VIII. *The Development of the Head of the Imago of* Chironomus.

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(Plates XXVIII.–XXXI.)

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Contents.

I. Introduction.—*Sketch of the Life-History of* Chironomus.

It will be desirable to begin by describing very briefly the life-history of *Chironomus*. The larva abounds in ditches, water-butts, and dirty streams, feeding upon decaying vegetable matter. It makes burrows of particles of earth or leaves, which it weaves together with the very abundant secretion of its salivary glands. The confined situation in which it lives and the scanty supply of oxygen to be found at the bottom of deep pools probably explain the red colour of these larvæ, which is due to hæmoglobin contained in the blood. The larva often leaves its burrow, and swims through the water with a well-known looping movement. It sometimes rises to the surface, no doubt for respiratory purposes. It is careless about finding its way back to its burrow, and in a short time glues together enough fresh fragments to conceal its body. The red larva, twisting itself into figures of eight, suggested the name of *Chironomus*, which means *harlequin*.

The body of the larva (Pl. XXVIII. fig. 1) consists of a head and twelve segments. The prothorax carries a pair of appendages, armed with numerous hooks for grappling, which are particularly useful when the larva advances or retreats within its burrow. A pair of somewhat similar appendages is carried on the last segment of the body, together with two pairs of anal processes. The last segment but one bears two pairs of respiratory tubules. The head, which is small in proportion to the body, bears a pair of short antennæ, two pairs of eye-spots, a labrum, strong toothed mandibles, a pair of maxillæ, and a labium. The lower exposed surface of the labrum is furnished with a very elaborate set of teeth, hooks, and spines, some of which are probably concerned with guiding the filaments of silk which issue from the salivary glands.

As the time of pupation approaches, the thorax becomes swollen and its segments lose their distinctness. The wings and legs of the future fly may now be seen indistinctly through the larval skin (fig. 2).

The pupa (figs. 3 & 4) is distinguished from that of most other aquatic Diptera by the tufts of respiratory filaments which project from the prothorax. It lies half buried in the mud at the bottom of the water, with the thorax and respiratory filaments projecting; these are swayed and bent to and fro by the alternate flexion and extension of the abdomen. After two or three days the tracheal system, which was rudimentary in the larva, but is now greatly enlarged and extended, becomes filled with air, secreted from the water by the help of the respiratory tufts, and the pupa floats at the surface. Some of the air passes through the spiracles and inflates the pupal skin. At length the skin of the back splits, the fly extricates its limbs and appendages, pauses for a moment upon the floating pupa-case, as if to dry its wings, and then flies away.

The fly (figs. 5 & 6) is a common object on our window-panes, and would be called a gnat by most people. It can be easily distinguished from a gnat by its habit of raising the fore legs from the ground when at rest. It is entirely harmless, and the mouth-parts can neither pierce nor suck. Like many other Diptera, the flies of *Chironomus* associate in swarms, which are believed to consist entirely of males. The male fly has large plumose antennæ, with their dilated bases almost in contact. In the female fly the antennæ are smaller and simpler, and the bases are separated by an appreciable interval.

There are many species of *Chironomus*, and they are often hard to distinguish. Much of our work has been done upon a species which has been identified as *C. dorsalis*, Meig. (*C. venustus*, Zett.). For the identification of the species we are indebted to Mr. R. H. Meade, of Bradford. *C. nigroviridis*, which is probably the species investigated by Weismann, is regarded by Van der Wulp as merely a variety of *C. dorsalis*. Our species is also that mainly employed by Meinert in his researches *.

II. *The Imaginal Disks of Weismann.*

All biologists are acquainted with the remarkable discoveries of Weismann † on the development of the appendages of the fly of the Muscidæ. He originally maintained that the new appendages arose altogether independently of the larval cuticle and its generating epidermis (hypoderm), from structures which he called *imaginal disks*. These were described as internal ganglion-like masses of cells, each mass being enclosed within a special membrane.

A few years later Weismann added ‡ a description of a quite distinct mode of formation of the imaginal appendages in Diptera. In *Corethra*, as he then showed, the parts of the imaginal head are developed in close relation to the corresponding organs of the larva, and *Corethra* was accordingly set up by Weismann as the type of a mode of transformation distinguished from that of the Muscidæ "in the sharpest manner" (*am schärfsten*) by the absence of imaginal disks.

* 'De Eucephalo Myggelarver,' 1886.

† "Ueb. d. Entstehung d. vollendeten Insekts in der Larve u. Puppe," Abhandl. Senckenb. Ges. iv. 1862–3.

‡ "Die Metamorphose d. *Corethra plumicornis*," Zeitschr. f. wiss. Zool. Bd. xvi. 1866.

This clear division of Metabolic Insects into two groups, with names, typical examples, and definitions, was only possible when little was known of the subject. Dewitz * showed that the imaginal disks of the Muscidæ originate in deep invaginations of the epidermis, and differ rather in degree than in kind from the shallow invaginations of such insects as *Corethra*. They are, in fact, imaginal folds rather than imaginal disks, and it would be convenient so to describe them in future †. It is the purpose of this paper to describe a Dipterous type intermediate in certain respects between *Corethra* and *Musca*, and one which throws not a little light upon the origin of the extremely complex invaginations of the Muscidæ. Other types might be named which are less specialized even than *Corethra*. We have to get rid altogether of the hard-and-fast lines laid down by Weismann when the subject was being explored for the first time, and endeavour to see the origin and history of those complex imaginal folds which characterize the more specialized Diptera.

III. *Description of the Larval Head of* Chironomus.

We must first give a short description of the head and its appendages in the larva of *Chironomus*. The head (Pl. XXVIII. fig. 7) is relatively small and of oval figure, widest behind. The dorsal border of the occipital foramen projects backwards near the middle line, while the ventral border is cut away so as to allow of flexion upon the thorax. The middle of the dorsal surface of the head is occupied by a narrow plate—the clypeus, which tapers to a point behind, and extends to the bases of the antennæ in front. External to the clypeus are lateral tracts, which carry the eyes. There are two pairs of these eyes, which in *Chironomus* are apparently little more than pigment spots.

The labrum (fig. 8) is bent round to the ventral side of the head, so that its free border is directed backwards. This is armed with ten or more fine denticles. In the centre of the ventral surface of the labrum is a squarish space, x, surrounded by a thickened rim, and fringed by paired setæ and hooklets. The whole surface of the labrum is furnished with complicated organs of this kind, which are probably concerned with the operations of spinning.

The appendages of the larval head are the antennæ, the mandibles, the maxillæ, and the labium. The antennæ are short, and consist of about five joints, which diminish rapidly in size towards the tip. From the free end of the first joint proceeds a long seta. A little below the middle of the basal joint and on its inner side is a roundish space enclosed by a chitinous rim ‡. This is probably sensory, and may perhaps be a simple auditory organ. The details of the antennary joints vary according to the species examined.

* "Beitr. z. postembryonalen Gliedmassenbildung bei den Insecten," Zeitschr. f. wiss. Zool. Bd. xxx. (Suppl.), 1878.

† This is recognized in all recent works on the subject. See, for example, the very interesting discussion of imaginal disks in Graber's 'Insekten,' or Mr. Lowne's new book on the Blow-fly (part i. 1890). One clerical error in this last (footnote to page 77) requires to be noted here. The insect described by Weismann in the memoir quoted by Mr. Lowne was not *Chironomus* but *Corethra*.

‡ Described and figured by Meinert, 'De Eucephale Myggelarver,' p. 436, pl. iii. fig. 78.

The mandibles are long, pointed, and toothed. They do not, as is the case with most mandibulate insects, work in the same plane, but in planes at right angles to each other (fig. 9), and when closed their toothed extremities meet at the centre of the serrated plate described below as the submentum. The internal margin of each mandible is fringed with long setæ.

The maxillæ are stunted processes lying just behind the mandibles. The basal piece is of irregular shape, sometimes produced internally into a setose prominence; it bears a stunted palp, which is flexible and setose.

In the labium, which represents the second pair of maxillæ, all signs of the coalescence of paired organs have disappeared. A comb-like plate (*sm*, fig. 8) is conspicuous on the ventral surface of the head, its denticles being directed forwards, so as to suggest that they oppose the teeth of the mandibles. This comb-like plate one is at first sight inclined to regard as the true labium, and this is probably Weismann's interpretation *. But this plate is at least not the whole labium. On its dorsal surface, and wholly concealed by it, is a soft process (fig. 10) with free anterior margin. It is beset with minute chitinous plates and setæ, and with papillæ, some of which may perhaps be taste-organs. Above this, again, lies the lingua, and between the lingua and the last-mentioned soft process is the opening of the salivary duct. It would seem that in the course of development the labium, which was originally bifid †, becomes doubled upon itself. The basal joint encloses the rest of the organ, and its fore edge becomes denticulate. This basal joint, though usually named mentum, appears to correspond more closely with the submentum of orthopterous insects. The soft process referred to above may be the mentum. On each side of the submentum is a radiately striated plate or flap (*y*, fig. 8 & fig. 13).

The accompanying figures will explain many details which can hardly be made intelligible by the most lengthy verbal description.

IV. *Description of the Head of the Imago of* Chironomus.

The head of the fly (Pl. XXIX. fig. 14) exhibits large crescentic compound eyes, surrounding the bulbous basal joints of the antennæ, in front of which are the rostrum and mouth-organs.

The antennæ differ materially in the two sexes. In the male (Pl. XXVIII. fig. 11) each consists of twelve joints, the basal one being nearly spherical, and very large in comparison with those which succeed. The next ten joints are short, and at first sight appear to be cylindrical. These form, together with the elongate twelfth joint, the shaft of the antenna. On closer examination it is found that the shaft is really a split tube, with a double wall enclosing a central cavity (figs. 11 *a* & *b*). This striking peculiarity is a modification of the more usual cylindrical form of antenna, and is attained during pupal life by a doubling in of the wall of the organ upon itself throughout almost its whole length, as will be seen further on. The exposed surface bears the long sensory hairs, while

* "Entwicklung der Dipteren im Ei," Zeitschr. f. wiss. Zool. xiii. 1863, p. 131, Taf. ix. fig. 45.

† Weismann, *loc. cit.* figs. 41, 42, & 43.

the surface which adjoins the enclosed cavity is beset with very minute elevations of the cuticle. A similar structure occurs in more than one species of *Chironomus*, and is found, though less marked, in the female. The basal joints of the antennæ are closely approximated in the male.

The antennæ of the female (fig. 12) scarcely reach half the length of those of the male. They consist of seven joints only. The basal joint has the same shape as in the male, but is much smaller. Each of the next five joints is enlarged in the middle. The terminal joint is elongate, but much shorter, both absolutely and relatively, than that of the male. The sensory hairs upon the five intermediate joints are comparatively few and short, and the last joint only takes the form of a split tube. The basal joints are much more widely separated than in the male.

On the vertex, and between the posterior angles of the eye, are seen a pair of minute tegumentary processes (see also Pl. XXIX. fig. 14 *c*), probably of little, if any, functional significance. We find, however, that in the pupa they are connected with the brain by a single median nerve. It may be of interest in this connection to recall a statement of Dufour * that in *Tipula oleracea*, an insect belonging to a genus characterized by Meigen and Macquart as devoid of ocelli, he found at the posterior border of each compound eye a minute ocellary nerve terminated by a subglobular violet-coloured retina. He further found behind the insertion of each antenna a minute subhemispherical tegumentary prominence. Although failing to trace with certainty the connection between the nervous and tegumentary structures so described, he hazards the conjecture that they are really associated, and regards them as the functionless vestigiary representatives of the ocelli of other Dipterous genera.

The mouth-parts of the fly (fig. 14) are carried on a projecting process of the head (rostrum), and consist of a labrum, tongue (lingua or hypopharynx), a pair of maxillary palps, and a labium, subdivided into labellæ. All these parts are imperfectly developed, and almost or altogether functionless, except the maxillary palps.

The rostrum corresponds to the fulcrum, or basal joint of the proboscis, in the Blow-fly. Its upper surface is the part known as clypeus in Orthoptera and other insects. A transverse suture divides this from the paired epicranial plates, which carry the eyes and antennæ. The rostrum ends below in a remarkable vaulted prominence, furnished with sensory hairs—the epistome, to which the labrum is articulated.

The maxillary palps are four-jointed, the basal joint being short and the other three long. They retain in the imago the bent position in which they were developed within the larval head. The labellæ are devoid of pseudotracheæ.

At the base of the rostrum and on the dorsal surface are situated the superior orifices (*or*) of a pair of large irregular, chitinous cavities, which extend through the head (figs. 15 & 16), each opening by a second minute slit-like orifice on its lower membranous surface or gula. We are unable to give any explanation of these curious structures, but note the existence of similar tunnelled cavities in the head of certain Culicidæ, especially in *Anophiles maculipennis*.

* "Recherches anatomiques sur les Diptères," Mémoires présentés à l'Institut de France, tom. xi. 1851, p. 178.

V. *Imaginal Folds in the Head of the Larva of* Chironomus.

In larvæ about half an inch long the epidermis of the top of the head begins to be infolded along two nearly longitudinal lines (*lf*, fig. 17, Pl. XXIX), 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 (Pl. XXIX. figs. 19, 20, 21, & 22, and Pl. XXX. figs. 24 & 25) 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.

In larvæ 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 rendered possible by a transverse fold (*tf*, *tf'*, Pl. XXIX. fig. 17, Pl. XXX. fig. 24, &c.) 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, the longitudinal folds could not have extended 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 (Pl. XXIX. fig. 19, *tf*) and tapering behind (fig. 17, *tf'*). The enclosed space is very inconsiderable, and appears in section like a thin slit. The prothoracic prolongations of the longitudinal folds, which give rise to the compound eyes and antennæ of the fly, open into the floor of the transverse fold (fig. 19).

As the longitudinal folds gradually deepen, the growing antennæ of the fly, still enclosed within the pupal skin, grow with it. Their basal parts recede further and further into the thorax, remaining all the time attached to the wall of the longitudinal invaginations already formed (figs. 21 & 22). 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 * 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.

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 (Pl. XXIX. figs. 21 & 22). We have found it possible to determine with certainty the sex of living larvæ 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 larvæ 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.* facing the middle line) rather than posterior (Pl. XXX. fig. 25). In this stage it may be distinguished from that of the female by its larger size, and by its extending backward up to, and even a little beyond, the hindermost extremity of the compound eye, which it never does in the female.

In the compound eye of *Chironomus* before pupation the epidermic cells of the so-called vitreous layer are often much elongated and resemble fibres. They retain their power of forming cuticle to a late stage, ultimately producing lenses which are not biconvex, but hollow, convex externally and concave internally. The retinal cells are pigmented and form retinulæ of seven cells each. No crystalline cones are formed, and the eye of the fly is therefore *aconic*.

Simultaneously with the formation of the compound eyes and the imaginal antennæ, 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 (fig. 26). 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 † of the fly. In larvæ ready to change into pupæ the tips of the labellæ 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 maxilla and the

* We do not at present distinguish between the imaginal and the pupal antenna.

† See Meinert, 'Fluernes Munddele,' 1881, or Dimmock, 'Anat. of Mouth-parts of Diptera,' 1881. In Orthopterous insects what is apparently the same part is named *paraglossa*.

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 (fig. 27). 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.

The history of the invaginations which give rise to the head of the fly can be followed in a series of larvæ of different ages. They are not to be discovered even in a rudimentary state until after the last larval moult *. Weismann † 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 ante-pupal 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 Muscidæ 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 §.

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 larvæ 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. Fig. 23, Pl. XXIX., represents a moderately early stage. Here the invaginations are restricted to the larval head, and form comparatively simple paired folds of the dorsal epidermis. Behind and on the ventral side is a short extension (*lf''*), 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.

The prolongation of the cephalic invaginations into the thorax gradually advances as

* 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.

† "Metamorph. der *Corethra*," loc. cit. p. 115.

‡ Lowne on the Blow-fly, new edition, pp. 2, 41 (fig. 7).

§ 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 suspects that as many as four moults may take place (Entw. der Dipteren, p. 104).

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 (fig. 19). Later on, the facets extend round the much bent floor of the cavity, and reach to a certain height upon the inner wall (Pl. XXX. figs. 24, 25, & 28). This change appears to be due to a modification of the shape of the invagination rather than to a development of new facets, for in late stages there is a marked change of shape in transverse sections of the invaginations (compare Pl. XXIX. figs. 18, 19, & 20, with Pl. XXX. fig. 28, and Pl. XXXI. figs. 31 & 32). The antenna also undergoes, especially in the male, a considerable change of form. At first the bulb is posterior (Pl. XXIX. fig. 22) 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 (Pl. XXX. fig. 25).

VI. *The Process of Pupation in* Chironomus.

Larvæ about to undergo pupation can be easily distinguished by the thickened thorax. If a number of such larvæ 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 anal papillæ, the respiratory tubules, 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 prothorax of the pupa protrude from the dorsal surface, between the larval head and prothorax. The larval head, which has been suddenly emptied by the retraction of its contents, then slips round to the ventral surface. The exact 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 prothoracic and anal regions sets up a blood-pressure, which is the immediate agent in the protrusion of the 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.

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, not by any gradual widening of the fold, but by a steady extension of the convex surface at the expense of the concave fold (Pl. XXXI. fig. 33). The process is hard to describe, but may be closely imitated by cutting a hollow india-rubber ball into halves, and everting one of the hemispheres with the fingers. During the process of eversion the compound eyes are drawn downwards and backwards, so that they get behind and beneath the bases of the antennæ (Pl. XXX. fig. 29). The morphologically external surface of the eyes, which was previously turned towards the lumen of the invagination, now looks outwards (Pl. XXXI. fig. 33); the optic nerve, which was distributed to the (temporarily) convex and outer surface of the eye, still takes its course to the same surface, now become concave and internal; and the walls of the head now for the first time enclose the brain. The inner walls of the paired invaginations, which were very long and enclosed a narrow median space or sinus (s', Pl. XXIX. figs. 18–22), contract more and more, and give rise to the central parts of the head of the fly.

Sections taken through the pupal antenna indicate the change resulting in the formation of the split in that organ to which reference has been made (page 268). The portion of the wall destined to form the hollow of the shaft projects in a marked manner, and is much more delicate than the remaining portion (see Pl. XXX. fig. 30).

The muscles of the larval head, as well as of some other parts of the body which become completely transformed, disappear by a process which leaves behind a number of more or less empty sheaths. This process reminds us strongly of the histiolysis which takes place in Muscidæ, as well as in many other animals. We have not, however, in spite of many efforts, arrived at such proofs of histiolysis as can readily be obtained in Muscidæ. We have never, for example, seen unmistakable sarcolytes within the supposed phagocytes, and cannot therefore appeal to any of our preparations as furnishing a demonstration of the process of histiolysis in *Chironomus*, which is on general grounds highly probable.

VII. *Comparison of* Chironomus *with some other Insects.*

In the larva of *Culex*, as we find from Dr. C. H. Hurst's partly unpublished descriptions and preparations, there are no deep invaginations for the compound eyes or antennæ of the imago. The compound eye forms beneath the larval eye-spots, and is at first relatively simple and of few facets. The number increases by the gradual formation of partial and marginal invaginations, each of which forms a new element. The imaginal antenna grows to a much greater length than that of the larval antenna, and its base is accordingly telescoped into the head while the shaft becomes irregularly folded*. *Culex*, though more modified than *Chironomus* in many respects, *e. g.* in the mouth-parts, is relatively primitive with respect to the formation of the imaginal head, and shows a mode of development of the eye and antenna which we may suppose to have characterized a remote and comparatively unspecialized progenitor of *Chironomus*.

* "The Pupal Stage of *Culex*" (Studies from Biol. Lab. Owens Coll. vol. ii. 1890). See also Manch. Micr. Soc. 1890.

In *Corethra*, as Weismann has shown, the compound eye develops in immediate proximity to the larval eye, but the imaginal antenna forms by an invagination, reaching far back into the larval head.

In order of complexity of the invaginations which give rise to the head of the imago we should arrange the Dipterous types already mentioned as follows:—

1. *Culex*. Relatively simple. Invaginations shallow.
2. *Corethra, Simulium*. } Intermediate.
3. *Chironomus, Ceratopogon*. }
4. *Muscidæ*. Relatively complex. Invaginations deep, and apparently, but not really, unconnected with the epidermis.

The development of the head of the fly of *Chironomus* appears therefore to furnish a useful middle term between the *Adiscota* and the *Discota* of Weismann: that is, between the types in which the parts of the head of the fly are developed in close relation to those of the larva, and the types in which deep invaginations lead apparently to the formation of similar new parts far within the body, the seeming independence of the new parts being intensified by thorough-going histiolysis. Other Dipterous types intermediate between *Corethra* and *Chironomus*, or even simpler than *Corethra*, yet require description, and possibly types may be discovered intermediate between *Chironomus* and *Muscidæ*. It will also appear, when the subject is fully gone into, that insects of other orders, *e. g.* Lepidoptera, present good examples of the origin of imaginal organs by foldings-in of the larval epidermis *.

Mr. Poulton † has pointed out that it is entirely erroneous to speak and think of the various parts of the Lepidopterous pupa as mere cases for the corresponding parts of the imago. "If we examine a section of a pupal antenna or leg (in Lepidoptera) we shall find that there is no trace of the corresponding imaginal organ until shortly before the emergence of the imago. In the numerous species with a long pupal period the formation of imaginal appendages within those of the pupa is deferred until very late, and then takes place rapidly in the lapse of a few weeks. This also strengthens the conclusion that such pupal appendages are not mere cases for the parts of the imago, inasmuch as these latter are only contained within them for a very small proportion of the whole pupal period."

It would appear from this passage and from what we have seen of the development of the imago of *Chironomus* that there is a strong superficial contrast, as to the formation of the imaginal organs, between Lepidoptera and Tipularian Diptera. *Chironomus* and *Corethra* exhibit an early and protracted metamorphosis, which extends through the last larval stage, as well as the relatively short pupal stage. Before the larval skin is shed the compound eyes, the antennæ, the wings, the legs, and reproductive organs, both external and internal, are far advanced, and though not complete in all points (the corneal facets,

* J. Dewitz has shortly described (Biol. Centralblatt, Bd. iii. 1883–84) the formation of theimaginal antenna of *Pieris Brassicæ* by a process essentially the same as that described in *Chironomus*, though far simpler.

† "External Morphology of the Lepidopterous Pupa," Trans. Linn. Soc., 2nd ser. Zool. vol. v. p. 188 (1890).

for example, are not yet formed) they are substantially those of the imago, the muscles and other internal tissues being already differentiated, and in some cases highly specialized. With the exception of the prothoracic respiratory appendages and the tail-fin, there is little in the pupa of *Chironomus* which does not relate to the next stage.

The ancestral history of the pupa is so completely disguised by adaptive peculiarities, that in this insect it is reduced to little more than a transitional form, effecting the difficult passage from a wholly aquatic to a wholly aerial mode of existence. At the same time there is no reason to doubt the morphological equivalence of the Tipularian and other insect pupæ. All of them represent a stage comprised between two moults, which has become subordinated in various degrees to the succeeding imaginal stage. Their morphological correspondence is as well marked and as interesting as their adaptive differences.

VIII. *Conclusion.*

The most striking feature of the development of the fly of *Chironomus* is the formation of paired invaginations extending far into the thorax, and giving rise to a great part of the imaginal head. *Chironomus* furnishes, not the most complex, but the most intelligible case of equally extensive invaginations hitherto described. When we inquire, as we cannot help doing, why such invaginations exist at all, 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 12 (male fly) to 11 (larva); the breadths as 5 (male fly) to 3 (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.

We should be glad to be in a position to show in what way and to what extent the invaginations of *Chironomus* lead up to those of the Muscidæ. But this is at present hardly feasible. We look forward to a time when a well connected series of thoroughly investigated Dipterous types can be arranged so as to lead up to and explain the formation of the fly in the Muscidæ, and the hope of contributing to such a result has been a principal motive of the present study.

EXPLANATION OF THE PLATES.

PLATE XXVIII.

Fig. 1. Half-grown larva. The numerals indicate the numbers of the body-segments. *p.app*, prothoracic, and *a.app*, anal appendages; *r.t*, respiratory tubules; *a.p*, anal processes. × 10.

Fig. 2. Full-grown larva. Letters and numerals as before. *r.f*, respiratory filaments of the pupa; *l*, leg of fly; *w*, wing. All seen through the transparent cuticle. × 10.

Fig. 3. Male pupa, front view. *r.f*, respiratory filaments. × 10.

Fig. 4. Ditto, in profile. *ant'*, antenna; *v.p*, processes on vertex. × 10.

Fig. 5. Male fly. × 10.

Fig. 6. Female fly. × 10.

Fig. 7. Head of larva. *cly*, clypeus, the diverging margins of which are strongly marked, inasmuch as they indicate the course of the longitudinal invaginations or folds which lie beneath them; *lr*, labrum; *ant*, antenna; *md*, mandible; *o*, eye-spots. × 70.

Fig. 8. Ventral surface of ditto. *mx.p*, maxillary palp; *x*, square marking on ventral surface of labrum; *sm*, submentum; *y*, striated flap flanking the submentum. × 70.

Fig. 9. Front or anterior view of ditto, showing the position of the mandibles at right angles to each other; letters as before. × 90.

Fig. 10. The mentum. × 300.

Fig. 11. Antenna of male fly: × 30. 11 *a*. Portion of the shaft: × 150. 11 *b*. Diagrammatic section of the same: × 150.

Fig. 12. Antenna of female fly. × 30.

Fig. 13. One of the striated plates flanking the submentum. × 300. (For convenience of arrangement this has been placed in a vertical position.)

PLATE XXIX.

Fig. 14. Head of the male fly. The antennæ are removed with the exception of the bulbous basal joints *b*, in the centre of each of which is a hollow with radiate markings whence the shaft has been taken out. *v.p*, processes on the vertex; *s*, transverse suture; *or*, orifice of chitinous cephalic cavity; *e*, epistome; *lr*, labrum; *l*, labella; *mx.p*, maxillary palp. × 60. 14 *a*. Extremity of labrum: × 300. 14 *b*. Extremity of lingua: × 300. 14 *c*. One of the processes on the vertex: × 300.

Fig. 15. Section showing one of the chitinous cephalic cavities, *c.c*. *e*, epistome; *l*, labella; *b*, bulb of antenna. × 100.

Fig. 16. Dissection showing the cephalic cavities, *c.c*, in front view, attached behind the epistome. × 90.
16 *a*. Posterior extremity of one of the cavities showing the slit-like opening. × 90.

Fig. 17. Diagram showing the newly forming epidermis within the head and thorax of a larva in the last period of larval life, as it would be revealed by the removal of the cuticle which is still indicated in outline at *l.c*. Below the orifice, *t.f*, of the transverse fold, the external epidermis of the prothorax has been further removed, revealing the upper wall, *t.f'*, of the fold (compare *t.f'*, figs. 19, 20, 24, & 25), the cut margin of the removed epidermis being indicated by the jagged line *m*; the nerve-centres and the œsophagus are also seen. *l.c*, larval cuticle; *ant*, larval antenna; *a.n*, nerve of the antenna, around which the imaginal antenna is in course of formation; *l.f*, longitudinal folds; *ep*, surface of the exposed epidermis; *t.f*, orifice or cavity of transverse fold; *t.f'*, its upper wall exposed; *m*, cut margin of epidermis; *o*, extremities of the longitudinal folds seen beneath the

transverse fold and showing the optic elements in course of formation; *o.n*, optic nerve distributed to the convex surface of the eye, which surface afterwards becomes the concave inner surface; *a.n'*, root of antennary nerve; *br*, brain; *œs*, œsophagus; *d.v*, dorsal vessel. × 50. The letters *sec, sec', sec''*, indicate the levels of the transverse sections shown in figures 18, 19, and 20 respectively. The lettering used in this figure will be repeated in those following.

Fig. 18. Early condition of the invaginations. Transverse section at the junction of the head and thorax (*sec*, fig. 17). The longitudinal folds, *l.f*, only, are cut through. *ant'*, first trace of the imaginal antenna. × 50.

Fig. 19. Early condition of the invaginations. Transverse section through the broad part of the transverse fold (*sec'*, fig. 17). The cavity, *t.f*, of the fold appears as a thin crescentic slit, and the prolongations of the longitudinal folds are seen opening into its floor. The eyes, *o*, are seen on the outer walls of the longitudinal folds. *s'*, median space or sinus. × 50. The great thickness of the larval cuticle is partly due to the oblique passage of the section through it caused by the convergence of the body-walls toward the head.

Fig. 20. Early condition of the invaginations. Transverse section through the narrow posterior part of the transverse fold (*sec''* fig. 17). × 50.

Fig. 21. Horizontal section through the head and thorax of a female larva, showing the formation of the eyes and antenna within the longitudinal folds. The bulb of each antenna, *bb*, is seen in two parts projecting into the cavity of the lateral fold from its inner wall. The parts lightly shaded in this drawing and marked *s, s', s* represent body-cavity of the insect, the invaginations being left white. The central one, *s'*, is the median sinus referred to on p. 274; it contains muscles connected with the labrum and the œsophagus, into it also project the frontal ganglion and the termination of the dorsal vessel. The lateral ones contain the great muscles of the mandibles, &c. The remaining letters as before. × 50.

Fig. 22. Horizontal section through the head and thorax of a male larva. Condition tolerably advanced but not ready for pupation. The antennary bulbs are as yet posterior (p. 271). × 50.

Fig. 23. Earliest observed condition of the invaginations. Internal view as exposed by a median vertical section. Only the longitudinal fold, *l.f'*, is as yet present, the short extension of which, *l.f''*, is referred to on p. 272. × 50.

PLATE XXX.

Fig. 24. Female larva. Diagram showing the newly forming parts in a somewhat advanced condition as laid open by a median vertical section. The inner wall, *l.f'*, of the longitudinal fold is seen, and in its backward prolongation beneath the transverse fold, *t.f*, a large orifice is represented as having been made exposing its cavity, *l.f*, and the passage through it of the newly forming antenna, the further course of which can be traced beneath the wall of the fold. The pigmented facets of the eye are indicated on both the inner and outer wall of the fold, more especially on the latter, which is seen through the opening. *ant'*, imaginal antenna; *b*, its bulb; *f.g*, frontal ganglion; *d.v'*, dilated extremity of dorsal vessel; *s.g*, subœsophageal ganglion. The other letters as before. × 70. Note that the faceted inner wall of the longitudinal fold is continuous with the antennary bulb.

Fig. 25. Male larva. Same view as in the preceding figure. The bulb of the antenna is much larger and projects towards the eye and towards the middle line of the head from the surface of the longitudinal fold, instead of being sunk within it as in the female. The course of the shaft has become arched upwards as described on p. 273. × 70.

Fig. 26. Labial fold or invagination. × 70.

Fig. 27. Maxillary ditto. × 70.

Fig. 28. Transverse section through the prothorax of a male larva in an advanced condition, passing through the eyes and in front of the antennary bulbs. The longitudinal folds, *l.f*, have lost their original form as illustrated in figs. 18–20, and have become more complicated. Lettering as on fig. 17, &c., with the following additions:—*s'*, central blood-sinus; *p.s*, pupa-skin surrounding the shaft of the antenna, but separated therefrom by a considerable interspace; *s.d*, salivary ducts. × 90.

Fig. 29. Horizontal section through the eyes and antennary bulbs in a larva about to pupate, illustrating a stage in the process of eversion as described on p. 274. The small folds, *l.f*, represent the originally deep longitudinal invaginations. The eyes are drawn back behind the antennary bulbs within, which certain newly forming nervous structures are now conspicuous. *l.c*, larval cuticle of the prothorax. × 120.

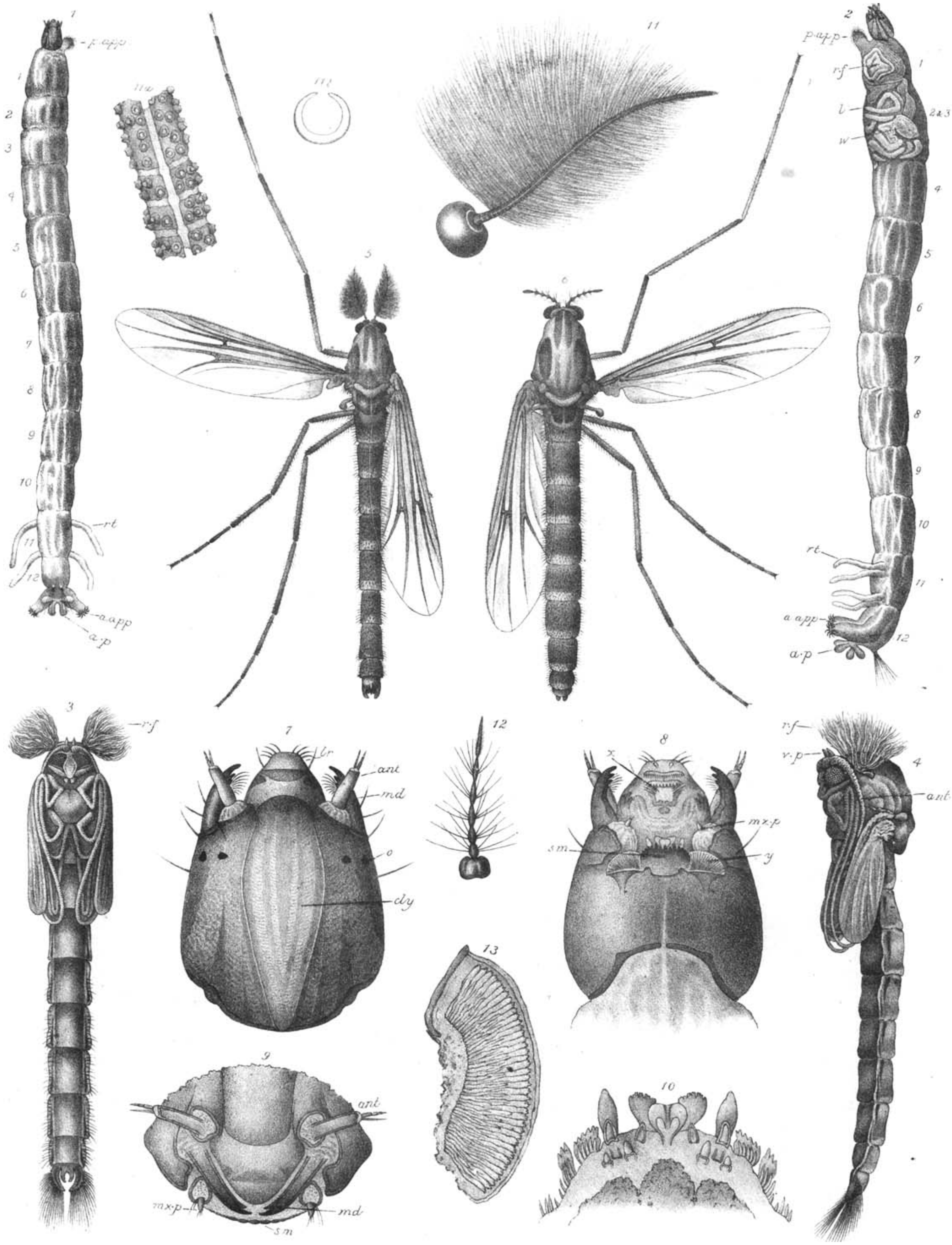
Fig. 30. Transverse section of the male pupal antenna showing the imaginal antenna surrounded by the pupa-skin. The part marked *x* is that which becomes invaginated to form the slit. *h*, sensory hairs. × 120.

PLATE XXXI.

Fig. 31. Transverse section through the prothorax of a male larva in an advanced condition, passing through the antennary bulbs and the ascending curvature of the shaft. The antennary nerve, *a.n*, of the larva is seen passing through the bulb and into the shaft, but there is reason to think that it subsequently to a great extent disappears and is replaced by new nervous structures within the bulb. *r.f*, respiratory filaments of the pupa. Other letters as before. × 90. This figure should follow fig. 28 in proper sequence, but it has been separated for convenience of arrangement.

Fig. 32. Transverse section through the posterior portions of the bulbs. Lettering as before: *v.p* are probably the minute processes on the head of the pupa seen in figs. 3 & 4, covering those of the fly alluded to on p. 269. × 90.

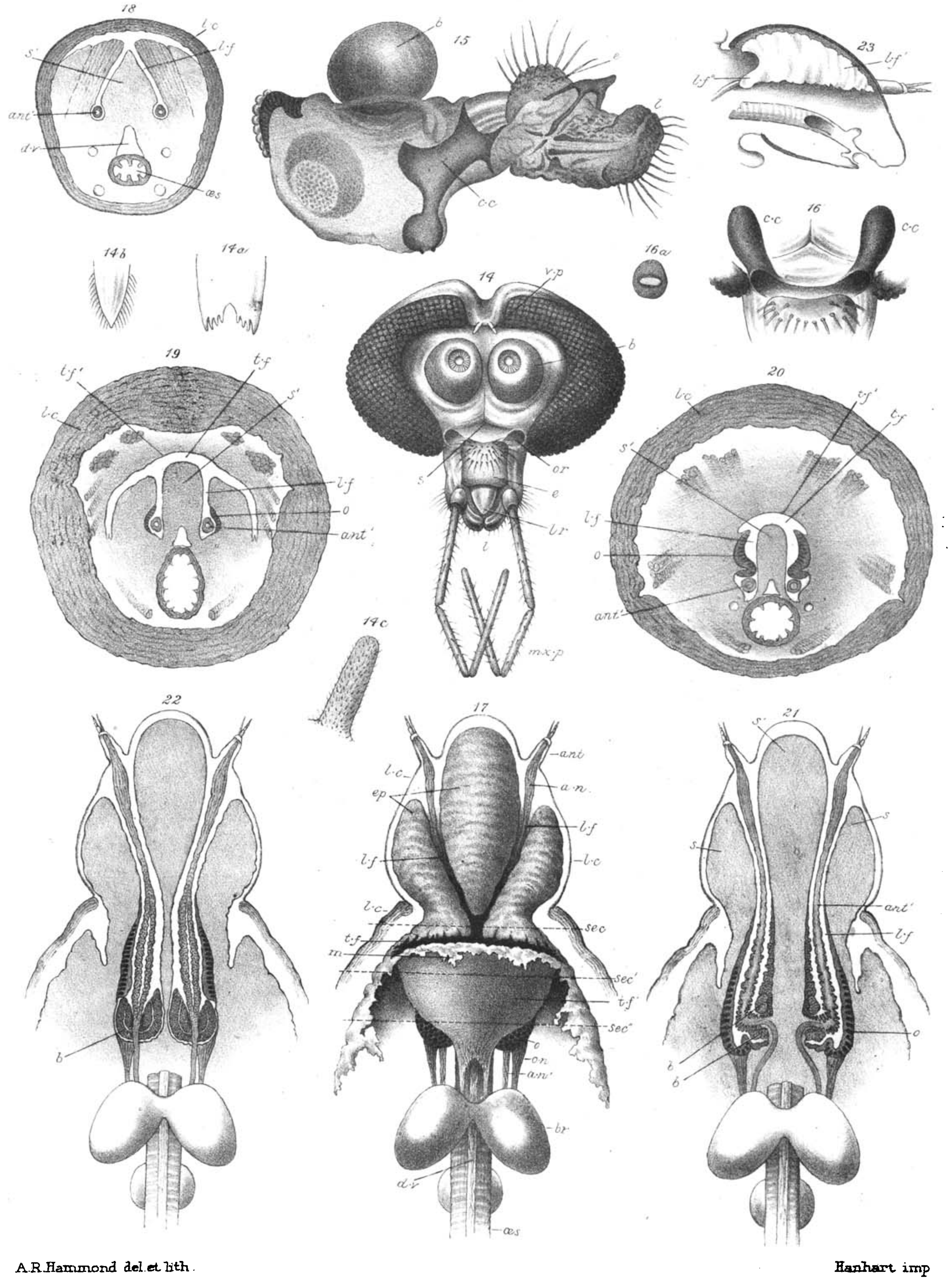
Fig. 33. Transverse section through the head of a recently emerged female pupa, showing the last traces of the folds, *l.f*, and the facets of the eye beginning to extend themselves around the convex surface of the head. × 90.



A. R. Hammond del. et lith.

Hanhart imp

DEVELOPMENT OF THE HEAD OF THE IMAGO OF CHIRONOMUS



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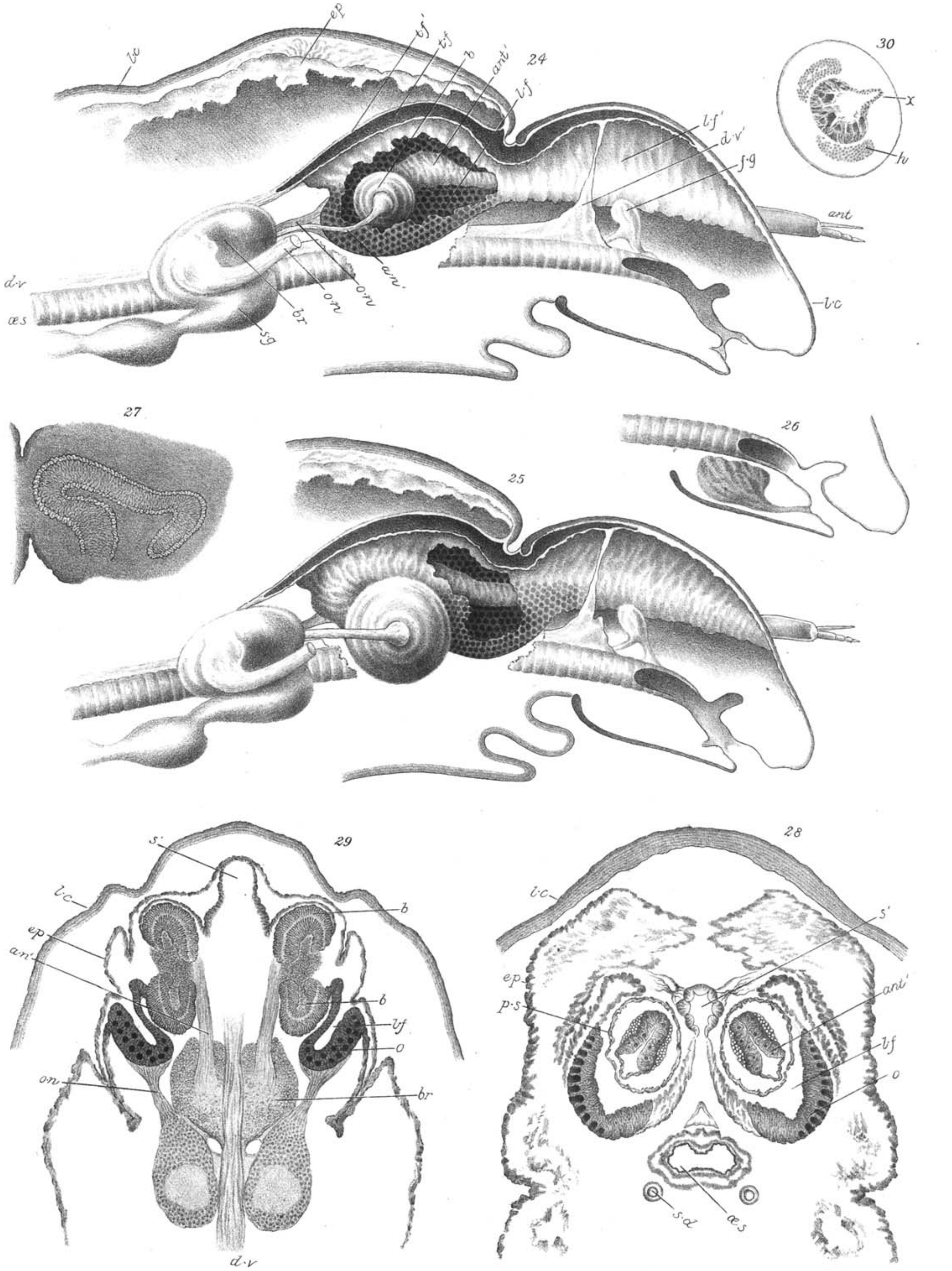

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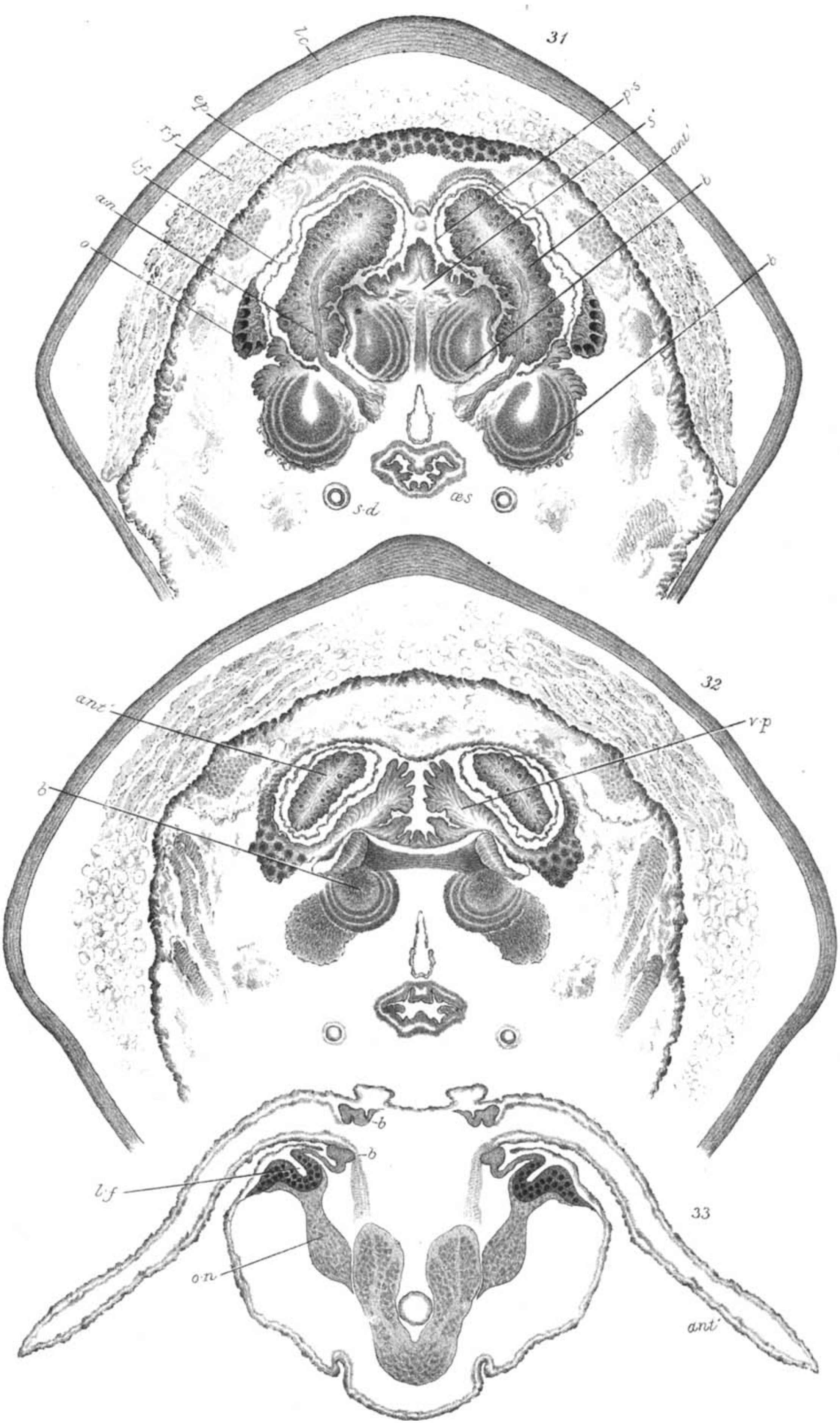

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DEVELOPMENT OF THE HEAD OF THE IMAGO OF CHIRONOMUS.