THE ANATOMICAL LIFE
OF THE MOSQUITO

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R. E. SNODGRASS

Research Associate
Smithsonian Institution

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INTRODUCTION

Mosquitoes are not popular with warm-blooded animals, but from their own standpoint they have been highly successful insects, until recently when they have been attacked with poison sprays and have had their larval habitats drained. Success, however, is always to be admired whether in man or an insect, and it is instructive to see how it has been achieved. The mosquitoes have attained their place in the world by the evolution of highly specialized anatomical characters. A study of their anatomy may help some in our war against them, and it will give a most interesting example of how insects have evolved structures fitting them for particular ways of living and of feeding that have made them so successful in the struggle for existence.

The family name of the mosquitoes is Culicidae, and they belong to the order Diptera, or two-winged flies, which in turn are members of that large group of insects in which the young, or larvae, are very different from their parents in form, structure, and habits, and must undergo a renewed growth to attain the adult state. We are so accustomed to seeing young animals grow up gradually into adults that it seems very remarkable that an animal can completely change its shape and structure in the middle of its life. The young mosquito, for example, hatches from the egg as an active larva having no resemblance to its parents but fully adapted in its structure for living and feeding in the water. During its life the larva sheds its cuticle four times. At each of the first three ecdyses it comes out a little larger than before, but with little change otherwise. On shedding the fourth cuticle, however, a very different creature, the pupa, emerges. The pupa has all the adult organs, though in an incomplete state of development, and is clearly a preliminary adult. With a final moult and ecdysis the completed mosquito appears, equipped for an entirely different life from that of the larva.

It is commonly said that the larva is metamorphosed into the adult

during the pupal stage. Actually it simply returns to its parental adult structure after having undergone during its evolutionary history a metamorphosis by which it took on a form and structure suited to a way of living quite different from that of its parents. The embryo, from its very beginning in the egg, develops into a larva. The egg, therefore, contains two distinct hereditary factors, one that first produces the larva, another that later generates the parent adult. When the larva does not differ too much from its parents, the adult may be formed mostly by a new growth of the larval tissues; but as the difference becomes more extreme, the larval tissues go into a state of dissolution and the adult is built up of embryonic cells that multiply but do not become organized during the larval stage. The transformation of the mosquito is intermediate between these two conditions.

Inasmuch as the word *metamorphosis* means simply a "change of form," we may say that the larva in its aberrant evolution has undergone a *divergent* metamorphosis, and that as an individual it resumes the parental form by a *convergent* metamorphosis.

Since the egg has the potentiality of developing into both the larval and the adult form, there must be some influence that allows the larva to develop first. The inhibition of adult development is effected by a hormone, known as the *juvenile*, or *status quo*, hormone. When the larva is mature and has served its purpose in the life of the insect, this hormone ceases to be effective, and the adult development proceeds under the stimulus of another hormone. This at least is the usual story of endocrinal regulation of insect growth and transformation, but, as will be seen, the mosquito does not comply fully with the rules of hormone control in its growth from larva to adult.

Before going on with anatomical descriptions of the larval, pupal, and adult stages of the mosquito, a few terms should be defined as they will be used. An *instar* is the insect between any two consecutive moults. *Moulting* is the physiological process of separating the old cuticle from a new cuticle being formed by the epidermis beneath it. The new instar begins its development when the moult is completed, but remains inside the old cuticle until it is fully formed. Then it breaks the cuticle and comes out. The emergence of the insect is its *ecdysis* (coming out). *Moulting* and *ecdysis*, therefore, refer to two different events, and are not synonymous terms, though many entomologists have not distinguished them as such. In life-history studies the "instar" is usually regarded as the insect between ecdyses, but since development begins inside the old cuticle, an instar is really the insect between moults. The concealed intracuticular period of the

instar has been appropriately named by Hinton (1946, 1958a) the *pharate,* or cloaked, stage of development. The pharate stage of the pupa in the larval skin is commonly called the "prepupal stage of the larva," but the larva has already ceased to be a larva, so the expression does not conform with the facts. The mosquito will demonstrate a number of other errors commonly made by entomologists.

The problem of explaining how an animal in its evolution has become adapted structurally to its environment and a special way of living is complicated in an insect such as the mosquito that lives two entirely different lives. If adaptation affects two or more organs separately, the matter is relatively simple, but when it involves coadaptation in all parts of the animal, it is hard to understand how evolution by means of natural selection has brought it about. On the other hand, the technique of "special creation" is entirely incomprehensible.

The writer began this work on a very meager acquaintance with the anatomy of mosquitoes, especially of the larva and pupa. For its completion he is deeply in debt to others, in particular to Dr. Alan Stone and Dr. Richard H. Foote at the U. S. National Museum for literature and the identification of species; to Dr. Paul Woke of the National Institutes of Health at Bethesda, Md., for an abundance of live larvae; to Dr. Ernestine B. Thurman, also of the Institutes of Health, and Dr. Jack Colvard Jones of the University of Maryland for much supplementary information and a critical reading of the manuscript; to various authors for copied drawings; and to Mrs. R. E. Snodgrass for the typing. For morphological interpretations the writer assumes entire responsibility.

I. THE LARVA

Mosquito larvae hardly need an introduction. They are the familiar aquatic "wrigglers" or "wigglers" that everybody knows turn into mosquitoes. Anatomically the most specialized parts of them are the head, the feeding organs, and the respiratory system. A number of good papers have been written on the larval anatomy, and the facts of structure have been well-enough described, but the writers, particularly on the head and feeding organs, mostly disagree as to the homologies of the parts, and consequently the different terminologies used must be very confusing to students. Hence, in the following text, the larval head and organs of feeding are given a disproportionate amount of space in an effort to arrive at reasonable interpretations and an acceptable terminology. Otherwise than in the head and feed-

ing apparatus, the principal specialization of the larva pertains to the respiratory system. The only functional respiratory apertures are a pair of dorsal spiracles near the end of the abdomen, the lateral spiracles being closed except at ecdysis when the tracheal linings are partly pulled out through them.

THE HEAD

The head of a mosquito larva projects forward from the thorax in line with the axis of the body, bringing the mouth parts to an anterior position. In most adult insects the head hangs downward on the thorax, so that the face is anterior and the mouth parts ventral. In the prognathous mosquito larva the face becomes dorsal and the mouth parts anterior. In going from adult to larva, therefore, instead of reversing the meaning of "dorsal" and "ventral," it will be better to speak of the *upper* and *lower* surfaces of the larval head, though "anterior" and "posterior" in either larva or adult will be directions relative to the axis of the body.

The typical shape of the mosquito larval head is oval or ovate, whether seen from above (fig. 1 A,B,C) or from the side (E), but the upper surface is more rounded than the lower. In some species, however, the head is almost rectangular in form (D). Anteriorly the head bears laterally a pair of large mustachelike brushes, and usually between them a small median brush, the three being supported by the labrum. Shortly behind the lateral brushes arise the slender, tapering, unsegmented antennae (E, *Ant*). Posteriorly on each side of the head is a large dark spot (*E*) varying in size with the age of the larva. These spots are the pigmented compound eyes of the adult developing in the epidermis beneath the larval cuticle. Behind or below each compound eye is a small, simple, presumably functional larval eye (*O*). The lateral area of the head between the antenna and the eye is the *gena* (*Ge*), that behind and below the eye the *postgena* (*Pge*). Posteriorly the head abruptly narrows to the occipital foramen, which is rimmed by a darkly sclerotized band, the *postocciput,* set off by a *postoccipital sulcus*. The membranous neck is usually cylindrical (fig. 1 A), but in *Anopheles* (fig. 3 C) it is narrowed where it joins the thorax, evidently to facilitate the turning of the head upside down while feeding.

The upper surface of the head (fig. 1) is differentiated into a large, shieldlike central area, narrow lateral areas bearing the antennae and the eyes, and a slender transverse anterior sclerite at the bases of the brushes. This sclerite (A,B, *Lm*) is the dorsal wall of the *labrum,*

as contended by Cook (1944a), though some writers have regarded it as a "preclypeus." The groove behind it (A, *cls*) then is the *clypeolabral sulcus*. The large central area of the head is bounded by lateral lines (*CL*) that diverge forward from a very short occipital cleft and become continuous with the clypeolabral sulcus. These lines, commonly called "frontal sutures," are merely lines of weakness
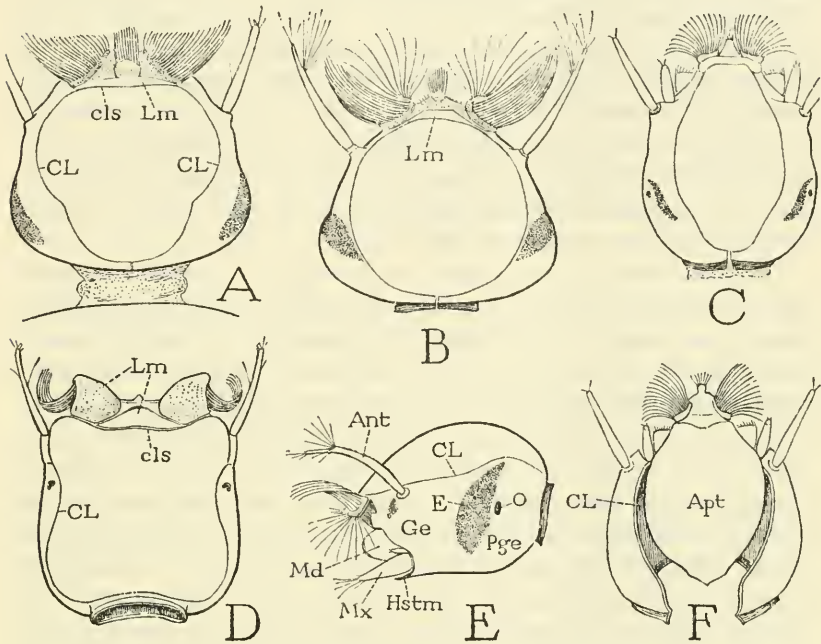
FIG. 1.—The larval head, dorsal and lateral.

A, *Aedes aegypti*. B, *Culex* sp. C, *Anopheles quadrimaculatus*. D, *Toxorhynchites rutilus*. E, *Culex* sp., lateral. F, *Anopheles farauti*, head exuviae. *Ant*, antenna; *Apt*, cephalic apotome; *CL*, cleavage line; *cls*, clypeolabral sulcus; *E*, compound eye; *Ge*, gena; *Hstm*, hypostomium; *Lm*, labrum; *Md*, mandible; *Mx*, maxilla; *O*, group of larval simple eyes; *Pge*, postgena.

in the cuticle where the latter will split at ecdysis (F, *CL*) to allow the emergence of the next instar, and are best termed the *cephalic cleavage lines*. In most young insects the cleavage lines take the form of a Y, which has been known as the "epicranial suture." In the mosquito larva the stem of the Y is the short occipital cleft. The frontal arms follow such very different courses in different insects that they can have no morphological significance (see DuPorte, 1946; Snodgrass, 1947), and hence do not define any specific part of the

head. The part of the head wall cut out at ecdysis may be termed the *cephalic apotome* (F, *Apt*).

The space between the arms of the cleavage lines and the clypeolabral sulcus in the mosquito larva has been variously called the "frons," the "clypeus," and the "frontoclypeus." The respective areas of the frons and the clypeus may be identified in other insects by specific groups of muscles that arise on them. In the mosquito larva the clypeal muscles arise anteriorly, the frontal muscles posteriorly on the central head area, but there is no external demarcation between the two regions. This area, therefore, is frontoclypeal in a limited sense, but it is not the entire clypeus or the entire frons. Ordinarily the clypeus extends laterally to the bases of the mandible, and in adult insects the frons is the facial area between the antennae and the eyes. The whole aspect of the mosquito head is changed at the transformation to the pupa and the adult.

The larval antennae are slender, unsegmented shafts bearing variously distributed spines and tufts of long hairs. Each terminates in a small apical papilla. The antenna of the pupa, being eventually much larger than the larval organ, does not develop within the latter but in a pocket extending posteriorly from the base of the larval antenna.

The eyes of the larva are each a group of simple lateral eyes; their structure in *Culex pipiens* has been described by Constantineanu (1930) and by Satô (1951b). According to Satô each eye consists of three parts, each with its own retinular cells. One part is central and has three retinulae, a second part is dorsal and has a single retinula of eight cells, the third part is a long band of about 40 cells surrounding the other two parts dorsally, anteriorly, and ventrally. Constantineanu, on the other hand, describes five parts in the eye of *Culex*, as in some other nematocerous larva. Probably the three retinulae of Satô's "central part" are regarded as three eyes. The larval eyes have no lenses, the ordinary head cuticle being continuous over them. They are present from the beginning of the larval stage and persist into the pupa, or even into the adult.

The presence of large, darkly pigmented compound eyes visible on the surface of the head gives the mosquito larva, as also the corethrid larva, a very unusual appearance. The compound eyes of other related Nematocera are developed likewise in the larva, but, because of the absence of pigment until the pupa stage, they are not apparent externally.

The undersurface of the larval head (fig. 3 C,D,E,F) is more difficult to understand than the upper surface. The mandibles and

maxillae are articulated on a transverse margin between the bases of the antennae. The long ventral cranial wall behind them is sclerotically closed by the union of the postgenae (C, *Pge*) along an incomplete median suture (C,D,E, *ms*). This same condition occurs in certain other insects, and to understand how it has come about we shall have to digress on some comparative studies.

The hypognathous position of the insect head in which the mouth parts are ventral (fig. 2 A) is clearly primitive, because the mouth parts, being modified legs, thus hang down from the head in the position of the thoracic legs. The prognathous condition has been attained in some cases by a mere turning forward of the head on the neck, involving a ventral elongation of the occipital foramen on the underside of the head (fig. 3 B). More commonly, however, the foramen remains in the vertical plane, as in the mosquito larva (fig. 1 E), and the underside of the head is lengthened by a ventral elongation of the postgenae (*Pge*).

With the elongation of the postgenae the entire labium, as in some beetles (fig. 2 B), may be simply enclosed between them, with a gular addition (*Gu*) to the submentum. This condition, however, does not occur in the larval mosquito, though some writers have so interpreted the mosquito head structure. More commonly, the postgenae come together medially and displace the labium. A primary stage of this transformation is seen at C, which might represent the head of a caterpillar or an adult honey bee, in which lobes of the hypostomal margins of the postgenae are intruded between the occipital foramen and the base of the labium. In other cases the lobes become united (D), forming a bridge between the foramen and the labium. An elongation of the bridge then produces the condition seen in the beetle larva at E, in which the labium is still fully exposed. Finally, as in the larvae of Chironomidae (F), the labium has become greatly reduced and is hidden from below by a median hypostomal lobe (*Hstm*) of the united postgenae.

This same process of closure and elongation of the postgenae and the reduction of the labium can be traced among nematocerous fly larvae. For example, in the primitive rhyphid larva of *Olbiogaster* (fig. 3 A) described by Anthon (1943b), a pair of small postgenal lobes are approximated behind the submentum (*Smt*) of the labium. In others, as in *Trichocera* and *Philosepedon* figured by Anthon (1943a, figs. 7, 10) the postgenal lobes are united in a bridge; the labium, though much reduced, is still mostly exposed. In the mosquito larva (fig. 3 C) the united postgenae form the long underwall of the

cranium and the greatly reduced labium is concealed above a median postgenal lobe (*Hstm*) between the maxillae (*Mx*).

The darkly sclerotized dentate lobe between the maxillae has commonly been regarded as a part of the labium, "mentum" or "submen-
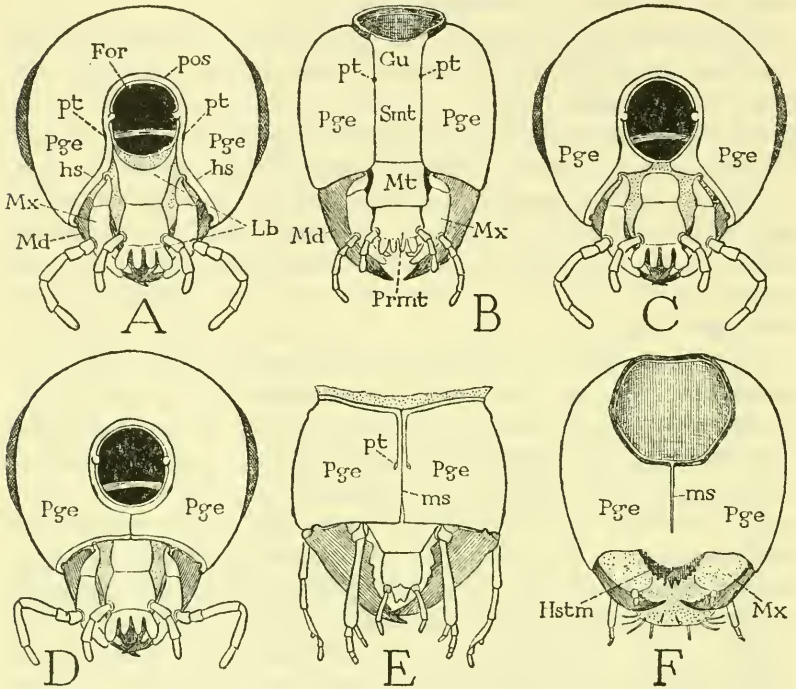

FIG. 2.—Structure of the posterior or ventral wall of the head in different insects, mostly diagrammatic.

A, Generalized structure of the posterior head wall and the mouth part attachments. B, The labium enclosed between the postgenae. C, The labium separated from the occipital foramen by intruding hypostomal lobes of the postgenae. D, The labium entirely separated from the foramen by union of postgenal lobes forming a postgenal bridge. E, Postgenal bridge lengthened. F, Larval head of *Chironomus*, postgenal bridge produced in a toothed lobe, labium displaced dorsally.

For, occipital foramen; *Gu*, gula; *hs*, hypostomal sulcus; *Hstm*, hypostomium, hypochilum; *Lb*, labium; *Md*, mandible; *ms*, median postgenal suture; *Mt*, mentum; *Mx*, maxilla; *Pge*, postgena; *pos*, postoccipital sulcus; *Prmt*, prementum; *pt*, posterior tentorial pit; *Smt*, submentum.

tum." To cut a long argument short, however, we have only to look at a tipulid larva (fig. 3 B) to see that the lobe is formed by the union of two processes extended forward from the anterior median angles of the postgenae, which themselves are not united in the tipulid. Above

this lobe are the united labium and hypopharynx (fig. 7 A, *Lb, Hphy*). We may, therefore, following Anthon (1943a), Hennig (1948, 1950), and Lawson (1951), appropriately call this lobe the *hypostomium* (*Hstm*), as it is termed also by Chiswell (1955) in the tipulid larva. Though Schremmer (1949) called it "mentum" in the mosquito larva, he later (1950) expressed doubt of the correctness of this designation, concluding that the lobe is rather a part of the cranial wall. More recently, Gouin (1959) has termed the dentate lobe the *hypochilum* (underlip).

From the base of the hypostomium there arises in some species a thin fold bearing a fringe of pectinate hairs or blunt teeth (fig. 15 A, *Aul*). The fold is the *aulaeum* (curtain) of Cook (1944a), but it has been variously named. Shalaby calls it the "glossa" on the assumption that it is formed by the union of a pair of labial glossae, a highly improbable interpretation since the hypostomium itself is no part of the labium. However, Shalaby has given detailed illustrations of the pectinate hairs of the lobe in *Aedes aegypti* (1957a) and *Culex quinquefasciatus* (1957b), and its armature of eight blunt teeth in *Anopheles quadrimaculatus* (1956). In *Psorophora ciliata* (1957c) he says the fold is absent.

In most mosquito larvae two dark lines in the ventral wall of the head diverge posteriorly from the basal angles of the hypostomium. In some species the lines are short (fig. 3 C,D, *r*), in others (E,F) they extend back to the posterior tentorial pits (*pt*); in *Chironomus* (fig. 2 F) they are absent. These lines when present are the external marks of internal ridges; their variable development suggests that the ridges are secondarily formed to strengthen the head wall. The surface area between the lines, however, has commonly been regarded as the basal part of the labium, probably because the structural pattern they produce resembles that of the head shown at B of figure 2. It has been suggested even that the median suture is the line where the two original labial appendages have united! Cook (1944a), for some obscure theoretical reason, calls the area in question the "maxillary segment," though the maxillae have no relation to it. That the ventral closure of the head results entirely from the union of the lateral cranial walls is clearly indicated in illustrations by Hennig (1948, figs. 31-37) of larval heads of Sciophilidae, in which are shown various degrees of approximation and union of the postgenal margins.

In most adult insects the lower edges of the cranium are reinforced by submarginal internal ridges formed by external grooves known as the *subgenal sulci*. The part of each groove on the postgena behind

the mandible is distinguished as the *hypostomal sulcus* (fig. 2 A, *hs*). Posteriorly these grooves become continuous with the postoccipital sulcus (*pos*) that surrounds the occipital foramen. In the mosquito larva the lower ends of the postoccipital sulcus have extended forward in the postgenal region carrying with them the minute rudiments of the posterior tentorial arms, the position of which is marked externally by a pair of pits (fig. 3 E,F, *pt*). The anterior tentorial arms are extremely slender bars arising from the cranial margins mesad of
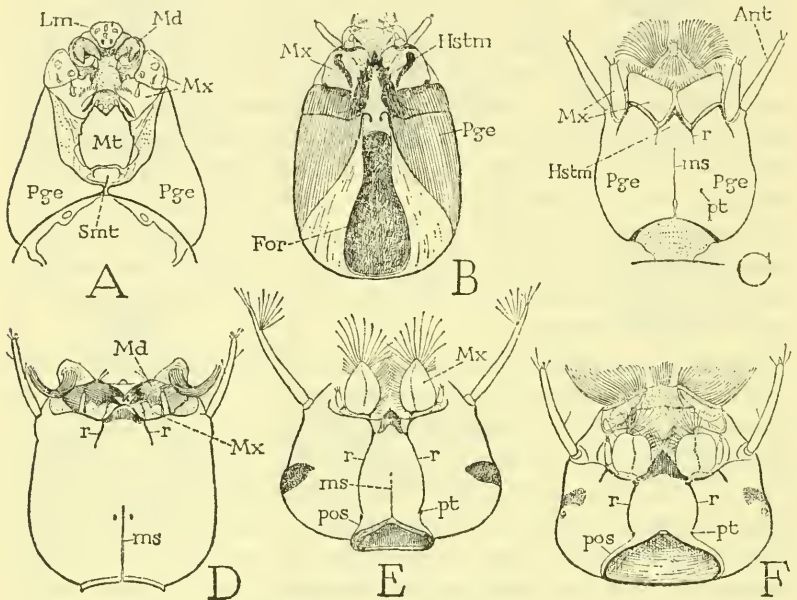
FIG. 3.—The larval head, undersurface.

A, *Olbiogaster* sp., Rhyphidae (from Anthon, 1943b). B, *Tipula* sp. C, *Anopheles quadrimaculatus*. D, *Toxorhynchites rutilus*. E, *Culex* sp. F, *Aedes aegypti*.

r, r, grooves in lower head wall. Other lettering as on figure 2.

the antennae that extend back to the posterior arms. Possibly it is the great lengthening of the postgenal regions of the head that has brought the posterior arms to their forward position.

The postgenal bridge is known also as the hypostomal bridge because it is the hypostomal margins of the postgenae that come together to form it. Lawson (1951) contends that the sclerotized ventral wall of the head behind the mouth parts cannot be derived from the postgenae because, he says, "the hypostomal sutures form the ventral

boundaries of the postgenae." This is clearly making anatomy con-
form with definitions. The lower parts of the postgenae are mechani-
cally strengthened by ridges formed by the submarginal hypostomal
grooves. The narrow strips below the grooves, therefore, are simply
the marginal parts of the postgenae, so it is immaterial whether we call
the bridge resulting from their union hypostomal or postgenal. The
grooves are sometimes absent, and the ridges may be marginal on the
postgenae. In the mosquito larva the anterior edge of the ventral
cranial wall on which the mandibles and maxillae are articulated is the
united hypostomal margins of the confluent postgenae.

From the free cranial margins just mesad of the antennal bases,
a slender bar on each side (fig. 7 B, *hb*) extends mesally, downward,
and somewhat posteriorly through the preoral epipharyngeal wall to
the base of the hypopharynx (*Hphy*). Each bar runs close before the
mandible of the same side and goes below the narrow lower lip of
the mouth (*Mth*). In *Dixa*, as shown by Schremmer (1950), similar
structures are present but are much wider than in the mosquito larva.
The mandibles have their anterior articulation on these rods, a very
unusual condition, since the anterior mandibular hinges are typically
on the basal angles of the clypeus. The rods have been called "cibarial
bars," but there is no defined cibarium in the culicid larva. Since the
rods appear to serve principally as suspensoria of the hypopharynx,
they are here termed *hypopharyngeal bars*. They are the *Verbindungs-
leisten* of Schremmer (1949). Since the hypopharyngeal bars carry
the anterior articulations of the mandibles, Menees (1958b) reason-
ably argues that the parts of the bars laterad of the articulation are
extensions of the clypeus. His identification of the posterior parts
with the "hypopharyngeal suspensorial bars of generalized insects,"
however, is less convincing, since these bars enter the mouth angles
and give attachment to the hypopharyngeal muscles, though each may
have a lateral preoral branch.

THE FEEDING ORGANS

One of the remarkable things about insects is the way their feeding
organs are variously adapted to feeding in different ways on different
kinds of food. Nothing comparable occurs among the vertebrates,
their only adaptation to the nature of their food is in the size, strength,
and dentition of their jaws or in the length of the neck. Yet the feed-
ing organs of all insects are made up of the same fundamental parts.
There is an upper lip known as the *labrum*, a pair of *mandibles*, a
median tonguelike *hypopharynx*, a pair of *maxillae*, and a lower lip, or

labium, composed of a united pair of second maxillae. The mandibles, maxillae, and labium, furthermore, have been fashioned from three pairs of legs, since the original arthropods had no other organs for feeding than their legs. The insect mouth parts, therefore, are all *outside* the mouth ; the space between them may be termed the *preoral food cavity,* but by a long-perpetuated error it has commonly been called the "pharynx." For want of a revised nomenclature we still speak of the upper wall of the preoral cavity as the *epipharyngeal surface,* and call the tonguelike lobe that projects below the mouth the *hypopharynx.* This is just a part of our heritage from the early insect anatomists, who had only vertebrate names to draw from, and applied them to insects on a functional rather than a morphological basis. The true *pharynx* is a part of the stomodaeal section of the alimentary canal behind the mouth.

The labrum.—The labrum of the mosquito larva includes the small transverse sclerite on the dorsal wall of the head before the clypeus (fig. 1 A, *Lm*), and a larger membranous undersurface that bears laterally the two vibratory feeding brushes (fig. 4 B), and usually a small median brush. The median brush is the "palatum" of mosquito students, another example of misuse of a borrowed vertebrate name, which in this case properly refers to the roof of the mouth cavity.

The lateral brushes of the labrum are the organs by which those larvae that feed on particles create currents in the water directed toward the head, and drive a stream of water back to the mouth along the epipharyngeal surface. The individual hairs of the brushes are finely pectinate and serve also as combs for retaining particles filtered from the water.

The vibratory movement of the brushes is produced by a pair of strongly musculated sclerites on the under side of the labrum. Similar sclerites are present in the larvae of Chironomidae (fig. 4 G, *Tor*), which have no brushes, but the posterior ends of the sclerite are produced into strong pointed processes (*Mes*) projecting freely from the epipharyngeal surface. These toothed sclerites were therefore called by most earlier writers "premandibles." Chaudonneret (1951), however, has shown that this term is entirely inappropriate. Cook (1944b) named the sclerites "messores" (harvesters) and carried the term over to the mosquito larvae, in which he has been followed by several recent writers, though the culicid sclerites are unarmed.

It must be noted that the insect labrum is commonly equipped with four muscles, one pair dorsal, the other ventral, all of which arise on the frons. The ventral muscles are usually attached on a pair of

sclerites in the lower labral wall known as the *tormae*. In a tipulid larva (fig. 4 A) the tormae (*Tor*) are simple sclerites, each giving attachment to a long muscle (*mcl*) from the frons. There is, therefore, no apparent reason why the similarly musculated sclerites of the mosquito larval labrum (C,D, *Tor*) should not be the tormae. On the other hand, Cook (1944b) has contended that the sclerites are
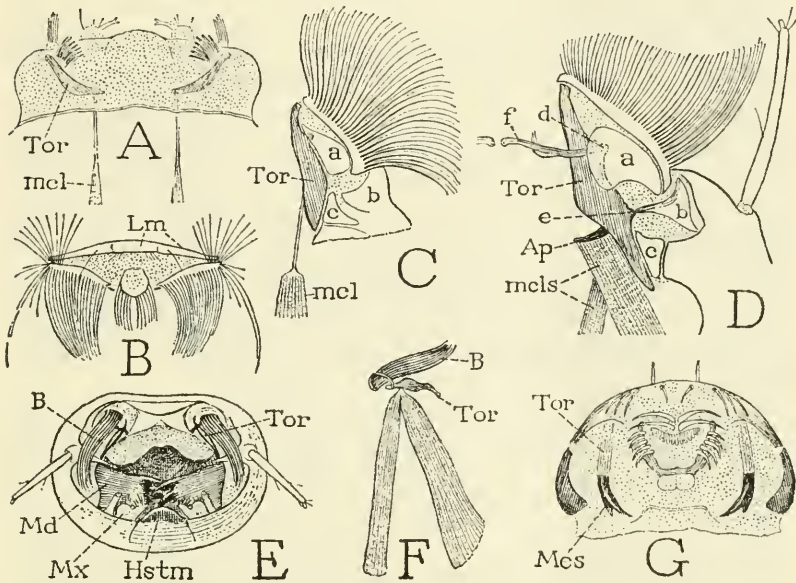

Fig. 4.—The larval labrum and tormae.

A, *Tipula* sp., underside of larval labrum. B, *Culex* sp., labrum of young larva, anterior. C, *Anopheles quadrimaculatus*, left labral brush and torma, undersurface. D, *Aedes aegypti*, same. E, *Toxorhynchites rutilus*, anterior view of larval head. F, Same, labral brush with torma and muscles. G, *Chironomus plumosus*, underside of larval labrum.

Ap, tormal apodeme; *B*, labral brush; *Hstm*, hypostomium; *Lm*, labrum; *mcl, mcls*, tormal muscle or muscles; *Md*, mandible; *Mes*, messorial teeth of torma; *Mx*, maxilla; *Tor*, torma.

a, connective sclerite between torma and brush; *b, c*, detached sclerites of cranial wall; *d, e*, anterior and posterior articulations of torma; *f*, epipharyngeal bar.

not the tormae because he finds in chironomid larvae another pair of muscles attached more dorsally and laterally on the labrum, which he insists are the true tormal muscles. These muscles, however, would appear to be the usual dorsal muscles of the labrum, which may have a lateral position. Furthermore, Cook adds that the ventral muscles are not tormal muscles because they arise on the clypeus, but what he calls

"clypeus" is the entire frontoclypeal area of the upper head wall between the cleavage lines. The sclerites in question, being in the ventral wall of the labrum and giving attachment to the ventral labral muscles, practically identify themselves as the tormae, and they have been regarded as such by Anthon (1943a), Schremmer (1949, 1950), and Menees (1958b). If it is desirable to keep the term "messor," it might be restricted to the free prongs of the tormae where they occur (fig. 4 G, *Mes*).

The tormae of an *Anopheles* larva (fig. 4 C, *Tor*) are elongate sclerites lying mesad of the brushes. Each torma is connected by its tapering anterior end with the base of the corresponding brush; posteriorly it is hinged to a small sclerite (*c*) in the cranial margin. A connective plate (*a*) lies between the torma and the base of the brush. A single muscle (*mcl*) from the frontal region is attached by a long tendon to a small point anteriorly on the lateral margin of the torma. Cook (1944a) ascribes a second posterior muscle to the torma of *Anopheles,* but this muscle, as shown by Farnsworth (1947) and by Schremmer (1949), belongs to a V-shaped sclerite of the epipharyngeal wall between the posterior ends of the tormae.

In the culicine mosquitoes the tormal apparatus is somewhat more complex than in *Anopheles.* In *Aedes aegypti* (fig. 4 D) the tormae have the same relation to the brushes and the cranial margin as in *Anopheles,* but each torma is specifically hinged posteriorly (*e*) to a detached triangular plate (*b*) of the cranial wall, and anteriorly (*d*) to the end of a transverse epipharyngeal bar (*f*). Since both this bar and the connective plate (*a*) underlap the torma, the anterior part of the latter appears to be sunk into the lower wall of the labrum. Posteriorly a strong apodeme (*Ap*) arises from the dorsal surface of the torma and curves mesally. On this apodeme are attached two large muscles (*mcls*) from the frontal region of the head. Contraction of the muscles evidently rocks the torma mesally on its articular points and thus gives a backward and mesal stroke to the connected brush. The reverse movement of the brush, as other writers have noted, results from the elasticity of its basal connections. According to Cook (1944a) in specimens of *Theobaldia* [*Culiseta*] killed and fixed with the brushes retracted, on cutting the muscles the brushes quickly spring back to the expanded condition.

The *Aedes* tormal mechanism is probably characteristic of the Culicinae. The same structure and musculature is shown to be present in *Culex* by Thompson (1905) and by Chaudonneret (1951), and in

species of *Theobaldia* [*Culiseta*], *Lutzia,* and *Armigeres* by Cook
(1944a).

In the predaceous larvae of *Toxorhynchites* the brushes are sup-
ported on prominently projecting lateral lobes of the labrum (figs.
1 D, 4 E). The brushes are narrow, stiff, and falciform, and appear
to be grasping organs, but as observed by Breland (1949) and by
Horsfall (1955) they are not used for obtaining prey. Just mesad of
the base of each brush is a small, slender sclerite (fig. 4 E, *Tor*).
Dissection reveals that this sclerite has a connection with the base
of the brush (F) and gives attachment to two large muscles, leaving
no doubt that it is the torma.

The preoral cavity.—The undersurface of the labrum is continuous
with the so-called epipharyngeal surface below the clypeal region,
which extends back to the mouth. In most adult insects the part of
the preoral cavity above the base of the hypopharynx becomes a special
food pocket, the *cibarium,* opening directly into the mouth. In the
mosquito larva the shortness of both the labium and the hypopharynx
leaves the entire preoral cavity open below, but still it serves as a
channel for water carrying food particles to the mouth. In the tipulid
larva, however, there is a short cibarial pocket (fig. 7 A, *Cb*) above
the hypopharyngiolabial lobe just in front of the mouth. In the adult
mosquito and other sucking insects the closed cibarium becomes a
preoral sucking pump. In the mosquito larva the pharynx assumes
the sucking function.

The epipharyngeal apparatus.—Lying in the epipharyngeal surface
between the posterior ends of the tormae is a structure that serves to
comb food particles from brushes on the mandibles. Since it is
musculated, and hence functions actively instead of passively, this in-
strument has been termed by Schremmer (1949) the *Epipharynx-
apparat.* Other writers have called it the "palatal bar," the "epi-
pharynx," and the "epipharyngeal armature." It includes a transverse
bar and groups of setae or other structures arising in front of the
bar. The crossbar is usually bow-shaped or V-shaped with the arms
diverging forward to the posterior ends of the labral tormae. The
setal accompaniment of the bar is quite different in different species.

In *Aedes* (fig. 8 A) the epipharyngeal apparatus is relatively simple.
The bar is slender, gently curved forward, and its ends appear to be
connected with the tormal apodemes. Arising in front of the bar
are two large brushes of stiff hairs that converge posteriorly beneath
the bar. At the sides of the brushes arise a pair of large, tapering,
hair-bearing processes directed posteriorly, and at the base of each are

two small clawlike structures. In *Culex* (B) the bar is strongly developed and angulated, its ends, as in *Aedes,* appear to be attached to the apodemes of the tormae. In front of the bar are two large oval masses of setae curving inward and posteriorly. From above these setal masses two brushes of long hairs project posteriorly. Medially there arise two pairs of short tapering processes that project beneath the bar, and from each angle of the bar a slender, bladelike, sharp-pointed process extends posteriorly.

The epipharyngeal apparatus of *Anopheles* as described by Schremmer (1949) is again quite different from that of either *Aedes* or *Culex.* The bar is V-shaped with an acute angle. Several brushes arise in front of the bar, but particularly developed are two long, wide combs of flattened, sharp-pointed bristles that extend posteriorly from a pair of triangular sclerites in front of the bar. These are the *Klingenborsten* of Schremmer, who says they are used for cleaning the food particles from the combs of the mandibles. In *Anopheles maculipennis,* as shown by Schremmer and by Farnsworth (1947), a large muscle from the clypeal region of the head is attached on each end of the epipharyngeal bar. These muscles the writer has not been able to find in *Aedes* and *Culex,* but the close connection of the bar with the apodemes of the tormae possibly coordinates the movements of the epipharyngeal apparatus with the movements of the labral brushes. In all three genera a pair of very slender, closely adjacent muscles is attached medially on the bar. Contraction of the lateral muscles of *Anopheles,* according to Schremmer, protracts the apparatus from the epipharyngeal wall, the median muscles are retractors. Thompson (1905) makes no mention of lateral muscles attached on the epipharyngeal bar in *Culex,* but he notes the presence of the median retractors.

The mandibles.—Both the mandibles and the maxillae lie on the underside of the head, where they are implanted obliquely in the membranous area that turns upward from the hypostomal margins of the postgenae to the hypopharyngeal bars (fig. 7 B, *Md, Mx*), the mandibles being above the maxillae.

The typical culicine and anopheline mandibles are flattened lobes (fig. 5 D,E,F) with their mesal ends produced into strongly sclerotized toothed processes and a lower seta-bearing lobe. The dorsal margins bear large comblike fringes of long setae directed mesally. The tips of the mandibles on opposite sides do not meet when the mandibles are closed, but come against the hypopharynx, which lies between them (fig. 7 B, *Hphy*). Each mandible has a posterior basal

articular point (fig. 5 E,F, *a*) that articulates with a process of the hypostomal margin just laterad of the base of the maxilla (fig. 7 B, *a*). Its anterior articulation (fig. 5 D, *c*) is with the hypopharyngeal bar (fig. 7 B, *hb*). The mandibles move in the transverse plane by strong abductor and adductor muscles. The principal function of mandibles of this type is the collection by their setal combs of food particles from
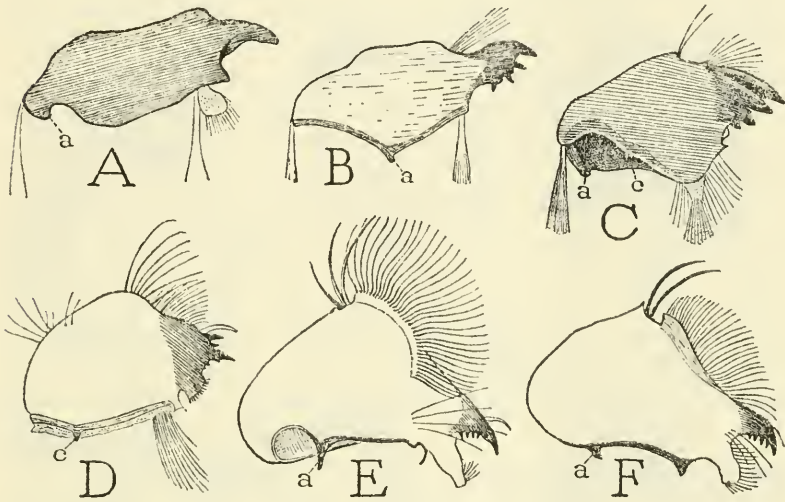

FIG. 5.—Larval mandibles.

A, *Tipula abdominalis*, right, ventral. B, *Lutzia* sp., right, ventral. C, *Toxorhynchites rutilus*, left, dorsal. D, *Anopheles quadrimaculatus*, left, dorsal. E, *Culex*, sp., right, ventral. F, *Aedes aegypti*, right, ventral.
a, posterior (ventral) articulation; *c*, anterior (dorsal) articulation.

the labral brushes, but the incisor points are said to break up larger particles that collect on the hypopharynx.

The mandibles of predaceous larvae, such as *Culex vorax* (fig. 5 B) and *Toxorhynchites* (C), are strongly toothed jaws, the points of which come together in adduction (fig. 4 E). Most larval Nematocera have jawlike mandibles (fig. 5 A), though they present many varieties of structure. *C. vorax* is a culicine mosquito, and its mandible (B) might be derived from the culicine type, but the mandible of *Toxorhynchites* (C) is a typical biting insect jaw.

The maxillae.—The maxillae of the mosquito larva (fig. 6 B-F) are so greatly simplified that they have lost the appearance and structure of an ordinary insect maxilla. They are borne on the transverse hypostomal margins of the postgenae at the sides of the hypostomium,

where they lie below the mandibles (fig. 3 C-F, *Mx*). The principal part of each maxilla is a flat lobe (fig. 6 D, *St*) of different shape in different species, bearing brushes of long setae or combs of shorter ones. Laterad of this lobe is a second cylindrical or fusiform lobe regarded as the palpus (*Plp*) varying in size relative to that of the mesal lobe. At the base of the palpus is usually a small sclerite (*x*) in the articular membrane.
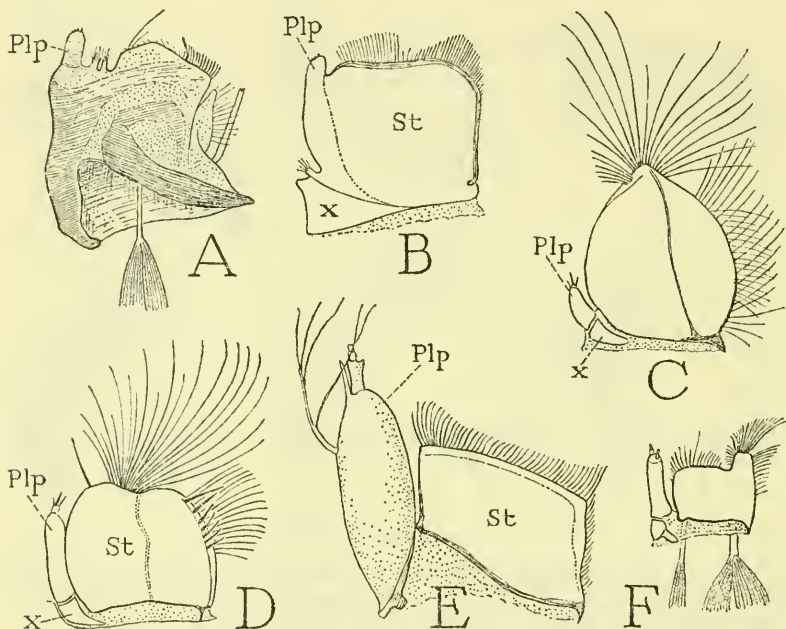
FIG. 6.—Larval maxillae, right, ventral.

A, *Tipula abdominalis*. B, *Culex vorax*. C, *Culex* sp. D, *Aedes aegypti*. E, *Anopheles quadrimaculatus*. F, *Toxorhynchites rutilus*. *Plp*, palpus; *St*, stipes; *x*, sclerite at base of palpus.

In other nematocerous larvae, as in *Tipula* (fig. 6 A), the maxillary palpus (*Plp*) is a small lateral appendage of the main maxillary lobe, as it is also in the culicid *Culex vorax* (B). In most mosquito larvae, however, the palpus appears to have somehow become separated from the rest of the maxilla (C-F). The main maxillary lobe in some nematocerous larvae, as shown by Anthon (1943a), may bear on its distal margin mesad of the palpus two variously developed outgrowths, which are identified as the galea and lacinia. The main maxillarly lobe, therefore, appears to be the stipes (*St*). The nature of the small sclerite (*x*) at the base of the palpus is uncertain. Cook

(1944a) calls it the "palpiger," but it might be referred to the cardo, though no muscles are attached on it.

The principal functional features of the culicid larval maxillae are their setal brushes and combs, which serve to collect food particles from the labral brushes. In the predaceous *Toxorhynchites* the maxillae (fig. 6 F) are similar to those of other species, but they are greatly reduced in size (fig. 4 E, *Mx*). The palpi are presumably sensory organs, but their disparity in size, as between *Culex* (fig. 6 C) and *Anopheles* (E), for example, is difficult to explain. The principal movements of the maxillae are in the transverse plane.

The labium and hypopharynx.—In most adult insects the salivary duct opens between the bases of the hypopharynx and the labium. In some larval insects, as in caterpillars and hymenopterous larvae, the labium and hypopharynx are united in a single suboral lobe traversed by the duct of the salivary, or silk, glands, which opens at the tip of the composite lobe. The same is true of some nematocerous fly larvae, as is well seen in the tipulid (fig. 7 A, *SlDct*). In the mosquito larvae the combined labium and hypopharynx are reduced to a flat or somewhat protruding vertical surface between the mouth and the hypostomium, with the salivary duct opening on it. The salivary orifice, therefore, separates the dorsal hypopharyngeal component from the ventral labial component.

The hypopharynx (fig. 7 B, *Hphy*) is supported by the hypopharyngeal bars (*hb*) from the lateral cranial walls; immediately above it is the wide mouth (*Mth*) opening into the pharynx. The labial area below the hypopharynx (D,E, *Lb*) is variously developed, usually strongly sclerotized and armed with spines or teeth. Other writers have well illustrated the details of the labial structure in different mosquito species. Some have attempted to analyze the larval labium into the parts of a typical insect prementum, but their results are not fully convincing. At C of figure 7 is shown the labiohypopharyngeal complex of *Toxorhynchites rutilus* in dorsal view, in which the salivary duct (*SlDct*) is seen opening between the two component parts. Attached laterally on the base of the labium are the tendons of a pair of muscles from the ventral head wall, as in the tipulid larva (A).

Inasmuch as all the cranial muscles of the insect labium are inserted on the prementum, the labium of the mosquito larva is evidently the prementum; the hypostomium and the ventral head wall, as already shown, being no part of the labium. Menees (1958a), however, has argued that the ventral head area behind the hypostomial lobe must be the labial submentum because the labial muscles have their origins on

it. He thus assumes that these muscles are the retractors of the prementum. The premental retractors, when present, do arise on the submentum, but they are always median in position. The muscles of the mosquito larval labium are lateral muscles, and therefore should
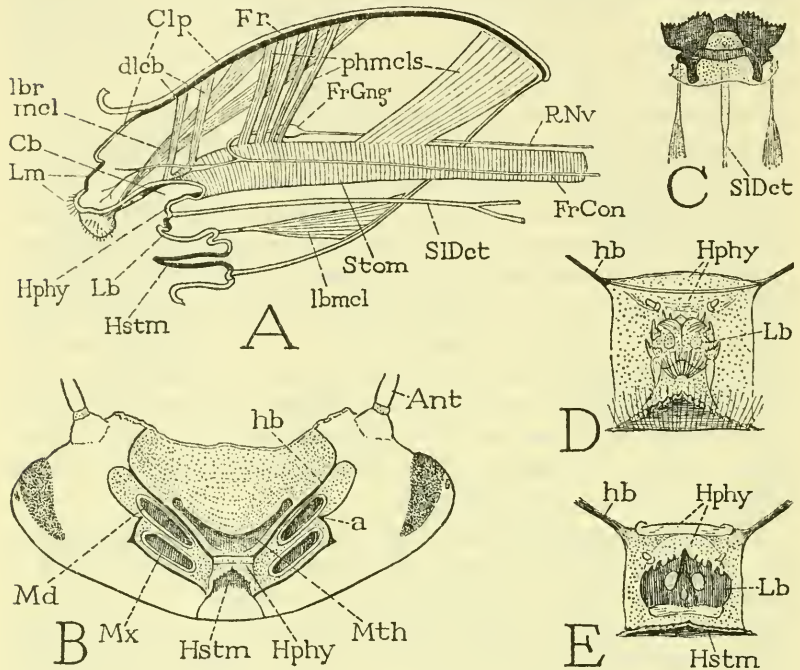

FIG. 7.—Labiohypopharyngeal complex of larvae, and associated structures.

A, *Tipula* sp., section of larval head. B, *Culex* sp., posterior part of head, anterior. C, *Toxorhynchites rutilus*, labiohypopharyngeal complex, dorsal. D, *Aedes aegypti*, same, anterior. E, *Culex* sp., same, anterior

a, posterior articulation of mandible; *Ant*, antenna; *c*, anterior articulation of mandible; *Cb*, cibarium; *Clp*, clypeus; *dlcb*, dilator muscles of cibarium; *Fr*, frons; *FrCon*, brain connective of frontal ganglion; *FrGng*, frontal ganglion; *hb*, hypopharyngeal bar; *Hphy*, hypopharynx; *Hstm*, hypostomium; *Lb*, labium; *lbmcl*, muscle of labium; *lbrmcl*, labral muscle; *Lm*, labrum; *Md*, mandible; *Mth*, mouth; *Mx*, maxilla; *phmcls*, pharyngeal muscles; *RNv*, recurrent nerve; *SlDct*, salivary duct; *Stom*, stomodaeum.

be one pair of the usual two pairs of cranial muscles of the prementum, which in other insects commonly arise on the tentorium. The same muscles in the tipulid larva (fig. 7 A, *lbmcl*) certainly have their origins on the head wall, since there is no sclerotization between the postgenae (fig. 3 B). The labial muscles of the mosquito larva, there-

fore, do not identify the head area on which they arise as any part of the labium.

The interpretation of these parts has been still further confused by Shalaby (1957d), who regards the median ventral head area as the labial submentum and mentum, the toothed hypostomial lobe as the paraglossa, the fringed lobe below it the glossa, and the entire complex above the toothed lobe the hypopharynx. Comparative studies, as already shown, give no basis for any such interpretation. Moreover, the adult labium is formed entirely from the rudiment beneath the cuticle of the larval labium (figs. 9 F, 15 A, *pLb*) and involves no part of the ventral head wall of the larva.

The larval labiohypopharynx is evidently retractile, but it plays no active part in feeding. Its principal function is said to be that of an "anvil" on which the incisor points of the mandibles strike to break up food particles.

Elaborate studies of the developmental changes in the mouth parts of larval instars of *Anopheles, Aedes, Culex,* and *Psorophora* have been made by Shalaby (1956, 1957a, 1957b, 1957c).

The pharynx.—The pharynx of larvae that feed on water-borne particles is a small, flattened, ovate or heart-shaped, thin-walled sac (fig. 8 C, *Phy*) opening directly from the wide mouth (fig. 7 B, *Mth*) and tilted upward and posteriorly in the head. From its posterior ventral surface is continued the thick-walled oesophagus (fig. 8 C, *Oe*). The ventral wall has an outer layer of semicircular muscles (E, *cmcl*) the dorsal wall is crossed by four wide muscle bands (C, *tmcl*) ; the extrinsic musculature includes dorsal and ventral dilator muscles from the head wall. The lateral margins of the pharynx are strengthened by two narrow, concentric, riblike thickenings on each side, convergent to the narrowed posterior end. Internally each of these ribs bears a long brush of fine hairs (D), suggestive of the brushes in the mouth of a baleen whale, and in fact they serve the same purpose, namely, that of filtering the food matter from the ingested water. A pharyngeal filter apparatus very similar to that of the mosquito larva is shown by Anthon (1943a) to be present in the larvae of several other nematocerous families. The pharynx of the predaceous culicid larva of *Toxorhynchites,* however, is a simple funnnel-shaped enlargement of the anterior end of the oesophagus, and has no filter brushes. In any case, the larval pharynx is not to be identified with the sucking pharynx of the adult mosquito, which lies in the posterior part of the head (fig. 24 A, *PhP*), and the larva has no cibarial pump.

Larval feeding.—The process of feeding by nonpredaceous larvae is not a mere matter of having food particles washed into the mouth by streams of water from the vibrating labral brushes. It involves cooperative action on the part of the labrum, the epipharyngeal apparatus, the mandibles, the maxillae, the labiohypopharynx, and the pharynx. The whole feeding process has been minutely described by Schremmer (1949) for the *Anopheles* larva, in which it is more readily
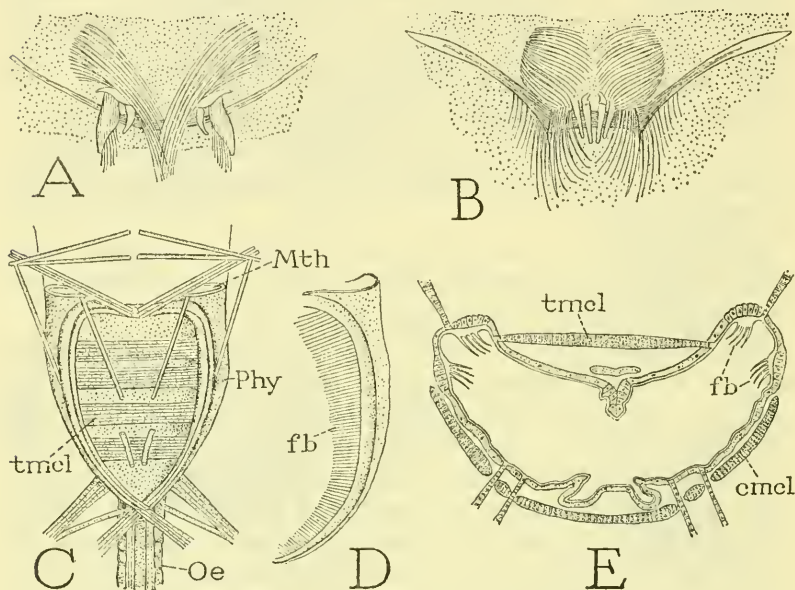
Fig. 8.—The larval epipharyngeal apparatus and the pharynx.

A, *Aedes aegypti*, epipharyngeal apparatus. B, *Culex* sp., same. C, *Anopheles maculipennis*, pharynx and its muscles, dorsal (from Schremmer, 1949). D, Same, filter-bearing rib of pharynx. E, Same, cross section of pharynx (from Imms, 1907).

cmcl, circular muscle; *fb*, filter brush; *Mth*, mouth; *Oe*, oesophagus; *Phy*, pharynx; *tmcl*, transverse muscles.

observed than in other species because the head is held with its underside turned upward against the surface of the water. Briefly, Schremmer's account is as follows.

The movements of the lateral brushes of the labrum create currents in the water that converge to the front of the head and are directed medially by the middle brush. With the backward stroke of the lateral brushes the mandibles and the maxillae are closed upon them, and as the brushes again go forward particles that may be adhering to

them are scraped off by the combs of the mandibles. Accompanying the opening of the mandibles, the epipharyngeal apparatus is protruded by action of its muscles and its bristles remove the food particles from the mandible combs. These freed particles and others that may be adhering to the epipharyngeal surface are then collected by the long basal brushes of the mandibles (fig. 5 D) and, with the closure of the mandibles, are pushed into the mouth of the pharynx. Though the mandibles and the maxillae close at the same time, the maxillae open first and the mandibles following remove whatever particles may be adhering to the maxillae, which lodge on the hypopharynx and with the next stroke of the maxillae are thrust into the pharynx. Large particles collected on the hypopharynx are broken up by the toothed lobes of the mandibles, which strike on the hypopharynx like hammers on an anvil.

The pharynx, by muscular expansion of its walls, functions as a sucking organ for drawing in a stream of water accompanying the mechanically ingested food particles. A contraction then follows in which the dorsal wall is deeply infolded by the action of the dorsal transverse muscles (fig. 8 E), reducing the pharyngeal lumen to two lateral channels containing the filter brushes (fb). At the same time the water is driven toward the mouth and the food particles are filtered out by the brushes. The water is then discharged through the open angles of the mouth, goes above the mandibles and escapes past the sides of the head. Schremmer made further experiments on a *Culex* larva by impregnating the water in a dish with carmine particles. After feeding by the larva, the carmine was found massed in the brushes along the sides of the pharynx. When the pharyngeal brushes have worked as filters for some time and have become well loaded, the pharynx makes a strong contraction which suddenly removes the carmine particles from the brushes and lodges them in small clumps at the mouth of the oesophagus, into which they are finally taken. The mosquito larva swallows no appreciable amount of water, its water balance being maintained by the anal lobes.

The extreme specialization of the mouth parts and the pharynx in the filter-feeding mosquito larvae gives a striking example of how independent of the adult structure an insect larva may become in its adaptation to a new way of feeding. In various mosquito genera, however, the larvae of some or all species are predaceous on other small aquatic animals, particularly on other mosquito larvae. Notable in this group are members of the subgenus *Lutzia* among the Culicini, and of the genus *Toxorhynchites*. In these forms the mandibles are

strongly developed jaws (fig. 5 B,C), the toothed lobes of which come together or overlap for grasping and biting. Yet these larvae have labral brushes and some of the other special features of particle-feeding larvae, so it is difficult to say whether they represent a partway stage in the evolution of filter feeding, or have been secondarily adapted for feeding on whole live prey. In some species the larvae are particle feeders in the first instar and become predaceous in their later instars. It would appear, therefore, as said by Bates (1949), "that the predacious habit has developed independently in the larvae of a number of mosquito groups, involving distinct adaptations both of structure and behavior."

THE THORAX

The larval thorax has a simple oval form, in which the intersegmental lines are but faintly marked as grooves of the cuticle, and there is no external trace of appendages. In the fourth instar the thorax becomes conspicuously enlarged (fig. 9 A). Beneath the cuticle on the ventral side are now plainly visible the extroverted wings and legs of the future pupa, and on the dorsal side the pupal respiratory trumpets. On removal of the cuticle (C) the legs are seen to be long, fully segmented appendages (E) closely folded in loops against the sides of the thorax. The forewings (W_2) are large pads corrugated in their basal parts (D) to allow expansion; the smaller hindwings (W_3) are more slender and tapering free folds of the metanotum. It has been shown by Imms (1908) that the rudiments of the wings, legs, and respiratory trumpets are formed in a young larval instar of *Anopheles* as integumental folds in pockets of the epidermis (B). Apparently they are extruded beneath the cuticle at the beginning of the fourth instar. This early eversion of the wings and legs occurs also in other nematocerous larvae, such as *Dixa, Corethra,* and *Chironomus,* shown by Miall and Hammond (1900) in *Chironomus.*

On each anterior lateral angle of the thoracic dorsum of *Anopheles* larvae there is usually to be seen a pair of minute, tapering, transparent lobes arising from a common base (fig. 9 A, *no*). These structures are known as the "notched organs." They are retractile and hence are not visible on all specimens, or only their tips may project. Between the lobes of each pair is a funnel-shaped depression that ends in a strand, which is said by Chang and Richart (1951) to be attached to the neighboring dorsal tracheal trunk. These writers contend, therefore, that the organs are the "prepupal respiratory trumpets." However, when the cuticle of a fourth-instar larva is removed,

the lobes and the funnel come off with it, showing that the organs are larval structures. Furthermore, the trumpets of the "prepupa" (i.e., the pharate pupa) are present beneath the larval cuticle. They appear to arise from the pupa just beneath the larval organs, but they project forward or mesally until the pupal ecdysis, when they stand out from the thorax.
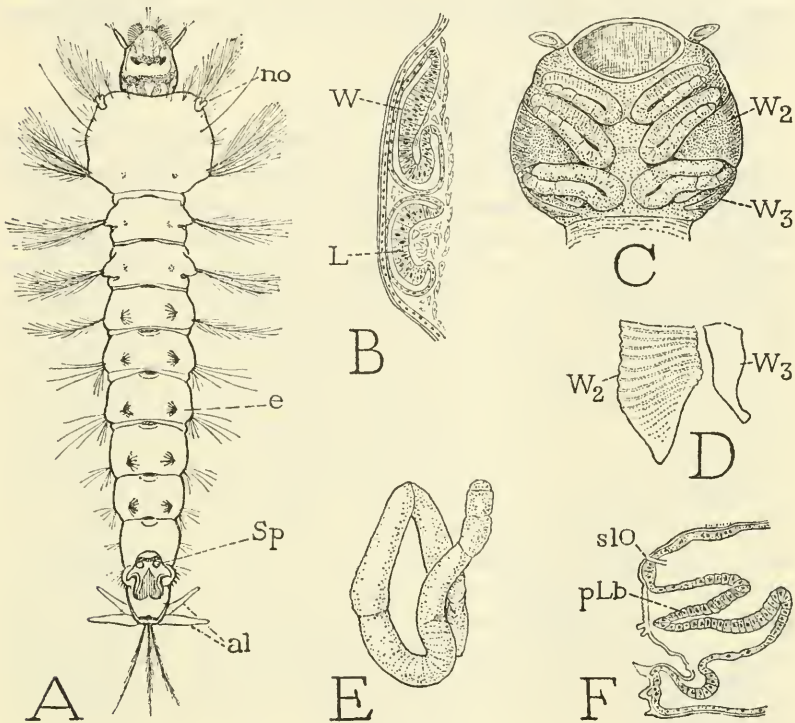

Fig. 9.—The larva, and developing pupal appendages.

A, *Anopheles punctipennis,* fourth instar larva, dorsal. B, *Anopheles maculipennis,* section of wing and leg buds in early larval instar (from Imms, 1908). C, *Aedes aegypti,* thorax of mature larva with cuticle removed, exposing extroverted legs and wings. D, Same, pupal wings of larva. E, Same, third left pupal leg of larva. F, *Anopheles maculipennis,* pupal labium developing inside larval labium (from Imms, 1908).

al, anal lobes; *e,* dorsal brush of larva; *L,* leg bud; *pLb,* pupal labium; *slO,* salivary orifice; *Sp,* spiracle; *W,* wing bud; W_2, W_3, pupal wings of larva.

The nature of the "notched organs" of the *Anopheles* larva is not clear. Their position on the dorsum of the thorax suggests that they might be remnants of anterior spiracles such as are present on larva of many other flies, including some Nematocera. Since these spiracles of successive instars are not formed in the usual manner within the

preceding spiracle, but as independent branches from a persisting spiracular atrium, it is perhaps possible that the pupal trumpets are in this manner related to the "notched organs" of the larva. Chang and Richart contend that the latter serve to keep the anterior part of the *Anopheles* larva afloat while feeding at the surface, but experiments have shown that the organs can be cut off without any apparent effect on the suspension of the larva (Jones, unpublished observations).

THE ABDOMEN

The larval abdomen (fig. 10 G) appears to have only nine segments, and it is usually represented as nine-segmented, with the respiratory apparatus on the eighth segment and the terminal segment enumerated as the ninth. However, there is reason for believing that a true ninth segment is combined with the eighth. Christophers (1922) contended that though "much of the apparent eighth segment is actually this structure, the greater part of the spiracular apparatus must be assigned to the tergite of a hitherto unrecognized ninth abdominal segment." Convincing evidence of this interpretation is the fact that the rudiments of the male genitalia are formed beneath the larval cuticle at the base of the terminal segment, and that in the adult male the genital claspers are carried on the *posterior* margin of a small but distinct ninth segment (fig. 27 B). Though this segment is not evident as a distinct annulus in the larva, it must be represented by some part of the apparent eighth segment immediately anterior to the genital rudiments. In the pupa, as will be shown (fig. 16 D,E) a small ninth-segment ring (*IX*) lies behind the eighth segment and carries the tail fins and the small anal lobe. The anal segment of the larva (fig. 10 B) must therefore be the tenth, as it is in the pupa and the adult.

The fully segmented abdomen of the mosquito embryo is shown by Telford (1957) in *Aedes* and by Menees (1958a) in *Anopheles* to have 10 segments. Telford says the tenth segment, or telson, disappears with the ingrowth of the proctodaeum, but since a tenth segment is present in the adult, the "telson" must be an eleventh segment. In some larvae, as seen in *Mansonia* (fig. 11 A) a small lobe (*XI*) protrudes from the end of the tenth segment, which would appear to be the evaginated anus-bearing telson. Even in the embryo, then, the ninth segment is not differentiated from the eighth. It appears as a distinct ring first in the pupa and as a definite segment in the adult.

The first seven segments of the larval abdomen have no distinctive features, except that in Anophelini (fig. 9 A) the last five or six of

them bear on the back pairs of small palmate brushes (*e*) that suspend the larva from the surface of the water in its usual horizontal feeding position. The respiratory apparatus on the dorsum of the ninth segmental region contains a pair of large open spiracles, which are either
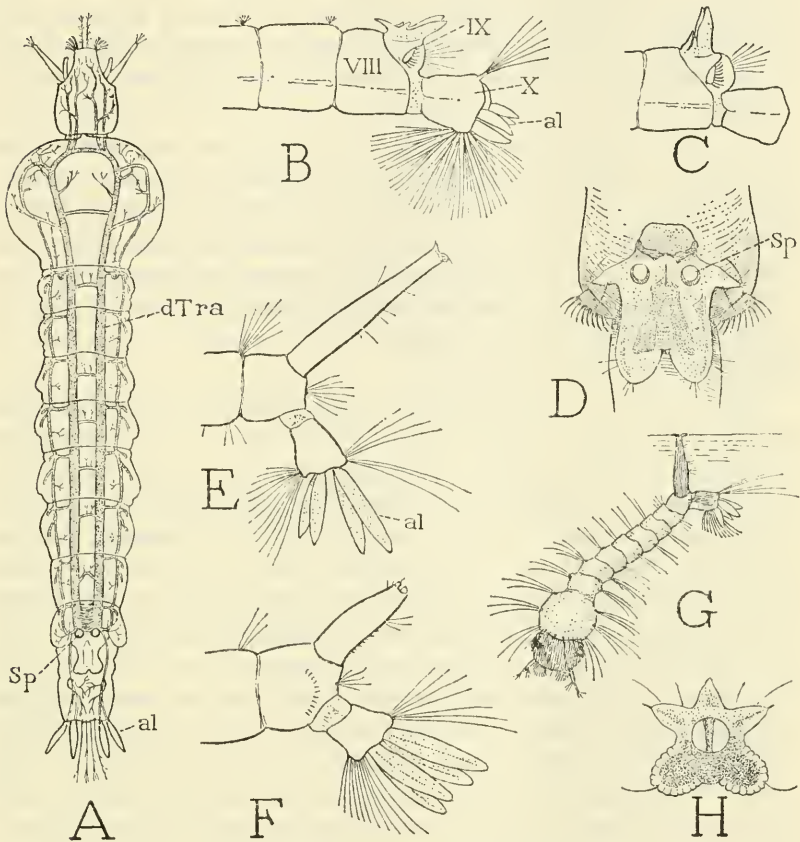
Fig. 10.—Larval respiratory organs.

A, *Anopheles maculipennis*, tracheal system, dorsal (from Imms, 1907). B, *Anopheles quadrimaculatus*, end of abdomen, spiracular apparatus open. C, Same, spiracular apparatus closed. D, Same, details of spiracular apparatus. E, *Culex pipiens*, end of abdomen. F, *Aedes aegypti*, same. G, *Culex quinquefasciatus*, larva in feeding position. H, *Culex pipiens*, end of respiratory siphon.

al, anal lobes; *dTra*, dorsal tracheal trunk; *Sp*, spiracle; *VIII-X*, abdominal segments.

flush with the surface (fig. 10 A, *Sp*) or carried out on the end of a respiratory tube (E,F,G). The tenth segment contains the functional anus at its end, and bears four lanceolate, thin-walled apical appendages, or *anal lobes* (A,B,E, *al*). Flat dorsal and ventral brushes

of long, spreading hairs are usually present on the end of the tenth segment, and perhaps serve as a rudder during swimming. Though mosquito larvae are commonly known as "wrigglers" or "wigglers" they swim by lashing movements of the abdomen, which drive them forward, backward, or sideways. The active larvae of *Culex* zigzag through the water like tumbling acrobats. *Anopheles,* however, is a true wriggler; it swims either on the surface or under the water by quick lateral movements of the abdomen and propels itself backward.

The dorsal spiracles of the abdomen are the only breathing apertures of the mosquito larva. The lateral spiracles are closed except at the ecdyses, when they are temporarily opened to allow the tracheal linings to be pulled out. Since the dorsal spiracles open into the dorsal trunks of the tracheal system and the lateral spiracles into the lateral trunks (fig. 10 A), the dorsal spiracles cannot be supposed to be a pair of lateral spiracles that have moved up onto the back. It may be conceded that spiracles can change their position, but they cannot change their tracheal connections.

The spiracles of anopheline larvae lie in the floor of a shallow, basinlike peritremal structure elevated on the back, the margins of which are variously produced into lobes (fig. 10 B). In *Anopheles maculipennis* (D) there are two large, thin posterior lobes, a pair of small tapering lateral lobes, and a single anterior lobe supported on a transverse basal bar. The spiracles (Sp) lie anteriorly; behind them is a median V-shaped sclerotization on the floor of the basin, and on each posterior lobe is a weak submarginal sclerotization. As the *Anopheles* larva feeds stretched out against the surface film of the water the peritremal basin projects just above the water with the spiracles freely exposed to the air. When the larva submerges, the whole apparatus folds up and the lobes clamp tight together (C). Imms (1908) describes three sets of paired muscles that effect the closing of the lobes, which retain a bubble of air between them. When the muscles relax the lobes open. Curving around the end of the ninth segment beneath the ends of the posterior lobes is a narrow semicircular bar that supports on each side a small plate bearing a comb of strong recurved bristles (D), or in some species is armed with spines or teeth.

In the larvae of Culicinae and Toxorhynchitinae the spiracles are carried out on the end of a tube, or siphon, varying in length and thickness in different genera (fig. 10 E,F). The spiracles are at the end of the tube and are surrounded by lobes similar to those in *Anopheles,* but necessarily much smaller (H). When the larva is at

the surface it hangs from the end of the siphon with the spiracles exposed to the air (G). Two strands of slender muscle fibers traverse the tube and converge to attachments on a strong apodeme from the terminal apparatus.

An extensive comparative study of the peritremal structure has been made by Montschadsky (1930) from a taxonomic standpoint. His illustrations are not realistic since they appear to have been drawn from flattened specimens, and the sclerotic parts are overemphasized by an unnaturally dark tone, but they show the great specific variation in the pattern of the peritremal lobes.

Glands associated with the spiracular apertures have been described by Keilin, Tate, and Vincent (1935). The secretion is oily and serves to give a hydrofuge quality to the peritremal surface, which prevents wetting and the entrance of water into the spiracles.

Though the respiratory siphon is primarily constructed for breathing air at the surface of the water, in species of *Mansonia* and a species of *Ficalbia* it is modified for insertion into the roots of aquatic plants. The siphon tapers distally and the apex is armed with spines, teeth, and hooks, which, operated by the inner muscles of the tube, enable the larva to insert the tip of the organ into the plant. In *Mansonia indubitans* (fig. 11 A) the siphon is large, conical in shape, and narrowed at the distal end. The apex is not sharp, but is armed with a pair of strongly toothed movable lobes (B), which can be retracted and brought together, or protracted with the teeth turned outward. The siphon in this case is a cutting and not a piercing instrument. It contains only one tracheal trunk, formed by the union of the dorsal body trunks in the eighth abdominal segment, and there is a single median, ventral spiracle between the bases of the toothed lobes. These larvae live entirely submerged and obtain their air from the air channels of the plant, to which they remain attached.

According to Iyengar (1935a, 1935b) species of *Mansonia* in India attach themselves only to the water plant *Pistia stratiotes*. To insert the siphon the larva moves backward with the siphon held horizontally and thrusts the tip against the root. It then wriggles actively backward, while it operates the apical armature with muscles attached on a rodlike apodeme, until the end of the siphon penetrates the root deep enough to enter an air chamber, when apical hooks anchor the larva to the root. The adult female lays her eggs only on submerged leaves of the *Pistia* plant, thrusting her abdomen into the water to do so, and where *Pistia* is not present she will lay no eggs.

While most other mosquito larvae spend most of their time at the

surface of the water, any of them can stay below without apparent discomfort, and some do so indefinitely. It was formerly supposed that the four thin-walled tracheated lobes borne on the end of the tenth abdominal segment were gills serving for underwater respiration. Wigglesworth (1933), however, has produced evidence that
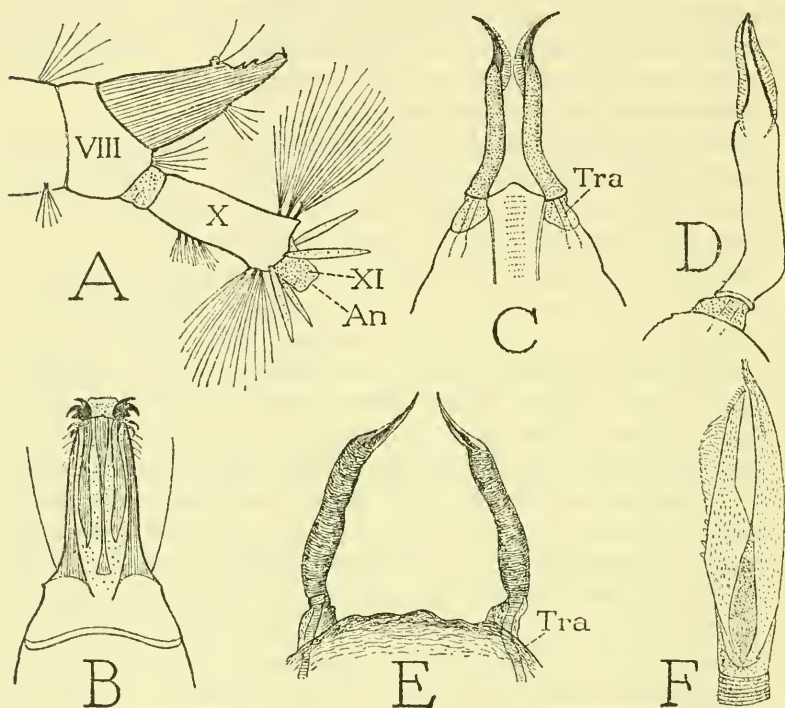

FIG. 11.—Respiratory tubes of larvae and pupae that get their air from the roots of aquatic plants.

A, *Mansonia indubitans,* terminal segments of larva. B, Same, apical part of siphon, ventral. C, *Mansonia* sp., thoracic respiratory horns of pupa, dorsal. D, Same, right horn, mesal. E, *Mansonia richiardii,* pupal respiratory horns, dorsal (from Wesenberg-Lund, 1920-21). F, *Ficalbia hybrida,* terminal part of pupal respiratory horn (from Bonne-Wepster, 1932).
An, anus; *Tra,* trachea.

these lobes are water-absorbing organs rather than gills. By immersing larvae in a water culture of the flagellate protozoon *Polytoma,* which is highly sensitive to the amount of oxygen in the water, he found that the flagellates first assemble at the posterior end of the larva and then spread all over the body surface. Soon, however, they move away in a mass, indicating that oxygen is being consumed by

the general integument of the larva as well as by the anal lobes. The submerged mosquito larva, therefore, breathes through its skin, and some other aquatic larvae are known to do the same.

From experimental ligaturing of the body of the larva in different places, Wigglesworth furthermore showed that the larva absorbs water from the posterior end of the body, presumably through the thin, permeable anal lobes. During feeding, the larva does not swallow the water taken into the pharynx with its food, this water, as already noted, being discharged from the mouth. The anal lobes thus serve to maintain the physiological balance of water in the larval body.

INTERNAL ANATOMY

Inasmuch as the principal specializations of the mosquito larva have to do with feeding and breathing, there is little in the internal organization that is essentially different from that of other insects.

The tracheal system.—The tracheal system of most insects includes a pair of lateral tracheal trunks running lengthwise through the body, with which the lateral spiracles are connected. Many insects, however, have also a pair of dorsal longitudinal trunks. In dipterous larvae, including the mosquito larva, that breathe through dorsal spiracles, the dorsal trunks are particularly large (fig. 10 A, *dTra*), and the lateral trunks connected with the closed lateral spiracles are much reduced. The dorsal spiracles of the ninth abdominal segment are evidently secondary respiratory apertures to allow the larva to breathe at the surface of the water, since it is hardly to be supposed that a primitive lateral spiracle could migrate dorsally and change its tracheal connections. In general the last pair of lateral spiracles is on the eighth segment. In the larvae of higher Diptera there is also a pair of secondary anterior dorsal spiracles on the thorax.

The fine end branches of the insect tracheal system in general go to the cells of the body tissues, which are thus directly oxygenated. In the larva of *Anopheles*, Imms (1907) describes a series of small tubes from the longitudinal trunks in the eighth abdominal segment that break up into fine branches going to the posterior end of the heart. Imms suggested that these branches may oxygenate the blood in the heart, but Jones (1954) says they end on the heart wall.

At each larval ecdysis the cuticular intima of the tracheal tubes is shed with the outer cuticle. In the mosquito larva, according to Wigglesworth (1949), the intima of the main tracheal trunks breaks between the segments, and the pieces attached to the shed cuticle are drawn out through the lateral and the posterior dorsal spiracles of

the new instar. The lateral spiracles are then closed again, since they are not functional in the larva for respiration. In the same manner, at the ecdysis of the pupa the tracheal trunks in *Culex* are said by Hurst (1890) to break up into segmental pieces, which are pulled out through the temporarily opened spiracles. The soft inner tissue of the respiratory siphon is withdrawn into the body where it is finally absorbed. The siphon itself is shed with the larval cuticle, and its two tracheal trunks break off at the base.

The tracheal system of the young larva on hatching is filled with a liquid. According to Frankenberg's (1937) observation on *Culex,* air enters the tracheae only when the end of the respiratory siphon comes above the water surface. One of the dorsal longitudinal trunks fills first, and then the other. The air is drawn into the tracheae as the embryonic liquid diffuses through the tracheal walls.

The dorsal blood vessel.—The dorsal blood vessel of the mosquito, particularly in *Anopheles quadrimaculatus,* has been elaborately described by Jones (1954). Structurally it differs in no essential respect from the vessel of other insects, except for a dilatation, or sinus, of the aorta in the thorax. The larval organ is a simple muscular tube extending along the midline of the back from the eighth abdominal segment into the head. The part in the abdomen, known specifically as the *heart,* is perforated along the sides by eight pairs of segmental openings, or ostia. The part in the thorax, called the *aorta,* is imperforate. In the head the aorta goes beneath the brain, where it is open ventrally allowing the blood to be freely discharged into the head cavity, whence it flows backward through the body to reenter the heart through the ostia. The larval heart, Jones says, always beats forward at an average of 85.2 pulsations a minute, but it has no nerve connections. Along the sides of the heart are attached the usual fan-shaped segmental groups of muscle fibers, the so-called *alary muscles,* that support the heart on the body wall.

The alimentary canal.—In the mosquito larva the alimentary canal (fig. 12) is a relatively simple tube. It consists of the usual three parts of the arthropod digestive tract, an ectodermal stomodaeum, an endodermal mesenteron, and an ectodermal proctodaeum. The stomodaeum begins in the head with the *pharynx* (*Phy*), which is followed by a narrow *oesophagus* (*Oe*) that goes through the neck into the thorax, where it enters the first part of the mesenteron, known as the *cardia* (*Car*). (This term, borrowed from vertebrate anatomy, has no literal significance in the insect.) Within the cardia the oesophageal walls are reflected to form the usual entrance funnel of the

stomodaeum into the mesenteron. The cardia is followed by a long, straight tube, the stomach, or *ventriculus* (*Vent*), that extends back into the seventh abdominal segment. The anterior end of the ventriculus bears a circle of eight large pouchlike diverticula, the *gastric caeca* (*GCa*). The dark mass of food particles in the ventriculus is contained in a thin tubular *peritrophic membrane* (*PMb*), shown by Wigglesworth (1930) to be secreted by the cell walls of the cardia surrounding the stomodaeal funnel. The proctodaeum, or intestine, is differentiated into a short anterior part (*AInt*), and a longer posterior part, or *rectum* (*Rect*). The anterior intestine begins as an expansion against the end of the ventriculus, and then narrows to a tube that makes an S-shaped bend to the saclike anterior enlargement
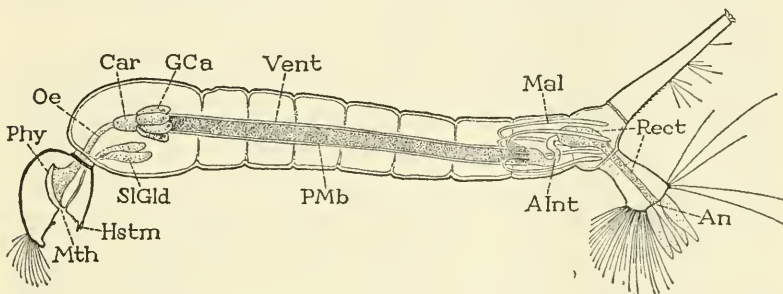

FIG. 12.—Lengthwise section of a *Culex* larva, showing the alimentary canal.

AInt, anterior intestine; *An,* anus; *Car,* cardia (anterior part of ventriculus); *GCa,* gastric caeca; *Hstm,* hypostomium; *Mal,* Malpighian tubules; *Mth,* mouth; *Oe,* oesophagus; *Phy,* larval pharynx; *PMb,* peritrophic membrane; *Rect,* rectum; *SlGld,* salivary glands; *Vent,* ventriculus (stomach).

of the rectum, which finally proceeds as a narrow tube to the anus (*An*).

For a detailed study of the general structure, histology, and movements of the larval alimentary canal of *Anopheles* the reader is referred to a forthcoming paper by Jones (in press).

The Malpighian tubules.—The excretory Malpighian tubules of the larva (fig. 12, *Mal*) are five in number. They arise from the anterior end of the proctodaeum, first going forward into the sixth abdominal segment, and then turning posteriorly to end in the subterminal segment around the rectal sac.

The salivary glands.—The larva has a pair of small salivary glands of various shapes lying ventrally in the thorax (fig. 12, *SlGld*). The ducts unite in a common outlet duct that enters the head and opens on the labiohypopharyngeal surface just below the mouth (fig. 15 A, *SlO*). The glands usually consist each of two parts of different shape

separated by a constriction. The histology of the glands in *Anopheles* larvae has been described by Jensen and Jones (1957). In *Anopheles albimanus* the globular anterior part of each gland consists of 12 to 15 large cells; the pear-shaped posterior part contains 50 to 60 much smaller cells. The glands of opposite sides are connected by a strand of nephrocytes. In other genera the relative size and shape of the two gland parts differ in various ways.

The nervous system.—The central nervous system of the larva includes a brain and suboesophageal ganglion in the head, and a ventral chain of segmental ganglia in the abdomen united by paired connectives. The last ganglion is that of the eighth abdominal segment.

The reproductive organs.—Rudiments of the reproductive organs are present in the young larva in a very elementary state; they slowly develop during the larval life.

Food reserves.—The insect larva has no idea of the meaning of its life or of what is to become of it. Its hereditary factors automatically determine its destiny by converting it into a pupa and finally into an adult. Yet, physiologically, the larva is loaded with responsibilities. Not only must it maintain its own existence, but at the same time it must provide for the future nutritional needs of the pupa and for its transformation to the adult. In the mosquito pupa there is a minimal breakdown of larval tissues to furnish food for the developing adult organs. The active mosquito pupa, moreover, is not a "resting stage," and, since it cannot eat, it is dependent upon the larva for everything except the air it breathes. An important function of the larva, therefore, is the storage of food reserves in its body to maintain the pupa and to insure the development of the adult. Only when the winged adult finally emerges from the pupal skin can the mosquito again take food and become once more an independent, self-sustaining insect.

The elaboration and storage of food reserves in the body of the fourth-instar mosquito larva is the subject of a special study by Wigglesworth (1942). The stored materials include principally protein, fat, and glycogen, which are shown by experiments to be rapidly consumed when the larva is subjected to starvation, and replenished on subsequent feeding. Normally, it is to be supposed, the stored products are passed on intact to the pupa, but Wigglesworth does not go into this phase of the subject, or follow the utilization of the reserves by the pupa. The matter, however, is well-enough known in other insects.

II. THE PUPA

The active pupa is familiar to all students of mosquitoes *after* its ecdysis from the larva. The fact, however, that it is already fully

formed shows that it became a pupa while still within the larval cuticle. It will therefore be of interest to follow the transformation processes that convert the larva into a pupa.

THE PUPAL DEVELOPMENT

As before noted, the primary buds of the pupal wings, legs, and respiratory trumpets are formed at an early larval period in pockets of the epidermis beneath the cuticle, as are also those of the antennae and the labium, and rudiments of the compound eyes are present in the first instar.
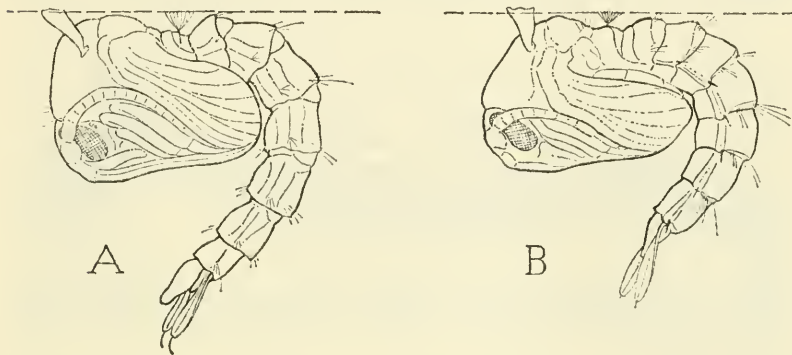

Fig. 13.—Pupae in natural floating position against the surface of the water. A, *Aedes atropalpus*. B, *Anopheles punctipennis*.

The development of the compound eyes of the mosquito has been described by Zavřel (1907), by Constantineanu (1930), and by Satô (1951a, 1953a, 1953b). The eye rudiments are first evident in the first larval instar as thickenings of the epidermis just in front of the larval eyes. With development of the eye pigment, the compound eyes become visible externally in the second instar or the early part of the third instar. From then on they increase in size as the ommatidia are slowly differentiated in the epidermis. During the larval stage the ommatidia are covered by the unmodified cuticle, but in the pupa the cuticle over each ommatidium becomes convex and the corneal facets are thus defined. After emergence of the adult the lenses become biconvex, and the ommatidia are completed in from 3 to 12 hours, but the lenses may continue to thicken during the first 24 hours of adult life.

The early development of the wings and legs in the mosquito larva is nothing unusual. The leg buds are always formed in the embryo, and all immature insects have legs, whether external or internal. Like-

wise the young of all winged insects have wing rudiments developing either externally or internally. The unusual thing about the mosquito and related Diptera is that the legs, wings, and pupal respiratory trumpets are fully extruded beneath the cuticle of the thorax at the third larval moult instead of at the moult to the pupa (fig. 9 C). The wings are still in the form of pads (W_2, W_3), but the legs (E) are already fully segmented appendages.

At a somewhat later period of the fourth instar, the larval cuticle is separated from the abdomen except at the posterior end (fig. 14), and beneath the cuticle on the back of the first segment are now seen the two small suspensory brushes of hairs characteristic of the pupal abdomen. The thorax and the abdomen inside the moulted larval
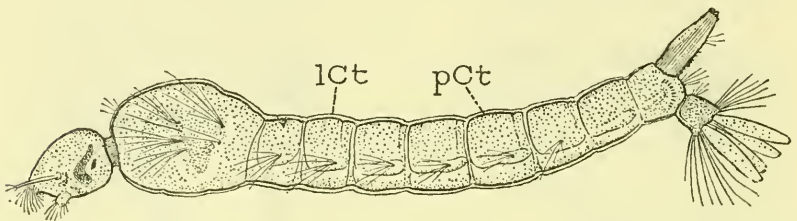

Fig. 14.—Fourth-instar larva of *Aedes aegypti* with larval cuticle (*lCt*) moulted over the thorax and most of the abdomen. The inner cuticle (*pCt*) is that of the pupa.

cuticle, therefore, pertain to the future pupa. The head cuticle of the larva has not yet been moulted, so that the larva in the fourth instar still feeds with its own mouth parts. It breathes with its posterior respiratory apparatus, and uses for locomotion the muscles now in the pupal abdomen.

The condition found in the mosquito is simpler than that described by Hinton (1958b) in *Simulium*. Here the fully formed pupa still within the larval skin is active for several days before ecdysis. Its activity is due to the fact that many of the former larval muscles, including those of the head, remain attached by tonofibrillae to the moulted cuticle of the larva. The pupa of *Simulium* is thus able to use the larval organs, and it not only continues to feed, but spins its own cocoon. In the mosquito there is no evidence of muscles retaining their attachment on the moulted larval cuticle; the insect feeds with the larval mouth parts until the latter are cast off at the final pupal moult.

The larval musculature of the thorax and abdomen is said by Thompson (1905) in *Anopheles* to go over into the pupa and the

adult with little alteration. The rudiments of the future wing muscles, however, are present in the thorax during the last larval instar. Hulst (1906), on the other hand, reports that in the larva of *Culex* there takes place an extensive histolysis and histogenesis of the body musculature, beginning when the larva is two-thirds grown. Some imaginal muscles thus appear first in the larva, particularly those of the wings and legs, prior to the advent of the pupal stage. Destruction of the larval muscles of the abdomen, however, Hulst says, is not complete even in a late stage of the pupa. In the Simuliidae, according to Hinton (1959), "the indirect flight muscles and the tergal depressor of the trochanter develop quite independently of the larval muscles in all post-embryonic stages."

Histological changes in the alimentary canal beginning in the larva have been described by Samtleben (1929), by Berger (1938) for *Culex,* and by Richins (1945) for *Aedes.* The replacement of functional cells from regenerative cells in the ventriculus during larval life is generally in other insects not a metamorphic process but the usual procedure of replacing worn-out digestive cells by new cells. At the fourth ecdysis to the pupa, however, Berger (1938) says, rapid changes take place. The alimentary canal of the pupa, well illustrated by Hurst (1890), differs from that of the larva, but is still not that of the adult. The short pupal stomach is said by Richins to be formed from only the posterior part of the larval stomach. According to Samtleben no specific pupal epithelium is formed for the pupal stomach.

Considering the precocious development of so many of the imaginal organs, the fourth instar of the mosquito larva presents the anomalous condition of being part larval and part pupal. In other words, the pupal development begins within the larva long before its completion at the pupal ecdysis. It ends with the formation of the pupal head, mouth parts, and tail fins.

In most young insects the endocrinologists find that the larval structure is maintained by the inhibitory action of the corpus allatum hormone on the adult development until the end of the larval life. The early origin of pupal organs in the mosquito larva and the continuance of their development through the larval period shows, however, that the *juvenile,* or *status quo,* hormone does not necessarily function as a complete inhibitor of adult development. In the mosquito it appears to be selective in its action, allowing the growth of pupal parts that do not interfere with the normal activities of the larva, while it maintains to the end of the larval period such parts as the head, feed-

ing organs, and respiratory apparatus that are essential to the life of the larva.

The corpora allata of the mosquito larva are described by Bodenstein (1945) as a "corpus allatum complex" composed of two small cellular bodies of elongate form, tapering posteriorly, attached laterally on the aorta just behind or within the neck. Anteriorly they adhere closely to a transverse trachea and are connected with each other by a loose chain of cells. Each body is entered by a slender nerve from the brain. Since the bodies contain different kinds of cells it is possible that they include elements of the usually separate corpora cardiaca. In higher Diptera the aorta is surrounded by a cellular ring, which is thought to include the corpora allata and corpora cardiaca, but according to Bodenstein the nature of the cells in the mosquito larva is not certain. The larval complex goes over into the adult in reduced form as two small, rounded bodies lying on the sides of the aorta.

If the fourth-instar larval mosquito behaves as other larvae have been shown to do when experimentally given an extra dose of juvenile hormone, it should go over into a fifth larval instar. In this case the larva issuing from the fourth-instar cuticle would have external legs and wings! We can only wait the results of some endocrinologist who may make the experiment.

When at last the cuticle of the larval head is moulted, taking with it the larval antennae and mouth parts, the corresponding pupal organs are rapidly developed within the still-unshed larval cuticle. The reconstruction of the mouth parts involves an extreme change from the specialized organs of the larva to the equally but differently specialized organs of the adult. The development of the pupal mouth parts has been described by Thompson (1905) for *Culex,* and by Imms (1908) for *Anopheles.*

The pupal labrum begins its growth as a fold of the epidermis at the anterior end of the dorsal wall of the head that first extends posteriorly beneath the cuticle (fig. 15 B, *pLm*). The fold elongates (C, *Lm*) and finally turns forward and downward over the other mouth parts. The buds of the new mandibles and maxillae are formed directly from the epidermis retracted into the bases of the larval organs. An early stage of their development still within the larval cuticle is seen at C of the figure taken from Thompson. The labium and the hypopharynx of the larva, as already shown, are greatly reduced and united in an area between the mouth and the hypostomium, the two components being separated only by the opening of the salivary duct. In *Aedes* the labiohypopharyngeal complex as shown by

Salem (1931) forms a distinct lobe below the mouth (fig. 15 A, *Hphy*, *Lb*), as it does also in a tipulid larva (fig. 7 A). The rudiment of the pupal labium within the larval labium (fig. 15 A, *pLb*) is said by Imms (1908) to be a pair of hollow lobes confluent at their bases. There is no separate rudiment of the adult hypopharynx. It is shown by Thompson (1905) that the hypopharynx is still united with the pupal labium (fig. 15 B) when the larval cuticle (*lCt*) is moulted. Later, as will be described, the hypopharynx of the adult female is separated from the labium. In their final stage of development the pupal mouth parts have become greatly lengthened and are closely pressed together in a long curved proboscis (D).

Rudiments of the pupal tail fins are formed beneath the cuticle of the fourth larval instar behind the respiratory apparatus, and the primary buds of the male external genital organs appear beneath the cuticle of the same instar behind the sternal region of the ninth abdominal segment.

THE MATURE PUPA

The pupa at ecdysis (fig. 16 A) is fully formed in all its outer parts and thereafter does not change externally. It is clearly a preliminary adult with the appendages in a halfway state of completion. The pupa can hardly represent a former active stage in the life of the mosquito, since its mouth parts are unfitted for any kind of feeding. The pupal thorax has already assumed the approximate size and shape of the adult thorax. In Simuliidae, Hinton (1959) says, the definitive thoracic structure is developed during the pharate stage of the pupa.

General external structure.—The head and thorax of the mosquito pupa are combined in a large cephalothorax, from which projects the slender abdomen (fig. 16 A). When at rest the pupa floats at the surface of the water (fig. 13), but it does not hang from its respiratory trumpets (as it often does in pictures). The back of the thorax and of the two anterior abdominal segments comes against the water, while the rest of the abdomen hangs downward as ballast. The open ends of the respiratory trumpets project just above the surface of the water, and two small brushes of spreading hairs on the back of the first abdominal segment help keep the pupa suspended. The floating position of the pupa is necessary for the future emergence of the adult, and is maintained by bubbles of air enmeshed in the folds of the legs and beneath the wings.

The source of the air that maintains the buoyancy of the pupa, according to Hurst (1890), appears to be a pair of large open spiracles
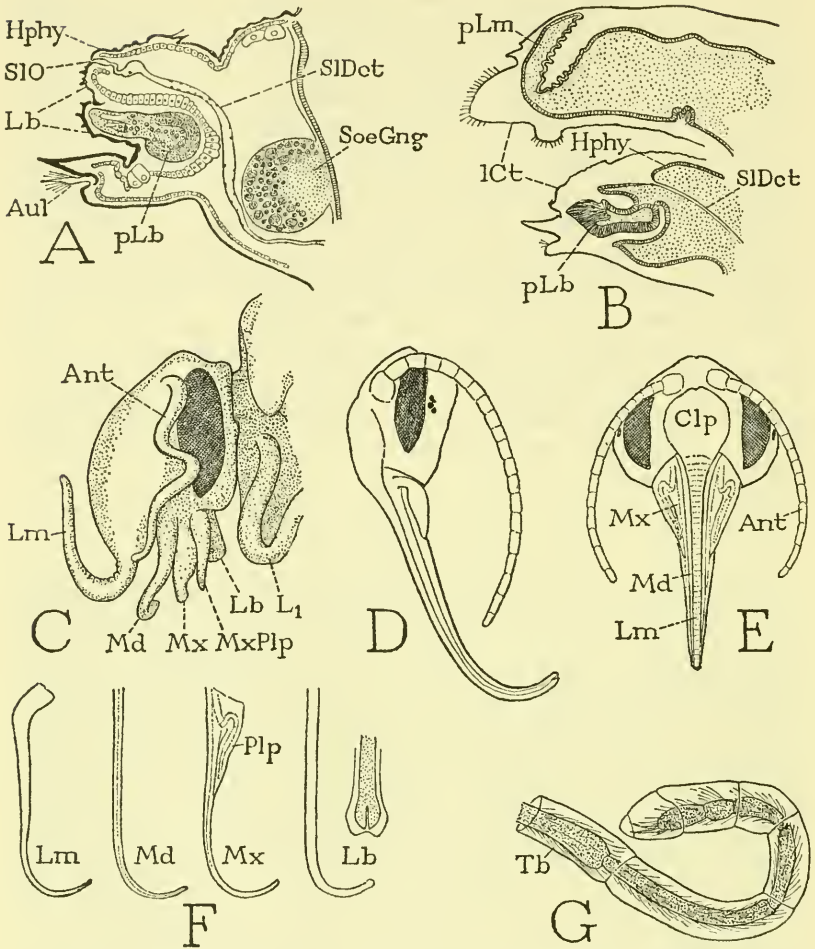
FIG. 15.—Development of pupal mouth parts and an adult leg.

A, Vertical median section through labiohypopharyngeal lobe of larva of *Aedes*, with contained rudiment of pupal labium (from Salem, 1931). B, Section of anterior part of head of *Culex* larva, with pupal labrum and labium forming inside the unshed larval cuticle (from Thompson, 1905). C, Head of *Culex* pupa removed from larval cuticle, with pupal mouth parts in early stage of development (from Thompson, 1905). D, Pupal head of *Aedes aegypti*, lateral. E, Same, anterior. F, Fully developed pupal mouth parts of *Aedes aegypti*. G, Distal part of a pupal leg with adult leg formed within it.

Ant, antenna; *Aul*, aulaeum; *Clp*, clypeus; *Hphy*, hypopharynx; *L₁*, first leg; *Lb*, labium; *lCt*, larval cuticle; *Lm*, labrum; *Md*, mandible; *Mx*, maxilla; *MxPlp*, maxillary palpus; *pLb*, pupal labium; *pLm*, pupal labrum; *Plp*, palpus; *SlDct*, salivary duct; *SlO*, salivary orifice; *SoeGng*, suboesophageal ganglion; *Tb*, tibia.

on the sides of the first abdominal segment of the pupa covered by the metathoracic wing pads. The tracheal system of the pupa, however, is so weakly developed that it would hardly seem capable of supplying the amount of air carried by the living pupa. Manzelli
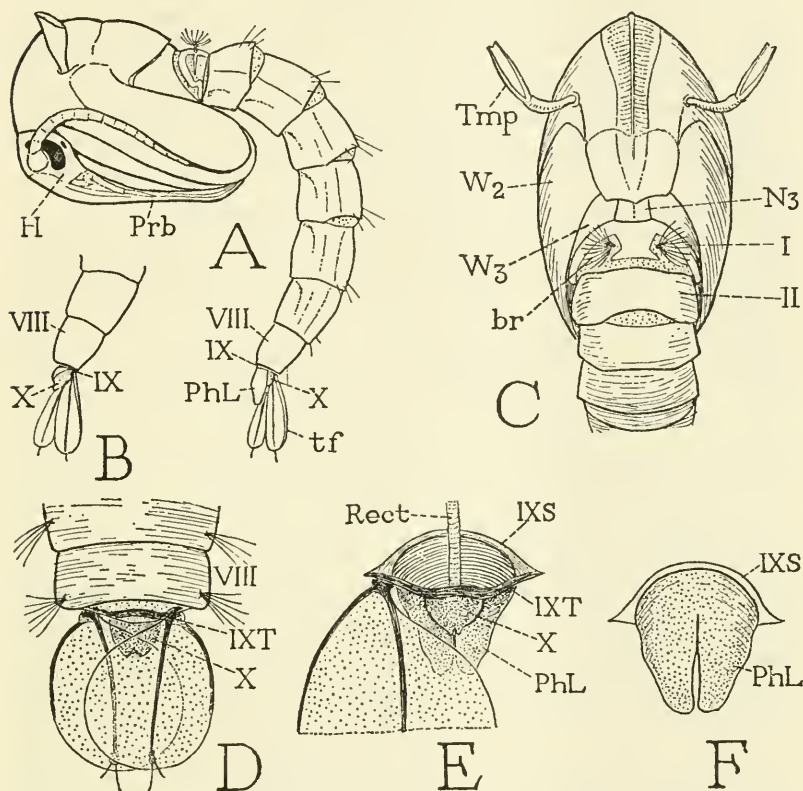
FIG. 16.—The pupa.

A, *Aedes aegypti*, male pupa, lateral. B, Same, terminal part of female abdomen. C, *Culex* sp., thorax and base of abdomen, dorsal. D, Same, end of female abdomen, dorsal. E, Same, apical structures of male abdomen. F, Same, phallic organ of male pupa, ventral.

br, suspensory brush of first abdominal tergum; H, head; N₃, metanotum; PhL, phallus; Prb, proboscis; Rect, rectum; S, sternum; T, tergum; tf, tail fin; Tmp, respiratory trumpet; W₂, mesothoracic wing; W₃, metathoracic wing; I-X, abdominal segments.

(1941) described and figured the pupa as "enclosed in a sac-like structure," which he says "has long been seen by all mosquito workers and is usually known to them as the pupal shell." This is a curious statement, since no such structure exists. Furthermore, the "shell" is said

to enclose a large air cavity, but on pressing a pupa in alcohol the air issues as free bubbles from beneath the legs and wings.

The pupa has two features that are peculiarly its own. First are the trumpet-shaped respiratory tubes projecting from the back of the thorax (fig. 16 C, *Tmp*), and second, a pair of thin, oval fan-shaped tail fins, or paddles, borne on the end of the abdomen (A, *tf*). Because it is necessary for the pupa to float with the back of its thorax against the surface of the water, with the abdomen hanging down, it had to discard the posterior spiracles of the larva and have its breathing apertures forward. The trumpets are connected with the anterior ends of the dorsal longitudinal tracheal trunks, and their open ends project just above the surface of the water.

It is a curious fact that in species of *Mansonia* and *Ficalbia,* the larva of which gets its respiratory air from the roots of aquatic plants, the pupa does the same thing by means of its thoracic trumpets. The trumpets in these species are drawn out into a pair of long horns directed forward from the thorax. In *Ficalbia hybrida* each horn ends in a pair of tapering blades (fig. 11 F), but in species of *Mansonia* each terminates with a strong, curved spine. The spines of *Mansonia richiardii* (E) are convergent and are said to be applied close against each other as inserted into the plant. In the species shown at C of the figure the spines are divergent, and, as in other species, each is bordered anteriorly and posteriorly (D) by a very thin, transparent, faintly striated flange. A trachea (C,E, *Tra*) is attached to the base of the organ, but does not penetrate the latter. The cylindrical basal stalk contains a wide lumen, which narrows abruptly where it enters the spine and opens by a minute aperture at the tip. Wesenberg-Lund (1920-21), however, says of *M. richiardii* that "the trachea runs through the whole tube," and Grossbeck (1908) figures a tube of *Culex perturbans* with a trachea going through it to the tip of the spine. It seems very unlikely, however, that the thoracic respiratory tubes in any case contain tracheae. They are merely elongated trumpets, and a typical trumpet is an open funnel with the trachea opening into its base (fig. 17 C, *Tra*).

As the pupa of *Mansonia* emerges from the larval skin, according to Galliard (1934) as quoted by Marshall (1938), it brings the tips of its horns together and searches for a neighboring root. Then it violently works its way out of the anchored larval skin and at the same time inserts its horns. When the adult is ready to emerge, the pupa breaks away from the plant and comes to the surface where it floats by reason of two tracheal air sacs in the thorax. The winged mosquito thus escapes into the air in the usual manner.

It is truly remarkable that the same kind of structural adaptation for the same purpose has occurred twice in the life of the same individual, affecting two different organs. Furthermore, with the acquisition of a new structure designed for a new use, the insect must be twice endowed with a new instinct for using the modified organs. It is enough to make us wonder if we really understand the nature of biological adaptation.

Though pupae that breathe free air ordinarily float at the surface of the water, they can escape danger by darting around on the surface or submerging quite as actively as the larvae by snapping movements of the flexible and well-musculated abdomen. The large tail fins are organs for increasing the motor efficiency of the abdomen. Functionally they are comparable to the tail fan of a crayfish. The pupa when swimming progressively on or below the surface kicks backward with its abdomen and propels itself forward, but the crayfish does just the opposite. When the pupa swims downward in the water, however, it goes tail first, and thus maintains its floating position. If it remains inactive it passively rises to the surface, otherwise it swims up by abdominal movements.

The head and mouth parts.—The head of the pupa (fig. 16 A, *H*) is closely attached to the lower anterior angle of the thorax, with its true dorsal surface directed anteriorly. It retains nothing of the structure of the larval head. The long, many-jointed antennae curve upward and backward beneath the lower edges of the wings. The large, black compound eyes (fig. 15 D, E) are conspicuous beneath the cuticle, and between them the clypeal region (E, *Clp*) makes a prominent bulge on the face. Posteriorly the head is produced into a long, tapering proboscis that lies beneath the thorax with its end upcurved behind the lower legs (fig. 16 A, *Prb*). The component elements of the proboscis are closely adherent (fig. 15 E), but are easily separated (F). Along the lower side is the relatively thick labrum (E, *Lm*) which is continuous from the clypeus. Flanking the labrum are the very delicate slender mandibles (*Md*), and bordering the mandibles are the maxillae (*Mx*). The wide base of each maxilla bears a free, tapering palpus (F. *Plp*). On the posterior (upper) side of the proboscis is the soft, slender, tubular labium ending in a bifid tip (F. *Lb*). There is no free hypopharynx in the young pupa.

As we have seen, the hypopharynx is not separated from the labium in the larva, and the two parts go over still united into the pupa, with the salivary duct enclosed between them. In most adult insects the hypopharynx is an independent suboral lobe, and the salivary duct

opens behind its base in front of the labium (fig. 23, *SlO*). The female of the mosquito and other adult Diptera possesses a free hypopharyngeal stylet, but it is traversed by the salivary duct. According to Thompson (1905) the hypopharynx of the female mosquito is differentiated by cellular growth from the median line of the anterior (lower) surface of the labium during the pupal stage. Since the hypopharynx, when it becomes a free stylet, contains the salivary duct, it would seem that in its separation from the labium it must take a part of the labium with it. In the male the hypopharynx is not separated from the labium, and the salivary channel remains in the labium. Dimmock (1881) says that in the male of *Culex* "the hypopharynx is, throughout its whole length, joined to the labium," and Hurst (1890) observes that it is "inseparable from the labium."

The fact that the hypopharynx of Diptera contains the salivary duct has given rise to the idea that this stylet is a new formation not homologous with the hypopharynx of other insects (see Demerec, 1950, pp. 375, 376). Yet the stylet in Diptera has all the usual relations of the hypopharynx to surrounding parts, and its base forms the floor of the preoral cibarial pump (fig. 24 E), just as in the cockroach (fig. 23) and other generalized insects.

The cuticle of the pupal mouth parts represents the organs as they are developed in the pupa. Inside the cuticular sheaths a renewed growth of the epidermis produces the final adult form of the stylets, just as the adult legs are formed within the cuticle of the pupal legs (figs. 15 G, 17 A). The segmented maxillary palpus of the adult, for example, is clearly seen inside the simple palpal sheath of the pupa (fig. 15 F, *Plp*), and within the end of the pupal labium (*Lb*) are visible the labellar lobes of the adult.

The thorax.—The large thorax of the pupa is indistinctly segmented, but it bears the legs and wings, and carries on its back the respiratory trumpets (fig. 16 A). The legs and the wings of the pupa have been taken over directly from the larva. The legs have increased in length and their joints are more distinct (fig. 17 A), but they are closely folded in loops against the sides of the thorax as in the larva. The mesothoracic wings are much larger and more winglike in shape; the hind wings are still triangular lobes of the metanotum. Within the cuticle of the pupal appendages are plainly seen the developing appendages of the adult. The venation of the forewing is already laid out (D). Within the hindwing may be seen the club-shaped halter (E, *Hlt*), which, whatever may be its evolutionary history, is not formed in ontogeny by a gradual modification of the wing.

The abdomen.—The abdomen of the pupa (fig. 16 A) resembles that of the larva except for the lack of the respiratory apparatus, the presence of the tail fins (*tf*), and the reduction of the tenth segment (*X*) to a small anus-bearing lobe. The dorsum of the first segment has a special pattern of sclerotization (figs. 16 C, 17 F) and bears the two brushes of spreading hairs that keep the base of the abdomen suspended at the surface of the water. It is suggested by Hurst (1890) that these brushes, besides serving as suspensoria, probably also are
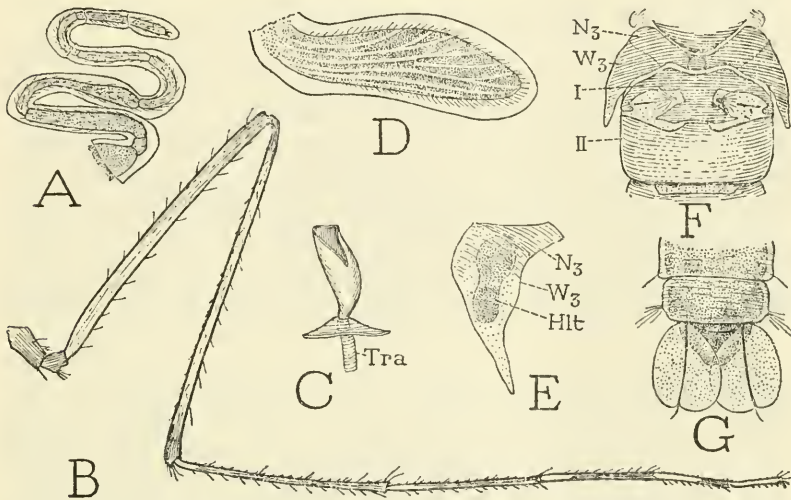

FIG. 17.—Pupal characters and an adult leg of *Aedes aegypti*.

A, Left third leg of pupa with adult leg formed inside the cuticle. B, Same leg of adult on emergence, same magnification. C, Right respiratory trumpet, mesal. D, Left mesothoracic wing with adult wing inside the cuticle. E, Left metathoracic wing with halter forming inside it. F, Metanotum and first two abdominal segments. G, End of abdomen with tail fins.

Hlt, halter; *N₃*, metanotum; *Tra*, trachea; *W₃*, metathoracic wing; *I, II*, first and second abdominal segments.

sensory organs responding to vibrations in the water. The pupa becomes immediately active on any disturbance of the water, even to a tap on the containing vessel.

The pupal tail fins, as usually drawn in illustration, appear to be attached to the end of the eighth abdominal segment (fig. 17 G). If they are pulled away from the eighth segment, however, they are seen to be carried by a transverse dorsal bar entirely separated from the tergum of the eighth segment (fig. 16 D,E, *IXT*), which, in fact, is the tergum of the ninth segment. On it is supported also the small tenth segment (*X*). In the male pupa (E) the ninth segment is a

complete narrow annulus (IXT, IXS) as in the adult male (fig. 27 B),
and below the small tenth segment projects a pair of large lobes (fig.
16 E, PhL) on a common base arising from the sternal arc of the ninth
segment (F). These lobes are the genital appendages of the male as
far as they are developed in the pupa. Male and female pupae, there-
fore, can be distinguished by the presence (A) or absence (B) of the
genital lobes (PhL), though in the male the lobes might be mistaken
for the tenth segment, since the latter is mostly concealed above them
(A, X).

THE PUPAL METAMORPHOSIS

The pupal life of most mosquitoes is very short, two or three days
or less, though with some species it is much longer. During this time
the contour of the adult is modeled by new growth of the epidermis
beneath the pupal cuticle, while the mouth parts, wings, halteres, and
legs take on the adult structure within their pupal sheaths. At the
same time reconstruction of internal organs takes place inside the
body. The degree of reconstruction necessary to change the larval
organs into those of the adult, however, is much less in the mosquito
than in many other insects, especially in the higher Diptera.

The mosquito pupa breaks with the tradition that a pupa is a "rest-
ing stage" in the life of the insect. When an ordinary pupa is broken
open it is seen to be full of a creamy mass of soft material resulting
from the disintegration of the larval tissues. The inside of a mosquito
pupa is as clean as that of the larva or the adult, and its organs appear
to be intact. Whatever reorganization is going on takes place mostly
inside the alimentary canal and the refuse is not thrown into the body
cavity.

The abdominal muscles are so well preserved that the pupa is an
extremely active stage of the mosquito, and the thoracic muscles are
so well developed that the pupa might be expected to fly if its wings
were more mature. As already noted, Hulst (1906) has described the
process of muscle histolysis and histogenesis as beginning in the larva,
but he is not explicit as to what larval muscles are destroyed or when
the imaginal musculature is completed. In *Culex,* according to Hurst
(1890), the muscles of the pupa are those of the imago; the principal
muscles are present in the young pupa, but they increase greatly in
size. A casual examination of the abdominal musculature in the larva,
pupa, and adult shows little difference between the stages, except for
the greater size of imaginal muscles. However, we need a more de-
tailed comparative study of the muscle pattern and more information
on the replacement of individual muscles.

The larval head musculature appears to be largely replaced by an imaginal musculature. According to Thompson (1905) there is an extensive histolysis of the larval head muscles, accompanied by a regeneration of muscles appropriate to the adult, which takes place in the eighth to tenth hour of pupal life.

The pupal tracheal system is weakly developed and is difficult to see in dissections. According to Hurst (1890) tracheae go from the base of each thoracic trumpet to various parts of the head and body, and a transverse trunk connects the two trumpets. A pair of longitudinal trunks runs back to the rear end of the body, giving off branches to the internal organs and to the site of each spiracle. Only the spiracles of the first abdominal segment remain open.

In his study of the heart of *Anopheles quadrimaculatus*, Jones (1954) reports that no evidence was found that the heart is "destroyed, reconstructed, or otherwise drastically modified during metamorphosis." In young pupae, according to Jones, the heart beats in a forward direction as in the larva, but later it may cease beating for prolonged periods of time. Circulation of the blood, therefore, appears to be unessential for the regenerative changes taking place in the pupa.

The alimentary canal of a young pupa, as described and illustrated by Hurst (1890) in *Culex*, might be supposed to be a functional organ if the pupa could feed. It more resembles the digestive tract of the larva than that of the adult, but since the adult feeds on a very different kind of food from that of the larva, the alimentary canal undergoes a complete reconstruction in the pupa, details of which have been described by Hurst (1890), Thompson (1905), Samtleben (1929), and Richins (1938). The oesophagus is least affected insofar as its epithelium goes over intact from larva to adult, but the larval pharynx is lost, and an enlargement in the back of the head forms the postcerebral sucking pump of the adult. In the thorax the dorsal and ventral diverticula of the adult grow out from the oesophageal wall. The larval gastric caeca are absorbed and not replaced in the adult. The larval epithelium of the stomach, according to Richins, degenerates completely and is cast off into the stomach lumen, as a new epithelium is formed by permanent regenerative cells. Transformation in the proctodaeum is brought about partly by histolysis and histogenesis of the epithelium and partly by regrowth. The five Malpighian tubules of the larva go over into the adult without change. In the rectal sac of the pupa are formed six invaginations of the wall that become the rectal papillae of the adult. The salivary glands of

the larva degenerate and each is replaced by three slender tubules generated from cells in the neck of the larval gland.

The central nervous system undergoes little change in the pupa other than growth and union of some of the ganglia. The first abdominal ganglion of the larva is drawn into the thorax, where it fuses with the metathoracic ganglion, and later the four ganglia now in the thorax condense into a single mass. The last abdominal ganglion of the larva unites with the ganglion of the seventh segment. In the adult mosquito, therefore, there are only six separate ganglia in the abdomen (fig. 30 C). In the head, as described by Woolley (1943) for *Aedes,* the brain and the optic lobes grow rapidly by peripheral formation of new cells. The circumoesophageal connectives shorten and the suboesophageal ganglion unites with the brain around the oesophagus.

Though the visible changes that take place in the nervous system are slight, there must be a considerable reorganization of the internal structure. The behavior and instincts of the adult mosquito are entirely different from those of the larva. Since the activities of the insect resulting from sensory stimuli are determined by established neuromuscular pathways and synapses in the central nervous system, the system that serves the larva must be entirely reorganized into one appropriate for the activities of the adult. Of this, however, we know little or nothing in any insect.

III. THE ADULT

The adult mosquito fully formed within the pupa has now only to cast off its pupal mold to gain its freedom in the garb of a mature winged insect. But this is not easily done since the confined mosquito has no instruments for cutting or breaking the pupal cuticle. Moreover, the wings, legs, antennae, and mouth parts are enclosed in tight-fitting sheaths, from which they must be slowly extracted. However, much as we might wish that the mosquito should remain a prisoner in the pupal skin, nature has made provision for its liberation.

As noted by several observers, the first evidence that the adult is about to emerge is the appearance of a film of air beneath the pupal cuticle on the back of the thorax. A slight retraction of the adult apparently breaks the connections of the pupal trumpets with the tracheal system and thus allows air to escape beneath the cuticle. Usually a short piece of trachea remains attached to the base of each trumpet. According to Marshall and Staley (1932) rhythmical movements now begin in the sucking pump of the adult which draw the air forward,

forming a bubble at the base of the proboscis. This air is then pumped into the stomach as a long narrow bubble that extends back to the fourth abdominal segment. Pressure by the distended abdomen now pushes the thorax forward until it ruptures the pupal cuticle in a median slit along the back from the neck to the end of the mesothorax. Outside air then enters the cleft and is rapidly swallowed, going back in the stomach as far as the sixth abdominal segment and greatly distending the abdomen. Knab (1909), in describing the role of air in the ecdysis of insects, says of the mosquito that on emergence from the pupa it is distended with air far beyond its natural size, the integument being stretched to its utmost. According to the writer's observations on emerging mosquitoes the degree of distention is highly variable, even with individuals of the same species.

Pupae of *Aedes aegypti,* before the adult ecdysis, are observed to have the abdomen extended straight back from the thorax, and during the emergence it is held, or floats, in this position with the tail fins against the water surface (fig. 18 A). When the pupal cuticle splits on the back of the thorax, the thorax of the adult bulges out and pushes apart the lips of the cleft. This produces a transverse split over the back of the pupal head, so that the pupal skin can now be widely opened anteriorly (B) to allow the egress of the adult. At the same time the cuticle on top of the pupal head between the eyes breaks out and folds forward as a free flap beyond the antennal bases (A,B). Behind the antennae the anterior tentorial arms project internally as a pair of slender tapering rods (B).

Inasmuch as the legs of the adult, as well as the wings and mouth parts, are enclosed in tight-fitting pupal sheaths, the mosquito cannot use its appendages for freeing itself. Yet, when the head and thorax are free, the abdomen follows and the entire adult slowly rises vertically from the pupal skin as if pushed out from below. The legs and wings are at first closely pressed against the body, but as the legs are freed they at once become active, and appear to be reaching for the surface of the water. The mosquito seems to know instinctively that now and henceforth it must support itself on its legs. It will be noted that the legs of the emerged adult are greatly longer than their pupal sheaths; the hindleg of an *Aedes* (fig. 17 B), for example, may lengthen to two and a half times the length of the corresponding folded leg of the pupa (A). When the end of the abdomen and the wings are finally out of the pupal thorax and the legs are all free, the new insect confidently steps out onto the surface of the water and calmly walks away from the discarded pupal skin. It may come to rest on

some nearby floating object (as a bit of cardboard in the aquarium), but usually in a very short time it is able to fly, and immediately is gone. Sometimes, however, mosquitoes in culture appear to have much difficulty in finally extracting their legs; often they fall over on the surface of the water, and some perish in this position with their tarsi still held in the pupal sheaths. It is probable that in such cases the larvae were not properly nourished.
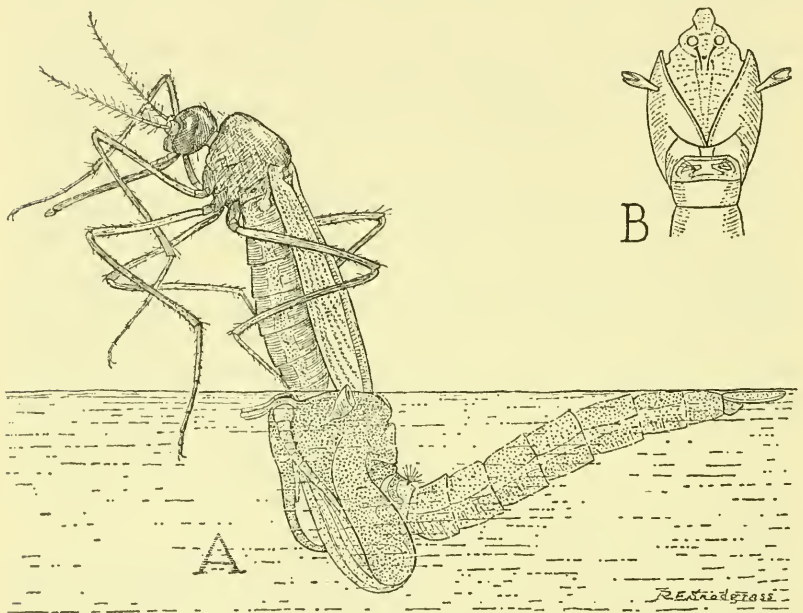

Fig. 18.—An adult female of *Aedes aegypti* emerging from the submerged pupal cuticle; and the open thorax of the discarded pupal cuticle of *Anopheles quadrimaculatus*.

A remarkable thing about the mosquito is that, after its whole previous life spent in the water, on emergence from the pupa it is at once at home in the air. Without a flutter of the wings or any practice trial, it makes a perfect takeoff, flight, and distant landing. During the pupal stage, therefore, the mosquito has not only been equipped with a complete mechanical apparatus of flight, but in its nervous system a mechanism of control has been fully elaborated. Compare this with the difficulty the young human has in learning even to walk, but of course his ancestors did not always walk upright on two legs.

The newly emerged mosquito (fig. 19) is really an elegant insect as it stands high on its long slender legs, the abdomen held straight back beneath the neatly folded wings, and the long proboscis extended from the head. The sexes of most species are readily distinguished at once by the antennae, those of the female having usually circles of short hairs, those of the male being large spreading plumes.
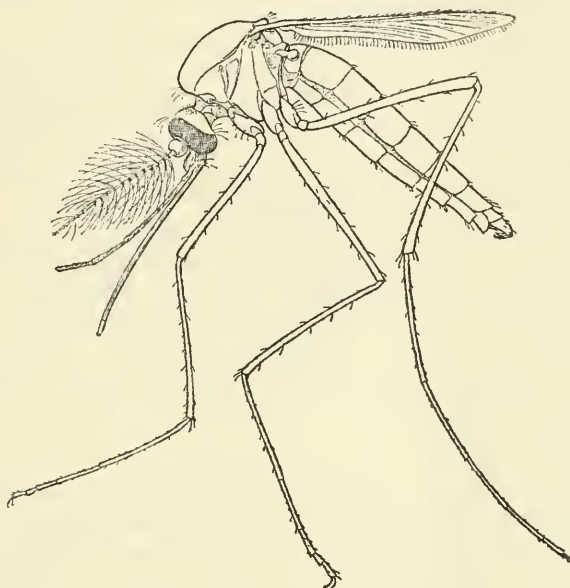

FIG. 19.—*Aedes aegypti,* adult male.

THE HEAD

The head of an adult mosquito has little likeness to that of the larva. It is an oval capsule (fig. 20 D) with the facial region carrying the antennae directed forward, and the long proboscis extended from its lower end. The sides are largely occupied by the great compound eyes, which almost meet dorsally and ventrally (A,B, *E*). The large bases of the antennae arise so close together on the face that the frons is reduced to a narrow verticle bar between them (A, *Fr*), but its lower end forks into diverging arms that support the clypeus (*Clp*). A median coronal sulcus (*cs*) on the vertex extends downward on the face through the frons. The strongly convex clypeus (A,C, *Clp*) forms a prominent lobe just above the base of the proboscis. The undersurface of the head (B) resembles that of the

larva in that it is completely closed from the occipital foramen to the base of the proboscis. The head is attached to the thorax by a slender membranous neck and is supported by a pair of lateral cervical sclerites (D,E). The head of the male is similar to that of the female, but is a little smaller. The internal head skeleton consists of a pair of simple tentorial arms extending from anterior pits above the lateral angles of the clypeus (A, *at*) to posterior pits (B, *pt*) on the ventral margin of the occipital foramen.

From the front of the face arise the long antennae (fig. 20 D,E). The hairy flagellum of each organ is borne on a large globose base (A, *Pdc*), which is the pedicel, or so-called torus, but when the pedicel is removed (right) it is seen to be itself supported on a narrow ring (*Scp*) that represents the usually much longer scape of other insects. The slender shaft of the flagellum is divided into 14 sections (errone-ously called "segments"), 13 of which carry each a whorl of hairs. In general the sexes are readily distinguished by the number and length of the flagellar hairs, which in the male (fig. 22 A) give the antennae a plumose appearance in contrast to the short-haired female antennae (D,E). The two types, however, intergrade, females of some species having bushy antennae, and some males short-haired antennae. In the female the hairs arise from clear areas near the bases of the flagellar units (B) ; in the male (C) they are borne on promi-nent, darkly sclerotized, subapical expansions of the units. Tulloch and Shapiro (1951) have shown from electron microscope studies that the flagellar hairs are armed with rows of minute teeth; in *Culex quinquefasciatus* they estimate there are at least 16 rows along each hair. These writers, however, are in error where they say the hairs "arise at the junctions of the flagellar segments."

The large globose pedicel of the antenna in each sex contains a highly developed sclopophorous sense organ, present also, though usually much smaller, in the antennal pedicel of most insects. The organ was first described in *Culex* as an auditory organ by Johnston (1855), who did not at all understand the nature of the structure in the pedicel, but it has since been known as *Johnston's organ*. Sub-sequently Child (1894) made good histological studies of the organ in various insects, including the mosquito, and his illustrations are now familiar in most entomological texts. A more recent comparative study of the organ in *Culex, Aedes,* and *Anopheles* is given by Risler (1955). The component sensory elements in the pedicel are attached to a plate or prongs on the base of the flagellum, and thus evidently register movements of the flagellum.
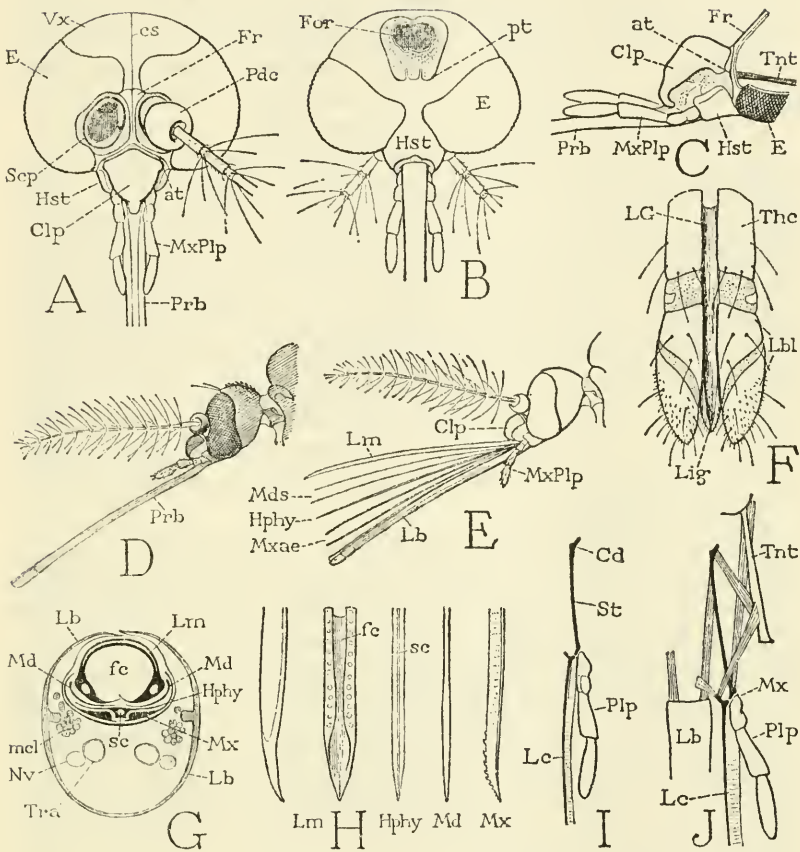
FIG. 20.—Head and mouth parts of an adult female mosquito, *Aedes aegypti* except G.

A, Head and base of proboscis, anterior. B, Same, posterior. C, Clypeus and base of proboscis, lateral. D, Head, lateral. E, Same, with mouth parts separated. F, End of labium, dorsal. G, Cross section of proboscis of *Anopheles* (from Vogel, 1921). H, Distal ends of mouth part stylets. I, Basal parts of maxilla. J, Proximal parts of right maxilla and labium, posterior.

at, anterior tentorial pit; *Cd,* cardo; *Clp,* clypeus; *cs,* median cranial sulcus; *E,* compound eye; *fc,* food canal; *For,* occipital foramen; *Fr,* frons; *Hphy,* hypopharynx; *Hst,* hypostome; *Lb,* labium; *Lbl,* labellum; *Lc,* lacinia; *LG,* labial gutter; *Lig,* ligula; *Lm,* labrum; *mcl,* muscle; *Md,Mds,* mandible, mandibles; *Mx,Mxae,* maxilla, maxillae; *MxPlp,* maxillary palpus; *Nv,* nerve; *Pdc,* antennal pedicel; *Plp,* palpus; *Prb,* proboscis; *pt,* posterior tentorail pit; *sc,* salivary canal; *Scp,* antennal scape; *St,* stipes; *Thc,* theca; *Tnt,* anterior tentorial arm; *Tra,* trachea; *Vx,* vertex.

While it is probable that the organ of Johnston in the antenna of most insects registers the movements of the flagellum, the elaborate experimental work of Roth (1948) leaves no doubt that the highly developed organ in the male mosquito is responsive to the effect of sound waves on the flagellum. This, of course, does not imply that the mosquito has an auditory "sense"; mechanical reaction to stimuli is all that we can attribute to the insects. Male mosquitoes are attracted to the females in flight by the tone produced by their wings. Roth showed that males with intact antennae, when subjected to the sound of a tuning fork at 480 vibrations a second held behind a suspended piece of cloth, fly to the source of the sound where they exhibit typical mating activities though no females are present. Even after complete removal of the flagellar hairs, males still respond to more intense sounds apparently by vibrations of the shaft alone, but on complete removal of the flagella they give no reaction. Roth's tests were made particularly on *Aedes,* but males of other genera were found to react similarly. Females of *Aedes aegypti* gave no evidence of being attracted to sounds, "though they may give shock-reaction to certain intensities."

Further experimental work of Roth (1951) on females of *Aedes* seems to show that the antennae function as directional distance thermoreceptors and probably also as chemoreceptors. Females deprived of their antennae are unable to locate a host from a distance. The antennae and the palpi are said to be the chief organs responding to stimuli that induce probing by the proboscis. The receptor organs of the antennae, however, are not described, but along the shaft of the female antennae (fig. 22 B) are numerous hairs, and on the male antenna (C) a ring of very short hairs encircles the distal end of each flagellar section. The antennae of insects in general are known to be the principal seat of chemoreception.

The compound eyes of the mosquito are so large that they almost encircle the head. Satô (1950, 1953a, 1953b) reports that by actual count there are from 440 to 462 facets in the eye of a male *Culex pipiens,* and 503 to 566 in the female; and that in *Aedes japonicus* the male eye contains 440 to 462 facets, the female eye 504 to 527. The surface area of the eye in each genus is larger in the female than in the male. The internal structure of the compound eye in *Culex* is described by Constantineanu (1930) and by Satô (1950).

An extensive experimental study of the visual responses of flying mosquitoes made by Kennedy (1939) on unfed females of *Aedes aegypti* shows that the mosquitoes react negatively to light, and are

attracted to dark objects. Experimentally they orient toward black stripes on a white background, and continue to do so when the stripes are rotated about them. When confronted by two black stripes, they face one or the other and not the intervening space. In a wind tunnel freely flying mosquitoes move against the current.

THE ORGANS OF FEEDING

The feeding organs of the adult mosquito include the *proboscis* and two sucking pumps. One of the latter is a preoral *cibarial pump* beneath the clypeus, the other is a *pharyngeal pump,* being a part of the alimentary canal behind the brain in the back of the head. In describing the feeding organs of the adult it will be better to take the female first, because in most mosquitoes she is the biting and bloodsucking member of the species and has the mouth parts fully developed. In the nectar-feeding male some of the parts are much reduced or absent.

The proboscis.—The slender, rodlike proboscis in the female mosquito is usually composed of all the mouth parts possessed by insects that feed on solid food, namely, a *labrum,* a pair of *mandibles,* a *hypopharynx,* a pair of *maxillae,* and a *labium,* but the parts are all structurally modified in adaptation to the mosquito's way of feeding. The relation of the parts in the undisturbed proboscis is best seen in a cross section (fig. 20 G). In the deeply channeled upper side of the labium (Lb) are enclosed the labrum (Lm), the mandibles (Md), the hypopharynx ($Hphy$), and the maxillae (Mx). The labrum itself is practically an inverted tube, since its margins are curved downward and may overlap. The enclosed labral canal (fc) is the food conduit. The hypopharynx contains the salivary canal (sc). By careful manipulation with a dissecting needle all these parts can be separated as shown at E.

The labrum (fig. 20 H, Lm) is the thickest and the strongest of the stylets. It is movable by muscles from the clypeus attached on its base (fig. 24 D), but the muscles simply elevate and depress the labrum, which is firmly hinged on the clypeus. The term "labrum-epipharynx" often applied to the labrum is quite unnecessary, since in its general form the labrum is a flat lobe of the head and therefore has an upper and lower surface. In the mosquito the decurvature of the lateral parts converts the labrum into a tube through which the ingested liquid food is drawn up by the sucking apparatus at its base. At the sharp-pointed distal end (fig. 20 H, Lm) the walls of the channel diverge to make an opening like that of a hypodermic needle.

The mandibles are the slenderest of the stylets, but they vary somewhat in thickness and shape in different species. In *Aedes* here illustrated (fig. 20 H, *Md*) each is slightly enlarged toward the tapering distal end. The base of each mandible is movably connected with the lower part of the cranial wall by a small suspensory sclerite, and a slender muscle from the tentorium is inserted on the mandibular base. The mandibles are thus retractile for a short distance, and, when retracted, their withdrawn tips give free entrance to liquid into the open end of the labral food canal. Protraction results from the elasticity of the suspensory mechanism on relaxation of the muscles.

The single, median hypopharynx, present as an independent stylet only in the female, is a simple, flattened rod (fig. 20 H, *Hphy*) traversed by the salivary outlet canal (*sc*), which opens on its acute tip. The hypopharynx is not individually movable; its anterior wall is continued basally into the floor of the cibarial pump.

The maxillae are less reduced than the other mouth parts, and are well equipped with muscles. The principal part of each maxilla (fig. 20 I) is a long, flattened, sharp-pointed blade (*Lc*) armed with recurved teeth near the end of its outer margin (H, *Mx*). From the base of the blade projects a usually short four-segmented palpus (I, *Plp*). The maxillary blade has been regarded as the galea by some writers (Robinson, 1939; Snodgrass, 1944), but it is more reasonably interpreted by Schiemenz (1957) as the lacinia, which is usually the operative part of a generalized maxilla. From its base a long, strongly sclerotized, apodemelike rod extends backward in the head and gives attachment to muscles (J). This rod is evidently the stipes, or more probably stipes (*St*) and cardo (*Cd*) combined, sunk into the head, since in some related flies, such as *Phlebotomus* (fig. 22 G), it is superficial on the back of the head and articulates on the cranial margin.

The maxillary musculature of *Aedes* (fig. 20 J) includes a long retractor arising on the head wall close to the posterior end of the tentorial arm (*Tnt*) inserted on the distal end of the stipes, and two protractors attached proximally on the stipito-cardinal rod. One of these muscles arises on the tentorium, the other, very curiously, on the base of the labium. A lateral muscle from the tentorium and a short mesal muscle both attached on the base of the lacinia are regarded by Schiemenz (1957) in *Theobaldia* [*Culiseta*] as an abductor and adductor respectively of the maxilla. A short muscle from the stipes is inserted on the base of the palpus, and each palpal segment contains a small muscle inserted on the segment distal to it.

The long, gutterlike labium of the mosquito is the so-called prementum of a generalized labium, the usual basal part of the labium being absent, though a small postmental sclerite may be present in other Nematocera (fig. 22 G, *Pmt*). The prementum in Diptera is known as the *theca* because it ensheaths the other mouth parts. Apically it bears two small movable lobes, the *labella* (fig. 20 F, *Lbl*), and ends between them in a slender median projection, or *ligula* (*Lig*). The labella appear to be two-segmented, and evidently represent the labial palpi because each is provided with an abductor and an adductor muscle from the prementum. The only muscles attached on the base of the labium are the two already noted that arise on the maxillary stipites (J) and probably act as protractors of the maxilla, since the labium is firmly fixed to the head.

The styliform mouth parts within the labial theca adhere to one another in a compact fascicle. They are usually said to be held together by an oil liquid, but Bhatia and Wattal (1957) have described rings issuing from the margins of the labrum that surround the hypopharynx, mandibles, and maxillae and bind these stylets to the labrum. However, no other investigator has reported the presence of any such structures, and the writer has failed to see them in *Aedes, Culex,* or *Anopheles*. The incurved lower edges of the labrum enclose only the food canal.

When the female mosquito is about to take a meal of blood, she places the tip of the proboscis against the skin of the victim (fig. 21 A), closely holding the end of the stylet fascicle between the labial labella. The movable maxillary stylets are the active piercing organs. Acting alternately, first one is protracted and holds its position in the flesh by means of its recurved teeth, then the other is forced in beyond the first and takes a deeper hold. The labrum, mandibles, and hypopharynx penetrate along with the maxillae. The retractor muscles of the maxillae, instead of pulling the stylets out of the wound, where they are held by the maxillary teeth, bring the head down closer to the feeding surface. The labrum, still holding the stylet fascicle between the labella, is thus forced to bend backward (B) and the bend becomes greater the deeper the stylets penetrate (C). When finally the stylets pierce and enter a small blood vessel, or let out a pool of blood, the mandibles are drawn back from the end of the labrum to allow the blood to enter the food canal in response to the suction of the cibarial pump. Saliva discharged from the hypopharynx in some species serves to prevent coagulation of the blood. A more detailed account of the feeding act and of accompanying movements by the maxillary palpi is

given by Robinson (1939). After feeding, the maxillary stylets are retracted, the female braces herself against the skin of the victim with her legs, and forcibly pulls out the fascicle of stylets, which again is ensheathed in the straightened labium.

In discussing the feeding of mosquitoes, we must not overlook the fact that not all females are bloodsuckers. A prominent exception to the rule are species of *Toxorhynchites,* in which both sexes feed on
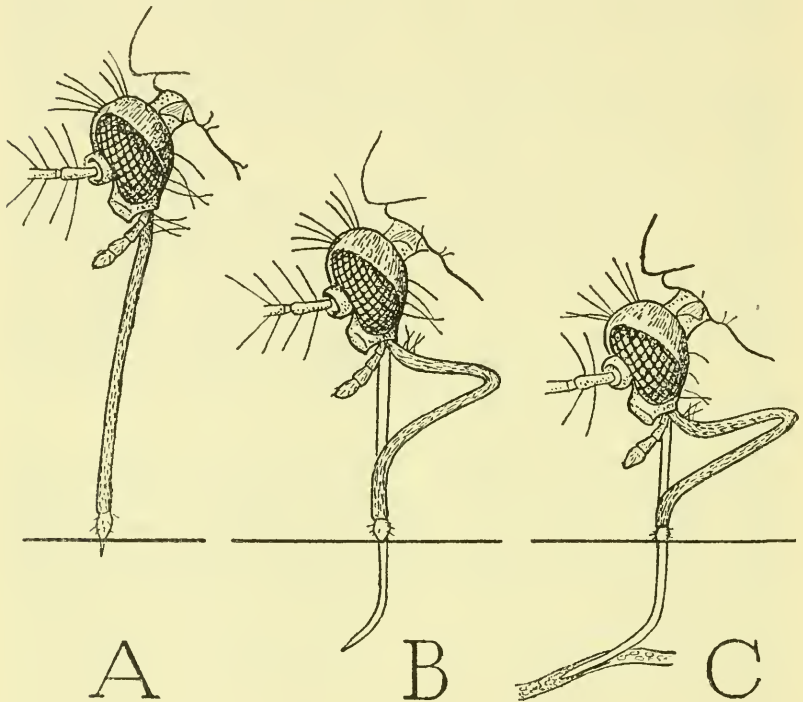

Fig. 21.—Successive stages in the penetration of the stylets of a female mosquito feeding on blood. (B, C, from Gordon and Lumsden, 1939, with neck plate added.)

nectar or other plant juices. In this genus (fig. 22 D) the proboscis is very long, tapering, and strongly decurved. The maxillary palpi projecting from the base of the proboscis are long and four-segmented. The laciniae by contrast are weak and taper into filaments reaching only a little beyond the end of the first palpal segment; evidently they play no part in feeding. A slender labrum extends to the tip of the proboscis, but mandibles appear to be absent.

Then there are species of *Malaya* (=*Harpagomyia*) that get their

food from ants. In these the proboscis is curved forward at its lower end (fig. 22 E) ; the distal part is thickened and armed with long hairs. The elongate labella terminate with a pair of small transparent lobes. The species of *Malaya* are minute mosquitoes, much smaller than ordinary ants. As described by Jacobson (1911) they sit on branches
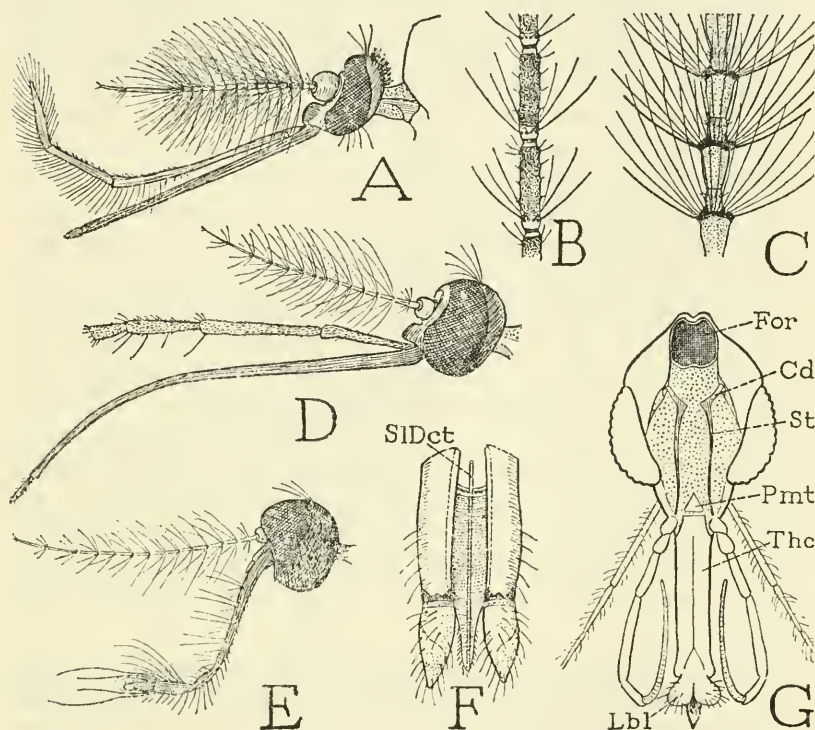

Fig. 22.—Various types of antennae, palpi, proboscides, and labia of adult mosquitoes.

A, *Culex* sp., head of male. B, Same, part of female antenna. C, Same, part of male antenna. D, *Toxorhynchites rutilus,* head and proboscis of female. E, *Malaya jacobsoni,* head and proboscis of female. F, *Culex,* distal end of male labium, showing salivary duct. G, *Phlebotomus verrucarum* (Ceratopogonidae), head and proboscis, posterior.

Cd, cardo; *For,* occipital foramen; *Lbl,* labellum; *Pmt,* postmentum; *SlDct,* salivary duct; *St,* stipes; *Thc,* theca (prementum).

inhabited by ants, and when an ant runs between the legs of one of them the mosquito thrusts the end of its proboscis between the open mandibles of the ant, which accommodatingly gives up its dinner to the mosquito. The proboscis of the adult *Malaya* lacks mandibles and maxillae. According to de Meijere (1911) these members are present

in the pupa, but the imaginal parts formed inside of them are short and disappear.

The mouth parts of the male mosquito are much simplified by the great reduction of the mandibular and maxillary stylets and the entire absence of a hypopharyngeal stylet. The male proboscis, therefore, consists principally of only the labrum and the labium, but the maxillary palpi are usually highly developed and may be much longer than the proboscis (fig. 22 A). Mandibular stylets when present are seldom longer than half the length of the proboscis and are usually much shorter. Marshall and Staley (1935) report that they are present in all genera examined except *"Aedes* and *Ochlerotatus."* These writers found maxillary stylets to be present in representatives of all genera examined, but the length is highly variable, even in species of the same genus. The labium is a deep trough, as in the female, and ends with a tapering median ligular lobe between the labella (fig. 22 F). It will be recalled that the hypopharynx of the male mosquito is not separated from the labium, as in the female. The hypopharynx thus retains in the adult male the larval condition of union with the labium. The male "labium" is, therefore, really a labiohypopharynx. The hypopharyngeal component in *Anopheles* is identified by Vizzi (1953) as a sclerotic plate on the floor of the labial gutter. In sectional figures he shows the salivary canal in an apparent median thickening of the plate. In *Culex* (fig. 22 F) the salivary duct (*SlDct*) is a thread-like tube that traverses internally the floor of the labial gutter and opens on the tip of the ligula, but it appears to be free in the labial lumen.

The cibarial pump.—The structure here termed the cibarial pump lies just beneath the clypeus at the base of the proboscis, and is the organ that sucks the liquid food up through the canal of the labrum. The same pump is present in all Diptera and is the sucking apparatus of other liquid-feeding insects, such as the Hemiptera. It has long been erroneously called the "pharynx," and even some recent writers continue to call it such on the pretext of not wishing to confuse students. It is possible, however, that some students might prefer to know the facts. The organ in question is entirely outside the mouth, as no true pharynx could be, but admittedly it is difficult to understand its anatomical status in the mosquito. We must therefore turn to some other more generalized insect for light on the nature of the preoral sucking organ, and for this purpose the cockroach will be particularly illuminating.

In a vertical lengthwise section of the head of a cockroach (fig.

23) the mouth (*Mth*) is seen to lie beneath the upper end of the clypeal region (*Clp*) of the cranial wall. Below the mouth projects the large tonguelike lobe commonly termed the hypopharynx (*Hphy*), which has a long base sloping up to the mouth. On this basal part of the hypopharynx is a depression that forms the floor of a pocketlike space (*Cb*) in front of the mouth beneath the inner wall of the clypeus. The masticated food passed back from the mandibles is stored in this pocket before it is swallowed. The pocket, therefore, is named the
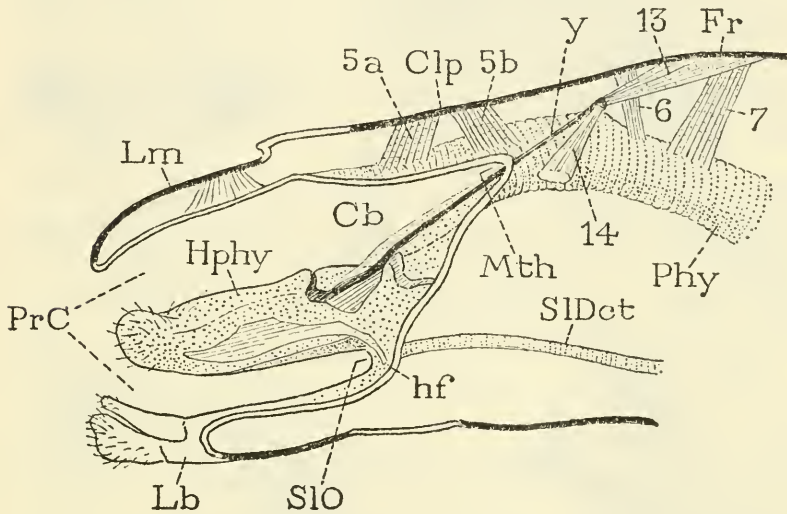

Fig. 23.—Vertical section through the left side of the head of a cockroach, exposing the preoral cavity.

Cb, cibarium; *Clp*, clypeus; *Fr*, frons; *hf*, hypopharyngeal fulcrum; *Hphy*, hypopharynx; *Lb*, labium; *Lm*, labrum; *Mth*, mouth; *Phy*, pharynx; *PrC*, preoral cavity; *SlDct*, salivary duct; *SlO*, salivary orifice; *y*, oral suspensory arm of hypopharynx.

5a,5b, dilator muscles of cibarium; *6,7*, frontal muscles of stomodaeum; *13*, adductor of hypopharynx; *14*, abductor of hypopharynx.

cibarium (food container). On its dorsal wall are attached strong muscles (*5a, 5b*) from the clypeus. The hypopharynx can be pressed against the inner clypeal wall by muscles (*13*) attached to arms (*y*) from its base. The cibarium then becomes a closed chamber that can be dilated by the clypeal muscles, and probably serves as a sucking organ when the cockroach drinks liquids. In insects that habitually feed on liquid food, the cibarium becomes elaborated to form a permanent sucking pump.

When we turn now to the mosquito, a section of the head (fig. 24 A) will show beneath the bulging clypeus (*Clp*) a small elongate capsule (*CbP*), which is the primary sucking pump. The basinlike lower wall is strongly sclerotized and, in the female, is directly con-
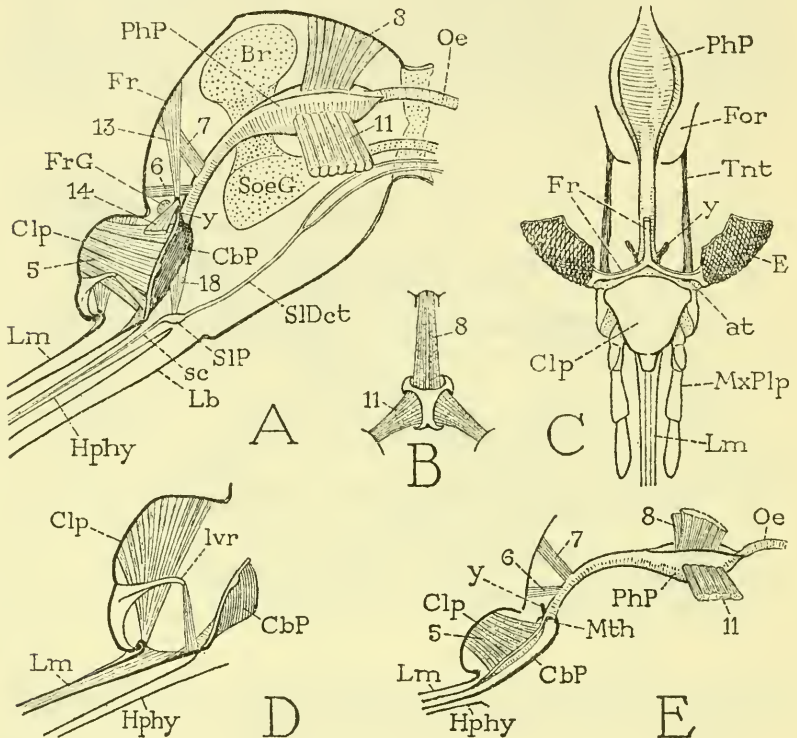

FIG. 24.—The sucking apparatus of an adult mosquito.

A, Diagrammatic section of female head. B, *Culex* sp., section of pharyngeal pump (from Thompson, 1905). C, *Aedes aegypti*, pharyngeal pump exposed by removal of anterior head wall. D, Same, muscles of labrum. E, Same, cibarial and pharyngeal pumps, left, cibarial pump opened to show lumen and dilator muscles.

at, anterior tentorial pit; *Br,* brain; *CbP,* cibarial pump; *For,* occipital foramen; *FrG,* frontal ganglion; *lvr,* labral lever; *MxPlp,* maxillary palpus; *Oe,* oesophagus; *PhP,* pharyngeal pump; *sc,* salivary canal; *SlP,* salivary pump; *SoeG,* suboesophageal ganglion; *Tnt,* tentorial arm; *y,* oral arm of cibarial pump. Other lettering as on figure 23.

tinuous with the supper surface of the hypopharynx (*Hphy*). The dorsal wall (E) is the so-called epipharyngeal surface from the labrum (*Lm*) to the mouth (*Mth*), and is thin and flexible. On it is attached a great mass of dilator muscles (*5*) from the clypeus. The

inner end of the organ opens through the mouth (*Mth*) into the narrow first part of the alimentary canal, and at each side of the mouth projects a small process (*y*) on which are attached two antagonistic muscles (A, *13, 14*), as in the cockroach. All these features so closely duplicate those of the cibarium in the cockroach as to leave no doubt that the preoral sucking pump of the mosquito is the cibarium. In the mosquito, however, the organ has been made into a much more efficient sucking apparatus than that of the cockroach by the union of the edges of its lower hypopharyngeal wall with the epipharyngeal wall, thereby converting the lumen into a closed cavity. The clypeal muscles on contraction lift the flexible dorsal wall and expand the lumen, drawing in the liquid food from the canal of the labrum. On relaxation of the muscles the dorsal wall snaps back by its own elasticity and drives the liquid from the pump back through the mouth.

On the epipharyngeal wall of the cibarial pump are small spines and papillae of various kinds, some of which are sense organs. A comparative study of these structures and an armature of ventral teeth at the mouth entrance has been made by Sinton and Covell (1927), and Chwatt and Major (1945) in the anophelines, and by Barraud and Covell (1928) in anopheline and culicine species. The epipharyngeal sense organs are described by Day (1954).

The pharyngeal pump.—From the mouth at the inner end of the cibarial pump the stomodaeal section of the alimentary canal begins as a narrow tube (fig. 24 A,E) that curves upward and backward in the head, going between the brain (A, *Br*) and the suboesophageal ganglion (*SoeG*). Behind the brain it expands into a large, bulblike structure, which is the pharyngeal pump (*PhP*). The walls of the organ when relaxed are deeply concave above and on each side, as seen in cross section at B. Into the concavity of the dorsal wall is inserted a pair of large muscles (A,B,E, *8*) from the dorsal wall of the head behind the brain, and into each lateral concavity a large flat muscle (*11*) from the side of the cranium. Contraction of the muscles dilates the lumen of the pump; on their relaxation the walls spring together again by their own elasticity. From the rear end of the pump, the narrow oesophagus (*Oe*) proceeds through the neck into the thorax. A cibarial and a pharyngeal pump like those of the mosquito are common to bloodsucking nematocerous flies. Presumably the two pumps work in alternate phases to keep the ingested blood flowing freely back into the stomach. In the nectar-feeding male mosquito the sucking apparatus is less strongly developed than in the female.

THE THORAX

The thorax of a winged insect may truly be said to be the most re-markable anatomical mechanism developed anywhere in the animal kingdom. It is remarkable both for its efficiency as a flight mechanism and for its structural simplicity. In insects with two pairs of wings the two wing-bearing segments have essentially the same structure, and are equipped with duplicating sets of muscles. In the Diptera, however, in which the flight function has been taken over entirely by the first pair of wings, the mesothoracic wing muscles have to do the work of the muscles of both winged segments in four-winged insects. Consequently, the mesothorax of the flies has been greatly enlarged and the metathorax much reduced. The knobbed stalks known as *halteres* borne on the metathorax are undoubtedly reduced wings, since, as seen in the mosquito pupa (fig. 17 E), they are developed in flat wing lobes of the metanotum. They are still important accessories of flight, being vibratory organs for maintaining the equilibrium of the flying insect, but their musculature is very simple, and the usual wing musculature of the segment has been eliminated.

In the adult mosquito (fig. 25) the mesothorax appears as a great wedge inserted between the narrow prothorax and metathorax. It alone retains the structure typical of a thoracic segment. Two princi-pal plates, an anterior *notum* (AN_2) and a posterior *postnotum* (PN_2), cover almost the entire dorsum of the thorax. The strongly convex postnotum, furthermore, is deeply infolded posteriorly be-neath the narrow metanotum (N_3) and extends into the first ab-dominal segment as a bilobed *phragma* (fig. 27 D, *Ph*). A narrow paranotal fold (*pnf*) borders the edge of the notum between the first spiracle and the wing. The pleural area tapers downward and becomes continuous with the sternum (S_2) between the first and second legs. A typical *pleural sulcus* (PlS_2) extends from the base of the middle leg to the wing fulcrum at the base of the wing (W). The area before the groove is episternal, that behind it epimeral. The episternal area includes a major episternal plate (Eps_2) continuous below with the sternum, and a smaller preepisternum (eps_2). The epimeron (Epm_2) is a simple quadrate plate. Below it is a small triangular plate (S_3), which in the mosquito appears to be a postcoxal lobe of the sternum; but a plate in the same position in higher flies is the detached meron of the coxa. In some species the episternum is divided into an upper and a lower part (fig. 27 A).

The prothorax is so reduced and modified that it is difficult to interpret its parts. The notum (fig. 25 N_1) includes a narrow plate

across the back beneath the overhanging front end of the mesonotum, and apparently a larger posterior plate on each side. This posterior plate, however, tapers narrowly down to the coxa so that its lower part must be epimeral. The episternum then is represented by a short plate (Eps_1) between the first notal plate and the coxa. A plate in the side of the neck ($CvPl$) that supports the head is unquestionably a cervical sclerite.
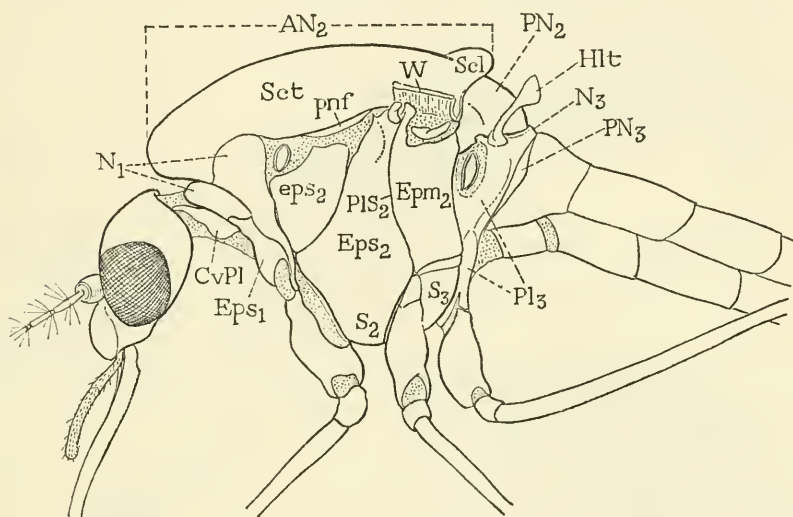

FIG. 25.—Thorax of *Psorophora*, with head and base of abdomen (from the author's illustration in Howard, Dyar, and Knab, 1912).

AN, wing-bearing notal plate; *CvPl*, cervical plate; *Epm*, epimeron; *Eps*, episternum; *eps*, preepisternum; *Hlt*, halter; *N*, notum; *Pl*, pleuron; *PlS*, pleural sulcus; *PN*, postnotum; *pnf*, paranotal fold; *S*, sternum; *Scl*, scutellum; *Sct*, scutum; *W*, wing.
Subnumbers *1,2,3* designate parts of prothorax, mesothorax, and metathorax.

The metathorax is even more simplified than the prothorax. The notum (fig. 25, N_3) is much narrowed across the back, but it expands on the sides where it carries the halteres (Hlt). From the notum the pleural region continues downward on the side, tapering to the hind coxa. Close to its posterior margin is a faint line that perhaps represents the pleural sulcus. A narrow strip (PN_3) between the metanotum and the first abdominal segment, more plainly seen in *Aedes* (fig. 27 C,D, PN_3), is clearly the metapostnotum, since it gives attachment to the first abdominal muscles (G).

The wings of the mosquito have a simple pattern of venation, shown at A of figure 26, in which the veins are named according to the Com-

stock-Needham system. Mosquito taxonomists, however, usually designate the veins behind the subcosta by numbers. In this scheme R_1 is vein 1, R_2 and R_3 are branches of vein 2, R_{4+5} is vein 3, M and its two branches are vein 4, Cu and its two branches are vein 5, and A is vein 6. The veins are densely clothed on both sides of the wing with long, slender, fusiform, or scalelike setae (omitted in the figure).

While the simple venation of the mosquito wing is of a fairly generalized pattern, the basal wing structure has little resemblance
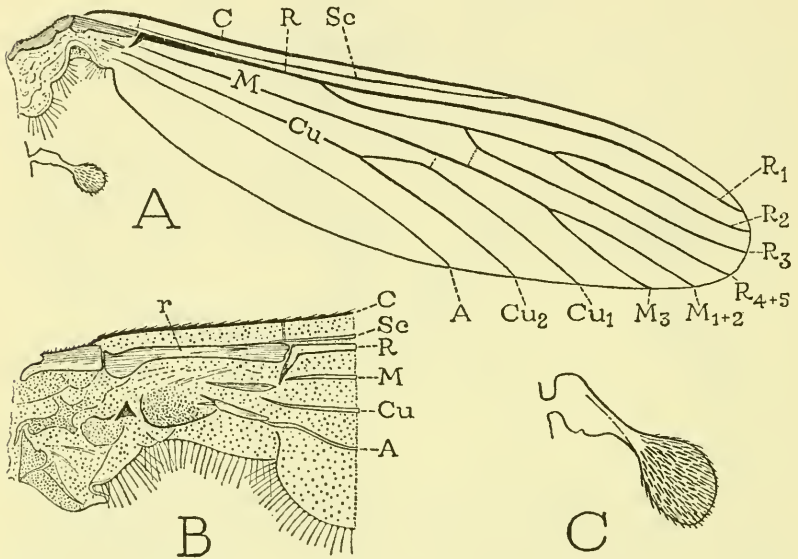

Fig. 26.—The wing and halter.

A, *Culex*, left wing and halter, wing partly flexed on basal lobe, scales removed to show venation. B, *Anopheles*, base of wing, flattened. C, *Culex*, halter enlarged, posterior.

A, anal vein; C, costa; Cu, cubitus; M, media; R, radius; Sc, subcosta.

to that of most other insects, and would appear to be specialized by elimination of the usual axillary sclerites. When the wing is flexed (fig. 26 A) a fold near the base sets off a triangular basal lobe by which the wing is attached to the thorax. During flexion the wing turns posteriorly over the basal lobe, which is then covered from above by the fully flexed wing, and gives the wing the appearance of being supported on a lobe of the thorax. The principal sclerotization of the wing base is a long, anterior jointed bar (B, r) that supports the radial vein, and bends at the joint when the wing is flexed (A).

Otherwise the membrane of the whole basal area is occupied by irregular thickenings or weak sclerotizations that are hardly sclerites and seem to have no mechanical significance. They are better developed in *Anopheles* (B) than in *Culex* (A). The same structure in modified form is present also in some related Nematocera, but not in Tipulidae.

The wing mechanism of extension and flexion is not understood, but all the direct muscles of flight appear to be attached on the basal lobe. The indirect flight muscles are as fully developed as in any other fly. They include great masses of dorsal longitudinal fibers and lateral vertical fibers that almost completely fill the thorax. The weight of the flight muscles of *Aedes* has been calculated by Hocking (1953) as from 16.5 to 18.7 percent of the total body weight, which, however, is small as compared with *Tabanus* in which the flight muscles are 23 to 35 percent of the body weight.

The rate of the wing vibration in flight, measured in wing beats per second, is given by Sotavalta (1947) for females as 165 to 196 for *Culex pipiens,* 165 to 247 for *Anopheles maculipennis,* 241 to 311 for *Aedes cantans* and *Aedes punctor.* With males the rate is consistently higher, from 330 to 587 beats per second by *Anopheles* and *Aedes.* Hocking (1953) has measured the flying speed of five species of *Aedes.* In ordinary cruising flight they go from 75 to 110 centimeters per second, but for short distances they can make 220 to 252 centimeters in a second.

The legs of the mosquito have no unusual features, except for their length and relative slenderness. Each leg (fig. 17 B) has the usual six segments of an insect leg, a coxa, trochanter, femur, tibia, tarsus, and pretarsus. The long tarsus is subdivided into five tarsomeres. The pretarsus has two decurved claws but no arolium. In some species, as in *Culex,* the foot is provided with a pair of small padlike pulvilli; in others there is only a heel-like hairy swelling at the bases of the claws. Most mosquitoes, however, whether they have foot pads or not, are able to cling to smooth vertical surfaces, such as window panes or the walls of a glass jar.

THE ABDOMEN

The abdomen of the adult mosquito (fig. 27 A) is broadly joined to the thorax and tapers posteriorly. The tergal and sternal plates are separated on the sides by membranous areas containing the spiracles, which are present on segments I to VII. In each sex the abdomen has 10 segments, as in the pupa, but in the females of some species the eighth segment is ordinarily retracted into the seventh, and in the male the ninth segment is concealed within the eighth.
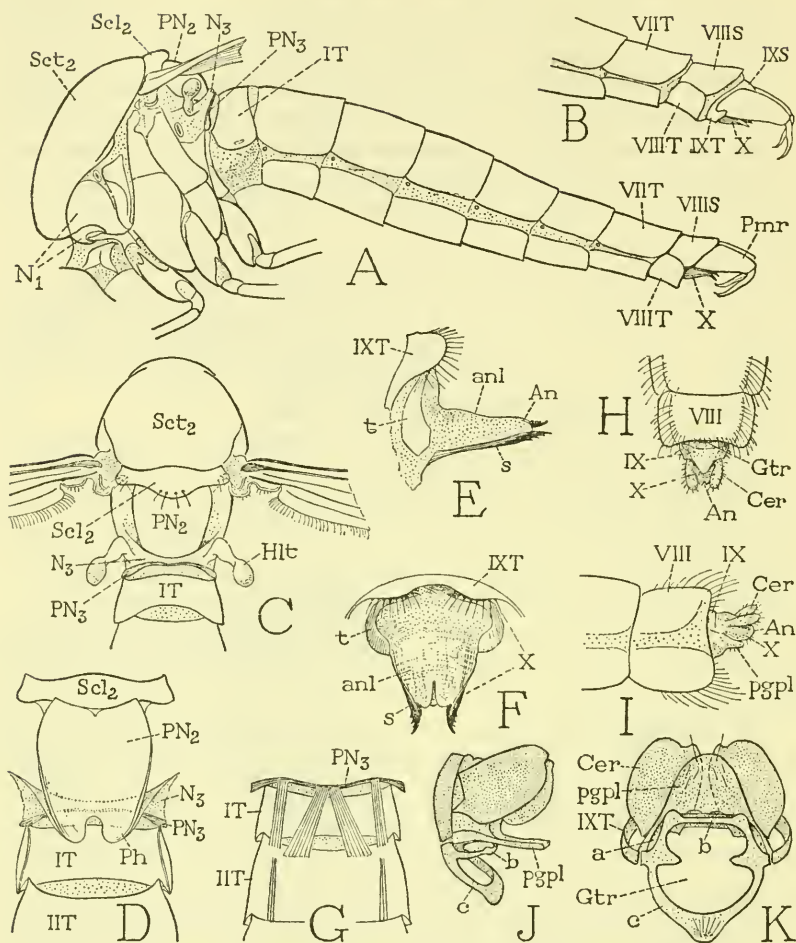
Fig. 27.—Details of the adult thorax and abdomen.

A, *Aedes aegypti*, male thorax and abdomen. B, Same, end of abdomen extended. C, Same, thorax and base of abdomen, dorsal. D, Same, postnotum of metathorax extended as a phragma into base of abdomen, ventral. E, Same, tenth abdominal segment of male, lateral. F, Same, undersurface (dorsal). G, Same, showing dorsal muscles of first abdominal segment. H, *Culex*, end of female abdomen, ventral. I, Same, lateral. J, Composite diagram of female terminalia, lateral (from Gerry 1932). K, Same, ventral, with ventral arc of sigma (*c*) turned forward (from Gerry 1932).

a, cowl; *An*, anus; *b*, dorsal arc of sigma (ninth sternum?); *c*, ventral arc of sigma; *Cer*, cercus; *Gtr*, gonotreme (opening of genital chamber); *Hlt*, halter; *N*, notum; *pgpl*, postgenital plate; *Ph*, phragma; *Pmr*, paramere; *PN*, postnotum; *s*, lateroventral prong of tenth segment; *S*, sternum; *Scl*, scutellum; *Sct*, scutum; *t*, tergum of tenth segment; *T*, tergum.

Subnumbers *1-3*, thoracic segments; *I-X*, abdominal segments.

The male mosquito is readily distinguished from the female by the presence of a pair of large, two-segmented genital claspers, or *parameres,* projecting from the end of the abdomen (fig. 27 A, *Pmr*). Though the ninth segment is ordinarily concealed by retraction into the eighth, on pulling out the end of the abdomen (B), it is seen to be a small sclerotic ring (*IX*) carrying the parameres. The anus-bearing tenth segment, or proctiger (*X*), is mostly hidden between the bases of the parameres, and is *apparently* ventral in position. In fact, the whole terminal part of the male abdomen beyond the seventh segment, except in newly emerged individuals, is turned upside down, so that the tergal plates are ventral and the sternal plates dorsal. The inversion takes place slowly during the first 24 to 48 hours after emergence from the pupa.

The tenth abdominal segment of the male is a flattened anal lobe with an expanded base projecting from above the inverted tergum of the ninth segment (fig. 27 E,F). In its base are two dorsolateral sclerites (*t*) that may be regarded as tergites. On the ventral (upper) surface are two marginal bars (*s*), the ends of which project as a pair of free, toothed prongs. These bars have commonly been regarded as sternites, but Christophers (1923) says they are the cerci united with the anal lobe.

The external genital organs of the male insect, because of their generic and specific variations, are important diagnostic features for taxonomists. In the mosquito they include primarily the paired lateral claspers and a median intromittent organ, carried by the ninth abdominal segment. Various names are given to these parts by different specialists, but the organs have essentially the same origin in all insects, and there is no need for special terms in the several orders, and certainly there is no excuse for specialists in one order to use different names for the same parts in different species. For simplicity the claspers are here termed the *parameres,* and the intromittent organ the *aedeagus.* Various secondarily developed accessory parts, of course, must have more specific names.

In the insects in general the male genitalia take their origin from a pair of *primary phallic lobes* that develop in a late instar of the nymph or larva on the posterior part of the ninth abdominal segment at the sides of the future gonopore. Later, each lobe divides into two parts, a mesal *mesomere* and a lateral *paramere.* Eventually the mesomeres unite around the gonopore to form the aedeagus, and the parameres become the claspers.

The development of the genital organs in the male mosquito has been shown by Christophers (1922) to proceed in the usual manner.

Early in the fourth instar of the larva paired thickenings of the epidermis appear behind the region of the ninth sternum. These "genital plaques" soon take on the form of budlike outgrowths, which are the primary phallic lobes (fig. 28 A, *PhL*). With further development the lobes elongate and unite at their bases, forming the genital ap-
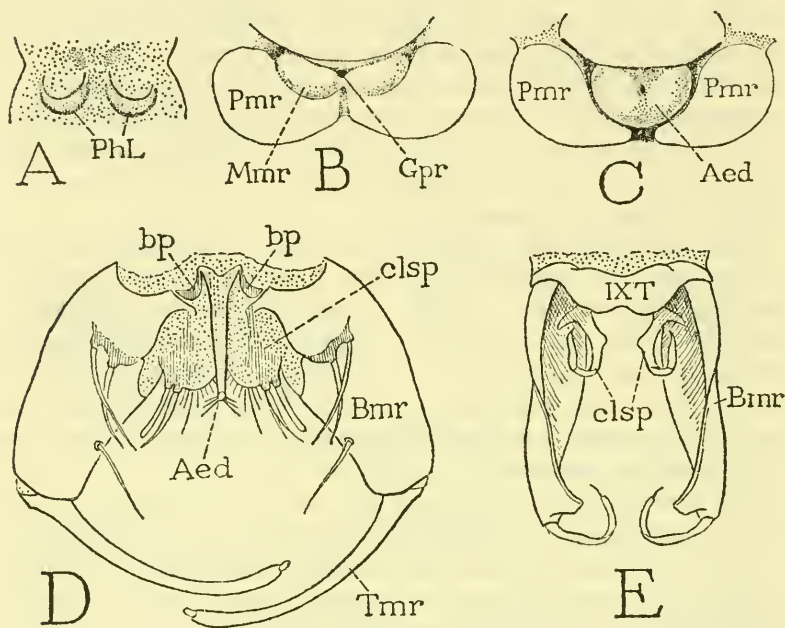

FIG. 28.—External genital organs of the adult male, and their development. (A,B,C, from Christophers, 1922.)

A, The primary phallic lobes that appear in a late instar larva behind the sternal region of the ninth abdominal segment. B, Later stage of same, each primary lobe divided into a mesomere and a paramere. C, Still later stage, mesomeres united around the gonopore to form the aedeagus. D, Adult genital apparatus of *Anopheles quadrimaculatus*, lower surface (dorsal). E, Parameres and claspettes of *Aedes pullatus*.

Aed, aedeagus; *Bmr*, basimere; *bp*, basal plate; *clsp*, claspette; *Gpr*, gonopore; *IXT*, ninth abdominal tergum; *Mmr*, mesomere; *PhL*, primary phallic lobes; *Pmr*, paramere; *Tmr*, telomere.

pendages as they appear in the pupa (fig. 16 F). At this stage the lobes are termed "proandropodites" by Christophers (1922), but this term literally translated would mean "primitive male parts of legs" (as "coxopodite" means the "coxal part of a leg"). Since there is no real evidence that the male genital organs of insects represent primitive legs, the genital organs of the pupa are simply the developed phallic lobes. Within them are formed the definitive genitalia of the

adult. From the base of each lobe inside the pupal cuticle, as de-
scribed by Christophers, is cut off a small median lobe (fig. 28 B,
Mmr), and the lateral part becomes the rudiment of the clasper
(*Pmr*). Finally, the two median lobes unite around the gonopore
to form the aedeagus (C, *Aed*), while the lateral parameral lobes
elongate to become the two-segmented claspers of the adult (D,E).

In the mature condition the genitalia take on a great variety of
forms and are complicated by the development of accessory parts.
All this is a great boon to taxonomists, but it often creates difficulty
for the morphologist. *Anopheles quadrimaculatus* (fig. 28 D) gives
a good example of one type of structure. Each paramere is divided
into a large *basimere* (*Bmr*) and a long slender *telomere* (*Tmr*).
The telomere is movable on the basimere by strong antagonistic
muscles arising in the latter. The slender aedeagus (*Aed*) lies between
the bases of the parameres and is connected with the basimeres by a
pair of small *basal plates* (*bp*). The basimeres are equipped with
long spines, and proximally each bears a membranous median lobe
(*clsp*) united with the one from the opposite side. Each lobe is armed
with strong spines and is known as a *claspette,* or *claspette lobe*. In
other genera the claspettes are more commonly independent ap-
pendages of the parameres, as seen in *Aedes* (E). The claspettes,
according to Christophers (1922), are cut out from the parameres
by secondary incisions of the latter.

For illustrations of generic and specific variations in the male
genital structure the student must consult taxonomic papers, but the
nomenclature will be confusing. In the current terminology of
mosquito specialists, the aedeagus is called the "mesosome" or "phallo-
some," the basal plates (*bp*) that connect it with the claspers are the
"parameres," and the claspers are the "side pieces." In this scheme
the term "paramere" is entirely misapplied, since it was first given to
the claspers, and moreover, "side piece" is a direct English translation
of "paramere." The segments of the claspers are known also as the
"basistyles" and "dististyles," but as shown by their development the
claspers have no relation whatever to legs or abdominal styli. The
terminology given on figure 28 is recommended for its simplicity and
because it can be applied, on the basis of development, to the male
genitalia in all the principal orders of insects (see Snodgrass, 1957).

The terminal parts of the female abdomen are much simpler than
those of the male, but their homologies are more difficult to under-
stand. Beyond the eighth segment projects a small lobe (fig. 27 I)
representing the combined ninth and tenth segments. The dorsum of

the ninth segment is a transverse basal arc (*IX*) usually containing a small tergal sclerite. Beyond it is the tenth segment (*X*) bearing a pair of lateral cerci (*Cer*) and the terminal anus (*An*). Ventrally is a lobe known as the *postgenital plate* (*pgpl*) because the gonotreme (H, *Gtr*), or opening of the genital atrium, is situated at its base above the sternum of the eighth segment (*VIII*). The nature of the postgenital plate is doubtful; it looks as if it should be the projecting sternum of the ninth segment. On its base there is generally a transverse fold known as the *cowl* (K, *a*) because it is sometimes reflected to form a hoodlike pocket. Surrounding the gonotreme above the end of the eighth sternum is a sclerotized ring (*b, c*) named the *sigma* by Christophers (1923). In figure K the ventral arc of the sigma (*c*) is turned forward; normally it is directed posteriorly (J, *c*). The sigma thus, as described by Christophers, resembles the lips of a half-opened clasp purse, in which it is represented by the metal framework of the purse. Some writers, however, without adducing specific evidence, regard the dorsal arc of the sigma as the ninth sternum. According to Christophers the whole structure is formed as a sclerotization in the intersegmental membrane of the gonotreme.

All parts of the female terminalia are subject to much variation, as shown in comparative studies by Macfie and Ingram (1922), Christophers (1923), Davis (1926), Gerry (1932), Gjullin (1937), Roth (1946), Rees and Onishi (1951), and Hara (1957). The student, however, will be somewhat confused by the different ways the parts are represented and named. The drawings J and K on figure 27, taken from Gerry, are composite diagrams showing all the parts that have been described, but they probably do not present the exact structure in any one species.

The gonotreme surrounded by the sigma above the eighth abdominal sternum leads into a small infolded pouch, the *genital chamber,* or *atrium.* In its anterior wall is the female gonopore, which is the opening of the median oviduct. Behind the gonopore the globular spermathecae (one, two, or three in number) open through the dorsal wall of the atrium, and into a posterior pouch of the dorsal wall, the *caecus,* opens the single accessory gland, called the "mucus gland," but the nature of its secretion is not known (fig. 30 B).

INTERNAL ANATOMY

A thorough study of the internal anatomy of the mosquito has not been made, but the parts of principal interest will be the alimentary canal and the reproductive organs. The muscular and tracheal systems

have no features peculiar to the mosquito, and even the unusual characters of the reproductive organs are common to other Diptera. The simple nervous system is that of the larva with an elaboration of the brain and the optic lobes in the head, a transposition of the first abdominal ganglion to the thorax, and the union of the eighth abdominal ganglion with the ganglion of the seventh segment. In the abdomen of the adult, therefore, the first ganglion is in the second segment (fig. 30 C, *GngII*), and the last is a composite ganglion (*Gng VII+VIII*) in the seventh segment. The tracheal system has lost the large dorsal trunks of the larva, and the lateral trunks along the spiracles have been enlarged.

The circulatory organs.—In the adult mosquito, as described by Jones (1954) in *Anopheles,* the dorsal blood vessel has in general the same structure as that of the larva. The part in the abdomen, however, is more distinctly "chambered" because of segmental swellings before the ostia. An aortic sinus is said by Jones (1952) to be present in the adult as in the larva and pupa of *Anopheles, Culex,* and *Aedes.* The sinus is a dilatation of the aorta in the dorsal part of the thorax, with the corpora allata-cardiaca attached to it laterally. Anteriorly the sinus is continued into the cephalic aorta. The adult heart, according to Jones, beats predominantly forward, but periodically reverses the direction of the beat. The heart has no innervation from any source and therefore its pulsations are myogenic, that is, engendered by the muscles themselves of the heart wall. Lateral alary muscles support the heart, but they do not vibrate, and when cut the heart keeps on beating.

A vibratile muscular membrane across the cavity of the mesothoracic scutellum appears to be an accessory pulsatile organ, as in some other insects. A frontal bulblike organ between the bases of the antennae has been described by Day (1955) as a sense organ, and by Clements (1956) as a pulsating organ for driving blood into the antennae. If it is a sense organ, it is a newly discovered one as Day claims; if it is a pulsating organ it is not unique since a pulsatile organ in the same place is present in various other insects.

The alimentary canal.—The alimentary canal of the adult mosquito (fig. 29 A) in its general form is quite different from that of the larva. From the pharyngeal pump in the head (*PhP*) a short, narrow oesophagus (*Oe*) extends into the front of the thorax, where it joins a wider tube, which is the beginning of the stomach, or *ventriculus* (*Vent*). Shortly before its junction with the stomach the oesophagus gives off three pouches, known as the *oesophageal diverticula,* two

of which are dorsal and one ventral. In *Aedes aegypti* the dorsal diverticula (A, *ddv*) are small, flat, elongate sacs with slender necks diverging forward and laterally from the oesophagus (C). The single ventral diverticulum (*A, vdv*) has a long, slender neck which expands into a large sac in the anterior half of the abdomen. This ventral diverticulum corresponds with the usual "crop" of other Diptera.
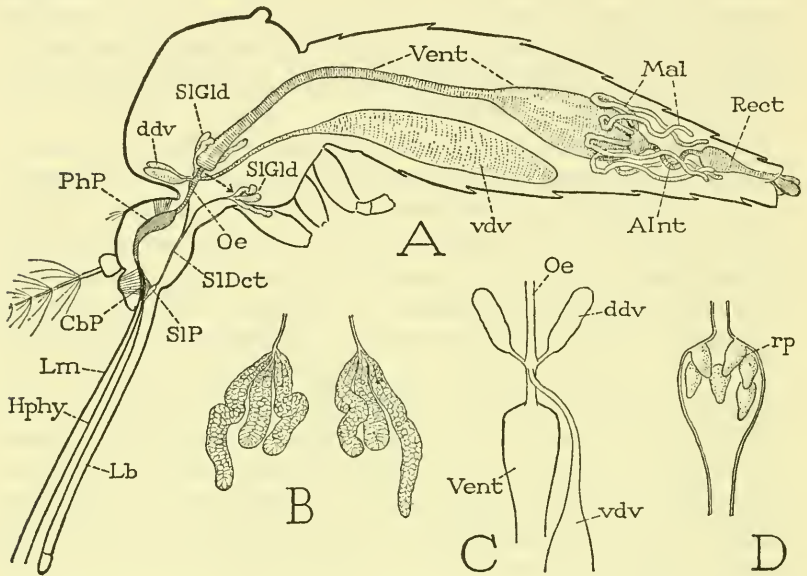

FIG. 29.—Alimentary canal and salivary glands of the adult female of
Aedes aegypti.

A, Sectional view of body showing alimentary canal and salivary system (glands on left displaced). B, The salivary glands. C, The oesophageal diverticula, ventral. D, Rectal sac and papillae.

AInt, anterior intestine; *CbP,* cibarial pump; *ddv,* dorsal diverticulum; *Hphy,* hypopharynx; *Lb,* labium; *Lm,* labrum; *Mal,* Malpighian tubules; *Oe,* oesophagus; *PhP,* pharyngeal pump; *Rect,* rectum; *rp,* rectal papillae; *SlDct,* salivary duct; *SlGld,* salivary glands; *SlP,* salivary pump; *vdv,* ventral diverticulum; *Vent,* ventriculus.

The ventriculus (fig. 29 A, *Vent*), which is the functional stomach of the insect, for most of its length in the female mosquito is a narrow tube that extends upward through the thorax and then turns backward into the abdomen where it ends in a saclike enlargement that joins the intestine. The first part of the latter, or *anterior intestine* (*AInt*), is a short, slender tube thrown into a small loop. Its anterior end, the pyloric region, joins the ventriculus by a funnel-shaped expansion. At the other end the anterior intestine is continued into the

posterior intestine, or *rectum* (*Rect*), which is much enlarged anteriorly and tapers back to the anus. The inner wall of the pyloric funnel is armed in some species with numerous small spines directed posteriorly. These pyloric spines have been described and well illustrated by Trembley (1951) in species of *Anopheles, Aedes,* and *Culex.* In the anterior end of the rectum are six small, soft, conical rectal papillae (D, *rp*) projecting inward from the rectal wall. Five Malpighian tubules (A, *Mal*) arise from the pyloric region of the intestine as in the larva.

The oesophageal diverticula are said to be empty on emergence of the mosquito from the pupa. Within an hour after ecdysis, however, according to Marshall and Staley (1932), the air that was pumped into the stomach begins to pass forward into the diverticula, and in 12 to 22 hours the stomach is empty.

The function of the oesophageal diverticula in relation to food intake has been studied by a number of investigators, but, though using the same experimental methods of feeding, the latter have not all come to the same conclusions. The subject has recently been well reviewed by Trembley (1952) and by Megahed (1958), and good bibliographies are given by both these writers. In general it is found that ingested blood goes directly to the stomach, while fruit juices and sugar solutions go first into the diverticula, to be later delivered to the stomach. According to Trembley, blood in small amounts may occasionally go to the diverticula, and sugar solutions sometimes go direct to the stomach. The work of Megahed on *Culicoides* gives essentially the same results, the stomach being ordinarily the receptacle for blood, the diverticula for concentrated sugar solutions, but water and dilute sugar solutions go direct to the stomach. Most observations seem to apply to the female insect. Day (1954), however, in experiments on male mosquitoes, found that the sexes react similarly: "blood went to the mid-gut and sugar to the diverticulum in the male in spite of the fact that males do not ingest blood under natural conditions."

The "switching mechanism" that determines whether the ingested food goes into the stomach or the diverticula, Day (1954) has proposed, is governed by the different kinds of sense organs in the wall of the cibarial pump (buccal cavity). If receptors of one type are stimulated by sugar it may be supposed that they cause a relaxation of sphincter muscles of the diverticula; if others are sensitive to blood components, they may effect a relaxation of the cardiac sphincter of the stomach. In the neck of the ventral diverticulum, Day notes the presence of a group of spines, which would appear to assist in keeping

blood corpuscles out of the diverticulum when the circular muscles in the neck of the diverticulum are contracted.

The salivary glands.—The salivary glands of the mosquito consist each of three lobes (fig. 29 B), of which the middle lobe is shorter than the other two. The glands lie at the sides of the anterior end of the ventriculus (A, *SlGld;* the left gland is displaced in the figure). The two ducts extend into the back of the head, where they unite in a single outlet tube (fig. 24 A, *SlDct*), which ends at the base of the hypopharynx in a small syringelike swelling that acts as a salivary ejection pump (*SlP*). On the elastic dorsal wall of the pump is inserted a dilator muscle (*18*) from the floor of the cibarial pump. The salivary pump discharges through the salivary canal (*sc*) of the hypopharynx in the female; in the male the duct traverses the labium (fig. 22 F). The salivary secretion in species of *Anopheles,* according to Metcalf (1945), contains both an anticoagulin and an agglutinin, but in other pest species neither appears to be present.

The salivary glands are of particular interest in connection with the transmission of disease by mosquitoes. They offer the only avenue of escape for disease organisms from the body cavity of the mosquito into the blood of an alternate host. The sporozoites of malaria, for example, that penetrate into the salivary glands are carried in the saliva of the biting mosquito directly into the vertebrate host, which is necessary for the completion of the complex life history of the malaria parasite, *Plasmodium.* This suggests the question of how it became obligatory for some parasites to divide their developmental history between two different animals, but the known facts give no answer. Mosquitoes do not bite each other, and there is no way by which the malaria parasite can be normally transferred from one vertebrate to another.

The reproductive system.—The organs of reproduction in the Diptera include the parts common to all insects, but their structure in two respects is exceptional. Each testis appears to correspond with a single testicular tube in other insects; the egg tubes of each ovary are extremely small, and all are enclosed in a cellular sheath.

The male organs of the mosquito include a pair of *testes* (fig. 30 E, *Tes*), a pair of testicular ducts, or *vasa deferentia* (*Vd*), which enlarge posteriorly to form a pair of *seminal vesicles* (*SV*) that in some species are united (D). The vesicles end in a very short common *ductus ejaculatorius* (*Dej*), which receives a pair of large *accessory glands* (*AcGld*) and then opens directly into the base of the aedeagus (*Aed*). In the normal condition the reproductive organs lie beneath the alimentary canal, but, with the inversion of the terminal segments of the abdomen, the relation is reversed (fig. 30 A)—the ejaculatory
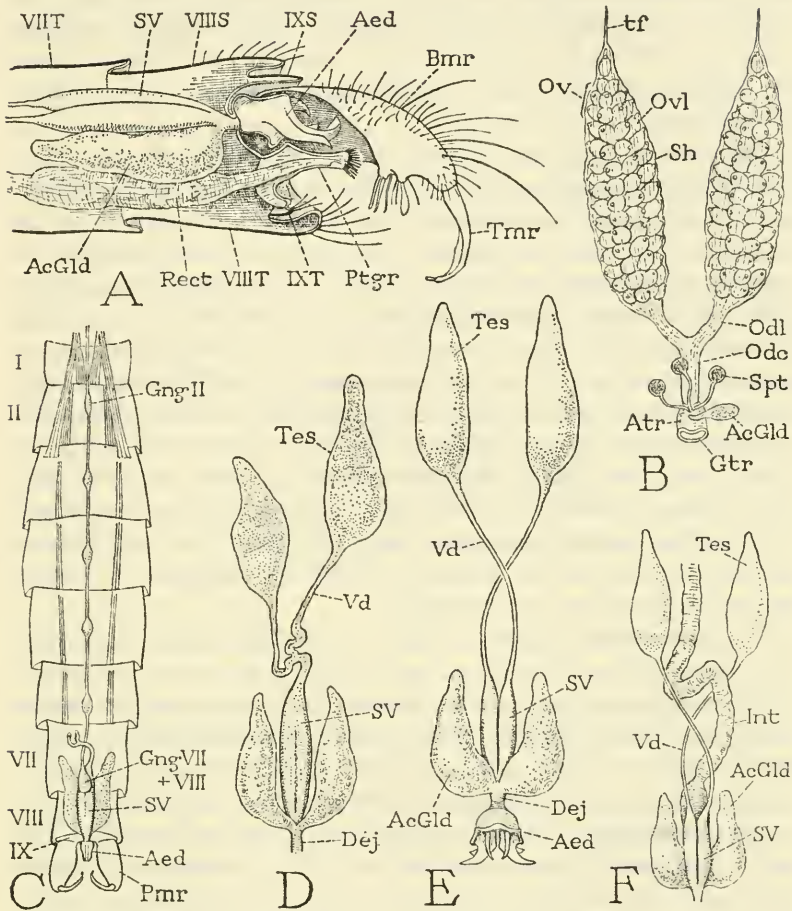
FIG. 30.—Reproductive organs and the abdominal nerve cord of the adult mosquito.

A, *Culex quinquefasciatus,* end of male abdomen, left side removed, exposing the inverted reproductive organs and rectum. B, Diagram of female reproductive organs, dorsal (adapted from Christophers, 1901). C, *Aedes aegypti,* male, ventral nerve cord of abdomen and genital outlets, dorsal. D, Same, male reproductive organs, ventral. E, *Culex quinquefasciatus,* male reproductive organs after inversion, lower side (dorsal). F, Same, with part of intestine, upper side (ventral).

AcGld, accessory gland; *Aed,* aedeagus; *Atr,* atrium, genital chamber; *Bmr,* basimere; *Dej,* ductus ejaculatorius; *Gng,* ganglion; *Gtr,* gonotreme; *Int,* intestine; *Odc,* oviductus communis; *Odl,* oviductus lateralis; *Ov,* ovary; *Ovl,* ovariole; *Pmr,* paramere; *Ptgr,* proctiger; *Rect,* rectum; *S,* sternum; *Sh,* sheath of ovary; *Spt,* spermatheca; *SV,* seminal vesicle; *T,* tergum; *Tes,* testis; *tf,* terminal filament of ovary; *Tmr,* telomere; *Vd,* vas deferens.

duct, the seminal vesicles, and the accessory glands now lie above the intestine. Since the testes are not affected by the inversion, the long *vasa deferentia* as in *Culex* (E) cross each other, but when the ducts are united as in *Aedes* (D) a simple twist takes place at the junction of the ducts.

The testis of most insects consists of a number of individual tubes in which the spermatozoa are formed as are the eggs in the ovarian tubes, and, except in the apterygotes, the tubes of each testis are enclosed in an investing sheath. The testes of the mosquito are elongate, pear-shaped bodies (fig. 30 D,E,F, *Tes*) continuous with the ducts. Each testis, however, appears in its entirety to be a single testicular tube. The same is true of the testes in other Diptera. In the narrowed upper end of each organ is a mass of undifferentiated cells; the rest of the lumen is filled with spermatocytes and spermatozoa in various stages of development. The mature spermatozoa are extremely long and threadlike; when liberated from the testis they exhibit active undulatory movements. The spermatozoa are stored in the seminal vesicles preliminary to mating, and the accessory glands probably have a prostate function, giving the spermatozoa a liquid medium in which they are discharged.

The reproductive organs of the female mosquito, represented diagrammatically at B of figure 30, include the parts characteristic of the female organs of insects in general. These are a pair of *ovaries* (*Ov*), the lateral *oviducts* (*Odl*) from the ovaries, and a median *common oviduct* (*Odc*) with which the lateral ducts are joined. The common duct opens by the primary genital aperture, or *gonopore,* into a small pocket above the end of the eighth abdominal sternum. This pocket, the *genital chamber,* or *atrium,* being a secondary inflection of the body wall between the eighth and ninth abdominal segments, is therefore not a part of the primary genital passage. The external opening of the atrium may be designated the *gonotreme* (*Gtr*). Into the dorsal wall of the atrium just behind the gonopore open the ducts of the spermathecae (*Spt*), which are usually three in number, though in *Anopheles* there is only a single spermatheca. Behind the spermathecal openings arises an *accessory gland* (*AcGld*), the function of which is not known in the mosquito. In other insects accessory glands usually secrete a cement for attaching the eggs to a support, or a material to form an egg covering.

The atrium serves as a copulatory pouch at the time of mating, and the spermatozoa from the male are stored in the spermathecae. Then when the eggs leave the oviduct they are received in the atrium and

are here fertilized by sperm discharged from the spermathecae. Finally the eggs are passed out through the gonotreme at the time of laying.

The ovaries of the mosquito differ in several respects from the usual structure of these organs in other insects. A typical insect ovary consists of a group of slender tubes known as *ovarioles* opening into the end of a lateral oviduct. The ovarioles taper upward and end in filaments that unite in a common strand attached to tissues in the neighborhood of the heart. A mature ovariole contains a series of ripening egg cells of successively larger size, with the mature egg in its lower end. Each egg is accompanied by a number of nutritive cells, or so-called *nurse cells,* which are absorbed by the egg as it matures. Each egg and its nurse cells are contained in a compartment of the ovariole known as a *follicle.* The follicles appear as swellings along the ovariole, increasing in size with the growth of the egg. The egg cell and the nurse cells are formed by division of the undifferentiated cells in a chamber, the *germarium,* in the upper end of the follicle. The eggs do not pass down the ovarioles; each ovariole grows from the germarium as an egg leaves the lowermost follicle and the latter disintegrates.

In the mosquito ovary (fig. 30 B) the ovarioles (*Ovl*) are very short and are arranged in rows along an axial cavity of the ovary. As in other Diptera, each ovary is invested in a thin membranous sheath (*Sh*) in which there are fine muscle fibers, and the sheath itself ends in a terminal filament (*tf*) attached to tissues along the sides of the heart. The muscle fibers of the ovarian sheath in *Anopheles* are said by Nicholson (1921) to be striated, but Jones (1958) finds that those of *Aedes* do not show a distinct striation in live, unstained whole mounts at 1,000 magnification under phase optics.

Each ovariole consists of a large egg-containing follicle with a small projection on its free end representing the germarium and one or two minute undeveloped follicles. The structure of the egg follicle of *Culex* has been described by Nath (1924), and an account of the development of the ovary and the development and nutrition of the eggs in the ovary of *Anopheles* is given by Nicholson (1921), by Christophers, Sinton, and Covell (1928), and by Mer (1936). The developmental processes described in the mosquito differ little from those in insects generally.

Many female mosquitoes need a meal of blood for the production of eggs. The eggs of *Anopheles* and *Aedes* are fully developed in two to three days after the female has fed. It is said by Roy (1936) that in

Aedes there is "a definite quantitative relationship between the weight of the blood meal and the number of eggs produced." As noted by Christophers, Sinton, and Covell (1928), the eggs in the lower follicles of all the ovarioles mature at the same time, so that as many eggs are ready for laying as there are ovarioles. When these eggs are deposited the eggs in the next follicles above mature, and so the production of fresh lots of eggs "seems to have no limit other than the life of the mosquito."

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