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Bureau of Entomology and Plant Quarantine
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CONTENTS

INTRODUCTION

All armies in the field have to contend with biting and disease-carrying insects. Every known method of control for such pests must be available to the members of the sanitary corps. Effective control methods cannot be devised extemporaneously; they must be worked out long in advance of the need for immediate application, and, just as battles are not won without knowledge of the enemy, nor diseases cured without knowledge of the organisms that produce them, so insects are not to be fought successfully without knowing the insects. We have at present a number of good textbooks on medical entomology, now widely used in the medical schools; they are broad in scope, including not only insects that are dangerous to man, but also those that afflict domestic animals and birds; but they have in common one defect—they do not adequately describe the feeding organs of the insects, the very instruments by which biting species produce pain in their victims and introduce disease-causing organisms. The present paper is intended to supplement the texts in so far as it deals with the biting flies, and thus to make available to teachers and students wherever medical entomology is being taught a condensed account of what entomologists now know concerning the various types of feeding organs found in the biting species of flies. The insects properly called flies belong to the Order Diptera, so named because they never have more than one pair of wings. The flies include the most dangerous of the disease and parasite vectors that attack man, other mammals, and birds.

Biting insects are always to their victims potential inoculators of parasites and diseases. Infection from outside the body requires, first an abrasion of the skin, second the introduction of a disease-producing virus or organism. The biting insects furnish both of these conditions. By their bite, which in most cases is more truly a puncture, the skin is pierced, and if the biter happens to carry disease organisms on the body, particularly on the biting organs, or in the saliva, infection of the victim is likely to result. Parasitic worms in the blood cavity of the insect even are transmissible, at least by flies, through the thin membranous lining of the proboscis.

Though specialists on the Diptera are not agreed as to how the flies should be classified within the order, for practical purposes it is most convenient to recognize three groups, which are called the NEMATOCERA, the BRACHYCERA, and the CYCLORRHAPHA. Differences in the feeding apparatus of biting species appear to be consistent with this arrangement. The Nematocera may be distinguished superficially by their antennae, which are generally long and slender and contain usually many small segments. The Brachycera have short antenna, and the number of segments is generally small but is variable. In the Cyclorrhapha the antennae are also short, but they never have more than three segments; these flies are named and distinguished by the fact that the adult fly emerges from a pupa case by pushing off a circular cap from the anterior end of the latter. Of the insects described in this paper, the mosquitoes, the sand flies, the biting midges, and the black flies belong to the Nematocera; the horse flies, the snipe flies, and the robber flies are members of the Brachycera; the eye gnats, the tsetse flies, the horn flies and stable flies, the louse flies, and the bat "ticks" are included in the Cyclorrhapha.

The generic and specific names and their authors given in this paper are those approved by the specialists in taxonomy of the Division of Insect Identification, United States Bureau of Entomology and Plant Quarantine.

The structure of the feeding organs of all the biting flies is well known; representative species in each group have been thoroughly studied by a number of competent investigators. As so frequently happens, however, the most thorough students are specialists in a particular group, and do not give sufficient attention to other insects to make reliable interpretations of the anatomical correspondence, or homology, of parts in their own group with those of insects constructed on a more generalized plan. This condition is particularly prevalent in the study of the feeding apparatus of the Diptera. To correct it, the structure of the fly's head, its mouth parts, and its sucking mechanism must be compared with that of corresponding organs in insects having a more primitive organization. For such a comparison no insect will serve our purpose better than the common household cockroach, *Blattella germanica* (L.), which is the subject of the first section following.

I. THE COCKROACH. FAMILY BLATTIDAE

The cockroach is regarded as a generalized insect because its anatomy gives evidence in many ways of conforming more closely than does that of most winged insects to the structure of primitive insects. In a study of specialized forms, such as the Diptera, we must endeavor, therefore, to trace the origin of their specializations in the more simple organization of a generalized insect such as the cockroach. Mechanisms may change radically from one insect to another through minor anatomical alterations, while fundamental structural relations remain the same, so that new uses for old organs are readily evolved. Yet no insect, or any other animal, can get completely away from the structural foundation of its ancestors.

A facial view of the head of the cockroach is shown at A of figure 1. The top of the cranium is called the vertex (*Vx*), between the antennae is the frontal region (*Fr*), and from the latter there is extended downward a broad lobe, which is the *clypeus* (*Clp*). The clypeus bears a free flap, the *labrum* (*Lm*), which serves as a front lip hanging before the jaws. In some insects the frontal region, or *frons* (*Fr*), is defined by a pair of lateral grooves converging upward between the antennae to a point below the vertex, and in most insects it is separated from the clypeus by a transverse groove, the *epistomal* *sulcus.* The latter is to be identified in most cases by a pair of depressions in its lateral parts; the depressions are present in the cockroach (*at, at*), but the connecting groove is absent. The depressions mark the anterior roots of an internal framework of the head known as the *tentorium,* and are hence termed the *anterior tentorial pits.* They are important landmarks. A pair of *posterior tentorial pits* lies on the back of the head close to the neck foramen.

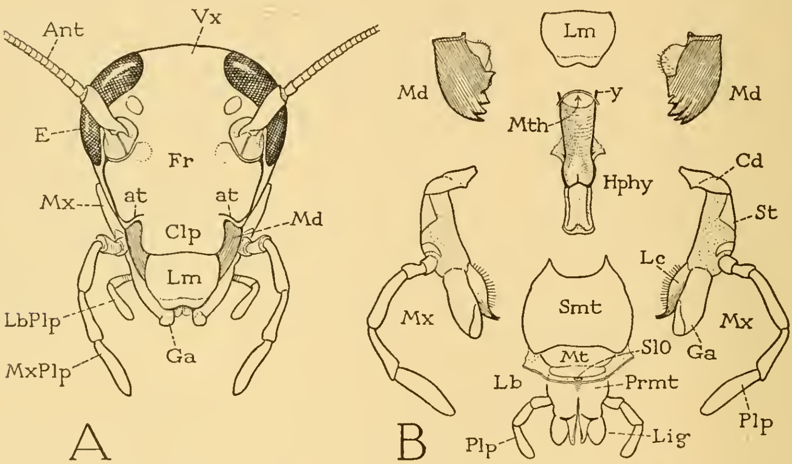

FIG. 1.—Head and mouth parts of a cockroach, *Blattella germanica* (L.). A, facial view of the head. B, the mouth parts.
Ant, antenna; *at,* anterior tentorial pit; *Cd,* cardo; *Clp,* clypeus; *E,* compound eye; *Fr,* frons; *Ga,* galea; *Hphy,* hypopharynx; *Lb,* labium. *LbPlp,* labial palpus; *Lc,* lacinia; *Lig,* ligula; *Lm,* labrum; *Md,* mandible; *Mt,* mentum; *Mth,* mouth; *Mx,* maxilla; *MxPlp,* maxillary palpus; *Plp,* palpus; *Prmt,* prementum; *SlO,* orifice of salivary duct; *Smt,* submentum; *St,* stipes; *Vx,* vertex; *y,* oral arm of hypopharynx.

Behind the clypeus and labrum are the external feeding organs, known collectively as the *mouth parts.* First is a pair of jaws, or *mandibles* (*Md*), shown detached at B. Each mandible of the cockroach has four muscles, two arising on the head wall, one on the tentorium, and one on the side of the tongue, or hypopharynx. The muscles open and close the mandibles in an approximately transverse plane.

Following the mandibles are the maxillae (fig. 1 A, B, *Mx*). Each maxilla (B, *Mx*) has a basal part subdivided into a *cardo* (*Cd*) and a *stipes* (*St*). The stipes bears a five-segmented *palpus* (*Plp*), and two terminal lobes, the *galea* (*Ga*) and the *lacinia* (*Lc*).

Suspended from the back of the head behind the maxillae is the *labium* (fig. 1 B, *Lb*). Its two basal plates, the *mentum* (*Mt*) and *submentum* (*Smt*), collectively the *postmentum,* lie in the rear wall of the head below the neck foramen. The rest of the organ is a free posterior lip, the body of which is the *prementum* (*Prmt*) ; the appendicular parts are the lateral *palpi* (*Plp*), and four terminal lobes, the *glossae* in the middle and the *paraglossae* at the sides, which together constitute the *ligula* (*Lig*).

Enclosed between all these organs is the median tonguelike lobe of the ventral head wall known as the *hypopharynx* (fig. 1 B, *Hphy*), but most inappropriately so named because it has no anatomical relation to the pharynx, which is inside the head. The position of the hypopharynx between the clypeus and labrum in front and the prementum of the labium behind is shown in a vertical section of the head at A of figure 2. In front of the hypopharynx at the base of the clypeus is the *mouth* (*Mth*), behind it at the base of the prementum is the opening of the salivary duct (*SlO*).

Just outside the mouth, between the inner wall of the clypeus and the proximal part of the hypopharynx, is a food pocket, the *cibarium* (fig. 2 A, *Cb*), in which is deposited the masticated food before it is delivered through the mouth into the alimentary canal. The hypopharyngeal floor of the cibarium is shown at B of figure 2, and is seen to be flanked by two elongate sclerites (*HS*), from which a pair of *oral rods* (*y*) are extended into the angles of the mouth. The inner ends of these rods project as free points, and on each are inserted two muscles, one (*13*) arising on the frons, the other (*14*) laterally on the head wall. The floor of the cibarium (*Cb*) forms a depression of the hypopharyngeal surface that leads directly into the mouth. The anterior wall, or roof, is the inner wall of the clypeus (A), and on it are attached two pairs of thick muscles (*5a, 5b*) arising on the outer clypeal plate. These muscles, since they compress the clypeus, are therefore *dilators of the cibarium.* The inner end of the cibarium extends a short distance into the mouth; it is separated from the stomodaeum, or first part of the alimentary canal, by a fold between the inner ends of the oral rods (B, *y*). The entire cibarial structure and mechanism as developed in the cockroach is taken over by the Diptera and converted into a sucking pump.

The principal salivary system of the cockroach consists of a pair of glands in the thorax and their ducts; the latter unite at the back of the head to form a common salivary duct (fig. 2 A, *SlDct*) that goes downward to open into a pocket, the *salivarium* (*Slv*), between the base of the hypopharynx and the prementum (*Prmt*) of the labium. Associated with the salivarium are four pairs of muscles, two arising within the hypopharynx and two in the labium. In the Diptera the salivarium retains one pair of the hypopharyngeal muscles, and is converted into a force pump for expelling the saliva. The outlet

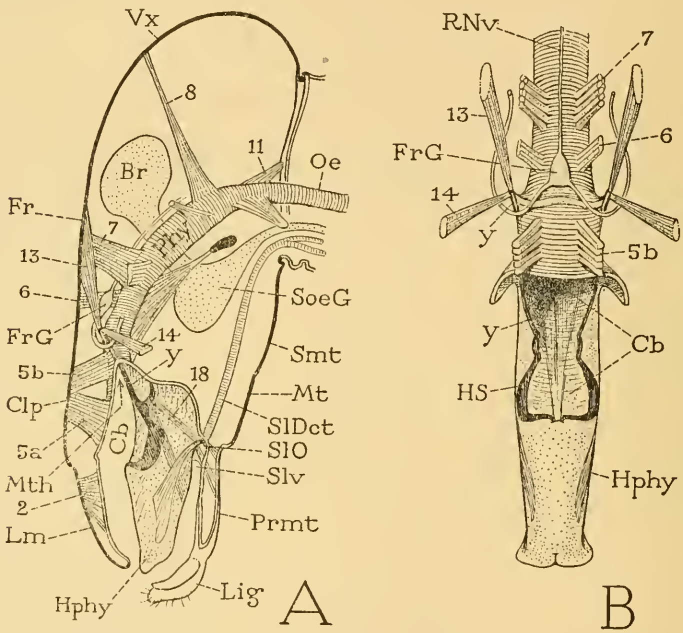

FIG. 2.—Cibarial and pharyngeal regions of the food tract of a cockroach.

A, vertical section of head to left of median plane, diagrammatic. B, hypopharynx and first part of pharynx, anterior (dorsal) view.

Br, brain; *Cb*, cibarium; *Clp*, clypeus, *Fr*, frons; *FrG*, frontal ganglion; *Hphy*, hypopharynx; *HS*, sclerites of hypopharynx on margins of floor of cibarium; *Lig*, ligula; *Lm*, labrum; *Mt*, mentum; *Mth*, mouth; *Oe*, oesophagus; *Phy*, pharynx; *Prmt*, prementum; *RNv*, recurrent nerve; *SlDct*, salivary duct; *SlO*, orifice of salivary duct; *Slv*, salivarium; *Smt*, submentum; *SoeG*, suboesophageal ganglion; *Vx*, vertex; *y*, oral arm of hypopharynx.

Muscles.—*2*, compressor of labrum; *5a*, *5b*, dilators of cibarium; *6*, *7*, precerebral dilators of pharynx; *8*, postcerebral dorsal dilator of pharynx; *11*, posterior lateral dilator of pharynx; *18*, hypopharyngeal dilator of salivarium; *13*, frontal retractor of hypopharynx; *14*, protractor of hypopharynx.

of the pump in the flies, however, penetrates the hypopharynx and opens usually at the tip of the latter.

The first part of the alimentary canal of an insect, which is of ectodermal derivation, is the *stomodaeum*. In the cockroach the stomodaeum begins at the inner end of the cibarium; it goes upward and backward in the head and enlarges somewhat between the brain and the suboesophageal ganglia to form a *pharynx* (fig. 2 A, *Phy*);

beyond the pharynx it contracts to a slender oesophageal tube (*Oe*) that enters the thorax through the neck. The degree of differentiation of the pharynx varies in different insects; in some of the Diptera it is developed into a second sucking pump; in others there is no pharyngeal dilatation of the stomodaeum, and the oesophagus may be said to begin at the inner end of the cibarium.

The pharyngeal section of the stomodaeum is provided with dilator muscles arising on the head wall and the tentorium. In the roach these muscles fall into dorsal, lateral, and ventral sets. Of the dorsal dilators two pairs (fig. 2 A, B, *6*, *7*) are precerebral in position, and one pair (A, *8*) is postcerebral. The lateral dilators include three consecutive muscles on each side, of which the last (A, *11*) arises at the margin of the neck foramen. The ventral dilators are a group of fibers spreading downward from the tentorium. In the Diptera the dorsal dilators and the last pair of lateral dilators are present as they are in the cockroach; the others are absent. It is important to note that the first dorsal dilators of the stomodaeum (fig. 2 B, *6*) are separated from the dilators of the cibarium (*5b*) by the frontal ganglion (*FrG*) and its recurving brain connectives. This relation is fundamental; the position of the frontal ganglion often serves as a key to the anatomical relations of parts that may appear confused in the cibariopharyngeal region of the food tract.

The structure of the head and the feeding organs exemplified in the cockroach recurs in similar form in all the biting and chewing insects, and from it have been derived the various types of specialized feeding organs found in the piercing and sucking insects, and also in those that are purely suctorial.

II. MOSQUITOES. FAMILY CULICIDAE

The head and proboscis of a mosquito (fig. 4 D) at first sight would appear to have little in common structurally with the head and mouth parts of the cockroach, but a closer study shows that there is an entire conformity, except for simplification of the mouth parts in the mosquito and other superficial modifications adaptive to a different manner of feeding.

On the front of the mosquito's head (fig. 4 A) the large bases of the antennae lie close together and are set into such wide membranous areas that the frons (*Fr*) is reduced to a narrow median bar, somewhat expanded above the antennal bases, and forked below into a pair of arms diverging laterally to the lower ends of the huge compound eyes. The vertical bar of the frons is marked by a median groove continuous from the coronal sulcus (*cs*) that divides the vertex (*Vx*). Below the frons is the strongly protruding, triangular clypeus (A, C, *Clp*). In the groove between the frons and the clypeus are the anterior tentorial pits (*at*) having the same relative position as in the cockroach (fig. 1 A, *at*). Many writers have made the mistake of regarding the frons of the Diptera as a part of the vertex, and have therefore called the clypeus the "frontoclypeus." On the back of the

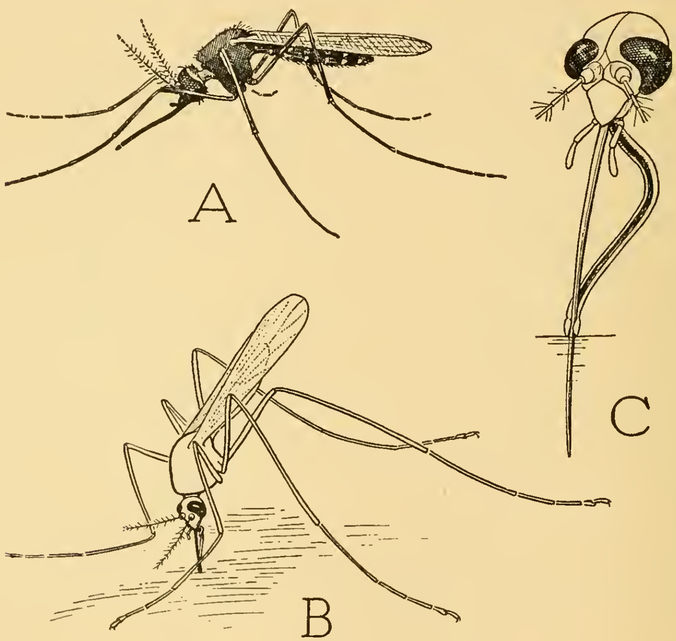

FIG. 3.—Mosquitoes. Culicidae.

A, a female *Culex* mosquito at rest. B, *Anopheles maculipennis* Meigen, female in act of feeding (adapted from Herms, 1939). C, head of a feeding mosquito, showing bending of the labium (from Weber, 1933).

head in the mosquito the small neck foramen (fig. 4 B, *For*) lies above the level of the eyes, and the cranium is closed below by a hypostomal sclerotization (*Hst*) that gives a rigid support to the base of the proboscis. The narrow neck is mostly membranous (D), but on each side is a small cervical sclerite uniting the head with the thorax.

The mouth parts of the mosquito are all much elongated and simplified as compared with those of the cockroach, and in the natural condition (fig. 4 D) only the beaklike labium is seen, since the other parts are enclosed in a deep groove of the labium, except for the maxillary palpi, which project freely at the base of the proboscis. The full complement of parts, present at least in the female, may be exposed by manipulation (E), and it is then seen that the proboscis is made up of six slender stylets representing the labrum, the mandibles, the hypopharynx, and the maxillae, in addition to the ensheathing labium.

The labrum (fig. 4 E, *Lm*) is the thickest and strongest of the stylets; it is sharp-pointed terminally and deeply channeled on its under surface (H, *Lm*). On its base is attached a large muscle arising on the median part of the clypeus (fig. 5 D), and on each side a smaller muscle from a lateral leverlike apodeme of the clypeus. The muscles serve evidently to lift the labrum or close it against the labium, but the labrum is firmly hinged to the clypeus and cannot be independently protracted or retracted. Most students of Diptera term the labrum the "labrum-epipharynx," as if it were composed of two primarily separate parts. Robinson (1939), however, properly rejects this dual concept and nomenclature. The insect labrum in its origin is a simple, preoral outgrowth of the head, and, though its posterior wall is called the "epipharyngeal" surface, the labrum itself is a single appendicular lobe.

The mandibles vary in shape in different species of mosquitoes, but they are generally the slenderest of the mouth parts; in the species here illustrated they are needlelike bristles (fig. 4 H, *Md*) somewhat expanded near the ends. The mandibles of the mosquito are said to have each only one muscle, termed a retractor by Robinson (1939), which arises on the tentorium. In most mosquitoes mandibles have been observed to be present only in the females, but Vogel (1921) says that very short, weak mandibles occur in the males of *Culex* and *Anopheles*.

The maxillae are less simple than the other members of the mosquito's mouth parts, since each includes a long flattened blade (fig. 4 I, *Ga*) and a four-segmented palpus (*Plp*), and is provided with an internal apodemal rod (*Ap*) for the attachment of muscles. The maxillary blade, which is sharp-pointed and armed with recurved teeth near the end (H, *Mx*), is commonly interpreted as the galea, the absent lobe being presumably the lacinia. The palpus is generally short in the female, but in the male it may be as long as the proboscis. The internal muscle-bearing rod is often regarded as the maxillary stipes, since there are no external parts in the mosquito representing the basal plates of the maxillae. The rod is of an apodemal nature, however, and no evidence has been given of its supposed stipital

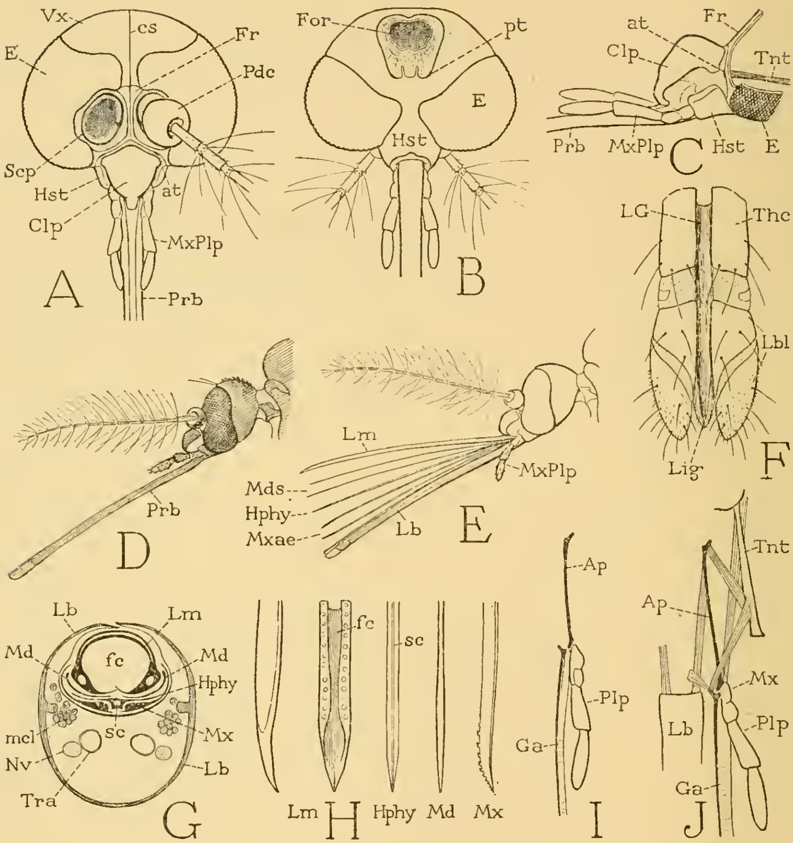

FIG. 4.—Head and mouth parts of a female mosquito. A-F, H, I, *Aedes aegypti* (L.); G, *Anopheles maculipennis* Meigen.

A, head and proboscis, anterior. B, same, posterior. C, base of proboscis, clypeus, and associated structures, left side. D, head and proboscis. E, same, stylets separated from labium. F, distal end of labium, anterior. G, cross section of proboscis (from Vogel, 1921). H, distal parts of stylets. I, basal parts of maxilla. J, musculature of a maxilla, diagrammatic.

Ap, maxillary apodeme; *at*, anterior tentorial pit; *Clp*, clypeus; *cs*, coronal sulcus; *E*, compound eye; *fc*, food canal; *For*, neck foramen; *Fr*, frons; *Ga*, galea; *Hphy*, hypopharynx; *Hst*, hypostoma; *Lb*, labium; *Lbl*, labellum; *LG*, labial gutter; *Lig*, ligula; *Lm*, labrum; *mcl*, labellar muscles; *Md*, mandible; *Mds*, mandibles; *Mx*, maxilla; *Mxae*, maxillae; *MxPlp*, maxillary palpus; *Nv*, nerve; *Pdc*, pedicel of antenna; *Plp*, palpus; *Prb*, proboscis; *pt*, posterior tentorial pit; *sc*, salivary canal of hypopharynx; *Scp*, scape of antenna; *Tnt*, tentorium; *Thc*, theca; *Tra*, trachea; *Vx*, vertex.

derivation. The maxilla is provided with protractor and retractor muscles (J), the protractors being inserted on the end of the apodeme, the retractors on the base of the galea and palpus. The maxillary blades, therefore, are the only stylets that are freely protractile and retractile by independent movements.

The hypopharynx is a slender, flattened stylet (fig. 4 H, *Hphy*), traversed throughout its length by the salivary canal (*sc*), which opens on the pointed tip. The hypopharynx has no muscles and hence no independent movement; it probably serves principally for the hypodermic injection of the saliva into the wound made by the other stylets.

The elongate labium of the mosquito corresponds with the distal appendicular part of the labium in the cockroach, known as the prementum (fig. 1 B, *Prmt*), the basal plates (mentum and submentum) being absent in the mosquito. The labium of all Diptera terminates with a pair of variously shaped lobes called the *labella,* which probably represent the labial palpi of other insects. In the mosquito the labella are somewhat oval and each labellum is two-segmented (fig. 4 F, *Lbl*). Between the labella is a tapering median lobe, the ligula (*Lig*), which in Diptera is not subdivided. The sclerotized outer wall of the dipterous labium, proximal to the labella, is termed the *theca* (*Thc*); the anterior wall, invaginated to form the groove containing the stylets, is the *labial gutter* (*LG*), which terminates on the ligula. The labella are movable by muscles arising within the theca, each lobe being provided with an abductor and an adductor muscle. The only muscles attached on the base of the labium are a pair arising on the maxillary apodemes (J), which, since the labium can have little movement on the head, are probably protractors of the maxillae.

The position of the stylets within the labial gutter is shown in cross section of the proboscis at G of figure 4. The almost tubular labrum (*Lm*) lies on top well enclosed by the labial margins. Below the labrum is the hypopharynx (*Hphy*), but the mandibles (*Md*) intervene between the labrum and the hypopharynx, except at the base of the proboscis, just as they do in the cockroach, though if they are slender they may assume a lateral position. Finally, beneath the hypopharynx against the floor of the labial gutter are the maxillary blades (*Mx*). The food canal of the proboscis, through which the imbibed liquid ascends to the mouth, is the channel of the labrum (*fc*). The saliva is conducted in the opposite direction to the tip of the proboscis through the salivary canal (*sc*) of the hypopharynx. The internal cavity of the labium contains blood, the labellar muscles (*mcl*), nerve trunks (*Nv*), and tracheae (*Tra*).

The general conformation of the head and proboscis of the mosquito (figs. 3 A, 4 D) would suggest that the insect attacks its victim first by a vicious jab. And yet the labium, which looks so formidable, is not a piercing organ nor does it enter the wound (fig. 3 C). The only stylet that appears strong enough to effect a puncture by a thrust of the head is the labrum. The hypopharynx is an injection needle; the mandibles in most species are too weak for effective piercing. The maxillae alone have a musculature capable of giving them an independent back-and-forth movement on the head. The biting procedure of the mosquito, as deduced by Robinson (1939) from direct observation and a study of the mechanism of the feeding apparatus, is essentially as follows: A puncture of the skin is first effected by a thrust of the head transmitted to the bundle of stylets held in the labial groove. The maxillary blades are then alternately by their own muscles protracted deeper into the wound, each holding by means of its recurved teeth against the action of the retractors, which draw the head down and stretch the protractors of the opposite side. By repeated action of the maxillae, each blade successively overreaching the other, the whole bundle of stylets is drawn into the wound. As the stylets sink into the skin, the labium, holding the fascicle between the labella, bends backward beneath the head (fig. 3 C).

The above explanation of the biting procedure of the mosquito is in entire harmony with the puncturing methods of other insects, whether with the mouth parts, the ovipositor, or a sting. Robinson found that mosquitoes are able to feed, though with difficulty, after the amputation of one maxillary blade, but that they could not be induced to feed when both blades were removed. The fact that the stylets do not separate from one another with the bending back of the labium he explains as due to the adhesive influence of a viscous liquid that bathes them in the labial gutter. The bending of the labium appears to be a passive result of the lowering of the head, but Robinson is of the opinion that it results from the tension of the muscles attached on the base of the labium.

When at last the stylets of the piercing mosquito penetrate a vein, the activity of the stylets ceases, and there begins the sucking phase of the feeding act, which proceeds quietly until repletion. Withdrawal of the stylets is effected in a manner reverse to that of penetration and is assisted by tension on the head exerted by the legs.

The sucking apparatus of the mosquito consists of two powerful pumps (*antliae*) contained within the head. One lies in the clypeal region (fig. 5 A, *CbP*) and is a derivative of the preoral cibarial pocket of such insects as the cockroach (fig. 2 A, *Cb*); the other (fig. 5 A, *PhP-p*) lies in the back part of the head and is a modification of the pharynx. The first pump, however, has generally been called the "pharynx," or "pharyngeal pump," and the second the "oesophageal pump," though some writers, following Nuttall and Shipley (1901-3), term the first pump the "buccal cavity" and recognize the second as the pharynx.

The cibarial pump (*antlia cibarialis*) is an elongate capsule with the upper or anterior wall ordinarily collapsed against the posterior wall, so that the lumen of the organ in cross section is narrowly crescent-shaped. The posterior wall (fig. 5 A, E, *CbP*) is strongly sclerotized and has the form of a basinlike trough; it is directly continuous distally with the anterior wall of the hypopharynx (*Hphy*), and its inner end is produced into a pair of short lateral cornua (*y*), on which are attached two muscles (A, *13, 14*) clearly corresponding with the muscles inserted on the oral arms of the hypopharynx in the cockroach (fig. 2 A, B, *13, 14*). There can be little doubt, therefore, that the floor of the first pump in the mosquito is the concave proximal part of the anterior wall of the hypopharynx in the cockroach (fig. 2 B, *Cb*). The dorsal wall of this pump in the mosquito is continuous with the inner, or epipharyngeal, wall of the labrum (fig. 5 A, E, *Lm*); it is flexible and elastic and on its midline are inserted paired sets of powerful dilator muscles (5) having their origins on the strongly arched clypeus (*Clp*). These muscles thus correspond with the dilators of the preoral cibarial pocket of the cockroach (fig. 2 A, *5a, 5b*). The transformation from the generalized cockroach type of structure in the mouth region to the specialized dipterous structure illustrated in the mosquito may be conceived to have been brought about by carrying the primitive mouth angles out from the base of the clypeus to the base of the labrum, or, in other words, by a lateral union of the inner surface of the clypeus with the edges of the cibarial surface of the hypopharynx. In some such way, at least, the functional mouth-opening has been reestablished at the base of the labrum, and what was primarily a preoral food space between the clypeus and the hypopharynx has been converted into a closed chamber. This chamber is potentially a sucking organ by reason of the clypeal muscles attached on its roof, which by contraction function as dilators of the lumen.

The cibarial pump is present in all Diptera, and in similar form is the only sucking organ of such insects as Thysanoptera and Hemiptera; in Lepidoptera and Hymenoptera it is combined with the pharynx.

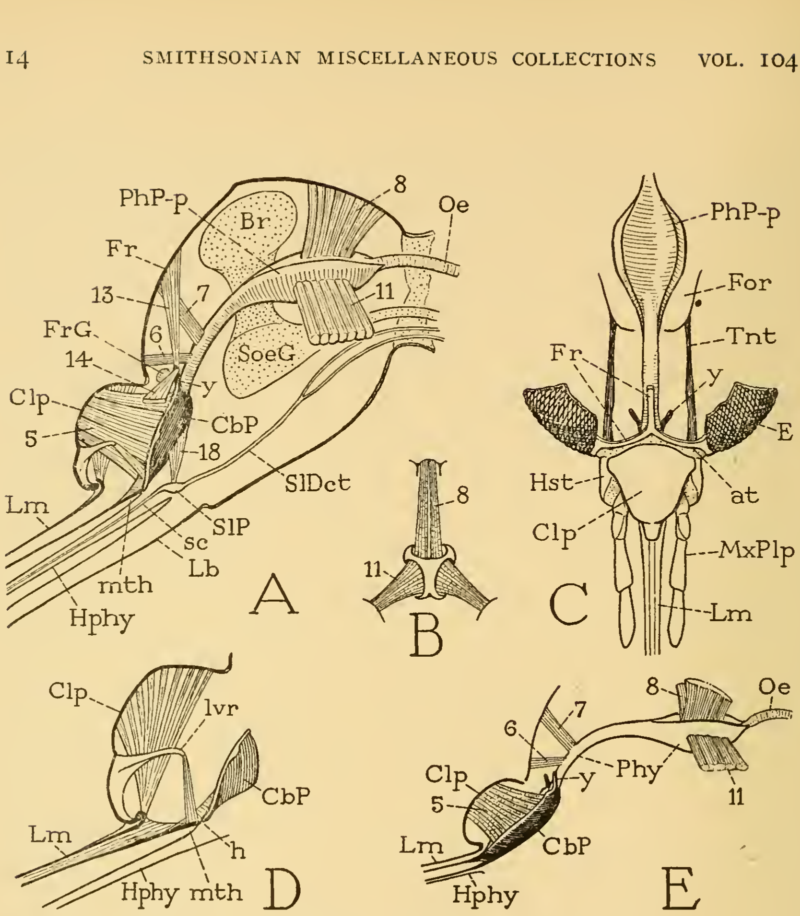

FIG. 5.—The sucking apparatus of a mosquito.

A, diagrammatic vertical section of head of a female mosquito, to left of median plane. B, cross section of pharyngeal pump of *Culex* (from Thompson, 1905). C, *Aedes aegypti* (L.), pharyngeal pump exposed by removal of facial wall of head. D, same, muscles of labrum. E, same, cibarial and pharyngeal pumps and their musculature, left side.

at, anterior tentorial pit; *Br*, brain; *CbP*, cibarial pump; *Clp*, clypeus; *For*, neck foramen; *Fr*, frons; *FrG*, frontal ganglion; *h*, hinge of labrum or cibarial pump; *Hphy*, hypopharynx; *Hst*, hypostoma; *Lb*, labium; *Lm*, labrum; *lvr*, clypeal lever; *MxPlp*, maxillary palpus; *mth*, mouth of cibarial pump; *Oe*, oesophagus; *PhP-p*, pharyngeal pump, posterior in the mosquito and other Nematocera; *Phy*, pharynx; *sc*, salivary canal; *SlDct*, salivary duct; *SlP*, salivary pump; *SoeG;* suboesophageal ganglion; *Tnt*, tentorium; *y*, cornu of cibarial pump, oral arm of hypopharynx in cockroach (fig. 2).

Muscles.—*5*, dilators of cibarial pump; *6, 7*, precerebral dilators of pharyngeal pump; *8*, postcerebral dorsal dilator of pharyngeal pump; *11*, lateral dilator of pharyngeal pump; *13*, retractor of cibarial pump; *14*, protractor of cibarial pump; *18*, dilator of salivary pump. (Compare with muscles of cockroach, fig. 2.)

The pharyngeal pump (*antlia pharyngealis*) of the mosquito is an elongate, gourd-shaped organ (fig. 5 E, *Phy*; A, C, *PhP-p*) with a slender neck curving upward and backward from the cibarial pump and expanding behind the nerve ganglia of the head into a large bulb. from which the oesophagus (*Oe*) proceeds through the neck into the thorax. This pump is a part of the stomodaeal section of the alimentary canal, but it lacks the usual stomodaeal sheath of circular muscle fibers, except at the anterior and posterior ends. The walls of the bulb are hardened to form three plates, one dorsal, the other two lateroventral, which are flexibly hinged to each other along their margins. Four huge muscles activate the pharyngeal pump, a dorsal pair (fig. 5 A, B, E, *8*) arising on the vertex behind the brain, corresponding thus with the postcerebral dorsal dilators of the pharynx in the cockroach (fig. 2 A, *8*), and a lateral muscle on each side (fig. 5 A, B, E, *11*), corresponding with the posterior lateral dilator of the pharynx in the cockroach (fig. 2 A, *11*). When the pharyngeal pump is collapsed (fig. 5 B) its three plates are curved inward by their own elasticity, almost obliterating the lumen between them; contraction of the opposing muscles then causes a wide expansion of the lumen by springing the plates outward. Two other pairs of muscles, (A, E, *6, 7*) are attached on the neck of the pharyngeal pump, which represent the two precerebral dilators of the pharynx in the cockroach arising on the frons (fig. 2 A, B, *6, 7*). The frontal ganglion (*FrG*) and its brain connectives in each insect separate these frontal pharyngeal muscles from the clypeal muscles of the cibarium.

A pharyngeal pump like that of the mosquito is present at least in all bloodsucking flies of the group Nematocera. The Brachycera also have a pharyngeal pump, but it is formed from the anterior part of the pharynx (figs. 11 J, 13 C, *PhP-a*) and is activated by the precerebral dilator muscles. It is necessary, therefore, to distinguish between the *posterior pharyngeal pump* of Nematocera and the *anterior pharyngeal pump* of Brachycera. The Cyclorrhapha have only the cibarial pump.

No information is at present available as to the functional relations of the two pumps, but it may be supposed that their respective expansions and contractions have opposite rhythms, one contracting as the other expands, so as to give a continuous flow to the stream of liquid food. Valvular structures within the pumps have not been noted, but sphincter muscles at the junction of the cibarial and pharyngeal pumps and behind the second pump are present in most cases. presumably so in the mosquito, which constitute regulatory apparatus.

Beneath the cibarial pump is still another pumping mechanism present in all Diptera, which is the *salivary pump* (*antlia salivarialis*). The salivary pump of the mosquito (fig. 5 A, *SlP*) is a small capsule with a strong, cup-shaped lower wall and a thin, elastic upper wall ordinarily collapsed into the cavity of the lower wall. The common salivary duct of the head (*SlDct*) opens into the rear end of the pump, and the distal end of the latter is continued into the slender, tubular salivary canal (*sc*) that traverses the hypopharynx to its tip (fig. 4 H, *Hphy*). The salivary pump is operated by a pair of dilator muscles (fig. 5 A, *18*) arising on the posterior wall of the cibarial pump, evidently corresponding with one pair of the hypopharyngeal muscles of the salivarium in the cockroach (fig. 2 A, *18*). The expulsive power of the pump results from the elasticity of the elevated anterior wall, which forcibly springs back into the concavity of the posterior wall when the muscles relax. The salivary pump is clearly a derivative of the salivarium of generalized insects, but the Diptera differ from most other insects in that the saliva is discharged through a canal of the hypopharynx.

Diseases of which mosquitoes are known to be vectors, or have been shown to be possible vectors, include malaria of man, bird malaria, yellow fever, dengue fever, human and equine encephalomyelitis, fowl pox, and filariasis. Malaria, caused by a blood-inhabiting protozoon, *Plasmodium,* of which mosquitoes are necessary intermediate hosts, is transmitted to man by species of *Anopheles* mosquitoes; the bird form of the disease is carried by species of *Culex* and *Aedes.* Yellow fever, now regarded as a virus disease, is transmitted normally by *Aedes aegypti* (L.), but other species have been shown experimentally to be capable of its transmission. Dengue fever, a virus disease of the Tropics, but sometimes epidemic in Temperate regions, is carried by species of *Aedes,* including *aegypti.* The virus of equine encephalomyelitis, which in the United States occurs in an eastern and in a western type, and the virus of human encephalitis have been shown to cause sleeping sickness in both horses and man. Many other mammals and also birds are susceptible to the disease. Mosquitoes have long been suspected of being vectors, and various species of *Aedes* have been shown experimentally capable of transmitting one form or the other of equine encephalomyelitis, while *Culex tarsalis* Coq. has been found in nature infected with the western form of equine encephalomyelitis, and with that of human encephalitis. (See Hammon et al., 1941; Giltner and Shahan, 1942.) Species of *Aedes* have been demonstrated to be potential vectors of the virus of fowl pox; and finally, both *Aedes* and *Culex* are known transmitters of nematode worms producing filariasis of man.

III. SAND FLIES. FAMILY PSYCHODIDAE

Most members of the psychodid family are small, harmless, nectar-feeding flies that look like tiny moths on account of their dense hairy covering and the way the wings are spread out flat or slopingly over the body when at rest. Species of the genus *Flebotomus* Rondani, known as sand flies, however, are bloodsuckers and painful biters. The species are relatively few, but they are widely distributed, particularly in warm regions; only one species has been recorded from the United States.

FIG. 6.—A sand fly, *Flebotomus verrucarum* Towns., female. Psychodidae. A very hairy fly, but hairs removed to show structure. (Length of body 2 mm.)

Flebotomus is a small, long-legged, very hairy fly a few millimeters in length (fig. 6, hairs not shown). When not in flight the wings are held upward and outward at an angle of about 45 degrees from the body with their inner margins sloping downward toward each other. The wing venation shows that the insect belongs to the Psychodidae, though otherwise it has little resemblance to other members of its family. The long head with its strong proboscis projects downward from beneath the thorax at right angles to the axis of the body, which is elevated on the slender legs, so that the whole configuration of the insect is one suggestive of readiness for giving a vigorous stab with the beak.

The head of *Flebotomus* (fig. 7 A, B, C) is elongate dorsoventrally, and is suspended from the neck (B, *Cvx*) by its upper part. The front of the head (A) has the same structure as in the mosquito. The frons

(Fr) consists of a median bar expanded above the antennae, and forked below into a pair of arms extending laterally to the lower ends of the eyes. The large clypeus (*Clp*) is separated from the frontal arms by an epistomal groove containing laterally the anterior tentorial pits (*at*). The back of the head (C), unlike that of the mosquito, is mostly nonsclerotized, there being an extensive membranous area from the neck foramen to the base of the proboscis.

The feeding apparatus of *Flebotomus argentipes* Ann. and Brun. has been well described and illustrated by Christophers, Shortt, and Barraud (1926), and that of *F. papatasii* Scopoli by Adler and Theodor (1926). The species here figured, *F. verrucarum* Towns. of South America, does not differ essentially from the others. The proboscis is relatively short as compared with that of the mosquito, but it is thick and strong (fig. 7 A, B, C) ; the long maxillary palpi are doubled up at its sides. The broad labrum (A, *Lm*) tapers to a spiny point (F) ; the mandibles (present only in the female) are bladelike (D), finely toothed near the ends (H), and each is provided with an abductor and an adductor muscle (D, *27, 28*) inserted on opposite sides of an articular point (*a*) ; the broad hypopharynx is traversed to its tip by the salivary canal (G). The maxillae differ from those of the mosquito in that they are suspended by a pair of slender rods lying in the membranous posterior wall of the head (C, *St*) and attached to the cranial margins below the neck foramen. These rods clearly represent the stipes, or stipes and cardo, of a generalized maxilla. The maxillary blade, or galea (E, *Ga*), is slender, finely serrate on its inner margin, and provided with a row of small subapical teeth on the outer margin (I). The theca of the broad, strong labium (C, *Thc*) bears a pair of soft labellar lobes at its end; proximal to its base is a small triangular plate (*Pmt*), probably a postmental sclerite.

The musculature of the mouth parts of *Flebotomus* is fully described by Christophers, Shortt, and Barraud (1926). As in the mosquito, the maxillae alone are capable of an independent back-and-forth movement on the head. The musculature of the mandibles can give the latter only movements in a transverse plane. While ordinarily the mandibles lie between the labrum and the hypopharynx, according to Adler and Theodor (1926) they are moved apart during feeding, perhaps to enlarge the wound, and allow the hypopharynx to come into apposition with the labrum. The channel of the latter is thus closed by the hypopharynx, and the slender spines on the ends of the two apposing blades (fig. 7 F, G) interlock to form a strainer guarding the entrance of the food canal. With the penetration of the

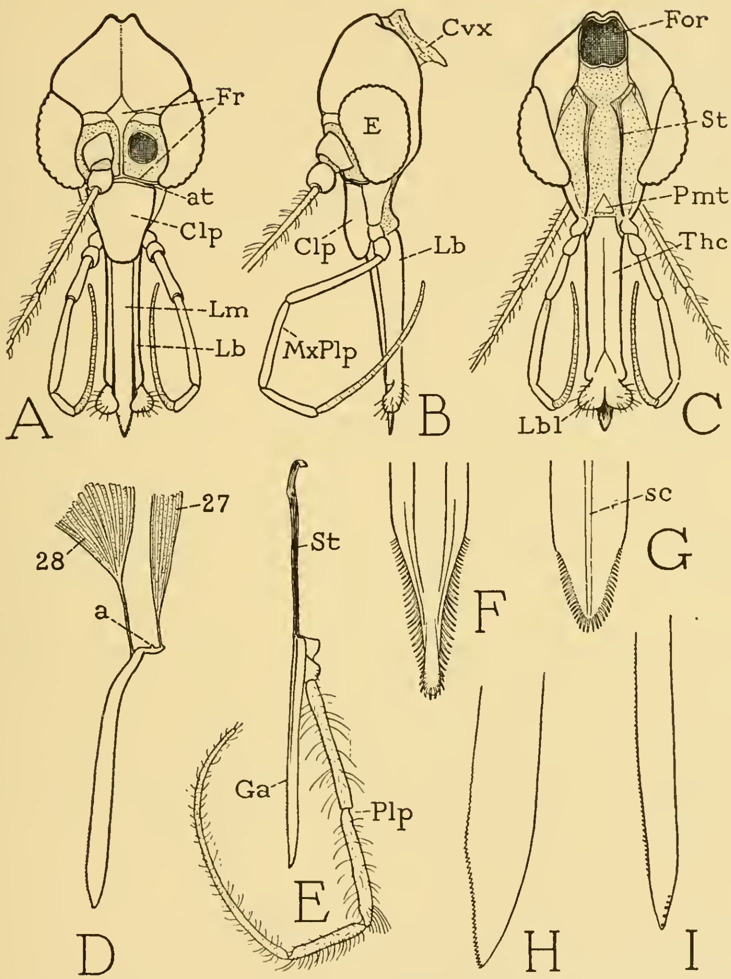

FIG. 7.—Head and mouth parts of *Flebotomus verrucarum* Towns., female.

A, head and proboscis, anterior, left antenna removed. B, same, lateral. C, same, posterior. D, left mandible and its muscles, anterior. E, left maxilla, anterior. F, distal end of labrum. G, distal end of hypopharynx. H, distal end of mandible. I, distal end of maxillary galea.

a, articular point of mandible; *at,* anterior tentorial pit; *Clp,* clypeus; *Cvx,* neck; *E,* compound eye; *For,* neck foramen; *Fr,* frons; *Ga,* galea; *Lb,* labium; *Lbl,* labellum; *Lm,* labrum; *MxPlp,* maxillary palpus; *Plp,* palpus; *Pmt,* postmentum; *sc,* salivary canal; *St,* stipes; *Thc,* theca.

Muscles.—27, abductor of mandible; *28,* adductor of mandible.

stylets into the wound, the labium is probably pushed up into the membranous posterior wall of the head. The labellar lobes are said by Adler and Theodor to spread apart and expose the broad ligula which supports the stylets.

The sucking apparatus of *Flebotomus* consists of the same two pumps as in Culicidae, the first cibarial, the second pharyngeal.

Sand flies, because of their biting propensities and prevalence where certain diseases abound, have been suspected of being carriers of a number of diseases, and have been subjected to several thorough investigations. Only in the case of pappataci fever, however, a filterable virus disease of southern Europe, northern Africa, and the Mediterranean region generally, has a positive conviction been obtained, the species involved here being *Flebotomus papatasii* Scopoli. Circumstantial evidence points strongly against *F. verrucarum* Towns. as being the natural vector of South American verruga, a disease caused by a rodlike coccoid organism named *Bartonella bacilliformis,* endemic in certain high valleys on the western slopes of the Andes in Peru, and reported from Colombia and Ecuador. It has been shown by Hertig (1942) that verruga can be transmitted experimentally to monkeys by the bite of an infected *Flebotomus,* and yet only in a very small percentage of flies collected in the verruga zone has the causative organism been found. Less convincing is the evidence against *F. argentipes* Ann. and Brun. as the vector of kala-azar, or black sickness, a leishmanian disease of India and China. Nor has the bite of *Flebotomus* been shown definitely to be responsible for the spread of Oriental sore, or the forms of South American leishmaniasis, but Southwell and Kirshner (1938) suggest that possibly inoculation may result from the crushing of infected flies on the skin.

IV. BITING MIDGES. FAMILY HELEIDAE

The family of the biting midges, which are called also punkies and no-see-ums, has more commonly been known as Ceratopogonidae, or included in the Chironomidae. The members of the family are small or minute gnatlike flies, notable principally as biting pests, though some are vectors of parasitic nematodes. The species best known anatomically belong to the genus *Culicoides* Latr. The structure of the head and mouth parts of *C. pulicaris* (L.) is the subject of a detailed account by Jobling (1928); *C. furens* (Poey) is here given (fig. 8) as a representative of the genus.

Culicoides (fig. 8 J) is short-legged by comparison with *Flebotomus,* the head is small, the proboscis short, but the head hangs downward from the receding anterior wall of the thorax, against which it can be braced for giving a punch with the proboscis. An anterior view of the head (A) shows that the clypeus is not projected as in the mosquitoes and sand flies, and is united with the frons above it. At each side of the clypeus is a wide membranous area, which is crossed ventrally by a slender bar (*mda*) that supports the mandible. The back of the head (B) resembles that of *Flebotomus,* its median part below the neck foramen being membranous; the membrane contains a pair of stipital rods (*St*) of the maxillae, and a small postmental plate (*Pmt*) of the labium.

The mouth parts of *Culicoides* include the usual stylets, enclosed in the labial gutter, which is covered in front by the broad labrum (fig. 8 A, *Lm*). The shape and relative size of the labrum, the mandibles, the hypopharynx, and the maxillae are shown at C, D, E, and F of the figure; apical details of the labrum, the maxillary galea, and the hypopharynx are more enlarged at G, H, and I. The salivary canal of *Culicoides,* as shown by Jobling (1928), traverses the proximal third of the hypopharynx and then, emerging on the anterior surface of the latter, continues its course to the apex as an open channel (K, *sc*).

The mandibles deserve particular attention. According to Jobling they are present in both sexes of *Culicoides pulicaris* but are relatively weak in the male. Each mandible of the female (fig. 8 D) is a thin flat blade, narrowed proximally but having an obliquely truncate, finely toothed distal margin receding mesally. At about the middle of the upper surface is an elongate depression, which is shown by Jobling to be reflected on the under surface as a corresponding elevation. The mandibles overlap, the left always on top of the right, and in this position the elevation on the under surface of the left mandible fits into the upper depression of the right (K). When thus interlocked the two mandibles resemble a pair of scissors. On the base of each mandible are inserted three muscles (D), two of which (*27, 28*) are the usual cranial abductor and adductor, the third (*30*) is an accessory adductor arising on the tentorium. The mandibles of *Culicoides,* therefore, have transverse movements as in other insects, and in spite of their scissorlike appearance it is improbable that they can work in the manner of a pair of scissors; furthermore, the elevation on the lower side of the right mandible (K, *rMd*) fits into the open salivary channel of the hypopharynx (*sc*). Between the left mandible and the concave under surface of the labrum is the food canal of the proboscis (K, *fc*).

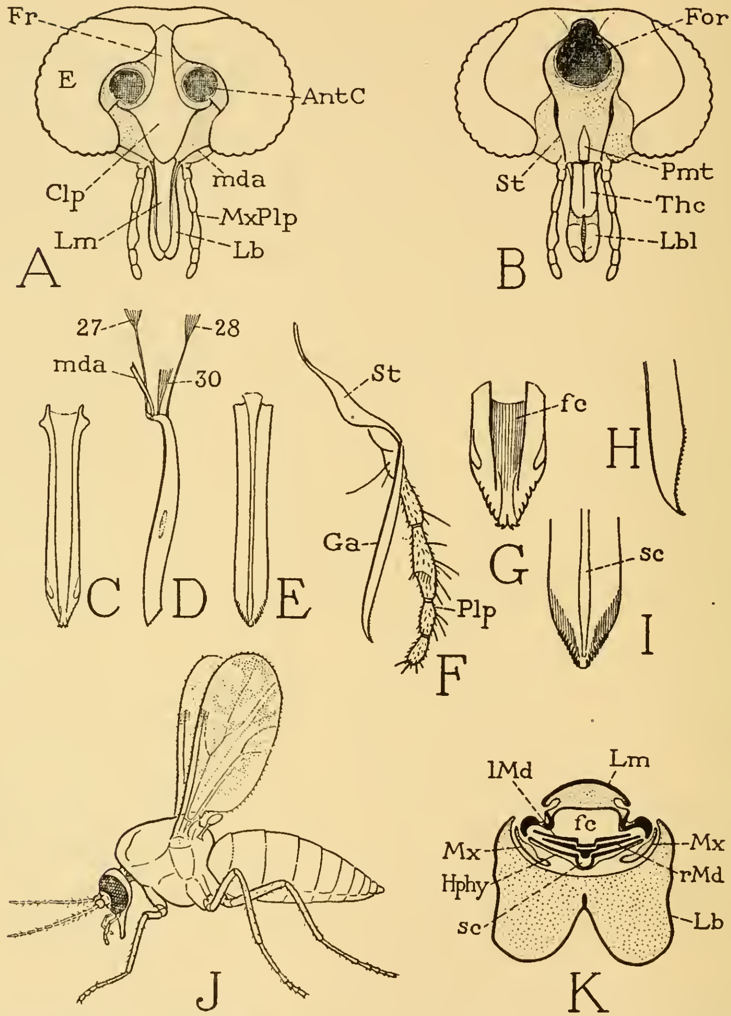

FIG. 8.—A biting midge, *Culicoides*, female, head and mouth parts. Heleidae. A-J, *Culicoides furens* (Poey); K, *Culicoides vexans* (Staeger).

A, head and proboscis, anterior, antennae removed. B, same, posterior. C, labrum. D, right mandible, anterior. E, hypopharynx. F, maxilla. G, end of labrum more enlarged, showing food canal on under surface. H, end of galea. I, end of hypopharynx. J, *Culicoides furens* (Poey), female (length 1.75 mm.). K, cross section through middle of proboscis of *Culicoides vexans* (from Jobling, 1928).

AntC, cavity where antenna removed; *Clp*, clypeus; *E*, compound eye; *fc*, food canal; *For*, neck foramen; *Fr*, frons; *Ga*, galea; *Hphy*, hypopharynx; *Lb*, labium; *Lbl*, labellum; *Lm*, labrum; *lMd*, left mandible; *mda*, mandibular arm of head; *Mx*, maxilla; *MxPlp*, maxillary palpus; *Plp*, palpus; *Pmt*, postmentum; *rMd*, right mandible; *sc*, salivary canal; *St*, stipes; *Thc*, theca.

Muscles.—27, cranial abductor of mandible; *28*, cranial adductor of mandible; *30* tentorial adductor of mandible.

The sucking apparatus of *Culicoides* is the same as that of Culicidae and *Flebotomus;* the cibarial and pharyngeal pumps of *C. pulicaris* are fully described by Jobling (1928), though the first is termed the "pharynx," and the second the "oesophageal pump."

The action of the mouth parts of *Culicoides* during feeding has been observed by Jobling, who says that the labrum, the hypopharynx, and the mandibles together compose a piercing organ, which performs forward and backward movements, the mandibles remaining locked together between the other two parts. Though the maxillary blades cannot be seen, their muscular equipment would indicate that their movements are also those of protraction and retraction. It may be noted that the membranization of large parts of the lower facial area and the back of the head in *Culicoides* allows the whole group of stylets and also the labium to be mobile. As the stylets penetrate the wound, the long labella of the labium bend backward and the short theca is retracted.

The most annoying species of biting midges in the United States belong to the genera *Culicoides* Latr., *Helea* Meigen (*Ceratopogon* Meigen), and *Leptoconops* Skuse. The bite of these flies is painful and the irritation may last for several days. The midges are obnoxious principally as pests at summer resorts and to agricultural workers. Certain tropical or subtropical species, however, such as *Culicoides austeni* Carter, Ingram, and Macfie of Africa, and *C. furens* (Poey) of the Antilles and the Gulf of Mexico are intermediate hosts and vectors of parasitic filarial worms of man.

V. BLACK FLIES. FAMILY SIMULIIDAE

The members of this family, known as black flies because of their dull and blackish color, or also as buffalo gnats because of the humped appearance of the thorax (fig. 9), are small flies characterized by the strongly declivous front of the thorax and the pendent head, which hangs on the neck below the level of the body. Many of the species are notorious biting pests, not only of man but of domestic animals and birds, and some are vectors of disease agents. Gibbins (1938) says, "among the insects which torment man there is perhaps none which inflicts so cruel a bite as *Simulium damnosum,*" of Africa. Only the females are known to be bloodsuckers; the males are said to have the same mouth parts as the females, but the stylets are much weaker. The familiar species belong to the genera *Simulium, Prosimulium,* and *Eusimulium,* but formerly all were included under the first name. The structure of the head and mouth parts is well known; the more recent papers on the subject are by Smart (1935) on *Simulium ornatum* Meigen, by Gibbins (1938) on *Simulium damnosum* Theobald, and by Krafchick (1942) on *Eusimulium lascivum* Twinn. *Simulium venustum* Say is here described and figured.

The head of *Simulium* is almost circular as seen from in front (fig. 10 A), or behind (B). On the face, the clypeus (A, *Clp*) sits like a broad shield below the antennae, while the frons (*Fr*) is almost obliterated between the antennal bases. On the back of the head (B)

FIG. 9.—A black fly, *Simulium venustum* Say, female. Simuliidae. (Length 3.5 mm.)

the cranial walls come together below the neck foramen (*For*) and separate the latter from a wide ventral plate (*Pmt*), which is probably the postmentum of the labium.

The proboscis is short and thick (fig. 10 A, B) and is far overreached by the long maxillary palpi. The broad labrum is hinged to the lower edge of the clypeus (A, C, *Lm*), and is armed distally (E) with a pair of strong, recurved tricuspid teeth; its under surface (D) is deeply channeled. The mandibles (C, *Md*, G) much resemble those of *Culicoides;* they overlap each other, the left over the right, and are held in this position by an interlocking mechanism as in *Culicoides,* so that they strikingly resemble a pair of scissors (J). Though Gibbins

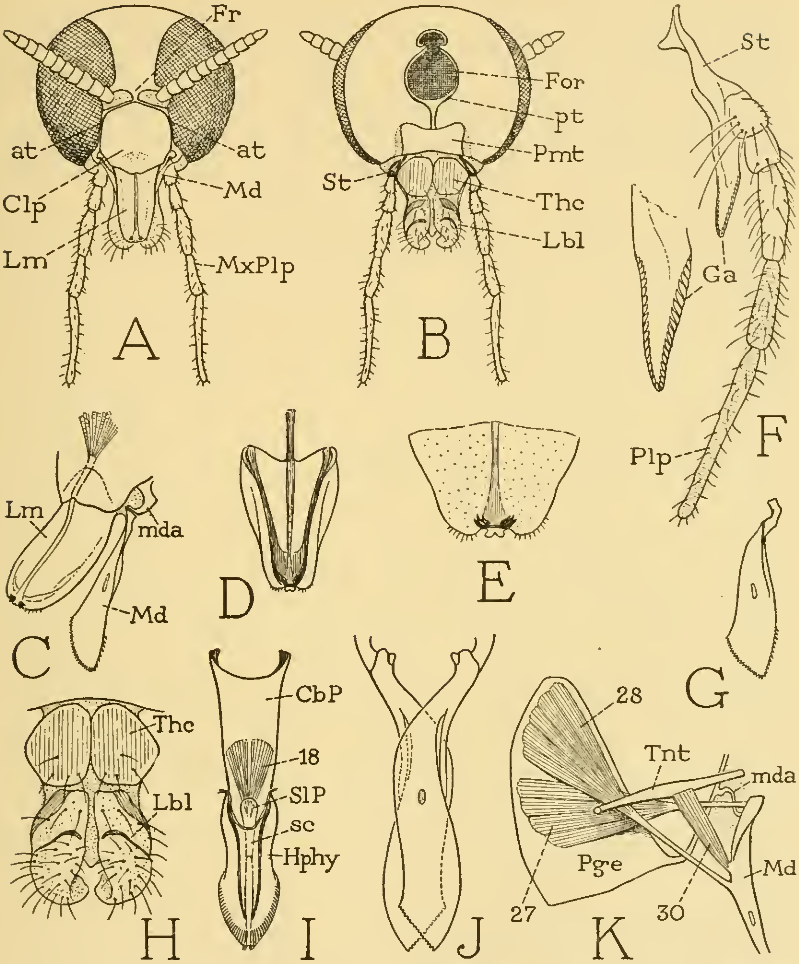

FIG. 10.—Head and mouth parts of *Simulium*, female. A-I, *Simulium venustum* Say; J, *Simulium damnosum* Theobald; K, *Prosimulium magnum* D. and S.

A, head and proboscis, anterior. B, same, posterior. C, labrum and left mandible. D, labrum, posterior. E, tip of labrum more enlarged, anterior. F, maxilla and detail of galea. G, mandible. H, labium, posterior. I, hypopharynx and floor of cibarial pump, posterior. J, mandibles in crossed and locked position, anterior (from Gibbins, 1938). K, base of left mandible and its muscles, mesal (from Krafchick, 1942).

at, anterior tentorial pit; *CbP,* cibarial pump; *Clp,* clypeus; *For,* neck foramen; *Fr,* frons; *Ga,* galea; *Hphy,* hypopharynx; *Lbl,* labellum; *Lm,* labrum; *Md,* mandible; *mda,* mandibular arm of head; *MxPlp,* maxillary palpus; *Pge,* postgena; *Plp,* palpus; *Pmt,* postmentum; *pt,* posterior tentorial pit; *sc,* salivary canal; *SlP,* salivary pump; *St,* stipes; *Thc,* theca; *Tnt,* tentorium.

Muscles.—27, cranial abductor of mandible; *28,* cranial adductor of mandible; *30,* tentorial adductor of mandible.

(1938) says of the mandibles of *Simulium damnosum* that they lie "right over left," his figure shows them in the reverse position. Each mandible is articulated at its base on a short arm of the cranium (C, *mda*), and is provided with strong abductor and adductor muscles (K). The hypopharynx (I, *Hphy*) is a broad, somewhat spatulate blade, the anterior wall of which is directly continuous with the floor of the cibarial pump (*CbP*). At its base is the salivary pump (*SlP*), and the wide salivary canal from the pump opens, as in *Culicoides*, on the proximal half of the anterior hypopharyngeal wall, whence it is continued distally as an open channel. The maxillae have each (F) a short but strong basal stipes (*St*) by which the appendage is attached to the head at the side of the postmental plate of the labium (B, *St*). The galea (F, *Ga*) is thick, tapering, and strongly armed with recurved marginal teeth. The five-segmented palpus (*Plp*) is relatively long. The short, wide labium (H) is soft and compressible; on its posterior surface is a pair of thecal plates (*Thc*), but they are shorter than the large, mostly membranous labella (*Lbl*). The labial gutter encloses the mandibles, the hypopharynx, and the maxillary galeae, which are ordinarily concealed beneath the labrum (A, *Lm*).

The method of feeding by *Simulium* is discussed by Gibbins (1938), who says the "biting appears to be performed in two stages. First, the initial incision is made by the mandibles, which function in the manner of a pair of scissors; the maxillae are then inserted and the puncture is enlarged sufficiently to allow the food channel to reach the blood level." That the mandibles can "snip the skin" between their serrated distal ends as Gibbins suggests does not seem plausible considering that their musculature (fig. 10 K) is of the usual abductor-adductor type, and does not appear to be in any way adapted to giving the mandibles a scissor movement on their interlocking mechanism. Jobling (1928), as already noted, says that the mandibles of *Culicoides* remain locked together during the act of puncturing the skin.

Simulium has a strong cibarial pump, but the pharyngeal pump is much less developed than in the other bloodsucking Nematocera. Krafchick (1942) describes the sucking apparatus of *Eusimulium lascivum* Twinn, a nonbiting species, and shows that the usual musculature is present. The protractor and retractor muscles inserted on the posterior cornua of the cibarial pump, he says, effect also a movement of the hypopharynx, and produce an elevation and depression of the labrum.

The biting simuliids in the northeastern parts of the United States and eastern Canada are perhaps the worst of the pests that detract from the pleasures of outdoor life; in the southern States they are a scourge to livestock and other animals. *Prosimulium hirtipes* (Fries) and *Simulium venustum* Say are well known to campers and fishermen in the Adirondacks as daytime pests, for, unlike the mosquitoes, the black flies swarm in bright sunshine and in the heat of the day. In the South the torment of animals by the bites of black flies is extreme. Of the southern buffalo gnat, *Eusimulium pecuarum* (Riley), Bishopp (1942) says: "In severe outbreaks of the southern buffalo gnat in the lower Mississippi Valley many mules die, cattle and horses are reduced in flesh, milk flow is cut, and the coats of the animals become rough and unsightly." In 1923 great numbers of domestic and wild animals were killed in Rumania by invading swarms of *Simulium columbaczense* (Schönberg) (Patton and Evans, 1929; Herms, 1939). Another pest of domestic animals in the southern part of the United States is *Simulium meridionale* Riley, known as the turkey gnat because it is particularly injurious to setting turkeys.

In addition to the annoyance and damage caused by their bites, the simuliids are further indicted on the charge of spreading disease. Various species are involved in the transmission of filarial worms of man in Mexico, Central America, and Africa, and of cattle in Australia. The parasites taken into the stomach of the fly undergo a metamorphosis, escape into the blood cavity, and soon find their way into the head and proboscis. The exit of the microfilariae from the proboscis, as Gibbins (1938) suggests, is probably made by penetrating the delicate, membranous inner walls of the labial labella, whence the parasites enter the wound made by the piercing stylets of the fly. Among wild and domesticated ducks in various parts of the United States a high mortality, especially in the young, is sometimes caused by the blood-inhabiting protozoon *Leucocytozoon anatis* Wickware, said to be transmitted by *Simulium venustum* Say.

VI. HORSE FLIES. FAMILY TABANIDAE

The Tabanidae, called horse flies, deer flies, and gad flies, are well-known insects because some of them viciously and persistently attack us when their haunts are invaded, especially along country roadsides and in dry wooded areas; they are probably the most severe biting pests against which horses, cattle, and deer have to contend. Furthermore, certain species are accused, on experimental evidence at least, of being vectors of such diseases as anthrax and surra, carriers of the filarial parasite *Loa loa,* and possible transmitters of tularemia.

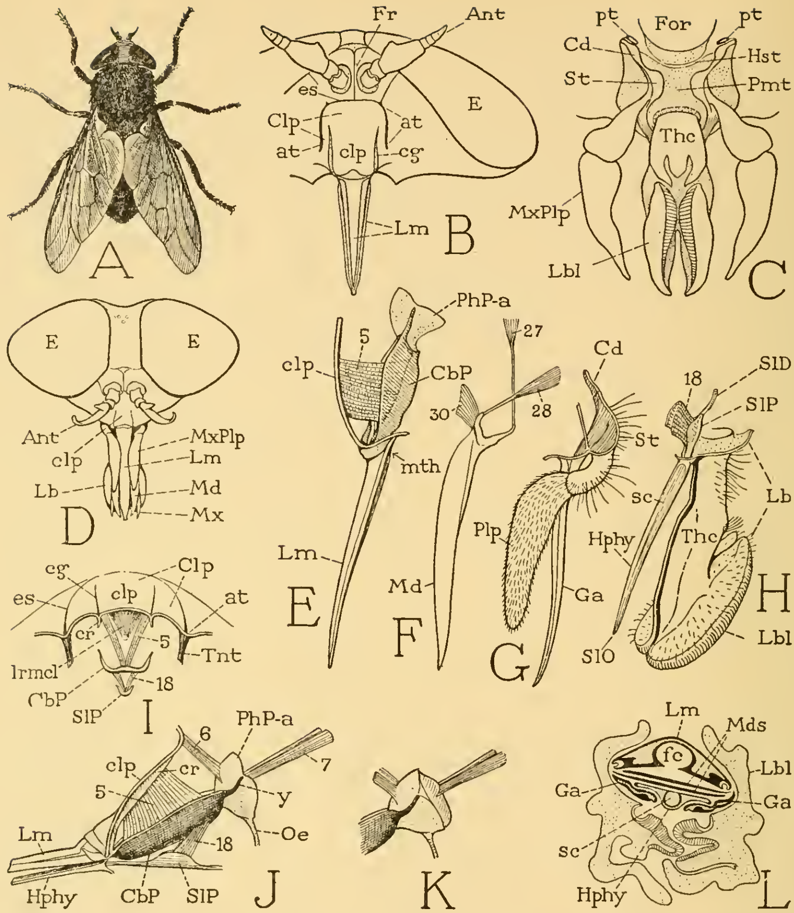

FIG. 11.—Horse fly, *Tabanus*, head, mouth parts, and sucking apparatus. Tabanidae. A-H, *Tabanus atratus* Fabr.; I-K, *Tabanus sulcifrons* Macq.

A, the black horse fly, *Tabanus atratus* Fabr., female (natural size). B, anteroventral view of head and labrum. C, mouth parts and their attachments on the head, posterior. D, head and mouth parts, anterior. E, labrum and sucking apparatus, left side. F, mandible. G, left maxilla. H, hypopharynx, labium, and salivary pump, left side. I, transverse section through clypeus and cibarial pump, diagrammatic. J, sucking apparatus and associated parts, left side. K, pharyngeal pump expanded. L, cross section of proboscis (from Vogel, 1921).

Ant, antenna; *at,* anterior tentorial pit; *CbP,* cibarial pump; *cd,* cardo; *cg,* clypeal groove; *Clp,* clypeus; *clp,* median plate of clypeus; *cr,* clypeal ridge; *E,* compound eye; *es,* epistomal suture; *fc,* food canal; *For,* neck foramen; *Fr,* frons; *Ga,* galea; *Hphy,* hypopharynx; *Hst,* hypostoma; *Lb,* labium; *Lbl,* labella; *Lm,* labrum; *lrmcl,* labral muscle; *Md, Mds,* mandible, mandibles; *mth,* mouth of cibrarial pump; *Mx,* maxilla; *MxPlp,* maxillary palpus; *Oe,* oesophagus; *Plp,* palpus; *PhP-a,* pharyngeal pump, anterior in Brachycera; *Pmt,* postmentum; *pt,* posterior tentorial pit; *sc,* salivary canal; *SlD,* salivary duct; *SlO,* salivary orifice; *SlP,* salivary pump; *St,* stipes; *Thc,* theca; *Tnt,* tentorium; *y,* cornu of cibarial pump.

Muscles.—*5,* dilators of cibarial pump; *6, 7,* precerebral dilators of pharyngeal pump; *18,* dilators of salivary pump; *27,* abductor of mandible; *28,* cranial adductor of mandible; *30,* tentorial adductor of mandible.

The species are mostly large for flies, and the black horse fly (fig. 11 A) is one of the largest of the Diptera.

The horse flies introduce us to the second major group of the Diptera, known as the Brachycera because the antennae (fig. 11 B, *Ant*) are shorter than in most Nematocera and have fewer segments. Though the mouth parts of the tabanids do not differ essentially from those of Nematocera, there are features in the head and the sucking apparatus that are characteristic of Brachycera.

An examination of the anteroventral aspect of the head of *Tabanus* (fig. 11 B) shows that the clypeal area (*Clp*) is defined, though not completely set off from the rest of the cranium, by an epistomal sulcus (*es*) strongly arched upward almost to the bases of the antennae. In the lateral parts of the sulcus are the elongate anterior tentorial pits (*at, at*). The median part of the clypeus is marked by two vertical grooves, one on each side (*cg*), which cut out a small median area (*clp*) to which the labrum (*Lm*) is attached. On the inner surface of the head the clypeal grooves form two ridges (I, *cr*) running just laterad of the attachments of the dilator muscles (5) of the cibarial pump (*CbP*). These features are perhaps of little significance in a study of the horse fly, but they should be kept in mind because of their bearing on the interpretation of less easily understood modifications in the clypeal region of the Cyclorrhapha.

The stylets of the horse fly are all large and are easy to study since they are not so completely concealed in the trough of the labium (fig. 11 D) as are those of the biting Nematocera. The labrum (B, E, *Lm*) is broad and tapering, but its soft edges and blunt point suggest that it is not an effective piercing organ; its under surface is deeply excavated to form the food canal (L, *fc*). The mandibles of the female are large, sharp-pointed blades (F) overlapping each other in the labial gutter (L, *Mds*) beneath the labrum, and thus closing the food canal except at the base of the proboscis, where the mandibles diverge laterally to their attachments on the head. Each mandible is firmly affixed to the cranial wall, so that it evidently can have no movements of protraction and retraction, but it is provided with the usual equipment of abductor and adductor muscles (F) and is readily moved in a transverse plane. The maxillae have strong stipitocardinal bases (G, *St, Cd*) implanted in the membranous posterior wall of the head (C), from which are suspended the slender galeal stylets (G, *Ga*) that converge into the labial gutter, and the thick two-segmented palpi (*Plp*) that project as free appendages at the sides of the proboscis (D). In the labial gutter (L) the galeae lie beneath the mandibles and the hypopharynx. The slender, relatively weak hypopharynx (H, *Hphy*) is a trifle shorter than the labrum, and is traversed to its rounded tip by the salivary canal (*sc*) from the salivary pump (*SlP*).

The labium (fig. 11 H, *Lb*) has a long basal stalk, the external sclerotization of which is the theca (C, H, *Thc*), and a pair of large terminal lobes (*Lbl*), which are the labella. Within the theca is the labial gutter. In their size, shape, and structure the labella of the Tabanidae differ from these organs in the other bloodsucking Diptera, and much resemble the labella of the nonpiercing Cyclorrhapha that feed on exposed liquids. Ordinarily the labellar lobes of *Tabanus* are folded together (C), but they can be spread out (H) to form a large, flat, oval disk. Their soft under surfaces are traversed crosswise by numerous fine, closely set channels ("pseudotracheae") that lead into a pair of median lengthwise channels. In the spread position of the labella the labellar disk is deeply cleft anteriorly between the lobes as far as the end of the labial gutter. There is no projecting ligular lobe; the labial gutter terminates with a narrow, slightly concave margin.

The method of biting and feeding by the horse flies has not been carefully observed, but the structure of the mouth parts suggests that the puncture is formed by the mandibles and the maxillary galeae, and that the labial labella are used in the manner of nonpiercing flies for collecting the exuding blood. When the labrum is pressed down between the labella it overreaches the end of the labial gutter, and if the tips of the mandibles are now separated from beneath the labrum the entrance to the food canal of the latter is directly exposed in the labellar cleft.

The male of *Tabanus* has a complete set of feeding organs, including the mandibles, but the parts are less strongly developed than in the female. Male horse flies are not known to suck blood, and are said to feed on plant juices.

The sucking apparatus of the horse flies includes a strongly developed cibarial pump and a pharyngeal pump. The cibarial pump is of the usual type of structure (fig. 11 J, *CbP*); its dilator muscles arise on the median plate of the clypeus (I, J, *clp*) between the clypeal ridges (*cr*). The pharyngeal pump (J, *PhP-a*), on the other hand, differs entirely from that of the bloodsucking Nematocera; it is formed from the pharyngeal region immediately following the cibarial pump, and is activated by the precerebral dilators of the pharynx (*6, 7*). The pharyngeal pump of *Tabanus* is a conical suction cup held between the posterior cornua (J, *y*) of the cibarial pump. Its broad inner end, ordinarily collapsed into the cup, is an elastic disk on which is attached the second pair of dilator muscles (7). These muscles by contraction pull out the disk (K), which, on relaxation of the muscles, snaps back by its own elasticity. The action is easily demonstrated on a dead specimen. The blood evidently is sucked out of the cibarial pump and driven on into the oesophagus.

VII. SNIPE FLIES. FAMILY RHAGIONIDAE

The family of the snipe flies has been more commonly known as Leptidae. At least two genera include biting and bloodsucking species; one is *Symphoromyia* Frauenfeld with several species in the western parts of the United States, the other is *Spaniopsis* White of Australia.

Symphoromyia atripes Bigot, here illustrated (fig. 12 A), is somewhat smaller than a house fly. The head is set on the front of the thorax as in the horse flies, instead of hanging below it as in most of the biting Nematocera. On the face (B) the large clypeus (*Clp*) is distinctly defined, and in its lower part a small median lobe (*clp*) supporting the labrum is set off by a pair of lateral grooves. The frons is represented by wide lateral areas between the eyes and the clypeus, but it is almost obliterated between the antennae by the upward encroachment of the clypeus. The piercing and sucking organs, as shown in the figure (C, D, E, F), resemble those of the Tabanidae. The female snipe flies are said to be vicious biters, but they are not known to be involved in the spread of disease.

VIII. ROBBER FLIES. FAMILY ASILIDAE

The robber flies do not attack man or any vertebrate animals; their victims are other insects or spiders, which is fortunate for us since as biting insects they probably have no equal. They kill their prey outright, and suck out not only its blood but all the softer tissue of the body as well. The asilids (fig. 13, B) are insects of medium or large size; their favorite haunt is any dry, open, sunny place where flight is not obstructed, visibility is good, and prospective victims have little protection. They capture other insects of all kinds and sizes, including members of their own family, but they show a preference for flies and Hymenoptera, and do not hesitate to attack stinging species such as bees and wasps.

The piercing organ of the robber flies is the hypopharynx (fig. 13 A, *Hphy*), a strong, sharp-pointed shaft that can be protruded beyond the other mouth parts. In a study of the feeding habits of the

Asilidae, Whitfield (1925) has shown that the victim is stabbed usually in the head or the thorax, and that in such cases death is generally instantaneous. The head puncture in most cases is inflicted just above the neck. Death evidently results from the injection of a lethal

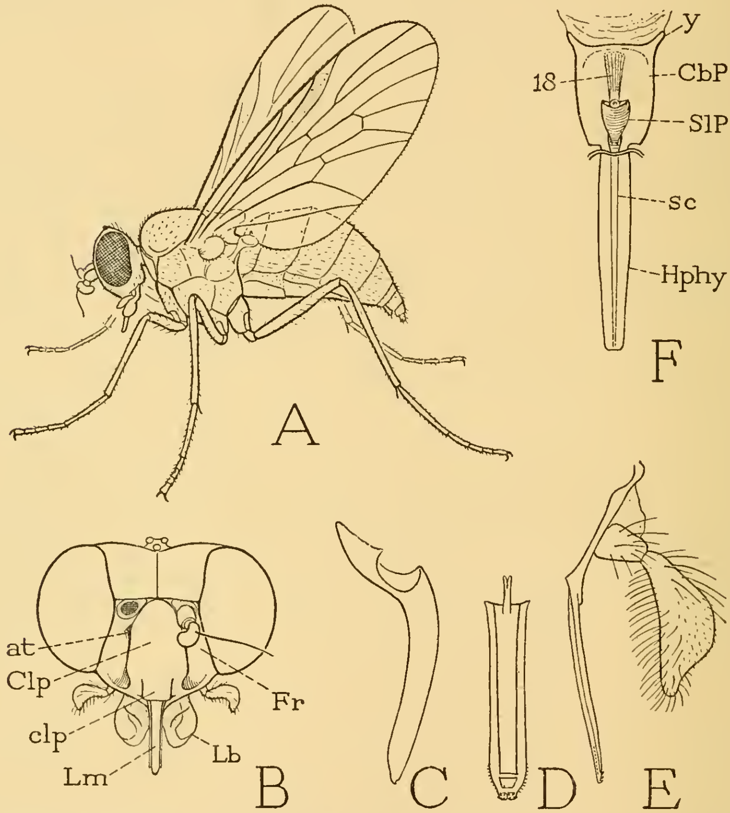

FIG. 12.—A snipe fly, *Symphoromyia atripes* Bigot, female, head and mouth parts. Rhagionidae.

A, female fly (length 5.5 mm.). B, head and proboscis, anterior. C, mandible. D, labrum, anterior. E, maxilla. F, hypopharynx, floor of cibarial pump, and salivary pump with its muscles (*18*), posterior.

at, anterior tentorial pit; *CbP*, cibarial pump; *Clp*, clypeus; *clp*, median lobe of clypeus; *Fr*, frons; *Hphy*, hypopharynx; *Lb*, labium; *Lm*, labrum; *sc*, salivary canal; *SlP*, salivary pump; *y*, cornu of cibarial pump.

secretion, since insects are not readily killed by mere wounds. The same, or another, secretion introduced into the body of the captive soon reduces to a liquid condition the entire body content, which is then sucked out so completely that the victim when discarded is little more than an empty skin. According to Whitfield the killing secretion must be that of the thoracic glands corresponding with the usual salivary glands of other insects, which, being discharged through the hypopharynx, is injected at the time of the fatal stroke. The secretion that subsequently digests the visceral organs Whitfield believes is pro-

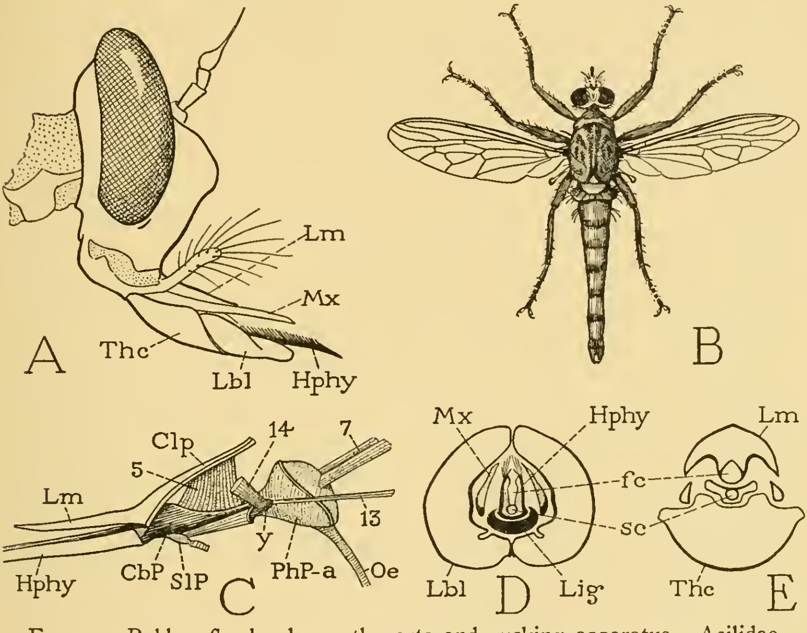

FIG. 13.—Robber fly, head, mouth parts and sucking apparatus. Asilidae.

A, *Proctacanthus* sp., head and proboscis. B, example of an asilid. C, *Diognites discolor* Loew, male, sucking apparatus and associated parts, left side. D, *Machimus atricapillus* Fln., cross section of proboscis through labella (simplified from Whitfield, 1925). E, same, section of proboscis near base (from Whitfield).

CbP, cibarial pump; *Clp*, clypeus; *fc*, food canal; *Hphy*, hypopharynx; *Lbl*, labellum; *Lig*, ligula; *Lm*, labrum; *Mx*, maxilla; *Oe* oesophagus; *PhP-a*, pharyngeal pump (anterior); *sc*, salivary canal; *SlP*, salivary pump; *Thc*, theca; *y*, cornu of cibarial pump.

Muscles.—*5*, dilators of cibarial pump; *7*, precerebral dilators of pharyngeal pump; *13*, retractor of cibarial pump; *14*, protractor of cibarial pump.

duced by a pair of glands in the labium that open into the distal part of the labial gutter.

The formidable proboscis of the asilids projects forward menacingly from the lower part of the head (fig. 13 A). It is composed of the labrum, a pair of maxillae, the hypopharynx, and the labium; mandibles are absent in each sex. The labrum (*Lm*) is short and triangular. The maxillae have slender galeal blades (*Mx*), concave on their inner surfaces, which normally are applied against the sides of the hypopharynx; the bristly palpi are unsegmented. The labium is hard and rigid; its base contains a large thecal sclerite (*Thc*) and supports the pair of long, horny labella (*Lbl*), which ensheath the distal parts of the maxillae and hypopharynx (D). The labial gutter is produced into a strong ligular tongue between the labella (D, *Lig*), on which slides the hypopharynx (*Hphy*). Just proximal to its sharp apical point the hypopharynx is deeply grooved on its upper surface (D) and fringed above with stiff hairs slanted backward (A). The hypopharyngeal groove is the first part of the food canal (D, *fc*); farther back, as shown by Whitfield, the function of conduction is taken over by the canal of the labrum, which toward the mouth becomes a closed channel (E, *fc*). Beneath the labrum the hypopharynx flattens out and contains only the salivary canal (*sc*).

The sucking apparatus of the Asilidae is of the same type of structure as that of the Tabanidae in that it consists of a cibarial pump (fig. 13 C, *CbP*) and an anterior pharyngeal pump (*PhP-a*). The pharyngeal pump, however, has an external sheath of circular muscle fibers, and lacks the first pair of cranial muscles of the tabanids (fig. 11 J, *6*). On each cornu of the cibarial pump are inserted a slender retractor muscle (fig. 13 C, *13*) and a stronger protractor (*14*). These muscles, directly effecting movements of the cibarial pump, Whitfield says, "are the means of extruding and retracting the hypopharynx." The cibarial pump has no connection with the head wall, and is movable by reason of the flexibility of the clypeus at the base of the labrum.

IX. THE CYCLORRHAPHA

Because of certain distinctive features in the feeding apparatus of the Cyclorrhapha, a study of the biting species included in this group may be expedited by a preliminary discussion of the typical cyclorrhaphous structure. The familiar nonbiting cyclorrhaphous flies are the fruit flies, the pomace flies, the house flies, the blow flies, and the flesh flies; biting species include the horn flies, the stable flies, the tsetse flies, and the louse flies.

The Cyclorrhapha lack mandibles, and most of them have no maxillary blades though the maxillary palpi are retained. The proboscis, therefore, consists generally of only the unpaired members of the mouth parts, namely, the labrum, the hypopharynx, and the labium (fig. 14 F). These parts are suspended from a conical, membranous projection of the lower part of the head, known as the *rostrum,* or *basiproboscis* (A, *Rst*). The true proboscis, corresponding with the proboscis of Nematocera and Brachycera, is termed the *haustellum* (*Hstl*). The anterior wall of the rostrum contains one or two clypeal plates (*clp*), and supports the maxillary palpi (*MxPlp*) ; within the rostrum are a pair of labral apodemes, the cibarial pump, and the salivary pump.

The labrum and the hypopharynx have the same structure in the Cyclorrhapha as in other flies; the labrum is excavated by the food canal (fig. 14 F, *fc*), which is closed by the hypopharynx below it, and the latter is traversed by the salivary canal (*sc*). The labrum, however, is provided with a pair of long internal apodemal rods (I, J, *lrAp*) for the attachment of muscles. These rods are often regarded as being parts of the maxillae, but they are articulated to the basal angles of the labrum, and their muscles move the proboscis. The labium consists of a proximal stalk, the prementum, and of a pair of labellar lobes (A, *Lbl*). The prementum is covered posteriorly by a thecal sclerite (F, *Thc*), and is excavated anteriorly by the labial gutter (*LG*), in which are lodged the labrum and the hypopharynx. In most of the nonbiting Cyclorrhapha the entire proboscis can be folded up against the lower side of the head, or even completely retracted within the peristomal margin of the cranium; in biting forms it is usually rigid and projecting, though it may be retractile into a pouch of the head wall.

The labial labella in most nonbiting species are large, soft, oval lobes that can be flexed upward against the sides of the haustellum or spread out flat to form a broad disk, the so-called "oral sucker," by which liquid food may be collected and conveyed to the food canal of the haustellum. When the labella are thus spread out (fig. 14 B), the cleft between their anterior parts is ordinarily closed by the apposition of the lobes except for an oval aperture at its inner end, which is termed the *prestomum* because it lies at the entrance to the food canal of the labrum and thus constitutes a provisional mouth of the proboscis. The under surfaces of the labella, as in the horse flies, are grooved transversely by canaliculi ("pseudotracheae") that serve as food conductors. The canals are kept open, and their flexibility preserved, by minute riblike thickenings of their walls, forked at one end and simply expanded at the other, that leave an open line along the exposed surfaces of the grooves, and entrance holes at their own forked extremities. In the blow fly (B) the first 6 or 8 and the last 11 or 12 transverse canaliculi of each labellum open respectively into anterior and posterior longitudinal collecting channels that lead toward the prestomum; the intermediate canaliculi, 12 in number on each side, discharge directly into the latter. At the mesal ends of the intermediate canaliculi is an armature of intercanicular spines, or toothlike processes (*t*), three rows of them on each labellum, and, in addition, flanking the open ends of the canals themselves are pairs of canalicular teeth. These labellar spines collectively are known as the *prestomal teeth;* their number, size, shape, and arrangement vary in different species.

The spines or teeth of the labella give many of the nonbiting flies a means of rasping, scraping, or even of puncturing the feeding surface. The various methods of feeding employed by the blow fly are graphically illustrated by Graham-Smith (1930). Certain other species have carried the development of the labellar teeth so far that the proboscis becomes an effective scarifying organ, as in *Philaematomyia crassirostris* (Stein) a bloodsucking fly of Africa, in which the soft, protrusible, strongly armed, terminal lobe of the labium (fig. 14 C) is evidently a cutting instrument. This fly, Austen (1909) says, "in all probability feeds by cutting through the epidermis with the teeth at the end of the tubular extension (of the labium), and then sucking up the blood in the ordinary way." In most of the biting flies of the cyclorrhaphous group, however, in which the prestomal teeth are cutting organs, the labella have become reduced to small, horny plates, and the labium itself has been converted into a strong piercing shaft.

A case of direct development of the labella into a pair of biting jaws occurs in *Melanderia mandibulata* Aldrich, a brachycerous fly of the family Dolichopodidae, which feeds on soft-bodied invertebrates along the seashore.

The sucking apparatus of the cyclorrhaphous Diptera consists of the cibarial pump alone, the head stomodaeum being a narrow oesophageal tube with no pharyngeal dilatation. The pump has the same structure and mechanism as in other Diptera (fig. 14 D), but its side margins are united with lateral plates (*lpl*) deeply inflected from the edges of the clypeus (*clp*). The associated parts thus form a stirrup-shaped structure, known as the *fulcrum* because the entire proboscis, including the pump, swings on the clypeal hinge with the frons.

To understand the nature of the fulcrum in the Cyclorrhapha we must refer back to the horse fly, in which it was noted that the median part of the clypeus, giving attachment to the dilators of the cibarial pump (fig. 11 B, *clp*), is partially cut out by a pair of grooves (*cg*) that form ridges on the inner surface (I, *cr*). In the Cyclorrhapha and some of the Brachycera, the median, muscle-bearing plate of the

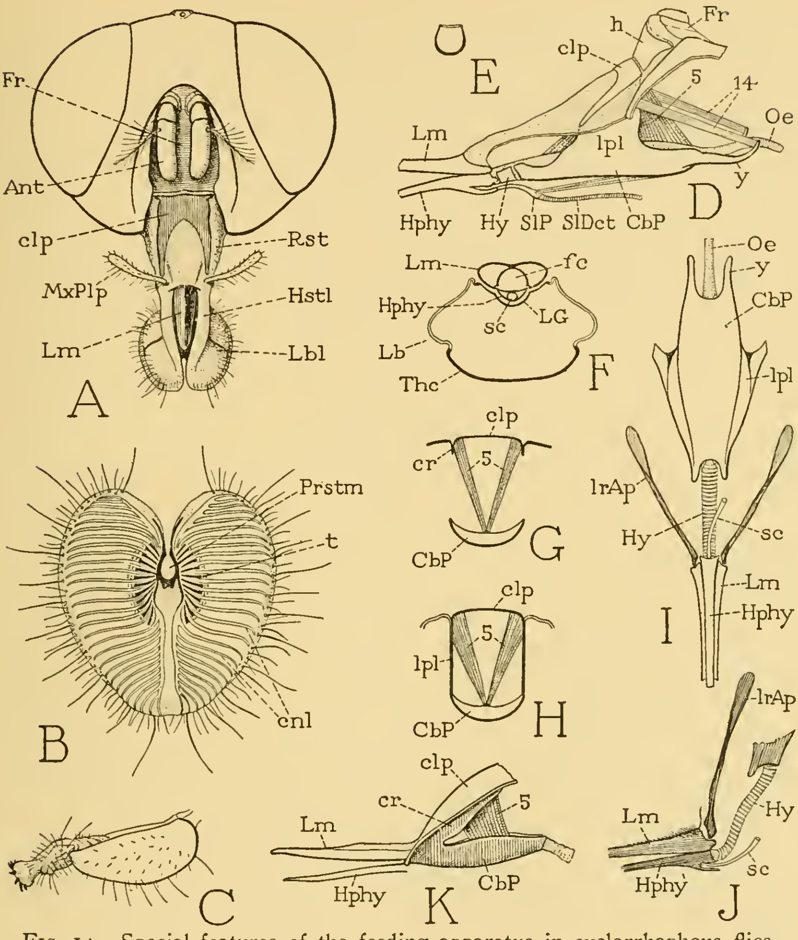

FIG. 14.—Special features of the feeding apparatus in cyclorrhaphous flies.

A, head of a female house fly, *Musca domestica* L., with proboscis extended. B, under surface of the labellar disk of a female blow fly, *Calliphora*. C, proboscis of *Philaematomyia crassirostris* (Stein) (*insignis* Austen), with strongly developed prestomal teeth (from Austen, 1909). D, fulcrum and associated parts of *Calliphora*, left side. E, cross section of the hyoid of *Calliphora*. F, cross section of the haustellum of a female house fly. G, diagrammatic cross section through clypeus and cibarial pump of a horse fly (see fig. 11 I). H, corresponding section of the fulcrum of a cyclorrhaphous fly. I, labrum, hypopharynx, hyoid, and cibarial pump of a stable fly, *Stomoxys calcitrans* (L.), posterior surface. J, showing relation of hyoid to bases of labrum and hypopharynx in the stable fly, left side. K, clypeus and cibarial pump of *Mydas clavatus* Drury, a brachycerous fly.

Ant, antenna; *CbP*, cibarial pump; *clp*, clypeus; *cnl*, canaliculi of labellum; *cr*, clypeal ridge; *fc*, food canal; *Fr*, frons; *h*, hinge plate of clypeus; *Hphy*, hypopharynx; *Hstl*, haustellum; *Hy*, hyoid; *Lbl*, labellum; *LG*, labial gutter; *Lm*, labrum; *lpl*, lateral plate of fulcrum; *lrAp*, labral apodeme; *MxPlp*, maxillary palpus; *Oe*, oesophagus; *Prstm*, prestomum; *Rst*, rostrum; *sc*, salivary canal; *SlDct*, salivary duct; *SlP*, salivary pump; *t*, prestomal teeth; *Thc*, theca; *y*, cornu of cibarial pump.

clypeus becomes isolated by a membranization of the surrounding clypeal area, and is thus flexible on its hinge with the frons. The clypeal plate in such cases takes on various shapes, but in the Cyclorrhapha it has typically the form of an inverted V (fig. 14 A, *clp*), sometimes with an accessory hinge plate (D, *h*) uniting it with the frons. To brace the now unsupported clypeus against the pull of the dilator muscles of the pump, the clypeal ridges (G, *cr*) have been extended inward as a pair of plates (H, *lpl*) that unite with the edges of the pump (*CbP*). The whole structure, or so-called fulcrum, is thus movably suspended in the peripheral clypeal membrane of the rostrum, but is hinged to the frons by the upper edge of the clypeal plate, or by an intervening hinge plate, and hence swings forward or backward with the protraction or retraction of the proboscis.

The clypeal plate of the Cyclorrhapha, recognized as such by Patton and Cragg (1913), is termed by Graham-Smith (1930) the "anterior arch of the fulcrum," which literally it is in a structural sense, but almost all other recent writers on Diptera have followed Peterson (1916) in calling this plate the "torma," on the mistaken idea that it is derived from lateral basal processes of the labrum, properly named *tormae*. The muscle relations between the plate in question and the pump show that this latter interpretation is impossible, as is clearly seen by referring back to the horse fly (fig. 11 B, I) and the cockroach (fig. 2 A). In some of the Brachycera a bracing of the pump on the clypeus is effected by a strong union of the lower parts of the clypeal ridges with the edges of the pump (fig. 14 K).

Between the food canal of the proboscis and the mouth of the sucking pump in such flies as the house fly and the blow fly there is interposed a short cylindrical passage. The wall of this tubular entrance to the pump contains a sclerite (fig. 14 D, *Hy*), which, being U-shaped in cross section (E), has been appropriately named the *hyoid*. Later writers, however, have applied the term "hyoid" to the passageway itself, which is unfortunate because the latter in some flies, as in *Stomoxys* (I, J, *Hy*), is drawn out into a long flexible tube, reaching its greatest length in connection with the retractile proboscis of the Hippoboscidae (fig. 17 I, *Hy*). The name is retained in this paper to avoid confusion.

The salivary pump of the Cyclorrhapha (fig. 14 D, *SlP*) has the same structure and musculature as in other flies. (See Cornwall, 1923.)

X. EYE GNATS. FAMILY CHLOROPIDAE

The flies of this family, known also as Oscinidae, are very small insects somewhat resembling the pomace flies (Drosophilidae), and often occur in swarms. They have a propensity for feeding on animal exudations, and are most annoying because of their persistent efforts to get into the eyes. Certain species, therefore, are accused, and on good circumstantial evidence, of spreading eye infections and the germs of suppurative sores; their habits alone are sufficient to put them under suspicion. *Siphunculina funicola* (de Meijère) of India, Ceylon, and Java, and *Hippelates pusio* Loew of the southern and western parts of the United States are probably each involved in the dissemination of conjunctivitis, while the first, in Ceylon, and *Hippelates pallipes* Loew, in Jamaica, have been strongly suspected of being vectors, respectively, of parangi and of yaws. Mastitis of cattle, or inflammation of the udder, has been shown to be spread by eye gnats.

The Chloropidae do not have piercing mouth parts of any of the usual types of structure, but they are able to make small punctures in delicate surfaces by means of minute spines or points along the edges of the channels on the under surfaces of the labella. The feeding organs of *Siphunculina funicola* have been described by Senior-White (1923), those of *Hippelates pusio* by Graham-Smith (1930a). The labella in these flies have each only six of the so-called pseudotracheal channels, and the latter run in a longitudinal direction. The rings that keep the channels open are not closed outwardly, but end in projecting points that become spinous proximally along the channel margins. "When the flies are feeding on abrasions or the conjunctival epithelium," Graham-Smith says, "these spines apparently act as cutting instruments capable of producing minute multiple incisions, likely to assist pathogenic organisms carried by the insects in gaining a foothold."

XI. HORN FLIES, STABLE FLIES, AND TSETSE FLIES. FAMILIES MUSCIDAE AND GLOSSINIDAE

The Muscidae are the family of the house fly, *Musca domestica* L., which though a common pest in many ways, is not guilty of the offense of biting, since it has no effective piercing mechanism; yet, within its family are some notorious biters, the horn flies (*Siphona*) and the stable flies (*Stomoxys*). Closely related to these flies also are the tsetse flies (*Glossina*), which some dipterists place in a separate family, the Glossinidae. In all these genera it is the labium that forms the piercing organ; the theca and the labial gutter are drawn out into a long, rigid shaft, and the labella, instead of being soft, spreading lobes as in most of the muscids, are reduced to a pair of small hard plates at the tip of the theca, armed internally with eversible teeth. The labrum and the hypopharynx are contained within the gutter of the labium. The beaklike haustellum of the proboscis, when not in use, projects forward from the lower part of the head (fig. 15 B, *Prb*).

The structure of the head and the feeding mechanism of *Glossina palpalis* (R.-D.) have been fully described by Jobling (1933). The head of *Glossina* (fig. 15 B) has the usual muscoid structure, but the proboscis (*Prb*) is long and slender with a bulblike swelling at the base, and normally is ensheathed between the long maxillary palpi (*MxPlp*). The proboscis, or, more strictly speaking, the haustellum of the proboscis (E, *Hstl*), arises from a relatively small, membranous rostrum (*Rst*), which is usually swung back, allowing the bulbous base of the haustellum to be firmly braced against the lower part of the head. The haustellum is composed of the labium, the labrum (*Lm*), and the hypopharynx (*Hphy*). It is the base of the labium that forms the bulb (*b*); the theca (*Thc*) is a thick plate on the outer posterior wall of the labium (G); the labial gutter (G, *LG*) embraces the labrum (*Lm*) and encloses the hypopharynx (*Hphy*). The food canal (*fc*) is the channel of the labrum closed below by the labial gutter; the salivary canal (*sc*) traverses the slender hypopharynx. The theca and the wall of the gutter are united by membranes along their edges, allowing the two parts of the labium a limited movement on each other. The labrum is held in the labial gutter by several interlocking ridges on each side. The horny platelike labella (E, *Lbl*) when pressed together form a small apical lobe of the haustellum. Their inner walls have a complicated armature of teeth and sensory papillae (H), a detailed description of which is given by Jobling (1933).

Since the theca and the labial gutter are movable lengthwise on each other because of the amplitude of the lateral membranes uniting them along the sides of the labium, the theca and the labella are retractile and protractile on the relatively fixed gutter. The retraction of the labellar plates (fig. 15 H, *Lbl*) on the end of the gutter (*LG*), therefore, everts the inner armature of the labella and gives the teeth a reversed position on the end of the haustellum. The movements of the theca are said by Jobling (1933) to be produced by the oppositely inclined sets of oblique muscles in the labial bulb (fig. 15 F), which are attached at one end on the gutter and at the other

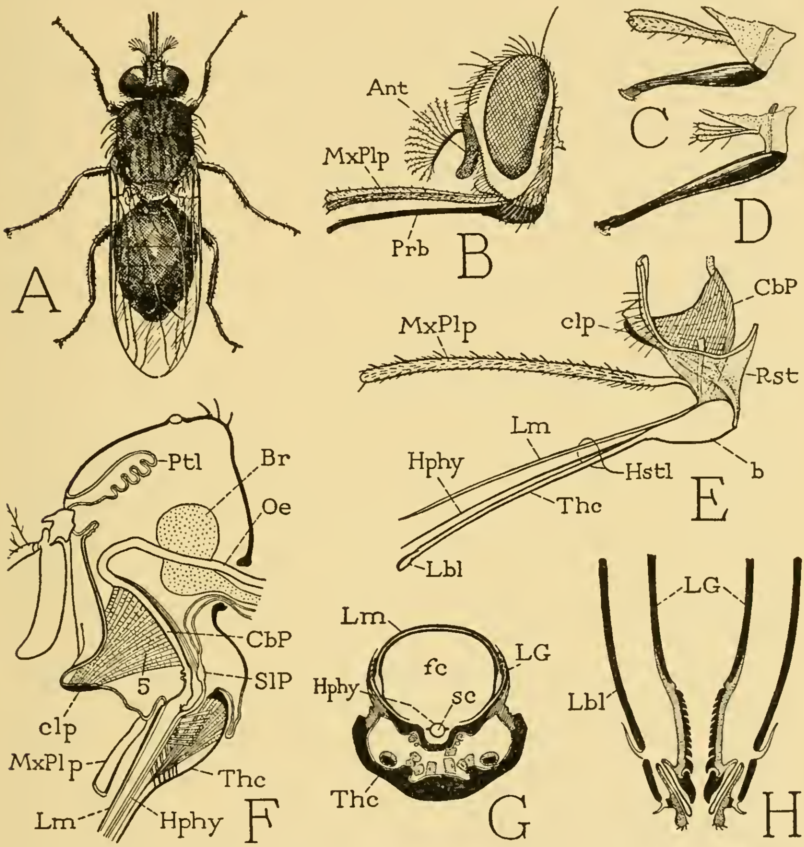

FIG. 15.—Tsetse fly, *Glossina*, horn fly, *Siphona*, and stable fly, *Stomoxys*, head and feeding apparatus. Glossinidae and Muscidae.

A, *Glossina palpalis* R.-D., male (length 11 mm.). B, same, head and proboscis. C, *Siphona irritans* (L.), proboscis. D, *Stomoxys calcitrans* (L.) proboscis. E, *Glossina palpalis*, proboscis and sucking pump, stylets separated from labium. F, same, vertical section of head and base of proboscis (simplified from Jobling, 1933). G, *Glossina fusca* (Walker), cross section of proboscis (from Vogel, 1921). H, *Glossina palpalis*, horizontal section of distal end of labium (simplified from Jobling, 1933).

Ant, antenna; *b*, bulb of labium; *Br*, brain; *CbP*, cibarial pump; *clp*, clypeus; *fc*, food canal; *Hphy*, hypopharynx; *Hstl*, haustellum; *Lbl* labellum; *Lm*, labrum; *LG*, labial gutter; *MxPlp*, maxillary palpus; *Oe*, oesophagus; *Prb*, proboscis; *Ptl*, invaginated ptilinum; *Rst*, rostrum; *sc*, salivary canal; *SlP*, salivary pump; *Thc*, theca.

on the theca. The corresponding muscles in the proboscis of *Stomoxys* were believed by Stephens and Newstead (1907) to effect a rotation of the theca, thus enabling the labellar teeth to exert a cutting action on the skin. Another pair of larger muscles in the bulb of the theca (F) have long tendons that traverse the labium to be attached on the labella, and these muscles effect directly a retraction of the labellar plates. Protraction of the theca reverses the movement and introverts the labellar teeth. While it would appear that the appressed labella in the protracted position are themselves sufficiently rigid to serve as a penetrating point for the proboscis, it is generally said that the everted teeth are the effective cutting agents that puncture the skin, the proboscis being then sunken into the flesh. Movements of the proboscis in the wound probably cause a laceration that increases the blood flow.

The sucking apparatus of *Glossina* has the typical muscoid structure. The cibarial pump (termed the "pharynx" by Jobling, 1933) lies within the rostrum of the proboscis (fig. 15 E, *CbP*), but when the haustellum is retracted the pump is pushed up into the head (F). The dilator muscles (5) take their origins on the small clypeal plate (*clp*) in the anterior rostral wall, and the clypeal plate is attached to the pump by a pair of internal lateral plates, the whole complex forming a typical fulcrum. The stomodaeum turns back from the upper end of the pump as a narrow oesophageal tube (F, *Oe*) without a pharyngeal differentiation. The salivary pump (*SlP*) is of the usual structure and has long dilator muscles arising on the floor of the cibarial pump.

There are about 20 known species of the genus *Glossina* Wied., confined almost entirely to tropical and southern Africa. The eggs of the tsetse flies are hatched and the larvae matured within the body of the female, so that the larvae at birth transform very shortly into pupae. *Glossina palpalis* (R.-D.) (fig. 15 A) is the principal vector of the Gambian form of African sleeping sickness of man, but it is said to live mainly on reptiles (Herms, 1939). The Rhodesian form of the disease is transmitted by *Glossina morsitans* Westwood and *G. swynnertoni* Austen. The last named and other species are also vectors of the trypanosomes of nagana, a disease of horses, cattle, camels, dogs, and other mammals.

The horn flies and the stable flies resemble the tsetse flies in the structure of the proboscis and their manner of biting. Their common names are merely distinctive titles, since the horn fly only incidentally settles on the horns of cattle, and the stable fly is not confined to stables; both species abound in pastures where horses and cattle are grazing, and are a source of great annoyance and distress to the animals because of their persistent and painful biting. The sharp bite of the stable fly is not unfamiliar to us, but it is usually attributed to a "biting house fly."

The horn flies have been known entomologically under the generic names of *Haematobia* R.-D. and *Lyperosia* Rondani, but are now included in one genus, *Siphona* Meigen. They comprise about 34 species indigenous to the Old World, of which the most common species in Europe are *stimulans* Meigen, *irritans* L., and *exigua* de Meij., but all three species have become more widely distributed, and the second, *Siphona irritans,* since 1887 has become an abundant pest in the United States and Canada. The stable flies belong to the genus *Stomoxys* Geoffroy, the species of which are most abundant in Africa, but *S. calcitrans* (L.) is now of general distribution, and is the only species occurring in the New World.

The proboscis both in the horn flies (fig. 15 C) and the stable flies (D) is thicker and relatively shorter than in the tsetse flies (B), but it is similar in structure and mechanism in the three forms. The maxillary palpi of the horn flies are long and ensheath the proboscis as in *Glossina;* the palpi of the stable flies are short and project straight out from the rostrum. The haustellum, when not in use, is extended horizontally from the head, but when the fly bites, the organ is said to be turned vertically and driven for a third or more of its length into the flesh of the victim. The structure of the proboscis of *Stomoxys,* including the labellar armature, has been fully described and amply illustrated by Stephens and Newstead (1907).

Horses and cattle suffer severely from the attacks of these flies. Horn flies settle by thousands on the bodies of cattle, and the irritation of their incessant biting, together with loss of blood, results in a lowered vitality and reduced milk production. The stable fly is perhaps a more painful biter even than the horn fly, on account of its longer proboscis; when present in great numbers it has been known to kill horses and cattle through induced nervousness and the loss of blood. It is serious also as a pest of humans, particularly where abundant in the neighborhood of summer resorts. Both the horn fly and the stable fly are potential carriers of such livestock diseases as anthrax and surra. The horn fly has been claimed, from experiments on monkeys, to be a vector of human poliomyelitis, but more recent tests (Herms, 1939) appear to give negative results. In any case, these flies well illustrate how an ordinarily harmless organ such as the insect labium, by a few anatomical alterations can be converted into an instrument of torture.

XII. LOUSE FLIES. FAMILY HIPPOBOSCIDAE

The Hippoboscidae are a family of winged or wingless bloodsucking flies parasitic on mammals and birds. They cause their hosts much physical annoyance, but because they do not ordinarily leave an animal until the latter dies, they have little relation to the spread of

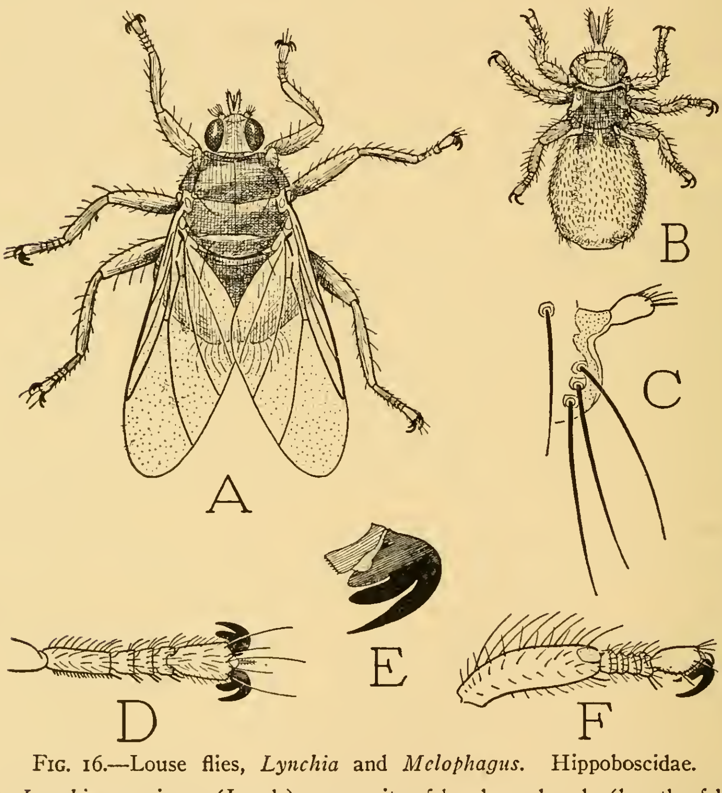

FIG. 16.—Louse flies, *Lynchia* and *Melophagus*. Hippoboscidae.

A, *Lynchia americana* (Leach), a parasite of hawks and owls (length of head and body about 8 mm.). B, *Melophagus ovinus* L., the sheep "tick" (largest about 8 mm. long). C, same, vestigial wing and associated bristles. D, *Lynchia americana*, right hind tarsus and claws. E, same, single foot claw. F, *Melophagus ovinus*, right fore tarsus and claws.

disease, though certain species have been shown to be vectors of pigeon and quail malaria. Most of the species are permanently winged (fig. 16 A), some shed the wings after having established themselves on a host, and a few are practically wingless (B), the wings in such species being reduced to minute lobes (C.). In all species the claws of the feet are conspicuously large and recurved (D, F). Those of the winged species shown in the figure are two-branched, each claw having a large basal lobe (E) separated from the outer branch by a deep, narrow cleft, by which evidently the insect is enabled to grasp the hairs or barbs of feathers amongst which it lives. In the wingless sheep "tick," *Melophagus ovinus* L. (B), the claws have a double appearance (F) but the apparent inner branch is a part of the base of the claw itself.

The head of a winged hippoboscid, though flattened and held horizontally so that the mouth parts project forward (fig. 16 A), resembles the head of any ordinary fly and is set on the thorax by a narrow neck. The eyes are large (fig. 17 A), the antennae (*Ant*) exposed, but the rostrum is concealed by the retraction of the haustellum. In *Melophagus ovinus,* however, the eyes are small (B), the antennae sunken into pits on the dorsal head surface, and the ventral part of the head is extended far back into the thorax. The proboscis is ordinarily inconspicuous; when not in use it is so deeply retracted into a pouch of the head that only its slender distal part is to be seen (A, B, *Prb*) between the long maxillary palpi (*MxPlp*). When protracted, however, it is fully everted (C) and now extends far beyond the ensheathing palpi. The lower lip of the pouch projects as a small lobe (*lp*) beneath the base of the proboscis.

The best published account of the structure and mechanism of the feeding apparatus of the Hippoboscidae is that of Jobling (1926), in which are described particularly *Pseudolynchia canariensis* (Macq.) (*maura* Bigot) and *Melophagus ovinus* L. The feeding organs in this family do not differ essentially from those of the biting muscoid flies described in the preceding section, the piercing instrument being the labium with an armature of eversible teeth on the labella. Both the labrum and the hypopharynx are contained within the labial gutter. The distinctive feature of the Hippoboscidae is the retraction of the haustellum into a deep pouch in the ventral part of the head (fig. 17 G), from which the organ is protractile for feeding. The haustellum is bulbous at the base, slender, and more or less decurved.

The wall of the labium, as is well shown in Jobling's cross section of the haustellum (fig. 17 F), is distinctly divided lengthwise into a strong posterior thecal section (*Thc*) and a deep anterior labial gutter (*LG*), the two parts being united by wide membranes deeply inflected on each side. The labrum (*Lm*) is embraced by the elevated sides of the gutter, and is held in place by interlocking ridges on the apposed surfaces of the two parts. The almost tubular channel of the labrum is the food canal (*fc*). Between the labrum and the floor of the

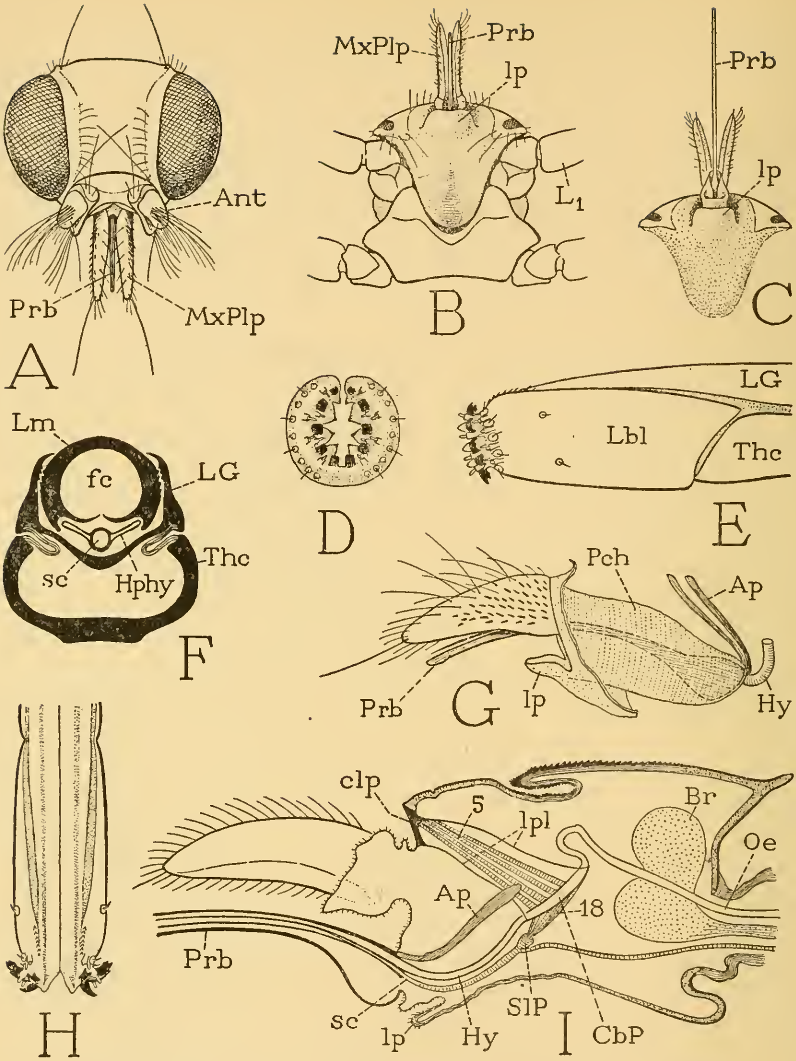

FIG. 17.—Head and feeding apparatus of *Lynchia* and *Melophagus*.

A, *Lynchia americana* (Leach), head and exposed part of retracted proboscis, anterior. B, *Melophagus ovinus* L., head and first two segments of thorax, ventral, proboscis retracted. C, same, head, proboscis protracted. D, *Pseudolynchia canariensis* (Macq.) (*Lynchia maura* Bigot), end view of labium, prestomal teeth introverted (from Jobling, 1926). E, same, distal part of labium, lateral, prestomal teeth everted (from Jobling, 1926). F, same, cross section through middle of proboscis (simplified from Jobling, 1926). G, *Lynchia americana*, proboscis retracted into pouch of head. H, *Melophagus ovinus*, distal part of proboscis, dorsal, prestomal teeth everted (from Jobling, 1926). I, *Pseudolynchia canariensis*, vertical section of head, proboscis protracted (from Jobling, 1926).

Ant, antenna; *Ap*, labral apodeme; *Br*, brain; *CbP*, cibarial pump; *clp*, clypeus; *fc*, food canal; *Hphy*, hypopharynx; *Hy*, hyoid; L_1, first leg; *LG*, labial gutter; *Lm*, labrum; *lp*, projecting lip of proboscis pouch; *lpl*, lateral plate of fulcrum; *MxPlp*, maxillary palpus; *Oe*, oesophagus; *Pch*, proboscis pouch; *Prb*, proboscis; *sc*, salivary canal; *SlP*, salivary pump; *Thc*, theca.

Muscles.—*5*, dilators of cibarial pump; *18*, dilators of salivary pump.

labial gutter lies the hypopharynx (*Hphy*), which is traversed by the salivary canal (*sc*).

The long slender theca of the labium bears distally a pair of lateral labellar lobes (fig. 17 E, *Lbl*), the outer surfaces of which are hard, smooth plates, while the inner surfaces are membranous and support an armature of strong teeth and associated sensory papillae (D). The teeth are everted and exposed externally (E, H) by the same mechanism as in the biting muscoids, namely, by the retraction of the theca and labella on the labial gutter.

The sucking apparatus of the Hippoboscidae consists, as in other Cyclorrhapha, of the cibarial pump (fig. 17 I, *CbP*), the cephalic stomodaeum being a slender oesophageal tube (*Oe*). The pump is supported on the clypeus (*clp*) by long, narrow lateral plates (*lpl*), which enclose the dilator muscles (5). To allow for the retraction of the proboscis, the so-called hyoid (*Hy*) connecting the pump with the food canal of the haustellum is drawn out into a long flexible tube. The salivary pump (*SlP*) has the usual relation to the cibarial pump, but is far separated from the base of the hypopharynx, necessitating a lengthening of the salivary canal (*sc*) proximal to the hypopharynx.

The Hippoboscidae undoubtedly are related to the muscoid flies, but they are placed in a separate superfamily, termed the Pupipara, because they give birth to full-grown larvae ready for pupation, as do the tsetse flies. Generally included also in the Pupipara are the two following families of bat parasites, the Streblidae and Nycteribiidae, but the relation of these flies to the hippoboscids is questionable.

XIII. BAT "TICKS." FAMILIES STREBLIDAE AND NYCTERIBIIDAE

The members of these two families, parasitic on bats, are of interest to us chiefly because of their queer shapes (fig. 18) and their structural adaptations to their habitat, but undoubtedly they are obnoxious pests to the animals on which they live. The Streblidae include some species with fully developed wings (B), others that have reduced wings (A), and still others that are wingless. The Nycteribiidae (C) are all wingless. In the Streblidae the head projects forward from the body in the usual manner (A); in the Nycteribiidae the small, basally narrowed head (D) arises from the dorsal surface of the thorax (C, *H*), on which it stands upright or bends backward. Just how these latter insects manage to insert the short proboscis into the skin of the host is not explained. The foot claws in both families are conspicuously large and recurved as in the Hippoboscidae, and have thick bases (E) like those of *Melophagus ovinus*.

For a detailed account of the structure of the head, the mouth parts, and the sucking pump of the bat "ticks," the reader is again referred to papers by Jobling, one (1928a) on the Nycteribiidae, another (1929) on the Streblidae. In general, the feeding apparatus resembles that of the Hippoboscidae and the biting Muscidae. The labium, armed with eversible labellar teeth, is the piercing organ. In some of the Streblidae the proboscis is short, and the thecal part of

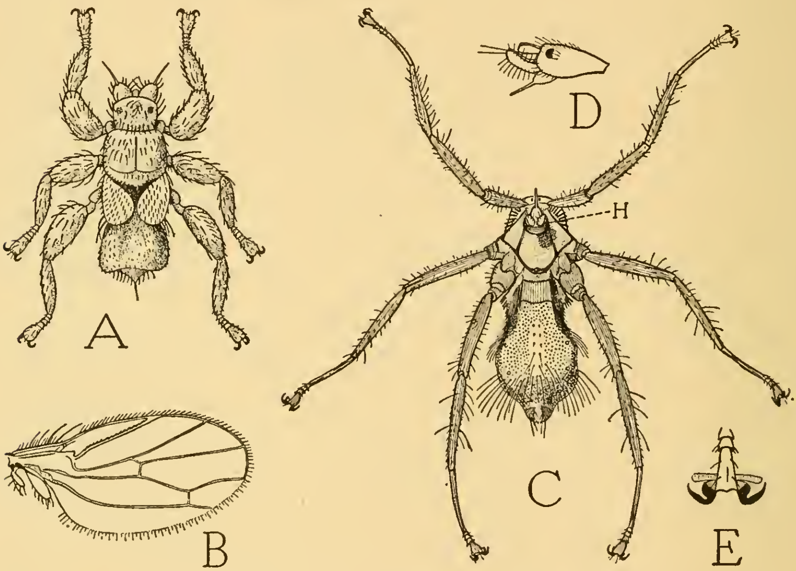

FIG. 18.—Bat "ticks." Streblidae and Nycteribiidae.

A, *Aspidoptera phyllostomatis* (Perty), a streblid with reduced wings (length 1.5 mm.) (from Speiser, 1900). B, *Raymondia lobulata* Speiser, wing of a fully winged streblid (from Jobling, 1930). C, *Cyclopodia sykesi* (Westw.), Nycteribiidae (length of body 5.5 mm.). D, same, head. E, same, end of hind tarsus, and claws.

H, head, projecting upward from thorax.

the labium is bulbous and bears a pair of small labella. In other species the proboscis is elongate, but the elongation results from a lengthening of the labella and not of the theca. The proboscis of the Nycteribiidae is relatively long and slender; the theca, however, forms only the basal bulb of the labium, the rest being the greatly elongate labella. While it is the labium that has been modified to form the piercing organ in the bloodsucking Muscidae, the Hippoboscidae, the Streblidae, and the Nycteribiidae, Jobling (1929) points out that "it is not the same part of the labium which has undergone this modification in all these families." Furthermore, Jobling gives reasons for believing that the resemblance of the bat "ticks" to the Hippoboscidae is the result of adaptation to the same mode of life and feeding; he would assign the Streblidae and the Nycteribiidae to the acalypterate section of the Cyclorrhapha.

Finally, it may be noted that the bee "louse," a minute wingless fly named *Braula coeca* Nitzsch, formerly classed with the hippoboscids and the bat "ticks," has been shown definitely by Imms (1942), from the structure of its larva, to be unrelated to these insects and to have its closest affinities in the Acalypterae. Moreover, *Braula coeca* is not a piercing insect. It is parasitic in the sense that it lives on the bodies of bees, and is regarded as a pest by beekeepers, but it is said to feed on saliva discharged from the mouth of the bee.

REFERENCES, AND TEXTBOOKS ON MEDICAL ENTOMOLOGY

ADLER, S., and THEODOR, O.

1926. The mouth-parts, alimentary tract, and salivary apparatus of the female in Phlebotomus papatasii. Ann. Trop. Med. Parasitol., vol. 20, pp. 109-142, pls. 8-14, 3 text figs.

AUSTEN, E. E.

1909. Illustrations of African blood-sucking flies other than mosquitoes and tsetse flies. 221 pp., 13 pls. British Mus. Nat. Hist., London.

BISHOPP, F. C.

1942. Some insect pests of horses and mules. Yearbook for 1942, U. S. Dep. Agr., pp. 492-500.

CHRISTOPHERS, S. R., SHORTT, H. E., and BARRAUD, P. J.

1926. The anatomy of the sandfly Phlebotomus argentipes, Ann. and Brun. (Diptera). I. The head and mouth parts of the imago. Indian Med. Res. Mem. No. 4, pp. 177-204, pls. 16-25.

CORNWALL, J. W.

1923. On the structure of the salivary pump in certain blood-sucking and other insects. Indian Journ. Med. Res., vol. 10, pp. 996-1007, pls. 75-80, 15 text figs.

GIBBINS, E. G.

1938. The mouth parts of the female in Simulium damnosum Theobald, with special reference to the transmission of Onchocerca volvulus Leuckart. Ann. Trop. Med. Parasitol., vol. 32, pp. 9-20, 8 figs.

GILTNER, L. T., and SHAHAN, M. S.

1942. Equine encephalomyelitis. Yearbook for 1942, U. S. Dep. Agr., pp. 375-391.

GRAHAM-SMITH, G. S.

1930. Further observations on the anatomy and function of the proboscis of the blow-fly, Calliphora erythrocephala L. Parasitology, vol. 22, pp. 47-115, pls. 19-22, 36 text figs.

1930a. The Oscinidae (Diptera) as vectors of conjunctivitis, and the anatomy of their mouth parts. Parasitology, vol. 22, pp. 457-467, pl. 40.

Hammon, W. M., Reeves, W. C., Brookman, B., Izumi, E. M., and Gjullin, C. M.
1941. Isolation of the viruses of western equine and St. Louis encephalitis from Culex tarsalis mosquitoes. Science, vol. 94, pp. 328-330.

Herms, W. B.
1939. Medical entomology. 3d ed., 582 pp. 196 figs. New York.

Hertig, M.
1942. Phlebotomus and Carrion's disease. Amer. Journ. Trop. Med., vol. 22, No. 5, suppl., 80 pp., 9 pls.

Imms, A. D.
1942. On Braula coeca Nitzsch and its affinities. Parasitology, vol. 34, pp. 88-100, 8 figs.

Jobling, B.
1926. A comparative study of the structure of the head and mouth parts in the Hippoboscidae (Diptera Pupipara). Parasitology, vol. 18, pp. 319-349, pls. 11-15, 4 text figs.
1928. The structure of the head and mouth parts in Culicoides pulicaris L. (Diptera Nematocera). Bull. Ent. Res., vol. 18, pp. 211-236, pls. 9-12, 10 text figs.
1928a. The structure of the head and mouth parts in the Nycteribiidae (Diptera Pupipara). Parasitology, vol. 20, pp. 254-272, pls. 14-16, 4 text figs.
1929. A comparative study of the structure of the head and mouth parts in the Streblidae (Diptera Pupipara). Parasitology, vol. 21, pp. 417-445, pls. 18-20, 6 text figs.
1930. A revision of the genus Ramondia Frauenfeld (Diptera Pupipara, Streblidae). Parasitology, vol. 22, pp. 283-301, 10 figs.
1933. A revision of the structure of the head, mouth-parts and salivary glands of Glossina palpalis Rob.-Desv. Parasitology, vol. 24, pp. 449-490, pls. 18-22, 11 text figs.

Krafchick, B.
1942. The mouthparts of blackflies with special reference to Eusimulium lascivum Twinn. Ann. Ent. Soc. Amer., vol. 35, pp. 426-434, 2 pls.

MacArthur, W. P.
1942. Medical diseases in tropical and sub-tropical areas. 282 pp., 108 figs. 6th British ed., London; 1st American ed., Brooklyn.

Matheson, R.
1932. Medical entomology. 489 pp., 211 figs. Springfield and Baltimore.

Nuttall, G. H. F., and Shipley, A. E.
1901-3. Studies in relation to malaria. II. The structure and biology of Anopheles. Journ. Hyg., vol. 1, pp. 45-74, 269-276, 451-483, pls. 1-2, 8-10; vol. 2, pp. 58-84; vol. 3, pp. 166-201, pls. 6-9.

Patton, W. S., and Cragg, F. W.
1913. A text book of medical entomology. 764 pp., 89 pls. London, Madras, and Calcutta.

Patton, W. S., and Evans, A. M.
1929. Insects, ticks, mites and venomous animals of medical and veterinary importance, 786 pp., 60 pls., 374 text figs. Croydon, England.

Peterson, A.
1916. The head-capsule and the mouth parts of Diptera. Illinois Biol. Monogr., vol. 3, No. 2, 112 pp., 25 pls.
Pierce, W. D.
1921. Sanitary entomology. 518 pp., 88 figs. Boston.
Riley, W. A., and Johannsen, O. A.
1938. Medical entomology. 2d ed., 483 pp., 184 figs. New York and London.
Robinson, G. G.
1939. The mouth parts and their function in the female mosquito, Anopheles maculipennis. Parasitology, vol. 31, pp. 212-242, 9 figs.
Senior-White, R.
1923. A note on pseudo-tracheal teeth in the 'eye-fly' (Siphunculina funicola, de Meijère). Indian Journ. Med. Res., vol. 10, pp. 825-826, pl. 61.
Smart, J.
1935. The internal anatomy of the black-fly Simulium ornatum. Ann. Trop. Med. Parasitol., vol. 29, pp. 160-170, 12 figs.
Southwell, T., and Kirshner, A.
1938. On the transmission of leishmaniasis. Ann. Trop. Med. Parasitol., vol. 32, pp. 95-102.
Speiser, P.
1900. Ueber die Strebliden, Fledermausparasiten aus der Gruppe der pupiparen Dipteren. Archiv Naturg., Jahrg. 66, Bd. 1, pp. 31-70, pls. 3, 4.
Stephens, J. W. W., and Newstead, R.
1907. The anatomy of the proboscis of biting flies. Pt. 2. Stomoxys. Ann. Trop. Med. Parasitol., vol. 1, pp. 171-198, pls. 12-19.
Thompson, M. T.
1905. Alimentary canal of the mosquito. Proc. Boston Soc. Nat. Hist., vol. 32, pp. 145-202, pls. 13-17.
Vogel, R.
1921. Kritische und ergänzende Mitteilungen zur Anatomie des Stechapparats der Culiciden und Tabaniden. Zool. Jahrb., Anat., vol. 42, pp. 259-282, pl. 15, 10 text figs.
Weber, H.
1933. Lehrbuch der Entomologie. 726 pp., 555 figs. Jena.
Whitfield, F. G. S.
1925. The relation between the feeding-habits and the structure of the mouth-parts in the Asilidae (Diptera). Proc. Zool. Soc. London, vol. for 1925, pp. 599-638, 2 pls., 15 text figs.