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THE HARLEQUIN FLY

MIALL AND HAMMOND

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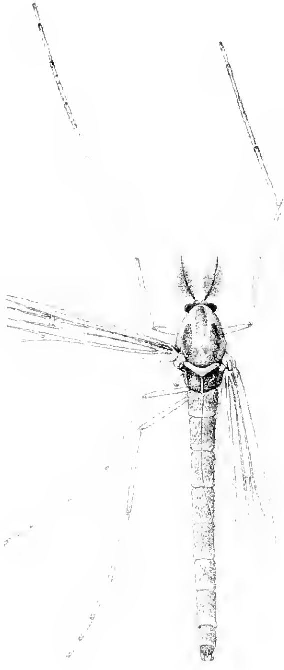

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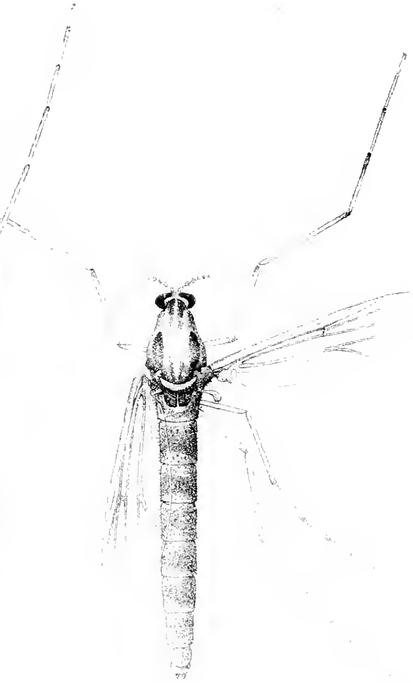

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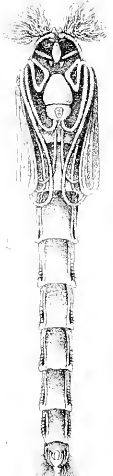

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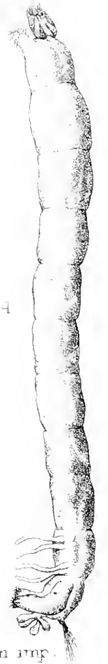

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The Harlequin Fly *(Chironomus dorsalis)*

THE
STRUCTURE AND LIFE-HISTORY
OF
THE HARLEQUIN FLY
(CHIRONOMUS)

BY

L. C. MIALL, F.R.S.

AND

A. R. HAMMOND, F.L.S.

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PREFACE

We have undertaken to give an account of this insect because we believe that its abundance nearly all round the year, its transparency, and the ease with which it can be reared, render it peculiarly fit for study by inland naturalists. Chironomus in its various stages has a very special biological interest, and we have thought that its inclusion in ordinary teaching-courses would be facilitated by such a description as is now offered. This insect has long been a favourite object with histologists, embryologists, and others, but its many points of interest had not been exhausted by our predecessors; we are well aware that they have not been exhausted by ourselves.

It would be a real service to biology if we could incite the members of naturalists' clubs and other non-academic biologists to take up the study of life-histories. The lists of species, which are now printed so freely, have no particular scientific value. Meanwhile the life-histories of insects, which have in the past yielded facts of the greatest biological importance, are almost totally neglected. The great majority of Dipterous insects, for instance, have never been reared, and only an insignificant minority have been closely examined.

In determining flies for the purposes of this book, we have been aided by the experience and accurate knowledge of the late Mr. R. H. Meade, of Bradford. Mr. G. H. Verrall has been good enough to identify for us the fly of Orthocladius. We have acknowledged in the proper places our obligations to Miss Dorothy Phillips and Mr. T. H. Taylor, both of the Yorkshire College. We hope that these two naturalists of the new generation may succeed as well in the independent labours that await them as in what they have done for us. Lastly, we have to thank the Delegates of the Clarendon Press for the liberality with which they have produced a book, whose numerous illustrations render it costly, while it appeals only to a limited public.

CONTENTS

CHAPTER I.

PAGE

Outline of Life-History; Relations of Chironomus to other Diptera 1

CHAPTER II.

The Larva of Chironomus 25

CHAPTER III.

The Fly of Chironomus 88

CHAPTER IV.

Development of the Pupa and Fly within the Larva 118

CHAPTER V.

The Pupa of Chironomus 138

CHAPTER VI.

The Embryonic Development of Chironomus 153

APPENDIX. Methods of Anatomical and Histological Investigation 177

Additional Note on the Swarming and Buzzing of Harlequin-flies 183

BIBLIOGRAPHY 185

INDEX 193

DESCRIPTION OF PLATE

(FRONTISPIECE)

FIG. 1. Male fly (*Chironomus dorsalis*). × 8.
FIG. 2. Female fly. × 8.
FIG. 3. Dorsal view of half-grown larva. × 8.
FIG. 4. Side view of older larva.
FIG. 5. Ventral view of pupa. × 8.
FIG. 6. Side view of pupa. × 8.

The full-grown larva of *C. dorsalis* is about 20 mm. long; the fly varies from 5·75 to 7·5 mm.; and the pupa is a little longer than the fly.

THE HARLEQUIN FLY

CHAPTER I

OUTLINE OF LIFE-HISTORY; RELATIONS OF CHIRONOMUS TO OTHER DIPTERA

NOTE.—When an author's name is followed by a date, the work cited will be found in the bibliographical list at the end.

Habitat, food, movements.

THE naturalist who searches the mud at the bottom of a slow stream will often meet with crimson larvae, an inch or less in length, which when full-fed turn to pupae, and shortly afterwards emerge as two-winged flies. These larvae are popularly called *blood-worms*. They feed chiefly on dead leaves and other vegetable refuse. Microscopic examination of the contents of the stomach reveals a blackish mass of vegetable fragments, besides diatoms, infusoria, eggs of other aquatic animals, and grains of sand. The larvae usually hide themselves from view, and in deep mud form nearly vertical tubes which open at the surface. When captured, their chief anxiety is to bury themselves in mud or vegetation. If a larva is placed in a saucer with a few bits of dead leaves, it will gather them about its body, weaving them together with viscid threads passed out from its mouth, and in a quarter of an hour it will be completely concealed by a rude sheath, which is not easily distinguished from the similar objects which lie around. If the remains of plants are not to be had, it will weave together grains of sand or particles of mud. In summer the proportion of saliva is greater, and the tubes are lined with felted fibres. These summer-tubes may be so coherent that they can be picked up with forceps and suffer no injury. The tubes are, if possible, attached to some fixed object, and are often much longer than the body of the larva. Larvae kept in a clean saucer with nothing but water make transparent tubes of saliva only. In winter the larvae often inhabit galleries, whose walls have little or no cohesion. The larva holds on to its tube, and travels along it, when necessary, by the help of two pairs of limbs, which are crowned with circles of hooklets. One pair is just behind the head, the other at the tail (fig. 1). The limbs are aided in locomotion

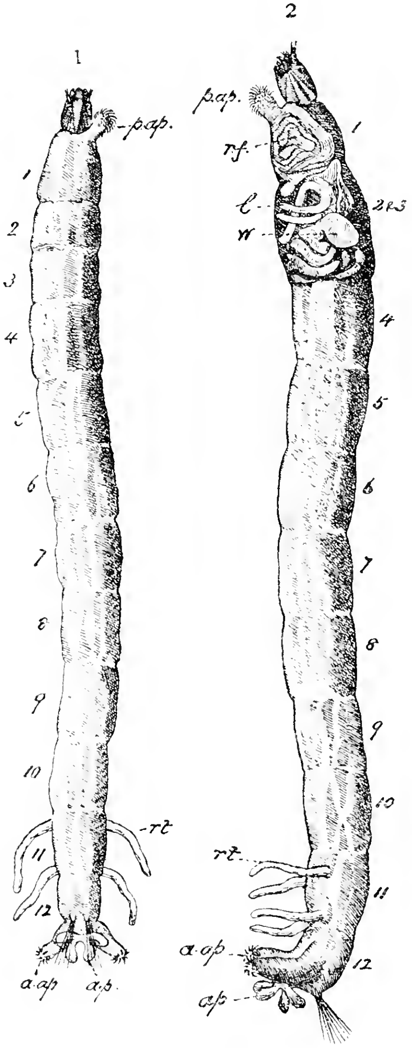

Fig. 1.—Larva of *Chironomus dorsalis* 1, half-grown. × 9. 2, full-grown. × 9. The numerals indicate the segments. *p ap*, prothoracic appendages. *rt*, ventral blood-gills. *a.ap*, anal feet. *a.p*, anal blood-gills. In 2 the following are seen through the larval skin. *r.f*, tracheal gill of pupa. *l*, leg. *w*, wing.

by the labrum (fig. 16), a flap hanging down in front of the mouth, which is armed with an elaborate provision of hooks and spines, and is often used to drag the body forwards. This use of the mouth for locomotion can be observed in other Dipterous larvae. Sometimes the larva sticks out the fore end of its body in search of food; at other times the hinder end is pushed out, and swayed up and down in the water; by a similar movement of the body a current of water can be made to flow through the burrow[1]. The larva, if undisturbed, seldom or never leaves its retreat by day, but at night it ventures out and swims near the surface of the water, writhing in figures-of-eight. The body is violently doubled up, and then suddenly bent to the opposite side, and the blows thus given to the water propel the larva slowly along. During these nightly excursions a store of oxygen is obtained, which amply suffices for the following day, when the helpless larva dares not quit its shelter. Captive larvae are careless about returning to their old burrows, being able to make new ones so easily, but in a small vessel they will come back time after time to the same burrows. If the water is well aërated and food plentiful, they often remain in their tubes day and night. Sometimes a number of larvae weave a felted mass of earth and threads, in which each animal has its own tube.

The larvae commonly inhabit slow streams, but they are also met with in pools and troughs. They can exist at great depths, and have been fished up, sometimes in company with Tanypus, from the bottom of Lake Geneva, Lake Superior, and other deep lakes. They have often been found in salt water. Packard was the first to

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[1] Caddis-worms and the aquatic caterpillar of Paraponyx, as well as the Chironomus-larva, keep up an undulatory movement of the body, which continually renews the water within the sheath, case, or burrow.

observe this; he found them abundant at low-water mark in Salem harbour; Verrill dredged one from a depth of twenty fathoms at Eastport, Maine; and they have also been found on the coasts of Denmark[1]. Swainson has found them in the sea at the Mumbles, Swansea, and has dredged them in fifteen fathoms off the Isle of Man. At Sheerness they inhabit salt-marshes, which are overflowed by the tide every day.

Parasites.

As might be expected from its place of abode and the nature of its food, the blood-worm is much infested by parasites. Stalked infusoria attach themselves to its head as well as to other parts of the body; nematoid worms coil themselves up in the body-cavity, and even distend the whole integument; Gregarines lurk in the intestine. According to Villot[2] a species of hair-worm (Gordius), while still of microscopic size, bores into the Chironomus-larva, and becomes encysted within it. If the larva is swallowed by a fish, the Gordius is set free; it now fastens upon the mucous lining of the intestine of its new host, and again encysts itself. When it has grown to its full size, it escapes into the water, elongates

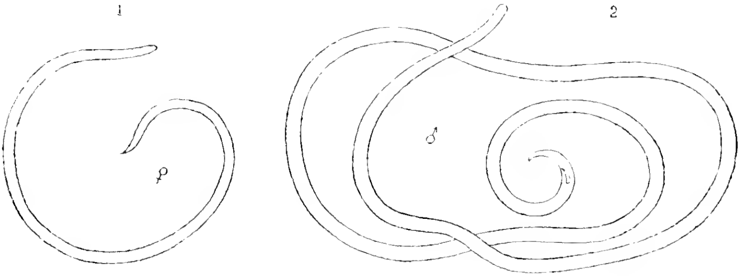

Fig. 2.—Gordian worm, infesting larva of Chironomus. 1, immature female, from larva, $\frac{1}{3}$ in. long. 2, adult male, from mud of stream, about 1 in. long. The adult female has no spicule, and the genital orifice is $\frac{1}{3}$ of the length of the body from the head end.

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[1] Meinert, 1886, p. 73; Packard, 1870; Monnier, 1874.

[2] Villot, 1874.

its body to a surprising degree, loses the cephalic armature, and becomes capable of propagation[1].

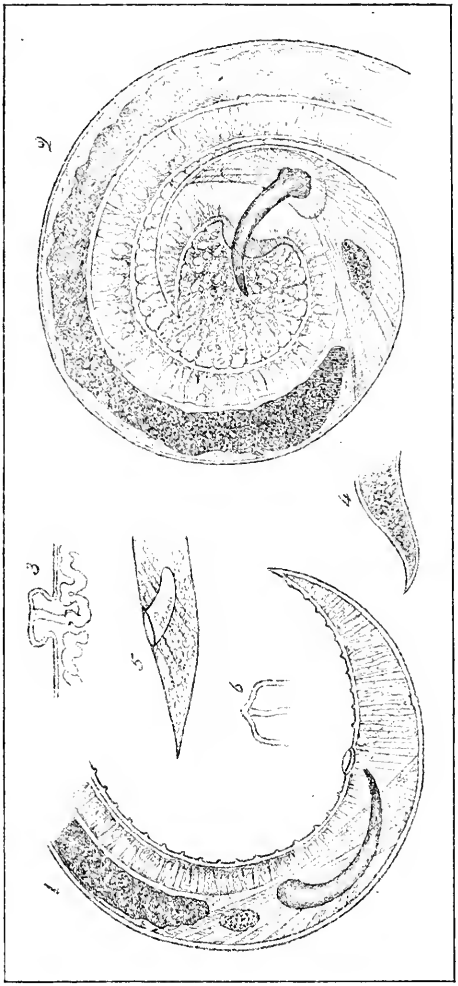

Fig. 3.—Gordian worm, infesting larva of Chironomus. 1, tail of adult male, showing spicule and one row of glandular papillae. 2, the same after slight pressure for an hour. The spicule is now everted, and the papillae have discharged a viscid secretion. 3, vulva of adult female. 4, tail of adult female. 5, tail of immature male, showing spicule-sac. 6, head of adult, with beginning of tube.

A nematoid worm (figs. 2, 3) which we have found in Chironomus is hard to identify, but it appears to be

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[1] We have seen Chironomus-larvae, pointed out to us by Mr. T. H. Taylor, in which the worm escaped through one of the anal feet.

either a Gordius or a Mermis. In its first condition it infests the larva, but a later stage has been found in the pupa and in the newly emerged fly, coiled in the body-cavity about the abdominal viscera. At length the worm quits its host, and then lives free in the mud, attaining a length of about an inch. The sexes are distinct, the male being distinguished by a spicule near the end of the tail. The intestine runs almost the whole length of the body, and is at first filled with granular matter. It ends blindly at both ends. An oesophagus extends backwards for some distance from the head-end, but does not enter the intestine[1]. The eggs are formed within a convoluted tube, but ultimately escape into the body-cavity, which they distend to such a degree that the female worm becomes little more than an egg-sac. What appears to be the outlet of the female reproductive organs is distant about one-third of the length of the body from the head. In the mature male the testis extends along nearly the whole length. The spicule is imperforate, and no outlet to the reproductive organs has been discovered. A double row of minute papillae runs along the inside of the curved tail, near the spicule. These seem to be glandular, for slight pressure (e. g. the weight of a cover-glass) causes them to exude a viscid fluid, which takes the form of threads mingled with loose cells. These occupy all the centre of the close coil formed by the tail, while the spicule is protruded (fig. 3, [2]). Neither the double spicule of the male Mermis nor the cleft tail of the male Gordius was seen.

The following species are said to infest Chironomus:—*Gordius tolosanus*, Duj., *Mermis albicans*, Sieb., *M. acuminata*, Sieb., *M. chironomi*, Sieb., *M. crassa*, Linst. They are parasitic on the larva and pupa, and *Mermis albicans* at least is not uncommon in the fly. The identification of the species in the second larval stage is difficult, and we have often been in doubt as to the forms observed.

Those who make many sections of Chironomus-larvae and pupae will be sure to come across specimens which harbour Gordian worms, and it may save them much time if they bear this in mind. It has happened to us to waste many hours over a singular new structure which at last revealed itself as a Gordius.

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[1] A similar break of continuity has been described in Mermis.

Enemies. Blood-worms are preyed upon by many aquatic insects, as well as by fishes. Caddis-worms, Perla-larvae, Sialis-larvae, and Tanypus-larvae devour them greedily. A number of empty heads of the blood-worm may often be seen in the stomach of a single Perla or Tanypus larva.

Method of collecting. If it is desired to get a supply of blood-worms, a slow, muddy stream, abounding in decaying organic matter, should be visited. Pure water is not at all necessary to the health of the larvae, and they often abound in foul streams. A long-handled iron spoon or ladle, which can be tied to a walking-stick if necessary, is a convenient collecting implement. The larvae may be picked or washed out of the mud, and brought home in a wide-mouthed collecting bottle. They can be kept alive for weeks with very little attention. Decaying vegetation and fresh water now and then are all that they require. A shallow vessel is better than a deep one for these and most other aquatic insects.

Transformations. In winter captive larvae continue a long time without marked change. Young ones grow bigger, and now and then moult, though it is rare that we see anything of the operation. A cast skin enables us to make out that the dorsal wall of the thorax splits along the middle line, while the head breaks up along two sutures which define the central plate (clypeus), and also along the mid-ventral line. When the larvae are nearly an inch long, they will often remain for many weeks together without visible alteration. But in summer, in a particularly warm winter-season, or in a well-warmed room, matters advance more rapidly. If we see larvae with the rings behind the head swollen, we know that they will shortly turn to pupae. When the last larval skin is cast, there emerges a very different-looking animal, in which we can make out with a little pains a pair of wings, six long legs, and a head with big, compound eyes. These organs belong to the fly; for the moment they are shrouded in a delicate, transparent envelope, the pupa-skin. The pupa commonly lies within its burrow, or half in and half out, until the time of extrication of the fly is at hand; it neither feeds nor swims about. Sometimes it lies with its tail buried in mud, the head and tracheal gills sticking out, or it may excavate a little basin in the mud by the movements of the tail, and lie in it. The tail or abdomen is always the part which bends to and fro. When kept in a saucer of muddy water, the pupa lies on the surface of the mud, and being insufficiently supported by the mud, takes an unnatural position, lying on its side.

The red colour of the fresh-emerged pupa soon darkens, and two bunches of silvery filaments just behind the head show out with great distinctness. In two or three days the pupa becomes buoyant, and rises to the surface, where it remains until the fly escapes. The process of extrication from the pupa-skin is accomplished so quickly that it is hard to see in detail what happens. The cast skin floating on the water tells us that the back of the thorax splits lengthwise, as at an ordinary larval moult, and that the fly emerges through the cleft. Considering that the long and slender legs, the antennae, the new mouth-parts, the wings, and the abdomen have all to be drawn out frcm their sheaths, it is startling to find the fly taking wing before one is able to focus the eye upon it. In the case of a fly which escaped more slowly than usual, we estimated that the whole process occupied ten seconds. Now and then something catches, and the fly extricates itself with great effort, or not at all.

Most of the larvae which we find in winter are destined to pupate and turn to flies in early spring. These lay eggs, and produce a fresh crop of young larvae. There is a rapid succession of broods until late autumn. A live fly is occasionally seen on the window-pane even in the depth of winter. Some of these unseasonable examples have lately emerged from the pupa-skin; others have lingered on from the previous warm season. An insect which has been unable to mate sometimes survives its companions for a long time.

The fly.

The fly of the blood-worm is a gnat-like creature, which is often seen in summer on the window-pane, or hovering in swarms over streams and pools. When at rest, it usually stretches out its fore-legs, raising them altogether from the ground[1]. Unlike the gnat, it has no biting or piercing organs, and is quite harmless. The mouth is almost closed, and feeding seems to be impossible. The head is furnished with great compound eyes, and in the male, with large plumed antennae. The female has simpler antennae, and the eyes are not so large as in the male. Swarms of flies, composed almost entirely of males, dance in the air of an evening. Now and then a pair falls towards the ground; the male soon rejoins the swarm, but the female flies off. (See additional note, p. 183.)

Egg-laying.

The fertile female skims over the surface of the water, touching it lightly from time to time with her legs. This is preliminary to the laying of the eggs, which commonly takes place in the late evening or early morning. She settles at last on the margin of a pool or stream, and brings the tip of the abdomen close to the surface of the water. A dark gelatinous mass, consisting of eggs thinly covered with mucilage, is then protruded until it touches the water, when it at once begins to swell up. After all the eggs are passed out, the whole mass, which forms a gelatinous cylinder, is secured by the female to some fixed object close to the water's edge. The attachment varies according to the species of the fly, but often takes

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[1] Gnats may be seen to lift the hind-legs, and wave them slowly about, as if to explore.

the form of a double cord, which traverses the egg-mass and projects beyond it at one end (fig. 116). During the process of oviposition the female is not easily induced to break off; if she is forcibly removed from the surface of the water, she sometimes flies a short distance with the egg-mass protruding, which disproves the statement formerly accepted, that she begins by making fast the end of the cord [1]. The eggs are almost transparent, and can be studied microscopically while still alive. They hatch out in three to six days.

Peculiarities of fresh-hatched larva.

When fresh-hatched, the Chironomus-larva is somewhat less peculiar than after its first moult; it has at first no red colour, and no blood-gills on the last segment but one; the brain is not retracted into the prothorax, but enclosed in the head, and the nerve-cord is visibly double throughout its whole length. This is an example of what zoologists call *Recapitulation*, the earlier stage retaining more of what we take to be the primitive structure.

Some common species of Chironomus.

There are many species of Chironomus, and it is remarkable that while the flies are very similar, the larvae are sometimes notably different. Two forms occur frequently. In one group of species the larva often has four long tubules (blood-gills) on the under-side of the body at the tail-end (fig. 1); the pupa bears bunches of long filaments (tracheal gills) behind the head, and has a fringed tail-plate (Plate, figs. 5, 6). To this group belong the comparatively large red larvae, which are called *blood-worms*. In a second group the larval tubules are absent; the pupa has a pair of short and simple trumpets in place of the bunches of filaments (fig. 7); the tail-plate is not fringed, but merely furnished with two bunches of short bristles [2].

Most of the larvae of the first group burrow; the larvae

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[1] Ritter, 1890, p. 411.

[2] Meinert, 1886, p. 75.

of the second group often live at the surface of the water, and feed upon weeds. Some of these surface-larvae are green instead of red, the green colour being due to a pigment in the fat. In at least one species the green pigment coexists with red blood. One greenish larva of the second group mines the floating leaves of Potamogeton (pond-weed), and another smaller kind, with pale red blood, does the same[1].

C. minutus.

Mr. T. H. Taylor, Assistant-Lecturer in Zoology at the Yorkshire College, favours us with a short account of the larva of *Chironomus minutus*, Zett., which has not, so far as we know, been previously described. The fly, which was reared in captivity, was identified by Mr. R. H. Meade.

'The larva of *C. minutus* is found on stones in streams both quick and slow. It escapes observation by surrounding itself with an irregular gelatinous tube, which is fixed to a stone, and coated with foreign particles. When disturbed, the creature leaves its case and crawls over the stones like a leech or a Geometer-larva, bringing the anal feet up to the prothorax, extending the body again, and so on. It swims vigorously with a figure-of-eight movement.

'The larva is of pale green colour, and about seven mm. long. It is similar in general appearance to the blood-worm, except that the blood-gills on the last segment but one are absent. The hooks on the prothoracic feet are toothed like a comb; the hooks on the anal feet are simpler (fig. 4). The tracheal system is well developed, longitudinal trunks with numerous branches extending throughout the body.

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[1] These two groups are not exhaustive. Thus the larva of *Chironomus niveipennis* has red blood, but no ventral blood-gills. The pupa has a fringed tail-plate, and the branches of the tracheal gill are comparatively few. See p. 13 for further details.

‘Larvae about to pupate have the thorax much swollen. The pupal stage is passed in a gelatinous case, which adheres to a stone in the stream (fig. 5). The wall of the case is structureless, but seems to have a fibrous texture within. At each end of the case is a spout-like aperture, and by the undulations of the body a constant current is kept up, flowing in at the fore aperture, and out behind. The head of the pupa lies in a part of the

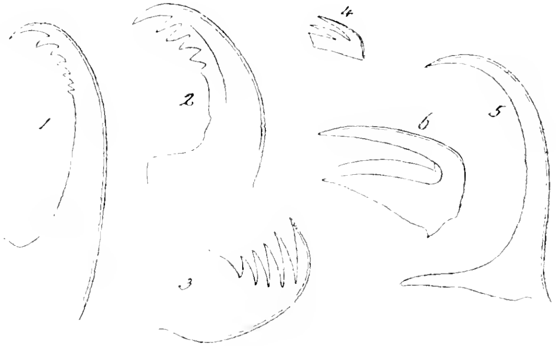

Fig. 4.—Larva of *Chironomus minutus.* 1–4, hooks on prothoracic appendages. 5, 6, hooks on anal appendages.

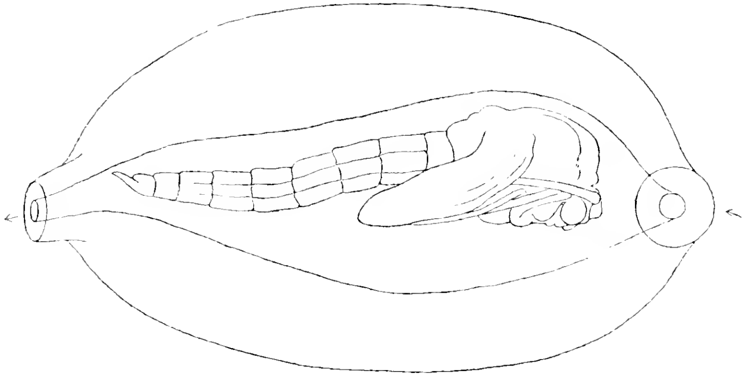

Fig. 5.—Pupa of *Chironomus minutus*, lying in its transparent sheath. The arrows show the current of water. × 15.

chamber which is considerably wider than the rest. It not uncommonly happens that two pupae are enveloped in a common case. Each however has its own separate chamber, which lies alongside the other, but with the ends reversed—an arrangement which saves space. The pupa has no tracheal gills, but small respiratory trumpets (figs. 6 7). The minute size of the trumpets, and the complete submergence of the pupa, indicate that respiration is carried on independently of these organs.

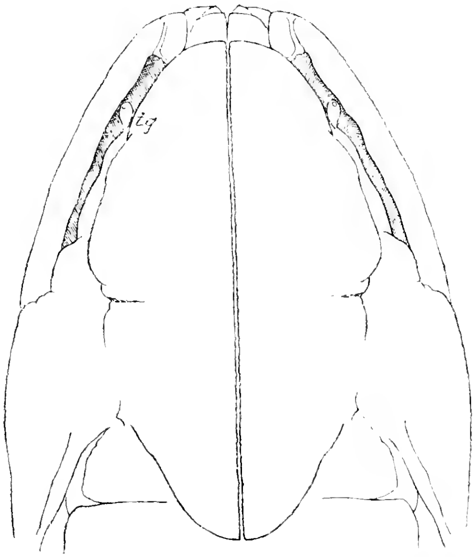

FIG. 6.—Dorsal surface of pupal thorax of *Chironomus minutus*, showing the respiratory trumpets, *tg*. × 50.

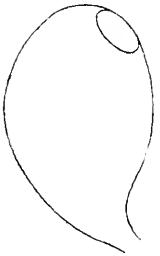

FIG. 7.—Respiratory trumpet of *Chironomus minutus*. × 400.

When ready to emerge, the pupa works its way through the wall of its case, aided doubtless by the strong hooks on the abdominal segments. It soon floats at the surface of the water, the thorax splits, and the fly escapes.'

C. niveipennis.

The larva and pupa of *C. niveipennis* have been pointed out to us by Mr. T. H. Taylor. The fly was named by Mr. R. H. Meade.

The larva inhabits a tube, and possesses red blood. There are no ventral blood-gills.

The pupa has a tail-fin composed of thirty to forty long setae, and the abdominal segments are laterally expanded. On the second abdominal segment are paired postero-lateral transparent appendages of small size, enclosing minute blood-spaces. There are two conical prominences, each bearing a long seta, on the vertex of the head. Corresponding structures were not found in the fly. The tracheal gill divides into three primary branches as usual. The secondary branches are comparatively few; each encloses a number of tracheae, which pass to the ultimate branches.

In the legs of the fly the variety of colouration, noted by Zetterstedt, was very apparent, though all the specimens were taken at the same time and place (Meanwood Beck, June, 1899).

Chironomus (Orthocladius) feeding upon Spirogyra.

Lyonet met with a tube-dwelling larva, of which an account is given in his *Anatomie et Métamorphoses de différentes espèces d'Insectes*, a posthumous work edited by De Haan. He speaks of the tube as formed of silk and a sort of moss, plentiful in ditches; it is open at both ends, enlarged in the middle, and sufficiently transparent to allow the movements of the larva to be watched. Unlike most other tubes secreted or built up by insect-larvae, the one in question is so flexible as to follow the bendings of the body when this is energetically contorted. He describes the method of feeding of the larva, which seizes the moss between its mandibles and fore-legs, and drags it into the tube, and its way of moving about, by grasping with the mandibles and fore-legs alternately. If the tube becomes lodged so as to be immovable, the larva quits it and makes another. When free, it swims with a looping action. The full-fed larva pupates in its tube. Beyond this point the description does not go, as Lyonet had mislaid his notes. He figures the tube, the larva, the pupa, and the male and female fly. De Haan identifies the insect as a Tanypus, perhaps *T. nervosus*, but it is really a Chironomus. Flies have been reared and sent to Mr. G. H. Verrall, who says of the species: 'It belongs to the group of Chironomi which Van der Wulp called Orthocladius, which have bare wings, the basal joint of the front tarsi shorter than the tibia, and the thorax not cowled. It is a large species for that genus, and is near *O. dilatatus*, V. d. Wulp, but is I think quite distinct, as Van der Wulp says nothing about the bearded front tarsi.' This insect has been rediscovered and studied in all its stages by Mr. T. H. Taylor, whom we have to thank for the following description and for the illustrative figures:—

Mode of life of Orthocladius.

'The larva finds its abode in a floating flock of Spirogyra. It makes a case of jelly-like substance, probably out of the secretion of its salivary glands. With a high power a faintly fibrous structure can be seen in the jelly; filaments of Spirogyra and also chain diatoms, &c., are interwoven, and this seems to be the result of a purposive act. The creature frequently stretches its body out of the tube and draws filaments towards the outlet, where they adhere to the viscous material and form a miniature arbour, like a porch over which creeping plants have been trained. There is nothing so elaborate in the construction as happens, for example, when a caddis-larva

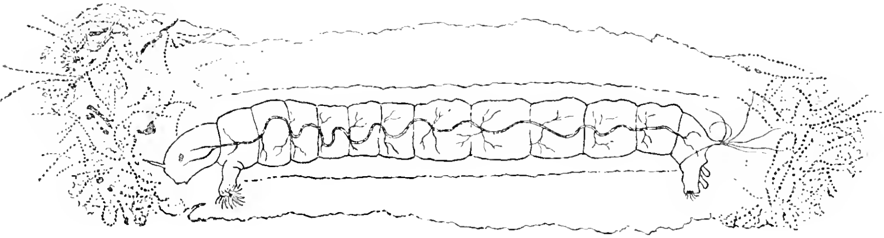

FIG. 8.—Half-grown larva of *Chironomus* (*Orthocladius*) *sp.* in its case. × 12.

builds its case; the Orthocladius-larva appears to rely almost solely on its own secretion. It feeds voraciously on the surrounding Spirogyra, and the filaments which are interwoven are those which have already passed through its alimentary canal.

'On account of the transparency of its tube, the larva of Orthocladius is a convenient form for study. Its activities are: (1) *Feeding.* A filament of Spirogyra is seized by the mandibles and bitten in two. Then the labrum, beginning at one end of the filament, draws it into the gullet by a stroking action. In the case of *Spirogyra condensata*, amongst which the larva was first obtained, a filament was very soon eaten, but when *Sp. orthospira* was supplied, the feeding was much slower and apparently more laborious, probably on account of the thick gelatinous sheath of this alga. If there is no food near, the larva, clinging to the tube by its anal feet, projects far out, and sweeps rapidly around until it gathers in a fresh wisp of filaments. In captivity, when the food-supply is exhausted, it will feed on other filamentous forms, e. g. Oedogonium. From time to time, the larva, protruding the tail-end from the tube, evacuates a bolus of digested Spirogyra, which at once disperses. This was rather surprising until microscopic examination showed that the filaments are not masticated, but simply crumpled up, and the contents removed, except remnants of the green protoplasm, so that when the filaments are released, the elasticity of the cell-wall straightens them out. (2) *Respiration.* The larva, when lying in its case, waves its body up and down; this sets up a current of water, which flows in at the front-end and out behind; either end may be the front-end, as the creature often reverses its position. The action is quiet and leisurely. (3) *Locomotion.* As the case is not fixed, the larva can travel without leaving it. It does not creep like a caddis-larva, but jerks itself forward by a few powerful undulations in which the flexible case participates. It is unlikely that the creature swims by this method, which demands considerable effort, and is not continued long at a stretch. When it swims it leaves the case altogether, and loops through the water like a blood-worm. In captivity it has been seen to return to its tube after swimming in this manner. (4) *Building.* At intervals the larva apparently adds fresh material to its case. It withdraws its head towards the middle, and then works over the inner surface with its mandibles, from behind forwards, testing the wall continually with its prothoracic legs. It has not been seen to work in this way on the outer surface.

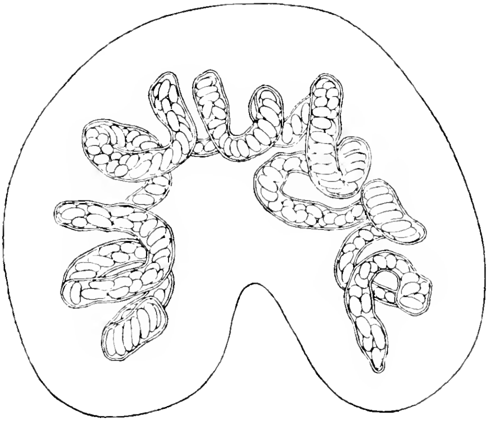

FIG. 9.—Egg-mass of Chironomus (Orthocladius). × 10.

'The larva grows rapidly, and pupates in about a fortnight. The cast larval skin is passed out of the pupal tube, which is now attached at one end to some fixed object. The pupa executes respiratory movements inside the tube, and after a short time—two days or less—comes out and floats at the surface of the water, where the fly escapes.

'The eggs are laid in a jelly-mass, about 250 being counted in one instance. The row of eggs is contained within a hollow gelatinous rope of firm consistency. The egg-rope is bent into a series of frequently reversed loops, and its two ends are approximated, so that it is horse-shoe shaped. The whole is enveloped in a mass of much softer jelly. The larvae hatch out in about five days, and escape into the hollow egg-rope. By the end of the first day after hatching they become altogether free and take up their abode in the Spirogyra. They select a point where several filaments intersect, and begin building their case. This at first is of very irregular form, but by the third or fourth day it assumes a tube-like character.

Structural peculiarities of Orthocladius.

'The full-grown larva measures ten to twelve mm. in length. The general colour is pale green, and the green food in the alimentary canal is conspicuous. Four anal blood-gills are present, while those of the ventral series on the penultimate segment are wanting. The paired sensory filaments are set on short stalks, and each consists of six long bristles. The tracheal system is well developed, and in this connexion the well-aërated habitat of this larva may be mentioned. The longitudinal tracheae are much larger than in *C. dorsalis*; they are relatively wide in front, but narrow backwards. Numerous segmentally arranged branches are given off. The epithelium of the main tracheal trunks shows a purple colouration. Two thoracic intersegmental and eight abdominal intra-

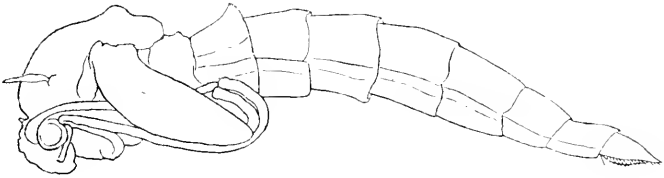

FIG. 10.—Pupa of Chironomus (Orthocladius). × 12.

segmental spiracles are present; all are closed. A pair of small processes were seen on the vertex of the pupa, like those of *C. dorsalis.* The pupa has a pair of respiratory trumpets, which are long, narrowed at each end, and spinous. The second abdominal segment bears a median dorsal prominence beset with spines; this perhaps serves to steady the pupa in its case. The tail-fin is expanded laterally, and fringed with about 100 setae on each side.

'The fresh-hatched larva does not differ materially in structure from the full-grown. The setae of the sensory filaments are not so numerous, and the tracheal system, if present at all, is not filled with air at this time.'

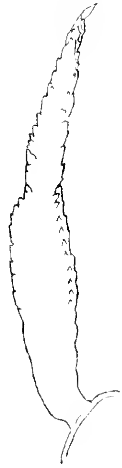

FIG. 11. — Respiratory trumpet of Chironomus (Orthocladius). × 100.

This book will be occupied by a description of species belonging to the first group (p. 10), which includes the common large red larvae or blood-worms. The insect which we have chiefly studied is called *Chironomus dorsalis* (*C. venustus* is a synonym). There are other larvae which differ only in minute details, such as the number and form of the joints of the antenna. For most purposes all large red larvae may be taken as practically identical; by *large* is meant a larva nearly an inch long when full-fed.

We have noted elsewhere (p. 150) the remarkable variety of structure presented by the larvae and pupae of the Chironomidae, and even by those of the single genus Chironomus.

Chironomus and other Diptera.

Baron Osten Sacken divides the order *Diptera* into three *sub-orders*:—

I. *Orthorrhapha Nemocera.* II. *Orthorrhapha Brachycera.* III. *Cyclorrhapha Athericera.*

The names adopted for these sub-orders have the advantage, as he says, 'of being descriptive of a character taken from their metamorphoses on one side, and of another character taken from the imago and its principal organ of orientation (the antennae) on the other. The names *Orthorrhapha* and *Cyclorrhapha* were very happily chosen by Brauer to characterize the metamorphoses of each of these groups, and should therefore be preserved. The names *Nemocera* and *Athericera* were adopted for two groups by Latreille, and should likewise be retained [1].'

Chironomus belongs to the sub-order *Orthorrhapha Nemocera*, in which the only pupal envelope is a thin membrane, the proper pupal skin. The antennae are slender and many-jointed.

Simplification of larva: complication of fly.

If a number of different Dipterous larvae are examined, a series can be traced which exhibits a twofold gradation, affecting the larva and the imago in opposite directions, the larva becoming simplified as the imago becomes complicated. This apparently results from the gradual transference of certain functions and responsibilities from the larva to the imago. In the more primitive forms the larva is active, and moves about to seek its food. Its structure is relatively complex, and its intelligence relatively high. The winged insect is short-lived, and the eggs are laid all together. The development of the fly within the body of the larva is gradual, and compatible with active life. Though the pupa does not feed, it never becomes motionless, and the pupal stage is brief. In proportion as the fly becomes more expert in seeking out stores of highly nutritious and easily assimilated food for its offspring, the larva degenerates. Some flies lay their eggs in green leaves, in living fungi, or in decaying carcases, and to find out a site which is exactly suitable they often require a comparatively long life, keen senses,

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[1] *Entomol. M. Mag.*, 1893, pp 149 150.

and good powers of flight. The eggs must, as a rule, be laid a few together in carefully selected spots. The larvae have little to do except to feed; their limbs, sense-organs, and even their mouth-parts become reduced or lost, and the ultimate result may be a headless and footless maggot. So great is the contrast between the larva and the fly that an elaborate process of reconstruction is necessary to effect the passage from one to the other. The grub feeds voraciously, goes to sleep within the hardened larval skin, and there undergoes a complete renewal of all its organs and tissues, emerging as a fly, which, in accordance with the difficulty of its task, is peculiarly active and gifted. A few insects may be quoted to illustrate the progressive simplification of the larva and the simultaneous complication of the fly.

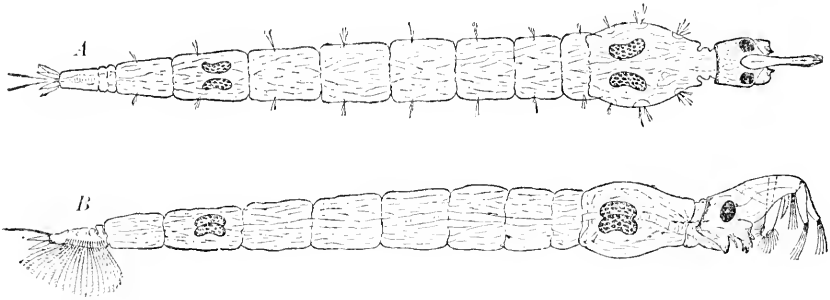

FIG. 12.—Larva of Corethra. *A*, dorsal view; *B*, side view. × 8. The two pairs of air-sacs are seen in the first and eighth segments behind the head. (From Miall's *Natural History of Aquatic Insects.*)

1. *Corethra* (fig. 12).—Larva active, carnivorous, with prehensile antennae and mouth-parts. Larval head not retractile; eye-spots; a tail-fin. No complete resting-stage; the pupa lasts four to five days. Fly short-lived: lays the eggs in a floating mass all together.

2. *Chironomus.*—Larva active, concealed, often feeding on decaying vegetable matter. Larval head often small, not retractile; eye-spots and antennae distinct, though

small. No complete resting-stage: the pupa lasts three to five days. Fly short lived; lays the eggs all together on the margin of a stream.

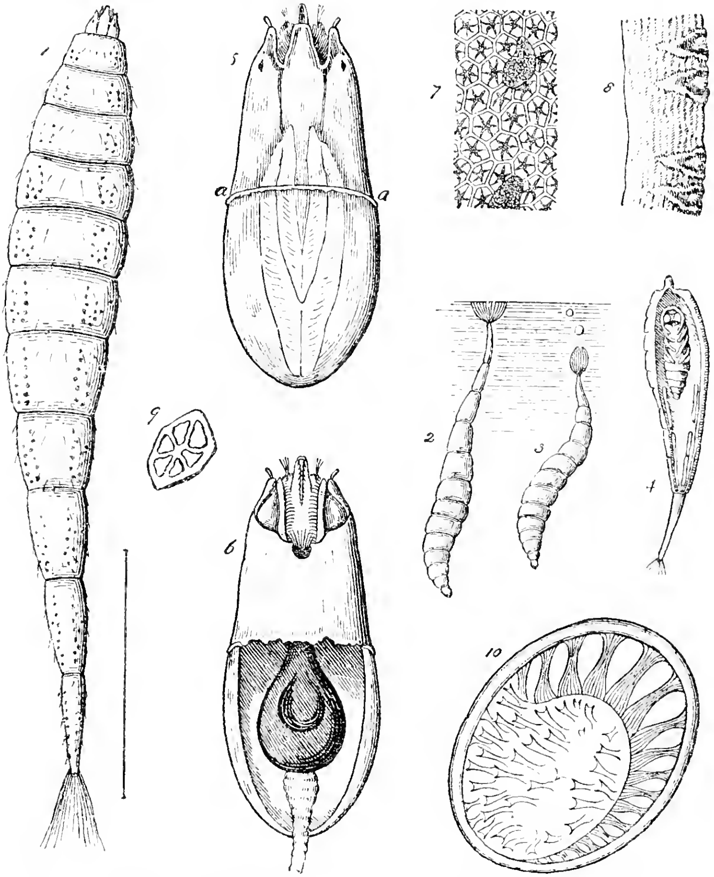

Fig. 13.—*Stratiomys chamaeleon*. 1, larva. 2, larva floating at surface of water. 3, larva descending. 4, pupa within larval skin. 5, head of larva, dorsal view (*a a* marks the attachment of the thoracic integument). 6, head of larva, ventral view. The ventral wall is incomplete behind, and the pharynx and gullet are exposed. 7, piece of integument. 8, ditto, in section, with conical, calcareous nails. 9, a single calcareous nail (surface view). 10, spiracle, lying in centre of tail-coronet. (From Miall's *Natural History of Aquatic Insects*. 2, 3, and 4 are copied from Swammerdam)

3. *Stratiomys* (fig. 13).—Larva fairly active, but only in rising and sinking; feeds on microscopic organisms.

Larval head minute, half-retractile; the mouth-parts, antennae, and eye-spots much reduced. Pupa inactive, enclosed within the larval skin; commonly lasts through the winter (five to seven days in summer). Eggs laid all together on water-weeds.

4. *Calliphora* (Blow-fly).—Larva very sluggish, immersed in putrid flesh. Head minute, rudimentary, completely retractile, without antennae or eye-spots, and with only a pair of hooks in place of mouth-parts. Resting-stage complete, passed within the hardened larval skin; the pupa lasts fourteen to thirty days according to the season, during which time the body is completely reformed. Fly active and long-lived, laying eggs in several batches, and feeding on nutritious fluids.

Brauer's classification.

Brauer (1880) has attempted to make use of such differences as these for the purpose of classification, and has published a system in which larval characters, and especially the degree of reduction of the larval head, are employed to denote extensive divisions of Diptera. The attempt has not proved satisfactory. Very few Diptera have been studied anatomically in their early stages, and Brauer has sometimes from defective information placed the genera wrongly in his own system (Chironomus and Phalacrocera are examples). Moreover, the organization of the larva is strongly adaptive, and varies with external circumstances. Almost every degree of reduction of the larval head can be found in nature, but the amount of reduction may give little information as to the affinities of the insect. Adaptive and finely graded characters prove here, as elsewhere, untrustworthy for the definition of large groups.

Adaptive resemblances and differences in Nemocera.

The flies of the many species of Chironomus are distinguished with difficulty, to judge from the characters employed in systematic books, which are largely drawn from colour, from the relative length of tarsal joints, and from the arrangement of the setae on the legs. Though the flies are so similar, the larvae and pupae may differ notably according to their species. Some larvae, for instance, have red blood, others not; some have blood-gills on the eleventh segment, which are wanting in others. Some pupae have prothoracic respiratory trumpets; others have branched tracheal gills instead. This adaptive specialization of particular stages is no new thing in zoology. Natural selection seems to act upon the separate stages of certain life-histories almost as it acts upon species.

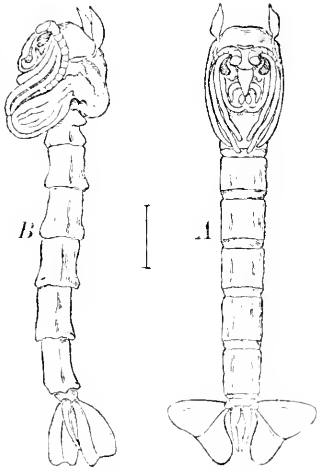

FIG. 14.—Pupa of Corethra. *A*, ventral view. *B*, side view. To show the prothoracic respiratory trumpets. (From Miall's *Natural History of Aquatic Insects.*)

Baron Osten Sacken [1] quotes two cases of Nemocera in which the reverse relation obtains, that is, the larvae are closely similar, but the flies so unlike as to be referred to different families. The two cases are (*a*) Mycetobia and Rhyphus, (*b*) Anopheles and Dixa. We are unacquainted with the early stages of Rhyphus, and will therefore offer no remarks on case *a*. The larvae of Anopheles and Dixa, though so like as to have deceived one experienced entomologist, are not, we think, so like as to raise any new biological question. They are easily and certainly distinguished by an attentive observer, and many definite points of difference could be brought forward. They are only superficially alike, and the resemblance is merely adaptive, like the resemblance of some Isopod Crustacea to Millipedes [2].

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[1] 1892, pp. 418, 465.

[2] It has been remarked that larvae of Noctuae (e.g. Agrotis), though almost exactly alike, may produce moths of very different appearance.

CHAPTER II

THE LARVA OF CHIRONOMUS

1. *External form.*

Method of examination.

MANY external features of the larva can be made out with the help of simple lenses, magnifying from five to thirty diameters, but the details require the compound microscope. Larvae are easily killed by placing them for a few seconds in water heated till it feels hot to the finger. Then they may be placed in water on a glass slip, and covered with a glass circle. It is often desirable to take off the weight of the cover by cotton-wool or three small glass beads. When it is desired to examine a larva alive, small specimens, not more than half-grown, are to be preferred. A little cell is made of cotton-wool; this is filled with water; then the larva is picked up with a clean brush, and dropped inside the cell; lastly, a glass cover is gently lowered upon it. The cotton-wool keeps off the pressure of the cover, and also restrains the movements of the larva. The space enclosed by the ring of cotton-wool should be clear of threads or nearly so, in order that the object may not be obscured. The beating of the heart, the contractions of the intestine, the action of the jaws, and many other operations of the living animal can be conveniently studied in this way. The details of the larval head can be made out by treating the parts with caustic potash. Soak several heads in a ten per cent. solution for two or three days, wash thoroughly with water, and mount in glycerine, or (after dehydration) in

Canada balsam. Some of the heads should be broken up with needles. For surface-views, larvae hardened in Flemming's solution or some similar fluid are particularly useful. Further descriptions of methods are given in the Appendix.

Segments and appendages

The body (fig. 1) consists of a head and twelve segments[1]. The head is rather small, and defended by a dense armour. The first three segments behind the head correspond to the thorax of the fly, and are distinguished as *pro-*, *meso-*, and *metathorax*. The prothorax has a pair of stumpy claw-bearing feet. The only other pair of feet, the *anal feet*, are carried on the last segment.

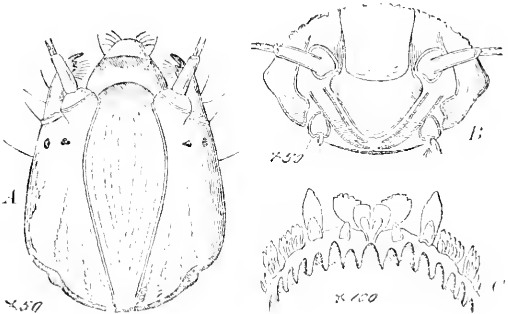

FIG. 15.—Larva of *Chironomus dorsalis*. *A*, head, dorsal view. *B*, ditto, front view. *C*, edge of labium, with its teeth and papillae. (From Miall's *Natural History of Aquatic Insects*.)

The larval head.

The larval head (figs. 15, 17) is protected on its upper or dorsal surface by three plates, one median and two lateral. The median plate (clypeus) carries the labrum, which hangs like a flap in front of the mouth, and can be bent backwards. The epipharynx or hind surface of the labrum, which looks towards the mouth, is furnished with an elaborate armature, which will be better understood by reference to fig. 16 than by any explanation in words.

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[1] This is the usual number in Nemoceran larvae. Pericoma and Phalacrocera have only eleven segments behind the head.

The hooks and spines no doubt aid the larva to grasp firmly with the mouth, as it continually does, not only in feeding, but in creeping; we have also thought it possible that some of these curious hooks may be used to guide the threads of silk as they are paid out from the salivary duct[1]. The lateral (*epicranial*) plates bear two pairs of rudimentary eyes (which are mere pigment-spots without lenses), as well as the antennae and the jaws. The epicranial plates curve round to the under-side of the head, and meet along the middle line in a faintly marked suture, along which the head splits at times of moult. In insects whose head is capable of considerable retraction into the thorax, there may be no suture here, but a wide gap (many Dipterous larvae); where the mouth-parts are large, they may almost completely fill the gap, or a separate piece (*submentum* or *gula*) may defend the space (Orthoptera, Coleoptera). The fusion of the epicranial plates on the lower surface of the head of the Chironomus-larva is well suited to an insect whose head is small, exposed, and furnished with minute mouth-parts. The genae, which in the cockroach and many other insects lie along the sides of the clypeus and bear the mandibles, are hardly separable in the Chironomus-larva.

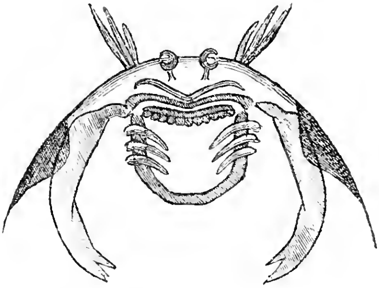
FIG. 16.—Under surface of labrum of larva, with its armature.

The larval antennae are small; each consists of a comparatively long basal joint, on which is a small, circular,

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[1] The mouth of the tadpole is armed with rows of horny teeth, which are not very unlike those of a Chironomus-larva.

sensory spot; beyond this are two terminal pieces of nearly equal length, one jointed, the other simple; the number of joints varies with the species.

The jaws.

In insects generally the jaws form three pairs of appendages, which somewhat resemble legs in their form, attachment, and mode of development. The *mandibles*, or foremost pair, are the least like legs, being unjointed and usually toothed. They divide the food, and may also be used in grasping, fighting, &c. Two pairs of *maxillae* follow, which are generally weaker than the mandibles, divided into many parts, and furnished with palps or feelers. The second pair of maxillae may closely resemble the first (Orthoptera, &c.), but they are often greatly modified for special purposes.

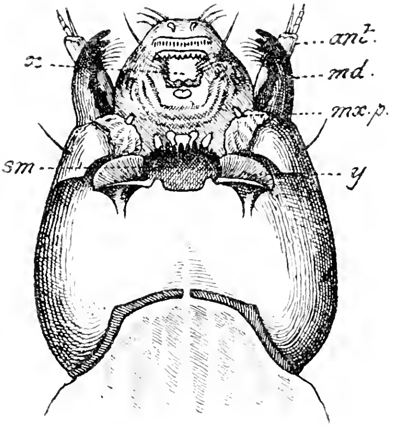

Fig. 17.—Ventral surface of head of larva. *ant*, antenna. *md*, mandible. *mx p* maxillary palp. *sm*, submentum. *x*, tooth-bearing surface of labrum. *y*, striated flap bordering the submentum.

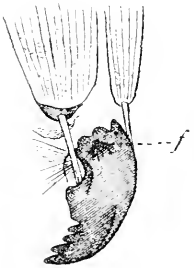

Fig. 18.—Mandible of larva, with chitinous tendons and muscles attached. *f*, fulcrum.

The mandibles of the Chironomus-larva (figs. 17, 18) are strong and toothed, and so placed that in closing they do not move in the same plane, but at angles of 45° with a vertical plane. They are not opposed to each other, but rather to the strongly toothed submentum. On the inner side of each mandible is a bunch of setae, which help to close-in the mouth. The first pair of maxillae are not so easy to make out, for they are reduced to stumps, which are concealed from view when the head is at rest. There is a rudimentary setose prominence internally, which in some species bears a row of tooth-like projections, and a minute palp on the outer side. The maxillae of the second pair, which often unite to form a single organ, the *labium*, can only be understood by comparison with other insects. In the Chironomus-larva they have lost so many of the original parts that at first sight they seem to consist of a single comb-like plate, whose teeth point forwards, and are opposed to the mandibles, helping them to grasp or divide the food. On close examination a second plate is discovered above the other, and almost hidden by it. The upper plate is of softer texture, and furnished with many spines and bulb-like projections some of which may be connected with the sense of taste (fig. 15, *C*). The fore-edges of these two plates form the hinder border of the mouth-opening. In Orthopterous insects, which with respect to the mouth-parts are less specialized than most others, there are two successive plates at the base of the labium, a basal and larger piece, called the *submentum*, and a distal piece, the *mentum*, to which the terminal parts are attached. It seems to us probable that the mentum of the Chironomus-larva has gradually slipped behind the submentum, which now almost completely conceals it. On each side of the labium is a striated and rather flexible flap (fig. 17, *y*), which helps to close-in the mouth.

Organs enclosed within the larval head.

The interior of the larval head is largely occupied by the muscles of the jaws. The slender gullet passes backwards from the mouth into the body. The salivary ducts pass forwards to open above the mentum, and behind a minute projection in the floor of the mouth (*lingua*). We should naturally expect to find the brain in the head, but in the blood-worm it has been retracted into the segment next behind (prothorax). In the fresh-hatched larva, however, it occupies its normal position in the head. A few words of explanation may be given here, though the subject is more fully discussed in chapter iv. The larval head is small in *Chironomus dorsalis* and other blood-worms, as in many other insects which feed upon dead organic matter. Their food is plentiful and ready to hand, so that highly developed sense-organs are not required in this stage. But the head of the fly, which is larger, much more complex, and quite different in shape, has to be formed within the body of the larva. It is, we may remark, a very wide-spread error to suppose that the head and other organs of the imago form during the pupal stage; their development is nearly always far advanced when the pupal stage begins. The imaginal head is moulded out of folds of the

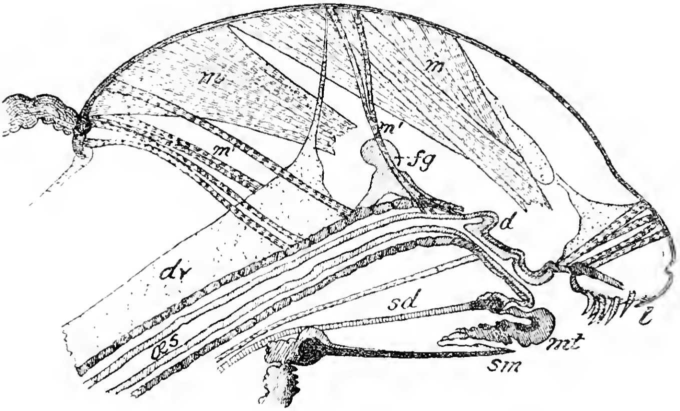

Fig. 10.—Median section through larval head. *œs*, oesophagus. *d*, its diverticulum. *dv*, dorsal vessel. *fg*, frontal ganglion. *l*, labrum. *mt*, mentum. *sm*, submentum. *mm*, muscles of mandibles, &c. *m'm'*, muscles which hold the oesophagus in place. *sd*, salivary duct.

larval epidermis, in a way which will be particularly described hereafter, and much more space is required for these folds than the small, hard head of the Chironomus-larva can supply. Since the imaginal head has to enclose the brain, it must form about the larval brain, and this makes it intelligible that in certain species of Chironomus the larval brain and the rudiments of the imaginal head should both shift into the relatively spacious prothorax. It may well be that the removal of these parts has led to a further reduction of the larval head.

Reduction of larval head in other Nemocera.

Many Nemoceran larvae, including some Chironomus-larvae, have a well-developed head, which lodges the brain and sub-oesophageal ganglion, bears eyes or eye-spots, antennae, and three pairs of jaws, and is externally defended by a dense and complete chitinous armour. The eyes are often compound in the larvae of Culicidae (Culex, Anopheles, Corethra, Mochlonyx). But where the larva is addicted to burrowing, and especially where it buries itself in its food, the head undergoes more or less reduction in size, which is nearly always associated with complete or partial retraction into the thorax. Sometimes only the hinder part of the head is retractile, and then its chitinous cuticle becomes thinner, or is excavated by notches, as if only those parts which serve for muscular attachment were retained. Larval head-reduction is not unknown in Nemocera, but it is universal, so far as we know, in Brachycera, where it is often carried much further than in any Nemocera. The back part of the retractile head shows, at least when not extremely reduced, a median and a pair of lateral projections, the remnants of a continuous cephalic shield. Any of the three principal divisions may be again subdivided. In heads which are still further reduced the principal parts which remain are not threefold, but paired, and are, we are inclined to think, rather paired apodemes than remnants of the cephalic shield. There are often two such pairs, which are long, slender, and exclusively concerned with muscular insertion. In extreme cases, e.g. in the leaf-mining larva of Phytomyza, only a single pair remains, and this is reduced almost beyond recognition.

The eyes and antennae often disappear altogether in larval Brachycera, while the mouth-parts may be represented, if at all, only by a pair of large hooks (larvae of Muscidae), whose homology with true mouth-parts is not yet adequately established, or by a single crescentic plate armed with saw teeth, which is perhaps the last vestige of the submentum. This extreme phase of reduction occurs in the larva of Phytomyza. The fore part of the head consists in this larva of a hammer-shaped chitinous rod, which bears in front the toothed crescentic plate. The rod is articulated behind to a rudimentary skeleton, consisting mainly of a pair of apodemes for muscular attachment. The hammer-shaped rod is swept to and fro like a scythe, and knocks off the green cells of the leaf, which are passed down the gullet.

Retraction and reduction of the larval head are usually associated with retraction of the brain, which often recedes into the prothorax, or, in the case of the blow-fly larva, into the metathorax.

The appendages of the thorax and abdomen.

The prothoracic appendages are short, united at the base, and armed with numerous hooks; they are used in grasping the food, in creeping, and in holding on to the burrow. Shortly before a moult new sets of hooks may be seen within the functional appendages; these become exposed when the old skin is cast (fig. 1). Segments 2–11 (not counting the head) bear no locomotive appendages. The twelfth and last segment bears a pair of long, straight appendages, often called the anal feet (figs. 1, 20) They are armed with a few stout curved spines, which show projecting cusps where they are attached to the chitinous cuticle, resembling in this the setae of some Oligochaet worms, or the hooks on the head of a tapeworm. Before a moult the new coronet of hooks may be

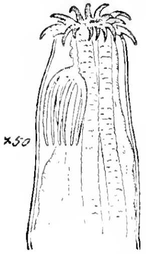

FIG. 20.—Larva of *Chironomus dorsalis.* Anal foot, showing its crown of hooks, the retractor muscles, and the formation of a new crown of hooks, preparatory to change of skin. (From Miall's *Natural History of Aquatic Insects.*)

discerned on the ventral side of the appendage, a short distance from its extremity. The anal feet are stiff, and possess a very limited range of movement. De Geer compared the long anal feet of the Tanypus-larva to wooden legs.

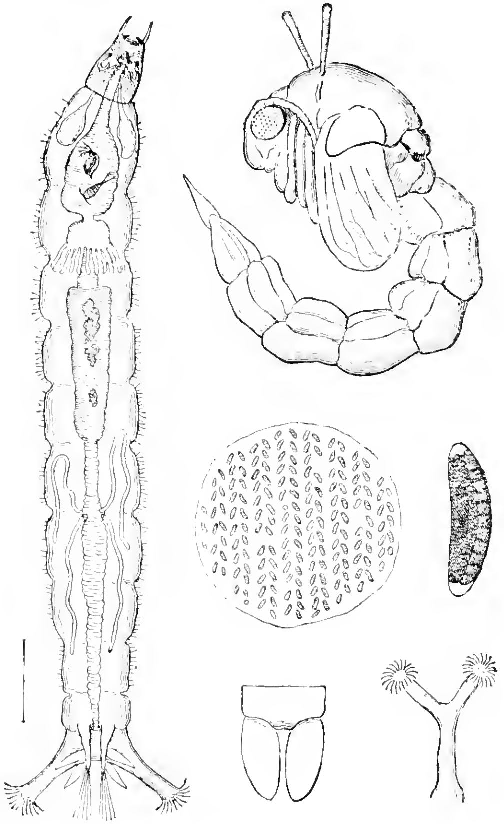

FIG. 21.—Larva and pupa of *Tanypus maculatus*, together with the egg-mass, a developing egg in side view, tail-plates of pupa in front view, and the prothoracic feet of the larva. (From Miall's *Natural History of Aquatic Insects*.)

The appendages of Nemoceran larvae.

Nemoceran larvae are often footless, but pseudopods, or provisional larval feet, occur in most of the families. The larva sometimes creeps by means of thickened segmental rings, which may be armed with spines, and it is a question whether the pseudopods are anything more than local developments of such rings. They vary much in number and position; three or four may be borne upon the same segment instead of the usual pair; and such facts point to their secondary, adaptive character. On the other hand, their usual segmental arrangement, and the normal occurrence of generally similar parts in insect-embryos, in the larvae of several different orders of insects, especially Lepidoptera and Hymenoptera (Saw-flies), in adult Myriopods and Peripatus, tend to support the view that they are true appendages, homologous with the thoracic legs of many insects.

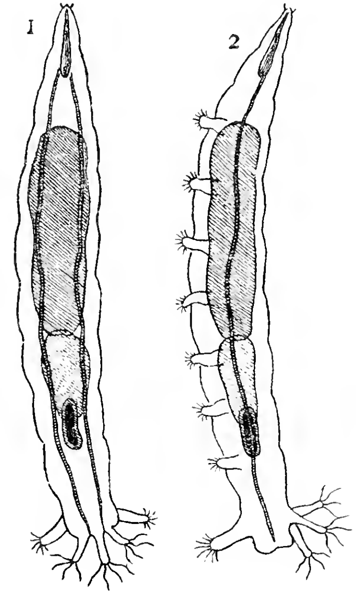

Fig. 22.—Larva of Clinocera showing pseudopods on eight segments. 1, dorsal view. 2, side view. × 20.

Chironomidae often, but not always, exhibit such an arrangement of pseudopods as we have described in the Chironomus-larva. The larva of Ceratopogon is footless. One of us found some years ago in a stream near London a Dipterous larva with remarkable pseudopods (fig. 22). This has since been rediscovered and identified. The head was very small and retractile. The stomach was filled with a red fluid, as if the larva had been feeding upon Tubifex. The body, which was a quarter of an inch long, apparently consisted of a head and eleven segments; eight segments (4–11) were provided with hooked ventral appendages, most of which were minute, but the last pair were comparable in size to the anal feet of the Chironomus-larva. From the dorsal surface of the last segment projected three small, cylindrical processes, each of which bore four filaments, and resembled the sensory processes of Chironomus[1] or Tanypus. No prothoracic

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[1] See pp. 35, 49.

appendages were seen. It is therefore possible that the prothoracic and anal feet of a Chironomus-larva may be the remnants of a series which once extended over many segments[1].

In the larva of Simulium both the prothoracic and the anal feet are recognizable, though they are largely fused, especially the anal pair, which constitute the posterior sucker.

The anal feet of caddis-worms.

Caddis-worms, which also inhabit tubes of various materials woven together, possess a pair of hooked feet at the hinder end of the body, and hold on by means of them, in the same way as Chironomus-larvae.

Blood-gills.

The eleventh segment of the Chironomus-larva has two pairs of ventral appendages, which are slender, thin-walled and tubular; these are believed to be respiratory; they are wanting in fresh-hatched larvae, as also in the surface-haunting species.

Appendages of the last segment.

From the dorsal surface of the twelfth segment project two bunches, each of five long setae. With each bunch a small ganglion is associated, so that they are apparently sensory in function[2]. Close to the anus are two pairs of small anal papillae, or blood-gills (see figs. 1, 24). These are tubular, and, we believe, respiratory. In some species a long seta springs from the base of each papilla of the upper pair. Either end of the body may require to be protruded from the tube; each is therefore furnished with organs for holding on and for perception. There are respiratory organs only at the tail-end, for these can be

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[1] As these sheets are passing through the press, Mr. T. H. Taylor has reared the fly from the larva described above, which is the hitherto unknown larva of Clinocera (fam. Empidae). Some Hemerodromia-larvae are similar, but have only seven pairs of pseudopods.

[2] In the larva of Tanypus (fig. 21) two similar bunches of filaments are carried on long cylindrical joints. The larvae of two undetermined species of Chironomus, which burrow in the leaves of *Potamogeton natans*, show tufts of setae, standing out from the sides of most of the segments. The thoracic segments and the twelfth abdominal segment in one species, the prothorax and the last two abdominal segments in the other, have no such tufts. The dorsal sensory tufts of ordinary Chironomus-larvae may be serially homologous with these.

effectively employed whether the tail is in the tube or out of it, owing to the power which the larva possesses of maintaining a regular flow of water through the tube (p. 3).

2. *Epidermis and Chitinous Cuticle.*

Chitinous cuticle.

In most parts of the body of the larva the chitinous cuticle is transparent and flexible. In the head, however, it is harder, and of deeper colour than elsewhere. In the prothorax it attains its greatest thickness, perhaps for the greater security of the brain and the important imaginal organs which develop within, and consists of numerous layers.

Fig. 23.—1, Epidermis from ventral blood-gill of larva. 2, ditto from dorsal wall. 3, portion of detached basement-membrane with dead cells, found floating in the body-cavity.

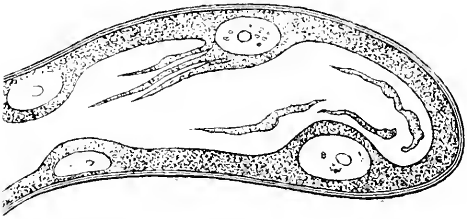

Fig. 24.—Anal blood-gill of larva, showing epidermis and floating filaments.

Epidermis.

The underlying epidermis consists in part of a single layer of minute and close-fitting cells, resting on a basement-membrane (fig. 23). The epidermic cells are best seen towards the middle of each segment; in other places, such as at the fore part of the prothorax, at the junctions of the segments, or in the anal blood-gills, they take the form of an undifferentiated layer of protoplasm, in which nuclei lie scattered. In these situations no cell-divisions can be made out either in the living larva or in sections[1]. The protoplasmic layer is here very unequally distributed, being often drawn out into irregular internal processes.

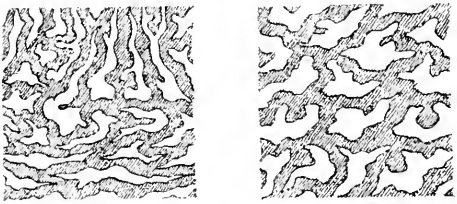

FIG. 25.—Internal elevations or thickenings of epidermis, as seen in dorsal wall of prothorax of living larva, surface view.

In the anal blood-gills it attains its greatest thickness, and here the large nuclei, thinly covered by protoplasm, bulge into the blood-cavity.

Folds of epidermis.

The epidermis often exhibits small folds which do not affect the chitinous cuticle outside. They become particularly evident shortly before a moult. At such time

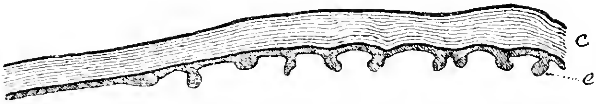

FIG. 26.—Section through dorsal wall of prothorax, showing thickenings of undifferentiated epidermis. *c*, cuticle. *e*, epidermis.

there may be seen within the transparent blood-gills, for instance, a wrinkled epidermis, whose surface is plainly larger than that of the cuticle within which it lies (fig. 28).

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[1] A syncytium, or continuous layer of protoplasm with scattered nuclei, has often been observed in the epidermis of Arthropods, especially in early stages, as also in Rotifera, Gordiidae, &c. See Leydig, 1864 b, pp. 21, 34, and the text-books of Comparative Anatomy.

Protoplasmic prominences also, which may be the beginnings of folds, are often seen on the inner surface of the epidermis, especially on the dorsal wall of the prothorax.

Filamentous corpuscles.

Peculiar filaments, often much drawn out, as if they were composed of protoplasm or some other plastic substance, are common in the blood-current, and are demonstrable in the more transparent parts of the body, such as the anal feet or the blood-gills (fig. 29, 1). No nuclei have been clearly seen within them, and any proper motion, or any power of spontaneously changing their shape which they may have, is masked by the rapidity of their translation. They are so like the drawn-out protoplasmic processes of the epidermis as to suggest that they have been detached therefrom to float for a time in the blood.

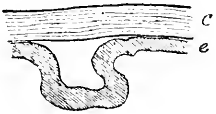

FIG. 27.—Diagram to illustrate the probable mode of conversion of one of the thickenings into a fold. *c*, cuticle. *e*, epidermis.

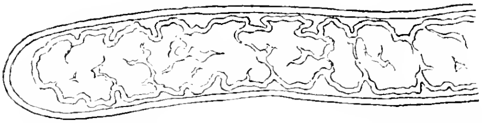

FIG. 28.—Ventral blood-gill during ecdysis, showing the epidermis retracted from the old cuticle.

Wandering cells.

Other corpuscles may be found aggregated beneath the epidermis, and these too are best demonstrated in the more transparent parts of the body. They are irregular in shape, but not extremely elongate (fig. 29, 2). Sometimes they become densely aggregated; they are not carried along by the blood-stream, so far as we know, though they probably travel. Nuclei

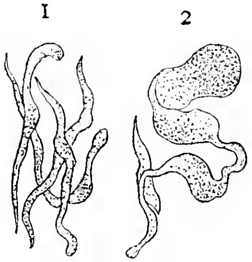

FIG. 29.—Filamentous corpuscles of blood. 1, as seen in the circulation. 2, as seen undergoing amoeboid changes in the ventral blood-gill.

have been observed within them, and they appear to undergo very slow amoeboid changes. Such cells, adherent to the inner face of the epidermis, have been found also in the blow-fly larva; they are the wandering cells (Wanderzellen) of Metschnikoff and Kowalewsky[1]. From the various states of aggregation which these cells exhibit, and from their slow change of figure, it is probable that, like the corresponding cells of the blow-fly, they can move from place to place, and that, however they may be scattered, they retain the power of combining into an epithelium. The blastoderm of many insect-embryos is formed out of cells which previously moved about in

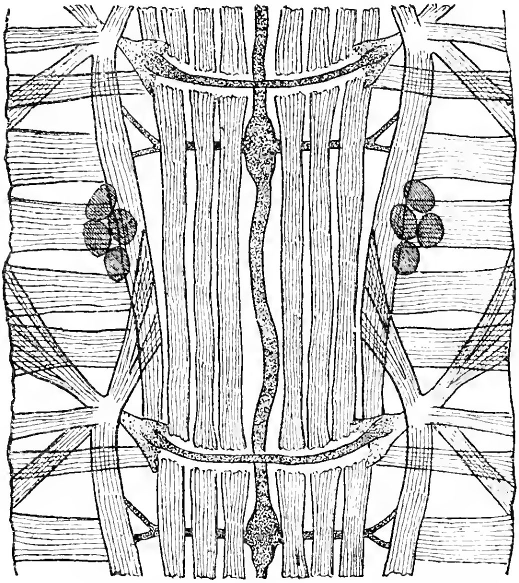

FIG. 30.—Third abdominal segment of larva and parts of two others laid open from above. In the middle line is the nerve-cord with the fourth and fifth abdominal ganglia, and paired nerves passing to the body-wall. In front of each ganglion a transverse nerve crosses the nerve-cord. The recti ventrales muscles lie next to the nerve-cord, and outside these are the transverse and oblique muscles. A pair of groups of oenocytes are also seen.

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[1] Metschnikoff, 1885; Kowalewsky, 1887, pl. xxvi (fig. 4).

the yolk. In Hydroids, in Echinoderms, and even in vertebrates, cells are known to detach themselves from an epithelium and to wander about the body, afterwards arranging themselves into an epithelium again[1].

Oenocytes. Closely associated with the epidermis of the Chironomus-larva are some peculiar cells, named *oenocytes* by Wielowiejski[2] from their colour, which is that of yellow wine (figs. 30, 31). The oenocytes are of two sizes, one much larger than the other. The large ones occur only in the abdominal segments, rather nearer to the ventral than to the dorsal surface. They form paired and segmentally arranged groups of four cells, which are often, but not uniformly, arranged in a lozenge close together. The cells are oval, nucleated, and attached to the epidermis by threads of protoplasm and fine tracheal branches. The nucleus may occupy nearly half the diameter of the cell, but is sometimes much smaller. The colour is due, according to Wielowiejski, to minute granules; no oil-drops are present. There is also a fifth cell, of spherical

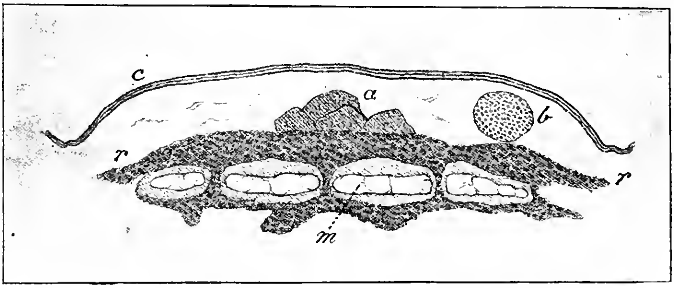

FIG. 31.—Oenocytes and outer fatty layer, as seen in third abdominal segment of living larva. *c*, cuticle. *a*, group of oenocytes. *b*, solitary spherical oenocyte in front of the group. *r*, outer fatty layer. *m*, muscles in transverse section.

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[1] Kleinenberg, 1886, p. 6; Metschnikoff, 1885.

[2] 1886.

shape, lying in front of the group; according to Wielowiejski it always contains two nuclei, one large and central, the other very small and peripheral[1]; it is more distinctly granular than the grouped cells. The twelfth segment (ninth abdominal) has no group of four cells, but one pair of spherical cells, and also a single cell at the base of each anal foot. The large oenocytes do not occur in young larvae, though they are conspicuous in those which are full-grown; they persist in the pupa and imago, but undergo some reduction in size. According to Graber (1891) the oenocytes are developed from the ectoderm.

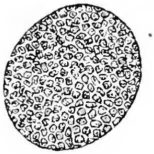

Fig. 32.—A solitary spherical oenocyte, with contained granules.

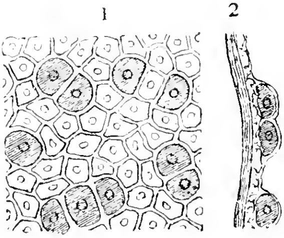

Fig. 33.—Small oenocytes, attached to inner face of epidermis. 1, surface view. 2, section.

The small oenocytes are very numerous on the inner surface of the epidermis of the last thoracic and the abdominal segments, especially towards the ventral surface. They contain yellow granules, like those of the large oenocytes, and often occur in pairs. Both readily stain with carmine.

Oenocytes occur in Culex, Corethra, and many other Diptera, and also in insects of other orders (Wielowiejski). Nothing has been definitely ascertained respecting their function. Wielowiejski points out their resemblance to

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[1] The same is true of Phalacrocera (Miall and Shelford, 1897, pl. xi, fig. 33).

blood-corpuscles, and also to the pericardial cells and the cells of the fat-body. They are bathed by blood, and he thinks that they probably secrete and discharge into the blood some unknown constituent.

We are disposed to entertain, though we cannot fully establish, the view held in whole or in part by Weismann, Graber, Wielowiejski, Schäffer, Tichomoroff, and Korotneff, viz. that the blood-corpuscles and oenocytes of insects are derived, directly or indirectly, from the ectoderm. With respect to the fat-cells and the pericardial cells, want of evidence prevents us from throwing them into the same group, as Graber and Wielowiejski would do[1].

Insertion of muscles.

Weismann[2] remarks of the larva of Musca that the epidermis is continued beneath the insertion of the muscles of the body-wall, a necessary provision, it would seem, for the renewal of the chitinous cuticle without disorganization of the muscles. The same is true of Chironomus (fig. 96), and it is remarkable how little the epidermic cells alter in size or appearance at the places of muscular insertion. It is probable that the remark holds good of Arthropods in general.

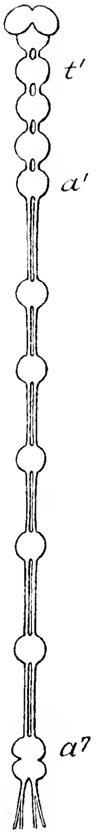

FIG. 34.—Nervous system of young larva. t', first thoracic ganglion. a', first abdominal ditto. a^7, seventh abdominal ditto. The connectives still retain their double character.

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[1] Graber, *Ueber die embryonale Anlage des Blut- und Fettgewebes der Insekten. Biol. Centralblatt*, Bd. xi, pp. 212-224 (1891).

[2] 1863.

3. *The Nervous System.*

The nervous system of the Chironomus-larva (figs. 34-39) consists of a brain or supra-oesophageal ganglion, a sub-oesophageal ganglion, three thoracic, and eight abdominal ganglia, the last of which supplies two segments, and is closely applied to the last but one. Ganglia.

The brain is, as usual, two-lobed, the lobes bulging outwards and downwards. Oesophageal connectives can hardly be said to exist, and the sub-oesophageal ganglion lies not behind, but beneath the brain. Both the brain and the sub-oesophageal ganglion properly belong to the head, in which they are actually lodged in most insects. In the larvae of *Diptera Nemocera* their position varies; they may lie in the head (Culex, Simulium, Phalacrocera, some species of Chironomus), half in and half out (Tipula, Ptychoptera), or altogether behind it (some species of Chironomus, Dicranota). In the 'acephalous' larva of the blow-fly they occupy the metathoracic segment. In the embryo and very young larva of *Chironomus dorsalis* the brain lies in the head, from which it gradually shifts backwards during the first few days after hatching[1]. After the first moult the small larval head is almost entirely filled by the jaw-muscles. Hence the nerve-centres, as well as the rudiments of the head of the fly, which begin to form in a later stage, can only find the room which they require in the thorax. Brain.

The first thoracic ganglion of the Chironomus-larva lies in the prothorax, the second and third in the mesothorax. The first abdominal is shifted forwards from its proper segment to the metathorax (fig. 35). Ganglia and connectives of ventral cord.

The connectives between the ganglia, though really double, appear to form a single cord behind the first abdominal ganglion, except in very young larvae, where

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[1] Weismann, 1863.

they are still distinct[1]. The nerve-cord has the usual connective-tissue sheath. In the ganglia the masses of

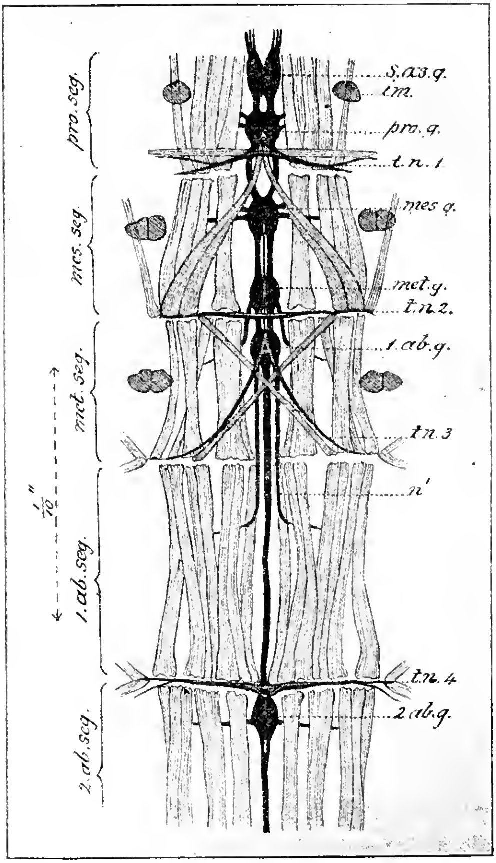

FIG. 35.—Nervous system of adult larva (fore part, extending to second abdominal ganglion, together with muscles of body-wall). The nerves are black. *s.œs.g*, sub-oesophageal ganglion. *im*, rudiments of imaginal legs. *pro.g*, prothoracic ganglion. *t.n.* 1–10, transverse nerves. *mes g*, mesothoracic ganglion. *met.g*, metathoracic ganglion. 1–8 *ab.g*, abdominal ganglia. *n'*, nerves passing from first abdominal ganglion to muscles of that segment. N.B.—The brain is not shown.

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[1] The connectives between the pro- and mesothoracic ganglia enclose between them the insertions of a pair of strong muscles, which arise from the hinder margin of the mesothorax. The separation of the thoracic connectives by muscles is more evident in large and active insects, such as the cockroach. (See Miall and Denny, 1886, fig. 34.)

nerve-cells are, as in other insects, ventral to the fibrous tracts.

Branches of distribution.

Each ganglion sends branches to its own segment. Where the ganglion is shifted out of its proper segment the branches retain their primitive distribution.

The last ganglion sends a pair of nerves to the ventral surfaces of each of the last two abdominal segments. There are probably nerves, which we have not clearly seen, connected with the ganglia at the bases of the bunches of sensory hairs (pp. 35, 49).

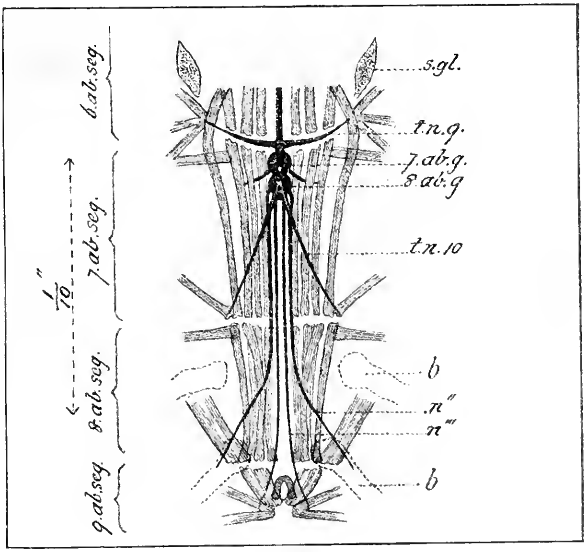

Fig. 36.—Nervous system of adult larva (hinder part). *s.gl*, sexual glands. *n''*, *n'''*, nerves passing from last ganglion to muscles of eighth and ninth abdominal segments. *b*, ventral blood-gills. The rest as in fig. 35.

Transverse nerves.

A transverse nerve proceeds from each of the thoracic and abdominal ganglia, except the first abdominal, and runs transversely above the ventral cord, usually along the junction of two segments (figs. 35, 36). Each is connected by a longer or shorter median nerve with one of the ganglia in front or behind; and at the junction of the median and transverse nerves there is a minute triangular plexus. The first, second, third, and tenth transverse nerves are thus connected with the thoracic ganglia in front of them, while the fourth to the ninth inclusive join the second to the seventh abdominal ganglia behind. The origin of the tenth and last transverse nerve lies immediately above the eighth abdominal ganglion, and its median nerve is too short for observation. The first abdominal ganglion has no transverse nerve, owing to the concentration of the ganglia in this region, where there is more than one ganglion to a segment. Each transverse nerve lies along the junction of two segments, and the figures show that every junction between the prothorax and the eighth abdominal segment has its nerve. The third and tenth transverse nerves take an oblique course owing to the forward displacement of the ganglia from which they spring.

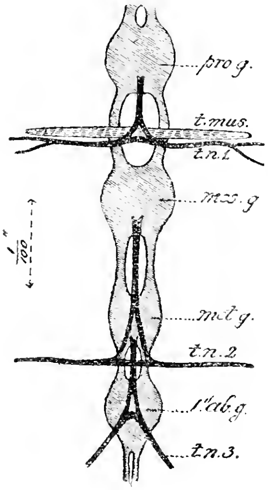

Fig. 37.—Thoracic ganglia and transverse nerves of larva, the latter in black. Letters as in fig. 35. *t.mus.* transverse muscle.

Similar nerves have been elaborately figured and described by Lyonet[1] in the caterpillar of *Cossus ligniperda*; by Newport[2] in the caterpillar of *Sphinx ligustri*; by Leydig[3] in *Locusta viridissima*; they have also been found in various other insects[4]. Lyonet gives no

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[1] *Traité anatomique*, p. 201, pl. ix, fig. 1.

[2] 1834, p. 401, pl. xvi.

[3] 1864 a, pl. vi, fig. 3. See also Leydig, 1864 b, p. 203.

[4] *Ann. Sci. Nat., Zool.*, x, pp. 5–10 (1858).

explanation of their special function, but notes that they communicate with branches of the ventral cord, and send branches towards the spiracles. Newport calls them *transverse* nerves from the direction of their principal branches, and also *respiratory* nerves from their special distribution to the breathing organs. Blanchard and Leydig[1] identify them with the sympathetic nervous system of Vertebrates. Since there is no experimental proof of their function, we adopt the neutral name of *transverse nerves*[2]. Their regular development throughout the body of the Chironomus-larva, which (in our species) has no open spiracles, and

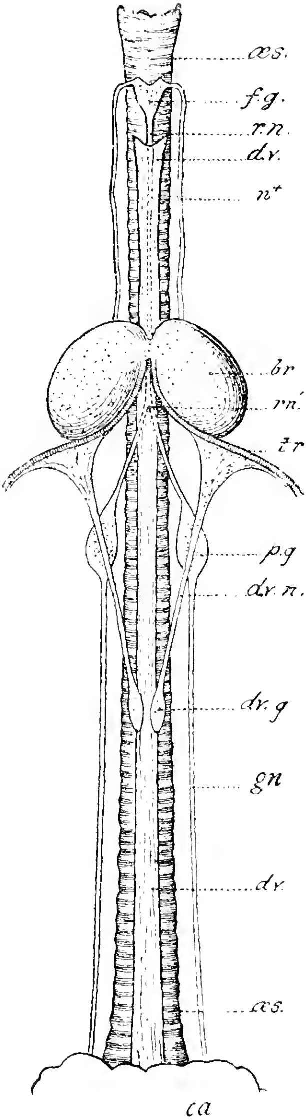

Fig. 38.—Stomato-gastric nerves of larva. *œs*, oesophagus. *ca*, cardiac chamber of stomach. *d.v*, dorsal vessel. *br*, brain. *f.g*, frontal ganglion. *r.n*, recurrent nerve. *n*^{4}, nerve passing from brain to frontal ganglion (Newport's fourth nerve). *rn′*, point of division of recurrent nerve. *tr*, trachea. *p.g*, paired ganglia. *dv.n*, nerve to dorsal vessel. *dv.g*, ganglia of dorsal vessel. *gn*, gastric nerve, to cardiac chamber. The course of the recurrent nerve beneath the dorsal vessel is dotted.

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[1] (1864 b), p. 203.

[2] H. Landois, in his juvenile thesis, *De systemate nervorum transversorum* (Greifswald, 1863), thinks that transverse nerves are particularly well developed in insects which have in the winged state a mobile abdomen (p. 24).

only vestiges of a tracheal system, is an argument against their respiratory character—not a conclusive argument, however, for at a later time spiracles form close to the junctions of the segments.

Stomato-gastric nerves.

A special system of *stomato-gastric* nerves and ganglia is found upon the oesophagus and the fore part of the aorta (fig. 38)[1]. Paired nerves proceed forwards from the lobes of the brain, and unite to form a frontal ganglion on the oesophagus. From the frontal ganglion a median recurrent nerve passes backwards between the aorta and the oesophagus. Beneath the brain this divides into two branches, which enter paired ganglia, and continue beyond them to the stomach. In some other Dipterous larvae[2], paired nerves are found, which pass backwards from the brain, and enter small ganglia on either side of the aorta. In the Chironomus-larva similar ganglia are seen (fig. 38, *dv.g*); we are not, however, quite satisfied in this case as to the nervous connexion with the brain. In some other insects a more extensive system of paired ganglia exists, sending branches to the oesophagus, aorta, and occasionally to the salivary glands.

Sense-organs.

The organs of special sense found in the larva are the eye-spots, the antennae, and the sensory prominences on the last segment. The eye-spots are little more than blotches of pigment without lenses. There are two pairs of them. In the larvae of several Culicidae the anterior pair become complex. In Corethra, Weismann found that the fresh-hatched larva possesses only one pair; that the second pair are developed in front of the first as a series of folds in two deep invaginations of the epidermis; that the first pair then begin to degenerate; and that the second pair are true compound

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[1] This is the *sympathetic* system of Johannes Müller, 1828.

[2] Phalacrocera (Miall and Shelford, 1897, pl. x, figs. 19, 20).

eyes, which are never replaced, but persist as the eyes of the fly. If this is really the case, the number of elements must be greatly increased during transformation. Weismann believes that the imaginal eye of Corethra, though not superficial, is functional in the transparent larva[1].

The antennae consist of a basal piece, relatively large, which carries two terminal pieces of nearly equal length, one jointed and one simple, the former consisting of four joints; a stout seta projects from the basal joint. There is a circular sensory spot about the middle of the basal joint; a similar spot occurs on the maxillary palp of the Phalacrocera-larva.

It seems probable that the antennae of the Chironomus-larva are of limited physiological importance; they are minute and of comparatively simple structure.

On the dorsal surface of the last segment, and at the very end of the body, are a pair of sensory appendages. Each bears several long setae, and is in close connexion with a ganglion at its base. The ganglion is no doubt connected with the abdominal nerve-cord, but we have not made out the connexion to our satisfaction (see p. 45). In the Tanypus-larva these prominences are long, and the setae numerous (see p. 33).

4. *Alimentary Canal.*

General description.

The alimentary canal of the larva takes a nearly straight course through the body, which it slightly exceeds in length (fig. 40). It is subdivided into oesophagus, stomach, and intestine. The stomach includes a distinct anterior region, which we shall call the *cardia* or *cardiac chamber*, while the intestine is divisible into a small intestine in front, and a large intestine or colon

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[1] Weismann, 1866, p. 16.

behind. There is no separate rectum, and the parts known in other insects as crop and gizzard are not distinguishable from the rest of the oesophagus. The stomach, small intestine, and colon all begin at their maximum width and gradually narrow behind.

The usual appendages of the alimentary canal are the salivary glands, the glandular caeca, and the Malpighian tubules. All these are found in our larva.

Nomenclature.

We shall devote a few lines to the nomenclature of the parts of the alimentary canal in insects generally, and to the definition of the terms which will be employed here. The alimentary canal in all insects is divided on developmental grounds into three primary sections:—(1) the *fore-gut* or *stomodaeum*, Fr. *préintestin*, Ger. *Vorderdarm*; (2) the *mid-gut* or *mesenteron*, Fr. *médi-intestin*[1], Ger. *Mitteldarm*: (3) the *hind-gut* or *proctodaeum*, Fr. *postintestin*, Ger. *Hinterdarm*. The mid-gut is the primitive alimentary canal, and in animals which pass through a well-marked gastrula-stage, it is at first a large internal cavity, formed by infolding of the hollow blastosphere, and lined by entoderm (hypoblast). The fore-gut and hind-gut arise by infolding of the ectoderm from the mouth and anus respectively. In all Arthropods they are lined by chitinous cuticle. The beginning of the hind-gut is marked, in nearly all insects, by the insertion of the Malpighian tubules[2].

The fore-gut of insects includes the oesophagus, and often exhibits a large dilatation, which may be followed by a chamber with thickened muscular wall and dense chitinous lining. The lining may be shaped into internal teeth or ridges. For the dilatation the name *crop* (Fr. *jabot*, Ger. *Kropf*) is in general use, while the muscular chamber is called *gizzard* (Fr. *gésier*, Ger. *Kaumagen*). Plateau[3] objects that the so-called gizzard of insects has no analogy with that of birds. This is put strongly;

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[1] This term is proposed by Balbiani, 1890, p. 3.

[2] Ptychoptera, according to Gehuchten, 1890, and Meloidae, according to Beauregard, 1886, are exceptions. Here the Malpighian tubules are said to pass off from the mid-gut. The same peculiarity is believed to obtain in scorpions.

[3] 1874, p. 114.

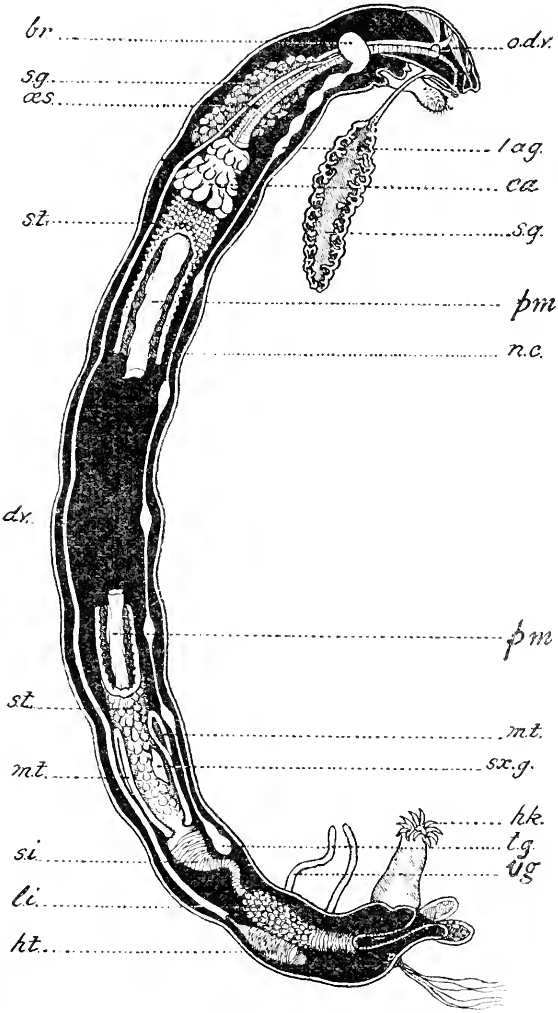

FIG. 39.—Bisected larva. *br*, brain. *s.g*, salivary gland. *œs*, oesophagus. *d.v*, dorsal vessel. *o.d.v*, outlet of ditto. *st*, stomach. *m.t*, Malpighian tubule. *s.i*, small intestine. *l.i*, large intestine. *ht*, heart. 1 *a.g*, first abdominal ganglion. *ca*, cardiac chamber of stomach. *pm*, peritrophic membrane. *n.c*, nerve-cord. *sx.g.* sexual gland. *hk*, hooks of anal feet. *t.g*, terminal ganglion of nerve-cord. *vg*, ventral blood-gills.

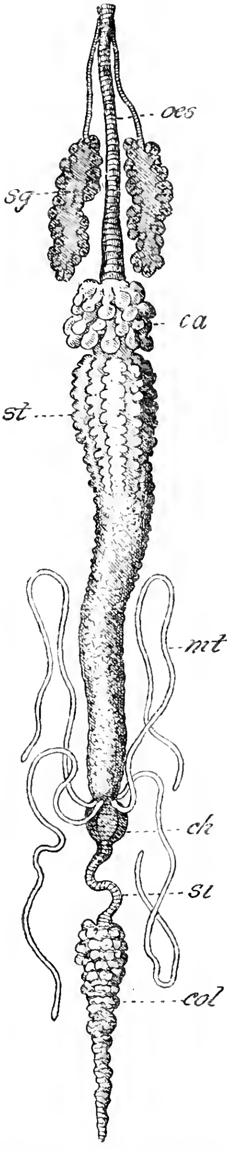

FIG. 40.—Alimentary canal of larva. *œs*, oesophagus. *sg*, salivary gland. *ca*, cardiac chamber of stomach. *st*, stomach. *mt*, Malpighian tubules. *ch*, dilated chamber at beginning of intestine. *si*, small intestine. *col*, colon.

there is at least the resemblance implied in a thick muscular wall and a dense cuticle. Of course the gizzard of the bird is part of the vertebrate *stomach*, while that of the insect is part of the arthropod *oesophagus*. If we will employ no vertebrate terms except strictly in the vertebrate sense, we shall be forced to invent unfamiliar and cumbrous expressions of our own. Plateau's *appareil valvulaire*, which he proposes to substitute for *gizzard*, is liable to be confounded with the oesophageal valve next to be mentioned. The lower end of the oesophagus of insects commonly protrudes into the mid-gut, and is then reflected, forming a circular valve, the *cardiac* or *oesophageal valve* of authors. The latter designation is preferable.

For the mid-gut or mesenteron in the completely developed insect, *stomach* is a convenient term. Plateau points out that the so-called stomach of insects is absorbent, but not secretory. It is not, however, clear that such physiological distinctions, even if well founded [1], need affect our nomenclature. The fore part of the stomach sometimes forms a distinct *cardiac chamber*, and into this, if present, the *glandular caeca*, which often project from the stomach, usually, but not always open.

The name *intestine* may be applied to all parts developed from the hind-gut. The intestine is often divisible into a fore section (*small intestine*), a middle section (*colon*), and a terminal section (*rectum*). The walls of the rectum are often longitudinally folded.

Mouth.

The mouth lies between the labrum in front and the labium behind; on either side are the mandibles and the greatly reduced maxillae (fig. 19). The labrum has the form of a flap; its free border is bent backwards when at rest, and the surface which faces the mouth (*epipharynx* of some authors) is armed with many teeth, raspers and setae, whose disposition can be seen in fig. 16. Some of these are probably sensory, others defensive, and others again masticatory or prehensile. The labrum is muscular and mobile; it is often employed to assist the mandibles in rasping the food, grinding it

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[1] See Secretion of the stomach, p. 57.

against the toothed labium, or cramming it into the mouth. In the floor of the mouth above the mentum (see p. 29) is a small forward projection, the lingua, behind which the salivary ducts open.

Oesophagus.

The oesophagus or gullet is a straight and narrow tube of simple structure. It is lined by an epithelium (not easily seen, and often only to be discerned by the cell-nuclei) and a chitinous cuticle, which is sharply folded lengthwise, so that the enclosed cavity is almost obliterated except when food is actually passing along it[1]. Outside the epithelium comes a muscular coat, invested inside and out by a thin membrane, which sometimes becomes separated in a macerated gullet. The muscular coat consists of a number of transverse rings, each of which is a cell, with thin cell-wall and nucleus. The ends of the cells are in contact on the ventral side, and form oblique sutures. In optical section they often look deceptively like an epithelium. Each cell, except in very young larvae, encloses a skein of fibres, which show cross-striation. The fibres lie in the direction of the length of the cell, i.e. at right angles to the oesophagus[2]. In the head the gullet is held in place by several pairs of slender muscles, which pass downwards and forwards from the occipital region (fig. 19). A small pouch extends forwards from its dorsal wall near the mouth.

Oesophageal valve.

The dilatations of the oesophagus, known as crop and gizzard, which in many insects and myriopods facilitate a process of oesophageal digestion, as explained by Plateau[3], do not occur in the Chironomus-larva. The

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[1] In a cast skin the chitinous lining is drawn out, and remains attached to the skeleton of the head as a long crumpled band.

[2] A much finer striation, which we believe to be due to local and temporary aggregations of the cell-protoplasm, often forms across the cell from side to side. This is shown in fig. 52.

[3] 1875, 1878.

tube enlarges a little behind, and then seems suddenly to dilate into the much wider stomach. A longitudinal section of the parts shows, however, that the oesophagus protrudes well into the larger chamber, and then returns upon itself, forming in this manner a circular valve, which we call, with Balbiani[1], the *oesophageal valve* (fig. 47). It lies in the fore part of the larval metathorax. The oesophageal cuticle is here very sharply folded so that it appears rosette-like in cross-section; in the Chironomus-larva this is only a more pronounced form of the folding which extends throughout the oesophagus, but in some other insects it is a special feature of the included termination of the oesophagus.

The oesophageal valve retards the passage of solid food into the stomach, and further, delivers it, not into the beginning of the stomach, but some way down. The epithelium of the cardiac chamber, into which the caeca usually open when they exist, is therefore not brought into direct contact with the solid food. Only dissolved food, microscopic particles, and digestive fluids actually reach this epithelium. In the Chironomus-larva and many other insects an inner tube, which will shortly be described under the name of the *peritrophic membrane*, conducts the solid food to the very end of the stomach, and thus completely protects every part of the epithelium of the stomach from abrasion[2].

Stomach. The *stomach*, mid-gut, or mesenteron is a long cylindrical tube, which occupies more than half the length of the alimentary canal. It is widest in front, gradually tapering to its junction with the small intestine, which is indicated by the four Malpighian tubules.

Cardia. The chamber which encloses the oesophageal valve is

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[1] 1890. p. 26.

[2] For fuller information respecting the oesophageal valve, see p. 60.

often called *proventriculus*, in the belief that it is, like the crop or gizzard of many insects, a dilatation of the oesophagus. Weismann indeed expressly asserts that it is such[1]. Our sections of Chironomus-embryos (fig. 127) lead us to a different conclusion, which is confirmed by the study of other insects. In Ptychoptera[2], Dicranota[3], and the cockroach[4] the break in the epithelium is quite unmistakable, and shows that the outer wall, which in the cockroach is drawn out into caecal projections, is mesenteric and not stomodaeal. The bee[5] and many other insects show essentially the same structure. The chitinous lining of the stomodaeum can often be distinctly traced as far as the break in the epithelium, where it disappears; in other cases the peritrophic membrane described below introduces complications, or the chitinous lining disappears gradually. We believe that all or very nearly all of the outer wall of the tube which encloses the oesophageal valve is developed from the mesenteron, and that caeca in this region always belong to the mesenteron. It is therefore inappropriate in our opinion to apply the term *proventriculus* to the part in question, which when distinct we call the *cardia*, or the *cardiac chamber of the stomach*. The term *proventriculus* has been long associated with the gizzard of insects.

Structure of stomach.

The cardiac chamber, or beginning of the stomach, lies in the metathorax; it is externally well marked. Three sets of short caeca project from its outer surface (fig. 41); they have no muscular wall[6]. A pair of muscles, arising,

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[1] 1863, p. 35 and fig. 96.

[2] Gehuchten, 1890.

[3] Miall, 1893, fig. 18.

[4] Miall and Denny, 1886, fig. 64, p. 120.

[5] Schiemenz, 1883.

[6] These caeca vary much in different Dipterous larvae; they are usually short, but long in the blow-fly larva; the number may be two (Ctenophora), four (Tipula, Simulium, &c.), or many.

we believe, from the junction of the meso- and metathorax on the ventral surface, are inserted into the fore part of the chamber (fig. 41)[1]. The outer surface of the succeeding part of the stomach is studded over by very numerous prominences, which bulge out between the crossed fibres of the muscular coat, being covered only by a thin connective-tissue layer. They are not caecal processes but solid outgrowths, consisting each of a single epithelial cell, or parts of two such cells; when seen in face they form a tolerably regular mosaic. Before the middle of the stomach is reached these prominences

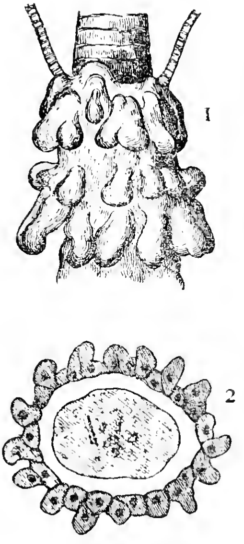

FIG. 41.—1, cardiac chamber of stomach of larva, showing its three tiers of caeca. 2, transverse section of fore part of stomach, showing the epithelium, and the food enclosed in a peritrophic membrane.

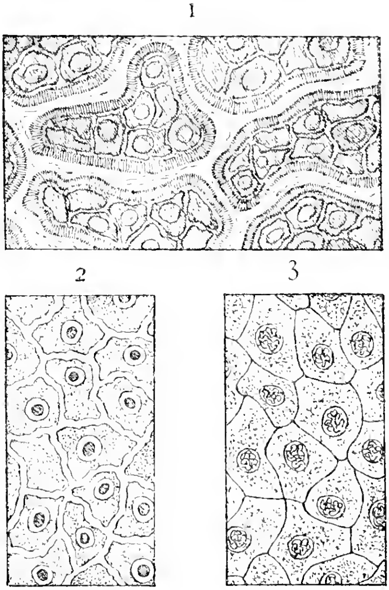

FIG. 42.—Epithelium of larval stomach. 1, 2, from middle; 3, from fore end. In 1 the striated seam can be observed around the island-like folds of epithelium; in 3 the nuclear figures are shown.

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[1] Similar muscles are found in the crane-fly larva.

subside. In the middle and hinder part the epithelium is sometimes thrown into shallow folds of irregular shape, which, when seen in face, look like islands with intervening channels (fig. 42, 1). The epithelial cells here assume a character which is usual in the stomach of insects, though by no means peculiar to it, being drawn out into numerous filaments, which are sometimes very long[1]; they may resemble, when contracted, the 'striated hem' usual in the intestinal epithelium of vertebrates.

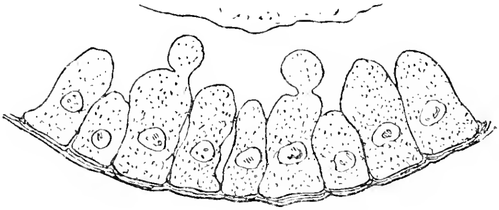

FIG. 43.—Epithelium of stomach, showing protrusions and detached peritrophic membrane. The striated hem is not drawn.

Secretion of the stomach.

Protrusions from the glandular epithelium of the stomach (such as those described and figured by Gehuchten in the larva of Ptychoptera) are easily seen at certain times in the stomach of the Chironomus-larva: they are finely granular, and protrude through the striated hem (fig. 43). In an earlier phase the granular substance (mucigen) collects along the inner face of every cell, and is readily distinguished from the ordinary cell-protoplasm in which the nucleus lies[2]. During active secretion large drops of mucus are squeezed out, and blend with the drops from neighbouring cells to form a viscid mass. Empty cells, with only the basal protoplasm and the nucleus, are occasionally but rarely seen. We agree with Gehuchten in believing that the secreted fluid

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[1] Frenzel, 1885.

[2] But see note to p. 60.

does not at once come into contact with the food; it is separated therefrom by the peritrophic membrane, which extends throughout the stomach. Between the epithelium and the membrane is a narrow space, which is occupied by a granular fluid, probably derived from the protrusions; it contains also granules of larger size, which we suppose to come from the food. It is not necessary to suppose with Gehuchten that the secreted fluid *diffuses through* the peritrophic membrane; the granules just noted indicate that another communication exists. We think it probable that fluid squeezed out from the food in the oesophagus and oesophageal valve passes down the cylindrical tube formed by the peritrophic membrane, and that it is regurgitated into the outer space by the contractions of the muscular chamber in which the small intestine begins (see p. 66).

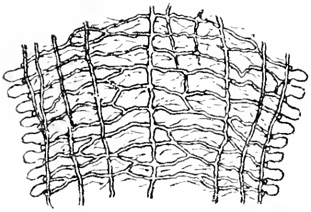

FIG. 44.—Muscular coat of stomach of larva, after immersion in 1 per cent. sodic carbonate, showing longitudinal and transverse fibres. The basement-membrane bulges out between the muscles on the sides.

Muscular coat of stomach.

The muscular coat of the stomach consists of two layers, an internal layer of annular fibres with frequent anastomoses, and an external longitudinal layer (fig. 44). A connective-tissue membrane invests both the inside and outside of the muscular layer, and is sometimes seen detached from the underlying epithelium in the meshes between the muscles [1].

Peritrophic membrane of stomach.

The proper chitinous lining of the stomodaeum usually ceases in insects at the lower end of the oesophagus. Nevertheless it is not uncommon [2] to find that the stomach

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[1] e.g. when the epithelium is macerated in weak alkali.

[2] Examples have been discovered in all the chief orders of insects (see

also is lined by a chitinous tube, which is not usually in contact with the epithelium. This is the *funnel* (Trichter) of Schneider, the *peritrophic membrane* of Balbiani. Its chitinous nature is inferred from its resistance to alkalis. It invests the food, and may be a provision for keeping rough particles from abrading the delicate epithelium. At times of moult, and in some Myriopods and Crustacea at all times, the peritrophic membrane breaks off, and passes out of the stomach with the faeces, which are thus enclosed in a kind of bag. In the Chironomus-larva it can at times be seen to begin exactly where the mesenteron begins; sometimes its fore edge is included in the first fold of the epithelium of the mesenteron (fig. 48). The peritrophic membrane has been found in nearly every Dipterous larva examined; Dicranota is an exception. It occurs also in many insects of other orders.

We have not been able to obtain entirely satisfactory evidence of the actual formation of the peritrophic membrane in Chironomus. In the larva of Simulium there may occasionally be seen a very copious fluid, coagulable by alcohol, in the cardiac caeca, and investing the food in the stomach. We have thought it possible that this may be the peritrophic membrane in a nascent condition. The membrane may in Chironomus also be a special secretion of the cardiac caeca, but of this we have still less evidence. Gehuchten (Ptychoptera), Cuénot (Orthoptera), besides Plateau and Balbiani (Chilopoda), agree that the membrane originates in the mesenteron.

The membrane extends throughout the stomach, though without attachment to its wall, except at its fore end,

Schneider, 1887, p. 95), in some Myriopods, Crustacea (Cirripeds, Cladocera), and Gasteropoda (Limnaeus, Helix, Limax). References to the literature are given by Balbiani, 1890, p. 30; Schneider, loc. cit.; and Gehuchten, 1890, p. 91.

and forms a loose inner tube of relatively small diameter (fig. 39, *pm*); sometimes it is thrown into loops or bends which do not affect the stomach itself. Black masses of food usually occupy the inner tube, and distinguish it from the surrounding cavity of the stomach. At the beginning of the small intestine the chitinous intima of the proctodaeum begins, and a little beyond this place the peritrophic membrane thins out and ceases. If the alimentary canal is removed from a fresh larva, and divided at the junction of the stomach and small intestine, the muscular and epithelial coats above the section contract, while the chitinous tube lies passive, and soon protrudes considerably from the cut end. This gives a ready proof of the want of adhesion between the membrane and the surrounding epithelium[1].

Miss Phillips' account of the oesophageal valve.

At our request, Miss Dorothy Phillips, a student of the Yorkshire College, has investigated more fully the structure of the oesophageal valve and peritrophic membrane, and furnishes us with the following account, as well as with sketches for the accompanying illustrations:—

'The oesophageal valve of the Chironomus-larva is a complicated structure, and will be better understood when compared with a simpler case. Simulium has been chosen as a convenient term of comparison.

'The layers of the oesophageal wall of the larva of Simulium and Chironomus, in order from within, are as follows:—

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[1] Vignon (1899) has published a preliminary note on the histology of the alimentary canal of the Chironomus-larva, in which he states (1) that the cavities or transparent spaces beneath the striated hem of the cells of the gastric epithelium are not visible in the living larva, and are due to pressure or the action of reagents; (2) that the peritrophic membrane is secreted in the neighbourhood of the gastric caeca, and gradually pushed downwards by the pressure of the food extruded from the oesophagus; he describes certain details, for which we must await the fuller account to be published in *Arch. de Zool. expér.*; (3) that vibratile cilia occur in the stomach and beginning of the intestine.

‘1. The *chitinous intima*, secreted by

‘2. The *epithelium*.

‘3. A *muscular layer*, of which the circular muscles form the principal part.

‘The oesophagus is continued into the cardiac chamber as an inner tube, whose wall becomes abruptly reflected, and passes upwards again, to the point where the epithelium of the stomach begins. There is thus an *upper* and a *lower bend* in the tube. The part of the oesophagus which is doubled into the cardiac chamber is called the oesophageal valve.

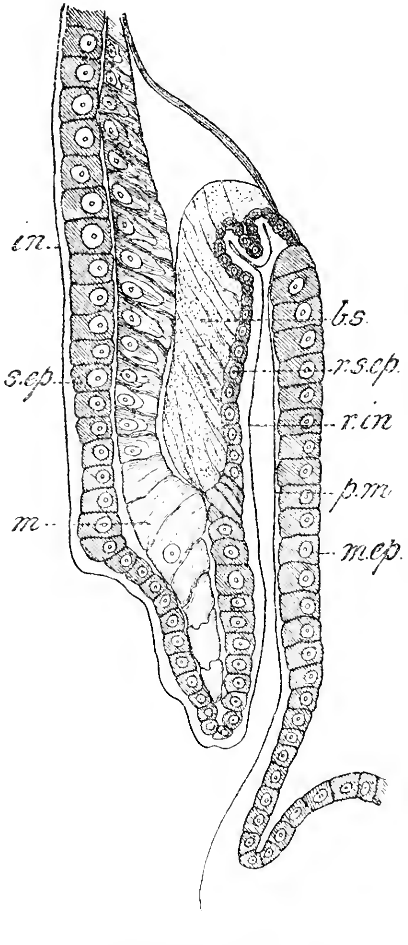

Fig. 45.—Oesophageal valve of Simulium-larva, one-half of a longitudinal section. *in*, chitinous intima. *s.ep*, stomodaeal epithelium. *m*, muscle-cells. *b.s*, blood-space. *r.s.ep*, reflected stomodaeal epithelium. *r.in*, reflected intima. *p.m*, peritrophic membrane. *m.ep*, mesenteric epithelium.

‘We will now describe, in more detail, the oesophageal valve of the Simulium-larva (fig. 45). In the reflected wall, i.e. the part between the upper and lower bends, the layers behave in the following manner:—The intima and epithelium extend to the upper bend. The epithelial layer decreases in thickness on approaching the upper bend, and is there bent into a small secondary fold which projects into the stomach. It then abuts upon the mesenteric epithelium. The passage from one epithelium to the other is abrupt, without transition. The muscular layer is not reflected, but ends at the lower bend.

'Between the oesophageal wall and its reflected continuation is a blood-space, which does not quite reach the lower bend. It has a proper wall, in the form of a thin membrane, and is crossed by a number of oblique connective tissue-fibres (fig. 45).

'In the larva of Chironomus (fig. 47) the layers of the wall of the oesophagus, in order from within, are as follows:—

'1. The *chitinous intima*, thrown into deep, longitudinal folds; and secreted by

'2. The *epithelial layer*, which is thin, and consists of a single layer of cells. This layer is generally inconspicuous and sometimes becomes much attenuated, probably after it has performed its function of secreting the chitinous layers.

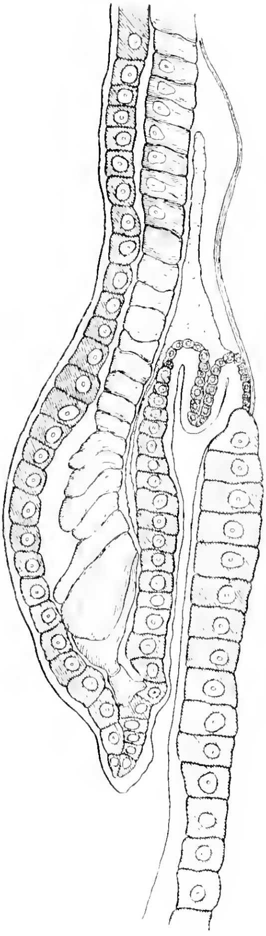

FIG. 46.—The same parts as in fig. 45 The blood-space is now contracted.

'3. The *basement-membrane* is a thin and apparently chitinous layer which lies close to the epithelium, by which it is secreted; it is also closely applied to the muscular layer. Like the generating epithelium, it is thrown into longitudinal folds, which alternate with the folds of the intima[1].

'4. The *muscles*, circular and longitudinal. The circular muscles form the innermost layer, and are large and conspicuous. At first they are simple, annular

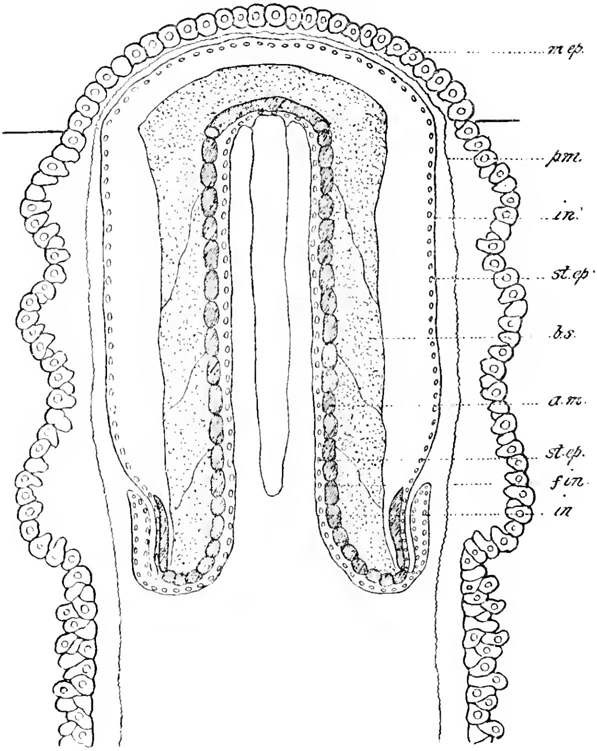

FIG. 47.—Diagram of oesophageal valve of Chironomus-larva. A transverse and a longitudinal section are here combined, the place of intersection being marked by a thick line. *m.ep*, mesenteric epithelium. *pm*, peritrophic membrane. *in'*, reflected intima. *st.ep'*, reflected stomodaeal epithelium. *b.s*, blood-space. *a.m*, annular muscle-cells. *st.ep*, stomodaeal epithelium. *in*, chitinous intima. *f.in*, longitudinal folds of intima.

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[1] Weismann has noted the presence of this chitinous layer in the oesophagus of Muscidae, and in the stomach and intestine of Corethra.

muscle-cells, each surrounding the oesophagus, and showing a line of junction on the ventral side, where the ends of the cell meet; each cell contains a large nucleus. At a later stage, the nucleus breaks up, and the whole cell-substance divides into a number of striated fibres, lying more or less parallel to the original cell. The wall of each muscle-cell appears in transverse section as a clear, wavy, fairly distinct line on the superficial side, but somewhat difficult to determine on the deep side. The longitudinal muscles of this part of the alimentary canal are restricted to the neighbourhood of the upper bend; they are few, and lie outside the circular muscles, stretching across the mouth of the blood-space from the oesophagus to the cardiac wall (figs. 45, 46).

'The oesophageal valve of Chironomus has the same general arrangement as in Simulium and many other insects, but is complicated by secondary folds of the epithelium and intima, which are the *upper and lower intermediate bends.*

'In the reflected wall of the oesophageal valve the behaviour of the different layers is difficult to determine; but it is probably as follows:—

'1. The *chitinous intima* continues to the upper bend, where it ends in an uneven edge. At a distance from the lower bend equal to about one-fifth of the total length of the valve it becomes abruptly folded inwards and backwards to the lower bend, thus forming the upper intermediate bend. Arrived at this point, it is again sharply reflected upwards (lower intermediate bend), and lying parallel to its former course, passes straight to the upper bend. Two of the three layers formed by this repeated folding are closely applied to each other, but between these and the third is a space, filled with a clear coagulable fluid, which is not obliterated even when the oesophagus is distended with food. This folding of the intima gives the appearance of a deep chitinous band, encircling the base of the valve externally, and best seen in fresh specimens from which the epithelium of the cardiac chamber has been removed.

'2. *The epithelium* is difficult to observe, but it closely follows the course of the chitinous intima. It consists of polygonal, nucleated cells, which decrease in size towards the upper bend. When it is in an inactive condition the nuclei of the epithelium are relatively very small.

'3 .It is not clear whether the *basement-membrane* continues to the upper bend, or, as seems more probable, disappears in the region of the lower bend.

'4. The *muscular layer* is reflected for about half the length of the valve. The boundaries of the muscle-cells become faint, and their thickness gradually diminishes as the reflected layer passes upwards.

'Between the muscular layer and its reflected continuation is a blood-space similar to that already described in the Simulium larva. During the passage of large masses of food along the lower part of the oesophagus the inner tube may be so greatly distended as to obliterate the space and squeeze out the blood (fig. 46). A number of oblique fibres may be seen to pass from the inner to the reflected muscular layer across the lower half of the blood-space. These fibres, which are probably of connective tissue, bind the walls of the fold together, but so loosely as to admit of considerable relative movement. It is obvious that fibres passing directly across would be much shorter, and would restrain the movements within much narrower limits. The fibres at their inner ends seem to be attached directly to the walls of the oesophageal muscle-cells, but at their outer extremities they are attached to a more or less cylindrical layer of connective tissue, which forms the outer boundary of the blood-space; it is generally applied to the surface of the reflected muscular layer, but occasionally is seen to be separated from it. This connective-tissue layer extends upwards beyond the reflected layers in some cases, and passes out from the blood-space, at the level of the upper bend, into the body-cavity. Gehuchten (1890) has described a somewhat similar structure in the oesophageal valve of *Ptychoptera contaminata*. The blood-space, however, in this case does not appear to communicate freely with the body-cavity, as in Chironomus; and it is traversed by radial membranes, some of which are described as muscular, others as elastic, not simply by connective-tissue fibres, as in Chironomus.

Miss Phillips' account of the peritrophic membrane.

'The whole of the stomach is lined by a distinct chitinous membrane, the peritrophic membrane of Balbiani. It is thinner than the oesophageal intima, and shows no longitudinal folds. A space, filled with fluid and food-particles, separates it, except at one point, from the epithelium of the stomach. The one place of attachment is at the beginning of the mesenteric epithelium, where it comes in contact with the oesophageal epithelium.

'The peritrophic membrane is renewed from time to time, and is occasionally double throughout. In such cases the inner tube is evidently the old one, which has failed to be carried away with the food as usual. The times of renewal of the membrane have not been ascertained.

'All the facts point to the derivation of the peritrophic membrane from the epithelium of the stomach, either by secretion or conversion, but the process has not been directly observed in Chironomus.'

Small intestine.

The small intestine begins in a pear-shaped chamber, which receives the four Malpighian tubules. It may be seen to contract suddenly from time to time, and then slowly to dilate. There is some reason to suppose that, when it contracts, the fluids extracted from the food are impelled into the space between the wall of the stomach and the peritrophic membrane. The rest of the tube is narrow and uniform. Its wall closely resembles that of the oesophagus, consisting chiefly of annular muscle-cells, each enclosing a number of obscurely striated fibres; within the muscular coat is a mosaic epithelium.

The colon, or large intestine, begins as a wide tube with rather distant bundles of striated muscular fibres, all annular. In this part of the colon the epithelial cells form transverse rows of large nucleated cells lying between the muscles, and bulging externally (fig. 49). Colon.

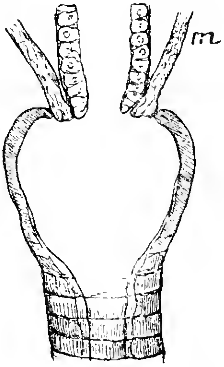

FIG. 48.—Chamber at beginning of larval intestine. *m*, origin of two of the Malpighian tubules.

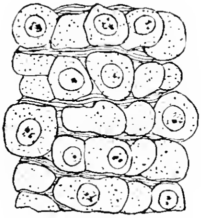

FIG. 49. — Epithelium and annular muscles of larval colon.

Lower down, the epithelium becomes thinner and less distinct, so that the muscular coat constitutes nearly the whole thickness of the wall. At the same time the diameter of the tube steadily diminishes. There is no rectum, or terminal enlargement, and the colon is continued to the anus, which is situated in the last segment.

The salivary glands of the larva (fig. 50) form a pair of thin hollow sacs, situated in the second and third thoracic segments. Each is slightly curved in Salivary glands conformity with the wall of the body, the concavity being turned towards the oesophagus, which lies between them. The lining epithelium is not continuous throughout, but ceases along the middle of the broad surfaces. The cells form a single layer, and are of large size, while the nuclei are enormous, being easily studied with a quarter-inch objective (fig. 50, 5). Sometimes the cells, probably in a special phase of activity, are flattish, while at other times the nuclei, surrounded by a thin coat of protoplasm, project into the lumen of the gland, being connected with the wall only by a slender neck [1]. Balbiani [2] has described the very interesting nuclei of these glands. They are easily prepared for examination, and the object is well suited in every way to the young

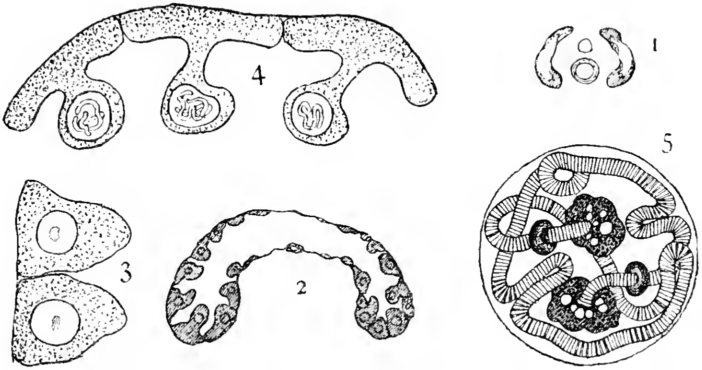

Fig. 50.—Salivary glands of larva. 1, position of glands on either side of oesophagus and dorsal vessel. 2, transverse section of gland, showing the disposition of the secreting cells. 3, two epithelial cells. 4, epithelial cells standing out into cavity of gland. 5, nucleus of epithelial cells, the last from Balbiani, 1881.

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[1] The projection of the nuclei of these cells into the cavity of the gland seems to be an extreme case of what may be noticed elsewhere; for instance, in the epithelium of the Malpighian tubules, and sometimes in certain cells of the epidermis, especially in those of the anal blood gills. Occasionally small cells have been noticed in the basal portions of the epithelium, as if for replacement of the existing functional ones.

[2] 1881, p. 637.

histologist. A full-grown larva is decapitated on a glass slip. The glands often float out with the blood; if this does not happen, gentle pressure should be applied. The tissue may be examined at once, while still bathed in the blood of the insect, but the finer details cannot be made out until the glands are stained. The cells do not take the stain until they are killed, and it is instructive to note that they remain long unstained in non-poisonous, aqueous, staining fluids. Strong alcohol or osmic acid (the latter is preferable) kills the cells, and then the stain penetrates. The following procedure will be found to answer well :—Immerse a gland momentarily in a mixture of equal parts of 1 % solutions of osmic and acetic acids, wash in distilled water, stain with acetized methyl green, followed by carmine, and mount in glycerine. The nuclei vary much in shape, being circular, oval, club-shaped, &c. Sometimes they send out radiating projections into the cell-protoplasm. They slowly change their figure. Each nucleus contains one or two nucleoli, besides a long convoluted, transversely striated cord. The ends of the cord are attached to the nucleolus (one to each, if there are two nucleoli). The transverse striation of the cord suggests that it is composed of a number of component disks, which are sometimes seen separated into small groups in a broken-up nucleus. Korschelt[1] believes, however, that the striation is due to infolding of the surface. He considers that Balbiani's figure is too regular. The nucleoli differ much in shape, being cup-shaped, oval, lobed, &c. They do not stain with acetized methyl green, though they readily take a carmine stain. The cord stains with methyl green, but very feebly with carmine.

Similar nuclei have been found in the Malpighian tubules, as well as in the epithelium of the stomach and

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[1] *Zool. Anz.*, vii, pp. 189, 221, 241 (1884).

colon; they have also been found in young embryos of Hydrophilus[1], and in plants (endosperm of Fritillaria, &c.). The physiological meaning of the structures has not been elucidated.

The salivary fluid is used in the form of silken threads to weave together the vegetable or earthy particles of which the wall of the burrow is composed. We have no reason to attribute to it any digestive property, and its rapid coagulation on contact with water renders it hard to suppose that it can act upon food which is necessarily mixed with water.

The salivary ducts pass off from the inner or concave sides of the glands. They have a ringed ('pseudo-tracheal') structure, like that of insect air-tubes. They pass forwards to the head, and enter the floor of the mouth beneath the lingua (fig. 19, *sd*). The common duct is extremely short.

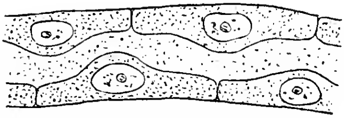

FIG. 51.—Epithelial cells of Malpighian tubule of larva.

Ganin[2] and Bugnion[3] find that in Hymenoptera the salivary glands are developed independently of the alimentary canal from a special ectodermal invagination. Carrière (1897), adopting the earlier suggestions of Bütschli and Grassi, derives them from the prothoracic spiracles, which, he says, in Hymenoptera open at first inside the second maxillae, and become approximated and at length fused as the maxillae unite to form the labium.

Malpighian tubules.

There are four long *Malpighian tubules*, which enter the dilated beginning of the small intestine. They are lined by an epithelium of flattish cells with large

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[1] Carnoy, 1885.

[2] 'Ueb. d. Embryonalhütte der Hymenopteren u. Lepidopteren-Embryonen.' *Petersb. Acad. Sci.*, xiv (1870).

[3] 'Anat. et mœurs de l'Encyrtus fuscicollis.' *Rec. Zool. Suisse*, tom. v, p. 454 (1891).

nuclei, which often project into the lumen of the tubule (fig. 51).

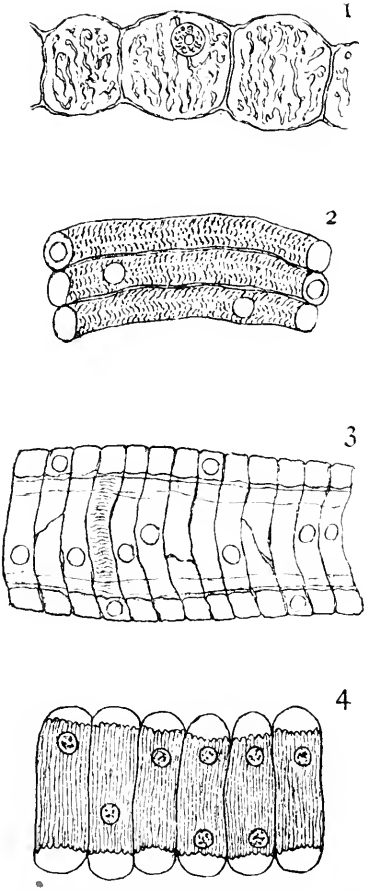

Fig. 52.—Muscle-cells of larval alimentary canal. 1, optical sections of fresh oesophageal muscle-cells, showing differentiation of contractile substance. The same appearance occurs in the intestinal muscle-cells; sometimes it cannot be found. 2, striated contractile substance and nuclei of muscle-cells of oesophagus. 3, muscle-cells of intestine, examined in blood of larva. 4, the same, after the addition of acetic acid.

Development of striped muscular fibres.

The muscular wall of the alimentary canal is well suited to the study of the development of striped muscular fibres from simple muscle-cells. We have made some progress with the investigation, but found it necessary to leave this and many other special features incomplete, in order to bring our work to a close in moderate time. The valuable *Recherches* of Viallanes (1882) would be a useful guide to any one who might be disposed to pursue the inquiry.

5. *The Heart and Circulation.*

Dorsal vessel.

When a live larva is examined under the microscope, the *dorsal vessel* is easily seen on the back of the hinder part of the body (fig. 39). In Dipterous larvae the dorsal vessel is divisible into two parts—the *heart*, which is posterior, and the *aorta*, which runs forwards from the heart. In a larva of one of the larger species of Chironomus the heart lies in the eleventh post-cephalic segment, and forms a single chamber with a muscular and rhythmically contractile wall. A pericardium can be seen in transverse sections which pass through the hinder part of the heart: elsewhere it is deficient. Two pairs of *ostia* or *lateral inlets*, of which the hinder pair are the larger, lead from the pericardium or from the body-cavity into the heart. The aorta leads from the heart to the head, lying above the alimentary canal. It passes beneath the commissure of the supra-oesophageal ganglia, and becomes enlarged further forward. A pair of rather large *aortic valves* guard the passage from the heart to the aorta; in front of these neither valves nor ostia are to be found, at least in young larvae. We have several times observed small bodies, which may be ganglia, set alternately on opposite sides of the aorta.

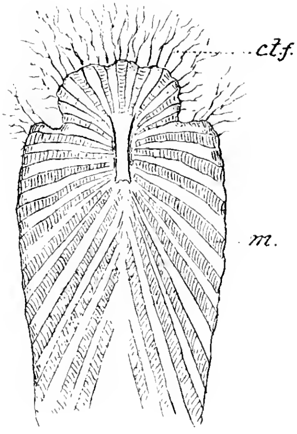

FIG. 53.—Heart of larva, ventral view, showing muscles (*m*) and connective-tissue fibres, which hold it in its place (*ct.f.*).

FIG. 54.—Heart of larva, dorsal view, showing ostia and muscles of wall.

The aorta ends in the head by a trumpet-shaped orifice, and here the blood escapes into the body-cavity.

In the living larva the energetic contractions of the heart are seen to drive the blood along the aorta, and the pulse can be followed by the eye as far as to the fore end of the stomach. The blood with its corpuscles can be seen to stream into the ostia during the dilatation of the heart.

Muscles of heart.

The muscles of the heart, when seen from above, are transverse, except behind the posterior ostia, where they radiate, and become nearly longitudinal (fig. 54). They do not extend completely across the heart, but thin away towards the middle line. On the ventral side the muscles have a radiate disposition; many of them converge towards a median space just in front of the posterior ostia; none extend completely across. A high power shows that all the muscles of the heart are striated.

Aortic valves.

The valves at the beginning of the aorta resemble triangular pockets, and when seen from the dorsal side their pointed tips seem to meet in a point; a side view shows that this is not really the case: the tips are separate, and attached to the wall of the aorta by bundles of fibres, rather like the tendinous cords of the mammalian auriculo-ventricular valves[1].

Alary muscles

Six pairs of segmentally arranged *alary muscles* (so called because they form, as it were, the wings of the heart) are found in the abdomen (fig. 55). As a rule, they spring from the junctions of the segments on the sides of the abdomen: from each junction a muscle passes forwards and another backwards[2]. Each muscle expands at its insertion into a triangular fibrous sheet, with numerous

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[1] Jaworowski, 1879.

[2] The muscle in front of a junction and that behind would together correspond with one alary muscle of a more primitive insect. (Cf. Miall and Denny, 1866, p. 135, fig. 75.)

meshes, which appears to be attached to the ventral side of the heart; a large *multinucleate pericardial cell*, elongated in the direction of the dorsal vessel, overlies each of these expansions. There are also small pericardial cells, which are attached to the upper surface of the same alary tendons singly or in clusters They are uninucleate, and contain oil-drops, as well as minute brownish concretions, probably fatty (Wielowiejski). Kowalewsky has discovered indications that the pericardial cells perform an excretory function. They eliminate carminate of ammonia, and have an acid reaction A very small cell or nucleus (perhaps a nerve-cell) is found near the middle of each alary muscle. The aorta is held in place by a great number of very fine threads which pass to its dorsal side from the body-wall.

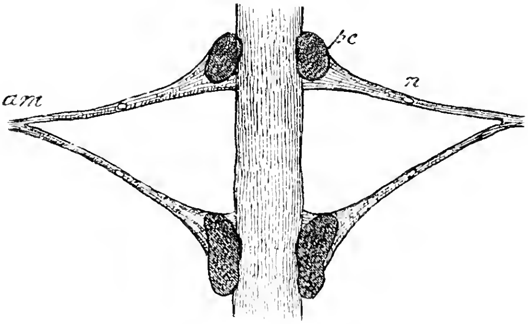

FIG. 55.—Part of dorsal vessel of larva, with pericardial cells and alary muscles of one segment. *am*, alary muscles. *pc*, pericardial cell. *n*, nucleus.

The stomato-gastric nerves of the aorta are described on p. 48.

Development of the dorsal vessel.

All Chironomus-larvae do not exhibit the same structure of the dorsal vessel, and the variations cannot be fully understood without some knowledge of the development of the organ. We learn from Jaworowski (1879) and Graber that the heart of an insect (Pyrrhocoris) may during embryonic development take the form of a nearly uniform tube, encircled by innumerable and close-set muscle-cells. The cells are usually deficient above and below, or united by non-muscular substance, so that they do not form complete circles about the dorsal vessel, but pairs of semicircles. The hinder part of such a tube may afterwards enlarge and form a heart, whose simple muscle-cells are often replaced by strands of striated muscle, as in the larger Chironomus-larvae. In the rest of the tube a great increase of length takes place without increase or even with considerable diminution in the number of the muscle-cells, which therefore become widely spaced. Certain of the muscle-cells become much enlarged, and send out nucleated projections into the cavity of the dorsal vessel. A pair of such projections, or in particular cases a single projection, forms a simple *cellular valve*, which, when the muscle contracts, prevents the passage of the blood. Such cellular valves are nearly always opposite, but in the dorsal vessel, or some part of it, of the larvae of Corethra, Ptychoptera, and Calliphora, they are not opposite, but alternate; in the Corethra-larva (where they are found only in the last chamber) they seem to be multicellular, but are not really so. Between two pairs of cellular valves, ostia, or inlets for the blood, may form; these too are specially associated with muscle-cells, and nuclei are often visible, one just in front and another just behind the inlet. The cellular valves and ostia often show something of a segmental arrangement, which is however usually effaced in the aorta and may disappear altogether.

Two types of dorsal vessel.

In Dipterous larvae two types of dorsal vessel have been described. In the first type, which is by far the commonest, both in Diptera and in insects generally, there is no important difference of structure between the heart and the rest of the abdominal dorsal vessel, which is contractile throughout, and provided with several pairs of inlets; of the many pairs of muscle-cells one pair here and there becomes enlarged, and forms cellular valves, whose free surface is often lobed; these cellular valves are intermediate between the inlets, and generally nearer to the one behind than to the one in front. There may be no enlargement of the hinder part of the dorsal vessel, and striated muscle-fibres are not found; aortic valves may be present or absent[1].

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[1] Jaworowski says that in Dipterous larvae which exhibit this type of

The larva of Tanypus exemplifies this type, as also do certain unnamed Chironomus-larvae.

The second type of dorsal vessel is found in the larva of *Chironomus dorsalis*. Here the heart and aorta are clearly differentiated, the heart being much the wider of the two; it is furnished with two pairs of valvular inlets, and its muscles, while still retaining something of the original semicircular arrangement, form bundles of striated fibres. The aorta has no muscle-cells, inlets, or valves, except the pair at its base (which properly belong to the heart); its wall, though very elastic, is not contractile.

In a dorsal vessel of the first type the valves are usually of very simple structure, and arise by modification of the muscle-cells; where inlets form, the adjacent muscle-cells do not altogether lose their original character; the more complex aortic valves may be absent altogether. In the other type the simple cellular valves almost or altogether disappear, aortic valves of complex structure are found, and the inlets themselves become valvular. Graber[1] has described and figured the appearance which the posterior inlets present, during contraction, in a Chironomus-larva of this kind. The muscular bands adjacent to the inlet, in which nuclei can often be distinguished, appear to cross one another and to unite where they cross, forming a figure-of-eight. During contraction, they appear to close the vessel and the inlets by one operation. All the valves found in the heart of any Chironomus, whether cellular, ostial, or aortic, appear to be derived from the semicircular muscle-cells.

Sections of dorsal vessel.

Thin sections through the heart of a Chironomus-larva show that there is an outer fibrous layer, an intermediate space in which the muscle-cells lie, and an inner membrane or *endocardium*.

Course of blood.

The blood passes from the heart to the aorta, and so to the head, where it escapes into the body-cavity, bathing all the viscera contained therein. A small portion of the blood is distributed to the respiratory tubules, and

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dorsal vessel the heart does not extend backwards into the eleventh postcephalic segment.

[1] 'Propulsat. Apparat d. Insekten.' *Sitzb. d. k. Akad. Wien*, 1872, fig. 7; Jaworowski, 1879, figs. 24, 25.

becomes aërated in them; the return-current during diastole passes by the ostia into the heart again.

Blood of larva.

The red colour of the larvae of some species of Chironomus has long been familiar. It must be due to something contained in the blood, for when a larva is cut open and gently squeezed, the body-wall and alimentary canal become pale, while the escaping fluid, if collected in fair quantity, for which a number of larvae must be sacrificed, is of a lively red. The colouring matter is dissolved in the fluid or plasma of the blood, and is not restricted to the corpuscles, as in vertebrates. A point of special interest is that the colouring matter is haemoglobin, the same substance which gives a red colour to the blood of man and other vertebrates. This was first shown by Rollett (1861). He collected the blood of Chironomus-larvae in quantity, and obtained from it crystals of haemoglobin; he also showed that it is *dichroic*, the light which has traversed a sufficiently thick stratum being red, while that which has passed through a very thin layer is green [1]. Brücke had shortly before (1853) shown that the venous blood of the frog is also dichroic. In 1867 Lankester [2] showed that the blood of Chironomus-larvae gives the characteristic absorption-spectrum of haemoglobin. It is a striking fact that haemoglobin should occur in a number of animals which are not closely related to one another. This peculiar respiratory pigment occurs in very nearly all vertebrates, as well as in the following invertebrates:—a small planarian, found at Suez by the late H. N. Moseley, some nemertines (where it is often specially associated with the nervous system, but may be found in red corpuscles), some leeches, many chaetopod

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[1] Attention to this dichroic property of the blood is necessary to avoid drawing wrong conclusions from the colours seen in the different tissues of Chironomus-larvae.

[2] *Journ. Anat. and Phys.*, ii, p. 114 (1867).

worms (such as the earthworm, Tubifex, Nais, *Capitella capitata*, in corpuscles, Terebella, Arenicola, &c.), gephyreans, crustaceans (among others Daphnia and Chirocephalus), the burrowing bivalve mollusk, *Solen legumen*, *Planorbis corneus*, Limnaeus, Paludina, Littorina, Aplysia, Patella, and Chiton. It seems to be absent only from the larval Muraenoids among vertebrate animals. Lankester[1] long ago remarked that haemoglobin occurs where increased facilities for oxidation are required, as by burrowing animals and inhabitants of stagnant pools, especially such as lurk in foul mud. It also occurs in animals which are particularly active, and in tissues which are frequently exercised (voluntary muscles of vertebrates, jaw-muscles of snails, &c.). It is well developed also in large thick-skinned animals with limited respiratory surface (vertebrates). Pelagic animals, which are of soft texture, usually of small size, and therefore with a relatively large surface, and which need above all things transparency so that they may escape the notice of their enemies, are nearly always ill-supplied with haemoglobin, or more commonly want it altogether. Certain Chironomus-larvae and various closely allied Dipterous larvae have no haemoglobin, and it is to be observed that these usually haunt the surface of the water, or at least do not bury themselves in mud. Thus the surface-feeding gnat-larva, and the phantom-larva (Corethra), which poises itself in the middle depths of clear water, have no haemoglobin. We cannot, however, explain on these or any other principles all the cases of presence or absence of haemoglobin in particular animals. We cannot tell, for instance, why caddis-worms or the larva of Dicranota, living in the same streams as red Chironomus-larvae, and leading a very similar life, should have no respiratory pigment at all.

[1] 1873, p. 9.

In the larger animals haemoglobin is chiefly important as a means of carrying oxygen from one part of the body to another; in the Chironomus-larva it seems to be rather employed as a means of storing the oxygen. In either case its usefulness depends upon its power of forming a very loose combination with oxygen, which it takes up easily, and easily parts with. Almost any reducing solution, a stream of hydrogen or some other indifferent gas, or diminished pressure, suffices to liberate much oxygen from its temporary combination with haemoglobin. Even in its crystalline form it gives off oxygen readily, changing colour like the blood itself, and becoming dichroic.

Either the storage capacity for oxygen of the Chironomus-larva is considerable, or the oxygen must be used very economically, for the animal can subsist long without a fresh supply. One of us took a flask of distilled water, boiled it for three-quarters of an hour, closed it tight with an india-rubber bung, and left it to cool. Then six larvae were introduced, the small space above the water being at the same time filled up with carbonic acid. The bung was replaced, and the larvae were watched from day to day. Four of them survived for forty-eight hours, and one till the fifth day, two of them meanwhile changing to pupae. Nevertheless the water was from the first exhausted of oxygen, or very nearly so.

Changes in dorsal vessel.

Dareste (1873) observes that in the pupa of Chironomus the dorsal vessel becomes contractile throughout, and divided into chambers by valves. We can confirm this statement, having found that in the abdomen of the pupa and late larva the dorsal vessel is provided with several pairs of opposite valves and ostia. The chambers contract in succession from behind forwards.

Following a suggestion made by Dareste, we may point out that the larval heart of *Chironomus dorsalis* is suited to a state of things in which the functional respiratory organs are limited to the hinder end of the body. But when, in the course of post-embryonic development, the insect acquires an extensive tracheal system, segmentally repeated, the circulatory apparatus becomes repeated too, and many segments are provided with contractile chambers.

6. *Organs of Respiration.*

(*a*) THE TRACHEAL SYSTEM.

Tracheal system.

The only means which the Chironomus-larva is known to employ for renewing its supply of oxygen is wriggling about in the comparatively well-aërated water near the surface of the stream. Owing to the circumstance that this exercise is usually taken by night, we have no detailed information as to its frequency or duration. The few observations which we have ourselves made only show that larvae kept in a deep tank with a sediment of mud and decaying leaves are frequently seen to rise to the top, nearly always by night.

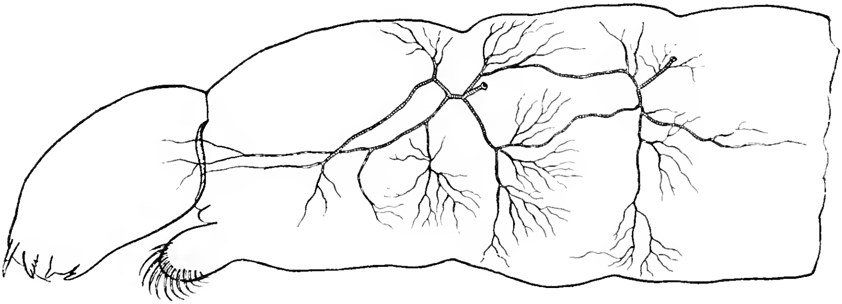

FIG. 56.—Tracheal system of larva, in side view. The head and thoracic segments are included. Two tracheal systems, with communicating branches, and two closed spiracles at the extremities of initial branches, are seen.

The larva has only a rudimentary tracheal system, which appears late in the larval stage (fig. 56). In *Chiro-*

nomus dorsalis there are two pairs of segmental tracheal systems in the thorax, of which the fore pair are much the larger. The segmental systems appear first in or close to the intersegmental boundaries, between the pro- and mesothorax, and again between the meso- and metathorax. At first they are independent of one another, but in the end they become slightly connected by longitudinal vessels. A very slender lateral or initial tube passes from each segmental system to the integument, but the spiracles are closed. The tracheae, with the exception of the initial tubes, are filled with air[1]. Each of the four initial tubes is plugged with dark chitinous deposit at the point where it reaches the skin; at these points the old tracheae are withdrawn during a moult as separate bunches, the slender longitudinal vessels being broken across.

No insect is known to us which has more completely departed from the habits and structure of an air-breathing animal. Yet even here we find visible proof of descent from a terrestrial insect with branching air-tubes.

It is noteworthy that these larvae can live at very great depths, where it is impossible for them to rise to the surface (see p. 3).

The account just given holds good of the blood-worms, which we have more particularly studied, but not of all larvae of the genus Chironomus, some of which have well-developed longitudinal tracheae.

Tracheal system of other Nemoceran larvae.

Terrestrial Nemoceran larvae may have numerous spiracles disposed along the sides of the body; such larvae are *peripneustic*[2]. Bibionidae, Cecidomyidae, and Mycetophilidae furnish many examples. The larva of

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[1] Forel (‘Matériaux pour servir à l'étude de la faune profonde du Léman, *Bull. Soc. Vaud. de Sci. Nat.*, 1874, p. 57) says that Chironomus-larvae brought up from great depths in the Lake of Geneva always had the tracheae devoid of air.

[2] Haliday, 1857, p. 179.

Mycetobia, however, is not peripneustic, but *amphipneustic*, having the middle spiracles closed, and only the prothoracic and terminal spiracles open. The larvae of Rhyphus, some Tipulidae, and some Psychodidae are also amphipneustic. Most Culicidae and Tipulidae, besides the aberrant genus Dixa, are *metapneustic*, with spiracles at the hinder end only. This gradual reduction in the number of open spiracles is no doubt due to increasing obstruction by water or earth.

As in other insects, initial tubes are usual in Nemoceran larvae; they lead inwards from the spiracles, one branch to each spiracle. The initial branches subdivide internally, forming local systems in each segment. The Chironomus-larva does not advance beyond this stage (we are speaking of the bottom-feeding species), and its imperfect tracheal apparatus consists at most of three thoracic segmental systems of very small extent. The local systems may be connected in a rather later stage by longitudinal trunks, from which branches to the viscera, body-wall, and limbs are given off. In the larva of Mochlonyx[1] the boundaries of the segmental systems of the abdomen are still marked by thin septa, which stretch across the longitudinal trunks.

In many Chironomidae, as well as in Corethra, Simulium, and Blepharocera, the tracheal system no longer opens at the surface of the body. The initial tubes become impervious, and may perhaps disappear altogether in some forms. The longitudinal trunks are usually retained in those larvae which have once acquired them, but in Corethra they subsequently become obliterated, two pairs of dilatations only persisting as hydrostatic vesicles.

Nemoceran larvae commonly bear the posterior spiracles on the eleventh segment, whether this is the last, as in Phalacrocera and Pericoma, or the last but one, as in Culex and Mochlonyx. In Dicranota and Ptychoptera, however, it is the twelfth segment which bears the spiracles.

The spiracles are usually flush with the general surface of the body, but may be sunk a little, as in Dixa, where a respiratory cup is formed, like that of some aquatic Coleopterous larvae (Hydrobius). In the Culex- and Mochlonyx-larvae, on the contrary, the spiracles are

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[1] Meinert, 1886, p. 60 (428).

elevated upon a long dorsal stalk, an outgrowth from the eleventh or penultimate segment. The aquatic larva of a Muscid, Ephydra, has two separate tubes, each fringed at its extremity by a circle of setae. In the larvae of Ptychoptera and Bittacomorpha the twelfth segment is very long, slender, and retractile, and the minute spiracles open at its extremity.

(*b*) THE BRANCHIAL SYSTEM.

Blood-gills.

Insect larvae which live immersed in water often develop gills, which are thin, transparent extensions of the body-wall, filled with blood, and employed for respiration. According as they contain tracheae or not, they may be distinguished as *tracheal gills* or *blood-gills*[1]. They have in general little morphological constancy, and vary much in position and number, as well as in minute structure. It is remarkable that functional gills are very rarely found in an adult insect, however aquatic its propensities (Packard, 1898, p. 476).

The larger species of Chironomus-larvae, such as *C. dorsalis* and *C. plumosus*, are furnished with two kinds of blood-gills, but tracheal gills are entirely absent. Two pairs of blood-gills are borne upon the lower surface of the last segment but one (fig. 1). These are long and flexible, but incapable of independent movement. From the last segment and close to the anus, two pairs of much shorter blood-gills project (fig. 1). We find, therefore, two pairs of *ventral*, and two pairs of *anal blood-gills*. The hinder end of the body, when the larva is not actually feeding, is often seen to be thrust out from the burrow. When the larva is completely concealed and apparently at rest, it keeps up a vertical undulatory movement of its body within the burrow, which continually renews

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[1] This distinction, though often convenient, is not strictly applicable to every known case. There are gills which are neither tracheal gills nor blood-gills.

the water. The larva has another mode of charging its blood with oxygen. It frequently comes up to the surface by night, and though it does not actually reach the air, it bathes its body in well-aërated water. The blood-gills no doubt effect an exchange of gases, giving off carbon dioxide and taking in oxygen. The only visible action which can be detected by the microscope is the in-and-out pulsation of the blood, driven to the gills by the heart.

Blood-gills of other Nemoceran larvae.

Blood-gills are not usual even in aquatic Nemoceran larvae. The ventral tubules described above seem to be peculiar to Chironomus. The larvae of Culex, Anopheles, Corethra, Mochlonyx, Tanypus, and others have four anal gills; the Simulium-larva has only three, which are retractile into the rectum. In the Dicranota-larva the anal gills are articulated and traversed by tracheae. The larvae of Eristalis and Helophilus, which are not Nemoceran, have about twenty long retractile anal gills, which are retractile into the rectum and traversed by tracheae. Such examples render it probable that the blood-gills of one larva may be replaced by tracheal gills in another larva[1].

Tracheal gills of Nemoceran larvae.

The Chironomus-larva has no tracheal gills, but they are common in other aquatic Nemoceran larvae. They occur in a variety of positions; thus they may be *ventral*, like the two pairs of articulated appendages on the last segment of the Dicranota-larva; *caudal* (i.e. terminating the body), like the last pair of the same larva[2]; lastly, they may be *segmental* (i.e. segmentally repeated), as in the larvae of Phalacrocera and Blepharocera[3]. Other variations probably exist, but full and exact descriptions are not always to be met with.

The tracheal gills of Nemoceran larvae seem to be derived in some cases, but not in all, from a set of *circum-spiracular papillae*, which surround the spiracles, and

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[1] The larva of Plectrocnemia (Trichoptera) has five retractile anal gills (T. H. Taylor in Miall, 1895, p. 266).

[2] The tracheal gills of the larvae of Ptychoptera and Bittacomorpha seem to be similarly placed, though the long, retractile, respiratory tube is continued beyond them.

[3] Cf. the larvae of Paraponyx, Sialis, and Trichoptera.

terminate the body in certain Tipula-larvae. In other larvae they are often reduced, and instead of being dorsal, lateral, and ventral, one pair only may be retained. The dorsal circumspiracular papillae may be two, four, or six in number[1]. One pair of these become large and fringed with long setae in the aquatic larva of Pericoma, and enclose the bubble of air which buoys up the tail[2]. In the Dicranota-larva only the ventral pair are retained; these become long and apparently respiratory[3]. Aquatic Nemoceran larvae which have no open spiracles, such as Chironomus, Tanypus, and Simulium, seem always to want the circumspiracular papillae.

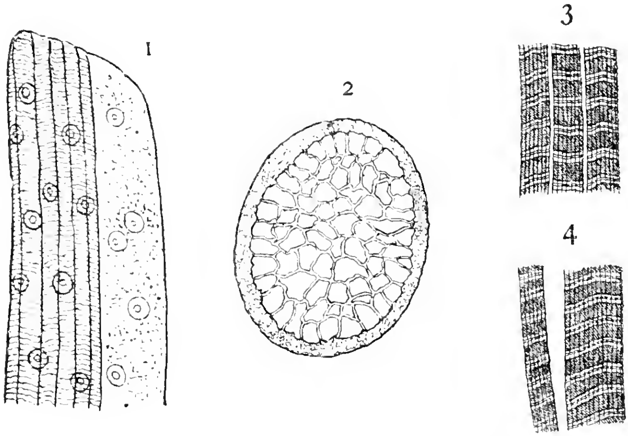

FIG. 57.—Histology of larval muscles. 1, subcutaneous larval muscle, showing contractile columns (to left), and protoplasm with nuclei (to right). × 200. 2, transverse section of ditto, showing muscle-fibres enclosed in protoplasm. × 125. 3, muscle-fibres, from body-wall. × 800. 4, ditto, from head. × 800.

7. *The Body-wall, Blood-space, and Fatty Tissues.*

Muscles of body-wall.

The muscles of the body-wall, of the prothoracic and anal feet, and of the head, are shown in figs. 19, 20, 30-36.

The muscles of the head and thorax are very different in arrangement from those of the fly, and are completely renewed during the transformation.

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[1] Osten Sacken, 1869, p. 7. In the blow-fly larva twelve small papillae are found in the same situation.

[2] Miall and Walker, 1895.

[3] Miall, 1893.

All the larger muscles of the larva are enclosed in connective-tissue sheaths, which become conspicuous, and sometimes perplex an inexperienced observer, when the muscles shrink, as they do a little while before pupation. This retraction of the muscles from their sheaths is particularly evident in the head of a late larva.

Blood-space and fatty tissues.

The space between the body-wall and the viscera is occupied by a large blood-sinus, which takes the place of a coelom or true body-cavity. In this space are lodged two fatty layers, inner and outer, which answer to the simpler fat-body of many other insects. As is usually the case, the fatty layers grow steadily throughout the larval stage, but are largely absorbed during the transformation. The *outer fatty layer* lies in the body-wall, partly without and partly within the muscles. It is segmentally arranged, being completely interrupted at the junctions of the segments. It consists of a network of lobes or strings, most of which take a longitudinal direction. The lobes may be thick, with relatively small, oval fenestrae between, or thin, with relatively large fenestrae, or mere threads stretching in various directions across open spaces in which single cells or groups of cells are disposed. The cells are enclosed in a thin membrane, and the threads are apparently drawn-out portions of the membrane only. The clusters of large oenocytes (see p. 40) are placed in oval fenestrae excavated in this layer. In young larvae the outer layer consists of a dense mass of cells, each with a central nucleus, surrounded by closely packed granules[1]. In a later stage oil-drops become plentiful, and gradually occupy more and more of the space within the cell[2]. By

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[1] According to Wielowiejski, 1886, p. 514, these granules are more or less soluble in acids and in alcohol.

[2] The fat-body in insects generally contains not only fat but proteid substances; it sinks in water (Bugnion, *Anat. et mœurs de l'Encyrtus fuscicollis*, p. 464)

clearing and staining, the nucleus, the parietal protoplasm, and the very numerous polygonal granules can be defined. In the larvae of some species of Chironomus the granules have a grass-green colour, which persists in the pupa and in the newly emerged fly. In the larva of *C. dorsalis* such granules occur in smaller proportion. The *inner layer* surrounds the alimentary canal, and has no segmental divisions. It is continuous from the hinder part of the thorax, or the beginning of the abdomen, to the ninth segment behind the head, ending opposite the reproductive bodies. Like the outer layer, it is composed of cells, packed into irregular lobes or strings, which show bulges and constrictions, with many cross-connexions. Detached cells and little groups of cells are also found. In older larvae the cells become charged with oil-drops and granules. Nuclei are easily demonstrated by clearing and staining; like the containing cells, they are larger than in the outer layer. The inner layer forms earlier than the outer, and is conspicuous in the embryo.

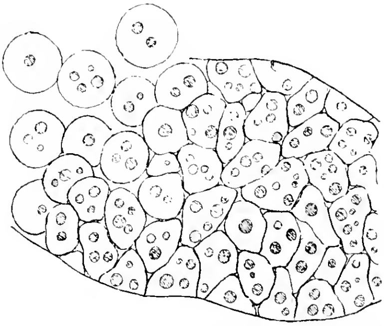

FIG. 58.—Inner fatty layer, from living larva. The fat-drops are shaded. Free cells take a spherical shape.

Connective tissue and tracheal tubes deficient.

The trabecular connective tissue, which in most insects invests the viscera, binds them together, and connects them with the body-wall, is very poorly developed in the Chironomus-larva, and seldom attracts the attention of the anatomist. The paucity of tracheal tubes further contributes to the lax and mobile condition of the organs in the body-cavity.

CHAPTER III

THE FLY OF CHIRONOMUS

Order of description.

THE larva of Chironomus, as of other metamorphic insects, is succeeded by a pupa, and this by a winged imago. It would therefore be natural to describe the pupa immediately after the larva. We do not, however, propose to follow that course here. The pupa of Chironomus is hardly more than the fly enclosed in a temporary skin, and the details of its structure cannot be understood without constant reference to the structure of the fly. It is necessary to know at least the general structure of the fly, in order to follow the changes which take place during the last larval stage.

The general appearance and habits of the fly have been shortly described on p. 9. See Plate.

Head.

The head is small. and flattened from before backwards (fig. 59). The lunate compound eyes occupy the sides, and almost meet above the antennary bulbs. From the lower or anterior part of the head projects a rostrum, on which the mouth-parts are carried. A narrow neck joins the head to the thorax.

When we compare the head of the Chironomus-fly with that of a more primitive insect, such as a cockroach, we see that the lateral lobes, which bear the compound eyes and antennae, have in Chironomus greatly encroached upon the median lobe, almost effacing the broad shield (clypeus), which is prominent in the larva, as in most insects. The small part of the clypeus which remains is seen as a narrow transverse plate, separated by a suture from the epistome or anterior clypeus, which carries the small triangular labrum (fig. 59).

Chitinous tunnels of head.

On each side of the suture between the clypeus and the epistome is a rounded orifice, which leads into the interior of the head, dilating there into an irregular cavity, which extends to the back of the head. The head is therefore tunnelled through by a pair of cavities, whose walls are stiffened by chitin, and are morphologically part of the external surface (fig. 60). Muscles are seen in our sections, which seem to pass from the tunnels to the bases of the

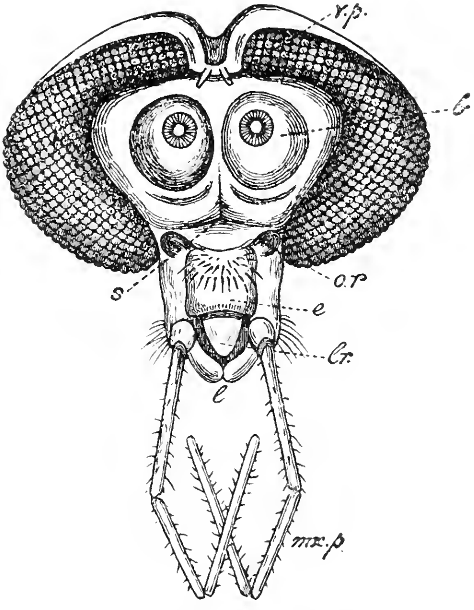

Fig. 59.—Head of male fly of *Chironomus dorsalis*, front view. The antennae are removed, with the exception of the large second joint (*b*) which shows the place of attachment of the shaft. *v.p*, processes on the vertex. *s*, transverse suture. *o.r*, orifice of chitinous cephalic cavity. *e*, epistome. *lr*, labrum. *l*, labella. *mx.p*, maxillary pulp.

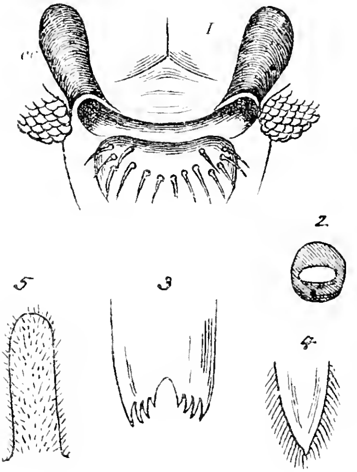

FIG. 60.—Details of imaginal head. 1, dissection to show the chitinous tunnels (cc) behind the epistome. 2, posterior end of one of the tunnels, with slit-like opening. 3, extremity of labrum. 4, extremity of lingua. 5, one of the processes on the vertex.

antennae. In many insects there occurs in a somewhat similar situation a *tentorium*, or internal skeleton for muscular attachment, which splits into halves at each ecdysis, and, according to Palmén's observations on Ephemera, is renewed from paired rudiments. Other writers[1] have traced the tentorium to the spiracles of the jaw-bearing segments. These identifications are still doubtful. Very similar hollow processes for muscular

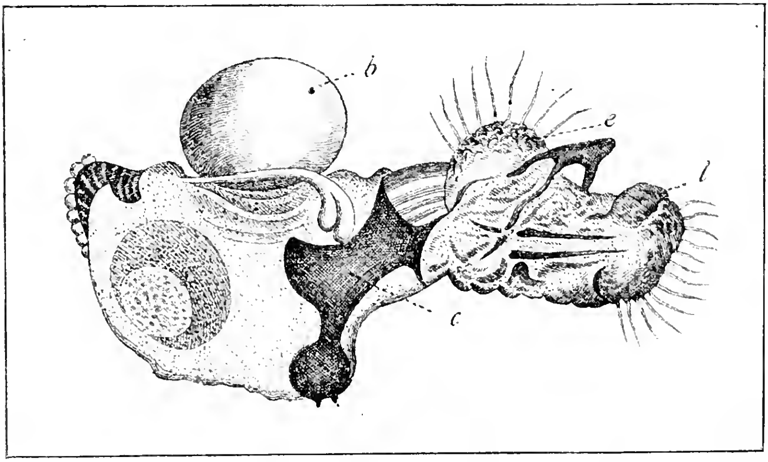

FIG. 61.—Section of imaginal head. *b*, enlarged second joint of antenna. *c*, chitinous tunnel. *e*, epistome. *l*, labella.

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[1] Carrière on Chalicodoma, 1897; Wheeler on Doryphora, 1889.

attachment are met with where there can be no question of spiracles, as in non-tracheate Arthropods, or in the median thoracic region (cockroach and many other insects). Chitinous tunnels like those of Chironomus occur in a gnat, Anopheles (fig. 62)[1].

Eyes.

The compound eyes are large in both sexes, but somewhat larger in the male than in the female. We estimate the number of facets in each eye as 225–250 in the male, considerably fewer in the female. The corneal facets are hemispherical on their outer faces, thick, and produced internally into prominences which look like crystalline cones, though they are really crystalline cells, four together. The outer layer of the facets is distinct and separable. No crystalline cones are formed. The pigmented retinal cells form retinulae of six or sometimes seven cells each.

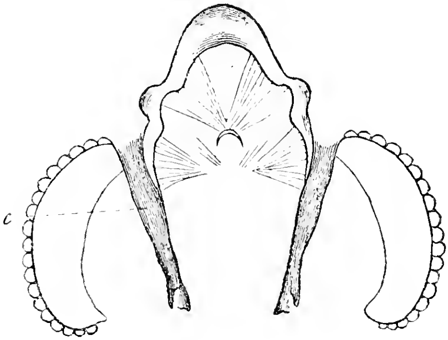

Fig. 62.—Horizontal section through head of *Anopheles maculipennis*, showing chitinous tunnels (c).

Vestiges of simple eyes.

There are no functional simple eyes, but between the compound eyes and near the top of the head are a pair of small stalks, which in the pupa are connected with the brain by a single median nerve. Dufour[2] has described, in the crane-fly (*Tipula oleracea*), a minute ocellary nerve terminated by a pigmented retina, and also a small

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[1] Mr. C. O. Waterhouse (*Labium and Submentum in Certain Mandibulate Insects*, 1895) mentions that certain beetles show a pair of pits on the submentum or gula. In Corydalis these are connected by a tube with two openings in front of the antennae on the upper side of the head, so that one can see daylight through the head, and a fine wire can be passed freely through.

[2] 1851, p. 178.

rounded prominence behind the insertion of each antenna. These he regards as the functionless representatives of the ocelli of other Dipterous families. The Culicidae, Chironomidae, Psychodidae, Tipulidae, like the Simulidae and most Cecidomyidae, have as a rule no ocelli. Schiner has however found traces of ocelli in some Chironomidae, especially Tanypus. Osten Sacken[1] notes that Trichocera has distinct ocelli, and he thinks that Pedicia has something like them.

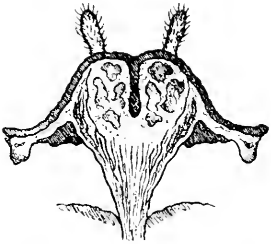

FIG. 63.—Section through processes on vertex of fly, showing nerve-pedicel connecting them with the brain. From pupa. × 300. Cf. fig. 140.

Antennae.

The antennae differ materially in the two sexes (fig. 64). In the male each consists of thirteen joints, most of which appear at first sight to be simple cylinders. On closer examination it is found that the shaft, composed of the last ten

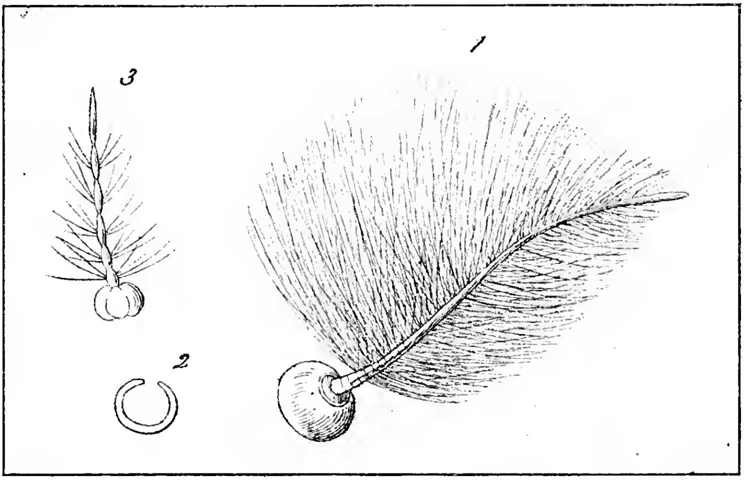

FIG. 64.—1, antenna of male fly. × 20. 2, section through shaft of ditto. 3, antenna of female fly. × 20.

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[1] 1887, p. 169; 1892, pp. 460–1.

joints, of which the terminal one is very elongate, is really a split tube (fig. 64, 2). This arises from the infolding of the wall of the antenna during the pupal stage. The completely exposed surface bears the long setae, while the folded-in surface is beset with minute elevations of the cuticle. A similar structure is found in other species of Chironomus, and in the female as well as in the male, though it is less marked in the female. The female antenna is scarcely half the length of the male, and consists of eight joints only. The second joint is dilated, but much less so than in the male; each of the next five joints is enlarged in the middle; the terminal joint is long, but not nearly so long as in the male, and only this takes the form of a split tube.

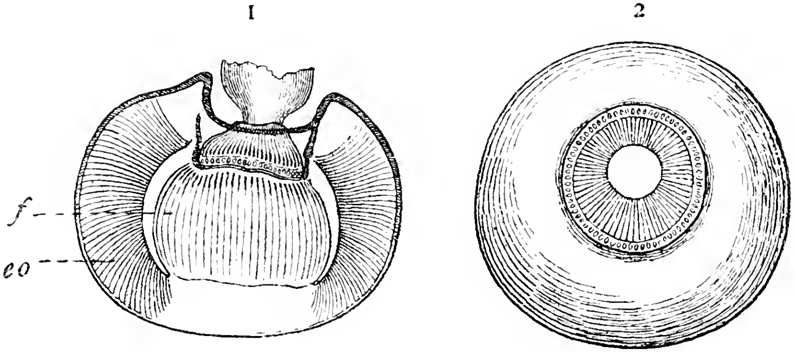

FIG. 65.—Enlarged second joint of antenna of male Chironomus-fly. 1, side view (transparent). *f*, peripheral fibres. *eo*, end-organs. × 150. 2, upper surface of ditto, the shaft being removed. × 150.

The three joints at the base of the antenna differ in structure from those immediately beyond them. The first joint is extremely short, sunk in the head, and almost entirely occupied by the muscles which move the antenna to and fro. The second joint is greatly enlarged, and constitutes a peculiar sense-organ; the third joint, unlike those beyond it, is smooth, and carries no large hairs or setae; it is much narrowed at its insertion into the second joint.

Auditory organ in the antenna.

The second joint in Chironomidae and Culicidae (especially in the males) exhibits a peculiar structure, which is believed to serve for the perception of sound (figs. 64-69). This joint swells out into a nearly globular capsule, four or five times as wide as any of the succeeding joints. On its upper surface[1] is the deep socket for the third joint, which is incompletely divided into an upper and a lower cavity by a horizontal, circular shelf. The chitinous roof of the lower cavity, which we shall call the *striated plate*, is convex upwards, and perforated by a central hole for the base of the third joint, from which radiate many close-set striae.

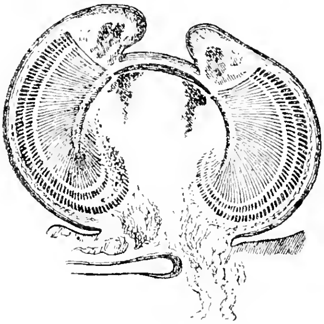

FIG. 66.—Vertical section of enlarged second joint of antenna of male Chironomus-fly. × 150.

The internal structure of the second joint can only be investigated by thin sections and other delicate methods. The striated plate is continued into the cavity of the joint as a thin sheet, stiffened by very numerous radiating fibres (the *peripheral fibres*), which, like the sheet which unites them, are of chitinous substance. In Chironomus the sheet curves downwards from the socket of the third joint, and forms a kind of dome (fig. 66). In the gnat (figs. 67, 68) it curves upwards from the socket, and forms a kind of basin. Each fibre is exactly in line with one of the radiating striae on the striated plate. Outside the peripheral fibres (i. e. between them and the outer wall of the second joint), and to a less extent on the

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[1] The antenna in this description is supposed to stand upright, with the attached base downwards.

inside also, are many *articulated branches*, which are connected with a regular and close-set layer of *end-organs* (fig. 67). These resemble slender cones, with the apex turned towards the peripheral fibres, and the base away from them. By maceration in weak chromic acid the articulated branches are resolved into their elements, slender rods with two to three elongate nuclei apiece. These elements are not closely connected, at least in the hardened tissues from which sections are cut. They are arranged in about three rather irregular, concentric zones, and appear slightly separated from the end-organs. Both the articulated branches and the end-organs appear to be peculiar modifications of epidermic cells, or of intercellular substance secreted by them. A deep circular fold of epidermis may be supposed to pass, during the development of the fly, far into the interior of the enlarged joint. The cells give rise to the elongate elements of the articulated branches and end-organs, which acquire a radiate arrangement, and the peripheral fibres with their connecting sheet form in the cavity of the fold. The outer (morphologically inner) surface of the end-organs is connected by delicate fibres with a ganglionic layer, and this in turn by a multitude of fibres with the antennary nerve (fig. 66). A much smaller branch of the antennary nerve passes along the centre of the antenna to the remaining joints.

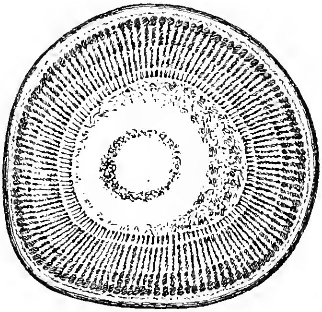

FIG. 67.—Transverse section of enlarged second joint of antenna of male Chironomus-fly, showing end-organs. × 150.

In the female fly the structure is similar, but far less complex. Tanypus has almost the same antennal structure as Chironomus. In the gnats (fig. 68), the free ends of the peripheral fibres turn upwards (i.e. towards the free end of the antenna), instead of downwards as in Chironomus. The general features are, however, much alike in all the Nemocera with enlarged second joint.

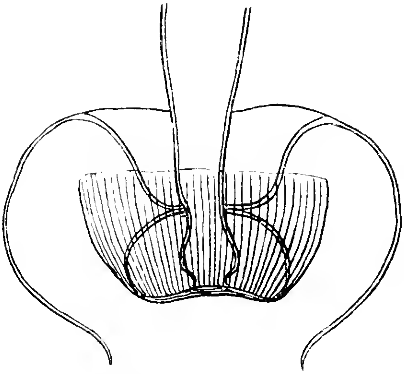

FIG. 68.—Enlarged second joint of antenna of male fly of *Anopheles maculipennis*, showing peripheral fibres. × 150.

Some of the peculiarities of the enlarged joint were described by Christopher Johnston (1855) from the male gnat or mosquito. He recognized the auditory function of the antenna, and supposed that

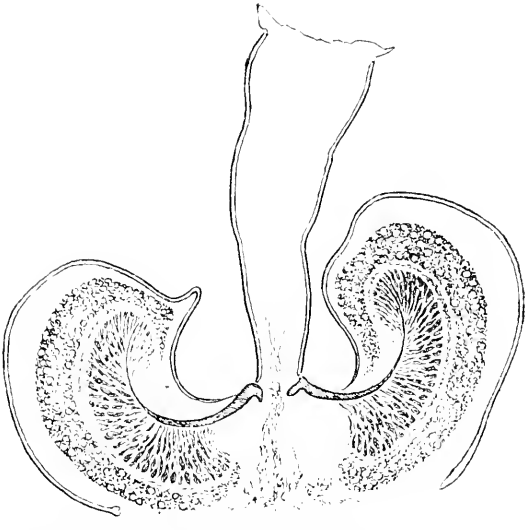

FIG. 69.—Vertical section of enlarged second joint of antenna of male gnat (*Culex sp.*), showing end-organs, &c.

it is set in action by sound-waves, which throw the setae into vibration; these vibrations he believed to be transmitted through the antenna to the cup or enlarged joint, and to the corpusculate fluid which he supposed to fill it, and which he compares to the endolymph of the vertebrate ear. The vibrations are ultimately communicated to the fibres of the antennary nerve. These early investigations are commemorated by the name of *Johnston's organ*, often given to the structures contained in the enlarged second joint of an insect's antenna.

The American physicist, A. M. Mayer (1874), made some interesting experiments on live gnats, glued to slips of glass. Tuning-forks were sounded in the neighbourhood of the gnats, and Mayer observed that some of the setae of the antennae were thrown into vigorous movement, especially when the fork Ut 4, giving 512 vibrations per second, was sounded. The forks Ut 3 and Ut 5 also set up more vibrations than intermediate notes. Other setae responded to other notes. We have repeated Mayer's experiments with the same general result. The fork Ut 4 caused a great amount of vibration in the setae of *Culex nemorosus*, affecting not merely a few setae of particular length, but many setae together; other forks produced a much smaller effect.

Mayer points out that the auditory hairs whose direction is transverse to the path of the sound-waves are most powerfully acted upon, while those which point to or from the source of sound are least affected. Hence the male can judge of the direction in which the female is to be found.

Sounds emitted by flies.

We have next to inquire what sounds the female emits which the male fly can perceive. On this point the observations and experiments of Landois (1867), though not made upon Chironomus, are instructive.

He tells us that when a blue-bottle is flying a loud buzz is heard. If the wings are held, a note of higher pitch is produced by movements of the abdomen. If such movements are stopped, a note of still higher pitch is given out.

The lowest of the three notes is due, directly or indirectly, to the vibration of the wings, and ceases when they are held or cut off. The middle note is caused by vibration of the abdominal rings, which are rubbed against one another from side to side; the sound may be increased by rubbing the head against the thorax. If the head, legs, wings, and abdomen of an active fly are all removed, so that the thorax is left with no vibratile parts except the halteres, the highest note continues to be heard. But if the thoracic spiracles, of which there are two pairs, are choked with gum or wax, the sound ceases. In the blue-bottle both pairs of thoracic spiracles are well developed, but in some other flies one or other pair may be useless for the production of sound.

By investigating the structure of the spiracles, Landois found that there is an air-chamber just within the external outlet, and that the wall of this chamber is folded, so as to give rise to a number of chitinous laminae, which, he supposes, are caused to vibrate by the forcible drawing of air in or out of the chamber. The laminae are prevented from collapsing by a special *vocal ring*, over which the vibrating membrane is stretched.

The flies of Culicidae can produce during flight the note d″. When the wings, legs, and head are removed, they emit a shriller note. There are two pairs of spiracles, of which the hinder pair are the larger. In each spiracle there is a slit-like outlet, a stretched membrane, and an elongate-oval vocal ring. The tension of the ring and membrane can be altered by muscular pull. The air-chamber of the blue-bottle is not found in Culicidae, and the spiracle opens direct into the lateral trachea. The note can be raised or lowered to some extent, and Landois gives the pitch of the female fly of *Culex annulatus* as ranging from a′ flat to b′ flat, while that of the male fly ranges from e″ to f″ sharp.

We suppose that in all cases the antenna of the male responds energetically to the note emitted by the female, though this has hardly been proved with the requisite nicety in any one case. The note of the female harlequin-fly (due to wing-vibration) is b, that of the male a′ sharp (see p. 183). In both gnats and harlequin-flies the male possesses a sound-producing organ, and the female a sound-perceiving organ, but this last is smaller and probably less efficient than the corresponding organ of the opposite sex.

Mouth-parts of fly.

The top of the rostrum (p. 90) is defended by a rounded chitinous plate, the epistome or anterior clypeus, which is prominent and beset with long, sensory hairs. It is supported in front and on the sides by a pair of slender, chitinous processes, which meet in front to form a narrow transverse arch (fig. 61). This forms also the base of the labrum, a bifid projection with membranous upper surface. Beneath the labrum lies the pointed, serrate tongue (lingua).

No trace of mandibles can be discovered. The maxillae are reduced to a pair of long, four-jointed palps. A pair of labellae represent the labium, and enclose the labrum. No food is taken by the fly, and the mouth-parts have no functional importance, except that the palps, from their large size, may be supposed to be useful as sense-organs.

Cervical sclerites.

The head is connected with the thorax by a neck, whose cuticle is membranous. Just behind the head, on the mid-dorsal line, is a lozenge-shaped piece, divided by a median suture; this appears to represent a pair of dorsal sclerites.

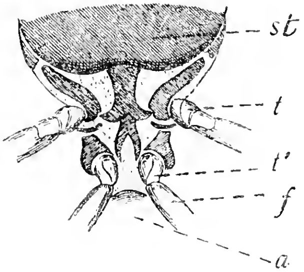

FIG. 70.—Ventral view of part of thorax of fly, with the attachments of intermediate and hind legs. *st*, mesosternum. *t*, trochanter of intermediate leg. *t'*, *f*, trochanter and femur of hind leg. *a*, abdomen. The medifurca and postfurca are seen in the middle line.

Thorax. A median section through the thorax shows plainly the limits of the segments upon the ventral surface, but on the sides the boundaries can only be traced with difficulty until the clue is discovered[1]. Upon the mid-ventral surface the prothorax is of moderate extent, the mesothorax very large, the metathorax short, and defined by two apodemes for muscular attachment, the medifurca and postfurca (fig. 70). Such apodemes are common in

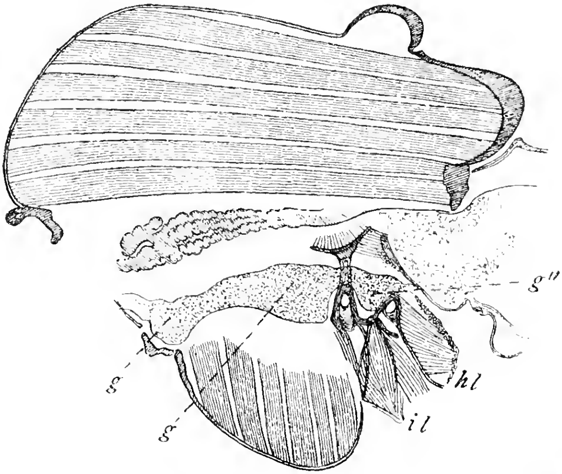

FIG. 71.—Nearly median section of fly, showing the longitudinal mesothoracic muscles above, and the vertical ones below. *g*, *g'*, *g''*, pro-, meso-, and metathoracic ganglia. *il*, intermediate leg. *hl*, hind-leg.

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[1] Note by A. Hammond. In my paper on the thorax of the blow-fly (*Journal Linn. Soc. Zool.*, vol. xv, 1881, pp. 9-31) I determined the whole of

insects; they are infoldings of the integument, which may either remain hollow or become filled with chitinous deposit. In the Chironomus-fly they are hollow. Each gives off from its upper part a pair of hollow, lateral extensions, so that it may be compared to a letter Y.

Each segment bears its own ganglion (fig. 71). The prothoracic and metathoracic ganglia occupy a large proportion of the length of their respective segments; the mesothoracic ganglion is placed

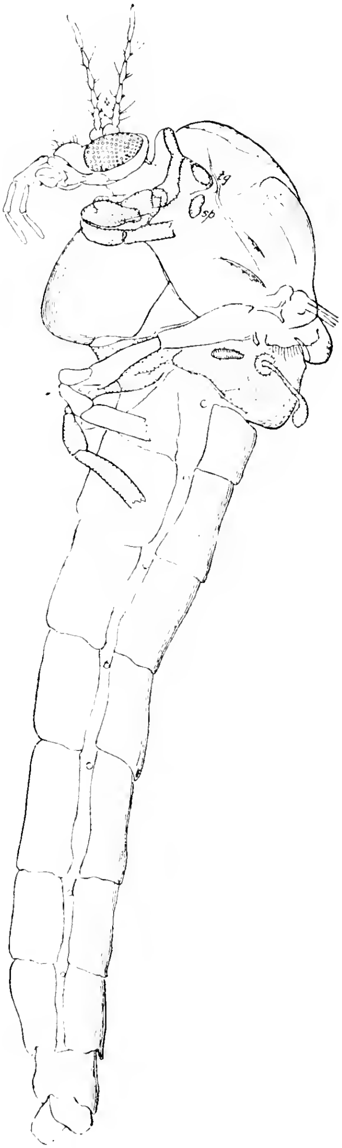

FIG. 72.—Side view of female Chironomus-fly. The prothorax and metathorax are dotted. *tg*, scar of pupal tracheal gill. *sp*, mesothoracic spiracle. The metathoracic and abdominal spiracles are also shown.

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the posterior portion of the cavity of the thorax to be mesothoracic. At that time I had not the advantage of the serial sections prepared for the present description of Chironomus. The section from which fig. 74 is taken shows the larval *recti ventrales* muscles still remaining amid the newly forming muscles of the imago. The metathoracic muscles of this series extend forwards to the medifurca, where the mesothoracic muscles begin. This observation shows me that my former view must be materially altered. I now concur in the views stated in the present chapter.

towards the hinder end of the large segment to which it belongs.

The chief part of the prothorax of the fly consists of an obliquely placed ring, which encloses the muscles of the fore-leg. On the dorsal surface it appears as a narrow band, with a median incisure and suture. The ring is thicker below, and defined by conspicuous grooves (fig. 72). At first sight it would appear that this ring formed the whole prothorax. But the tracheal gill of the pupa is certainly prothoracic (p. 142), and the scar left upon the thorax of the fly by this tracheal gill must be prothoracic also. We have therefore to extend the prothorax of the pupa or fly, so as to include the tracheal gill or its scar. The extension has been called the *humerus*, an unfortunate name for a part of the thorax; it is the *paratreme* of Lowne. This part of the prothorax has no clear boundary in Chironomus, but thins away gradually, and passes into the conjunctival membrane; in some other Diptera it is clearly defined.

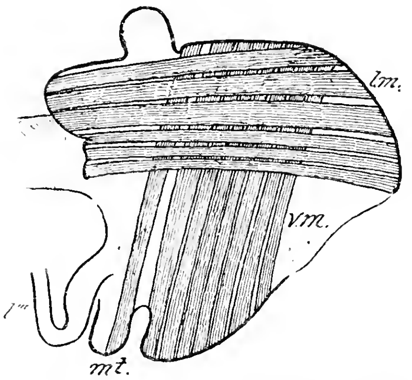

FIG. 73.—Mesothoracic muscles of fly. *l.m*, longitudinal muscles. *v.m*, vertical ditto *mt*, metathorax. *l'''* hind-leg.

The mesothorax is enormous, and chiefly occupied by the powerful muscles which are directly or indirectly concerned in flight. On its fore edge the anterior thoracic spiracle can be easily made out. The humped dorsal surface shows a prominent semi-cylindrical transverse ridge: this is the scutellum; the wings are attached on either side of it. Behind the scutellum the dorsal surface makes a step downwards to the post-scutellum, which exhibits on its dorsal surface a pair of plates; these meet along the middle line, and have together an oval outline. Below, the mesothorax swells into a great hemispherical prominence, the mesosternum, which is convex downwards, its depth allowing a great prolongation of the vertical mesothoracic muscles. The intermediate legs are attached to the hinder part of the mesosternum by oval sockets.

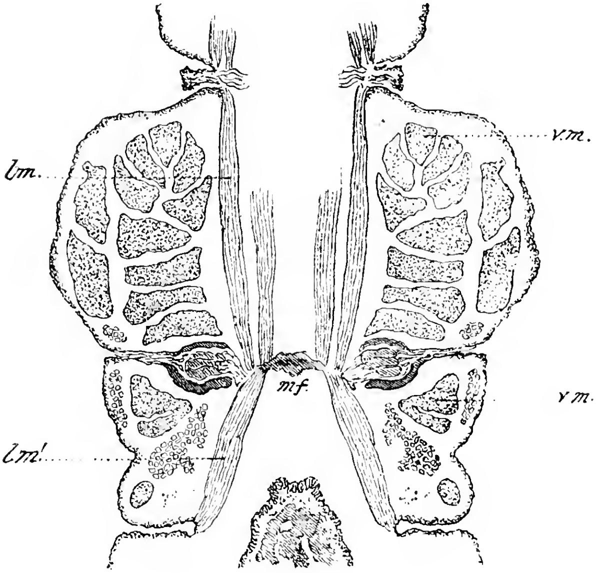

FIG. 74.—Horizontal section through meso- and metathorax of pupa (enclosed in larva). *mf*, medifurca. *lm*, *lm'*, remains of larval muscles as yet unabsorbed, the posterior series being those of the metathorax and indicating the extent of that segment. *vm*, vertical muscles.

The metathorax is small in comparison with the mesothorax. On its side may be seen the posterior thoracic spiracle, and above it the haltere, or rudimentary hind-wing. On the dorsal surface there is a small metathoracic plateau, on either side of the post-scutellum and at a considerably lower level: a deep groove separates the two. The metathorax possibly reaches the mid-dorsal line in the groove between the post-scutellum and the first abdominal segment. The ventral surface of the metathorax is both short and narrow; it is largely occupied by the insertion, close together, of the two hind legs.

Proof of the boundaries of the segments is in most places easily obtained by thin sections, though now and then the determination is difficult. The apodemes, the muscular intersections, and the intrinsic muscles of the metathorax furnish the chief evidence.

Legs.

The legs are long and slender. The fore pair, which are longer than the others, are usually raised in the air like feelers, when the insect is at rest. The last joint of the tarsus of each leg bears a pair of claws and a large, bifid empodium, which acts as an adhesive disc.

Wings.

The wings do not extend beyond the sixth abdominal segment; they are furnished with two small accessory lobes close to the root. When at rest, the wings cover the back and slope away on either side. The venation is fully described in systematic books.

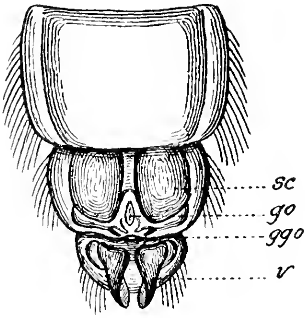

Fig. 75.—Last abdominal segments (vii, viii, ix) of female fly, ventral view. *sc*, sclerite. *go*, genital orifice. *ggo*, outlet of gluten-gland. *v*, valve.

Abdomen.

The abdomen is long and slender, especially in the male, and consists of nine segments, the hindmost being modified to form the reproductive armature.

In the female fly the seventh abdominal segment is normal (fig. 75), both the dorsal (tergum) and ventral plate (sternum) being well developed. The eighth segment shows a semi-lunar tergum and a pair of ventral sclerites; in the flexible membrane between them is the reproductive orifice, and close to it, the outlet of the gluten-gland (fig. 75, *ggo*). The ninth or terminal segment is small, and bears a pair of valves; the anus opens on its dorsal surface.

In the male fly (fig. 76) the eighth abdominal segment shows no unusual features; the ninth tergum is shield-like and bears a small median spine, which projects a little beyond its posterior edge. The ninth sternum is deeply bilobed. Three pairs of appendages are enclosed within it, diminishing regularly inwards. The innermost pair appears to be supported by a small median plate. These appendages are a little upturned; the outer ones are slightly curved, and form a forceps.

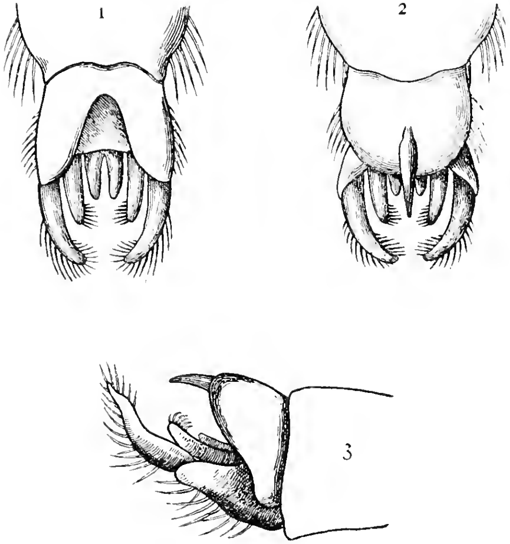

Fig. 76.—Genital armature of male fly. 1, ventral. 2, dorsal. 3, lateral.

These appendages of the male fly probably serve as claspers. It has been remarked that they do not occur in insects whose females bear an ovipositor. Similar appendages are found in Lepidoptera, Trichoptera, and Ephemeridae. The styles of the cockroach are borne upon the same segment. The median dorsal spine (suranal plate of some authors) has been explained as an undeveloped tenth segment.

Nervous system.

The following features distinguish the nervous system of the fly from that of the larva:—

The brain and sub-oesophageal ganglion, now enclosed in the head, are more widely separated from the rest of the nerve-cord. Each thoracic ganglion lies in its own segment. The first abdominal ganglion is closely united with the metathoracic, and the seventh and eighth become fused.

We may perhaps say that there is some amount of decentralization during the transformation of Chironomus. Certain families of Brachyceran Diptera, such as Stratiomyidae, Tabanidae, Syrphidae, Conopidae, and Acalypterate Muscidae, exhibit the same process of decentralization, the ganglia becoming separated during metamorphosis. In Calypterate Muscidae, Oestridae, Hippoboscidae, and Nycteribiidae the thoracic and abdominal ganglia, which were already fused in the larva, remain so. Decentralization may also occur in Coleoptera. Thus in most Lamellicorns, as well as in some Curculionidae and Scolytidae, the ganglia of the ventral cord are so closely approximated in the larva as to appear like a single ganglionic mass, while after transformation the thoracic ganglia at least are separated, and double connectives form between them.

Alimentary canal.

In the fly the whole alimentary canal is considerably reduced (fig. 80). The salivary glands may shrink to two minute and structureless membranous sacs[1], the epithelial cells of the stomach almost completely disappear (fig. 113), and the rectal folds, to be described below, are the only indication of a structure more complex in the alimentary canal of the fly than in that of the larva.

It is evident that Chironomus does not feed in the winged

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[1] In another species this shrinkage of the salivary glands was not found to occur.

state. The mouth-parts, though of elaborate structure, are never used in feeding, and the alimentary canal of the fly is empty, except for a greenish fluid, which fills the stomach of the pupa and newly emerged fly. In male flies the abdomen is empty and collapsed, the under-side being concave and applied to the upper, except in the segments which contain the reproductive organs. The pulsating dorsal vessel and the tracheal system can be seen by the microscope, but the stomach, subcutaneous muscles, and nerve-cord are hardly visible. In males reared in captivity the abdomen is comparatively plump for a day or two. The beginning of the stomach, which is enclosed in the metathorax of the larva, gets close to the head in the pupa and fly, in consequence of the shortening of the oesophagus and prothorax.

The rectum, which is undeveloped in the larva, is easily demonstrated in the fly. It forms a short, wide chamber, containing two oval papillae, which are largely supplied with tracheae (fig. 77). These appear to correspond to the 'rectal glands' or 'folds' found in many insects of different orders. They vary greatly in number. Chironomus has two, most other Diptera four, Pulex, most Hymenoptera, Neuroptera, and Orthoptera six, Lepidoptera 60–200, Coleoptera and Hemiptera none. They are absent in larvae, with a few exceptions. In many cases the rectal papillae are freely supplied with tracheae,

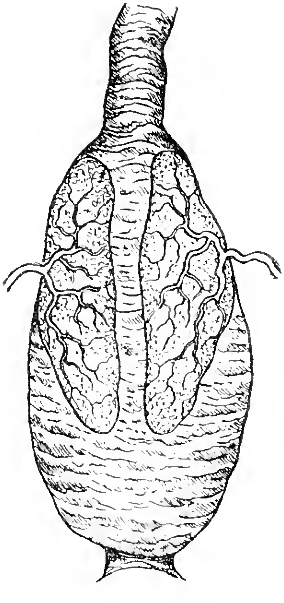

Fig. 77.—Rectal papilla of fly, with tracheae.

a circumstance which tells in favour of Leydig's supposition that they are primarily respiratory organs—a supposition which is far from general acceptance at present. We can give no account of the function of these organs in Chironomus.

The Malpighian tubules persist unchanged throughout the metamorphosis, being, we may suppose, still required for the elimination of the abundant waste material formed by the destruction of various larval tissues.

Heart.

We have seen (p. 71) that in the larva the contractile and valvular heart is restricted to the hinder part of the body. As the tracheal system attains a fuller development, the part of the dorsal vessel in front of the original heart becomes chambered. New inlets and valves appear, and the muscular tissues become more complex. In the late larva, pupa, and fly, the dorsal vessel is chambered throughout the abdomen. In the pupa and fly, the thoracic portion of the dorsal vessel exhibits a feature which we have not found in early larvae, viz. a numerous series of what we take to be ganglia, placed alternately on the right and left sides in the neighbourhood of the head. These were also found in the larva of Corethra by Dogiel (1877).

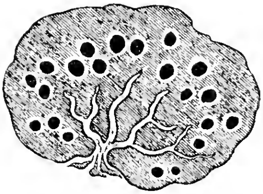

Fig. 78.—Transverse section of rectal papilla of fly (from larva). × 300.

Tracheal system.

The two pairs of thoracic spiracles of most insects are now believed to belong to the meso- and metathorax. This has been proved for several Coleoptera[1] and Hymenoptera (Apis, Hylotoma), Hemiptera (Coccidae), and Thysanura (Lepisma). We believe that no clear case of a prothoracic spiracle has been recorded in any winged

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[1] See Heider on Hydrophilus, Wheeler on Doryphora, Graber on Melolontha and Lina.

insect. In Chironomus the posterior thoracic spiracle is clearly metathoracic, while the anterior spiracle lies in the groove between the pro- and mesothorax. The tendency of the spiracles to shift into the intersegmental grooves in front may be attributed to the necessity of protection for an organ of vital importance.

In Aphis-larvae the whole series can be plainly seen. Each segment has its own pair of spiracles, that of the prothorax being of peculiar form; the spiracle in all cases is situated near the middle of the segment.

The tracheal system of the fly, though very much more extensive than that of the larva, is not so elaborate as in large insects of powerful flight. Its arrangement is as follows:—The anterior or mesothoracic spiracle is connected by a short branch with a longitudinal trunk, which sends off several branches to the head, and with an external branch which passes outside the vertical muscles of the mesothorax. There is a pair of good-sized air-sacs between the vertical and longitudinal muscles of the mesothorax. The main longitudinal trunks pass inside the vertical muscles, and are connected in front of them by a transverse branch. They are continued forwards to the head, and in this part of their course lie very near to the dorsal vessel. From each metathoracic spiracle a branch joins the main longitudinal trunk, which gives off at the same place a large descending branch. The trunks are then continued into the abdomen, and receive branches from the spiracles. The abdominal spiracles are so minute that it is hard to say how many of them are open; probably either four or five, viz. those lying in the intersegmental spaces behind the four or five anterior abdominal segments.

Reproductive organs.

In the more primitive insects, the reproductive organs are not very unlike in the two sexes, and the general arrangement is comparatively simple. A number of tubes, ovarian or seminal, enter paired ducts (oviducts or vasa deferentia), which run lengthwise through the abdomen. The ovarian or seminal tubes approximate to the number of the segments, and sometimes give indications of segmental arrangement[1]; they commonly enter the ducts at right angles or nearly so, and from one side only[2].

In Ephemeridae[3] the outlets are double in both sexes, and this we suppose to be the primitive arrangement. In the great majority of insects, however, the ducts unite behind; and there may be a common tube, divided into chambers of special functions, and receiving the secretions of accessory glands. The common tube is usually prolonged by the invagination, or inward telescoping, of the integument around the outlet; a considerable section may thus be added to the original ducts, and furnished with recesses, glands, &c., of its own. The invaginated portion is usually lined by a chitinous membrane, continuous with the chitinous cuticle of the external surface[4]. The ovarian or seminal tubes often deviate greatly from their original disposition. In the male all, or all but one, of the seminal tubules may be suppressed; and the functional testis is then either a dilatation of the sperm-duct, or a capsule of similar form. In the female the original number of ovarian tubes is often retained, but they may be reduced or greatly multiplied. In the earwig, for instance, there is only one ovarian tube on each side, but this gives off three longitudinal rows of short secondary tubes.[5] In female Diptera we often find a similar arrangement,

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[1] Japyx, according to Grassi, *Atti d. R. Ac. Lincei*, 1888.

[2] Oudemans, 1887, pl. iii, figs. 41–43.

[3] Palmén, *Paarige Ausführungsgänge d. Geschlechtsorgane bei Insecten* (1884).

[4] Palmén (loc. cit., pl. v) gives useful diagrams of the morphology of the reproductive passages in a number of insects.

[5] Dufour, *Ann. Sci. Nat.*, xiii. (1828).

a multitude of short tubes opening into one central passage.

The essential reproductive organs are the ovaries and testes, within which the ova and sperm-filaments (spermatozoa) are formed. Particular germinal cells, formed within a part of the ovary distinguished as the germarium, are converted into ova, nutritive cells, or follicular epithelial cells; particular cells of the epithelium of the testis undergo repeated division, and form multitudes of seminal filaments. In Chironomus we find the remarkable and almost unique phenomenon, that the eggs or sperm-filaments are developed from cells which have never formed part of a permanent tissue; they are believed to be merely handed on from generation to generation, and though some of the cells to which they give rise are differentiated for special purposes and used up, others undergo no change except division[1].

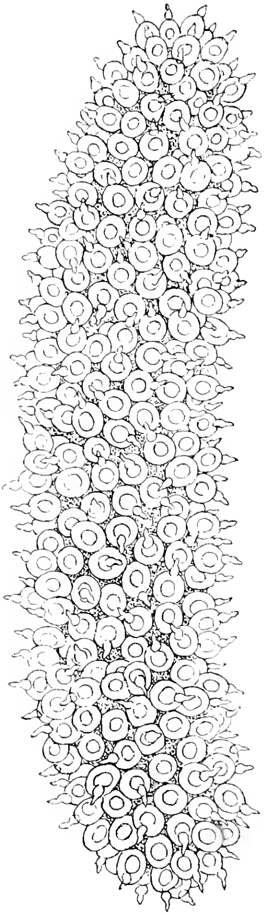

Fig. 79.—Ovary from full-grown larva. The external envelope is removed.

Female organs.

Let us now examine the structure of the female organs in the fly of Chironomus. The ovarian tubes (fig. 79) are short and extremely numerous, radiating from a central axis which takes the place of an oviduct, or else of a primary

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[1] Weismann, 1889.

ovarian tube. The axis is not visibly hollow, but that it is an actual oviduct may be inferred from the fact that all the eggs developed within the numerous tubes escape in a continuous egg-mass. The whole collection of ovarian tubes is enclosed within a transparent outer sheath, and constitutes the ovary, a smooth, sausage-shaped organ, which unites behind with its fellow. From the point of junction of the two ovaries a short, wide oviduct or uterus passes backwards, and is continued to the genital outlet by the ectodermal invagination described below. The two ovaries are applied to each other along almost their whole length, but are not everywhere in contact, for an unpaired sac, the gluten-gland (fig. 80), lies between them. The three together form a large semi-transparent mass,

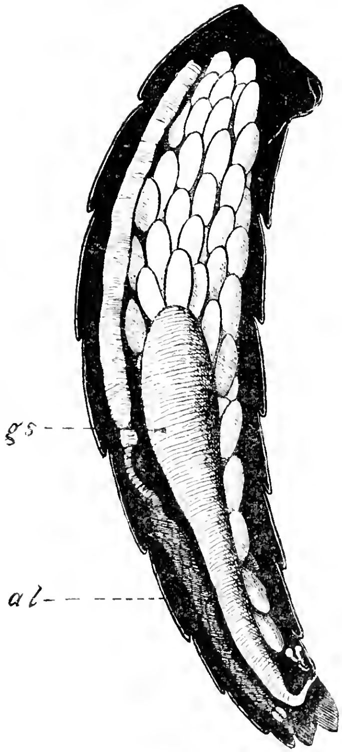

Fig. 80.—Abdominal cavity of female fly. *al*, alimentary canal. *gs*, gluten-gland. The ovary and the paired spermathecae are also seen. Dorsal surface to left, outlet below.

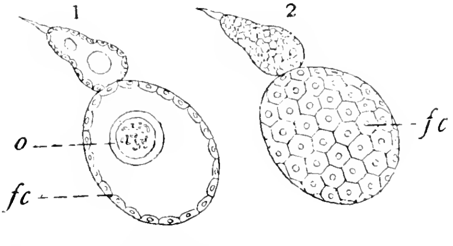

Fig. 81.—Two ovarioles. 1, optical section. 2, surface view. *fc*, follicular epithelium. *o*, ovum.

which fills almost the whole abdomen, and bulges a little into the thorax. Above it lies the empty alimentary canal. Many tracheae ramify on the surface of the ovaries.

A single ovarian tube consists of three successive chambers of unequal size, connected by narrow passages

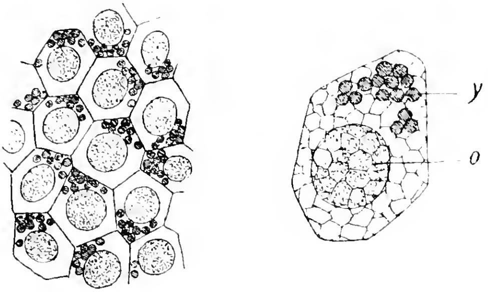

FIG. 82.—Ovary, from pupa. To left a number of follicles; to right a single follicle. *o*, ovum. *y*, yolk-granules.

(fig. 81). The free extremity is a short thread, and from the other end a narrow duct passes towards the axis of the ovary. Microscopic study of the large chamber in an oviduct not yet mature shows that it contains, as in other Diptera, an ovum, several nucleated cells, yolk, and a follicular epithelium. This last secretes the chorion or egg-shell, and afterwards disappears (fig. 83). The two chambers next above each contain a small ovum and a few nutritive cells; the distal portion or germarium is very minute, and its contents are not visibly differentiated.

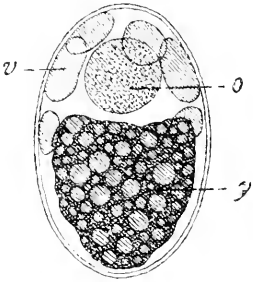

FIG. 83.—Ovarian chamber, from fly. *o*, ovum. *v*, nutritive cells. *y*, yolk.

The rest of the female reproductive organs is derived from invaginated epidermis, and lined with chitinous cuticle; it consists of the gluten-gland and a pair of spermathecae.

The gluten-gland extends between the ovaries for the greater part of the length of the abdomen. It is of elongate-oval shape, and externally smooth and undivided. A cross-section shows that it is occupied by four longitudinal segments (dorsal, ventral, and two lateral) of a coagulable, transparent secretion, from which is derived the bulk of the egg-mass (fig. 84). The wall of the gland is rather thick, and shows in order, beginning from the outside, a connective-tissue sheath, a layer of transverse muscle-fibres, a space filled with granules in several layers, a basement-membrane, and a lining epithelium, which in the pupa shows cells charged with secreted matter.

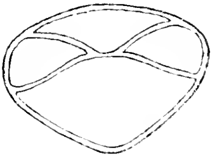
FIG. 84.—Transverse section of gluten-gland of female fly, showing the subdivision of the secretion into four masses.

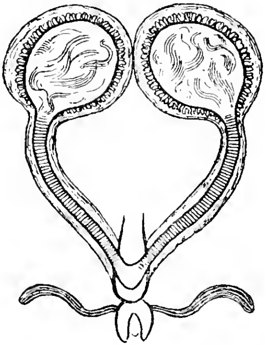
FIG. 85.—Spermathecae and their ringed ducts, from female fly.

A pair of spermathecae (fig. 85) lie on the ventral surface beneath the gluten-gland; they are derived from rudiments contained in the eleventh segment, and form nearly spherical capsules, about ·25 mm. in diameter, with short ducts, which converge to a common opening close to that of the gluten-gland. The ducts have muscular walls, and internally show a pseudo-tracheal structure, similar to that often seen in the salivary ducts of insects. Both the capsules and ducts may be filled with seminal filaments.

The common oviduct, the spermathecae, and the gluten-gland, all open close together into a deep intersegmental fold at the junction of the eleventh and twelfth segments of the larva (fig. 75, *go*, *ggo*).

Before egg-laying the epithelium of the ovarian tubes, and apparently that of the small egg-chambers, are completely absorbed. In a female fly, taken just before egg-laying, thin sections revealed hardly anything within the abdomen except the eggs, the gluten-gland, the spermathecae, the shrivelled alimentary canal, and the unaltered Malpighian tubules. A clear, thin line surrounded each egg, which we took to be the last trace of the wall of the ovarian tube. In some places this was found lying in actual contact with the epidermis of the body-wall.

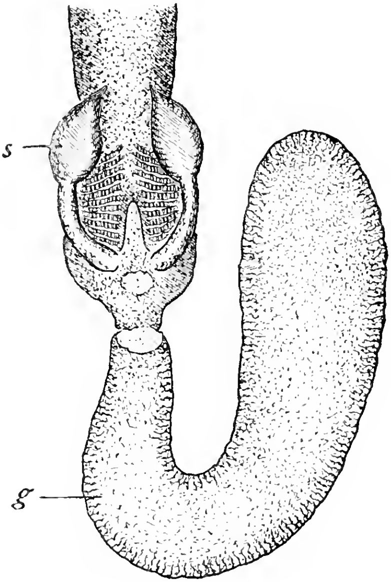

Fig. 86.—Female organs removed from the larva. *s*, spermatheca. *g*, gluten-gland.

The external female organs are described on p. 104.

During copulation the spermathecae are filled with seminal filaments from the male. One egg descends from each ovarian tube, the others remaining undeveloped. It is not known where fertilization is effected. The very numerous eggs as they pass out are enveloped by the secretion of the gluten-gland; this consists of transparent mucilage, and is shaped into a cylinder with rounded ends. The detailed structure of the cylinder is described in chap. vi. p. 153.

The contents of both ovaries and of the gluten-gland are discharged simultaneously. As in many other cases of coated eggs, the mucilage is at first scanty and dense, but swells enormously on reaching the water. In some species of Chironomus the contents of the two ovaries seem to remain distinct, except that they become fused at one place. In *C. dorsalis* they are intricately blended.

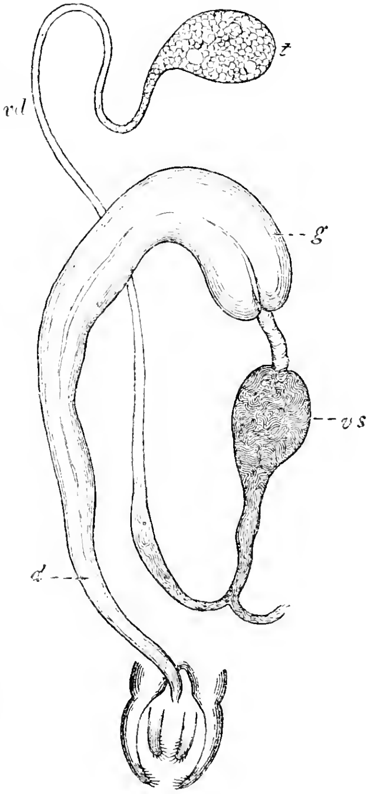

Fig. 87.—Male genital organs of fly. *t*, testis. *vd*, vas deferens. *g*, *d*, ejaculatory duct. *vs*, vesicula seminalis.

Male organs.

The male organs of the fly consist of a pair of testes, a pair of sperm-ducts, and an ejaculatory duct. The testis, when ripe, is filled with long simple sperm-filaments, developed as usual from compound cellular masses (spermospores) which arise by repeated division of single cells. The sperm-ducts are long and slender, and pass backwards as far as the junction of the penultimate with the last abdominal segment, where they open into the ejaculatory duct. This now passes forwards for a considerable distance, and is again bent backward to find its outlet in the last segment. A dilatation in the first part of its course is frequently seen to be filled with sperm-filaments; the walls are glandular, at least in the late larva and pupa, and perhaps in the fly also. Fig. 88 shows sections through the bight of the ejaculatory duct in the late larva, where each section exhibits a double tube lined with long cylinder epithelium. Many insects exhibit paired accessory glands, contributing a glutinous secretion to the spermatic fluid. In Chironomus, however, the same product appears to be secreted by the glandular wall of the duct itself. The wall of the duct has a delicate coat of transverse muscles.

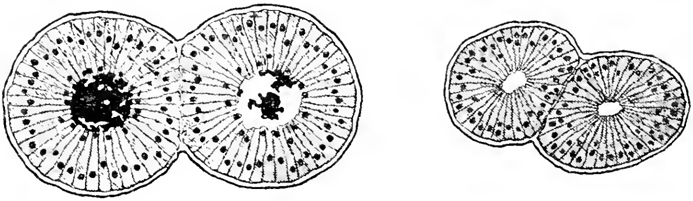

Fig. 88.—Sections across the bight of the ejaculatory duct (see line in fig. 102), from larva.

The external male parts are described on p. 105.

Oscar von Grimm (1870) has described the liberation of unfertilized eggs, capable of development, from a pair of genital orifices situated on the eighth abdominal segment of the pupa of a small species of Chironomus. Confirmation of this observation is much to be desired[1]. Many examples of parthenogenesis in insects have been recorded, and Cecidomyia (Miastor) is known to be capable of parthenogenetic and viviparous reproduction as a larva.

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[1] We have not found the ventral apertures of Grimm, but note that a pair of transparent rounded bodies, the spermathecae, lie exactly in the same place, and are seen through the skin of a female pupa.

CHAPTER IV

DEVELOPMENT OF THE PUPA AND FLY WITHIN THE LARVA

General explanations.

In Chironomus the fly differs so conspicuously from the larva that, without direct observation of the passage of the one into the other, no naturalist could have guessed that they were in any way related. In certain insects the transition from the creeping to the flying stage is mainly effected by small additions and modifications, which take place beneath the skin, and only become apparent at times of moult. Thus in a locust the wings, crumpled up within their sheaths, become longer and longer every time the skin is cast. While the wings are being perfected by definite, though not very conspicuous steps, the reproductive organs steadily increase in bulk and complexity, and at length the adult structure is attained without any sudden alteration of form, any change of food, or any resting-stage.

In most insects the larval stage is a time of voracious feeding, while the winged fly either does not feed at all, or feeds upon food which can be quickly taken into the body, and which does not materially hinder flight. A radical change of mouth-parts thus becomes necessary, and such a change involves a resting-stage. It is popularly believed that during the resting-stage the new mouth-parts, the compound eyes, the long antennae, the long legs, and the wings, all of which characterize the adult insect, are formed. The arguments long ago employed by Swammerdam, or a careful study of what happens in the transformation of any moth or butterfly, would be enough to refute such notions. The parts in question are complete (to outward appearance, at least) when the pupal stage begins, and can often be revealed by dissection before the pupal stage approaches. The microscopic rudiments of the imaginal organs can sometimes be found in a very young larva, or even in the embryo.

In the Muscidae, which happened to be the first Dipterous insects to be thoroughly investigated, the unlikeness of the larva to the winged fly becomes extreme. Buried in its food, the larva requires no limbs, and only a vestige of a head. The fly, on the contrary, is elaborate in structure beyond almost all other insects, more elaborate by reason of the simplicity of the maggot. It undertakes all the functions connected with the choice of a site and food suitable for the larva, and the contrast in activity and intelligence is as striking as the contrast in form.

The transformation of Chironomus

Chironomus is less complex in its latest stage, more complex in its larval stage, than a blow-fly, or perhaps any other Muscid. Hence its transformation, though difficult to make out, is much more intelligible than that of the Muscidae, upon which the labours of a generation of entomologists have already been bestowed. Other Dipterous insects are simpler than Chironomus in particular points, such as the development of the imaginal head and its appendages, but taking it as a whole, Chironomus is, of all the well-known Dipterous types, the fittest for an elementary study of imaginal development.

What may be conveniently called *imaginal folds* often play a great part in the development of the new organs of an insect. In the simplest cases they are shallow infoldings of the epidermis, but at times their real character is not evident without close inspection. They may penetrate far below the surface, and the invaginated layer, which connects them with the rest of the epidermis, may be hardly visible. The infolded cells may proliferate, and form solid masses within the body. Hence the name of *imaginal discs*, originally applied by Weismann to complex structures of this sort.

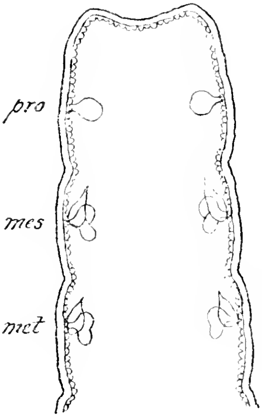

FIG. 89.—Early state of imaginal rudiments, from thorax of living larva. *pro*, prothorax (with one pair of rudiments only). *mes*, mesothorax (two pairs). *met*, metathorax (two pairs).

The chief alterations which are necessary to convert the larva of Chironomus into a flying insect are these. Biting mouth-parts are replaced by suctorial ones, suited to the nourishment of an insect which must not be loaded with food nor spend much time in feeding. In our common English species of Chironomus the fly does not feed at all, but the adaptation to a change of food takes place notwithstanding, and the mouth-organs of the fly, though not functional, are formed as in certain other Diptera which still occasionally feed upon the honey of open flowers (Tipula, Bibio, &c.). The eyes and antennae, which were rudimentary in the burrowing larva, become large and complex. Wings and long thoracic legs are developed. The hinder abdominal segments become modified for reproduction. The fly no longer inhabits the water, and it breathes by tracheae with open spiracles instead of by organs of aquatic respiration. Every part of the body undergoes change, and all the external organs are completely recast.

Until the last larval change of skin, which takes place when the larva is of about half its full length, the chief organs already developed which belong to the organization of the future fly are the nervous system and the reproductive glands, which grow steadily throughout the larval stage. Soon after the insect enters upon its last larval stage, the rudiments of the head, wings, and legs of the fly begin to form.

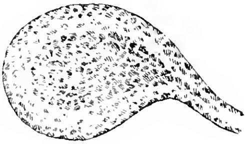

FIG. 90.—Early rudiment of prothoracic imaginal leg.

Imaginal rudiments in thorax.

If we take a larva at the beginning of its last stage, i.e. when it is about half an inch long, we shall discover new growths in the thorax, just beneath the skin. An alcohol-preserved larva is best, and we have found it a good plan to divide such larvae into lateral halves, remove the alimentary canal, stain the body-wall with picrocarmine,

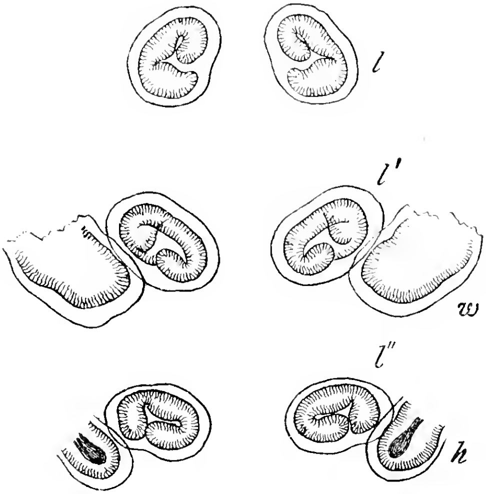

FIG. 91.—Imaginal rudiments from thorax of larva, more advanced than in fig. 95. The rudiments are enclosed in their capsules (outer walls of invaginations). *l*, *l'*, *l''*, first, second, and third legs. *w*, wing. *h*, haltere.

and mount in Farrant's medium. Several larvae, of different degrees of maturity, should be prepared in this way. The new rudiments will be found arranged in two rows, dorsal and ventral, and there is a dorsal and ventral set to each thoracic segment. The ventral rudiments ultimately yield the legs of the fly. They can be followed from the first simple buds, enclosed in transparent sheaths (the outer walls of the imaginal folds), until they become long and convoluted, divided into joints, and covered with hairs. Sections taken at different times reveal all the stages of tissue-development. As the legs increase in length they become folded beneath the larval skin in the manner represented in fig. 92.

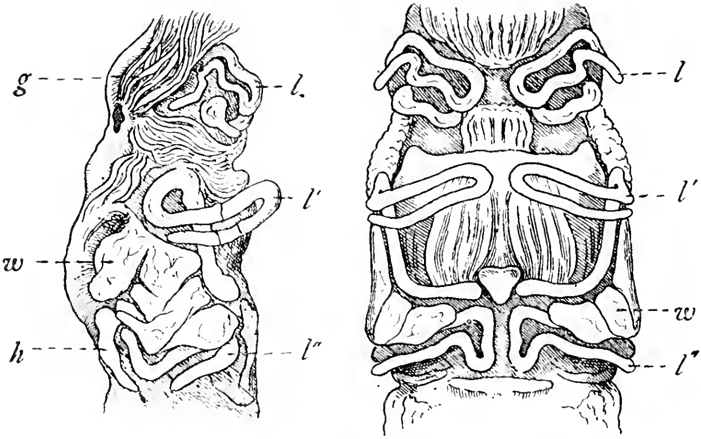

Fig. 92.—Thoracic appendages of pupa and fly, as seen in larva about to pupate. The larval skin has been removed. Left hand, side view: right hand, ventral view. *l*, *l′*, *l″*, first, second, and third legs. *w*, wing. *h*, haltere. *g*, prothoracic tracheal gill (of pupa).

The two hinder pairs of dorsal appendages give rise to the wings and halteres. The case of the prothoracic dorsal appendage presents some perplexing features. It develops into a short tube, from which three main branches proceed, and these by further division form a multitude of filaments, which are the tracheal gills, or respiratory organs of the pupa. Is it possible that this was ever wing-like, as the corresponding structures of the meso- and metathorax now are? Is it possible that the nervures of the prothoracic wing have persisted as branching tubes, while the intervening web has been suppressed? In some species of Chironomus and in many other Nemocera, we find pupal respiratory trumpets on the prothorax, instead of bunches of respiratory filaments. It has been conjectured that such trumpets represent wing-like rudiments, rolled up into tubes. But another origin for the pupal trumpet is suggested by the row of holes which we find upon its upper border in Dicranota. These favour the view that the trumpet is the basal tube greatly enlarged, and deprived of all its branching filaments, or else that the tracheal gill has arisen by the drawing out of the margins of the holes in a pupal respiratory trumpet. Wing-like dorsal appendages are not always restricted to the thoracic segments. In Ephemeridae flattened folds of integument are found on the abdominal segments of the larvae, as in the very common *Chloeon dipterum*, where they resemble in form and insertion the larger plates which enclose the future wings. The abdominal appendages of Ephemeridae are the tracheal gills of the larvae. By their vigorous flapping movements they continually bring a rush of water against their richly tracheated surfaces, and, as it would seem, promote the respiratory gas-exchange. It is possible, though not proved, that the original function of such appendages was respiratory, and that the conversion of some of them into wings is a secondary development. In certain Carboniferous Ephemeridae all three thoracic segments bear expansions, which have the form and the venation of true wings, and the narrowing of their bases seems to show that even the prothoracic pair were articulated like wings[1], though their forward position seems hardly compatible with the notion that they were serviceable in raising the body from the ground.

The patagia of Lepidoptera and Caddis-flies have been identified with prothoracic wings by Cholodkowsky, but Haase points out that they agree better with the tegulae found on the mesothorax of certain insects.

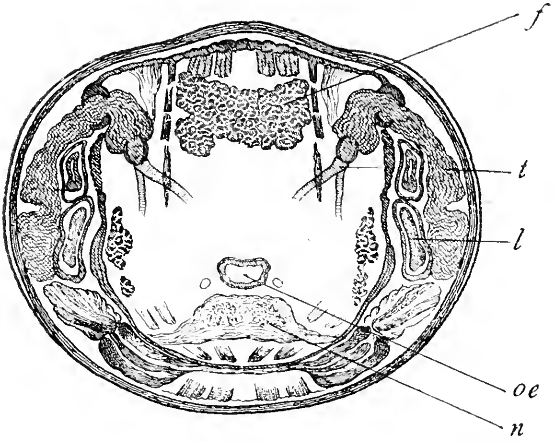

FIG. 93.—Transverse section of late larva, showing: *f*, fatty cells. *t*, tracheal gill of pupa. *l*, fore-leg. *oe*, oesophagus. *n*, nerve-cord.

It is to be observed, however, that the dorsal prothoracic rudiments, from which the pupal tracheal gills of Chironomus proceed, are the last to be developed. It is not till the larva is almost full-grown, and long after the other thoracic appendages are visible, that they appear. In the same way the corresponding organs of the blowfly, the prothoracic appendages of the pupa, are the only imaginal rudiments which cannot be traced back to the

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[1] Brongniart, *Rech. pour servir à l'histoire des Insectes fossiles des temps primaires.* 2 vols. 4to. St. Etienne, 1893.

embryo[1]. This may mean that the prothoracic tracheal gills are of comparatively recent origin, and that they are not truly in series with the dorsal appendages of the two hinder thoracic segments.

We feel no great confidence in any such explanations of the origin of the dorsal prothoracic rudiments as we or any others may have entertained. The possibility that they were once wing-like is not to be lost sight of till it is disproved, but it is at least possible that they have never existed in any other form than the bunch of filaments, the tube open or closed, or some other pupal respiratory organ.

In the Chironomus-pupa the wings are of simple outline, but they are too large to expand within the larval skin, and are therefore for a time much folded. The imaginal wings form within the pupal wings, and are also much folded.

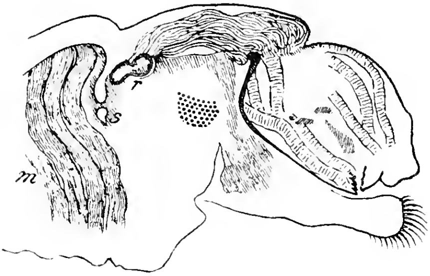

Fig. 94.—Sagittal section of larva, passing through base of pupal tracheal gill. The compound eye of the fly is seen within the prothorax; the muscles of the larval head are undergoing histolysis. *s*, anterior thoracic spiracle. *r*, tracheal gill. *m*, vertical mesothoracic muscles.

Shrinkage of larval prothorax.

The prothorax shrinks greatly during the last days of the larva. The head and the tracheal gill, which were widely separated, come gradually nearer together, and in the pupa the gill lies just behind the head. Fig. 95 shows a dorsal protrusion filled with disintegrated larval tissues, which represents the way in which a great part of the larval prothorax is made to disappear.

Phagocytes.

In the late larva and pupa the body-cavity, especially in the thorax, may contain clusters of cells which very

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[1] Weismann, *Entw. der Dipteren*, p. 145.

closely resemble the granular spheres (*Körnchenkugeln*) of Weismann, and are probably phagocytes gorged with the products of disintegration of larval structures. The eating up of the larval muscles by phagocytes is, however, much less striking than in the blow-fly. We have never seen in Chironomus larval muscles excavated by phagocytes, nor fragments of striped muscle lying inside phagocytes, though both can be demonstrated in the blow-fly. In Chironomus the disintegration of the larval organs of the thorax is relatively slow, and the muscles, for instance, seem to waste gradually and uniformly, while undergoing for a long time no marked change in external form.

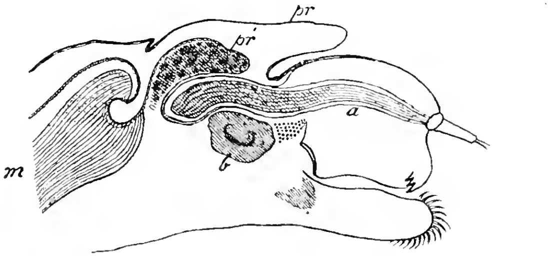

FIG. 95.—Sagittal (nearly median) section through head and prothorax of larva, shortly before pupation. *a*, antenna of fly. *b*, enlarged second joint of ditto. *pr*, larval prothorax. *pr'*, pupal prothorax, showing absorption of contents and marked retraction. *m*, mesothoracic muscles.

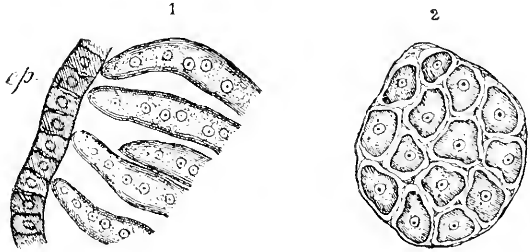

FIG. 96.—Developing imaginal muscles, with central nuclei, enclosed by contractile substance. 1, muscles attached to epidermis (*ep*). 2, transverse section of ditto.

Imaginal folds of head.

We have specially studied the development of the head of the imago within the larval head, and the following account is largely taken from our paper of 1892.

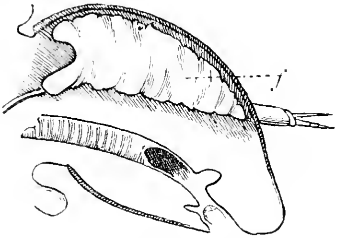

Fig. 97.—Early state of invagination for imaginal antenna, from larva, divided along middle line. *f*, longitudinal infolding.

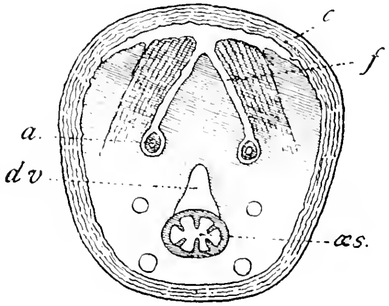

Fig 98.—Transverse section through invaginations for imaginal head (early state). The section passes through the junction of the head and prothorax. *c*, larval cuticle. *f*, longitudinal fold. *a*, antenna of imago. *dv*, dorsal vessel. *œs*, oesophagus.

In larvae about half an inch long the epidermis of the top of the head begins to be infolded along two longitudinal lines, which run forwards from the junction of the head and thorax, diverging a little as they do so. These lines correspond to the margins of the clypeus in the larval head. The epidermis, thus carried into the interior, gives rise to new cuticular organs, first to the pupal cuticle, and subsequently to the various external organs of the head of the fly. The cuticle of the head of the pupa is of less interest, and its formation need not be particularly described. The compound eye and antenna of the fly originate in these epidermic folds, and are therefore developed at a distance from the larval cuticle, though they are from the first external in their morphological position. The outer wall, the bottom, and ultimately the inner wall of each invagination develop facets, and thus give rise to the compound eye of the fly. In the larva this compound eye looks into the cavity of the invagination. and its concavity as well as its deeply sunk position contrast strongly with the convexity and exposed position of the imaginal eye. The imaginal antenna originates as a secondary duplication of the invagination around the antennal nerve of the larva. which duplication in all stages of growth is continued up to the larval antenna.

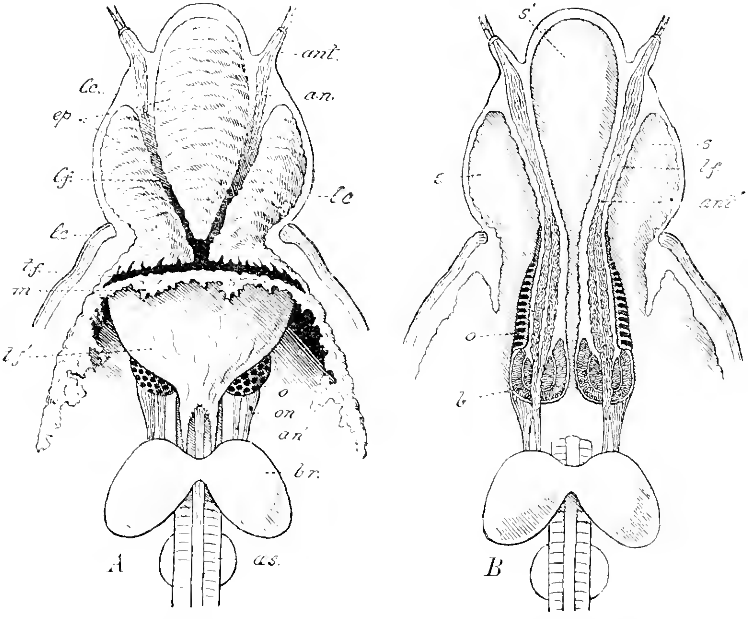

FIG. 90.—Formation of imaginal head in larva (male). *A*. The new epidermis thrown into folds, which have been cut away in places. *B*. The same parts in horizontal section. *lc*, larval cuticle. *t.f*, transverse fold. *t.f'*, upper wall of ditto. *ep*, epidermis. *m*, cut edge of new epidermis. *ant*, larval antenna. *a.n*, nerve to ditto. *ant'*, antenna of fly. *l.f*, longitudinal fold. *o*, eye of fly. *on*, optic nerve. *a.n'*, root of antennary nerve. *br*, brain. *æs*, oesophagus. *b*, enlarged second joint (bulb) of antenna of fly. *s*, *s*, *s'*, blood-spaces. (From Miall's *Natural History of Aquatic Insects*, after Miall and Hammond, 1892.)

In larvae which are not far from pupation, the folds are no longer confined to the region of the head. They extend backwards into the prothorax. and the part which forms the compound eyes comes to lie wholly behind the larval head. This backward extension is not brought about by any infolding of the epidermis of the dorsal surface of the prothorax, for the folds, though they lie deep in the prothorax, belong to the larval head exclusively. Weismann has shown that in Corethra the integument of the head of the fly is formed from the epidermis of the larval head, and the same thing is true of Chironomus, though here the cephalic invaginations are deeper and more complicated. Their backward prolongation is facilitated by a transverse fold which runs back from the junction of the larval head and prothorax, and is overarched by the uninterrupted epidermis of the latter. But for this transverse fold, it would not have been easy for the longitudinal folds to extend into the prothorax without implicating the prothoracic epidermis. The transverse fold is derived from the epidermis at the junction of the head with the thorax, and forms a sort of pocket, crescentic in transverse section, and tapering behind. The enclosed space is very inconsiderable, and appears in sections like a thin slit (fig. 98). The prothoracic prolongations of the longitudinal folds, which give rise to the compound eyes and antennae of the fly, open into the floor of the transverse fold.

As the longitudinal folds gradually deepen, the antennae of the fly, still enclosed within the pupal skin, grow at the same rate. Their basal parts recede further and further into the thorax, remaining all the time attached to the wall of the longitudinal invaginations already formed. The tip of the imaginal antenna is never withdrawn from the short larval antenna, which it is destined to replace. If we suppose a cloth to be spread out between two rails, then a hand grasping the cloth at one place may be made to push downwards and backwards until both hand and arm become buried in a deep fold. The fist will correspond to the bulb of the antenna, the arm to its shaft, and the fold in the cloth to the longitudinal invagination. This rude model will also show how it becomes necessary to introduce a transverse fold if the longitudinal fold is to extend beneath an undisturbed surface of cloth or epidermis. In all stages of larval growth the imaginal antenna[1] encloses the larval antennary nerve, the invagination being, in fact, formed about the nerve, but in the pupa this nerve becomes no longer traceable, and new structures appear to take its place.

Difference between imaginal rudiments in male and female.

The proportions of the male and female head differ materially in the adult fly. In the male the antennary bulbs are larger and closer together than in the female. This difference is already apparent in the antennary invaginations of the larva. We have found it possible to determine with certainty the sex of living larvae by observation of the form of the incipient generative organs. Having marked several specimens as male or female, we have cut sections through the growing heads of the larvae so marked. In the female the invaginations are wider apart, and the antennary bulb projects from the *inner* wall into the interior of the invagination. In the male the invaginations are so close that they almost or actually touch behind, and the antennary bulbs are at first connected with their *posterior* extremities. As the development of the imaginal head advances, the antennary bulb, even in the male, becomes to a great extent internal (i.e. adjoining the middle line) rather than posterior. In this stage it may be distinguished from that of the female by its larger size, and by its extending backwards up to, and even a little beyond, the hindermost extremity of the compound eye, which it never does in the female[2].

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[1] We do not at present distinguish between the imaginal and the pupal antenna.

[2] Ratzeburg, Reinhard, Packard, and Bugnion have remarked that in many Hymenoptera, but not in Tenthredinidae, the compound eyes of the imago form within the larval prothorax. Bugnion says that in Encyrtus the larval cephalic ganglia lie not in the head, but in the prothorax.

Formation of new mouth-parts.

Simultaneously with the formation of the compound eyes and the imaginal antennae, new mouth-parts are developed. As in Corethra, they develop within those of the larva. On either side of the salivary ducts and their common opening into the mouth, the epidermis of the larval head becomes infolded, and the pouches ultimately extend backwards to the back of the head. From the inner side of each pouch, and close to its hinder extremity, a secondary invagination pushes forwards and downwards, and this ultimately gives rise to the labella[1] of the fly. In larvae ready to change into pupae the tips of the labellae are bent inwards, towards each other, at a right angle. The invagination for the maxillary palp forms on the side of the larval head. The mouth of the primary fold is at first nearly equidistant from the larval maxillae and the occiput. The secondary forward-directed fold is long and narrow, and extends from the back of the head into the larval maxilla. As it lengthens it becomes coiled, and much resembles one of the developing imaginal legs. The new parts thus formed are those of the pupa, and the imaginal rudiments are enclosed within them. The pupal integument of the head, like that of some other parts of the body, recedes considerably from the larval cuticle, and the imaginal integument recedes again from that of the pupa, so that in sections of the pupal head a tolerably wide space separates the mouth-parts of the fly from the empty cuticle which represents the corresponding organs of the pupa.

Early stages of imaginal folds.

The history of the invaginations which give rise to

These authors seem to think that part of the larval prothorax is, so to speak, annexed by the imaginal head. It is desirable to inquire whether their observations do not admit of the same explanation that we have given in the case of Chironomus.

[1] The lateral halves of the labium, which become free distally. See Meinert, 1881, or Dimmock, 1881.

the head of the fly can be followed in a series of larvae of different ages. They are not to be discovered even in a rudimentary state until after the last larval moult[1]. Weismann[2] has given reasons for supposing that invaginated imaginal rudiments could not come into existence before the last larval moult in an insect whose life-history resembles that of Corethra or Chironomus. If the epidermis were invaginated in any stage before the antepupal one, the new cuticle, moulded closely upon the epidermis, would become invaginated also, and would appear at the next moult with projecting appendages like those of a pupa or imago. This is actually the way in which the wings are developed in some larval insects with incomplete metamorphosis. In Muscidae the invaginations for the head of the imago have been traced back to the embryo within the egg, but the almost total subsequent separation of the disks from the epidermis renders their development independent of the growth of the larval cuticle and of the moults that probably take place therein[3].

Very soon after the last larval moult, when the Chironomus-larva is about half an inch long, the first indications of the invaginations can be discovered by means of sections. They form rapidly, and among larvae quite similar in size and outward appearance some are found to exhibit tolerably advanced invaginations, while others do not possess even the rudiments of such structures. In an early stage the invaginations are restricted

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[1] There are probably four larval moults in Chironomus, as in Corethra, but the burrowing habits of the insect render it difficult to be quite certain of the exact number.

[2] 1866, p. 115.

[3] Leuckart and Weismann have inferred the occurrence of at least two moults in the larva of the blow-fly, from the changes observed in the stigmata and the hooks. Weismann (1863) suspects that as many as four moults may take place (p. 104).

to the larval head, and form comparatively simple paired folds of the dorsal epidermis (fig. 97). Behind and on the ventral side is a short extension, which will subsequently give rise to the compound eye and the antennary bulb. As the invaginations do not as yet extend into the thorax, the transverse fold described above is wholly wanting. In this early condition the invaginations of Chironomus are essentially similar to those of Corethra at the time of their fullest development.

Later stages.

The prolongation of the cephalic invaginations into the thorax gradually advances as the larva is nearing the time of pupation. The formation of the transverse fold already described is a necessary consequence. This fold may be regarded as an exaggeration of the slight fold which in so many insects forms in the new cuticle and epidermis at the junction of the head and thorax, as well as between other segments of the body shortly before a moult. While the backward extension of the invaginations is taking place considerable histological differentiation is in progress, and some change takes place in the form of the future sense-organs. The compound eye forms at first a vertical layer, not far from flat, occupying the outer wall of the invagination. Later on, the facets extend round the much bent floor of the cavity, and reach to a certain height upon the inner wall (fig. 99). The antenna also undergoes, especially in the male, a considerable change of form. At first the bulb is posterior, and the shaft takes a nearly straight course to the larval antenna, within which its tip is included; subsequently the bulb becomes internal, and the shaft is arched upwards in a bend of gradually increasing sharpness (fig. 95).

Eversion of head

The parts of the head thus formed within the larva, assume their final position by a process of eversion (turning inside out) which can be observed when the larva changes to a pupa. This is more fully described in the next chapter (p. 138).

Comparison with other Dipterous insects.

Comparison with allied insects shows that the formation of a new head is not accomplished in the same way in all Diptera. In a gnat the invaginations are shallow, and the compound eyes and antennae form within the larval head, though the base of the new antenna is telescoped into the head, and its shaft becomes folded. In Corethra the same process is carried a little further. *Chironomus dorsalis* comes next in the series, while in the Muscidae we reach the maximum of complexity. The invaginations are deep, and apparently, though not really, unconnected with the larval epidermis. In the Muscid pupa the epidermis, the muscles, the intestinal epithelium, and even a great part of the nervous system are regenerated; the old tissues are devoured by phagocytes, and only nests of cells persist as rudiments from which the new organs are developed.

Possible motive of invaginations.

Chironomus furnishes a particularly accessible and easily understood case of the development of what is practically a new head within the larva. When we inquire, as we cannot help doing, why the new head should be formed by imaginal folds in the thorax of the larva, the obvious facts suggest themselves that the head of the fly is utterly unlike the larval head in shape and that it is of larger size. The lengths are as twelve (male fly) to eleven (larva); the breadths as five (male fly) to three (larva). As a mere matter of dimensions, such a head as that of the male fly of Chironomus could not be developed within the larval head. This explanation at once provokes a further question: Why should any such disproportion exist between the head of the fly and that of the larva? We may say in reply that the fly is a nimble aerial insect, requiring keen senses and some degree of intelligence that it may escape danger, find a mate, and lay its eggs in a suitable position. The larva, on the contrary, is an animal of very simple mode of life, feeding upon dead vegetable matter at the bottom of dark and slow streams. The abundance of its food, and the ease with which it can be appropriated, have led in this, as in many other cases, to some degree of degeneration which is particularly apparent in the larval limbs and head[1]. We have already pointed out (p. 30) that the brain must be removed to the prothorax in an insect whose imaginal head develops in the prothorax, and that this shifting of the brain would naturally lead to further reduction of the larval head.

Variations

We find that within the family Chironomidae there are considerable variations in the mode of formation of the imaginal head. Thus in a large Chironomus-larva, of which we have not been able to procure the fly, the compound eyes are restricted, even in a late stage of formation, to the larval head. It is noteworthy that in this larva the head is much larger than in *C. dorsalis*. In some Tanypus-larvae the same thing has been found. In other Chironomus-larvae the compound eyes, just before pupation, lie half in and half out of the larval head, and here too the head is larger than in *C. dorsalis*.

Development of reproductive organs.

While the testes, sperm-ducts, and their contents are undergoing development, a paired ventral invagination forms in the last abdominal segment of the larva. This soon becomes double and lengthens greatly, bending first forward, then backward, and lastly again forward. From it are derived the paired ejaculatory ducts (ducts of Herold). They are the *ectadenes* (i. e. ectodermal glands) of Escherich, who distinguishes glandular mesodermal outgrowths, e.g. outgrowths from the sperm-ducts, by the

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[1] We have to thank the Linnean Society for permission to extract part of our paper of 1892, and to copy several figures from the illustrated plates.

term *mesadenes* (mesodermal glands)[1]. Near the posterior border of the penultimate segment, the extremities of the ejaculatory ducts come into contact with the backward extensions of the sperm-ducts, which have reached this point. Here an anterior genital rudiment appears to

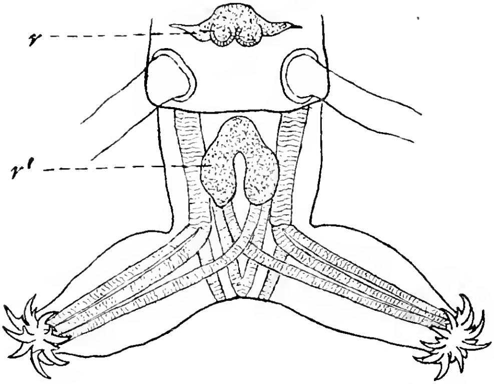

FIG. 100.—Ventral surface of eleventh and twelfth segments of male larva, showing the rudiments of the genital ducts, the muscles of the anal feet, and the ventral blood-gills. *r*, anterior genital rudiment. *r'*, posterior ditto. From living larva.

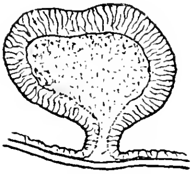

FIG. 101.—Rudiment of ejaculatory duct, from living larva.

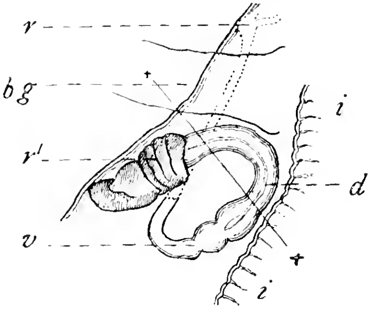

FIG. 102.—Developing ejaculatory duct of male from larva. More advanced than fig. 100. The line + + shows the plane of the section in fig. 88. *r*, rudiment in the eleventh segment. *r'*, ditto in the twelfth segment. *d*, ejaculatory duct. *v*, vesicula seminalis? *i*, intestine *bg*, blood-gill indicated by two nearly parallel lines. From living larva.

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[1] Escherich, 1894.

occupy a position on the ventral surface of the larva exactly corresponding to that of the rudiment which in the female gives rise to the seminal receptacles, but the connexion of the supposed anterior genital rudiment with the male ducts has not been satisfactorily ascertained, and is somewhat difficult to understand.

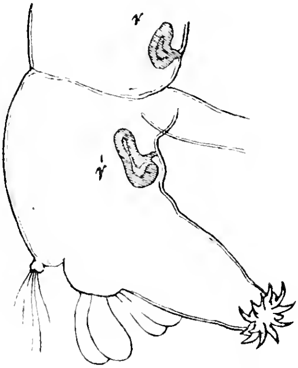

FIG. 103.—Development of female organs within the larva as seen in the eleventh and twelfth segments (side view). *r*, rudiment of spermatheca. *r'*, rudiment of gluten-gland. From living larva.

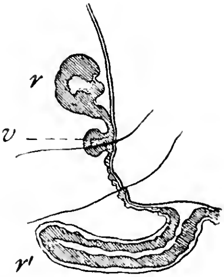

FIG. 104.—Development of female organs within the larva. More advanced than fig. 103. *r*, rudiment of spermatheca. *r'*, rudiment of gluten-gland. *v*, vulva. From living larva.

The female reproductive appendages develop within the larva as thickenings and invaginations of the ventral epidermis. From rudiments in the eleventh segment are derived the spermathecae, while a similar ingrowth in the twelfth segment gives rise to the unpaired gluten-gland.

CHAPTER V

THE PUPA OF CHIRONOMUS

The process of pupation.

LARVAE about to undergo pupation can be easily distinguished by the thickened thorax. If a number of such larvae are observed continuously for a few hours. the process of pupation can be studied without serious difficulty. The first distinct sign of change is the retraction of the epidermis and soft parts from the old cuticle of the prothoracic feet. Very shortly after this (about a minute) the same process takes place in the blood-gills, and a little later in the anal feet. After a further interval of a few seconds, or at most a minute or two, the head and thorax of the pupa protrude from the dorsal surface, between the larval head and prothorax. The larval head, which has been emptied by the retraction of its contents, then slips round to the ventral surface. The order of these events is not quite constant. Now and then the anal feet and other posterior appendages are seen to be unchanged in a larva which has already slipped off the larval head, but this is unusual. It is probable that the contraction of the thoracic and anal regions sets up a blood-pressure, which is the immediate agent in the protrusion of the pupal head. An independent indication of the existence of such blood-pressure at the time of pupation is given by the occasional escape of a large quantity of blood. which fills the space between the old cuticle and the retracted epidermis. In such cases we have found that the pupa dies within a short time. The complete removal of the larval cuticle from the body is a matter of time, and may occupy several hours. The old cuticle becomes much wrinkled, and is ultimately torn into shreds, being gradually rubbed off by the almost incessant movements of the pupa. Occasionally the larval skin is still adherent to the pupa when the fly emerges.

Sections taken through the pupal head a little after the time of change illustrate the eversion of the imaginal head. The compound eyes, which were deeply invaginated, become bit by bit convex, by progressive eversion of the folds. During the process they are drawn downwards and backwards, so that they get behind and beneath the bases of the antennae. The morphologically external surface of the eyes, which was previously turned inwards, now looks outwards; the optic nerve, which was distributed to the temporarily convex surface, still takes its course to the same surface, now concave; and the walls of the head, for the first time since the first larval moult, enclose the brain.

Characteristic pupal organs.

It will be understood from the history of its development that the pupa of Chironomus is structurally little more than the fly enclosed in a temporary skin. The compound eyes and antennae, the mouth-parts, legs, and wings of the fly are all there, complete in outward form, and usually exhibiting on microscopic examination all the histological detail of the same organs in their active condition. The only structures peculiar to the pupa seem to be the prothoracic respiratory appendages or tracheal gills, and the fin-like expansions of the abdomen (Plate, figs. 5, 6).

A pair of conical prominences are borne on the top of the pupal head; they enclose a pair of imaginal prominences (fig. 105). In *Chironomus niveipennis* each of these pupal prominences bears a long seta (see p. 14).

Legs and wings.

The legs of the pupa are doubled up in the manner shown in Plate, fig. 5. Short-legged Dipterous pupae have the legs extended. Legs, wings, and antennae have their own pupal sheaths, which fit closely, and are not glued to the body. The pupal wing is of simple outline, and much smaller than that of the fly, which is crumpled up within it. The haltere is relatively larger and more wing-like in the pupa than in the fly.

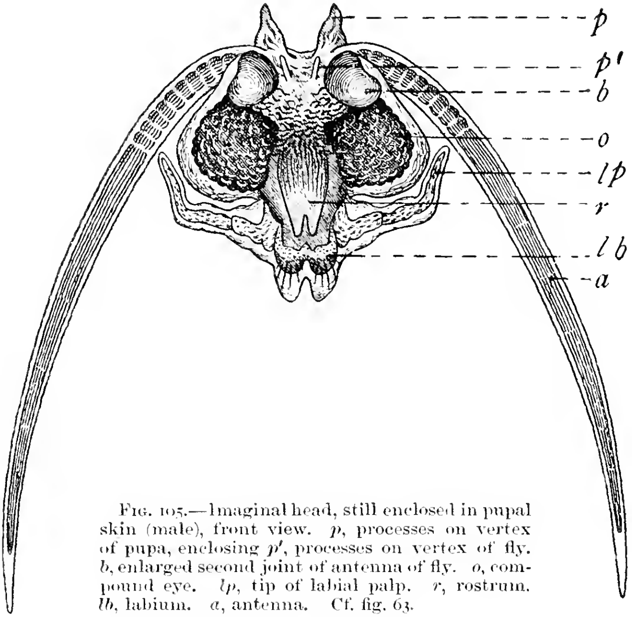

FIG. 105.—Imaginal head, still enclosed in pupal skin (male), front view. *p*, processes on vertex of pupa, enclosing *p′*, processes on vertex of fly. *b*, enlarged second joint of antenna of fly. *o*, compound eye. *lp*, tip of labial palp. *r*, rostrum. *lb*, labium. *a*, antenna. Cf. fig. 63.

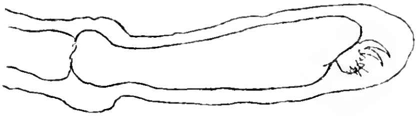

FIG. 106.—Foot of fly in pupal cuticle.

Pupal abdomen.

The pupal skin which invests the abdomen of the fly is expanded laterally into paired flanges, which are fringed with long setae. In some species the pupa has claw-like projections on the sides of the abdominal segments, a pair to each segment. In pupae of the *plumosus* section the flanges of the last abdominal segment are furnished with very long setae, and constitute a tail-fin (Plate, figs. 5, 6). The laterally expanded abdomen acts powerfully on the water in the incessant movements of flexion and extension, and drives it in a continual stream through the tube, in which, under normal circumstances, the pupal stage is passed.

Pupal tracheal system.

The pupa aerates its tissues by means of tracheal gills and a system of air-tubes.

The tracheal gill of the pupa forms in the hinder part of the larval prothorax. This might not of itself prove that it is truly prothoracic, since pupal and imaginal structures characteristic of a particular segment may form within a larval segment which does not occupy the same place in the series. The best proof that the tracheal gill is really prothoracic seems to be furnished by the following observations:—The larval skin was removed from a larva nearly ready to pupate (fig. 108). A well-marked transverse line was then seen, which apparently marked the junction of two segments. By a simple dissection with needles the longitudinal mesothoracic muscles were traced precisely to this line, and no further. It thus became clear that the line marks the

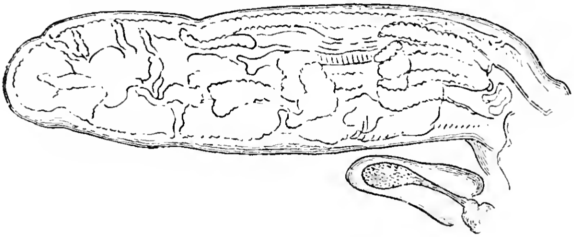

Fig. 107.—Wing and haltere of fly, enclosed in their pupal sheaths.

boundary between the pro- and mesothorax. The tracheal gill was clearly seen in front of the line, while the

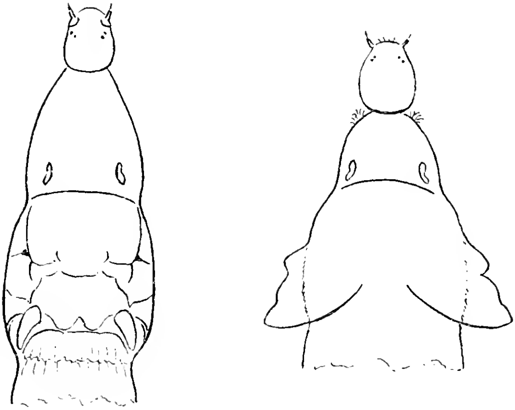

FIG. 108.—Dorsal views of the thorax of a late larva, showing the position of the paired bases of the tracheal gills of the pupa just in front of the strong transverse line that separates the pro- from the mesothorax. In the right figure the larval skin has been removed, except from the head, so that the wings are suffered to expand. The prothorax here has suffered some degree of contraction.

anterior or mesothoracic spiracle of the imago lies in the line.

The tracheal gill branches primarily into a larger anterior lobe and two posterior bifid lobes. These again

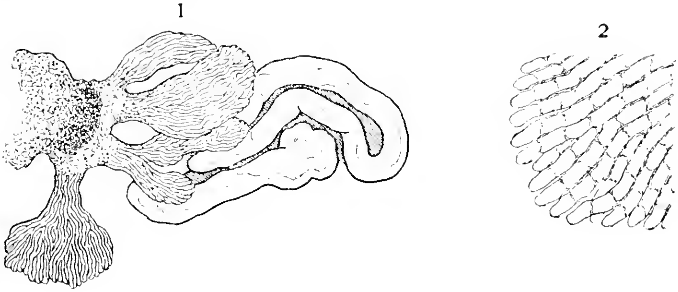

FIG. 109.—1, tracheal gill of pupa and adjoining fore-leg in side view, as seen through larval skin. 2, filaments of tracheal gill. × 350.

become divided into numerous long filaments, which float freely in the water (Plate, figs. 5, 6). A stiff cylindrical stem, slightly flattened, supports the base of the gill, and gives passage to a multitude of fine tracheae.

When the pupal skin is cast, two sets of branching tracheal tubes are found attached, one to its superficial and one to its deep surface, in the region of the tracheal gill. Those on the superficial face pass through the stem into the gill; those on the deep face are withdrawn from the tracheal system of the fly, which forms outside that of the pupa in the same way that this formed outside that of the larva. While one set of tracheae is withdrawn from the anterior spiracle of the fly, another much smaller set, further back, is withdrawn from the posterior or metathoracic spiracle.

The cast pupal skin in the prothorax and fore part of the mesothorax is marked by three scars, nearly in a line. The uppermost scar, which is also in front of the others, is oval and has a sieve-like appearance, which we are unable to explain. Next comes the base of the tracheal gill, fringed by innumerable broken tubes. Last and lowest is a pit-like depression of the pupal skin, which looks rather like a pupal spiracle, though we believe that it is impervious; it is in close relation to the imaginal spiracle beneath (fig. 111), and the pupal tracheae are withdrawn at this point.

In the abdomen of the pupa a pair of narrow longitudinal tracheae can be traced, which are placed in communication with impervious spiracles by minute initial branches. One spiracle lies near the middle of the second abdominal segment; the rest in the fore part of each of the segments from the third to the seventh inclusive.

The tracheal system of the pupa is larger and more continuous than that of the larva. Sections through the thorax now show a double wall in all the larger tracheae, the outer being the imaginal structure, while the inner is the comparatively narrow pupal trachea.

The casting of the tracheal gill.

The branches of the longitudinal tracheae which pass to the tracheal gill take origin near together, and are at first tortuous and crowded. They soon break up, nearly at the same level, into a multitude of much smaller tubes, which run parallel to one another up to and through the stem of the gill, and then break dichotomously into still finer branches, which pass along the tubules of the gill. Beyond the common stem the tracheae branch with the containing tubules until the ultimate tubules are reached: the tracheae then branch independently, so that one tubule may contain several tracheal branches.

FIG. 110.—Termination of filament of tracheal gill of pupa, with tracheae enclosed.

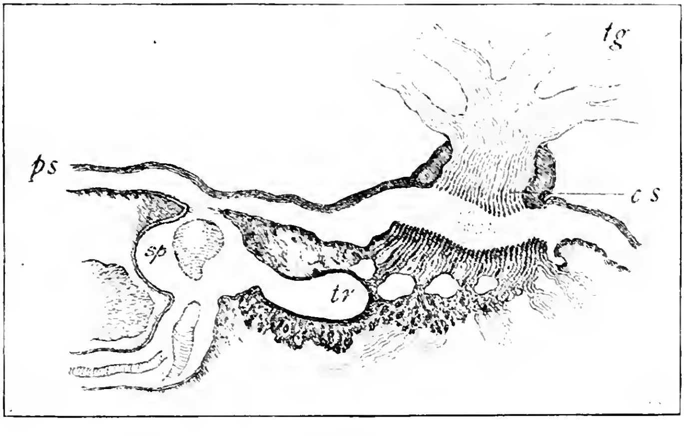

FIG. 111.—Sagittal section of pupa, passing through base of tracheal gill and mesothoracic spiracle. *ps*, pupal skin. *sp*, mesothoracic spiracle of fly. *tr*, large trachea. *cs*, chitinous septa at base of tracheal gill. *tg*, tracheal gill.

Within the stem of the gill the tracheae are supported by chitinous septa, which are easily distinguished in sections by their solidity and well-marked colouration.

The septa begin at the base of the stem, and die away gradually upwards. Between the tortuous tracheae within the thorax, and the strong chitinous septa, extend a number of straight, parallel, and relatively weak tubes (fig. 111).

It is here that the tracheae are ruptured when the pupal cuticle is about to be cast. The vigorous contractions of the body exert a pull upon the tracheae, which break across just where the abrupt change to the chitinous septa takes place, and the tracheal gill comes off with the pupal skin. After the separation a number of short threads (the broken ends of the tracheae) are seen to project from the chitinous septa. This provision for securing a clean fracture without undue violence reminds us of the process by which an autumn leaf is detached from the twig[1]. The sudden change in the strength of the chitinous septa is in itself a cause of weakness; the base of the gill is weaker than if its tracheae were not strengthened at all.

Just behind the common stem of the gill the anterior spiracle of the fly is formed, which opens to the air as soon as the pupal cuticle is removed.

The separation of the tracheal gill would seem likely to leave openings by which air could enter or leave the tracheal system of the fly. Such openings, which would be naturally incapable of regulation, would destroy the efficiency of the tracheal apparatus, for air can only be forced into the finer branches by closing all the outlets, and then compressing the main trunks. The torn ends of the tracheae are, however, quickly sealed up. The tubes themselves collapse, while their generating epithelium, which, it will be observed, is an extension inwards

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[1] In a pupa which had just cast the larval skin no inequality in the chitinous septa could be discovered. The generating cells, which secrete the thickenings and plug up the outlets, were plainly seen in this stage.

of the cuticle-secreting epidermis, resumes its activity. The cells multiply and enlarge, form a layer over the scar, and secrete new cuticle. In a few hours the only external indication of the place where a tracheal gill once projected is an oval scar, which is easily seen on the thorax of the fly (fig. 72).

We have already remarked (p. 10) that there is a section of Chironomus (the *motitator* group of Meinert) in which the pupa is provided, not with bunches of filaments, but with a pair of trumpets.

Pupal respiratory organs of other Nemocera.

Sedentary aquatic pupae, which are unable to come to the surface of the water, may be provided with branched and filamentous gills like those of Chironomus (*plumosus* section) or Simulium. Free aquatic pupae are able to float at the surface without effort, and are commonly provided with respiratory trumpets, whose tips just reach the surface of the water when the pupa is at rest. The trumpets, instead of a single orifice, may have a row of small holes; in particular cases the passage is closed by a thin membrane. The respiratory trumpet of the pupae of Culex, Corethra, certain species of Chironomus, &c., is perhaps the equivalent of the common stem of the pupal tracheal gill of *Chironomus dorsalis*, &c. The numerous holes in which the trumpet of the Dicranota-pupa ends may perhaps correspond to the short tubes which in *Chironomus dorsalis* lead from the tracheal trunk to the tracheal gill of the pupa (see p. 144).

The pupal trumpets are very long and slender in some species of Limnophila; one of the pair is longer than the body in Ptychoptera and Bittacomorpha. In Ptychoptera they exhibit a very peculiar and interesting structure[1].

Provision for escape of fly.

On the dorsal surface of the pupal thorax an interrupted median white line may be seen, and on either side of it a curved line of similar character (fig. 112). Along these lines the integument is slightly sunk, and thinner than elsewhere, while the close-set cuticular hairs, so prominent elsewhere, disappear. These hairs are pro-

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[1] Grobben, 1875; Miall, 1895.

bably casting-hairs, and facilitate the separation of the pupa from the larval skin, within which it was formed. We believe that the median line marks the place where the pupal thorax splits to allow of the escape of the fly, and that the lateral lines constitute, so to speak, the hinges on which a pair of flaps bend downwards and outwards, to enlarge the opening. These lines of weakness, prepared long in advance, facilitate the escape of the fly, and help to explain the wonderful speed with which it is accomplished (see p. 6).

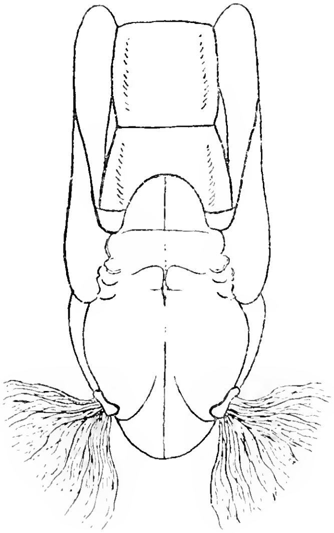

FIG. 112.—Dorsal surface of pupal thorax and anterior abdominal segments. The tracheal gills and wings are seen on the sides. Between the tracheal gills a median and two curved lateral lines appear, which in the fresh pupa are white upon a dark ground. The median line indicates the cleft by which the fly will escape; along the lateral lines the pupal integument is thin and flexible, and bends downwards and outwards to enlarge the cleft.

The mode of life of the pupa and the extrication of the fly have already been described (p. 8).

Changes in the alimentary canal.

Shortly before pupation the alimentary canal undergoes marked changes. The epithelium of the stomach becomes stripped, and large masses, in which shrunk nuclei are still apparent, lie in the cavity (fig. 113); this does not take place everywhere and at once. At the beginning and end of the stomach the epithelium persists for a time, but in a shrunk and probably functionless condition. The stomach of a late pupa or a fly contains hardly a trace of epithelium; its wall consists merely of muscular tissue and basement-membrane. A similar stripping of the epithelium of the mesenteron has been described in many insects[1]. The cast basement-membrane, or 'cyst,' observed in some other insects, was not found in Chironomus.

The changes which take place are not wholly destructive. In the oesophagus of the larva the epithelium is so thin as to require pains to make it evident, and even with careful staining and high powers we rarely see anything more than regularly spaced and minute nuclei. But in the pupa a relatively thick epithelium with large nuclei is often conspicuous in sections (fig. 114). We have not discovered how it is regenerated.

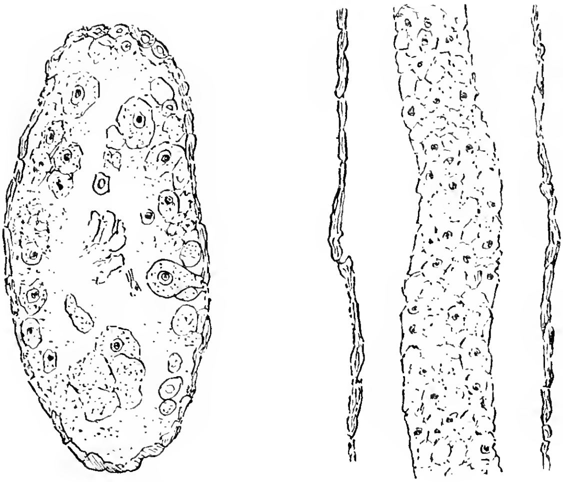

FIG. 113.—Stripped epithelium, from stomach of pupa. The left-hand figure shows scattered cells and nuclei; the right-hand one the more usual appearance of a coherent mass.

Just above the junction of the oesophagus with the stomach a hollow lateral outgrowth forms on one side, shortly before pupation. It grows fast, and soon takes the form of a ventral diverticulum (fig. 114). This is

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[1] Weismann, 1863; Kowalewsky, 1887, and authors there quoted; Rengel, 1896.

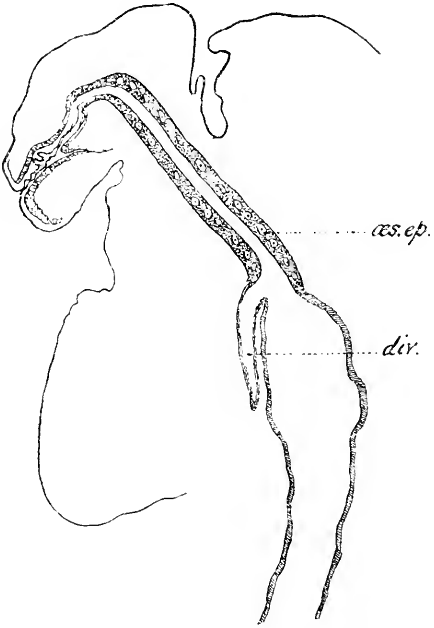

FIG. 114.—Sagittal section of fore-part of pupal alimentary canal. *œs.ep*, regenerated epithelium of stomodaeum. *div*, diverticulum or sucking stomach.

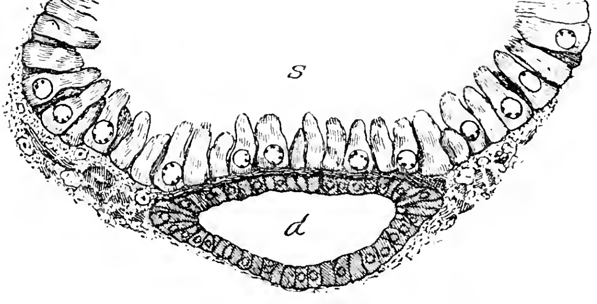

FIG. 115.—Transverse section of diverticulum or rudimentary sucking stomach of pupa. *s*, epithelium of stomach, not yet broken up in this region. *d*, cavity of diverticulum.

narrow and pointed behind; it extends to the end of the metathorax, the oesophagus having now contracted so much that the cardiac end of the stomach is close to the head, from which it is separated only by the length of the greatly reduced prothorax. The diverticulum is an outgrowth of the oesophagus, and probably represents the sucking stomach or honey-bag of some winged Diptera, Neuroptera, Lepidoptera, and Hymenoptera. It has a distinct epithelium with small nuclei, a rather thick muscular wall, and, like the oesophagus itself in this stage, secretes no chitinous intima. The cavity, which is at first conspicuous but not large, never contains food; it shrinks rather rapidly, and in the late pupa is nearly obliterated, the epithelium being then irregularly folded, and in course of disintegration.

The two groups of Chironomus larvae and pupae contrasted.

The tube-dwelling Chironomus-larvae are distinguished from the surface larvae by a number of adaptive characters, so marked that it is a matter for surprise to find that both groups can be comprised within one genus. The tube-dwelling larvae usually have red blood, four ventral and four anal blood-gills, and vestigial tracheae, reduced to two almost independent intersegmental systems. The pupa is furnished with tracheal gills on the prothorax. The larval head is usually small, and the invaginations for the compound eyes and antennae often extend far into the prothorax, where the larval brain is situated. In the surface larvae, on the other hand, the blood has rarely any red colour; the ventral blood-gills at least are wanting: the tracheal system may extend throughout the whole length of the body, its various parts being connected by longitudinal trunks of fair capacity. The pupa has prothoracic trumpets in place of tracheal gills. The larval head is sometimes decidedly larger in proportion to the body than in the other group; the invaginations for the compound eyes and antennae are therefore shorter, and it is possible, though we have not actually noted such a case, that the brain may sometimes be lodged within the larval head. It seems probable that Chironomus is less primitive than Tipula and some other Nemocera whose early stages are terrestrial. The species of Chironomus whose larvae dwell at the bottom of the water and make tubes appear to be less primitive than the surface-haunting species.

It must not be forgotten that of the many species of Chironomus only a minute proportion have had their life-history in any degree elucidated. Increased knowledge will no doubt greatly add to the list of adaptive modifications of the larval and pupal structures.

The pupal stage in insects generally.

The biological importance of the pupal stage is very unequal in different insects. Some undergo no transformation at all (Thysanura). In Orthoptera the so-called pupa is little more than a late larva with rudimentary wings. Where the larva is aquatic and the fly aerial, as in may-flies and dragon-flies, more conspicuous changes are effected during transformation, especially in the mode of respiration, but there is not of necessity a definite resting-stage. Where, as in Lepidoptera, Hymenoptera, and Diptera, the imago adopts a new mode of feeding, great and apparently sudden changes in the mouth-parts are set up, and the pupa ceases to feed, though it may still retain, as in Chironomus, a limited power of movement. In the Muscidae the divergence of the fly from the larva reaches its extreme. The body is reconstructed during the pupal stage, and the immobility of the pupa is rendered complete by its enclosure within the hard and dead larval skin. The gradations observed in existing insects with respect to the completeness of their transformation help us to understand that the elaborate metamorphosis of the Muscidae was attained by many steps. The stages by which holometabolous insects acquired their pupa are still extant, and those naturalists who consider such a series as this:—(1) Thysanura; (2) any locust; (3) any dragon-fly or may-fly; (4) Chironomus; (5) Muscidae—will probably admit that the transformation of insects does not agree either in motive or in its relation to the rest of the life-history with the *embryonic* transformation of most marine invertebrates. The transformation of an insect, like that of a frog, is an *adult* transformation [1].

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[1] Miall and Denny, 1886, pp. 196–203; Miall, *Nature*, Dec. 19, 1895; Address to Section D of Brit. Assoc., 1897; Boas, *Zool. Jahrb.*, Bd. xii, 385–402 (1899).

CHAPTER VI

THE EMBRYONIC DEVELOPMENT OF CHIRONOMUS

Egg-masses.

THE process of egg-laying has already been described (p. 9). In *C. dorsalis* the egg-mass is a transparent cylinder with rounded ends, about 2 cm. long, formed of a mucilage secreted by the gluten-gland, in which the

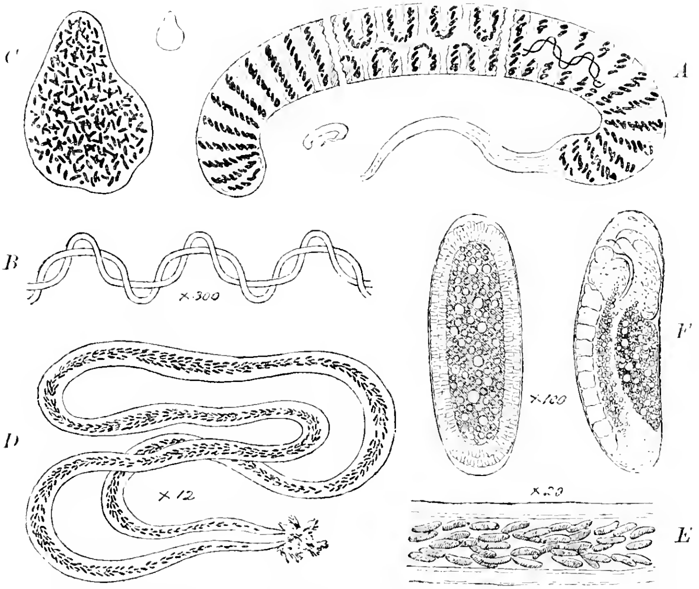

FIG. 116.—Egg-masses of Chironomus. *A*, egg rope of *C. dorsalis*, divided into sections, to show both sides. *B*, twisted fibres, which traverse the egg-rope. *C*, egg-mass of another species of Chironomus. *D*, egg-mass of a third species. *E*, part of the last, more highly magnified. *F*, developing eggs in two stages. (From Miall's *Natural History of Aquatic Insects*.)

brownish eggs are embedded. The eggs do not lie at random in the cylinder, but are lodged in a special winding tube or egg-pipe, which lies near the surface of the egg-mass, and makes many almost complete spires, curving round from right to left and from left to right alternately. The tube itself only becomes visible when the egg-mass is boiled or treated with hardening agents. The interior of the cylinder is traversed by interwoven cords, which are more fully described on p. 155. As many as nineteen spires have been counted on one egg-mass, and since each spire commonly contains about forty-five eggs, the total may amount to 850 or even more [1].

The various forms of egg-rope which characterize different species of Chironomus reach a climax of complication in *C. dorsalis*. In simpler cases the eggs may be enclosed in a globular or pear-shaped gelatinous mass, which is glued to a stone in the bed of a stream (fig. 116). Or the eggs may lie, almost at random, within a gelatinous pipe. Both a pipe, enclosing the eggs, and an outer gelatinous envelope may be present, and the pipe may be thrown into bends or spires which do not affect the outer covering. Lastly, a pair of interwoven cords may be added, which traverse the cylinder, on whose outer wall lie the spires of the egg-containing pipe. The egg-mass may contain three different kinds of gelatinous substance, one forming the pipe, a second the general investment, a third the interwoven cords. The two latter may be furnished by the gluten-gland, whose cavity when cut across shows sectors of what are probably two different secretions (fig. 84); the wall of the egg-pipe is perhaps secreted by the ovary or oviduct.

Since the larvae which issue from the eggs have to

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[1] In seven egg-chains the number of eggs was estimated at 668, 784, 817, 818, 828, 912, and 1102.

live in water, it is convenient that the egg-chains should be laid in water, and further that they should float at the surface, where they can be freely supplied with air, and run no risk of being smothered by silt or organic refuse. If the water were stagnant, the eggs might float free, as the egg-raft of the gnat does, but the eggs of *Chironomus dorsalis* are laid in slow streams, and must be secured, lest they should be swept away, and perhaps lodged in some unsuitable place, or even carried out to sea. The eggs of this species are therefore invested by a gelatinous envelope, which swells out, the moment it touches the water, into an abundant transparent mucilage, and the whole mass is moored to some fixed object by twisted cords. The mucilage has its special uses: it makes the egg-mass slippery, so that birds or insects cannot grasp it; moreover, it spaces the eggs, so that each is well exposed to the sunlight and air; lastly, it keeps off the attacks of the water-moulds (Chytrideae and allied Oomycetes), which abound in water and on the surface of decaying plants, or devour the substance of living insects and fishes. It may be that the mucilage of the egg-mass has some antiseptic property, for it remains unchanged by parasitic growth or putrefaction long after the eggs have hatched out.

During the summer months the egg-masses of *Chironomus dorsalis* are readily found. It is not indeed easy to detect them on the weedy bank of a stream, but the fly often lays them on the edge of a stone fountain, or in a watering trough by the side of a road. If an egg-mass is dipped into boiling water, the way in which it is moored becomes evident. An enclosed double cord, previously invisible, now becomes opaque enough to be examined by a lens (fig. 116, *B*). It passes through the cylinder in a series of loops, and then returns in as many reversed and intertwined loops, so as to give the appearance of a lock-stitch.

The cord is so tough that it can be stretched with a pair of needles without breaking. A steady pull at the ends of the cylinder will draw it out to nearly twice its original length without injury; if stretched beyond this point, the cord becomes strained, and does not perfectly recover its shape when released. The ends of the cord pass into an adhesive disk, which is attached at the surface of the water. Thus the whole mass, containing hundreds of eggs, is firmly moored, yet so moored that it floats without strain, and rises or falls with the level of the water. The eggs get all the sun and air which they require, and neither predatory insects, nor birds, nor water-moulds, nor rushing currents can injure them.

Facilities for study.

There are few animals which afford greater facilities than Chironomus for the study of embryonic development. The eggs are very plentiful, and can always be had during the summer months; they are so transparent as to admit of the use of fairly high powers of the microscope; and since they require no preparation for study as whole objects, they can be replaced in water after inspection, to continue their development. This diminishes the difficulty of ascertaining the order of the developmental changes, which is nevertheless considerable, even in Chironomus. The development is completed in six days or less, so that every part of the process can be observed without prolonged waiting. On the other hand, the small size of the eggs is a serious difficulty in the preparation of sections, and in some important respects the development is peculiar, and not typical of insects.

Writers on the development of Chironomus.

We have now three excellent accounts of the embryonic development of Chironomus. Weismann (1863) studied living or fresh embryos for his classical memoir. It was largely upon facts drawn from the development of Chironomus that he long afterwards based his theory of the Continuity of the Germ-plasm (1889). At the time of his first paper Weismann had not ascertained the destination of the 'polar globules' of Robin, and thought that they were subsequently cast out from the embryo, at least in part. After the appearance of Metschnikoff's account of the development of Miastor, and Balbiani's account of the development of Chironomus, Weismann adopted their view that the so-called polar globules are sexual germs. Balbiani (1885) contributed some new and interesting particulars, and traced the development of the reproductive organs from the so-called polar globules. Ritter (1890) was the first to apply the method of sections to the eggs of Chironomus. He gave the first satisfactory account of the origin of the layers of the alimentary canal, and furnished needful corrections as to the process of egg-laying.

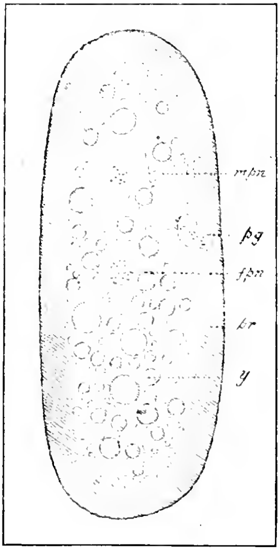

FIG. 117.—Egg just laid, in longitudinal section. *mpn*, male pronucleus. *fpn*, female ditto. *pg*, polar cells or globules. *pr*, external protoplasmic layer. *y*, yolk. (From Ritter, 1890, fig. 1.)

The egg.

The egg is of elongate-oval form, ·3 mm. (·012 in.) long, and ·1 mm. (·004 in.) broad. The anterior end, at which the head of the larva will appear, is rather blunter than the other, and one side is flattened. There is a transparent and structureless egg-shell, which is perforated at the anterior end by a minute micropyle for the entrance of the spermatozoa. Within the egg-shell is a vitelline membrane, hardly to be seen in an undeveloped egg, but becoming plain when the embryo shrinks, as it does in the course of development. Almost the whole space within the vitelline membrane is filled with a brownish yellow yolk, containing a multitude of fat-globules of various sizes (fig. 117). We can indistinctly make out a thin superficial layer of clear protoplasm, which becomes more evident in stained sections, where it is seen to send out many thread-like extensions into the yolk.

The ovarian egg of the pupa or imago is enclosed in a follicle of the egg-tube (fig. 83), which is lined, until the eggs are almost ready to be laid, by a scanty epithelium. The follicle in an early stage encloses a true egg-cell, whose nucleus is the germinal vesicle, and also several nutritive cells, which dwindle as the yolk increases (see p. 113).

The posterior end of the ovum is the first to pass into the oviduct, and it is probable that Hallez' law of orientation, viz. that the ends and faces of the ovum are placed similarly to the corresponding parts of the parent, obtains here as in all insects which have been investigated.

Methods.

In order to study the early embryonic stages to the best advantage, special preparation is necessary. The following method we have found to succeed:—The egg-chain is killed with hot 30% alcohol, half saturated with corrosive sublimate. It is then gradually transferred to absolute alcohol, and subsequently to chloroform and melted paraffin. Sections are cut by the microtome, and stained on the slide by Heidenhain's haematoxylin method. The observation of living embryos should not be omitted, and much may be learnt by those who are unable to prepare sections at all.

Fertilization and segmentation.

Before fertilization the egg-nucleus travels to the surface and divides. The two polar bodies thus formed are not ejected, but break up within the egg. After fertilization male and female pronuclei form in the usual way (fig. 117). Segmentation begins at the hinder pole about two hours after egg-laying. A few large nuclei appear in successive pairs at the surface of the egg, the protoplasm gathers round each, and forms constricted masses, which afterwards bud off, become free, and divide into four and eight (figs. 118, 119). After this the contained nuclei divide without separating, so that when we consider the subsequent history of the buds, we shall find that they consist of eight large cells, with four nuclei apiece. These cells have often been called *polar cells* or *polar globules*. In view of their ultimate destination, and to prevent confusion with the bodies broken up within the egg during maturation, we may call them the *sexual germs*[1]. The differentiation of sexual germs in this very early stage, before a blastoderm has been formed, is a phenomenon as yet observed only in Diptera In Distomum the germ-cells (ova ?), which give rise to the sporocysts and rediae, are set apart very early, at the end of cleavage (cf. Sagitta).

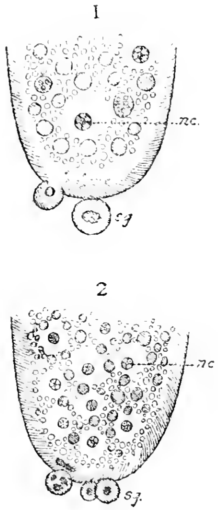

Fig. 118.—1, First formation of sexual germs (*sg*) and somatic nuclei (*nc*). 2, Later stage, both the sexual germs and the somatic nuclei having increased by division. (From Ritter, 1890, figs. 5, 6.)

Formation of blastoderm.

At the time when the sexual germs become defined, the yolk contains several scattered nuclei, which can sometimes be

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[1] The sexual germs in the egg of Chironomus were first observed by Robin (1862). Weismann (1863) observed that they subsequently became withdrawn into the yolk. Metschnikoff (1866) believed that in Cecidomyia he had observed the derivation of the reproductive organs from these germs. Balbiani (1885) traced the development of the germs into the testes and ovaries of Chironomus. Ritter (1890) demonstrated the validity of Balbiani's conclusions by means of thin sections.

seen to be connected by streaks or paths of clear protoplasm. These nuclei are the first indications of the somatic cells, from which the tissues of the body of the insect will be derived. They multiply with great rapidity, travel towards the surface of the egg, probably accompanied by protoplasm, and arrange themselves side by side in the peripheral protoplasmic layer, which bulges a little outwards over each nucleus, but is otherwise continuous and uniform; it is sharply separated from the yolk within (fig. 119). This layer is the *blastoderm*; it gives rise to the future body, and also to certain temporary structures connected with it. The nucleated blastoderm appears almost suddenly, and being transparent, curved, and refringent, it is a matter of great difficulty to study its formation at all closely. The nuclei are at first few and large, but rapidly increase in number and diminish in size. An inner, clear, protoplasmic blastema, deepest at the two poles, forms within the blastoderm; the investing cells extend into this, and absorb or appropriate it, thereby doubling the depth of the blastoderm; the nuclei at the same time become temporarily elongated in a direction perpendicular to the surface of the egg. The formation of a single cellular layer enclosing the yolk has often been cited as an example of

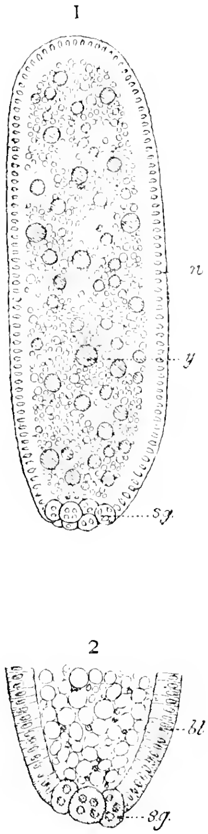

Fig. 119.—1, Longitudinal section of blastoderm. *n*, nuclei. *y*, yolk. *s.g*, sexual germs. 2, Hinder end of blastoderm, to illustrate the re-entry of the sexual germs. *bl*, blastoderm. *s.g*, sexual germs. (From Ritter, 1890, figs. 9, 10.)

the 'superficial cleavage' supposed to be characteristic of Arthropoda generally. The superficial cleavage of the insect-egg is however, as Carrière (1897) remarks, only apparent. The cells appear in the interior of the egg, and merely become superficial by migration.

Some of them, whose function is probably digestive, can be seen at a much later time in stained sections as small, branching, nucleated, protoplasmic masses scattered through the yolk. About twenty hours after egg-laying the sexual germs re-enter the egg (fig. 120), apparently forcing a passage in mass through the hinder end of the blastoderm.

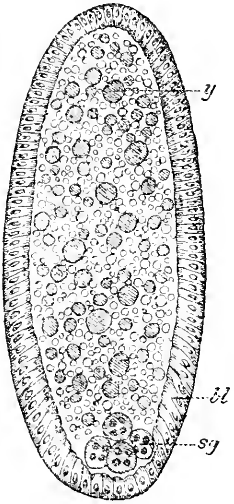

FIG. 120.—Longitudinal section of embryo. The sexual germs are now included, and the blastoderm is closed. *y*, yolk. *bl*, blastoderm. *sg*, sexual germs.

Ventral plate.

The cells of the blastoderm now divide rapidly along what will afterwards be the ventral surface of the embryo. There is thus formed a thickening, the *ventral plate* or *germ-band* (*Keimstreif*), which runs nearly round the egg lengthwise; it becomes unusually solid in the region of the future tail (fig. 122). As the ventral plate thickens, the cells on the dorsal surface thin out.

Ventral fold.

A longitudinal ventral infolding next appears, which deepens rapidly, and the median blastodermic cells are thereby pushed a little way into the yolk. The cavity of the fold is obliterated very early, and the infolded cells are cut off from the surface by the reunion beneath them of the outer layer.

The ventral groove is generally taken to be the cavity of a shallow and elongate gastraea; this identification only applies to the earlier stage, before the ectoderm reunites beneath the infolded cells.

Origin of inner germinal layers.

In most of the insects whose development has been carefully studied[1] the entoderm and the mesoderm are developed in the following way:—the infolded cells along the greater part of the length of the fold become mesoderm-cells, but at the oral and anal ends of the line median cell-masses form, which are the rudiments of the entoderm. These are pushed into the interior by the oral and anal invaginations (fore-gut and hind-gut). A pair of cellular strings then grow backwards from the anterior cell-mass, and a similar pair forwards from the posterior mass. The two pairs approach, meet on either side,

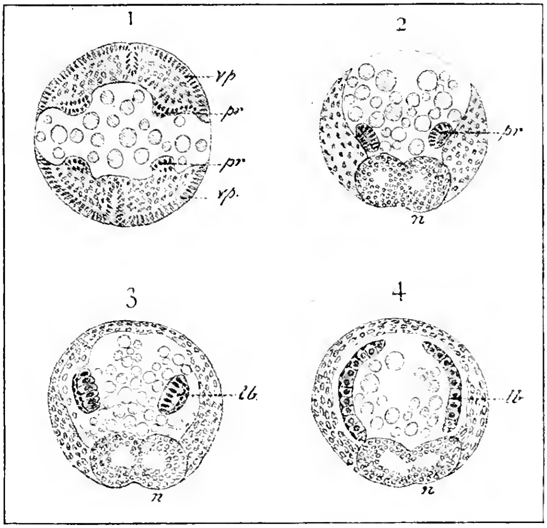

FIG. 121.—Transverse sections of embryo, showing successive stages of the developing mesenteron. *v.p*, ventral plate. *pr*, prominences from which the ento-mesoderm is derived. *lb*, lateral bands of ento-mesoderm. *n*, nerve-cord. (From Ritter, 1890, figs. 30-33.)

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[1] e. g. Musca (Kowalewsky), Apis (Grassi), Hydrophilus (Heider), Doryphora (Wheeler), and Chalicodoma (Carrière).

extend vertically until they are converted into sheets enclosing the yolk, and finally coalesce to form the mid-gut.

In Chironomus the formation of the entoderm, as first described by Ritter (1890), is somewhat different. The inward-projecting ridge, at first single and median, becomes paired by the formation of lateral thickenings, and then divided by constriction into segmentally arranged prominences, which are almost hemispherical, and bulge into the yolk. Secondary prominences (rudiments of the mid-gut) now form upon the hemispherical surfaces. These are at first segmental, distinct from one another, and paired, like the prominences from which they grow out; they consist of different kinds of cells on their inner and outer faces (i.e. on the faces which are turned towards and away from the middle line). The inner cells are relatively large, while the outer ones remain small. The secondary prominences project more and more into the yolk, fuse together on either side, and at length become detached as a pair of longitudinal bands, each consisting of an outer and an inner layer of cells (fig. 121). The inner layer, which comes next to the yolk, ultimately yields the mucous wall of the mid-gut, while the outer layer forms the muscular wall. The two bands are at first ventral to the chief mass of the yolk (fig. 121), but they soon extend until they meet and fuse above and below, thus completing the wall of the mid-gut, and enclosing the yolk.

Diversity of entoderm-formation.

It is not a little perplexing to the student that the entoderm should arise in a variety of ways in different animals. The variety of formation is illustrated by the fact familiar to every embryologist, that the yolk sometimes lies inside the entoderm and sometimes outside it. For instance, in the two primary divisions of Myriopods this difference seems to be regular and characteristic. In Chilopoda the mesenteron encloses the yolk; in Chilognatha it runs as a tube through the yolk[1]. In the less complex cases of animal development, which are usually chosen for elementary teaching, the entoderm arises by invagination of the blastoderm (Sagitta, Amphioxus, Echinoderms). Here there is little or no yolk. Where yolk becomes abundant we get the modifications known as epiboly, delamination, polar regression, &c. The continuity of the entoderm may be lost. Its cells may be gorged with yolk. Their nuclei may afterwards retreat outwards and form a new epithelium (Astacus, &c.) which encloses the yolk. Not only may the invagination for the entoderm disappear altogether, but when it is retained it may take the most unexpected forms. In Chironomus and other insects it is on general grounds likely that the tissue formed by infolding is really the entoderm, from which the mesoderm is afterwards differentiated. The details still require to be elucidated by practised embryologists.

Position of embryo at end of first day.

At this time (end of first day of hatching) the parts of the embryo are in the following position (fig. 122):—The body is curled up within the egg, lying in the median longitudinal plane, with its ventral surface close to the egg-shell, and the dorsal surface, which is largely open, in contact with the yolk. The head is thrown back and lies on the dorsal surface. The tail-end is at a short distance, and between the two is a thin sheet of extra-embryonic blastoderm. At this point the yolk projects between the head and tail, which are therefore distinctly marked out.

Envelopes

The edges of the ventral plate pass into the extra-embryonic blastoderm, which retains its original character of a single layer of cells. On the sides of the future body this tract will gradually be encroached upon by the extension of the ventral plate, which grows upwards on either side, and ultimately completes the body-wall; between the head and tail, temporarily in apposition, the

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[1] Metschnikoff, *Zeitsch. f. wiss. Zool.*, Bde. xxiv-v (1874-5).

extra-embryonic blastoderm gives rise to the envelopes of the embryo.

The tail-end, which is particularly thick in this stage, now bends inwards (i.e. towards the centre of the egg) and a little backwards (i.e. towards the hinder pole of the egg), pushing before it the sexual germs, which are, so to speak, caught in its concavity (fig. 122).

The extra-embryonic dorsal blastoderm now sends out a fold (tail-fold of the amnion) which grows backwards in close contact with the embryo as far as the hinder pole of the egg, and ultimately still further, bending round to the ventral surface. A little later a head-fold forms just behind the head from the same dorsal blastoderm, pushes forward, and then, curving round the anterior pole of the egg, grows backward along the ventral surface to meet the tail-fold. The two folds coalesce, and form a double embryonic membrane, which is singularly like the amnion of the higher vertebrates (fig. 123).

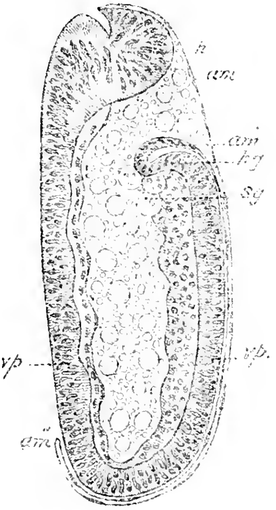

FIG. 122.—Longitudinal section of embryo during formation of tail-fold of amnion. *h*, head. *vp*, ventral plate. *am*, outer layer of amnion. *am'*, inner ditto. *am''*, termination of tail-fold upon future ventral surface. *hg*, hind-gut. *sg*, sexual germs. (From Ritter, 1890, fig. 19.)

The coalescence is not at first quite complete, for an oval space on the ventral wall remains for some time uncovered by the amniotic folds. The edges of the folds slowly extend until the whole embryo is enclosed.

The outer wall of the united folds is called, as in other animals, the *serosa*; it forms a complete investment to the embryo. The inner wall is called *amnion* or *true amnion*; it is continuous, except for a short distance

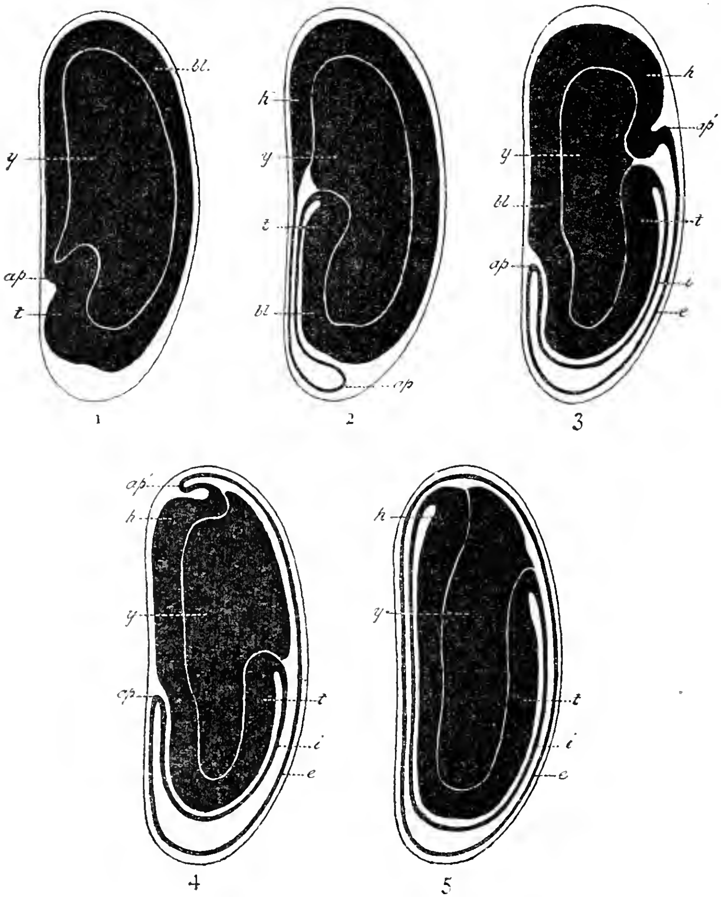

Fig. 123.—Diagrams to illustrate the formation of the amnion and serosa of Chironomus-embryo. 1, beginning of tail-fold on straight side of egg. 2, tail-fold reaches hinder pole. 3, (after rotation of embryo) head-fold appears on convex side. 4, head-fold growing over anterior pole. 5, coalescence of head- and tail-folds on ventral surface. *bl*, blastoderm. *y*, yolk. *t*, tail-fold. *h*, head-fold. *ap*, apex of tail-fold. *ap'*, apex of head-fold. *i*, inner embryonic membrane. *e*, outer ditto. (From Kupffer, *Arch. f. mikr. Anat.*, Bd. ii (1886).)

between the approximated ends of the body. Between the two a clear fluid can be detected with some difficulty.

The original motive, so to speak, of the amnion of insects can only be guessed at. It may be rudimentary (Muscidae), or wanting altogether (Poduridae, Cecidomyia, &c.), and its relation to the yolk varies greatly in different insects. One special use of the amniotic folds may be noted. In some insect-eggs (Chironomus, &c.) the embryo is long and peripherally coiled, so that the head and tail nearly meet; the intervening extra-embryonic blastoderm is naturally short. In a later stage the embryo straightens itself, so that the head gets to one end of the egg, and the tail to the other. This straightening is greatly facilitated by the extended folds of the blastoderm. Whatever circumstances may have led to the first development of an amnion, it seems to be now a protective structure, protecting the delicate body from friction. In a late stage the serosa of the Chironomus-egg has been found to be retracted into the dorsal surface of the embryo, and to be there incorporated with the yolk [1]. The amnion persists as a dead and shrivelled membrane, which can often be seen within an egg from which the larva has escaped [2].

Lateral tracts.

The ventral plate is from a rather early stage, when the amniotic folds are beginning to form, marked along the middle line of its free surface by a much more conspicuous and wider groove than that of the ventral fold already described. This runs along the body from the tail-end to the junction of the future head and thorax, where it ends by forking. The groove marks out a pair of thickenings, the *lateral tracts* (*Keimwülste*), which are prominent features of the embryo during the middle stages of its growth.

Rotation of embryo.

At the time when the lateral tracts appear the embryo

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[1] Graber, 1888, p. 34.

[2] Id. (loc. cit.).

rotates on its principal axis through an angle of 180°, and the parts corresponding to the future head and tail, which lay on the flat side of the egg, are shifted to the opposite, or convex side. The rotation is effected in about a quarter of an hour. The embryo of Simulium effects a similar rotation. In some Orthopterous eggs with copious yolk the embryo travels from the ventral to the dorsal surface, always returning to its original position before hatching[1]. The embryo of Chironomus, too, regains its original position by a second rotation.

Formation of segments and appendages

Early in the second day segmentation of the ventral plate sets in. The three jaw-segments are first defined (fig. 125). A little later the brain section of the head, in front of the jaw-segments, sends out a pair of lateral lobes, which almost touch in the middle line. The central unpaired lobe projects a little further forwards than the lateral lobes, and is a good deal smaller. From the central lobe will be developed the clypeus and labrum, while the lateral lobes will yield the epicranial plates; the rest of the body then rapidly segments from before backwards, until three thoracic and nine abdominal segments are developed[2].

Somewhat later, and after the formation of the rudiments of the nervous system, paired buds appear, first on the jaw-segments, and a little later on the first and last abdominal segments: these are the first signs of the appendages (fig. 125).

It seems that the full number of insect-segments is about twenty. Of these the first three are supposed to be indicated chiefly by the divisions of the brain; only one, the second, bears a pair of appendages, the antennae;

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[1] Wheeler, 1893, p. 68.

[2] The greatest number of abdominal segments clearly seen in any insect is eleven. Indications of a transitory premandibular segment have been detected in some insects, but not, so far as we know, in Chironomus.

the third is the premandibular segment, whose appendage, undeveloped in all insects of post-embryonic age, would apparently correspond to the second pair of antennae of Crustacea. The development of this region is peculiar, in that it proceeds from a central and two lateral masses. The central tract is believed to be relatively primitive; it becomes divisible into three, or, according to some authors, four successive lobes, each with its own ganglionic mass. The lateral tracts, which are outgrowths from the central one, yield the compound eyes, the antennae, and the ganglia specially associated with these organs. The antennae are at first placed on each side of the mouth, or even behind it: they grow forwards and soon become pre-oral. It has been thought that there was primitively a pair of simple eyes to each of the three median segments[1]. Behind these come the three or four jaw-segments, whose ganglia fuse to form the suboesophageal. Only the appendages of the jaw-segments are usually well developed; of the segments themselves doubtful remnants have been traced in the occipital or gular regions of the head. The brain-segments are therefore excessively developed dorsally and laterally, but incompletely ventrally; while the jaw-segments are incomplete dorsally, and only distinguishable by their ventral appendages. The three thoracic segments normally bear legs, and each encloses its own ganglion. The abdominal segments often bear appendages in some stage or other, but the morphological value of these appendages is not yet established. (See p. 33.)

Second rotation.

Towards the middle of the second day the embryo, which has for some hours been so placed in the egg that the head- and tail-ends of the ventral plate lay on the convex side, slowly rotates a second time through 180°.

Fore- and hind-gut.

In the course of the second day the fore- and hind-gut form. An invagination appears at the tail-end in the inturned extremity of the ventral plate. The proximal wall of the invagination is thick; the distal wall (nearer to the end of the body) is continuous with the extra-embryonic blastoderm. The fore-gut forms in the same

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[1] Patten, 'The Eyes of Acilius,' *Journal of Morphology*, vol. ii. 1888.

way by an infolding of ectoderm from the future mouth (fig. 126).

While the fore- and hind-gut are forming, the embryo has begun to shorten, and in a few hours the tail-end retreats to the hinder pole of the egg, while the body becomes almost straight (fig. 125).

Nerve-cord.

The details of the formation of the nerve-cord cannot be followed with advantage in Chironomus-eggs, which are small and hard to orientate. The main features of the development, so far as we have been able to observe them, agree with the beautiful results obtained by Wheeler in Xiphidium (1893).

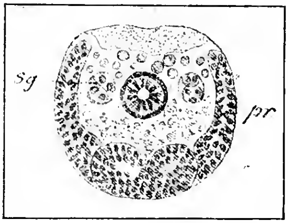

FIG. 124.—Transverse section of embryo, showing sexual germs (*sg*), proctodaeum or hind-gut (*pr*).

Large cells appear on the deep face of the ectoderm of the ventral plate. From these are derived by proliferation ganglion-cells which arrange themselves as columns of daughter-cells. Two lateral masses are thus formed, and we have seen indications of a middle element. The masses of nerve-cells grow rapidly, and are mainly responsible for the prominent lateral tracts already mentioned. There are at first as many ganglia as segments; they are large, extend throughout the segments, and are only interrupted by the intersegmental constrictions. Connectives and commissures form later. The neurilemma is an epithelium derived from the ectoderm. The original fifteen ganglia behind the brain are gradually reduced to twelve, the suboesophageal ganglion of the larva being a complex of three, and the last abdominal a complex of two. During development the anterior ganglia are always in advance of those further back.

The development of the brain is more complicated and more uncertain. Authors have recognized three or even four pairs of successive ganglia, which are taken to be the primitive elements of the brain. From the last brain-segment the oesophageal connectives are given off. From the second segment the antennae are innervated. The first segment constitutes the chief mass of the brain, including the optic ganglion[1].

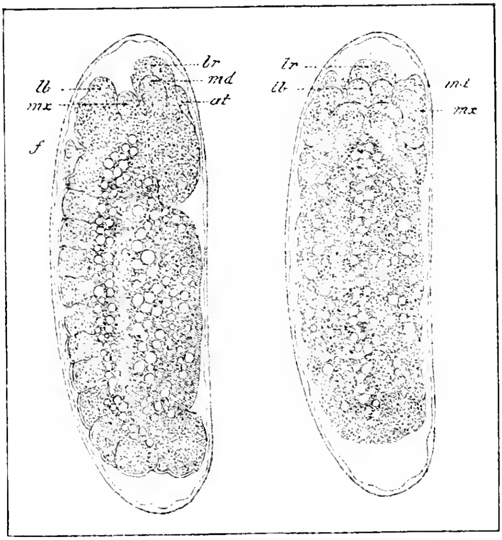

FIG. 125.—Living embryo within the egg, after shortening, in side and front (ventral) view. *lr*, labrum. *lb*, labium. *at*, antenna. *md*, mandible. *mx*, maxilla. *f*, prothoracic foot. Three thoracic and nine abdominal segments are seen in the side view.

According to Wheeler (1893) the peripheral nerves probably arise as outgrowths of the ganglia, while the stomato-gastric ganglia are developed from the ectoderm of the dorsal surface of the oesophagus.

Condition of embryo at end of second day.

At the end of the second day[2] the body is segmented,

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[1] Viallanes, 1890; Wheeler, 1893.

[2] The indications of date here and elsewhere are only approximate. On account of the very different rate of development at different seasons, and of the difficulty in procuring egg-chains immediately after they are laid, it is hard to make tolerably sure of even the order of events.

and already furnished with appendages. The jaws are three pairs of rounded prominences, and the antennae large, blunt outgrowths from the lateral lobes of the

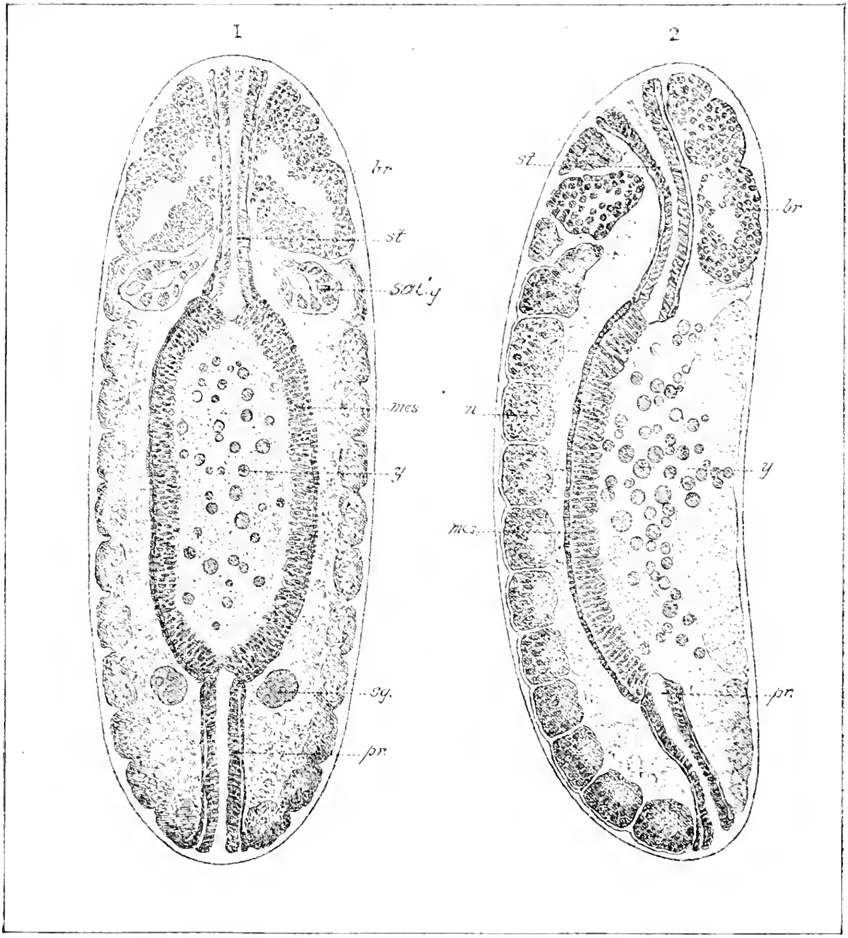

FIG. 120.—Sections of embryo before completion of mid-gut. 1, horizontal. 2, sagittal. *br*, brain. *st*, stomodaeum (fore-gut). *sal g*, salivary gland. *mes*, mesenteron (mid-gut) *n*, nerve-cord. *y*, yolk. *s.g*, sexual gland. *pr*, proctodaeum (hind-gut)

head (fig. 125). The prothoracic and anal feet are not yet visible. The head is externally complete, and bears a much larger proportion to the rest of the body than in the larva after hatching. The fore-gut and hind-gut are plainly visible, and about this time join the mid-gut, which is still very incomplete, not enclosing the yolk on the dorsal side (fig. 126). The fore-gut pushes into the mid-gut, which it indents and breaks through. Continuing to lengthen, the fore-gut protrudes for a certain distance, and is then reflected, meeting the wall of the mid-gut with a marked break in continuity, as fig. 126 shows. It is not true, as has been said by Weismann and others, that the wall of the cardia ('proventriculus') is derived from the fore-gut; it is altogether entodermic, as is evident from a careful examination in any stage. The future reproductive organs are represented by two cellular masses lying in the yolk within the hinder end of the abdomen, which is strongly bent inwards. The nervous system is a gangliated cord of relatively large size. The serosa completely invests the body.

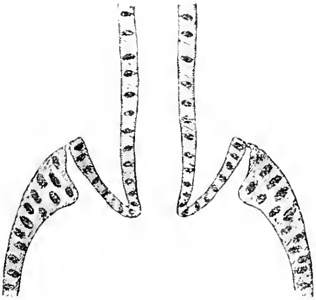

FIG. 127.—Diagram of development of oesophageal valve and cardiac chamber. × 300.

During the third day of development the jaws begin to assume their ultimate form and arrangement. The maxillae of the second pair unite to form a labium. The prothoracic limbs appear, and the first indications of the anal feet may sometimes be made out. The body has now contracted to such a degree that the anus lies at the posterior pole of the egg, the head being bent backwards on the dorsal surface, and resting upon a large mass of yolk. The ento-mesodermal rudiments are fast growing round the yolk, and the dorsal wall approaches com- Third day.

pletion, closing-in being facilitated by the shortening of the body.

The amnion tears across the ventral surface, and is retracted towards the middle of the back, where its remains continue for a time to be visible on the surface of the yolk.

Fourth day.

In the course of the fourth day all the parts rapidly advance. The wall of the mid-gut is completed. The envelopes of the reproductive bodies appear. The thoracic and abdominal limbs become quite plain. Eye-spots appear. The body enlarges in proportion to the head, and its dorsal wall is completed (fig. 128).

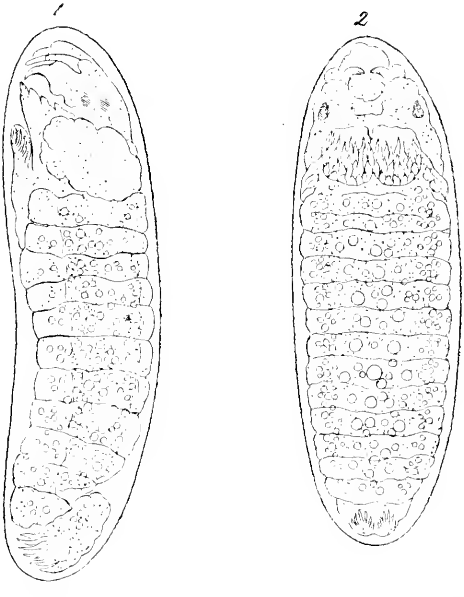

FIG. 128.—Late embryo in egg. 1, side view. 2, ventral view.

Tracheal system.

Chironomus is not well suited for the examination of the development of the tracheal system, which is quite rudimentary even in the fully formed larva of the tube-inhabiting species.

Body-cavity. Dorsal vessel. Our information respecting the development of the body-cavity and dorsal vessel is neither full nor altogether trustworthy. Very few of our sections illustrated the later stages of formation. The paired longitudinal thickenings on the inner face of the ventral plate, described on p. 163, become transversely segmented and hollow. The cavities soon unite on either side to form a coelom. Then the walls of the mesenteron become detached from the ridges, as described on p. 163. The ridges next begin slowly to grow upwards and to enclose both mesenteron and yolk. The narrow body-cavity extends of course at the same time. The outer layer yields the muscles of the body-wall, while much of the inner layer seems to break up, perhaps into wandering cells and blood-corpuscles. From the dorsal margin of the mesodermal layers are derived the halves of the dorsal vessel.

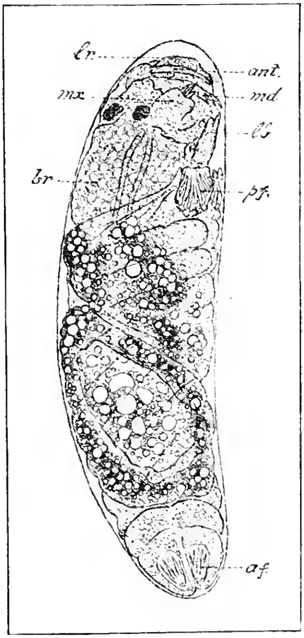

FIG. 129.—Larva coiled up within the egg, just before hatching. *lr*, labrum. *ant*, antenna. *md*, mandible. *mx*, maxilla. *lb*, labium. *br*, brain (within the head). *pf*, prothoracic foot. *a.f*, anal foot.

Fifth day. During the fifth day the head and jaws acquire very nearly their ultimate form. The salivary glands and ducts, which had a separate origin, now open into the mouth. The body is considerably longer than the egg, and somewhat coiled, as shown in fig. 128.

Sixth day. On the sixth day, the coiling increases, and the larva begins to move about. The chitinous cuticle becomes evident. The egg-shell is burst open, and the larva becomes free.

Fresh-hatched larva.

The fresh-hatched larva is half a millimeter long, and differs in various details from the larva of later stages. The blood has no red tinge; there are no ventral respiratory tubules; the head is relatively large, and as yet encloses the brain; the nervous system is proportionally large, and each ganglion seems to extend through the whole length of the enclosing segment, or nearly so; remnants of the yolk are still to be seen in the body-cavity, and within the alimentary canal. After the first moult, these peculiar features disappear, and the ordinary larval structure is attained.

APPENDIX

METHODS OF ANATOMICAL AND HISTOLOGICAL INVESTIGATION

(Additional remarks on methods will be found on pp. 7, 25, 69, 158.)

General instructions.

Much may be made out respecting the structure of the larva by simple examination of the living and uninjured animal under the microscope. A little dissection may also be done with the help of a dissecting microscope. This is particularly important for the purpose of getting true notions as to the relative situation of the organs. We have also made great use of comparatively thick but transparent sections made by the celloidin process. These are particularly serviceable in topographical anatomy. Lastly, continuous thin sections are indispensable for histological study.

Mr. Walker's methods of preparation for cutting.

The following directions incorporate the experience of Mr. Norman Walker, Demonstrator in Botany at the Yorkshire College, who has made many excellent series for us:—

'FIXING AND PRESERVING LARVAE.

'The two following fixing methods have been found to answer well.

'1. *Flemming's chromic-acetic-osmic acid.* Larvae are placed in this fluid for one hour. Each larva is halved and again placed in the mixture for another hour. They are then washed in running water for twenty-four hours.

This is best done by using a wide-mouthed bottle fitted with a cork bored with two holes. A straight glass inlet-tube is passed through one hole down to the bottom of the bottle. In the other is fitted a V-shaped outlet-tube, which is not allowed to descend quite through the cork. This allows a piece of copper gauze to be tacked over the outlet-aperture, to prevent the objects being swept out of the bottle. A current of water passing through the bottle keeps the larvae gently moving about in the water. Flemming's mixture, although an extremely faithful fixing agent, often renders staining by haematoxylin methods difficult, especially if the objects have not been thoroughly washed.

'2. *Perenyi's chromo-nitric acid.* Six hours are allowed in this fluid. At the end of three hours the larvae are cut in two. 70 per cent. alcohol is used for washing, and this should be continued for twenty-four hours. After fixing, the larvae may be preserved in 70 per cent. alcohol until required.

'STAINING AND PREPARING FOR CONTINUOUS SECTIONS.

'*Staining in bulk.* From distilled water the larvae are transferred to weak Delafield's haematoxylin solution. They remain in this fluid until stained a uniform blue. To determine this, the larvae must be occasionally examined with a pocket lens in distilled water. In about a week they will probably be sufficiently stained. The staining fluid is washed out by distilled water. After dehydration the larvae are cleared in clove oil. From absolute alcohol they are passed into a mixture of equal parts of clove oil and absolute alcohol for half an hour, and finally into pure oil for two or three hours.

'*Paraffin embedding.* From clove oil the larvae are transferred direct to the hard paraffin bath for six hours.

‘CUTTING IN CONTINUOUS SECTIONS.

‘In cutting insect-sections, where hard chitinous parts are encountered, it is often found difficult to keep a continuous ribbon. This may at times be due to the imperfect union of the hard paraffin and the coating of soft paraffin. This coating of soft paraffin, which has long been recommended, is very helpful in making obstinate sections stick together, when it is properly applied. Immediately before dipping the trimmed paraffin block into soft paraffin, the upper and lower sides[1] should be touched with a hot knife. By this means the soft paraffin is made to adhere firmly to the block, and is not liable to become detached during the cutting.

‘STAINING ON THE SLIDE.

‘The sections are cemented to the slide in serial order by Mayer's albumen. After melting and dissolving off the paraffin with turpentine, the sections are passed through the various strengths of alcohol into distilled water, and then into weak Delafield's haematoxylin solution. This stains very slowly, and by occasionally examining the sections under a microscope after washing in distilled water, a very precise result may be obtained. The weak Delafield's haematoxylin solution will keep in the dipping-bottle for a long time if a little camphor is added. For nuclear differentiation Heidenhain's haematoxylin will be found to give better results than the above method. From distilled water the sections are transferred to $\frac{1}{3}$ per cent. solution of haematoxylin in distilled water for about an hour, and then treated for the same length of time with $\frac{1}{2}$ per cent. solution of neutral chromate of potash. Wash in distilled water, dehydrate, clear in turpentine, and mount in balsam.

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[1] The block is supposed to project horizontally from the holder.

‘CELLOIDIN SECTIONS.

‘By the celloidin-embedding method very thick sections may be cut. Larvae fixed by the chromo-nitric acid method are stained in a borax-carmine solution for at least a week. After washing in acidulated alcohol and dehydrating, they are placed in a mixture of equal parts of absolute alcohol and ether for a few hours. A thick solution of celloidin in the same mixture should then be added, a few drops at a time, at intervals of a few hours, until the consistency of a thick syrup has been reached. The contents of the bottle are then poured into a paper tray, and the larvae arranged in the desired position by means of needles wet with the mixture of alcohol and ether. The tray is allowed to stand for about ten minutes, until the surface has set, and is then submerged in 80 per cent. alcohol for a day. The paper is now removed, and the celloidin mass cut up into blocks, which are carefully trimmed. These may be kept in 80 per cent. alcohol until required to be sectionized. To fix the celloidin block upon the object-holder of the microtome (or upon any wooden holder to be clamped in the microtome), pour a few drops of a celloidin solution upon the surface of the holder. Dip the celloidin block into a little ether in a watch-glass, and then press it firmly upon the holder. Allow it to stand for a few minutes, and then place it in 80 per cent. alcohol for a few hours. The sections should be made with a long slicing cut, the razor and the celloidin block being kept well wetted with spirit. The sections are arranged in serial order, close together, upon two or three slides, and the excess of 80 per cent. alcohol is removed with blotting-paper. To fix the sections to a slide, place in a covered dish (a Petrie's dish answers very well) with a little ether in the bottom. In a few seconds the celloidin in which the sections are embedded will soften and adhere to the slide. Before removing from the dish, add by means of a pipette a few drops of 95 per cent. alcohol, and then submerge the slide in spirit of the same strength in a dipping-bottle. Clear by transferring to a mixture of one part absolute phenol with four parts xylol. Entire larvae may be cut by this process if plenty of time is allowed for staining and embedding.'

MOUNTING OF ENTIRE LARVAE.

Mr. Wilkinson's method of mounting entire larvae.

Mr. J. J. Wilkinson, of Skipton, gives the following instructions for mounting aquatic larvae whole without pressure. Many of his preparations are extremely useful for anatomical study, as the internal organs can be examined microscopically *in situ.* For some reason which we can only guess at, the Chironomus-larvae hitherto put up are not quite so successful as others, but they have yielded good results. Perhaps the best proportion of alcohol and ether has not yet been exactly determined.

'Select transparent specimens, place them alive in clear water, and keep them without food for a day or two, so as to empty the alimentary canal. Have ready a number of small, wide-mouthed bottles, containing a suitable mixture of absolute alcohol and ether. If larvae are put into alcohol alone they shrink, as exosmose is greater than endosmose. In a mixture which contains too much ether the case is reversed, and the larvae will swell until they burst. From 15 to 20 per cent. of ether is suitable for most larvae, but those of Chironomus will not bear more than 10 per cent. When all is ready, put a larva into a watch-glass containing the mixture, and hold it in the desired position with two small sable brushes. As soon as it is set (that is, in from three to ten minutes, according to size), transfer it to one of the bottles containing the same mixture. Leave it for a few hours (or days, if more convenient) and then transfer to absolute alcohol unmixed. The ether must be got rid of before the next process; if any is left, a gas (ether vapour?) will appear in the tissues and spoil the preparation, causing it to appear black by transmitted light. From alcohol transfer to oil of cloves to clear, then mount in an excavated cell with balsam and benzine. New balsam should be used, or the mixture should be newly boiled, so as to diminish the risk of liberation of vapour.

'Certain delicate structures, such as the branchial filaments of the Sialis-larva, require special treatment. When the larva is immersed in the alcohol and ether mixture add about 10 per cent. of ether, and repeat this several times until the mixture is almost pure ether. Transfer quickly to a second bottle containing enough pure ether to cover the object entirely. To this add every day a few drops of balsam mixed with benzine, and leave the cork rather loose, so that the ether may slowly evaporate. When nothing remains but balsam and benzine, the preparation may be mounted. Only new balsam should be used.'

OTHER METHODS.

For the examination of the minute structure of the oesophageal valve sections were not found to be sufficient. Much useful information was got from fresh preparations treated with 2 per cent. caustic potash, and examined while the alkali was acting. Teased-out preparations, stained with haematoxylin or borax-carmine, and mounted in glycerine, were also very useful.

ADDITIONAL NOTE

ON THE SWARMING AND BUZZING OF HARLEQUIN-FLIES

(See pp. 9 and 99.)

Mr. T. H. Taylor furnishes the following observations on swarms of harlequin-flies, which were received too late for insertion in the proper place. The text has, however, been altered in accordance with the new information:—

'When a swarm of harlequin-flies is dancing some ten or fifteen feet from the ground, it is observed that at intervals a pair of flies leaves the rest, and descends. If the pair be captured, it will be generally found to consist of a male and a female. Occasionally it consists of two males. Sometimes there are three flies in a cluster; one captured triplet yielded two males and a female. After a mating pair has flown a short distance from the swarm, the union is broken; the male returns to its comrades, but the female flies away. The number of females in the swarm is probably never large; it seems to be affected by wind. In calm weather pairing is readily accomplished, and the females soon leave the swarm, but a high wind renders pairing difficult, and the females remain longer in the company of the males. On a calm evening a sweep of the net yielded 700 flies, all of which were males. On another evening, when the swarm was much disturbed by wind, 4,300 flies were captured, twenty-two of which were females.

'If the net with its captive flies be held to the ear. a distinct buzzing is heard. If a single fly be seized by the legs, so that the wings are free to vibrate, and held close to the ear, the note is plainly heard, and can easily be determined. The male fly yields the note a′ sharp (about 450 vibrations), the female b (about 240 vibrations). The pitch is not constant, but varies through three or four semitones. No evidence was obtained of any sound other than that due to the vibration of the wings.'

As different notations are quoted on pp. 97–9, it may be worth while to explain that Ut 3, Ut 4, and Ut 5 answer to c′, c″, and c‴.

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INDEX

Abdomen, of fly, 104; of pupa, 140.
Adult and embryonic transformation, 152.
Alary muscles of larva, 73.
Alimentary canal, of larva, 49; of insects, nomenclature of, 50; of fly, 106; changes in, 147.
Amnion of insects, 167.
Anopheles, 31, 84, 91.
Antennae, of larva, 27; of fly, 92; of pupa, 140; development of ditto, 172.
Aphis-larva, spiracles of, 109.
Auditory organ of fly, 94.

Balbiani, on salivary glands, 68; on embryonic development of Chironomus, 157.
Bibliography, 185.
Blastoderm, formation of, 159; of Chironomus, 160.
Blood of larva, 77.
Blood-gills, 83.
Blood-space of larva, 85.
Body-wall of larva, 85.
Branchial system of larva, 83.
Brauer's classification, 14.

Calliphora, 23, 75.
Cardia of larva, 52, 54.
Carrière on superficial cleavage of insect-egg, 161.
Ceratopogon, 34.
Chironomus, species of, 10; two groups of, 11, 146, 150; transformations of, 119.
Chironomus-eggs, 8, 153, 157; mucilage of, 155; facilities for study of, 156; methods of study of, 158; fertilization and segmentation of, 158.
Chironomus-fly, 9; extrication of, 8; in winter, 8; egg-laying of, 9; its head, 88; chitinous tunnels, 89; eyes, 91; antennae, 92; auditory organ, 94; sounds emitted by, 97; its mouth-parts, 99; thorax, 100; legs, 104; wings, 104; abdomen, 104; alimentary canal, 106; heart, 108; tracheal system, 108; reproductive organs, 109; female organs, 111; male organs, 116; development of, 118; of thorax of, 121; of thoracic appendages, 122; of head, 127; of reproductive organs, 135.
Chironomus-larva, its habitat, 1; tubes in mud, 1; food, 1; movements, 2; limbs, 2; labrum, 3; at great depths, 3; in salt water, 3; parasites of, 4; enemies of, 7; collecting of, 7; fresh-hatched, 10; varieties of, 10, 135, 150; external form, 25; examination of, 25; its segments, 26; appendages, 26, 32; thorax, 26; head, 26; antennae, 27, 49; eye-spots, 27, 48; jaws, 28; interior of head, 29; salivary ducts, 29, 70; lingua, 30; brain, 30; blood-gills, 35, 83; sensory setae, 35, 49; epidermis, 36; chitinous cuticle, 36; wandering cells, 40; insertion of muscles in, 42; its nervous system, 43; transverse nerves, 45; stomato-gastric nerves, 48; sense-organs, 48; alimentary canal, 49; oesophagus, 49, 53, 62; stomach, 49, 55; salivary glands, 50, 67; Malpighian tubules, 50, 70; mouth, 52; oesophageal valve, 53, 60; peritrophic membrane, 44, 58; cardia, 54; Vignon on histology of alimentary canal of, 60 (note); its dorsal vessel, 71; heart, 71; aorta, 71; alary muscles, 73; blood,

77; respiratory organs, 80; tracheal system, 80; branchial system, 83; body-wall, 85; fatty tissues, 85; peculiarities when fresh-hatched, 176.

Chironomus-pupa, 8; varieties of, 10, 150; development of, 118; characteristic organs of, 139; its legs, 140; wings, 140; abdomen, 140; antennae, 140; tail, 140; tracheal system, 141; tracheal gills, 141; changes in alimentary canal of, 147; diverticulum of ditto, 148.

Clinocera, larva of, 34.

Colon of larva, 67.

Corethra, 21, 31, 48, 75, 82, 84, 129, 146.

Culex, 31, 43, 82, 84, 96, 146.

Dareste on changes in dorsal vessel of larva and pupa, 79.

Decentralization in Diptera, 106.

Development, of pupa and fly, 118; embryonic, 156; methods of study of, 158.

Dicranota, 43, 55, 82, 84, 85, 146.

Diptera, sub-orders of, 19: larvae of, compared, 20; caeca of, 55; dorsal vessel of, 71; two types of dorsal vessel in, 75; Hammond on thorax of, 100 (note); formation of imaginal head in, 134; respiratory trumpets of, 146; decentralization in, 106.

Diverticulum of pupal oesophagus, 148.

Dixa, 82.

Dorsal vessel of larva, 71.

Ectadenes of Escherich, 135.

Eggs of Chironomus, 154.

Embryonic and adult transformation, 153; development, 156.

Enemies of larva, 7.

Ephemeridae, reproductive outlets of, 110; Carboniferous, 123; wing-like structures of, 123.

Ephydra, 83.

Eristalis, 84.

Escape of fly, 146.

Escherich on ectadenes and mesadenes, 135.

Eversion of head, 133.

Eyes of fly, 91; development of, 127.

Fatty tissues of lava, 85.

Female organs of fly, 111.

Gehuchten, oesophageal valve of Ptychoptera, 66.

Germs, sexual, 159.

Gordius, 4.

Graber on development of dorsal vessel of larva, 74.

Grimm on egg-laying by pupa, 117.

Haemoglobin, 77.

Hallez' law of orientation, 158.

Head of fly, eversion of, 133.

Heart, of larva, 71; of fly, 108.

Hemerodromia, larva of, 35 (note).

Hydrobius, 82.

Hymenoptera, salivary glands of, 70; formation of head of, 130 (note).

Imaginal folds, 119; of head, 127; rudiments in thorax, 121; head, formation of, 135.

Insects, nomenclature of alimentary canal of, 50; Malpighian tubules of, 50; oesophageal valve of, 54; peritrophic membrane of, 58; development of dorsal vessel of, 74; tracheal gills and blood-gills of, 83; tentorium of, 90; chitinous tunnels of, 91; rectal glands of, 107; thoracic spiracles of, 108; reproductive organs of, 109; larval stage of, 118; stripping of epithelium in, 147; pupal stage of, 151; development of entoderm and mesoderm of, 162; amnion of, 167; number of segments of, 168; development of brain of, 171.

Insect-transformation an adult transformation, 152.

Jaworowski, on dorsal vessel of larva, 73, 75; on development of ditto, 74.

Johnston on auditory organ of gnat, 96.

Kowalewsky on pericardial cells of larva, 74.

Landois, on transverse nerves, 47 (note); on sounds of insects, 97.

Lankester on haemoglobin, 78.

Larval moults of blow-fly, 132 (note).

Legs, of fly, 104; of pupa, 140.

Lyonet on Orthocladius, 14.

Male organs of fly, 116.
Malpighian tubules of larva, 70, 108; development of, 175.
Mayer on gnats, 97.
Meinert on two groups of Chironomus-larvae, 10.
Methods, of collecting, 7; of examining larvae, 25; of examining salivary glands, 69; of examining imaginal rudiments, 121; of examining eggs, 158; of fixing and preserving larvae, 177; of staining and preparing for continuous sections, 178; of cutting in continuous sections, 179; of staining on the slide, 179; of celloidin sections, 180; of mounting entire larvae, 181; of examining oesophageal valve, 182.
Mochlonyx, 31, 82, 84.
Moults of larva, 7, 132 (note).
Mouth-parts, of fly, 99; development of, in larva, 131.
Müller on sympathetic nervous system, 48 (note).
Muscidae, 119, 151; invaginations of, 132.

Nemocera, a sub-order of Diptera, 19; adaptive resemblances and differences in, 23; reduction of larval head in, 31; larval appendages of, 33; position of larval brain in, 43; tracheal system in larvae of, 81; blood-gills of, 84; tracheal gills of, 84; ocelli of, 91; respiratory trumpets of, 123; more and less primitive genera of, 131; pupal respiratory organs of, 146.
Nemoceran larvae, appendages of, 33; tracheal system of, 81; blood-gills of, 84; auditory organ of, 96.
Nervous system of Chironomus-larva, 43.

Oesophageal digestion, Plateau on, 53; valve of larva, 53.
Osten Sacken, on sub-orders of Diptera, 19; on Nemocera with similar larvae but unlike flies, 24.

Palmén, morphology of reproductive passages, 110 (note).
Parasites of larva, 4.
Patagia, 124.
Pericoma, 82, 85.
Peritrophic membrane of larva, 53, 58.
Phagocytes, 125.
Phalacrocera, 43, 49, 82, 84.
Phillips, Miss Dorothy, on oesophageal valve of larva, 60; on peritrophic membrane of larva, 60, 66.
Phytomyza, 31.
Plateau, on nomenclature of alimentary canal of insects, 50; on oesophageal digestion, 53.
Ptychoptera, 43, 55, 59, 75, 82, 83, 146.
Pupal organs, 139; skin, 143; stage of insects, 151.
Pupation, 138.

Recapitulation, 10.
Rectal papillae of fly, 107.
Reproductive organs, of fly, 109; development of, in larva, 135.
Respiration, organs of, 80.
Ritter on embryonic development of Chironomus, 157.
Rollett on haemoglobin in Chironomus-larva, 77.

Salivary glands of larva, 67.
Secretion of stomach of larva, 57, 60 (note).
Sense-organs, 48.
Sensory setae, 35, 49.
Sexual germs, 159.
Simulium, 35, 43, 59, 61, 82, 85, 146; peritrophic membrane of, 59; oesophageal valve of, 61.
Sounds emitted by fly, 97, 183.
Stomach of larva, 55.
Stomato-gastric nerves, 48.
Stratiomys, 22.
Swammerdam on transformation, 119
Swarms of Chironomus-flies, 9, 183.

Tail of pupa, 141.
Tanypus, 7, 33, 49, 76, 84, 85, 95, 135.
Taylor, on *Chironomus minutus*, 11; on *C. niveipennis*, 13; on Orthocladius, 14; on Clinocera, 34; on Hemerodromia, 35 (note); on swarms and buzzing, 183.
Tentorium, 90.
Thoracic appendages, development of, 121.
Thorax of fly, 100.
Tipula, 43.

Tracheal gill of pupa, 141; casting of, 144.
Tracheal gills, 83.
Transformation, of *Chironomus dorsalis*, 7, 119; of *C. minutus*, 12; of *C. niveipennis*, 13; of Orthocladius, 17; of insects, 151; embryonic and adult, 152.
Transverse nerves, 45.
Two groups of Chironomus-larvae and pupae, 11, 146, 150.

Ventral plate of embryo, 161.
Viallanes, *Recherches* of, 71.
Vignon on histology of alimentary canal, 60 (note).
Villot on hair-worms (Gordius), 4.

Walker on methods of fixing, staining, and cutting, 177.
Waterhouse on chitinous tunnels in heads of insects, 91.
Weismann, on insertion of larval muscles, 42; on Corethra, 49, 129; imaginal discs of, 120; on development of thoracic appendages, 124; on continuity of germ-plasm, 156; on embryonic development of Chironomus, 156.
Wielowiejski, on oenocytes, 40; on pericardial cells, 74.
Wilkinson on mounting entire larvae, 181.
Wings of fly, 104; of pupa, 140.

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