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A legless, almost headless, wormlike maggot hatches from the egg of a fly; but the maggot is not a young fly in the sense that a kitten is a young cat, or even in the sense that the nymph of a grasshopper is a young grasshopper. The maggot does not grow up into a fly, and neither does it literally transform into a fly. It is a highly specialized larval form of its species, which, though developed directly from the fly's egg, becomes a creature self-sufficient in all respects except that of procreation. Structurally the fly larva is so different from its parents that it cannot itself go over into the next fly generation. Consequently nearly all the larval tissues finally go into a state of dissolution, and the fly is then newly generated from groups of undifferentiated cells that are carried by the larva but which form no essential part of the larval organization.

This potentiality of dual development from a single egg becomes most accentuated among the Diptera in the cyclorrhaphous families. It affects not only the internal organs, but also the body wall, which is almost entirely replaced during the pupal stage from groups of cells, known as imaginal discs, that remain undeveloped from an early period, and at the end of the larval life begin an active growth that forms the integument and appendages of the pupa. The cells of the larval integument degenerate before the advancing new epidermis and are cast into the body cavity where they become food for the developing imaginal tissues. During larval life the regenerative discs of the thorax and head are contained in narrow-necked pouches of the epidermis, closed at their outer ends beneath the cuticle. Within these pouches the appendage rudiments may develop continuously through the larval instars without being exposed at the larval moults. Finally, however, during the prepupal or early pupal stage the pouches are everted and the appendages quickly grow to the state of development they have when the pupa is exposed by the shedding of the last larval cuticle, while the everted pouches themselves expand by cell proliferation and construct the pupal integument.

All this has been known for nearly a century. Weismann (1864) said that the thorax and head of the fly, together with their appendages, the halteres, the wings, legs, antennae, eyes, and mouth parts develop within the body of the larva, and the truth of this statement has been verified by numerous subsequent workers. Most of the earlier students of the structure and metamorphosis of the cyclorrhaphous larva, however, did not understand the morphology of the larval head. Though they correctly described facts, their identification of anatomical parts is often entirely erroneous, and later writers, taking their statements literally, either criticize them as false, or perpetuate their errors. In the following pages an attempt will be made first to understand the nature of the head of a cyclorrhaphous larva, and then to put together the story of the formation of the adult head as far as it can be compiled from our present information on the subject.

In the lower nematocerous flies the metamorphic changes between larva and adult are less intense than in the cyclorrhaphous families, and larval tissues may go over directly into adult tissues. In the larva of *Corethra,* for example, as described by Weismann (1866), the imaginal discs of the thorax are mere groups of cells in the larval epidermis, which begin development in the prepupal period and then form only the pupal appendages. The general integument of the pupal thorax in this case is a product of renewed growth activity in the cells of the larval epidermis, which simply remodel the thorax into the form of the pupal thorax. The same applies to changes of the head, the pupal head being formed by alterations in shape and size of the larval head within the unshed cuticle of the last larval instar. The imaginal mouth parts of Nematocera have been shown by Kellogg (1902) to be formed directly within the larval mouth parts; the adult antennae, however, which are generally much longer than the larval organs, develop with only their distal ends in the larval antennae. In some of the lower flies, as will be shown later, the imaginal antennae grow within pockets of the integument, and the pockets may include also the rudiments of the compound eyes.

The structural disparity between the larva and the adult in the Cyclorrhapha is due to the specialized form that the larva has acquired, rather than to that of the adult fly. The larval head of these flies in particular has become so highly modified in a specific way that it is difficult to understand how it has been evolved from a head of more usual structure. Only a small part of the adult head is derived directly from the larval head.

The apparent, or functional, head of a muscoid maggot is a small, rounded lobe at the anterior end of the body (fig. 2 A, *LH*) more or less sunken into the thorax. Apically this larval head bears a pair of large papillae, on each of which are situated two small sense organs, but there are no eyes of any kind. The under surface of the head (A) presents a median depression from which projects a pair of strongly

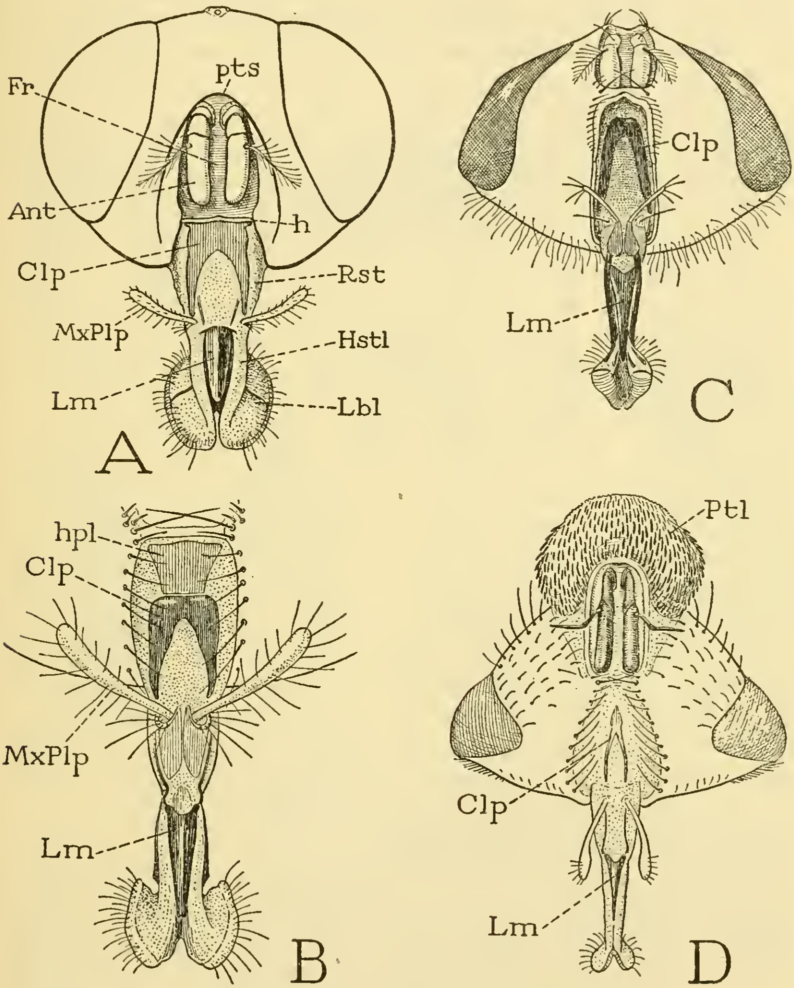

FIG. 1.—Head and proboscis of adult muscoid flies.

A, *Musca domestica* L., anterior. B, *Calliphora vicina* R.-D. (*erythrocephala* Meigen), clypeus and proboscis. C, *Callitroga macellaria* (F.), ventral. D, *Gonia* sp., with ptilinum everted.

sclerotized, decurved hooks (*mh*) partly covered by lateral folds of the integument. Below the bases of the hooks is a soft median lobe (*Lb*), which at least serves the larva as an under lip, and appears to be a true larval labium. Above the labium, between the bases of the hooks, is the food-intake orifice of the larva (*Atr*), but it leads immediately into an atrial chamber before the mouth of the larval sucking apparatus.

The larval organ of ingestion is a suction pump lying within the thorax, supported by a strongly sclerotized structure commonly called by students of cyclorrhaphous larvae the "buccopharyngeal skeleton" or the "cephalopharyngeal apparatus" (fig. 2 B). By whatever name this complex structure is known, it is an important part of the larval head retracted into the thorax. In details of shape it differs characteristically in different species, but the general form and structure of the organ is that shown here for the mature larva of *Callitroga macellaria*.

The dorsal part of the sucking apparatus (fig. 2 F) is a long, thin, hyaline plate having a strongly contrasting, dark U-shaped sclerotization around its anterior end with the arms extending posteriorly along the lateral margins. From the edges of this sclerotized part of the dorsal plate a strong lateral plate descends on each side (B) and expands below into a broad posterior extension. Supported between the lower edges of the lateral plates is the sucking pump of the larva (*CbP*), which is continuous anteriorly from the atrium above the labium (*Lb*) and posteriorly into the oesophagus (*Oe*). The lumen of the pump when contracted is crescent-shaped in cross section (D, *Cb*), but on its concave upper wall are attached two rows of large dilator muscles (*dlcb*) arising on the arms (*Clp*) of the U-shaped sclerotization of the dorsal plate. Anterior to the lateral plates is a smaller, independent, median, ventral plate (B, *e*) on which the mouth hooks (*mh*) are articulated. This plate, which lies on the base of the dorsal wall of the larval labium (C, *e*), is H-shaped in ventral view (E, *e*). In front of its crossbar are two small sclerites bearing minute sense organs, and a narrow anterior V-shaped sclerite. Just behind the crossbar is the opening of the salivary duct (B, E, *SlDct*), which discharges on the base of the labium.

The dorsal plate of the larval sucking apparatus is covered by a very delicate, closely adherent membrane (fig. 2 B, *a*). Anteriorly, however, the membrane becomes free, forming the dorsal wall of the atrium (*Atr*), and is then continued into the wall of the ventral depression of the external larval head (A). When the atrium is exposed by cutting away the covering membrane (C) there is seen projecting into it from the anterior end of the dorsal plate of the sucking apparatus a small conical lobe (*Lm*) with a minute sclerotic tip. This lobe is clearly the larval labrum; in a first instar larva the sclerotized tip is larger and forms a conspicuous tooth.

The "buccopharyngeal skeleton" of the cyclorrhaphous larva is perhaps generally regarded as a structure distinctive of the larva, since most entomologists do not seem to have observed that it is almost a replica of the supporting skeleton of the sucking pump of the adult fly, which is commonly known as the "fulcrum" of the proboscis. This structure in the fly (fig. 3 F) consists of the clypeus (*Clp*) and a pair of lateral plates (*f*), called the paraclypeal phragmata, inflected

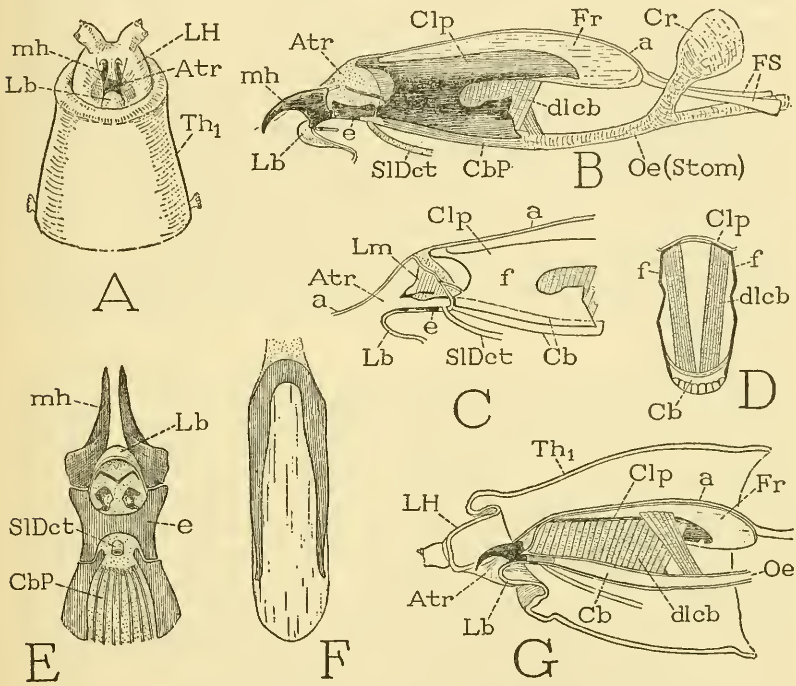

FIG. 2.—Larval head structures of *Callitroga macellaria* (F.).

A, head lobe of larva (*LH*), partly retracted into prothorax, ventral. B, feeding apparatus ("buccopharyngeal skeleton") of a mature larva, lateral. C, diagram of anterior end of sucking apparatus, with lateral wall of atrium (*Atr*) cut away, exposing the labrum (*Lm*). D, cross section of sucking apparatus, showing inflection of paraclypeal phragmata (*f, f*) from edges of clypeus, supporting the cibarial pump (*Cb*). E, ventral surface of anterior part of cibarial pump and H-shaped sclerite (*e*) supporting the mouth hooks (*mh*) and the labium (*Lb*). F, frontoclypeal plate of sucking apparatus, dorsal. G, diagrammatic lengthwise section of head and prothorax, mesal view of right half.

from the clypeal margins, which support between their lower edges the sucking pump (*CbP*) of the food tract. The dilator muscles of the pump (G, *dlcb*) arise on the clypeus and are enclosed between the paraclypeal phragmata. The cross section of the "fulcrum" of the fly (E), therefore, is an exact duplicate of a similar section of the "buccopharyngeal" apparatus of the larva (fig. 2 D), and there can scarcely be any question that the two structures are merely imaginal and larval forms of the same thing.

The clypeus of a muscoid fly is generally U-shaped or V-shaped with the closed end dorsal. In *Musca* and *Calliphora* (fig. 1 A, B) the clypeus (*Clp*) is fully exposed on the base of the proboscis; in *Callitroga* (C) it is deeply sunken in a cavity on the under side of the head; in *Gonia* (D) it is relatively very small. In *Musca* (A) the broad base of the clypeus is closely hinged to the lower margin of the frons (*Fr*); in *Calliphora* (B) a hinge plate (*hpl*) intervenes between the frons and the muscle-bearing plate of the clypeus; in *Callitroga* (C) the sunken clypeus is separated by membrane from the epistomal ridge beneath the frons; in *Gonia* (D) the diminutive clypeus is well removed from the frons. In any case, the proboscis, with the clypeus and the sucking apparatus, swings back and forth below the frons in the ample membranous connection of the clypeus with the head by muscles attached on the supporting skeleton of the sucking pump. The latter and the clypeus are, therefore, known as the "fulcrum" of the proboscis.

Finally, to understand the nature of the parts that compose the "fulcrum" of the adult muscoid fly, we must go back to the more primitive condition in the orthopteroid insects. A median section through the distal part of the head of a cockroach (fig. 3 A) shows that there is a specific preoral food pocket, the *cibarium* (*Cb*), between the epipharyngeal wall of the clypeus (*Clp*) and the sloping basal part of the hypopharynx (*Hphy*). Two suspensory rods on the cibarial floor extend up through the angles of the mouth (*y*) and give attachment to muscles from the frons. On the anterior or upper wall of the cibarium are attached thick bundles of muscle fibers (*dlcb*) arising on the external clypeal area of the head. These muscles are compressors of the clypeus, but their contraction expands the cibarium. If, then, the movable lobe of the hypopharynx is brought against the inner surface of the labrum (*Lm*), the cibarium will become practically a closed chamber opening anteriorly from the food meatus (*fm*) between the labrum and the free lobe of the hypopharynx, and proximally into the stomodaeum (*Stom*). It is very probable that the cibarium thus serves the cockroach as an organ for the ingestion of liquids. On its dorsal wall are transverse compressor muscles not shown in the figure. The true mouth of the cockroach is the opening of the cibarium (*Mth'*) into the stomodaeum. An important point to bear in mind is that the cibarial muscles of the clypeus are separated from muscles of the stomodaeum arising on the frons by the frontal ganglion and its brain connectives.

The homology of the sucking pump of the fly with the cibarium of the cockroach has been amply illustrated by Gouin (1949).

In various insects the cibarium becomes a permanently more or less closed chamber by a lateral union of the epipharyngeal wall with the base of the hypopharynx, so that the functional mouth opening may come to lie beneath the base of the labrum. The cibarium thus becomes more efficient as a sucking organ. Among the Diptera this condition is fully developed in the lower families, and is well illustrated in the mosquito (fig. 3 B). The cibarial pump of the mosquito (*CbP*) has a strongly sclerotized basinlike floor; the intake orifice lies beneath the base of the labrum and thus constitutes a *secondary mouth* (*Mth''*). Since the floor of the pump in the mosquito corresponds with the hypopharyngeal floor of the cibarium in the cockroach, the hypopharyngeal stylet of the mosquito (B, *Hphy*) represents only the free lingual lobe of the cockroach hypopharynx (A, *Hphy*). A section of the sucking pump of the mosquito (indicated by the arrow at B) shows two sets of strong dilator muscles (*dlcb*) from the clypeus to the concave upper wall of the pump.

The cibarial pump of the mosquito projects freely into the head (fig. 3 B), and, though it is strongly sclerotized and is suspended from the frons by muscles attached on a pair of proximal processes (*y*), it is still not braced against the pull of the dilator muscles. This condition has been remedied in the higher flies. In some of them, as in the mydas fly (C), a strong ridge is inflected from a groove on each side of the clypeus, and the distal ends of the ridges (*f*) are fused with the lateral walls of the pump, thus serving to hold the latter firmly in place. From this simple condition it is only a step to that in the muscoid flies in which the clypeal ridges have been enlarged into broad paraclypeal phragmata (F, *f*) supporting the full length of the pump. The dilator muscles of the pump (E, *dlcb*) are thus boxed in between lateral plates (*f*, *f*), and the pump is securely braced against the clypeus. As in the cockroach and the mosquito, the primary mouth of the muscoid fly is the opening of the cibarium into the stomodaeal oesophagus (F, *Mth'*), but the functional mouth (*Mth''*) is the entrance into the cibarium from the food meatus (*fm*) between the labrum and the hypopharyngeal stylet. However, in those flies in which the labellar lobes of the labium form a broad, food-collecting disc (D), the deep notch between the lobes (*Mth'''*) is the real intake aperture for liquid food, and has been termed the *prestomum.*

The paraclypeal phragmata are not primarily inflections from the extreme edges of the clypeus. In the adult male of *Tabanus,* as has been shown also by Bonhag (1951), the clypeus is divided longitudinally into three areas by a groove on each side well within the epistomal sulcus. These clypeal grooves in *Tabanus* form merely a pair of internal ridges, but it is clear that the ridges represent the beginning of paraclypeal phragmata in other flies. Developmentally the phragmata are first formed in the larva, and they may be well developed in brachycerous as well as in cyclorrhaphous larvae. Theoretically, however, it seems probable that the complex sucking apparatus must have been first evolved in the adult fly, since the larvae of lower dipterous families have biting and chewing mouth parts.

On returning now to the larva, it is clear that the sucking pump (fig. 2 B, *CbP*) is the cibarium, as it is in the fly. The dilator muscles of the larval cibarium lying in front of the frontal ganglion, therefore, should identify the part of the dorsal plate on which they take their origin as the clypeus (*Clp*), since these muscles entirely conform with the cibarial muscles of the adult. In the larva, however, there is an oblique posterior group of fibers just behind the frontal ganglion, attached below on the stomodaeal oesophagus (G) and arising on the posterior part of the dorsal plate of the sucking apparatus mesad of the cibarial muscles. In the cyclorrhaphous flies the stomodaeum proceeds from the cibarial pump as a simple tubular oesophagus (figs. 2 B, 3 F, *Oe*), but in adult Brachycera it is differentiated immediately behind the cibarium into a second, smaller pharyngeal pump, with its dilator muscles arising on the frons, and these muscles are those represented in the cyclorrhaphous larva by the oesophageal muscles arising on the posterior part of the dorsal plate of the sucking apparatus. The structure and mechanism of the pharyngeal pump in the adult of *Tabanus* are well described and illustrated by Bonhag (1951).

In the larvae of Stratiomydiae the pharyngeal pump has been converted into a crushing organ by the transformation of its dorsal wall into a thick plate with a convex, sometimes strongly ridged, under surface that fits like a broad pestle into the concave, mortarlike ventral wall. This pharyngeal organ is sclerotically continuous with the long, slender cibarial pump, from the end of which it turns upward like the bowl of a pipe from the stem (fig. 6 B, *Phy*). It is the *Schlundkopf* of Jusbaschjanz (1910), who calls the cibarium the "pharynx"; it is described in the larva of *Odontomyia alticola* by Cook (1949), and Schremmer (1951) gives a fully detailed account of its structure and probable use in the larva of *Stratiomys chamaeleon*. The organ is operated by dorsal muscles arising on the frontoclypeal area of the head. A large anterior muscle inserted at the junction with the cibarium is shown by Cook to lie before the frontal ganglion and its brain connectives. This muscle, therefore, is a cibarial muscle; the other, posterior muscles are true frontal pharyngeal muscles.

The attachment of both frontal muscles and clypeal muscles on the dorsal plate of the larval sucking apparatus should identify this plate as a *frontoclypeal* element of the head skeleton, which is a well-defined,

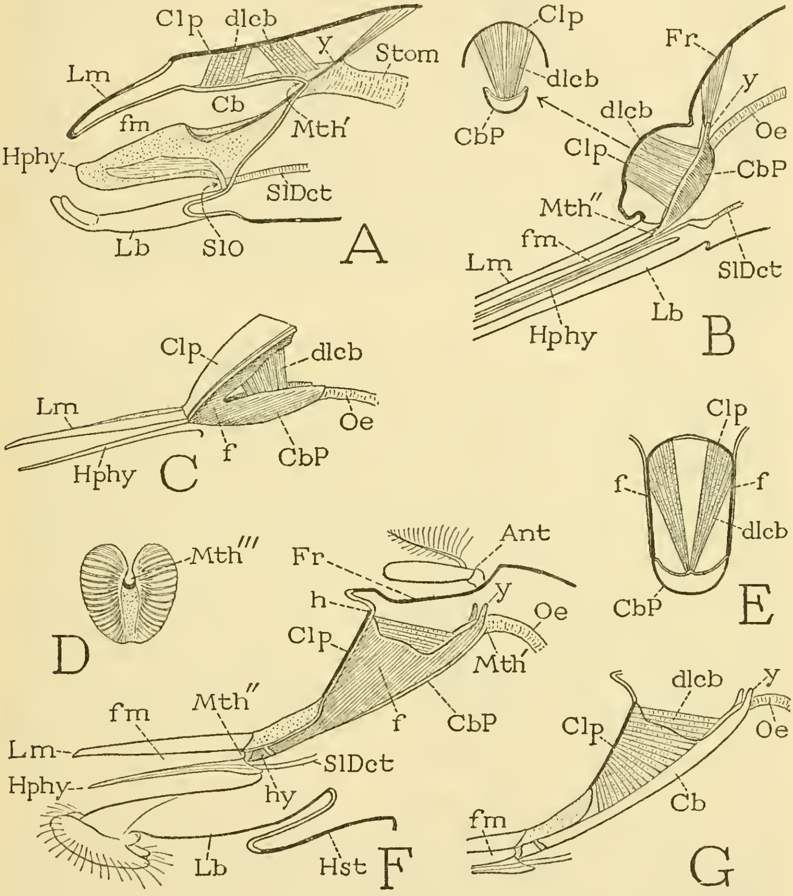

Fig. 3.—The sucking apparatus of adult Diptera, and comparison with the cibarium of a cockroach.

A, diagrammatic lengthwise section of head of a cockroach. B, diagram of sucking apparatus of a mosquito. C, same of a mydas fly. D, labellar disc of a muscoid fly. E, cross section of sucking apparatus of adult *Callitroga macellaria*. F, sucking apparatus and mouth parts of adult *Callitroga macellaria*, lateral. G, lengthwise section of sucking apparatus of same, showing clypeal dilator muscles of cibarium.

median dorsal area of the head in most nematocerous and brachycerous fly larvae (fig. 6 A). Cook (1949) has called this entire area the "clypeus," but in so doing he disregards the evidence from muscle attachments in insects having the clypeus separated from the frons, in which the cibarial muscles arise on the clypeus and the postcibarial muscles on the frons. The frontal and clypeal areas, however, are often continuous. Ludwig (1949) says merely that this area of the head in the larva of *Calliphora* "includes the clypeus and some additional part of the cranium." The sucking apparatus of the cyclorrhaphous larva, therefore, is a more complex structure than that of the adult fly in so far as it includes not only the clypeus and the cibarium, but also the frons and frontal muscles of the stomodaeum. The frontoclypeal plate and the sucking apparatus of the larva lie entirely within the thorax, a position they have acquired either by retraction or by the overgrowth of a fold from the thorax, or by both means. The frontoclypeal plate is connected with the external larval head (fig. 4 D, *LH*) by the membrane (*a*) extending back from the latter over the atrium.

The H-shaped plate of the larva that lies on the base of the labium and supports the mouth hooks (fig. 2 B, E, *e*) suggests by its position the hyoid sclerite of the adult (fig. 3 F, *hy*), but in the larva the salivary duct (*SlDct*) opens behind the H-shaped plate, while in the adult it enters the hypopharyngeal stylet anterior to the hyoid. The hypopharynx in the larva is represented only by the floor of the cibarium, a free hypopharyngeal lobe corresponding with that of the cockroach (fig. 3 A) or with the hypopharyngeal stylet of the fly (F, *Hphy*), being absent in the larva. The larval labium (fig. 2 A, C, *Lb*) does not become the labium of the adult; the labium of the fly is developed from a pair of histoblastic pouches formed inside the larval labium.

The nature of the mouth hooks of the cyclorrhaphous larva has been a subject of much discussion, some writers contending that the hooks are mandibles, others that they are not. The latest advocate of their mandibular nature is Ludwig (1949). If the larval mouth hooks are not mandibles, the question is, what are they? In the first place, it is curious that mandibles should have their only articulations on a plate on the base of the labium, and secondly, since the muscles of the hooks are attached on the paraclypeal phragmata of the sucking apparatus, it is an unusual thing for mandibular muscles to arise on any part of the clypeus. However, since the parietal walls of a typical insect cranium are obliterated in the fly larva, the phragmata offer the only available solid support for the muscles, and muscles do change their points of origin where efficiency demands a change. On the other hand, if the hooks are not mandibles, they cannot be homologized with any other structure of other insects, and it is hardly to be supposed that such highly developed feeding organs should be developed *de novo* for the express use of the larva. However, since the hooks disappear at the end of larval life and the adult fly has no mandibles, the larval hooks cannot be put to the crucial test of finding what they become in the imago, and for this same reason we may leave the matter without further discussion, inasmuch as the mouth hooks are not involved in the metamorphosis of the larva into the fly.

In most nematocerous and brachycerous families the head of the larva is more or less retracted into the thorax, so that it is at least partly ensheathed in a fold of the prothorax. In the cyclorrhaphous larva, however, the head appears to consist of an external part bearing the apical sense organs of the larva, and of a retracted part that includes only the frontoclypeal area, which carries the labrum and supports the cibarial sucking apparatus. The cyclorrhaphous larva thus presents a cephalic condition that is difficult to understand, and even the known facts of embryonic development do not make the condition entirely clear.

The head of the embryo at an early stage of its development is a simple structure. As shown by Pratt (1901) in *Melophagus ovinus* (fig. 4 A) the embryonic head presents a dorsal lobe above the entrance into the food tract (*Cb*) and a ventral lobe below it. The dorsal lobe, which contains a group of compressor muscles (*dlcb*), Pratt calls the "muscular sucking tongue," but we can easily recognize this lobe as the labrum and clypeus (*Lm, Clp*), and the muscles as the dilators of the future cibarial pump (*Cb*). The ventral lobe is clearly the larval labium. This stage of the embryo may be diagrammatically presented in a more conventional form as at C of the figure. The short dorsal wall of the embryonic head represents at least the clypeus of the larva (D, *Clp*) bearing the labrum and giving attachment to the dilator muscles of the cibarium.

The primary embryonic head now becomes covered by the forward growth of an integumental fold (fig. 4 A, C, *hf*) from behind it, which goes over the labrum (B) and forms the roof of an antechamber, the head *atrium* (*Atr*), before the mouth of the cibarium (*Cb*), while the fold itself becomes at least a part of the external head lobe of the larva (D, *LH*) bearing the larval sense organs. The overgrowth of the primitive head by this secondary dorsal head fold is well illustrated also in *Calliphora* by Ludwig (1949, fig. 58). According to Pratt (1901) there is a dorsal and a ventral fold in *Melophagus* (A, B, C, *hf, vf*). Unfortunately Pratt's terminology is confusing because he calls the newly formed atrium the "pharynx," and the cibarium the "stomodaeum." With the completion of the dorsal head fold the embryo acquires the essential head structure of the larva, represented diagrammatically at D of the figure. The frontoclypeal plate and the cibarial apparatus thus become enclosed within the thorax, and the major part of the external larval head lobe (*LH*) bearing the larval sense organs appears to be a secondary structure formed by the dorsal head fold extended from *c* to *d*. The original space (*b*) beneath the fold later becomes obliterated by the close apposition of the inner wall of the fold (*a*) on the frontoclypeal plate, but the labrum (*Lm*) is left projecting freely into the atrium (*Atr*).

Of the two sense organs on each of the apical papillae of the larva, the dorsal one, according to Ludwig (1949), represents the larval antenna, the ventral one the maxillary palpus. This opinion was also that of Weismann (1864), but other authors have considered the interpretation doubtful. The alleged antennal organ is shown by Ludwig to be innervated by a long branch from the labrofrontal nerve—a most unusual association for an antennal nerve, and neither the nerve nor the sense organ can have any relation to the antenna of the adult. The ventral sense organ, Ludwig says, "is the maxillary palp sense organ," but apparently the only basis for this statement is that the organ in question is innervated by a branch from the "mandibular-maxillary-labial nerve." A sense organ wherever located must have a nerve. The origin of the papillar sense-organ nerves from head ganglia is not proof that the organs are either antennal or maxillary, but it is convincing evidence that, whatever they are, they belong to the head, and Ludwig shows, moreover, that the organs originate in the epidermis of the lateral walls of the embryonic head. It becomes a problem, therefore, to understand how these sense organs in the larva come to be situated on the external head lobe formed by the head fold, and their position on this lobe raises the question as to whether the fold pertains to the thorax or to the head.

As seen in longitudinal sections the head fold of the cyclorrhaphous embryo (fig. 4 A, B, *hf*) suggests the prothoracic fold that partly ensheaths the head of many nematocerous and brachycerous larvae (fig. 6 A, B, *thf*). Schremmer (1951) asserts that there appears to be no remnant of a head in the cyclorrhaphous larva, and that as a result of the forward growth of the dorsal fold the larval sense organs come to be on the anterior end of the thorax. Holmgren (1904) apparently regarded the larval head lobe as a derivative of the thorax, but he says nothing of the sense organs. Pantel (1898) called the larval head lobe a "pseudocephalon." Ludwig (1949) also attributes at least a part of the head fold to the thorax because it contains a pair of muscles innervated from the prothoracic ganglion that "insert on a sclerotized area between the mandibles." In the *Callitroga* larva, however, these muscles do not arise in the head lobe itself but on the overhanging anterior part of the prothorax, so, if the larval head lobe is a part of the head, the muscles in question are merely prothoracic head muscles.

In a cross section of the embryonic head of *Calliphora* it is shown by Ludwig that the head fold (fig. 6 C, *hf*) covers only a narrow space (*b*) above the frontoclypeal surface (*Clp*). The inner lamella of the fold (*a*) arches immediately over the frontoclypeus, while the outer lamella has become continuous with the parietal walls of the head. If

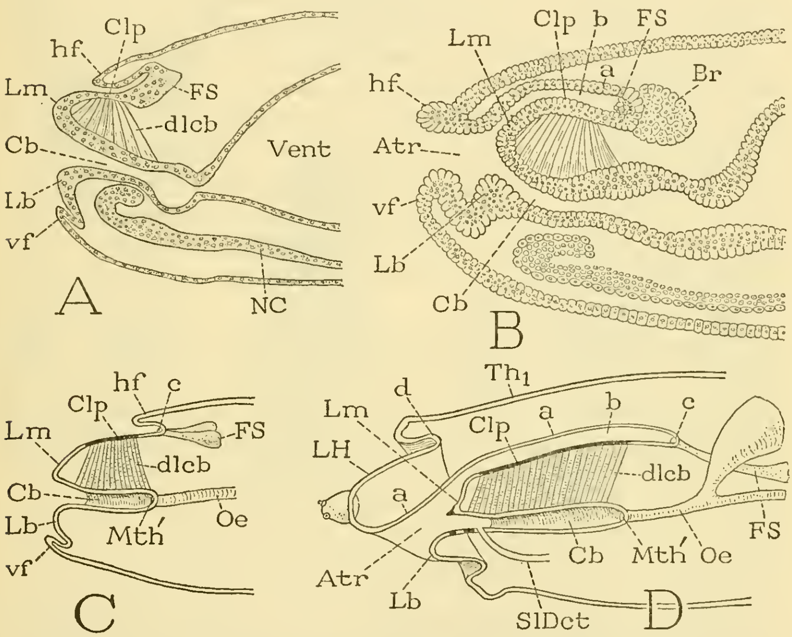

FIG. 4.—Development of the larval head of a cyclorrhaphous fly.

A, lengthwise section of embryonic head of *Melophagus ovinus* (from Pratt, 1901), showing beginning of head fold (*hf*). B, later stage of same (from Pratt, 1901), in which the head fold has grown forward over the labrum and labium, which are now enclosed in a secondary preoral atrial chamber (*Atr*). C, diagrammatic expression of A. D, diagrammatic analysis of the anterior larval structure based on B.

the fold proceeds over the head as a narrow median growth from the thorax alone, it is difficult to understand how it becomes so intimately a part of the head wall. In any case, it is evident that this head fold of the cyclorrhaphous larva is something quite different from the prothoracic fold that ensheaths the base of the head in a brachycerous larva.

The head fold of *Calliphora,* Ludwig (1949) says, appears at about the thirteenth hour of the developing embryo, and "is in the shape of a

U, with the open end pointed anteriorly." Its lateral margins lie mesad of the developing larval sense organs. If, therefore, the head fold grows forward in this manner with its arms extending along the edges of the frontoclypeal area, it would seem that, whatever its origin, the extension of the fold must be at the expense of the head wall itself, and that the arms of the fold close medially from the sides as the fold advances. If this is the manner of growth of the fold, the condition seen in cross sections of the embryonic head (fig. 6 C) becomes understandable. Furthermore, only by some such process of growth from the head wall could the lateral sense organs on the embryonic head be carried up over the labrum and finally come to be situated on the anterior end of the fold, which forms at least the dorsal part of the head lobe of the larva. It is, then, certainly more rational to regard the larval head lobe as a part of the head itself than as a derivative of the thorax. Clearly there is need for further study of the nature of the head fold and the manner of its growth, and Schremmer (1951, p. 362) has promised a new investigation "über die Enstehung des Cyclorrhaphenlarvenkopfes."

When a young insect in its development takes a path widely divergent from that of its parents, and acquires a head structure as extraordinarily specialized as that of the cyclorrhaphous larva, it is evident that the larval structure cannot be "transformed" into that of the adult. The head of the fly, therefore, is practically a new structure developed without reference to the larval head. In the evolution of the Diptera, however, the cyclorrhaphous way of forming the adult head has been derived from a more simple method retained in some of the lower flies.

Among the nematocerous Diptera, as has been shown by Kellogg (1902) in *Simulium* and *Bibiocephala,* the imaginal (pupal) head may be formed simply and entirely within the loosened cuticle of the larval head, and the imaginal mouth parts are formed inside the cuticle of the larval mouth parts. The antennae of the pupa, because they are much longer than those of the larva, find space for their growth between the pupal head and the cuticle of the larval head, but their tips are retained in the corresponding larval organs. In *Corethra,* as described by Weismann (1866), the long slender antennae of the pupa become sunken into pouches of the pupal head, from which they are everted when the larval cuticle is shed. In *Corethra* the compound eyes are formed on the surface of the pupal head beneath the larval cuticle. In *Tendipes* (*Chironomus*) Miall and Hammond (1900) showed that both the antennae and the compound eyes of the pupa are developed within longitudinal infoldings of the epidermis of the dorsal wall of the pupal head inside the larval cuticle. Dissection of a mature *Tendipes* larva reveals a pair of long pockets converging from the larval antennae to the posterior end of the head (fig. 5 A), each of which contains an axial tubular antenna (*Ant*) and, in the wall of its basal part, the developing rudiment of a compound eye (*E*). These elongate pockets

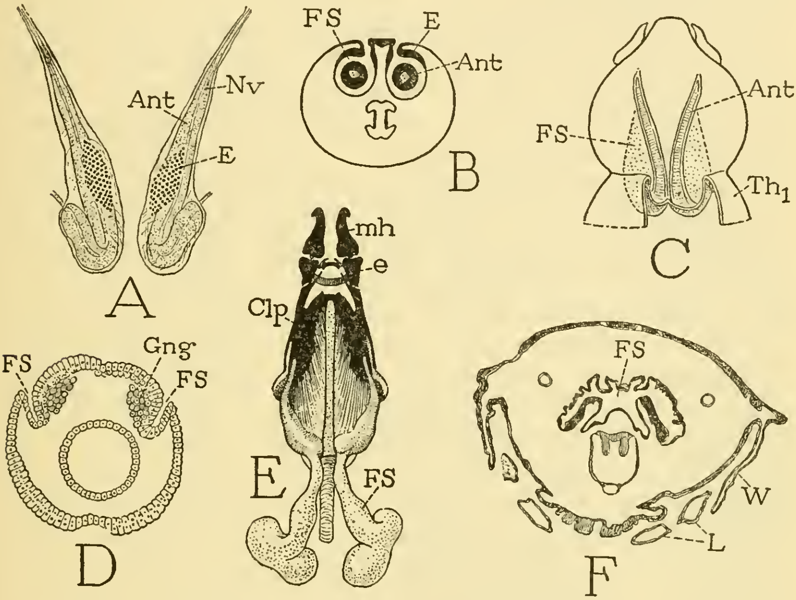

Fig. 5.—Development of the frontal sacs.

A, oculoantennal pockets from head of a mature tendipedid (chironomid) larva, *Tendipes plumosus* (L.), extending posteriorly from larval antennae. B, diagrammatic cross section of pupal head of *Psychoda alternata* showing open grooves (*FS*) containing imaginal antennae and rudiments of compound eyes (outline from Feuerborn, 1927). C, diagrammatic dorsal view of head of young pupa of same, showing oculoantennal grooves extended into pockets of prothorax (outline from Feuerborn, 1927). D, cross section of head of embryo of *Melophagus ovinus* showing origin of frontal sacs (*FS*) on sides of head (from Pratt, 1901). E, dorsal view of feeding apparatus of mature larva of *Rhagoletis pomonella,* with fully developed frontal sacs (*FS*) extending posteriorly from frontoclypeal plate (from Snodgrass, 1935). F, cross section of 7-hour prepupa of *Drosophila melanogaster* showing united frontal sacs produced into lateral pouches with folded walls (from Robertson, 1936).

lie immediately beneath the ecdysial cleavage grooves of the larval head. Very similar groovelike pockets of *Psychoda* are described and figured by Feuerborn (1927) as infoldings of the pupal head (B, *FS*) open by narrow slits on the surface, and containing the developing antennae (*Ant*) and compound eyes (*E*). In *Psychoda* the grooves extend into the front part of the thorax (C) as pockets, which deepen as the pupa develops.

It is probable that similar developmental processes occur in other Nematocera, though little attention has been given to the details of metamorphosis in these flies. The oculoantennal pockets of the head very clearly are equivalent to the peripodal pouches of the thorax in which the imaginal legs are developed and to the pouches that contain the wing rudiments.

In the higher Diptera the oculoantennal pockets, known as the *frontal sacs,* are present in the larvae as long-necked pouches extending from the posterior end of the frontoclypeal plate of the sucking apparatus into the thorax as far as the retracted brain, with which they are connected by ocular nerves (figs. 2 B, 5 E, 6 B, *FS*). In the stratiomyid *Odontomyia* Jusbaschjanz (1910) says the pouches contain only the histoblasts of the compound eyes (fig. 6 B, *FS*), the antennae arising from the surface of the head as in *Corethra.* In all cyclorrhaphous flies that have been described, however, the frontal sacs contain the rudiments of both the eyes and the antennae. These sacs are formed in the embryo and are present in all stages of the larva, but reach their full development only in the last larval instar. In their early origin, therefore, the frontal sacs of the head in the cyclorrhaphous flies more nearly resemble the thoracic peripodal pouches of the legs than do the oculoantennal pockets of the Nematocera, which appear only in the prepupal stage. Because in the late embryo the sacs appear to arise from the inner end of the passage between the inner lamella of the head fold and the underlying frontoclypeal plate (fig. 4 B, *FS*), this passage (*b*) has been regarded as an unpaired part of the sacs, and the latter have been erroneously said to be invaginations from the atrium (*Atr*), or from the "pharynx" if the atrium is mistaken for the pharynx. The point at which the sacs grow into the thorax (D, *c*) is simply overgrown by the head fold, and the true origin of the sacs is on the lateral parts of the embryonic head.

According to Ludwig (1949) the imaginal discs of the compound eyes in the embryo of *Calliphora* arise as ectodermal thickenings on the lateral walls of the head, but in the larva both the ocular and the antennal rudiments are contained in a pair of membranous sacs lying along the sides of the oesophagus. Ludwig does not explain how the sacs are developed, or how they come to contain the histoblasts of the eyes and antennae. In his figure 57 he shows the left sac exactly as all other writers have depicted the frontal sacs, and yet he says "embryonic studies reveal no such pouches." Furthermore, Ludwig attributes to Pratt (1901) the absurd statement that the common opening of the sacs "is drawn forward and downward, and then posteriorly through the mouth," and on this assertion he bases a criticism of Pratt's work.

However, Pratt makes no such statement, or anything like it. More concisely than does Ludwig himself, Pratt describes in *Melophagus ovinus* the origin of the frontal sacs ("dorsal head discs") as dorsolateral thickenings of the epidermis of the embryonic head. Early in their history the discs begin to invaginate in the form of crescentic slits (fig. 5 D, *FS*), and later they move dorsally to the back of the head, where their outer parts unite in a single, transverse depression, while the inner parts increase in length and extend separately into the

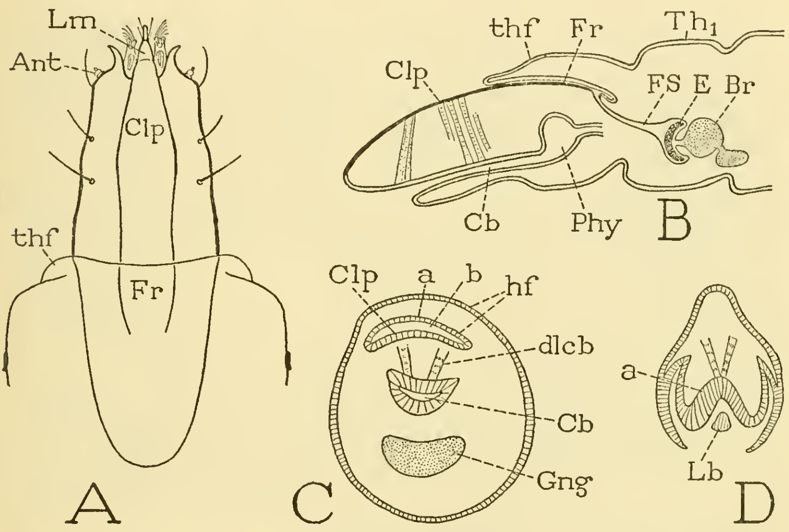

FIG. 6.—Head of stratiomyid larva and sections of embryonic head of *Calliphora*.

A, larval head of *Ptecticus trivittatus* (Say) partly ensheathed in fold of prothorax, dorsal. B, lengthwise section of larval head and prothorax of *Odontomyia* (combination diagram from Jusbaschjanz, 1910, relettered). C, cross section near base of head of 15-hour embryo of *Calliphora* (from Ludwig, 1949). D, cross section of head lobe of 16-hour embryo of *Calliphora*, overhanging the labium (from Ludwig, 1949).

body cavity as a pair of stalked sacs that lie in contact with the cerebral ganglion. Now there takes place, from behind the mouth of the sacs (fig. 4 C, *c*), the formation of the dorsal fold (*hf*), which grows forward over the head. Since the inner lamella of the fold becomes closely adherent to the frontoclypeal plate, it thus comes about that in the larva the sacs *appear* to be attached to the posterior end of the larval sucking apparatus (figs. 2 B, 5 E, *FS*). Their true opening at the posterior end of the head beneath a fold of the thorax (*thf*) is shown by Jusbaschjanz (1910) in his sectional figure of a stratiomyid larva (fig. 6 B, *FS*).

From the description of the early history of the frontal sacs given by Pratt it is clear that the frontal sacs of the cyclorrhaphous flies can be correlated in their origin with the oculoantennal grooves of the pupal head in the Nematocera. That, in the former, the sacs arise in the embryo instead of in the pupa shows that the imaginal discs of the head have followed the same course of evolution as have those of the thorax, which also in the higher flies have come to be formed in the embryo.

The further history of the frontal sacs has been followed by Wahl (1914) in *Calliphora* and by Robertson (1936) in *Drosophila.* Weismann (1864) observed that the head of the fly is formed from two "cell masses" (the frontal sacs), which at first are in contact and later become united. Jusbaschjanz (1910) noted that in a stratiomyid larva there is only one frontal sac (*Kopffalte*) at the time of pupation, from which fact he concluded that the two primary sacs must have united in a single pouch. Wahl (1914) specifically describes the formation of a single sac in the early pupa of *Calliphora* by a dissolution of the mesal walls of the original two sacs followed by a union of their outer walls. The resulting unpaired sac then increases in size by expansion of lateral pouches, and its walls become thrown into numerous irregular folds. In *Drosophila* Robertson (1936) says the closely appressed frontal sacs begin to fuse two hours after the formation of the puparium. The median walls break down and the broken edges of one sac unite with those of the other until the two sacs have completely united (fig. 5 F, *FS*) except at their posterior ends where the optic concavities are applied to the cerebral ganglia.

At pupation the cephalic fold of the larva retracts (fig. 7 B, *hf*), the passage (*b*) beneath it opens and becomes continuous with the lumen of the now single frontal sac (*FS*), so that, as Wahl (1914) shows in the early pupa of *Calliphora,* the frontal sac comes to open directly to the exterior above the mouth of the cibarium ("pharynx"). The same thing was noted by Pratt (1897) in *Melophagus,* but Pratt's language is somewhat confusing to a modern reader when he says "the lumen of the discs and that of the pharynx become completely merged and form together a single continuous space." The "discs" are the frontal sacs, the "pharynx" is the larval atrium. When now the pupa is first exposed by the shedding of the last larval cuticle within the puparium, there is to be seen at the anterior end of the body only a great hole in the front of the prothorax (fig. 7 A). This stage is the cryptocephalic phase of the pupa. Shortly thereafter the walls of the cavity are suddenly everted, and the pupa thus acquires a head (C). The pupal head is at first relatively small and not fully developed, but it takes on its definitive size and structure (D, E) during the rest of this phanerocephalic stage of the pupa. When the head of *Drosophila* is first everted, Robertson says, the eyes are brought to their final position, but are not yet histologically completed, and the antennae are simple thickenings of the front wall of the head. Bodenstein (1950) describes in detail the development of the compound eyes in *Drosophila*.

Ludwig (1949) emphatically denies that there is any process of invagination involved in the formation of the head of the fly. However,

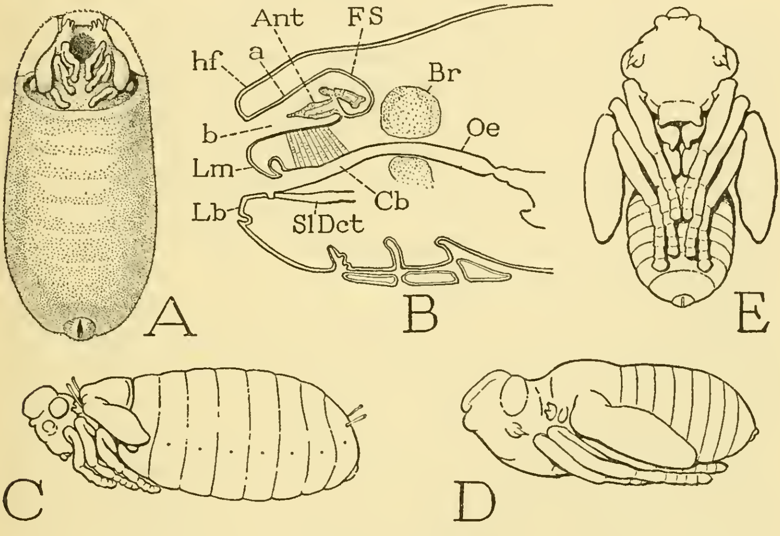

FIG. 7.—The pupa.

A, cryptocephalic pupal stage of *Rhagoletis pomonella*, ventral. B, lengthwise section of anterior end of 10-hour prepupa of *Drosophila melanogaster* showing opening of frontal sac just before pupation (from Robertson, 1936). C, early phanerocephalic pupal stage of *Rhagoletis pomonella*. D, mature pupa of *Rhagoletis*, lateral. E, same, ventral.

since the adult head is visibly everted in the pupal stage, it is not clear how it became introverted without a previous inversion. The frontal sacs are actually ingrowths of the embryonic integument, and an ingrowth is usually called an "invagination," though admittedly it is more properly an introversion. Furthermore, Ludwig criticizes a former statement by the writer (1935, p. 313) that "the entire facial region of the head, including the area of the frons and that of the imaginal antennae and compound eyes, is invaginated into the thorax." This statment is in accord with the findings of other writers, since the time of Weismann (1864), and all that is needed to demonstrate its truth is a glance at a pupa in the cryptocephalic stage, whether of

Musca, Calliphora, Drosophila, or *Rhagoletis* (fig. 7 A). When the frontal sac is everted, it brings with it the eyes and the antennal rudiments, and its walls form the epidermis of all parts of the fly's head except that part derived from the sucking apparatus of the larva. The cuticular skeleton of the latter is shed at the moult to the pupa, but the matrix of the organ must remain to form the more simple sucking apparatus (or "fulcrum") of the adult, though the transformation has not been observed.

In the change from the larva to the adult the frontoclypeal plate of the larva undergoes a very considerable modification. First, it is distinctly divided, in the fly, into frontal and clypeal elements; the clypeal area retains the muscles of the cibarium, the frons now carries the attachments of the postcibarial frontal muscles of the stomodaeum. The shape of the clypeus in the adult becomes reversed from that of the larva, in that, though U-shaped or V-shaped in both, the open end is distal in the adult (fig. 1, *Clp*). The frons of the fly is a part of the head wall, including specifically the depressed area of the face (*Fr*) in which the antennae are lodged.

Again we may point out that the frontal sacs of the cyclorrhaphous fly larva from which the imaginal head is formed are cephalic equivalents of the thoracic histoblasts, which latter not only give rise to the legs and wings, but in the higher flies regenerate the thoracic integument as well. As an example we may refer to Robertson's (1936) account of the formation of the imaginal thorax in *Drosophila.* As the histoblast pouches of the legs and wings open to allow the contained appendages to evert, their edges expand by cell proliferation, while the surrounding larval cells retreat and are gradually sloughed off into the body cavity to be devoured by phagocytes. The newly generated areas spread over the thorax, unite, and finally construct the entire thorax of the fly. In describing the formation of the thorax of *Melophagus,* Pratt (1897) says: "In proportion as the larval hypodermis disappears under the attack of the phagocytes, the edges of the imaginal discs grow and take its place, forming the imaginal hypodermis." The idea that the larval cells are *first* destroyed by phagocytes, however, is not in accord with results of later investigators. The cephalic histoblasts of the fly have no opposition from larval cells because of the great reduction of the larval head; the elaborate head of the cyclorrhaphous fly is practically a new structure with no counterpart in the larva.

Likewise, the mouth parts of the fly owe little to those of the larva. The larval mouth hooks are not re-formed in the pupa, and the fly has no trace of mandibles. The adult labium is formed from a pair of histoblastic pouches developed inside the larval labium. According to Wahl (1914) these ventral histoblasts give rise to the entire proboscis of the fly, including the hypopharynx, the maxillary remnants, and the labrum, which statement suggests that the matter should be reinvestigated. The cyclorrhaphous larva, as already observed, has no free hypopharyngeal lobe, and the salivary duct opens on the base of the labium (fig. 2 C, *SlDct*). In the fly, on the other hand, the salivary outlet duct traverses a median stylet arising at the base of the labium, which is commonly called the hypopharynx. Because this stylet gives passage to the salivary duct, however, Ferris (1950) asserts that it is not a hypopharynx, but a secondarily developed outgrowth containing the salivary outlet. According to the same interpretation the Hemiptera and Siphonaptera also should not have a hypopharynx. While it is generally true that the salivary outlet duct of insects opens between the base of the hypopharynx and the base of the labial prementum, the opening is sometimes on the base of the hypopharynx, as in the cockroach (fig. 3 A, *SlO*), in dragonflies, and, as shown by Weber (1938), in the Psocoidea. The hypopharynx is a median, postoral outgrowth of the ventral wall of the head, principally on the maxillary segment, but it may encroach on the labial segment. If the organ includes a labial element, therefore, it is nonetheless a hypopharynx, and if the salivary duct opens into a pocket on its base it might traverse its entire length. In the larvae of nematocerous flies a hypopharynx is present, but, as in other holometabolous insects, it is united with the labium in a composite suboral lobe and the outlet duct of the salivary glands opens distally between the two component parts of the latter. The ancestors of the Diptera, therefore, must have possessed a true hypopharynx, and there would seem to be no reason why it should not be restored in the adult, just as are the legs. Weismann (1864) called the median mouth stylet of the fly "die Kieferborste," and described it as formed by the union of paired parts about a cellular strand that became the salivary duct. Again, we can say only that the pupal development of the mouth parts of the cyclorrhaphous flies needs further investigation, since the ordinary criterion of correlating the adult parts with the larval parts cannot be invoked.

A comparison of the mouth parts of the fly with those of the cockroach shows at least that the stylet containing the salivary outlet of the fly (fig. 3 F, *Hphy*) corresponds exactly in position with the free lobe of the hypopharynx in the cockroach (A, *Hphy*). Its grooved dorsal surface, moreover, is continued into the floor of the sucking pump (F, *CbP*), which represents the floor of the cibarium on the base of the hypopharynx in the cockroach. Even the oral arms of the suspensory rods of the cockroach hypopharynx (A, *y*) may be retained in the flies as a pair of short cibarial processes (B, F, *y*) embracing the primary mouth (F, *Mth'*).

Finally, in connection with the metamorphosis of the fly's head, we should mention the ptilinum, since it constitutes an example of exceptional development in the pupa of a special structure for the temporary use of the fly. The ptilinum is a vesicular introversion of the front of the head of the pupa in the schizophorous families of the Cyclorrhapha, which is everted by the emerging fly to open the anterior end of the enclosing puparium. After emergence, the lips of the opening come together in the long groove of the head that arches over the bases of the antennae (fig. 1 A, *pts*). As described by Laing (1935), in *Calliphora* the ptilinum is formed in the young pupa from the head wall just above the antennae, which on the third day of pupal life begins to introvert and soon becomes a crumpled sac inside the head with a greatly thickened cuticle. Eversion of the ptilinum in the emerging fly is brought about by blood pressure resulting from contraction of the abdomen. The surface of the organ in different flies may be smooth, covered with fine spicules, or, as in *Gonia* (fig. 1 D), thickly coated with coarse spines. After the ptilinum has served its purpose it is again retracted and remains as a large though shrunken body in the fly's head. The retraction is caused by muscles, which are fully described by Laing. Some of the muscles are special ptilinal retractors, and these muscles disappear during the first two days of the life of the fly.

Metamorphosis in the cyclorrhaphous Diptera is a "change of form" in the insect as a whole, but it is not a transformation of the maggot into a fly. The maggot represents an extreme degree to which juvenile development among the insects has diverged from the evolutionary course that produced the adult, until the young insect has become an independent creature in no way structurally related to its parents. The embryo develops directly into the form of the larva and not into that of the insect that produced it, but certain cells of the larval tissues retain the potentiality of reproducing the corresponding adult tissues, while the rest of the larval tissues, after performing their temporary function, go into dissolution and become food for the growing imaginal tissues. The maggot is in no sense a recapitulation of any stage in the evolution of the fly, except larval stages of its more recent ancestors. The larval form is determined at an early period of development in the egg, and when the larva has completed its destiny it gives way to the ancestral development of the fly, but the manner in which the modern fly is developed has no phylogenetic significance. The larval development and the adult development are known to be under control of hormones, but the mechanism of dual inheritance has not been explained.

EXPLANATION OF LETTERING ON THE FIGURES

a, membrane over frontoclypeal plate of larva, inner wall of head fold.
Ant, antenna.
Atr, head atrium.

b, space between head fold of embryo and frontoclypeal plate.
Br, brain.

c, posterior end of frontoclypeal plate, origin of inner wall (*a*) of head fold.
Cb, cibarium.
CbP, cibarial pump.
Clp, clypeus.
Cr, crop.

d, end of dorsal wall of head fold.
dlcb, dilator muscles of cibarial pump.

e, H-shaped sclerite supporting mouth hooks.
E, rudiment of compound eye.

f, paraclypeal phragma.
fm, food meatus.
Fr, frons.
FS, frontal sac.

Gng, ganglion.

h, hinge of clypeus on frons.
hf, head fold.
Hphy, hypopharynx.
hpl, hinge plate of clypeus.
Hst, hypostome.
Hstl, haustellum.
hy, hyoid sclerite.

L, legs.
Lb, labium.
Lbl, labellum.
LH, external larval head lobe.
Lm, labrum.

mh, mouth hooks of larve.
Mth', primary mouth (entrance to stomodaeum).
Mth'', secondary mouth (entrance to cibarium).
Mth''', tertiary mouth, prestomum (aperture to food meatus between labella).
MxPlp, maxillary palpus.

NC, nerve cord.
Nv, antennal nerve.

Oe, oesophagus.

Phy, pharynx.
Ptl, ptilinum.
pts, ptilinal sulcus.

Rst, rostrum of proboscis.

SlDct, salivary duct.
SlO, salivary orifice.
Stom, stomodaeum.

Th, thorax.
thf, thoracic fold.

Vent, ventriculus.
vf, ventral head fold.

W, wing.

y, oral arm of hypopharyngeal suspensorium, or of floor of cibarium.

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