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AND SUCKING INSECTS AFFECTING
MAN AND ANIMALS

BY

R. E. SNODGRASS

Bureau of Entomology and Plant Quarantine
Agricultural Research Administration
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INTRODUCTION

The insects that entomologists understand by the term "biting insects" are those that obtain their food with a pair of jaws working against each other. These insects, mostly plant feeders, seldom molest us or attack animals, other than small invertebrates, for their flesh or blood. On the other hand, the insects that most people regard as "biters" are such as the mosquitoes, the bed bugs, the lice, and the fleas. These insects, however, attack their victims with a single point, or a group of stylets working side by side driven into the skin, and hence by professional entomologists are termed "piercing insects." The verbal distinction between the two groups thus depends on our definition of "biting," but after all there is no great difference whether a wound is made by two opposing points, a single point, or a pair of sliding points; if it is made with feeding organs (not a sting) it is essentially a bite, and undoubtedly the bitten public will continue to speak of "mosquito bites" and "flea bites," though some of the others may not be mentioned so freely. The essential difference between the insects of the two groups is not a question whether they "bite" or "pierce," but is in the nature of their food and the way they get it into the mouth. Most insects with jaws feed on solid food, which they bite off, chew, and swallow; the piercing insects feed on liquids, either the juices of plants or the blood of animals, and are provided with puncturing instruments and a pumping apparatus. All sucking insects, however, are not piercing insects, for there are the butterflies, the moths, and most of the two-winged flies, which live on liquids but do not "bite" in any sense of the word. Furthermore, most biting-and-chewing insects are also sucking insects; the wasps and the bees, for example, have jaws for biting and a pump for sucking, and even the cockroach, a typical biting-and-chewing insect, is found to be also a sucking insect, and to suck with the same mechanism as do the piercing-and-sucking insects.

The fact that it is difficult to establish definitions in biology is one of the proofs that living things are interrelated, and, though it brings much grief to the classifiers, it adds much to the interest of anatomical investigation, since we can follow the evolution of organs by observing the stages of their development in different forms, and by noting the various lines of divergence along which they have evolved in adaptation to different kinds of uses. We must always be cautious, however, in drawing conclusions as to the relationships of the animals themselves based on a study of any one organ or functional group of organs. There can be no doubt that the possession of jaws for biting and chewing the food is a character of primitive insects, and

that the other types of feeding organs are specialized adaptations evolved from the feeding organs of biting-and-chewing ancestors. Hence, though we are here particularly concerned with piercing, bloodsucking species, which are potential disease vectors, it will greatly facilitate an understanding of such forms if we begin with the study of a biting-chewing-and-sucking insect, such as any one of our common household cockroaches.

For purposes of description things described must have names. Most well-known insect species have so-called common names, and all that are known have scientific names. Common names are not standardized; current scientific names are always subject to change by priority of some older name. The generic and specific names and their authors of all species described in this paper are those at present regarded as authentic by the specialists in taxonomy of the Division of Insect Identification, United States Bureau of Entomology and Plant Quarantine. The anatomical parts of insects also have names, and here again students find some confusion on comparing the work of different writers, but discrepancies in anatomical terminology are more likely to be the result of differences of interpretation or of identification of the parts described.

The reader of the present paper will find that the text ignores the probability of his having any previous knowledge of insect anatomy or anatomical nomenclature. Furthermore, considering the paper shortage, the opinions of others that do not appear to conform with the facts now known are given short notice or none at all, and no apology is offered for the many inconsistencies with former statements by the writer himself. Inconsistency is the natural result of wider information and better vision.

I. THE COCKROACH. ORDER ORTHOPTERA

The cockroach, because of its structure and physiology, is not limited to any particular way of living or of feeding; it is capable of existing in almost any kind of surroundings, and it makes little choice of food. In its anatomy the cockroach gives evidence in many ways of conforming more closely than do most other winged insects to the structure of primitive insects, and, in fact, it is one of the oldest of insect forms, its ancestors being among the earliest insects recorded in the fossil records of insect life of the past. All the other insects included in this paper will be seen to be specialized either in their mode of life or in their manner of taking food. Hence, a knowledge of the basic anatomy of the insect head and feeding organs as retained in the cockroach will elucidate the structure of other forms and lighten the work of description.

THE HEAD AND THE ORGANS OF INGESTION

The head of an insect bears the principal sensory organs, eyes and antennae, and the organs of ingestion. The intake of food is a relatively complex process with the insects, involving the cooperation of a whole group of structures associated externally with the mouth, no one of which has anything like the motility of the vertebrate jaw, or the versatility of the human tongue. Feeding, as done by the insects, is a mechanical process, performed by parts that individually have limited movements, but which, working together, accomplish results most efficiently.



FIG. 1.—The common house cockroach, *Blattella germanica* (L.), often called "waterbug" or "crotonbug," female (length 15 mm.). Order Orthoptera, family Blattidae. Note the position of the head when the insect is active, and the open space between the wing and the abdomen for the admission of air to the spiracles on the back beneath the wings.

General structure of the head and mouth parts.—Though the cockroach of illustrations usually has its head bent downward beneath the front of the thorax (fig. 2 A), this attitude is merely one of repose, and is naturally assumed by museum specimens. When the insect is active the neck is stretched out and the face turned vertically (fig. 1); during feeding, the head may be directed even forward almost in line with the axis of the body in order to bring the mouth parts into contact with the food. For descriptive purposes, therefore, it is best to orient the head in the vertical plane, and to call *anterior* and *posterior* the opposite directions of a line through the head perpendicular to the face.

A facial view of the head of a cockroach is shown at B of figure 2. 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 the insect 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 median point below the

vertex, and in most insects it is separated from the clypeus by a transverse groove, the *epistomal sulcus*. The last is to be identified in most cases by a pair of depressions or pits in its lateral parts; though the groove is absent in the cockroach, the depressions are present (*at, at*), and serve as important landmarks. Behind the clypeus and the labrum are the external feeding organs, which, together with the labrum, are known collectively as the *mouth parts*.

On the back of the head (fig. 2 D) is seen the large *neck foramen* (*For*), called also *foramen magnum* and *occipital foramen*, by which the cavity of the head is continuous with that of the neck. Below the foramen are suspended the two maxillae (*Mx*) and the median labium (*Lb*). In the lateral margins of the foramen are a pair of slitlike pits (*pt, pt*), which are the posterior roots of an internal framework of the head called the *tentorium*. The tentorium of the cockroach (C) is a thin plate with a large median perforation, lying transversely within the head where it is supported on four stalks which are invaginations of the cranial walls at the anterior pits above the mandibles (B, *at, at*) and the posterior pits (D, *pt, pt*) just noted. In other insects the tentorium takes on various shapes, but in general it serves to strengthen the lower part of the head and to give attachment to muscles. The cockroach has a relatively long and flexible neck (fig. 1), which gives the head much freedom of movement and allows it to be retracted beneath the front of the thorax (fig. 2 A). The movements of the head are made by muscles, but they are controlled by a pair of fulcral sclerites (*cvs*) in the sides of the neck, and it is by movements of these sclerites that the neck is "stretched" and the head extended.

The group of feeding organs known as the mouth parts includes the *labrum* (fig. 2 B, *Lm*), a pair of jawlike *mandibles* (*Md*), a pair of *maxillae* (D, *Mx*), a single posterior *labium* (*Lb*), and, enclosed by these parts, a median tonguelike organ called the *hypopharynx* (E, *Hphy*). The flattened, strongly toothed mandibles, shown detached at E of figure 2 (*Md, Md*), lie in a transverse plane immediately behind the clypeus and labrum. Behind the mandibles are the maxillae (D, E, *Mx*). Each maxilla has a large basal part that bears a five-segmented lateral *palpus* (E, *Plp*), and two terminal lobes, the *galea* (*Ga*) and the *lacinia* (*Lc*); the base is subdivided into a proximal *cardo* (D, E, *Cd*), and a main stalk, or *stipes* (*St*). The labium is best seen on the back of the head (D, *Lb*); its two basal plates, the *submentum* (*Smt*) and *mentum* (*Mt*), collectively the *postmentum*, lie in the rear wall of the head, but the inflected margins of the submentum partly overlap the cardines and stipites of the

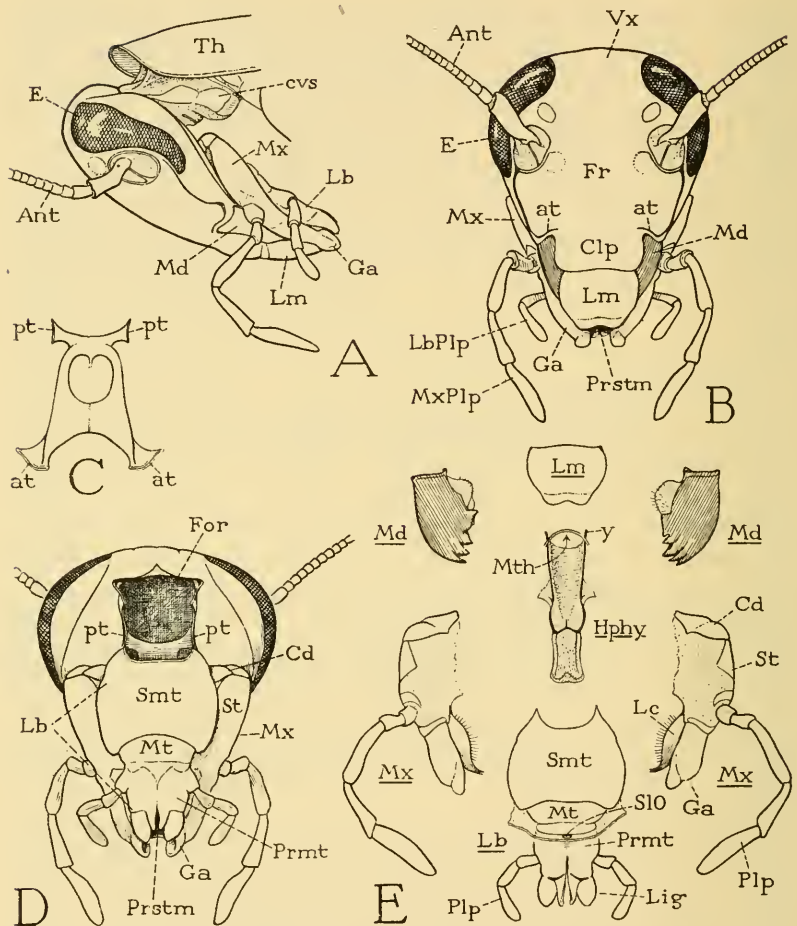


FIG. 2.—Head and mouth parts of a cockroach, *Blattella germanica* (L.).

A, lateral view of the head suspended by the neck on the body in position of repose. B, facial view of head. C, tentorium, dorsal surface. D, posterior view of head. E, the mouth parts separated from head and spread out in approximately relative positions, showing anterior surfaces.

Ant, antenna; *at*, anterior tentorial pit; *Cd*, cardo; *Clp*, clypeus; *cvs*, neck (cervical) sclerite; *E*, compound eye; *For*, neck foramen (foramen magnum, or occipital foramen); *Fr*, frontal region (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; *Prstm*, prementum; *pt*, posterior tentorial pit; *SIO*, orifice of salivary duct; *Smt*, submentum; *St*, stipes; *Th*, thorax; *Vx*, vertex; *y*, oral arm from base of hypopharynx.

maxillae. The distal part of the labium is a free posterior lip, the body of which is the *prementum* (D, E, *Prmt*); the appendicular parts are the lateral *palpi* (E, *Plp*), and four terminal lobes, the *glossae* in the middle and the *paraglossae* at the sides, which together constitute the *ligula* (*Lig*). The hypopharynx is a thick, elongate, tongue-like organ (E, *Hph*) arising at the base of the labial prementum, and extending anteriorly up to the mouth (*Mth*).

The mouth parts of the insect are appendages of the head surrounding the mouth, which latter lies in the ventral head wall between the inner surface of the clypeus and the base of the hypopharynx (fig. 7 A, *Mth*). The food is masticated or otherwise prepared for ingestion in the space enclosed by the mouth parts, but since this space lies entirely outside the true mouth it should not be called the "mouth cavity" or "buccal cavity"; more appropriately it may be termed the *preoral food cavity*. Furthermore since the aperture between the tips of the mouth parts is not anatomically the mouth of the insect, though it serves for the intake of food, it is better called the *prestomum* (figs. 2 B, D, 7 A, *Prstm*).

We may now attempt to understand how the cockroach feeds by the mechanism of its mouth parts. The mechanisms of an insect, however, cannot always be fully understood merely from a study of the joints between the movable parts and a determination of the muscle attachments; the elasticity of the skeleton itself is often an important factor, and may modify in a subtle manner the direct action of the muscles. The various thickenings and thinnings of the body-wall cuticle are generally found on close inspection to have some significance in relation to movements. The skeletal component of any movement, however, is elusive, and is likely to be inoperative in a dissected specimen. Hence we can get at best, by pulling on opposing muscles, only an approximate idea of how a mechanism works in the intact living insect, whose anatomy often seems inadequate for its performance. Again, however, in some cases it may be observed quite clearly that the antagonistic force of muscle contraction is skeletal elasticity, since various mechanical organs, especially sucking and pumping apparatus, are provided with only one muscle or a single group of muscles. The actions of an insect are almost purely mechanical because the parts of its skeleton are like the parts of a machine; whatever an insect does it must do always in the same way.

The labrum.—The labrum is a flat, hollow lobe of the head (fig. 2 B, *Lm*) flexibly suspended from the lower edge of the clypeus. Its outer surface is covered by a hard cuticle, its inner wall (fig. 5 A) is soft and mostly membranous except for two small sclerites at the

basal angles, known as the *tormae* (*tor*). The labral movements are small, though the labrum is provided with four strong muscles arising on the frontal area of the face. Two of these muscles (3) lie close together and are attached anteriorly on the base of the labrum; the other two (4) are attached laterally on arms of the *tormae*. The labrum is partly retractile beneath the flexible edge of the clypeus in order to expose the points of the mandibles, it can be lifted from the mandibles or closed against them, and it has slight lateral movements. All these labral movements are produced by the four frontal muscles according as the latter act together or as antagonists. The principal use of the labrum in feeding is to cover the mandibles so as to prevent the escape of food, and to form a closed passage over the hypopharynx for the intake of liquids.

The mandibles.—A typical, jawlike insect mandible (fig. 3 A) is somewhat conical in shape, triangular at the base, and usually more or less flattened distally. The lower, incisor end (*inc*) generally has several coarse teeth on its mesal edge, and on the same side near the base is a broad, variously developed molar area (*mol*) facing that of the opposite jaw. The mandible is attached to the head by a flexible articular membrane (*mb*) all around its base, but it is specifically hinged to the edge of the cranium by anterior and posterior points of articulation (*c*, *a*) near the outer side of its base. These hinges are external to the articular membrane, and are of the ball-and-socket type, but the parts are reversed in the two, the condyle being on the cranium in the anterior articulation and on the mandible in the posterior. An insect jaw of this kind swings in a transverse plane on its anteroposterior axis (*c-a*). Its principal muscles are a relatively slender *abductor* (*ab*) attached laterally close to the mandible (*d*), and a large *adductor* (*ad*) attached mesally (*e*). The power of the adductor muscle is increased by the length of its leverage (*b-e*) mesad of the mandibular axis.

The mandibles of the cockroach (fig. 3 B-H) are of the type of structure described above. The dentition is asymmetrical on the two jaws (B, C), and the molar areas are relatively small (B, H, *mol*). Arising anteriorly from the mesal angle of the base of each mandible is a small membranous flap (*f*). In the cockroach and most other orthopteroid insects (except grasshoppers) each mandible has *four* muscles. The huge cranial adductor of the cockroach arises in several bundles of fibers on the dorsal wall of the head (fig. 3 D, 28) and is attached by a large flat tendon (*t*) on the mesal angle of the mandible. The much smaller abductor (27) arises on the side of the head and its slender tendon is attached in the articular membrane

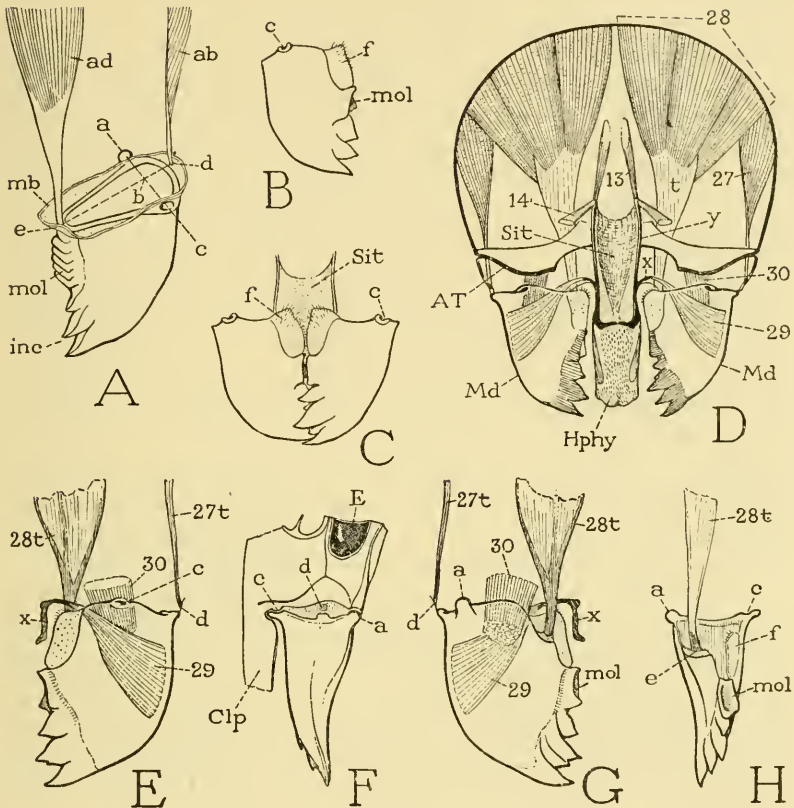


FIG. 3.—The mandibles of a cockroach.

A, diagram of the structure and mechanism of an insect mandible that serves as a biting and chewing jaw, movable in a transverse plane on the axis (*a-c*) by an abductor (*ab*) and an adductor muscle (*ad*). B, right mandible of *Blattella germanica* (L.), anterior. C, mandibles of same in closed position, anterior. D, diagrammatic cross section, anterior view, of head of a cockroach, showing mandibles, their musculature, and relation to hypopharynx. E-H, left mandible of *Blatta orientalis* L., anterior, lateral, posterior, and mesal views, respectively.

a, posterior articular condyle of mandible; *ab*, abductor muscle; *a-c*, axis of mandibular movement; *ad*, adductor muscle; *AT*, anterior tentorial arm; *c*, anterior articular socket of mandible; *Clp*, clypeus; *d*, attachment of tendon of abductor muscle; *e*, attachment of tendon of adductor muscle; *E*, compound eye; *f*, membranous flap on base of mandible; *Hphy*, hypopharynx; *inc*, incisor lobe of mandible; *mb*, articular membrane; *Md*, mandible; *mol*, molar lobe of mandible; *Sit*, sitophore (food receptacle on base of hypopharynx); *t*, muscle tendon; *x*, mandibular arm of hypopharyngeal suspensorium; *y*, oral arm of same.

Muscles.—13, frontal producer of hypopharynx; 14, frontal reducer of hypopharynx; 27, cranial abductor of mandible; 28, cranial adductor of mandible; 29, hypopharyngeal muscle of mandible; 30, tentorial muscle of mandible.

laterad of the mandibular base (E, F, *d*). (It should be noted that insect tendons are ingrowths of the body wall, not parts of the muscle tissue.) The third muscle of the cockroach mandible is a fan-shaped group of fibers arising inside the mandible on the lateral wall (D, E, G, 29), and converging mesally out of the base of the jaw to a small arm (*x*) from the side of the hypopharynx. The action of the hypopharyngeal muscles of the mandibles in the cockroach, whether they adduct the mandibles or widen the base of the hypopharynx, is not clear, but the muscles themselves are persisting remnants of powerful ventral adductors of the jaws present in most other arthropods. In some of the piercing and sucking insects these muscles are converted into protractors of the mandibles. The fourth muscle of the cockroach mandible (D, E, G, 30) is a short bundle of fibers arising on the anterior arm of the tentorium (D, *AT*) and attached inside the mandible on the posterior wall. Since the mandibular articulations are merely loose points of contact between the skeletal parts, and hence allow a slight anteroposterior movement of the jaw, the tentorial muscles of the mandibles probably have something to do with the grinding action of the opposed molar surfaces.

The mandibles lie in a transverse plane within the preoral food cavity between the labrum and the hypopharynx, with their points well back from the distal margin of the labrum except when the latter is retracted. When the two jaws are closed so that the molar surfaces are in contact (fig. 3 C), the teeth of the left mandible overlap anteriorly those of the right, and the two basal flaps (*f*) project mesally over the food trough (sitophore, *Sit*) on the base of the hypopharynx.

The maxillae.—The maxillae lie against the back of the head (fig. 2 D, *Mx*), but their relation to the other mouth parts is best seen in side view (A), showing the inclusion of the terminal lobes between the labrum and the labium. The cardo and stipes of each maxilla lie in a membranous fold of the head wall (fig. 4 A, *mb*), which is concealed posteriorly (fig. 2 D) by the projecting edge of the labial submentum. Each appendage, however, is attached to the cranium by a single point of articulation on the base of the cardo (fig. 4 A, *a*), and the cardo and stipes are hinged to each other in an elbowlike angle projecting laterally. By reason of the amplitude of the membrane uniting the maxilla to the head, the maxilla as a whole is freely movable on the head at the cardinal articulation, and the cardo and stipes are movable on each other at the elbow hinge between them. The palpus (*Plp*) arises laterally from the distal part of the stipes, and mesad to it are the galea (*Ga*) and lacinia (*Lc*). The galea

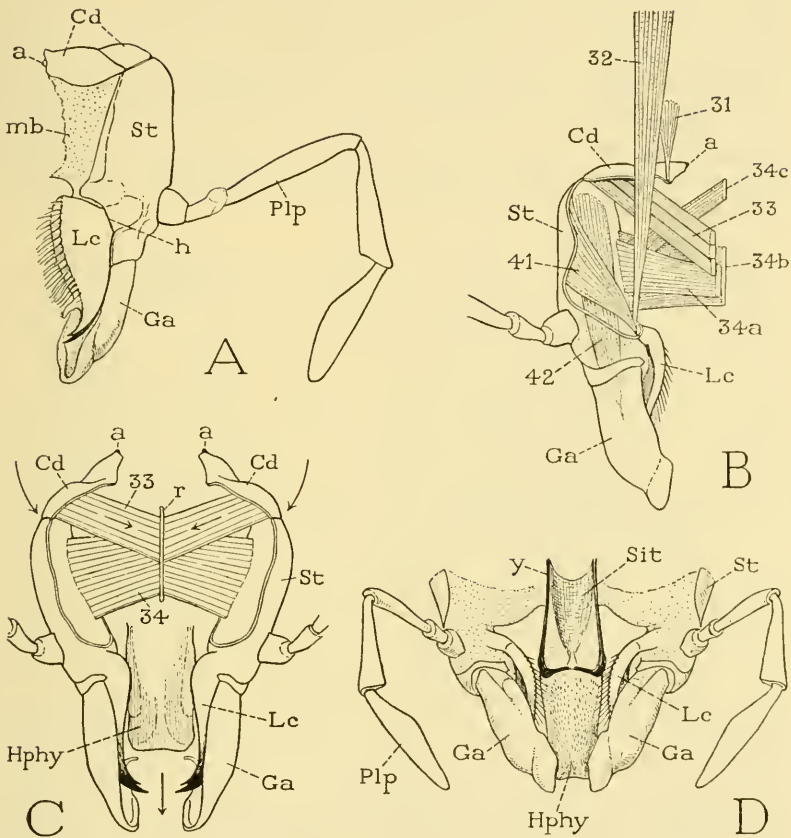


FIG. 4.—The maxillae of a cockroach.

A, right maxilla of *Periplaneta americana* (L.), posterior surface. B, same, anterior view, showing muscles, except those of the palpus. C, diagram of protractor-adductor mechanism of the maxillae: contraction of the cardinal muscles (33) turns the cardines (*Cd*) downward on their cranial articulations (*a*) and thereby protracts the galeae and laciniae (*Ga*, *Lc*) beyond the hypopharynx; a contraction of the adductor muscles (34) brings these lobes together. D, position of maxillary lobes in retraction against sides of hypopharynx.

a, articulation of cardo on head; *Cd*, cardo; *Ga*, galea; *h*, hinge of lacinia on stipes; *Hphy*, hypopharynx; *Lc*, lacinia; *mb*, articular membrane; *Plp*, palpus; *r*, median ventral ridge of tentorium; *Sit*, sitophore; *St*, stipes; *y*, oral arm of hypopharyngeal suspensorium.

Muscles.—31, rotator of cardo; 32, retractor of maxilla; 33, adductors of cardo, protractors of maxilla; 34, adductors of stipes; 41, producer of lacinia; 42, reductor of galea.

is a relatively soft, thick lobe with a hoodlike apical pad hollowed on its mesal surface. The lacinia is a rigid flattened lobe tapering distally and ending with two sharp, incurved teeth, proximal to which is a weak subapical projection. Though the galea is lateral and the lacinia mesal, the galea overlies anteriorly most of the lacinia and conceals the teeth of the latter in the hoodlike concavity of its apical pad. The opposite pairs of maxillary lobes lie close against the sides of the hypopharynx (D), between the labrum in front and the labium behind (fig. 2 A).

When the maxillae are in action they make rapid back-and-forth movements along the sides of the hypopharynx, accompanied by an adduction of the terminal lobes during protraction. The movements of the two appendages are simultaneous, in the same direction, and are never perceptibly varied; they are produced by retractor, protractor, and adductor muscles. Each maxilla has a single, long retractor muscle (fig. 4 B, 32) arising on the top of the head and inserted on the maxilla at the base of the lacinia. The protractors are three parallel bundles of fibers (33) going from the under surface of the tentorium to the lateral part of the cardo. The adductors (34a, 34b, 34c) arise also on the tentorium but are inserted on the mesal border of the stipes. When the maxillae are not active they are held in the retracted position with the galeae and laciniae close against the sides of the hypopharynx (D). Protraction results from the contraction of the cardinal muscles (C, 33), which turns the cardines downward on their cranial articulations (a), flattens the cardino-stipital angles, pushes the stipites ventrally, and protracts the galeae and laciniae well beyond the hypopharynx. The action of the stipital adductors (34) at the same time brings the free ends of the lobes together, or against any object grasped between them. The movements of the maxillae are exactly comparable to the extension and retraction of the human arms by bending the elbows and bringing the hands together with each outward thrust; if the palms are cupped to represent the galeal pads the imitation is complete, except for the absence of the lacinial points.

The lacinia and the galea have each a single muscle arising in the stipes (fig. 4 B, 41, 42), but these muscles serve merely to keep the two lobes in close apposition, neither lobe having any adductor movement. The lacinia has a firm hinge line on the stipes (A, h) that allows it to close against the galea, but prevents the toothed lacinial point from being turned mesally. Each pair of lobes thus forms a functional unit opposed to the pair of the other side, and their movements are always the same regardless of the inciting stimulus.

Yet the maxillary lobes are put to various uses; in addition to their function in feeding they are used for cleaning the antennae, the palps, and the front legs. An antenna is grasped near its base between the tips of the galeae and slowly drawn upward while the galeal pads, without losing their hold, work rapidly back and forth against it. The point of a needle or anything else placed between the lobes elicits the same response. In feeding, the action is no different, but now the hollowed galeal pads, armed with the lacinial teeth, serve

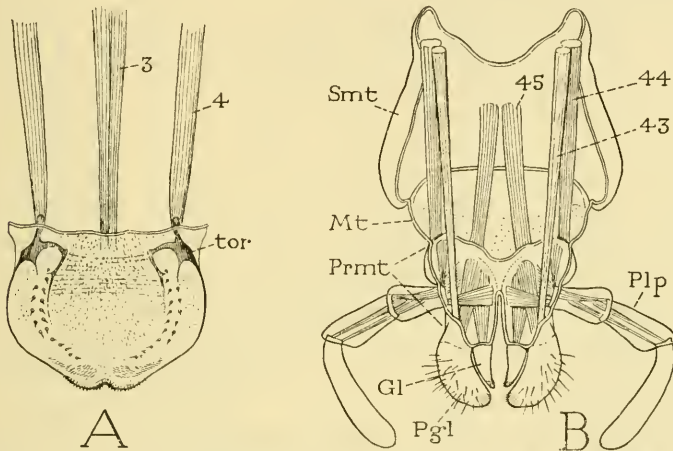


FIG. 5.—The labrum and the labium of a cockroach, *Periplaneta americana* (L.).

A, labrum and its frontal muscles, posterior surface. B, labium, anterior view, showing muscles.

Gl, glossa; *Mt*, mentum; *Pgl*, paraglossa; *Plp*, palpus; *Prmt*, prementum; *Smt*, submentum; *tor*, torus.

Muscles.—3, anterior frontal muscle of labrum; 4, posterior frontal muscle of labrum; 43, tentorial producer of labium; 44, tentorial retractor of labium; 45, retractor of prementum.

as scrapers for collecting particles of food and for drawing them back into the prestomum, where the food mass is taken over by the mandibles. The mandibles also may independently bite off pieces of food, but the main supply appears to be that brought in by the activity of the maxillary lobes. During the intake of water there is little movement of any of the mouth parts.

The labium.—The two basal plates of the labium, the mentum and submentum, as already noted, are immovably affixed to the back of the head below the neck foramen (fig. 2 D, *Mt*, *Smt*). Only the distal part of the labium, or prementum (*Prmt*), suspended from the mentum is a free and movable appendage. The labial muscles, therefore, are attached on the prementum (fig. 5 B), and the prementum

alone contains the muscles of the palpi and the distal lobes. The motors of the prementum are two pairs of long muscles (43, 44) arising on the posterior part of the tentorium, one pair (43) inserted anteriorly at the bases of the paraglossae (*Pgl*), the other (44) posteriorly on the basal angles of the prementum. These muscles, therefore, are respectively productors and reductors of the prementum, though they may give it also slight lateral movements on the mentum. A third pair of premental muscles (45) arises on the submentum and inserts on the base of the prementum. These muscles serve to retract the prementum against the mentum, the distal part of the latter being membranous and flexible. The palpi, the glossae, and the paraglossae are all provided with muscles taking their origins in the prementum, as shown in the figure (5 B).

The prementum serves passively to close the preoral food cavity behind the maxillae and hypopharynx. Though it shows no conspicuous activity during feeding, the strength of its musculature suggests that whatever movements are made, either by the prementum as a whole or by the terminal lobes, are of importance. The palpi on the other hand are extremely active; like a pair of fingers they feel around in all directions, tap the food and make motions toward the lips, but they do not appear to be prehensile; probably their function is mainly sensory.

The hypopharynx.—The organ commonly known as the hypopharynx is functionally the tongue of the insect and more appropriately might be named *lingua* since its only relation to the pharynx is that (in common with the other members of the mouth parts) it is *below* the pharynx.

The hypopharynx of the cockroach (fig. 7 A, *Hphy*) has a long oblique base in the ventral wall of the head, sloping downward and backward from the mouth (*Mth*) to the base of the prementum (*Prmt*). Only the distal part of the organ thus forms a free, tongue-like lobe. In the lateral and posterior walls of this lobe are two pairs of elongate lingual sclerites (fig. 6 A, B, *ls*), which in *Blatta* (D) are united proximally. The lateral sclerites, or the common bases of the two on each side, turn backward at their proximal ends and join from opposite sides in an arc (B, C, D, *f*) that rests on the base of the prementum and forms a *fulcrum* for the movement of the hypopharynx (C). Within the fulcral arc is the aperture of the salivary duct (D, *SIO*).

That part of the anterior hypopharyngeal wall that lies between the free lingual lobe and the mouth (fig. 6 A) is margined by a pair of linear sclerites (*HS*) that at their lower ends bend mesally in the

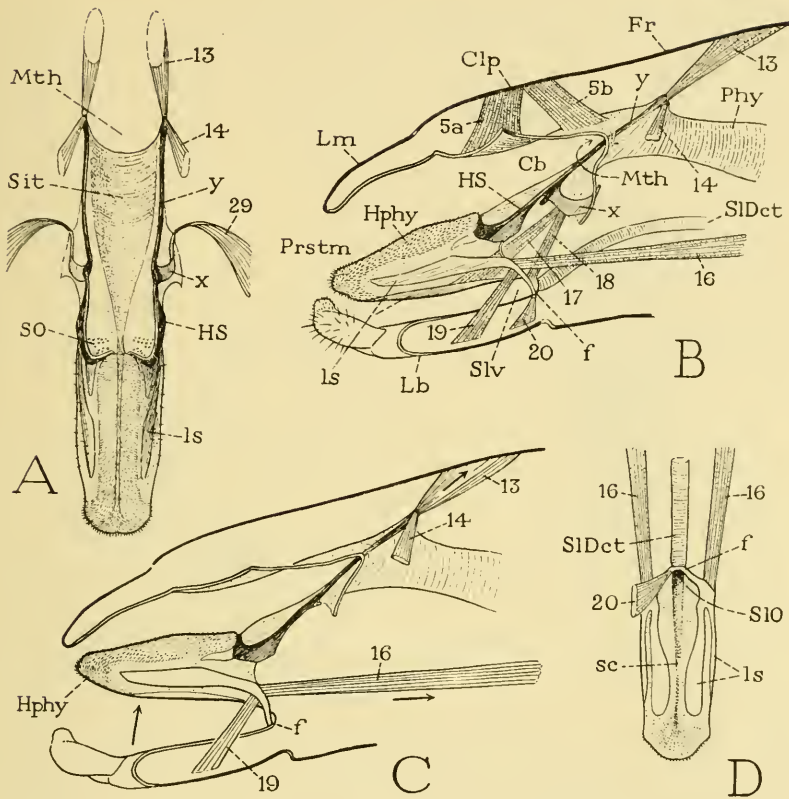


FIG. 6.—The hypopharynx of a cockroach.

A, hypopharynx of *Periplaneta americana* (L.), anterior surface, showing attachments of frontal and mandibular muscles. B, diagrammatic lengthwise section of lower part of head, showing position of hypopharynx in preoral cavity, with associated structures and muscles. C, diagram of productors of hypopharynx. D, posterior surface of free lingual lobe of the hypopharynx of *Blatta orientalis* L., with salivary orifice at its base.

Cb, cibarium; *Clp*, clypeus; *f*, fulcrum of hypopharynx; *Fr*, frons; *Hphy*, hypopharynx; *HS*, suspensorial sclerite of hypopharynx; *Lb*, labium; *Lm*, labrum; *ls*, lingual sclerite; *Mth*, mouth; *Phy*, pharynx; *Prstrn*, prestomum; *sc*, salivary canal; *Sit*, sitophore; *SIDet*, salivary duct; *SIO*, salivary orifice; *Slv*, salivarium; *SO*, sense organs; *x*, loral arm of hypopharyngeal suspensorium; *y*, oral arm of same.

Muscles.—*5a*, *5b*, clypeal dilators of cibarium; *13*, frontal producer of hypopharynx; *14*, frontal reductor of hypopharynx; *16*, tentorial producer of hypopharynx; *17*, *18*, hypopharyngeal muscles of salivarium; *19*, reductor of hypopharynx; *20*, labial muscle of hypopharyngeal fulcrum; *29*, hypopharyngeal muscle of mandible.

root of the lingua to form a U-shaped band, while their upper parts are continued as a pair of slender *oral arms* (*y*) that enter, and continue through, the mouth angles (B, C) to give attachment each to two muscles (13, 14) arising on the frontal area of the head wall. The hypopharynx thus appears to hang from the cranium by a long U-shaped *suspensorium*. Small lateral branches of the suspensorial sclerites (fig. 6 A, B, *x*) give attachment to the hypopharyngeal muscles (A, 29) of the mandibles (fig. 3 D, E, G). These branches may be termed the *loral arms* of the suspensory apparatus because they clearly represent the so-called *lora* in the head of Homoptera. Between the suspensory sclerites the surface of the hypopharynx is depressed in the form of a widening, troughlike channel (fig. 6 A, *Sit*) through which the food is conveyed to the mouth, and which, therefore, may be named the *sitophore*.

Associated with the hypopharynx of the cockroach are six pairs of muscles besides the hypopharyngeal muscles of the mandibles. Two pairs already mentioned are attached on the upper ends of the oral arms of the suspensory apparatus (fig. 6 A, B, 13, 14), one pair (13) arising medially on the frons in a direct line with the oral arms, the other pair arising laterally on the lower part of the frons. Attached on the proximal end of each lateral lingual sclerite is a long posterior muscle (B, 16) arising on the tentorium. This muscle is opposed by a shorter muscle (19) arising in the prementum. Two short muscles on each side (17, 18) take their origins on the loral arm (*x*) of the suspensory sclerite; one (17) goes to the posterior wall of the hypopharynx, the other (18) to the margin of the salivary orifice. Finally, a pair of very small muscles arising in the prementum (20) is inserted on the fulcral arc of the hypopharynx (D).

Though the musculature of the hypopharynx is somewhat complex, the movements of the organ are relatively simple. Since the median frontal muscles (fig. 6 B, C, 13) attached on the oral arms (*y*) of the suspensorium, and the tentorial muscles (16) attached on the lateral lingual sclerites both pull on the same (anterior) side of the hypopharyngeal fulcrum (*f*), it is evident that the two pairs are protractors inasmuch as their contraction swings the hypopharyngeal lobe forward (C). The labial muscles (19) of the lingual sclerites, and the lateral frontal muscles (14) of the oral arms are the reductors. The small labial muscles of the lingual arc (20) probably serve to hold the fulcrum in place. Muscles 17 and 18 are intra-hypopharyngeal; the first evidently expands the salivarium, the second dilates the salivary orifice.

The preoral food cavity.—The space enclosed by the peripheral mouth parts and containing the hypopharynx, as already noted, is not a true mouth cavity because it is not a part of the alimentary canal, and yet it is an important part of the feeding apparatus. Its

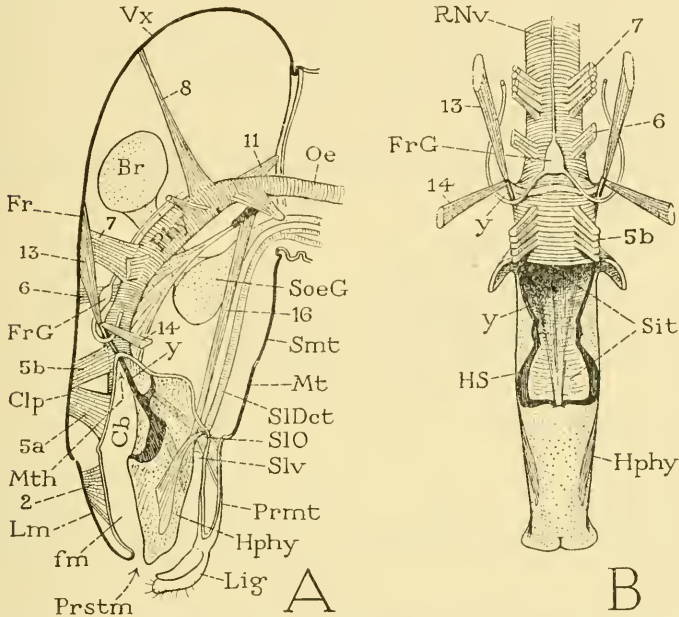


FIG. 7.—The preoral and the pharyngeal regions of the food tract of a cockroach.

A, vertical section of head somewhat to left of median plane, diagrammatic. B, hypopharynx and first part of pharynx, antero-dorsal view, showing attachment of muscles arising on anterior wall of head.

Br, brain; Cb, cibarium; Clp, clypeus; fm, food meatus; Fr, frons; FrG, frontal ganglion; Hphy, hypopharynx; HS, suspensorial sclerite of hypopharynx; Lig, ligula; Lm, labrum; Mt, mentum; Mth, mouth; Oe, oesophagus; Ph, pharynx; Prmt, prementum; Prstm, prestomum; RNv, recurrent nerve; Sit, sitophore; SIDct, salivary duct; SIO, salivary orifice; Slv, salivarium; Smt, submentum; SoeG, suboesophageal ganglion; Vx, vertex; x, loral arm of hypopharyngeal suspensorium; y, oral arm of same.

Muscles.—2, compressor of labrum; 5a, 5b, clypeal dilators of cibarium; 6, 7, precerebral dilators of pharynx; 8, postcerebral dorsal dilator of pharynx; 11, posterior lateral dilator of pharynx; 13, 14, muscles of oral arm (y) of hypopharyngeal suspensorium.

entrance, the prestomum (fig. 7 A, *Prstm*), leads first into a passage, the *food meatus* (*fm*), between the labrum and the lingual lobe of the hypopharynx. Within this passage the mandibles close upon each other during feeding. Proximal to the meatus, between the inner wall of the clypeus and the basal part of the hypopharynx, is a definite food pocket (figs. 6 B, 7 A, *Cb*) that receives the masticated food

material before delivery into the mouth (*Mth*). This pocket is the *cibarium*. The floor of the cibarium is the troughlike sitophore of the hypopharynx (figs. 6 A, 7 B, *Sit*); the roof is the inner wall of the clypeus. Thick bundles of intraclypeal muscle fibers (figs. 6 B, 7 A, 5a, 5b), which anatomically are compressors of the clypeus, at the same time serve to dilate the cibarium. The generalized cibarium of the cockroach contains the structural elements of the specialized sucking apparatus in the sucking insects. Similarly, between the base of the lingual lobe of the hypopharynx and the prementum of the labium is a posterior pocket, the *salivarium* (figs. 6 B, 7 A, *Slv*), into which discharges the salivary duct (*SIDct*). The salivarium, with muscles attached on it, is developed in many of the higher insects into a salivary ejection pump.

The mechanism of ingestion.—A lengthwise section through the middle of the head (fig. 7 A) will show the course that the food traverses in its passage from the prestomum (*Prstm*) to the true mouth (*Mth*) at the upper end of the hypopharynx. We have already seen how the food is taken into the prestomum by the action of the maxillary lobes and the mandibles. To reach the mouth it must go through the food meatus (*fm*) between the labrum and the free lobe of the hypopharynx, which is guarded laterally by the maxillary lobes (fig. 4 D), and is occupied by the mandibles. Here, if necessary, the food is cut, crushed, and masticated by the jaws, but in any case it appears to be the action of the mandibles that moves the food along and delivers it into the sitophore on the base of the hypopharynx. Probably the membranous flaps on the mandibular bases (fig. 3 C, f) help to push the comminuted food up toward the mouth. At this point, however, the sitophore acquires a sheet of transverse muscle fibers attached laterally on the suspensory arms, and the opposing clypeal surface is likewise covered with a layer of transverse fibers (fig. 7 B), which together would serve to constrict the cibarium. On the other hand, the cibarium is dilatable by the intraclypeal muscles (A, 5a, 5b) attached on its anterior wall, and by the lower fibers of a fan-shaped muscle from the tentorium attached on the sitophore. It is evident, therefore, that the food delivered from the mandibles into the cibarium is passed on into the mouth by muscular action of the cibarial walls, probably assisted by an adoral movement of the hypopharynx itself (fig. 6 C).

Sometimes the cockroach ingests bubbles of air. With the small *Blattella germanica* the bubbles can be seen through the semitransparent head wall passing rapidly and in close succession through the cibarium. No visible activity of any anatomical parts accompanies

the movement of the bubbles, but it is evident that some sucking mechanism carries them toward the mouth. If the base of the hypopharynx is pressed against the inner wall of the clypeus the concavity of the sitophore becomes a closed chamber, and the cibarium could now function as a *sucking pump* by the alternate action of the dilator and compressor muscles of its dorsal and ventral walls. Suction from the mouth would seem to be out of the question because there is no postoral pumping mechanism. With the same apparatus the roach imbibes water, but since the flow is continuous there is no visible evidence of the action of the cibarial pump. To find that the cibarium of a generalized biting-and-chewing insect such as the cockroach may

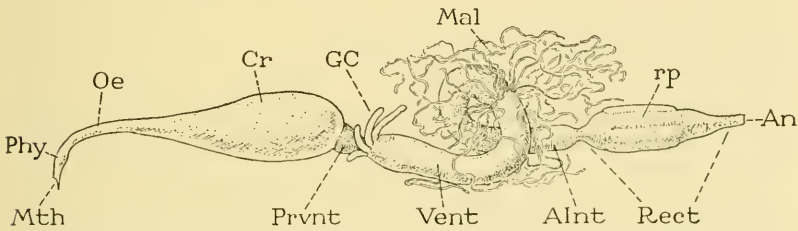


FIG. 8.—The alimentary canal of a cockroach, *Blattella germanica* (L.), left side.

Alnt, anterior intestine; *An*, anus; *Cr*, crop; *GC*, gastric caeca; *Mal*, Malpighian tubules; *Mth*, mouth; *Oe*, oesophagus; *Phy*, pharynx; *Prvnt*, proventriculus; *Rect*, rectum; *rp*, rectal pads; *Vent*, ventriculus (stomach).

function as a sucking organ is most interesting in that it shows there is no new function involved in the evolution of the sucking pump of the higher insects.

THE ALIMENTARY CANAL

The alimentary canal begins at the mouth between the upper ends of the suspensory arms of the hypopharynx (fig. 7 A, *Mth*). As it goes upward in the head between the two nerve ganglia it widens to form the *pharynx* (*Phy*), and then narrows as the *oesophagus* (*Oe*), which turns backward over the tentorium and goes through the neck foramen to enter the thorax. Here the canal enlarges into a baglike *crop*, or *ingluvies* (fig. 8, *Cr*), that extends into the abdomen and ends with an abrupt constriction separating it from a short *proventriculus* (*Prvnt*). The crop is a mere storage sack for the ingested food; its shape and size vary with the contents. The proventriculus, on the other hand, is a definite organ; it probably functions as a gizzard, since it has hard plates and teeth on its inner walls, but it also regulates the passage of the food to the next section of the

canal, which is the *stomach*, or *ventriculus* (*Vent*). The stomach is the principal seat of digestion and absorption; in the natural position in the cockroach it is looped more transversely than shown in the figure. Its anterior end bears on each side four fingerlike *gastric caeca* (*GC*). Following the stomach is the intestine, which extends to the anus (*An*), but is divided by a constriction into a looped anterior part, or *anterior intestine* (*Ant*), and a straight posterior part, the *rectum* (*Rect*). From the anterior end of the intestine are given off numerous long slender *Malpighian tubules* (*Mal*), many more than shown in the figure, that envelop this region of the alimentary canal in a dense mass of tangled threads. These tubules are excretory in function. The anterior part of the rectum shows externally six elongate opaque bands (*rp*) due to padlike thickenings of the inner wall (formerly known as "rectal glands").

The primary part of the alimentary canal as formed in the embryo is the ventriculus, termed midgut, or *mesenteron*; its cellular layer represents the endoderm of the insect. The anterior part including the proventriculus, and the intestine are secondary ingrowths of the ectodermal body wall, termed respectively the foregut, or *stomodaeum*, and the hindgut, or *proctodaeum*; each of these ectodermal sections has a chitinous intima. The part of the stomodaeum in the head of the cockroach must be given special attention in order to understand its modification in other insects.

The pharyngeal region of the stomodaeum is closely invested in a sheath of circular constrictor muscle fibers, and is provided with dilator muscles arising on the head wall and the tentorium. In the cockroach the dilator muscles fall into dorsal, lateral, and ventral sets (fig. 7). Of the dorsal dilators two pairs (*A*, *B*, δ , γ ,) are precerebral in position, and one pair (*A*, δ) is postcerebral. The lateral dilators include three consecutive muscles on each side, of which the last (*A*, *IX*) arises at the margin of the neck foramen. The ventral dilators are a group of fibers spreading downward from the tentorium as far as the floor of the upper part of the cibarium. It is important to note that the first dorsal dilators of the stomodaeum (*B*, δ) 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 thus often serves as a key to the anatomical relations of parts that may appear confused in the cibario-pharyngeal 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

head structures and feeding organs found in the piercing and sucking insects, and also in those that are purely suctorial.

II. THE BITING LICE AND BOOKLICE. ORDERS MALLOPHAGA AND CORRODENTIA

Of the numerous insects having mouth parts of the biting-and-chewing type, there is only one order, the Mallophaga, in which all the members habitually feed on vertebrate animals. Many others attack and devour their fellow insects, or other small invertebrates; such as these are said to be *predaceous*. The Mallophaga are called biting lice because they are louselike parasites of birds and mammals. The term "parasite" implies literally the taking of food (*sitos*) at the side of (*pará*) another. Parasites, in the original sense and usage of the word, were persons who fed regularly and gratuitously at the table of some rich patron. In zoology an animal that subsists on the food of another is called a *commensal* (from *mensa*, a table); a *parasite* is one that lives on the body of another living animal, called the *host*, and, instead of eating the host's food, attacks some part of the host himself. Some parasites are *external*, in that they live on the outside of the host, others are *internal* and feed on the blood or viscera of their victims. External parasites may be carriers, or *vectors*, of internal parasites, such as worms and microscopic disease-producing organisms. Besides the Mallophaga, there are a few other insects with the biting type of mouth parts that live on mammals. These include species related to the earwigs, Order Dermaptera, found on a bat and on African rats (fig. 9 E, F), and a small beetle (D) that inhabits the fur of the beaver.

The "biting" ascribed to the Mallophaga by the name "biting lice" refers to the ordinary manner of feeding by these insects and not to any wound they may inflict on the host, since with most species the food consists of feathers and hairs, though some are found to have an admixture of blood in their diet. Whatever their feeding habits may be, however, the Mallophaga are most annoying pests because of the irritation produced by their constant crawling and nibbling. Nearly all birds are infested by these lice, and domestic poultry and pigeons suffer particularly from them owing to the crowded conditions under which they live. Badly infested hens become nervous, their feeding is affected, and egg-laying reduced; death may result, particularly among young birds. On mammals Mallophaga are less widely distributed, but they occur on all domestic species, including cats and dogs. Man, apes, and bats, however, have no indigenous mallophagan parasites.

The Mallophaga are small, flattened, short-legged, wingless insects (fig. 9 A, B, C), the largest probably not over 10 mm. long, the smallest about a millimeter in length. They are classified in two

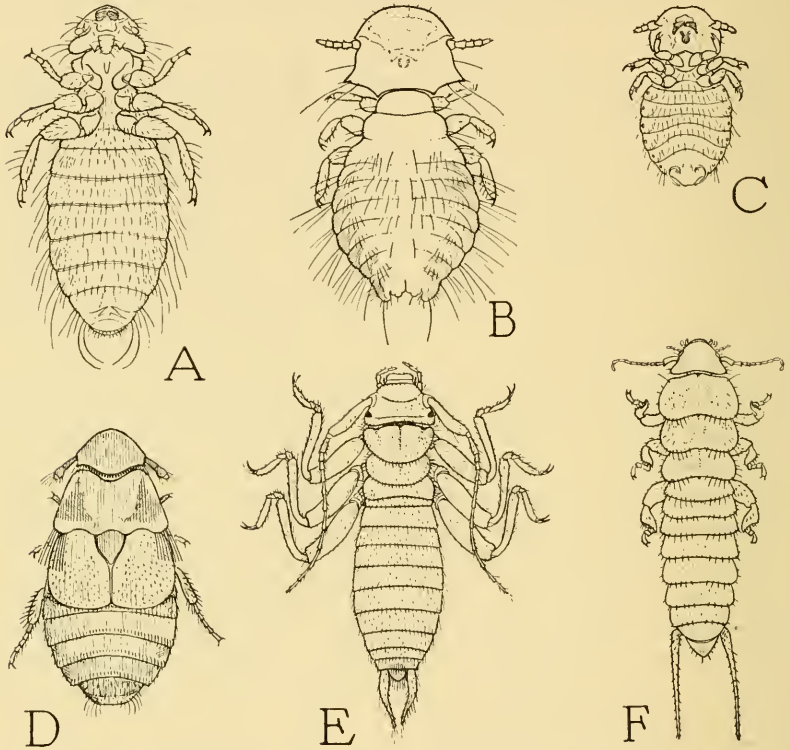


FIG. 9.—Examples of insects having the biting-and-chewing type of mouth parts that live on other animals, either as parasites or as scavengers.

A, a chicken body louse, *Menacanthus stramineus* (Nitz.), female, ventral (length a little more than 3 mm.), Mallophaga-Amblycera. B, the large chicken louse, *Goniocotes gigas* Tasch., female, dorsal (length $2\frac{3}{4}$ mm.), Mallophaga-Ischnocera. C, the dog louse, *Trichodectes canis* Deg., female, ventral (length $1\frac{3}{4}$ mm.), Mallophaga-Ischnocera. D, a beetle, *Platyssyllus castoris* Rits., that lives on beavers (length a little over 2 mm.). E, an insect related to earwigs, *Arixenia esau* Jordan, found on a bat (length 18 mm.) (from Jordan, 1909). F, another relative of the earwigs, *Hemimerus deceptus* Rehn, variety *ovatus* Deoras, that lives on African rats (length 12 mm.) (from Deoras, 1941).

suborders, the Amblycera and the Ischnocera. In the first group the short antennae are ordinarily concealed in grooves on the under surface of the head (figs. 9 A, 11 A), in the second the antennae project freely from the sides of the head (fig. 9 B, C). Other differences pertaining to the mouth parts will be noted later. While most of the species inhabit birds, each suborder contains a family of

mammal-infesting species, the Gyropidae in the Amblycera, the Trichodectidae in the Ischnocera.

The flattened head of the Mallophaga (fig. 11 A), which is relatively large for the body, is horizontal in position with the labrum (*Lm*) forward. The terms "dorsal" and "ventral," therefore, as applied to the mallophagan head, are equivalent respectively to "anterior" and "posterior" in the cockroach. The most conspicuous members of the mouth parts are the mandibles (*Md*); the maxillae and the labium are small and more or less imperfect, but the hypopharynx has some unusual features and is undoubtedly an important adjunct to the jaws. The feeding apparatus of the Mallophaga is difficult to study, and the structure of the mouth parts has been variously interpreted, even up to the present time. In the closely related order, the Corrodentia, known as booklice, however, the organs are more easily seen and their structure is better known. The mouth parts of the Mallophaga, therefore, will be better understood by an examination of the corresponding parts in a corrodentian.

The Corrodentia are called booklice because they are small soft insects seen most frequently perhaps in old books, but they live in many other places besides libraries. Sometimes they become pests by entering houses in great numbers, but they are not parasitic. The head of a corrodentian (fig. 10 A) sits vertically on the neck as in the cockroach. A prominent feature of the face is the large clypeus (*Clp*), below which is the labrum. The mouth parts have the same relative position as in the cockroach. The mandibles (*D*) are strong, toothed jaws. The maxillae present an unusual structure; each appendage (*G*) has a basal stalk, or stipes (*St*), bearing the palpus (*Plp*) and a soft galeal lobe (*Ga*), but the lacinia (*Lc*) is a long, slender rod toothed or forked at its apex and entirely free from the stipes except for protractor muscles (*pt*) arising on the latter. An opposing retractor muscle of the rod (*rt*) comes from the head wall. The laciniae are thus independently protractile and retractile. The labium has a broad base on the back of the head (*A*, *Lb*), which bears distally a pair of small palpi (*E*, *Plp*) and two median lobes (*Pgl*). From within the latter a membranous flap (*m*) curves back over the end of the hypopharynx.

The most characteristic features of the corrodentian mouth parts, which recur also in most of the Mallophaga, pertain to the hypopharynx. By spreading apart the outer mouth parts of a booklouse, the broad, thick hypopharynx is readily exposed, and on its posterior surface (fig. 10 F) are to be seen a pair of large, smooth, convex, ovoid sclerites (*ls*). An apodemal process (*ap*) on the base of each

sclerite gives attachment to a muscle arising on the laterodorsal wall of the head. These conspicuous ovoid sclerites of the Corrodentia very evidently correspond, therefore, with the lingual sclerites of the cockroach (fig. 6 B, D, *ls*). Yet for many years they have been called "lingual glands," and recently "salivary reservoirs," regardless of the fact that both Badonnel (1934) and Weber (1938) have shown conclusively that the plates in question are mere surface sclerotizations without a lumen, and that there is no glandular structure in the epithelium beneath them. The salivary glands of the Corrodentia open, as in the cockroach, into the pocket between the base of the hypopharynx and the base of the labium, somewhat on the hypopharyngeal surface of the pocket, but in no close relation to the lingual sclerites.

A second characteristic feature of the corrodentian hypopharynx, again present also in many Mallophaga, is a conspicuous cup-shaped sclerite on the anterior hypopharyngeal surface just before the mouth (fig. 10 B, *Sit*). Typically this sclerite has a pair of basal cornua (*y*) and a pair of distal arms (*a*), the size and shape of which are variable in different species. On the basal processes (*y*) are attached a pair of muscles arising on the frons, and on the sides of the sclerite a pair of muscles from the mandibles. The position and musculature of this preoral hypopharyngeal sclerite of Corrodentia and Mallophaga thus leave no doubt that the sclerite is a modification of the suspensory sclerites and sitophore of the cockroach hypopharynx (fig. 6 A, *Sit*). It may, therefore, be termed the *sitophore sclerite*. According to Weber (1936) it forms in Corrodentia the bowl of a "mortar-and-pestle" apparatus (C), the "pestle" being a small, hard, blunt process (*Pes*) of the clypeal wall of the preoral cavity operated by elasticity and a large group of muscle fibers (*5b*) arising on the outer wall of the clypeus. Weber suggests that the apparatus is used for crushing fungus filaments and spores on which the insects feed. The mortar and pestle of the Corrodentia is thus a special adaptation of the cibarium of the cockroach.

Finally it should be observed that the sitophore in both the Corrodentia and the Mallophaga is connected with the lingual sclerites by a branched filament (fig. 10 B, *cf*), the arms of which traverse the anterior surface of the hypopharynx, curve around the distal end, and attach on the lingual sclerites behind. It is the ductlike appearance of this filament that has given rise to the idea that the lingual sclerites are glands. The filament appears to be imbedded in the hypopharyngeal wall, but Armenante (1911), Badonnel (1934), and Weber (1938) all agree that it is merely a cuticular fiber and has no continuous lumen. If the filament were tubular it might be regarded

as a salivary conduit for the conveyance of saliva from the salivary pocket beneath the hypopharynx to the sitophore cup. Weber (1936) suggests that the purpose of the filament is to roll the hypopharynx

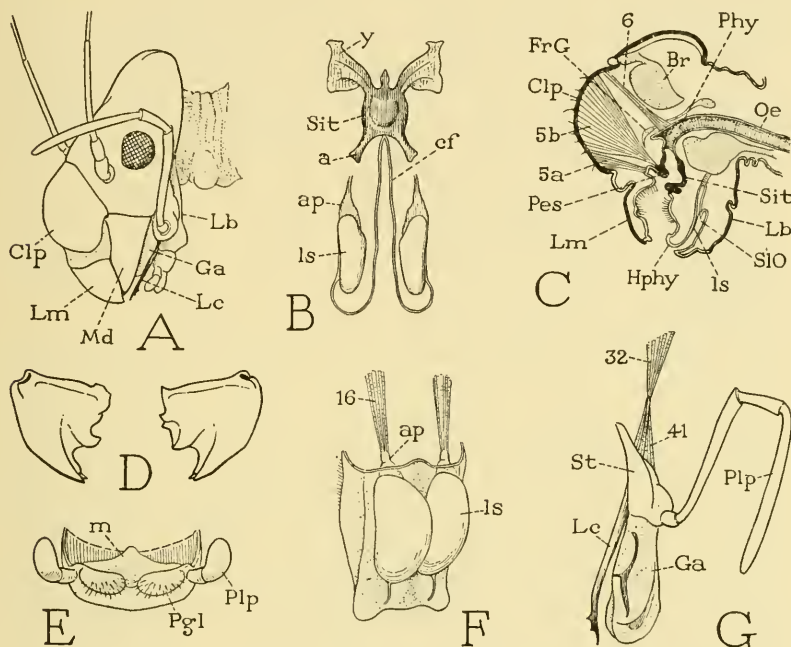


FIG. 10.—Head and feeding organs of booklice. Order Corrodentia.

A, head of *Speleketor flocki* Gurney, side view. B, hypopharyngeal sclerites of *Ectopsocus californicus* (Banks), ventral (hypopharynx itself not shown). C, median vertical section of head of *Ectopsocus briggsi* (McLachl.) (simplified from Weber, 1936, 1938). D, mandibles of *Troctes divinatorius* (Müll.), anterior. E, end view of labium of *Speleketor flocki* Gurney. F, posterior wall of hypopharynx of same, showing lingual sclerites and muscles, latero-posterior view. G, left maxilla of same, anterior.

a, distal arm of sitophore; ap, apodeme of lingual sclerite; cf, connecting filament; Clp, clypeus; FrG, frontal ganglion; Ga, galea; Hphy, hypopharynx; Lb, labium, Lc, lacinia; Lm, labrum; ls, lingual sclerite; m, ligular fold of labium; Md, mandible; Oe, oesophagus; Pes, pestle; Pgl, paraglossa; Phy, pharynx; Plp, palpus; Sit, sitophore (mortar); SIO, salivary orifice; St, stipes; y, oral arm of sitophore.

Muscles.—5a, 5b, clypeal muscles of cibarium (5b, retractor of pestle); 6, precerebral muscle of pharynx; 16, muscle of lingual sclerite; 32, retractor of lacinia; 41, protractor of lacinia.

toward the mouth when the sitophore sclerite, or "mortar," is retracted by its frontal muscles.

The food of most species of Corrodentia is said by Pearman (1928) to consist principally of the epiphytic green algae, *Pleurococci*, though some feed on microfungi, plant tissues, and even the dead bodies

and eggs of other insects. The food is gathered, according to Pearman's observations, with the mandibles; the lacinial forks are protruded against the feeding surface, and appear "to act as supporting props or levers during the vigorous grabbing bites with the mandibles," and they were not seen to be used in any other manner.

Returning now to the Mallophaga we find a striking resemblance in their mouth parts to those of the Corrodentia. The mallophagan mandibles have the typical biting type of structure (fig. 11 B); they are strongly toothed, and are hinged to the head by the usual ball-and-socket articulations. Their position relative to the head, however, differs characteristically in the two suborders. In the Amblycera the jaws lie in a plane parallel with the under surface of the head with their articulations dorsal and ventral; in the Ischnocera they hang vertically from anterior and posterior articulations.

The maxillae of the Ischnocera are simple lobes, usually serrate on their mesal margins, palpi being entirely absent. In the Amblycera the maxillae are better developed (fig. 11 C), each having a short, segmented palpus. Because of the close connections of the maxillae with the labium (D) some writers have regarded the palpi as labial organs, but a comparison with the Corrodentia leaves little question that the mallophagan palpi are maxillary. In a few species in both the Amblycera and the Ischnocera there is associated with each maxilla a slender rod (G), usually forked at its extremity, which freely projects mesad of the maxillary lobe (D). This rod exactly corresponds with the free, rodlike lacinia of the Corrodentia (fig. 10 G, *Lc*); it has the same retractor muscle (32) arising on the head wall, and protractor fibers (41) arising in the stipes. Among the Mallophaga, therefore, the lacinia has been lost in the majority of species, and the persisting maxillary lobe is the galea. The use of the "lacinial forks" is not known, but their position and musculature suggest that they serve as picks.

The labium of the Mallophaga is always a simple structure, consisting of a broad plate in the under wall of the head (fig. 11 A, D, *Lb*) bearing two or four small terminal lobes. The simplicity of the labium is in line with the simplification of the organ in the Corrodentia. The mallophagan labium can play only a passive role in feeding.

The hypopharynx has the same essential structure in the Mallophaga as in the Corrodentia. In most species a variously developed but typically cup-shaped sitophore sclerite lies in the dorsal surface just before the mouth; more distally on the ventral surface is a pair of ovoid sclerites (fig. 11 F, H); and, connecting the two, a forked filament (*cf*) runs forward from the sitophore, and its branches

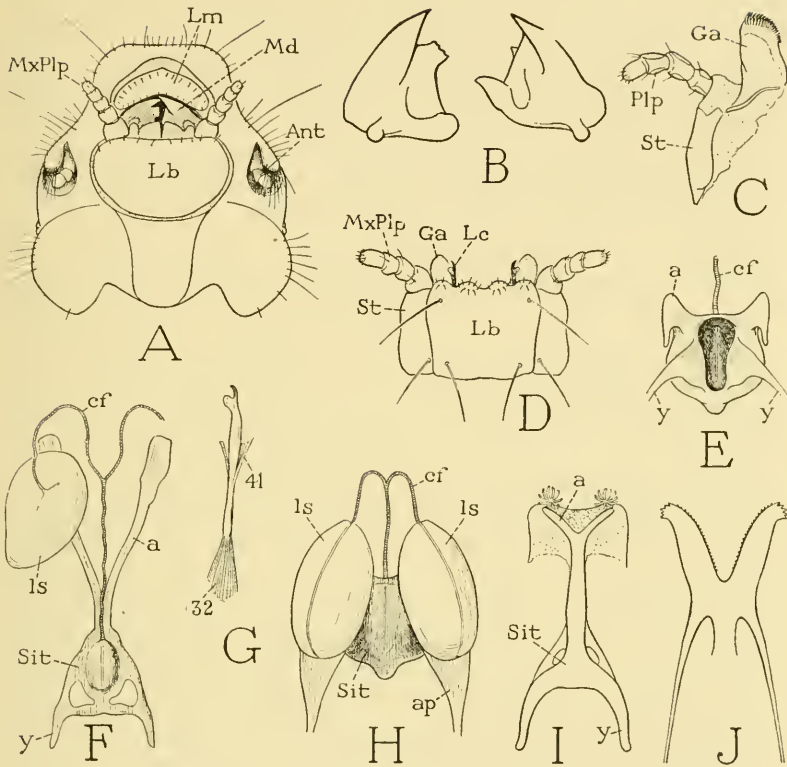


FIG. 11.—Head and mouth parts of biting lice. Order Mallophaga.

A, head of *Laemobothrion* sp., ventral. B, mandibles of same, ventral. C, maxilla of *Laemobothrion gypsis* Kellogg. D, labium and maxillae of *Ancistrona vagelli* (F.), ventral. E, sitophore sclerite on base of hypopharynx of *Docophoroides brevis* (Dufour), dorsal. F, hypopharyngeal sclerites of *Laemobothrion gypsis* Kellogg, ventral (hypopharynx itself not shown). G, maxillary fork (lacinia) of *Ancistrona vagelli* (F.). H, hypopharyngeal sclerites of *Docophoroides brevis* (Dufour), ventral. I, sitophore sclerite of hypopharynx of *Ancistrona vagelli* (F.). J, apical armature of hypopharynx of *Gliricola porcelli* (L.) (from Ewing, 1924).

a, distal arm of sitophore sclerite; Ant, antenna; ap, apodeme of lingual sclerite; cf, connecting filament; Ga, galea; Lb, labium; Lc, lacinia; Lm, labrum; ls, lingual sclerite; Md, mandible; MxPlp, maxillary palpus; Plp, palpus; Sit, sitophore; St, stipes; y, oral arm of sitophore.

Muscles.—32, retractor of lacinia; 41, protractor of lacinia.

curve over the end of the hypopharynx to unite with the lingual sclerites. The sitophore, when present, is usually to be seen in whole-mounted specimens as a dark object in the center of the head (fig. 9 B, C). In shape it varies from a simple thick-walled cup (fig. 11 E) with short anterior and posterior arms, to a more elaborate structure with long anterior arms (F). In the genus *Ancistrona* (I) the anterior arms are united basally in a long median stalk, from which the distal parts branch into the margin of the hypopharynx. Among the mammal-infesting Gyropidae, certain species of *Gliricola* have the distal end of the hypopharynx produced into a pair of flat lobes (fig. 11 J), serrate in some species, unarmed in others, which appear to be terminal branches of the sitophore sclerite. The ovoid lingual sclerites are more constant in shape than is the sitophore sclerite, but they appear to be always present in connection with the latter. Observations on the occurrence of the organs in different genera are given by Cummings (1913) and by Qadri (1936).

No convincing explanation of the function of the sitophore sclerite in the Mallophaga has yet been offered, and an opposing "pestle" such as that of the Corrodentia has not been observed in this order. Because of its shape the sclerite is termed the "lyriform organ" by Armenante (1911), but functionally he says it is an "isopogometer," meaning an instrument by which the mandibles are enabled to cut off equal lengths from the barb of a feather pushed back against the inner wall of the sitophore cup by the maxillae. Armenante's observations were made on *Menopon gallinae* L. (*pallidum* Nitz.) and an examination of the crop in a specimen of this species shows in fact that the barbs have been cut off at remarkably similar lengths; measurements give an average of about 308 microns, with but small variations either way. The distance from the base of the "meter" cup to the tips of the closed mandibles, however, is only 136 microns, and the incongruity can be seen in one of Armenante's own figures. The barbs in the crop are fully as long as the entire head, and must extend through the pharynx and well back into the oesophagus before they are cut by the jaws.

The food of the Mallophaga is principally feathers and hair, pieces of which, cut off by the mandibles, are stored in the crop, but no studies have been made on the process of digestion in the stomach. Certain species, however, have been observed to feed on blood or other exudations from abrasions of the skin. According to Ewing (1924) there is no evidence that *Gyropus ovalis* Nitz. or *Gliricola porcelli* (L.), parasitic on guinea pigs, feed on hairs. He says the second species may be seen to crawl down a hair until it comes to the

follicle, into which it appears to thrust the hypopharyngeal horns and to use them for abrading the skin, apparently to obtain oil from the follicle, and perhaps serum exuding from the wound. Finally, conclusive evidence has been given by Crutchfield and Hixson (1943) that two species of chicken body lice, *Menacanthus stramineus* Nitz. and *Menacanthus* sp., feed habitually on blood in addition to barbs and barbules of feathers. Nucleated red blood corpuscles were found in the crops of a majority of specimens examined, and made often a considerable part of the crop contents. The two species are said to "obtain blood by gnawing through the epidermis of the skin and rupturing the quill of pin feathers." The other species of chicken lice appear to feed entirely on feathers.

The alimentary canal of the Mallophaga presents two types of structure, according as the crop is a symmetrical enlargement of the oesophageal region (fig. 14 A, *Cr*), or a lateral diverticulum of the latter (B). The first condition is characteristic of the Amblycera, the second of the Ischnocera. In the ischnoceran Trichodectidae the crop has a narrow neck (C). The pieces of feathers or hairs swallowed by the insects are stored lengthwise in compact bundles in the crop, but no information is available on how they get from the crop into the stomach for digestion. The entire alimentary canal, except for the ischnoceran crop, is a simple tube. The Malpighian vessels (*Mal*) are always four in number, and there are six padlike bodies (*A, rp*) in the walls of the anterior end of the rectum.

The Mallophaga are not known to be vectors of diseases or internal parasites of birds, though *Rickettsia* bodies have been found in several mallophagan species, as well as in insects of most of the other orders. The dog louse, *Trichodectes canis* (Deg.) (fig. 9 C), however, is known to be a larval host of the common dog tapeworm, *Dipylidium caninum* (L.). The eggs of the worm, discharged with the feces of the dog and eaten by the louse, develop into larvae within the latter, and if an infested louse is then swallowed by the dog or another animal the larvae mature in the intestine of the host. The dog tapeworm sometimes occurs in man, especially in children, as a result of too intimate association with dogs.

The few other mammal-infesting insects that have the biting type of mouth parts may be given brief mention here because of their entomological interest, though they have no relation to the Mallophaga, nor are they of any economic importance. Of the two that belong to the earwig order Dermaptera, one, *Arixenia esau* Jordan (fig. 9 E), is known only from a few specimens taken from the breast pouch of an East Indian bat, the other is represented by a number of species

of the genus *Hemimerus* (fig. 9 F) found only on African rats of the genus *Cricetomys*. The feeding habits of *Arixenia* are not known. *Hemimerus* probably makes a diet of any eatable material it can obtain on the body of the rat; its mandibles are of the typical biting structure with sharp apical teeth. The minute beaver beetle, *Platypsyllus castoris* Rits. (fig. 9 D), occurs abundantly on beavers, but it cannot be regarded as a true parasite in the defined sense of the term, because its mandibles are so reduced in size and so far apart that they can have no function as biting jaws, and the small maxillae bear only a pair of thin lobes fringed with long hairs. It has been suggested that the beetles feed on mites that infest the beaver, but they are themselves scarcely larger than mites, and it is not clear how they could attack even a small mite with their weak mouth armature. Another and more plausible suggestion is that they feed on the oily secretion of the skin glands of the beaver. The larvae, on the other hand, said also to live on the beaver, have well-developed, sharp-pointed, overlapping mandibles. There are also beetles of the staphylinid genus *Amblyopinus* that live on marsupials and rodents in South and Central America, which are said to be "parasitic," but the nature of their food has not been determined.

III. THE ELEPHANT LOUSE

A remarkable louse found on elephants, *Haematomyzus elephantis* Piaget, has at present no abiding place in any of the recognized insect orders, nor has it been assigned an order of its own. It possesses many peculiar features that preclude its inclusion with the typical biting lice of the order Mallophaga, or with the typical sucking lice of the order Anoplura; it is a nonconformist louse that both bites and sucks, and bites in a most unusual manner.

The head of *Haematomyzus* (fig. 12 A) is extended anteriorly in a long, narrow beak, at the end of which are a pair of small mandibles and certain other structures that may be vestiges of the maxillae and labium. A detailed description of the external anatomy of the insect is given by Ferris (1931). The mandibular teeth are turned laterally (B) and the stronger movement of the jaws is outward. Ferris suggests that the beak is used to penetrate into the folds of the elephant's skin, where the mandibles cause lacerations that permit an exudation of blood, which is then sucked up through the beak. While *Haematomyzus* is thus in its own way a "biting" louse, its jaws have no resemblance to the mandibles of Mallophaga. That the insect is also a sucking louse is attested by the presence of a well-

developed pumping apparatus in its head, shown in a lengthwise section by Weber (1938a), whose figure is reproduced here (fig. 12 C) in simplified form. From the tip of the beak a long, slender, tubular food meatus (B, *fm*) leads back into the wide part of the head, where it enlarges into a bulbous chamber (C, *CbP*) provided with a huge bundle of dilator muscle fibers (5) arising on the clypeal region of the head wall. This chamber, therefore, clearly represents a conversion of the preoral cibarial pocket of the cockroach (fig. 7 A, *Cb*) into a sucking pump. Following it is a second pump (fig. 12 C,

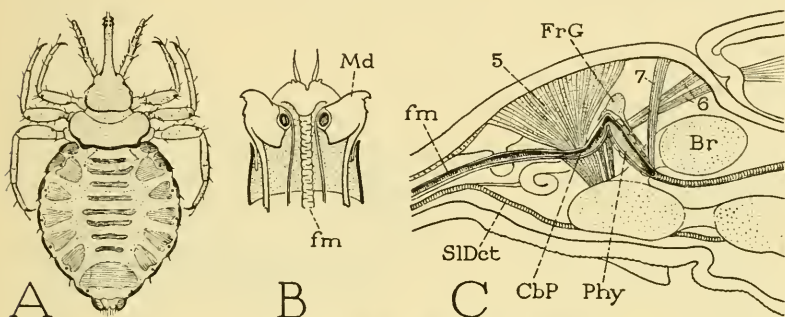


FIG. 12.—The elephant louse, *Haematomyzus elephantis* Piaget, its mandibles, and sucking apparatus.

A, whole insect, female (length 3 mm.), dorsal (redrawn from Ferris, 1931). B, end of proboscis, dorsal wall removed, showing mandibles and their tendons, with food meatus opening between them (from Ferris, 1931). C, median vertical section of head, showing sucking apparatus (simplified from Weber, 1938a).

Br, brain; *CbP*, cibarial pump; *fm*, food meatus; *FrG*, frontal ganglion; *Md*, mandible; *Phy*, pharynx; *SIDet*, salivary duct.

Muscles.—5, dilator of cibarial pump; 6, 7, precerebral dilators of pharynx.

Phy), which is the true pharynx, since its dilator muscles (6, 7) are separated from the cibarial dilators (5) by the frontal ganglion (*FrG*). *Haematomyzus*, therefore, is a mandibulate sucking louse. Its sucking apparatus is essentially identical with that of the piercing and sucking lice (fig. 13 D).

IV. THE SUCKING LICE. ORDER ANOPLURA

The lice of the order Anoplura are parasites of mammals only, including apes and man. Those that infest man are the human louse, *Pediculus humanus* L. (fig. 13 A), and the crab louse, *Phthirus pubis* (L.). The feeding apparatus of the Anoplura differs from that of the Mallophaga in three respects: first, the absence of functional mandibles; second, the presence of a group of piercing stylets; and third, the development of a highly efficient sucking mechanism. The

Anoplura are piercing-and-sucking lice, and feed entirely on blood. In their general appearance (fig. 13 A) they are readily distinguishable from the Mallophaga (fig. 9), but in details of structure, aside from the mouth parts, there are likenesses between the two orders.

The louse has a harmless appearance since no armature for inflicting a wound is ordinarily visible. The head is horizontal as in the Mallophaga (fig. 13 A); its bluntly conical anterior end is produced into a very small, snoutlike proboscis, probably formed of the labrum (D, *Lm*), in which is a terminal opening, the prestomum (*Prstm*), continued into a short slit on the ventral side. Through the under wall of the head, however, may be seen a bundle of minute rods almost as long as the head itself. These rods are the *piercing stylets* of the louse (D, *Stl*); they are protractile through the prestomum for at least half their length. The labrum is armed internally with small recurved teeth, and is eversible. When turned out (fig. 14 D), the teeth probably first secure a hold on the skin of the host, after which the stylets are inserted.

The prestomum opens into a spacious preoral cavity within the head (fig. 13 D), the upper part of which is directly continued into the chamber of the cibarial pump (*CbP*), while from the lower part there is extended a long sack (*Sac*) reaching almost to the rear end of the head, which contains the stylets (*Stl*). The stylets are usually said to be three in number, one dorsal in position (F, *dStl*), one ventral (*vStl*), and one intermediate (*iStl*), but there is a question as to whether the intermediate stylet may not be a part of the dorsal stylet. The stylets arise from the inner end of the ensheathing sack, and in the retracted position their tips lie just within the prestomum (D). The backward extension of the stylet sack beneath the mouth of the cibarial pump produces a transverse *suboral fold* (D, *sof*), the upper wall of which is the floor of the pump (*CbP*).

The stylets are extremely slender rods grouped in a fascicle that lies freely in the enclosing sack. They are forked at their bases (fig. 13 F), and the divergent arms are attached on the walls of conical ingrowths of the posterior end of the sheath. The dorsal stylet appears to be made of two united halves with the edges curved upward, and distally rolled over each other to form a tube (E, *dStl*). The tube thus formed is the food canal (*fc*). The ventral stylet is the effective piercing organ, and its apex is armed with small teeth (F, *vStl*); in cross section (E) it is seen to be channeled above and to embrace the other stylets. The intermediate stylet is extremely slender and contains the exit canal of the salivary duct (E, *sc*), which enters a bulbous enlargement of its base (F, *SIDct*). The form of the stylets

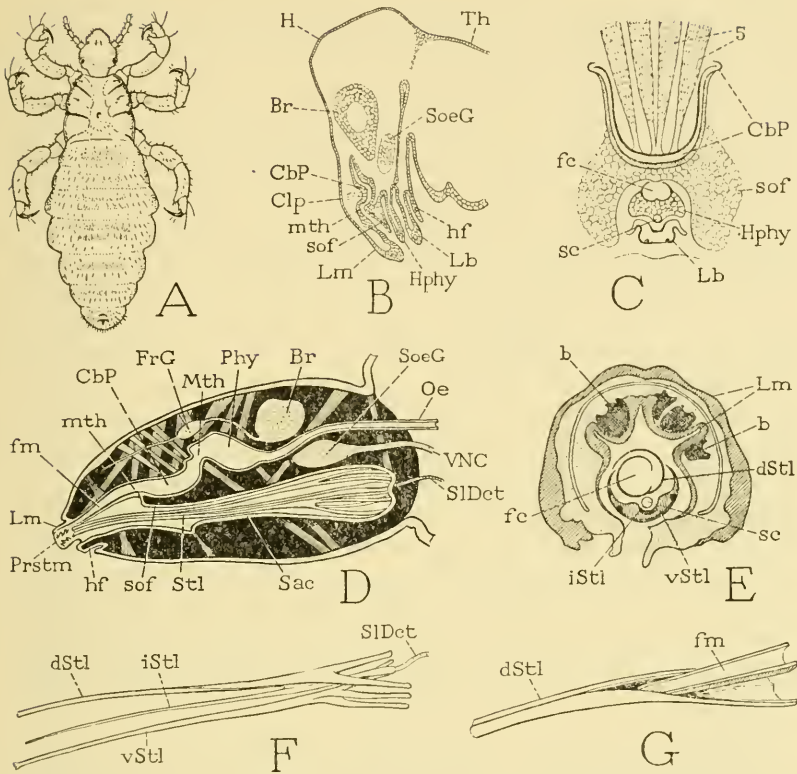


FIG. 13.—A sucking louse and its feeding organs. Order Anoplura.

A, the human louse, *Pediculus humanus* L., variety *corporis* Deg., adult male (length $2\frac{1}{2}$ mm.) (from Keilin and Nuttall, 1930). B, median vertical section of head of a late-stage embryo of *Haematopinus eurysternus* (Nitz.) (from Schölzel, 1937). C, cross section through sucking pump and stylets of embryo of same ready to emerge from egg (from Schölzel, 1937). D, diagrammatic median vertical section of louse head (combination from figures by Sikora, 1916, and others). E, cross section through labral proboscis and stylets of *Pediculus humanus* (from Vogel, 1921). F, diagram of stylets in relative position. G, diagram of probable relation of food meatus trough to dorsal stylet during feeding.

b, sclerites in inner wall of proboscis; *Br*, brain; *CbP*, cibarial pump; *Clp*, clypeus; *dStl*, dorsal stylet; *fc*, food canal of dorsal stylet; *fm*, food meatus; *FrG*, frontal ganglion; *H*, head; *hf*, hypostomal fold; *Hphy*, hypopharynx; *iStl*, intermediate stylet; *Lb*, labium; *Lm*, labrum; *mth*, mouth of sucking pump; *Mth*, true mouth, opening into pharynx; *Oe*, oesophagus; *Phy*, pharynx; *Prstm*, prestomum; *Sac*, sack containing the stylets; *sc*, salivary canal; *SIDct*, salivary duct; *SoeG*, suboesophageal ganglion; *sof*, suboral fold of hypopharynx; *Stl*, fascicle of stylets; *Th*, thorax; *VNC*, ventral nerve cord; *vStl*, ventral stylet.

Muscles.—5, dilators of cibarial pump.

probably differs in different species of lice, since descriptions by different writers are not entirely consistent. Protraction and retraction of the stylets is effected by muscles attached on their bases and on the walls of the enclosing sack.

The homology of the anopluran stylets with the mouth parts of biting insects has been a subject of dispute for many years. The mandibles of the sucking lice are generally conceded to be reduced to a pair of small plates buried in the walls of the preoral cavity. The dorsal stylet has been commonly regarded as the united maxillae, the intermediate stylet as the hypopharynx, the ventral stylet as the labium, and the embryological work of Fernando (1933) seemed to confirm this interpretation. More recently, however, Schölzel (1937) has reinvestigated the development of the mouth parts. He substantiates the claim that the ventral stylet is the labium, but he says that the maxillae as well as the mandibles are reduced, drawn aside, and merged into the lateral walls of the preoral cavity, and that the dorsal and intermediate stylets are both derived from the embryonic hypopharynx (fig. 13 B, C, *Hphy*). In an earlier paper, Peacock (1918) stated that the intermediate stylet in the adult of *Pediculus humanus* appears to be united with the dorsal stylet. Vogel (1921) says that the dorsal and intermediate stylets are united at their bases, but regards their distal parts as separate rods, though he observes that they are entirely "chitinous" without any cellular elements.

The interpretation of the anopluran stylets given by Schölzel seems most reasonable if we put any faith in the idea that the Anoplura are related to the Mallophaga. In the latter the maxillae are already much reduced and simplified, and it is not likely that they would form the important sucking tube of the Anoplura. On the other hand, since in any generalized insect the food passes over the hypopharynx on its way to the mouth, it would be only conformable with its function that the hypopharynx should form the food canal in a sucking louse. The salivary canal always pertains to the hypopharynx. Furthermore, however, it is clear that the suboral fold of the anopluran head (fig. 13 D, *sof*) must also be a part of the hypopharynx, since its dorsal wall is the floor of the cibarial pump (*CbP*), and therefore is specifically the sitophore of the cockroach.

The sucking apparatus of the louse consists of two pumps. The first is a cibarial pump (fig. 13 D, *CbP*), since it is formed by the cibarial pocket of the preoral cavity and its clypeal dilator muscles; the second is the pharynx (*Phy*). The identity of the two parts is attested by the position of the frontal ganglion (*FrG*) between the

respective sets of dorsal dilator muscles. The true mouth of the louse (*Mth*), corresponding with that of the cockroach (fig. 7 A, *Mth*), is the entrance to the pharynx; the mouth of the cibarial pump (fig. 13 D, *nth*) lies above the edge of the suboral fold (*sof*), the intake orifice to the preoral cavity is the prestomum (*Prstm*), and finally, the primary food aperture is at the apex of the dorsal stylet. The suction of the cibarial pump, therefore, must be exerted on the blood in the tubular part of the dorsal stylet, and to insure this action there is a closed passage, or food meatus (D, *fm*), from the prestomum to the mouth of the pump. The meatus is variously termed "haustellum," "buccal tube," and "pumping pharyngeal tube" by different writers. It is formed by two opposite folds with strongly sclerotized, overlapping mesal margins that extend along the lateral walls of the preoral cavity from the sides of the suboral fold to the prestomum. Together these folds make a trough closed over by the inner clypeal wall. Presumably during feeding the trough fits into the proximal end of the food canal of the dorsal stylet (G) just within the labral proboscis. In this way the blood is conveyed through a series of closed passages from the wound to the pharynx.

The salivary system of the Anoplura consists of two pairs of glands and their ducts lying in the thorax. The several ducts unite in the common duct of the head that enters the base of the intermediate stylet, through which the saliva may be conveyed into the puncture made by the ventral stylet. There appears to be in the Anoplura no mechanism for the forcible ejection of the saliva, such as is present in most other piercing insects. Three other glands are said to lie in the head and to open into the stylet sack; their secretion perhaps lubricates the stylets and probably serves also to hold them together in a fascicle during feeding.

The alimentary canal of the sucking lice (fig. 14 E) is simpler than that of the Mallophaga in that there is no crop, the oesophagus (*Oe*) being a slender tube from the pharynx to the stomach. On the other hand, as in Mallophaga, there are two gastric caeca, four Malpighian tubules, and six rectal pads.

The sucking lice, besides being highly undesirable parasites whose very presence may cause an unhealthy or diseased condition of the skin, are responsible for the spread of several human diseases. They have been shown to be capable of carrying the organisms of impetigo adhering to their legs or body hairs and to be infective when transferred from a diseased person to another. The human louse, *Pediculus humanus* L., may harbor within its body the agents of relapsing fever (*Spirochaeta recurrentis* Lebert), typhus fever (*Rickettsia*

proわざeki de Rocha-Lima), and trench fever (a virus or a *Rickettsia*?). Only the second is known to be transmitted from one person to another by the bite of the louse, but any one of the three diseases may be inoculated from lice crushed on the skin or under the fingernails.

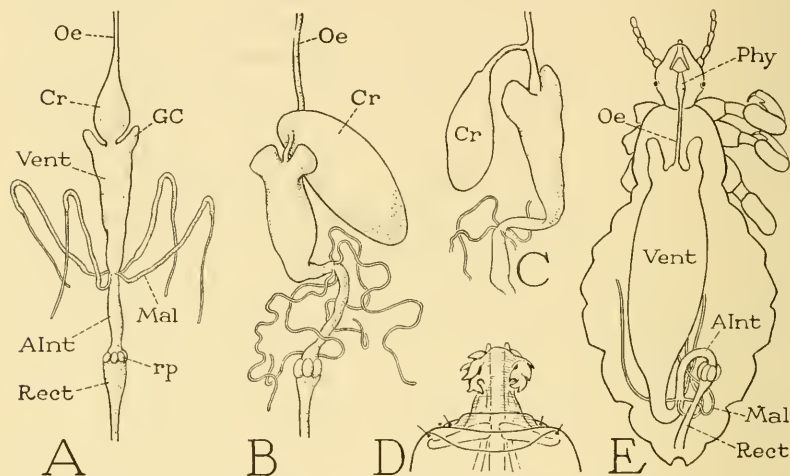


FIG. 14.—Alimentary tract of Mallophaga and Anoplura.

A, alimentary canal of *Tetroplthalmus titan* (Piaget), Mallophaga, Amblycera. B, alimentary canal of *Docophorooides brevis* (Dufour), Mallophaga, Ischnocera. C, crop and stomach of *Geomydoceus geomydis* (Osborn), Mallophaga, Ischnocera, Trichodectidae. D, everted proboscis of *Pediculus humanus* L., Anoplura (from Peacock, 1918). E, outline of *Pediculus humanus* L. and alimentary canal (from Sikora, 1916).

Alnt, anterior intestine; *Cr*, crop; *GC*, gastric caecum; *Mal*, Malpighian tubules; *Oe*, oesophagus; *Phy*, pharynx; *Rect*, rectum; *rp*, rectal pads; *Vent*, ventriculus (stomach).

V. THE FLIES. ORDER DIPTERA

The members of this order are named Diptera, meaning "two wings," because they never have more than two wings; but there are wingless species. They are regarded by entomologists as the insects properly termed *flies*, though some are known as mosquitoes, gnats, and midges. They do not include the Mayflies, the stoneflies, the dragonflies, the butterflies, and others with fly names but four wings. In writing, the true flies may be distinguished from these other so-called flies by separating the two words of their names, as sand fly, black fly, horse fly, house fly, etc.

The Diptera are all sucking insects; none of them bites in the ordinary sense of the word, since in none are the mandibles jawlike. The mouth parts of some species, however, are constituted for pierc-

ing, and such species that habitually feed on blood are those commonly known as "biting" flies. Though the species of flies are numerous, most of them are entirely harmless to us, and yet the order includes some of the most dangerous of the disease and parasite vectors that attack man, other mammals, and birds. The larvae of many species, moreover, live parasitically within the bodies of animals; those that thus destroy other insects are, from our standpoint, beneficial species, those that infest domestic animals or man are abhorred pests.

The dipterologists are not agreed as to how the flies should be classified within the order, but for practical purposes it is most convenient to recognize the three groups commonly known as the Nematocera, the Brachycera, and the Cyclorrhapha. Differences in the feeding apparatus of biting species appear to be consistent with this classification. 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 antennae, and the number of segments is generally small but is variable. In the Cyclorrhapha also the antennae are short, never having more than three segments, but each antenna bears a prominent plumed bristle; the flies of the cyclorrhaphous group are named and distinguished by the fact that the adult emerges from a pupa case by pushing off a circular cap from the anterior end of the latter. Of the flies described in this section, the mosquitoes, the sand flies, the biting midges, the black flies, and the net-winged midges 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 fly, the louse flies, and the bat "ticks" are included in the Cyclorrhapha.

MOSQUITOES. FAMILY CULICIDAE

The head and proboscis of a mosquito (fig. 16 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. 16 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. 2 B, *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 head in the mosquito the small neck foramen (fig. 16 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

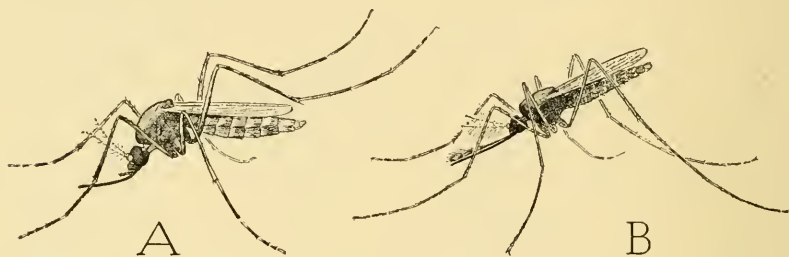


FIG. 15.—Examples of mosquitoes in natural positions. Order Diptera, family Culicidae.

A, female of *Aedes aegypti* (L.); *Culex* mosquitoes also often take this attitude. B, male of *Anopheles punctipennis* (Say); some *Anopheles* stand with the body more steeply tilted and the hind legs elevated.

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. 16 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. 16 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. 17 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. 16 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. 16 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 short in the female except in the Anophelini, but in the male it is usually 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 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. 16 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.

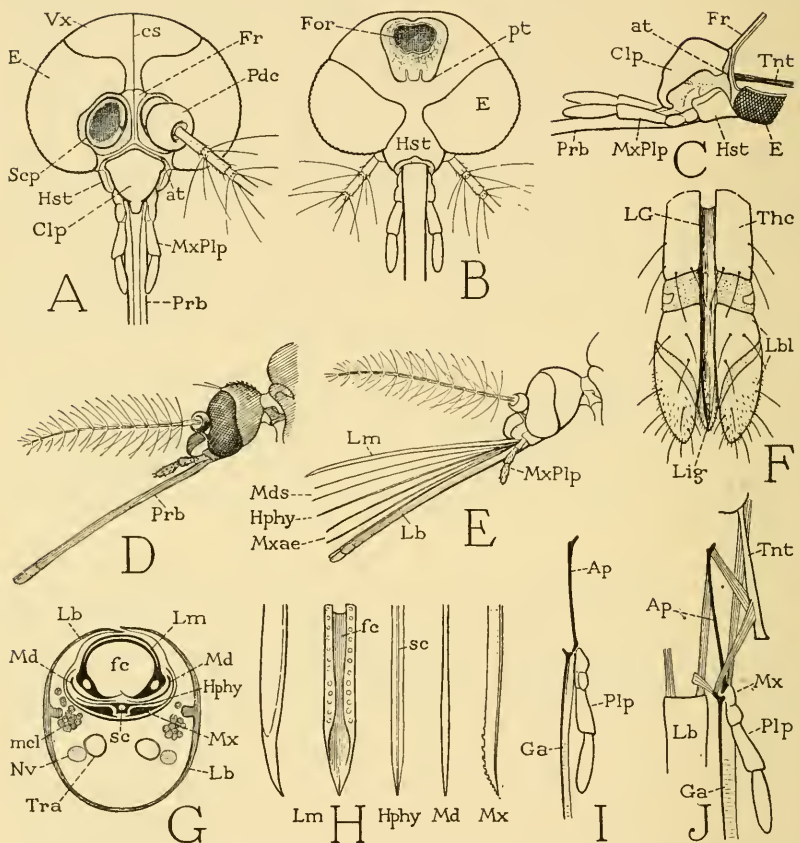


FIG. 16.—Head and mouth parts of a female mosquito. A-F, H, I, *Aedes acgypti* (L.), G, *Anopheles maculipennis* Meigen.

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, 1921a). 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.

The elongate labium of the mosquito corresponds with the distal appendicular part of the labium in the cockroach, known as the prementum (fig. 2 D, *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. 16 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 16. 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 sucking apparatus of the mosquito consists of two powerful pumps (*antliae*) contained within the head. One lies in the clypeal region (fig. 17 A, *CbP*) and is a derivative of the preoral cibarial pocket of such insects as the cockroach (fig. 7 A, *Cb*); the other (fig. 17 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. 17 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, *I3*, *I4*) clearly corresponding with the muscles inserted on the oral arms of the hypopharynx in the cockroach (fig. 6 A, B, *I3*, *I4*). There can be little doubt, therefore, that the floor of the first pump in the mosquito is the concave sitophore of the anterior wall of the hypopharynx in the cockroach (fig. 7 B, *Sit*). The dorsal wall of this pump in the mosquito is continuous with the inner wall of the labrum (fig. 17 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. 7 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.

The pharyngeal pump (*antlia pharyngealis*) of the mosquito is an elongate, gourd-shaped organ (fig. 17 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

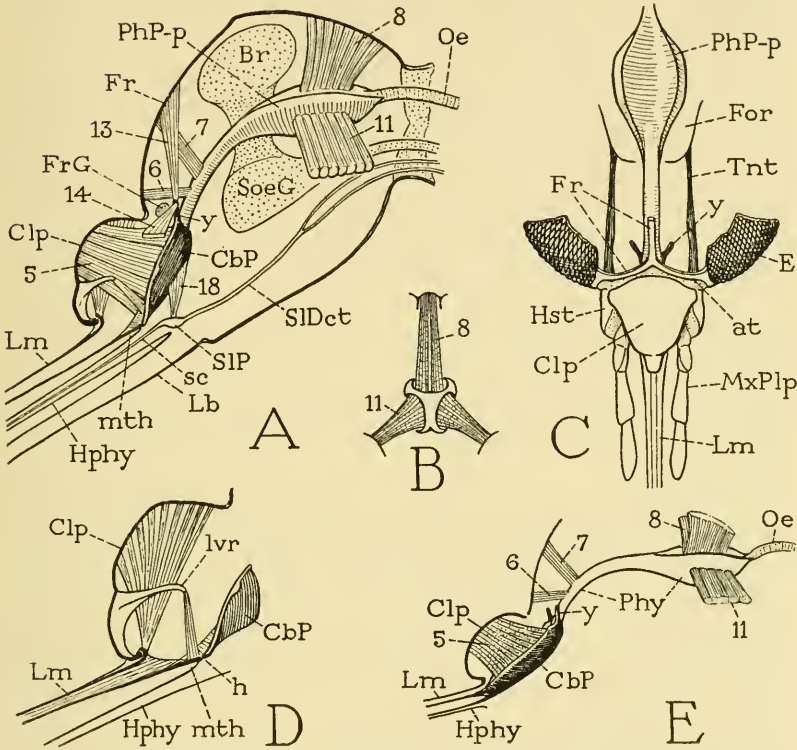


FIG. 17.—The sucking apparatus of a mosquito.

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 on 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; *SIDct*, salivary duct; *SIP*, salivary pump (oral arm of hypopharynx in cockroach, fig. 6A).

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. 7.)

other two lateroventral, which are flexibly hinged to each other along their margins. Four huge muscles activate the pharyngeal pump, a dorsal pair (fig. 17 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. 7 A, 8), and a lateral muscle on each side (fig. 17 A, B, E, 11), corresponding with the posterior lateral dilator of the pharynx in the cockroach (fig. 7 A, 11). When the pharyngeal pump is collapsed (fig. 17 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. 7 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. 25 J, 27 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 of the mosquito, 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. 17 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 (*SIDct*) 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. 16 H, *Hphy*). The salivary pump is operated by a pair of dilator muscles (fig. 17 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. 6 B, 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.

The salivary glands of the mosquito lie in the thorax (fig. 19 A, *SIGld*); their ducts converge forward into the head and unite to form the common duct (*SIDct*) that goes to the salivary pump. Each gland is three lobed (B), and each lobe contains a slender axial duct that branches from the end of the main duct. The gland cells are so large that the surfaces of the lobes have a coarsely reticulate appearance. In *Aedes aegypti* (fig. 19 A), the salivary glands embrace the anterior end of the ventriculus, but in the figure the left gland is shown displaced laterally. It is these glands that are penetrated in *Anopheles* mosquitoes by malarial plasmodia that have entered the body cavity from the alimentary canal, and it is through the common salivary duct that the parasites are conveyed into the blood of a vertebrate host for their further development. The salivary duct of *Anopheles*, therefore, as dramatically stated by Nuttall and Shipley (1901), has played a large part in human history, for along it has passed the cause of disease and death that has ruined cities and devastated countries, and that, it might be added, has conquered armies and brought about the downfall of nations.

The general conformation of the head and proboscis of the mosquito (fig. 16 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. 18). 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 driven deeper into the wound, each blade holding by means of its recurved teeth against the reverse pull of the retractors, which draw the head down and thus stretch the protractors of the opposite stylet. By repeated alternating 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

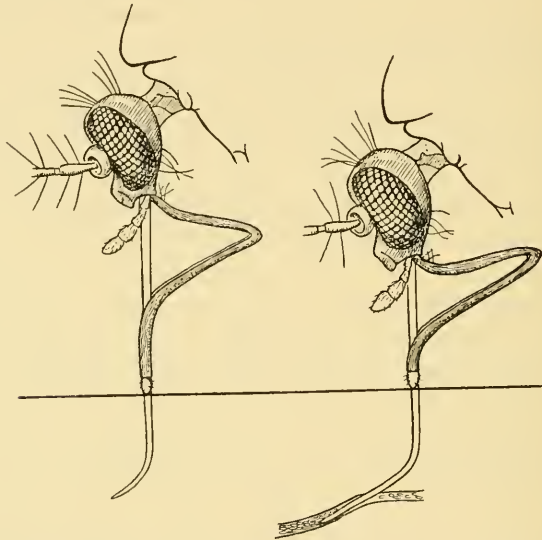


FIG. 18.—*Aedes aegypti* (L.) feeding in the web of a frog's foot. (Redrawn from Gordon and Lumsden, 1939, with addition of neck sclerite.)

At left, actively flexible end of stylet fascicle curved as it probes the tissue of the web. At right, the fascicle penetrated into a capillary.

the head (fig. 18). The bending of the labium, which appears to be a passive result of the lowering of the head, is believed by Robinson, and also by Gordon and Lumsden (1939) to be effected by muscles attached on its base. The adhesion of the stylets when the fascicle is freed from the labium is attributed by Robinson to the presence of a viscous liquid that bathes the stylets in the labial gutter.

The action of the stylets within the tissue of the victim has been studied by Gordon and Lumsden (1939) by allowing mosquitoes to bite the thin web of a frog's foot, the latter being so arranged that the course of the stylets in the transparent web could be observed under a microscope. The stylet fascicle, these writers report, is worked into the tissue by an oscillatory movement and a series of

minute forward thrusts. Within the web the fascicle usually makes a sharp curve in a horizontal plane (fig. 18), and the tip bends actively in various directions as if feeling its way. Apparently, however, the fascicle movements are entirely fortuitous, there being no evidence of sensory influence, the fascicle often going close to a capillary without entering it, or sometimes penetrating clear through a blood vessel. Probing may continue in some cases for some minutes, in others a blood source is found at once. Blood may be obtained either directly from within a capillary, or from a pool of blood that has escaped into the tissue from a punctured vessel. When a capillary is tapped by insertion of the fascicle there is no hemorrhage, the blood being all taken up by the mosquito. The entrance of the fascicle is said to cause an "enormously accelerated" flow of blood. The same writers observed the discharge of saliva from the probing fascicle into the tissue, and also its injection directly into a capillary.

The ability of the stylet fascicle to make the movements described above may seem remarkable, but independent motions of the fascicle when separated from the labium were earlier recorded by MacGregor (1931), who says the unsheathed fascicle "is capable of making vertical, horizontal and rotary movements, which enable the insect to replace the biting armament within the labium without much difficulty." The movements are perhaps to be explained by assuming some differential action of the muscles inserted on the bases of the stylets.

The alimentary canal of the mosquito (fig. 19 A) begins with the entrance to the pharyngeal pump (*PhP*), the cibarial pump, as already explained, being a development of the preoral food cavity. From the pharyngeal pump the slender oesophagus (*Oe*) goes through the neck into the front of the thorax, where it joins the ventriculus (*Vent*). Near its posterior end the oesophagus gives off three pouches, known as the *oesophageal diverticula*, two of which are dorsal (*ddv*), and one ventral (*vdv*). The diverticula vary in shape and size according to their contents, but in unfed specimens of *Aedes aegypti* the dorsal diverticula have the form of small, flat, elongate lobes with slender stalks (C); they diverge upward and outward from the oesophagus and lie against the anterior wall of the mesothorax. The single ventral diverticulum is a large sack (A, *vdv*) extending from a narrow neck far back into the ventral part of the abdomen. This diverticulum corresponds with the crop of other Diptera. The ventriculus, or stomach (A, *Vent*), for most of its length is a narrow tube. From the slightly enlarged anterior end, embraced by the salivary glands, it extends upward and posteriorly in the thorax.

turns backward into the abdomen, and beyond the third segment of the latter expands into a large sack, the rounded posterior end of which joins the enlarged anterior end of the intestine. The anterior intestine is a short, slender tube (*AInt*) thrown into a small loop before it unites with the rectum (*Rect*). The sacklike anterior part of

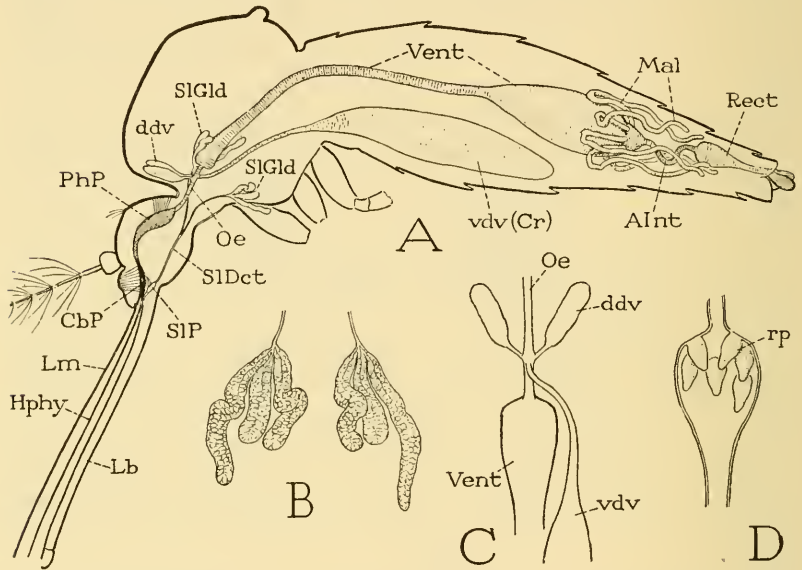


FIG. 19.—The alimentary canal and salivary glands of a mosquito, *Aedes aegypti* (L.)

A, outline of body and proboscis of a female, showing alimentary tract and salivary glands, the left gland displaced laterally. B, the salivary glands. C, the oesophageal diverticula shown in relation to the oesophagus and ventriculus, ventral view. D, outline of the rectal sac, showing rectal papillae projecting from inner wall.

AInt, anterior intestine; *CbP*, cibarial pump; *ddv*, dorsal diverticulum of oesophagus; *Hphy*, hypopharynx; *Lb*, labium; *Lm*, labrum; *Mal*, Malpighian tubules; *Oe*, oesophagus; *PhP*, pharyngeal pump; *Rect*, rectum; *rp*, rectal papillae; *SIDct*, salivary duct; *SIGld*, salivary gland; *SIP*, salivary pump; *vdv*, ventral diverticulum of oesophagus (crop); *Vent*, ventriculus, or stomach.

the rectum contains six small, soft, conical papillae projecting from its inner wall (D, *rp*). These rectal papillae, characteristic of Diptera and certain other insects, replace the padlike rectal organs of such insects as the cockroach (fig. 8, *rp*). From the anterior end of the intestine, close to the stomach, are given off five Malpighian tubules (fig. 19 A, *Mal*). These excretory tubules are relatively short and thick in the mosquito; they are looped and convoluted about the intestine and the posterior end of the stomach.

The nature of the sucking act and the destination of imbibed

liquids in the alimentary canal of the mosquito have been investigated by Kadletz and Kusmina (1929), MacGregor and Lee (1929), MacGregor (1929, 1931), and Fülleborn (1908, 1932). It is found that a mosquito having the stylets unsheathed from the labium, with the labium removed, or the tip of the proboscis cut off will feed much more readily and on a greater number of substances, even poisonous solutions, than will a mosquito with a normal proboscis. This method of experimentation is called "forcible feeding." Fülleborn claims that by its use the sucking act of the mosquito is demonstrated to be a pure reflex, that mosquitoes having the labium removed will always drink any liquid into which the stylets are inserted, and will continue to suck even to the bursting of the abdomen, or when the body is removed from the head. The other writers, on the contrary, contend that the action of the pump is a conditioned reflex, since they find that mosquitoes without a labium will not always feed, and may show a choice when different solutions are offered at the same time, and furthermore, they say that a rupture of the abdomen from "forcible feeding" was never observed in their experiments.

Blood taken by natural continuous feeding is said by MacGregor and Lee (1929) and MacGregor (1929, 1931) to go directly into the stomach (ventriculus), though Kadletz and Kusmina (1929) observe that it is found in both the crop and the stomach. In discontinuous feeding, however, MacGregor says the blood accumulates first in the oesophageal diverticula. On the other hand, nonprotein liquids, particularly sugar solutions, or blood with an admixture of honey, also glycerin and poisonous liquids are stored first in the diverticula, from which they are gradually delivered to the stomach. The oesophageal diverticula, according to MacGregor, serve also as "air separators" for the removal of air bubbles from the imbibed liquid.

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 and of dogs.

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.

Flebotomus is a small, long-legged, very hairy fly a few millimeters in length (fig. 20, 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 the fly 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. 21 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. papatasi* (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,



FIG. 20.—A sand fly, *Flebotomus verrucarum* Towns., female. Order Diptera, family Psychodidae. A very hairy fly, but hairs removed to show structure. (Length of body 2 mm.)

but it is thick and strong (fig. 21 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;

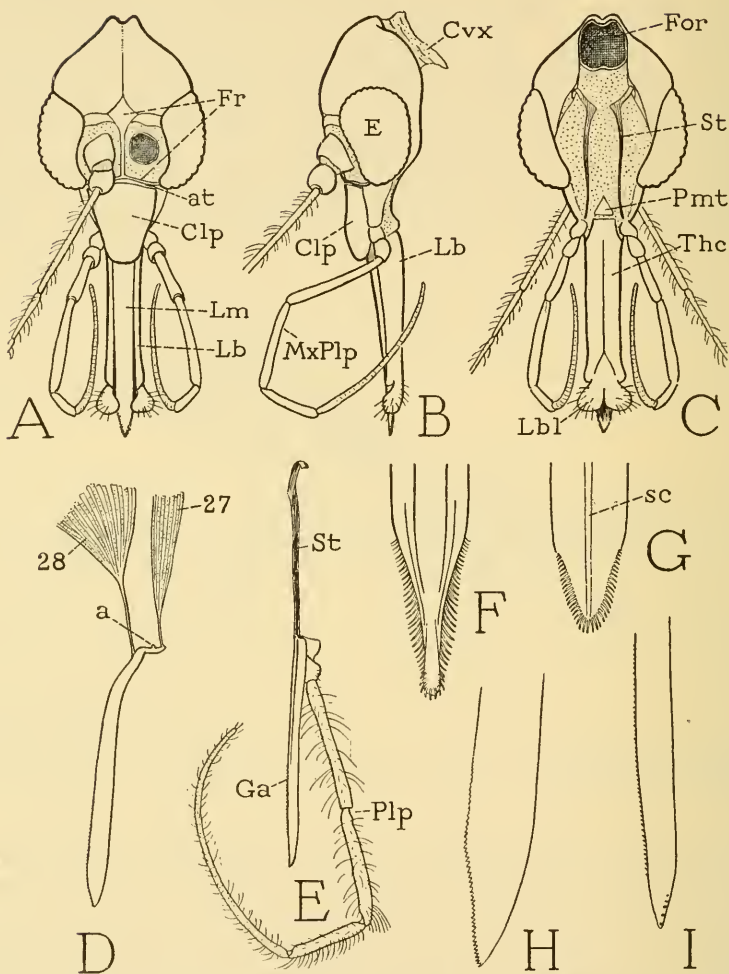


FIG. 21.—Head and mouth parts of *Flebotomus verrucarum* Towns., female.

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; *The*, theca.

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

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. 21 F, G) interlock to form a strainer guarding the entrance of the food canal. With the penetration of the 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 papatasi* (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 *Flebotomus* been shown 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.

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. 22) as a representative of the genus.

Culicoides (fig. 22 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 does not project, 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. 22 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. 22 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

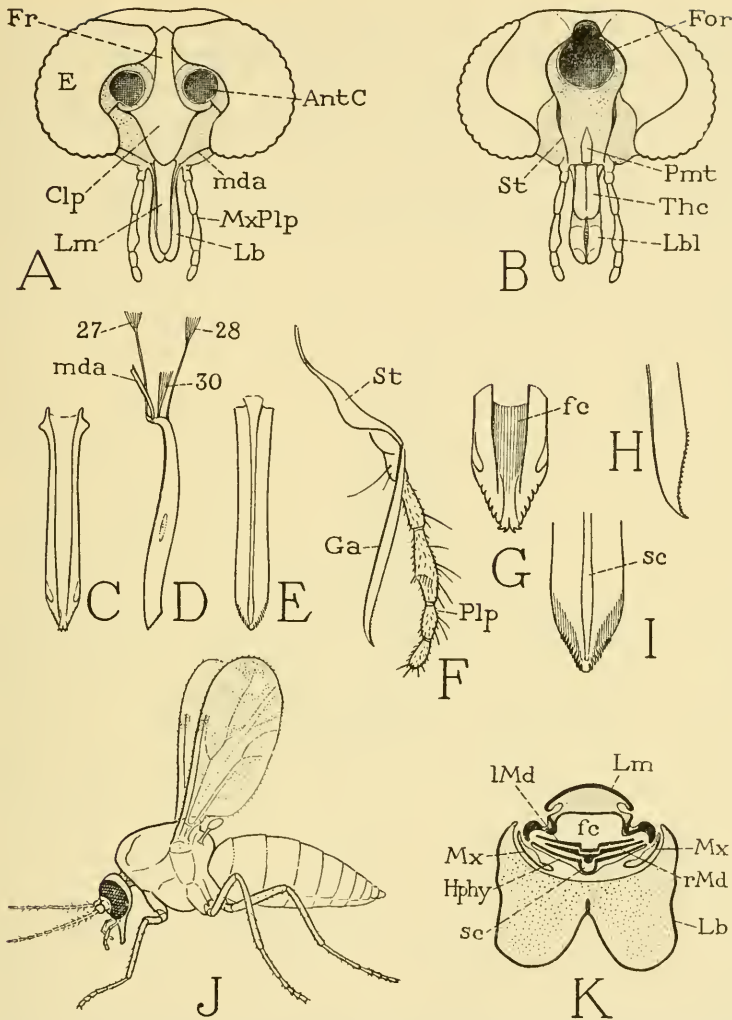


FIG. 22.—A biting midge, *Culicoides*, female, head and mouth parts. Order Diptera, family Heleidae. A-J, *Culicoides furens* (Poey); K, *Culicoides vexans* (Staeger).

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; *The*, theca.

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

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*).

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.

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. 23), 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



FIG. 23.—A black fly, *Simulium venustum* Say, female. Order Diptera, family Simuliidae. (Length 3.5 mm.)

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. 24 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) 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. 24 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 (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 (*SIP*), 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. 24 K) is of the usual abductor type, and does not appear to be in any way adapted to giving the mandibles a scissor movement on their interlocking mechanism.

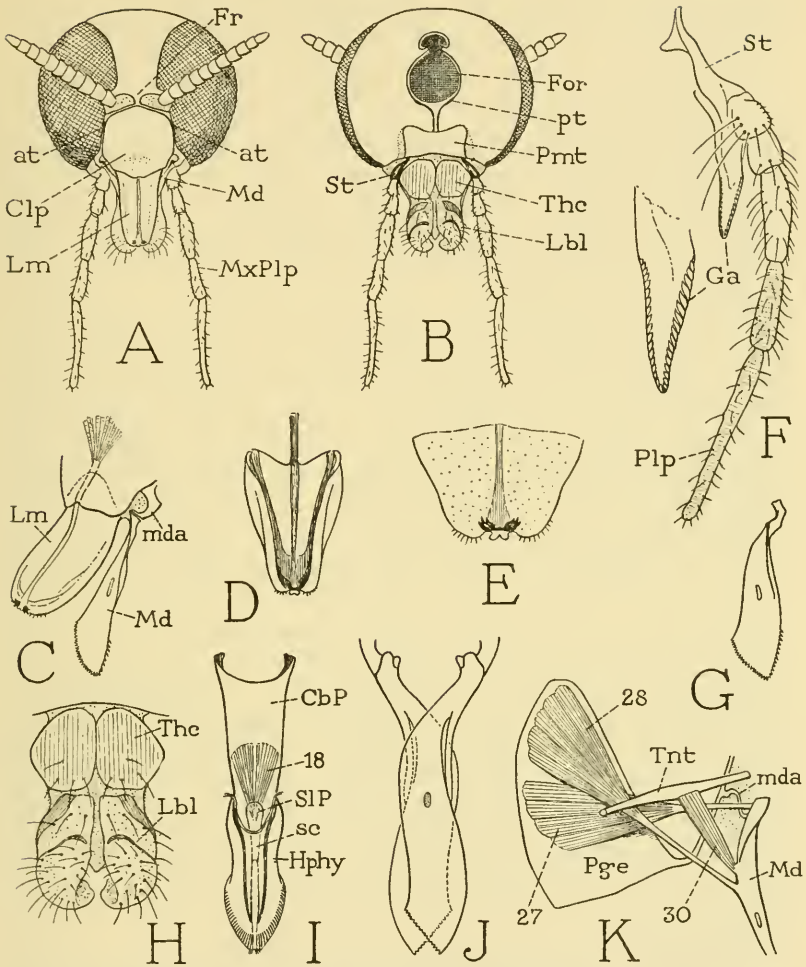


FIG. 24.—Head and mouth parts of *Simulium*, female. A-I, *Simulium venustum* Say; J, *Simulium daninosum* Theobald; K, *Prosimulium magnum* D. and S.

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; The, theca; Tnt, tentorium.

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

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 Romania 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 some-

times caused by the blood-inhabiting protozoon *Leucocytozoon anatis* Wickware, said to be transmitted by *Simulium venustum* Say.

NET-WINGED MIDGES. FAMILY BLEPHAROCERATIDAE

The members of this family are small, mosquitolike, nematocerous flies characterized by a network of fine lines in the wings extending irregularly between and across the true veins. The flies are found along water courses in hilly or mountainous country, since the larvae are aquatic and live only in fast-flowing streams. The females of the adult fly are predaceous, mostly on other insects, but some of them are bloodsuckers, and are therefore occasional "biters." The mouth parts resemble those of the Simuliidae, except that the mandibles are not interlocked. The mandibles of the female are long, strong, sharp-pointed blades, each armed along its inner edge with a fringe of long slender teeth slanted upward, and on the outer margin with a few smaller teeth directed downward. The net-winged midges occur in North and South America, Europe, Asia, Australia, and New Zealand, but as biting pests they are not important.

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 habitats 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. The species are mostly large for flies, and the black horse fly (fig. 25 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. 25 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. 25 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 Cyclorhapha.

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. 25 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 stipito-cardinal 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 (*SIP*).

The labium (fig. 25 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 Cyclorhapha 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

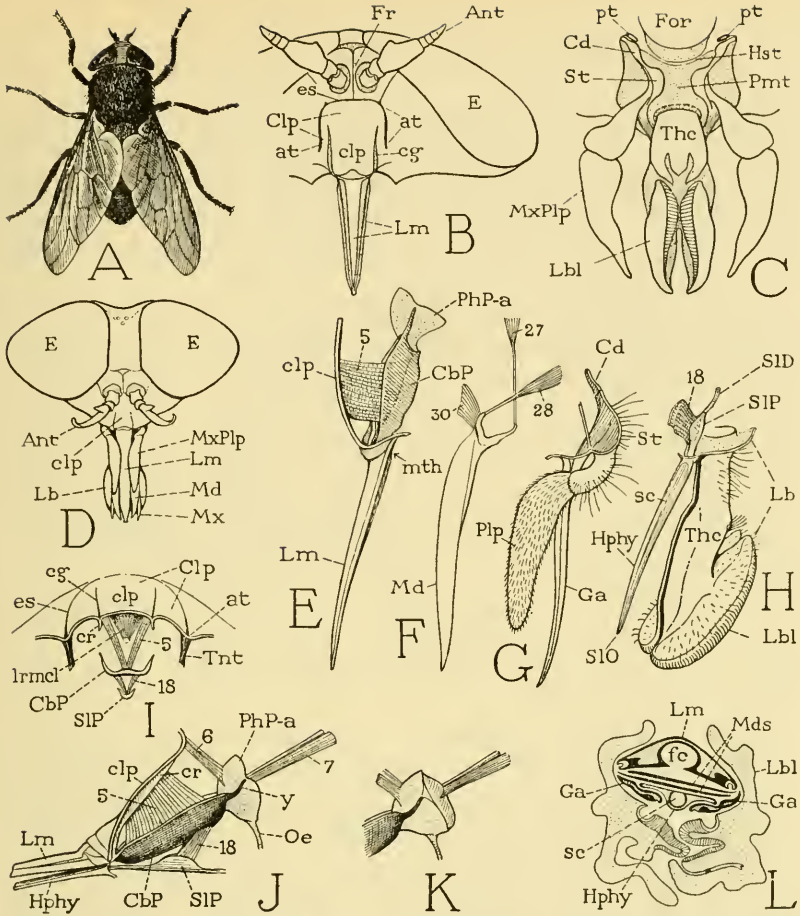


FIG. 25.—Horse fly, *Tabanus*, head, mouth parts, and sucking apparatus. Order Diptera, family Tabanidae. A-H, *Tabanus atratus* F.; I-K, *Tabanus sulcifrons* Macq.

A, the black horse fly, *Tabanus atratus* F., female (natural size). B, antero-ventral 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 cibarial 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; *SID*, salivary duct; *SIO*, salivary orifice; *SIP*, salivary pump; *St*, stipes; *Thec*, 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, adductor of mandible; 30, tentorial muscle of mandible.

traversed crosswise by numerous fine, closely set channels ("pseudo-tracheae") that lead into a pair of median lengthwise channels. In the spread position of the labella the labellar disk is deeply cleft anteriorly between its 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 of 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. 25 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 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, 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.

SNIFE 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. 26 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*)

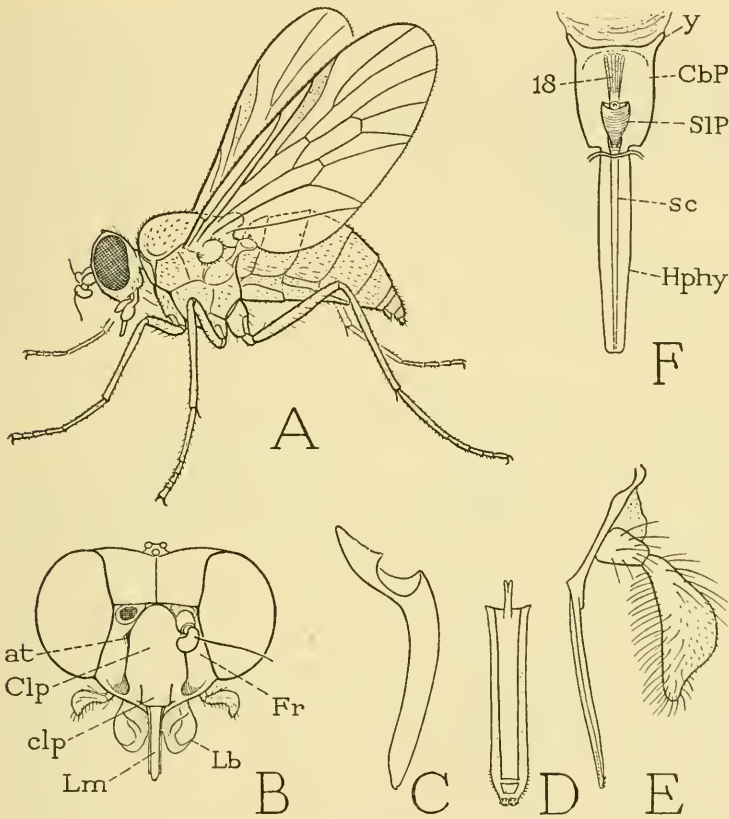


FIG. 26.—A snipe fly, *Symphoromyia atripes* Bigot, female, head and mouth parts. Order Diptera, family Rhagionidae.

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; *SIP*, salivary pump; *y*, cornu of cibarial pump.

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.

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. 27 B) are insects of medium or large size; their favorite habitat 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. 27 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 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 produced 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. 27 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

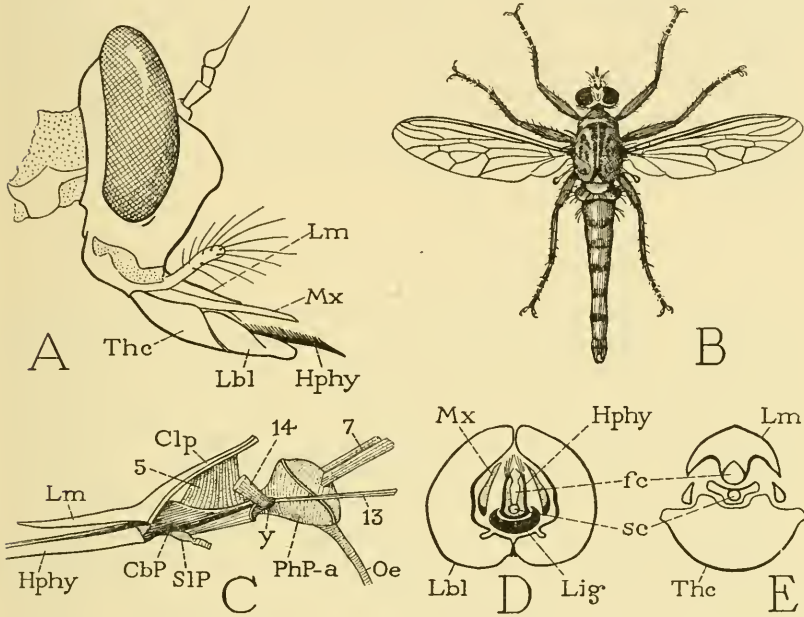


FIG. 27.—Robber fly, head, mouth parts, and sucking apparatus. Order Diptera, family Asilidae.

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* Flin., 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; *SIP*, salivary pump; *The*, 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.

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. 27 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. 25 J, 6). On each cornua of the cibarial pump are inserted a slender retractor muscle (fig. 27 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.

SPECIAL FEATURES OF 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. 28 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. 28 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. 28 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. 28 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. 28 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. 25 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 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. 28 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.

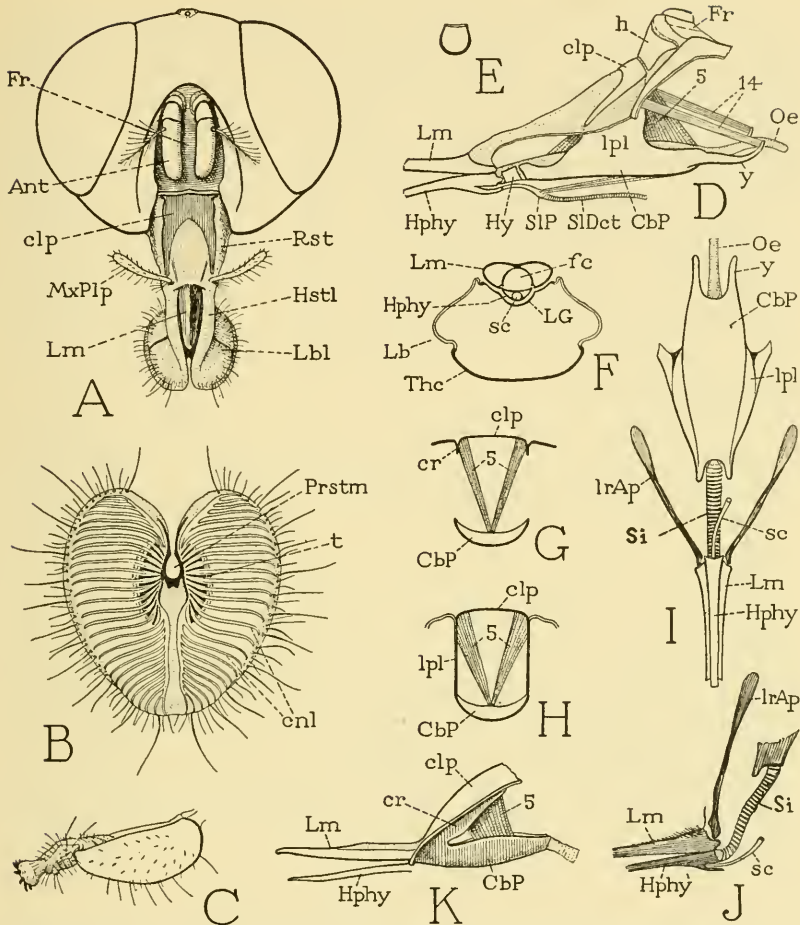


FIG. 28.—Special features of the feeding apparatus in cyclorrhaphous flies.

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. 25 I). H, corresponding section of the fulcrum of a cyclorrhaphous fly. I, labrum, hypopharynx, siphon, and cibarial pump of a stable fly, *Stomoxys calcitrans* (L.), posterior surface. J, showing relation of the siphon 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 sclerite; *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; *Si*, siphon; *SIDct*, salivary duct; *Slp*, salivary pump; *t*, prestomal teeth; *Thc*, theca; *y*, cornu of cibarial pump.

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, except Crampton (1942), 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. 25 B, I) and the cockroach (fig. 7 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. 28 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. 28 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, *Si*), is drawn out into a long flexible tube, reaching its greatest length in connection with the retractile proboscis of the Hippoboscidae (fig. 31 I, *Si*). The tube may be termed more appropriately the *siphon*.

The salivary pump of the Cyclorrhapha (fig. 28 D, *SIP*) has the same structure and musculature as in other flies. (See Cornwall, 1923.)

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."

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; 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. 29 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. 29 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. 29 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. 29 F), which are attached at one end on the gutter and at the other 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)

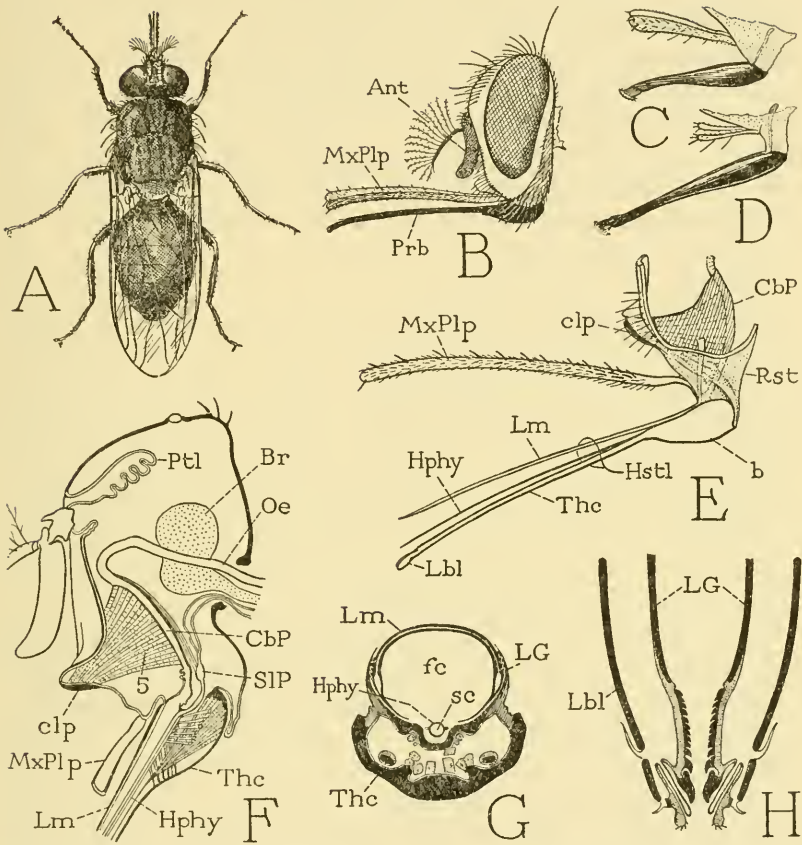


FIG. 29.—Tsetse fly, *Glossina*, horn fly, *Siphona*, and stable fly, *Stomoxys*, head and feeding apparatus. Order Diptera, families Glossinidae and Muscidae.

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; SIP, salivary pump; Thec, theca.

lies within the rostrum of the proboscis (fig. 29 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. 29 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. 29 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. Both the horn fly and the stable fly are to be regarded as potential carriers of such livestock diseases as anthrax and surra. The stable fly, because of its biting propensities, is also a most annoying pest of man, particularly where abundant in the neighborhood of summer resorts, but it has not as yet been convicted of being a natural transmitter of any human disease, though Berberian (1939) reports that transmissions of oriental sore from one human subject to another have been effected experimentally by the bite of the stable fly. The horn fly, from experiments on monkeys, has been accused of being a vector of human poliomyelitis, but more recent tests (see Herms, 1939) appear to give negative results.

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 since they do not ordinarily leave an animal until the latter dies, they probably have little relation to the spread of disease, though certain species have been shown to be vectors of pigeon and quail malaria. Various observers have reported the finding of Mallophaga attached to hippoboscid flies (see Warburton, 1928), and it is possible, therefore, that the flies play some role in the distribution of these parasites, since if they do leave a host they are most likely to go to another of the same species.

Most of the hippoboscids are permanently winged (fig. 30 A), some species shed their 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

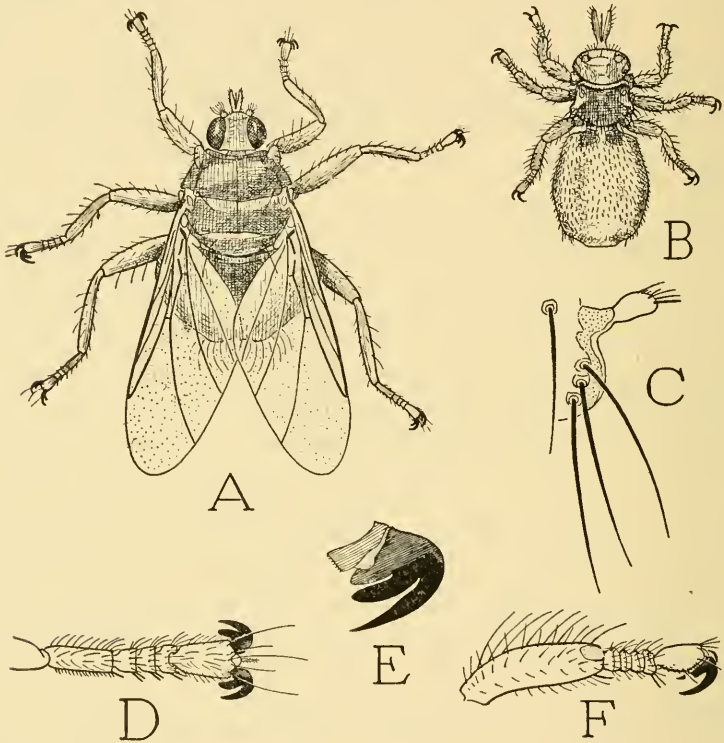


FIG. 30.—Louse flies, *Lynchia* and *Melophagus*. Order Diptera, family Hippoboscidae.

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 claw of foot. F, *Melophagus ovinus*, right fore tarsus and 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. 30 A), resembles the head of any ordinary fly (fig. 31 A) and is set on the thorax by a narrow neck. The eyes are large, the antennae (*Ant*) exposed, but the rostrum is concealed by the retraction of the haustellum. In *Melophagus ovinus* (fig. 30 B), however, the eyes are small (fig. 31 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. 31 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. 31 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 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. 31 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

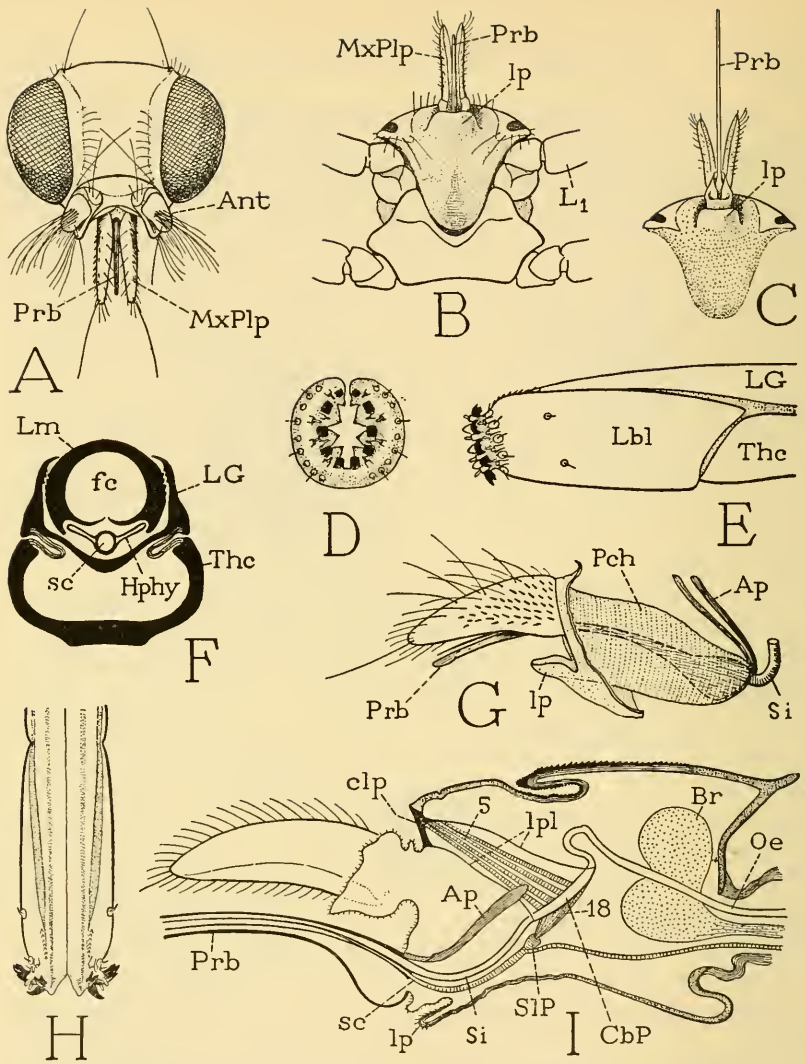


FIG. 31.—Head and feeding apparatus of *Lynchia* and *Melophagus*.

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; *L₁*, 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; *Si*, siphon; *SIP*, salivary pump; *Thec*, theca.

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

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. 31 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 siphon (*Si*) connecting the pump with the food canal of the haustellum is drawn out into a long flexible tube. The salivary pump (*SIP*) 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.

A detailed account of the process of feeding by *Hippobosca equina* L. is given by Hase (1927).

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.

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. 32) 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 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,

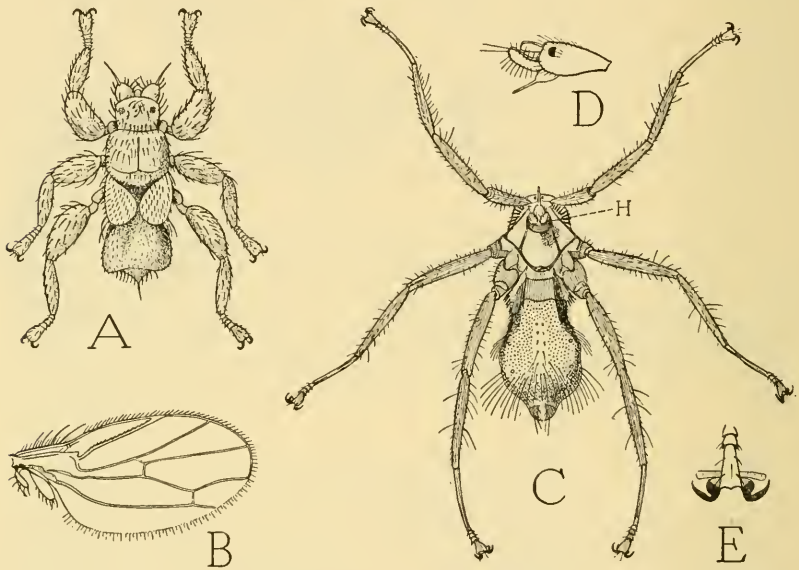


FIG. 32.—Bat "ticks." Order Diptera, families Streblidae and Nycteribiidae.

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.

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, Hippoboscidae, Streblidae, and 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 acalyptrate 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.

VI. THE FLEAS. ORDER SIPHONAPTERA

The common name of the flea order, Siphonaptera, refers to the fact that the fleas are wingless sucking insects; another name for them is Aphaniptera, which tells us that wings are invisible. Most parasitic insects, whether winged or wingless, are flattened in a plane parallel with the body surface of the host; the fleas are flattened in the opposite direction, giving them a shape conducive to rapid movement through closely massed hairs. The fleas also are notable jumpers; their leaping powers are of much importance to them because most species do not live continuously on the same animal, but go from one to another, and they can leave in a hurry when necessary. A flea at rest (fig. 33 C, D) sits with its six legs evenly spread out in the manner of any other insect, except that the knees are sharply bent upward; when it jumps it simply disappears without taking any preparatory attitude, though the leap is usually preceded by a sidewise shaking of the body. The large hind legs must be the principal jumping organs, but the flea appears to spring by extending all the legs at once, and the legs are all strongly muscled in the coxae and femora. The stiff hairs projecting from the body (fig. 33 C) evidently are conducive to forward movement through narrow spaces. Though most fleas are extremely restless and active, a species called the sticktight flea remains nearly all its life attached to the host if not artificially dislodged, and the female chigoe flea buries herself in the skin of the host, where she remains until she lays her eggs and dies. Some fleas are not strictly parasitic but live principally in the nests of the animals on which they feed.

The eggs of the fleas are generally deposited on the bodies of the hosts, but they readily fall off to the ground, into nests or bedding, or onto the floors of buildings. The young flea is a legless, wormlike larva, which lives wherever the eggs drop, and goes through a pupal stage before becoming an adult flea and adopting the parasitic, blood-sucking habit. The fleas, therefore, are the only bloodsucking insects

other than the flies that have what is called a "complete metamorphosis."

The fleas as parasites mostly attack mammals, but some of them live on birds and are particularly a pest of domestic poultry. Several hundred species of them have been named and described. Ewing and Fox (1943) record more than 200 from North America and the West Indies. The species that commonly annoy man and domestic animals are known as the human flea (fig. 33 A, B), the dog flea

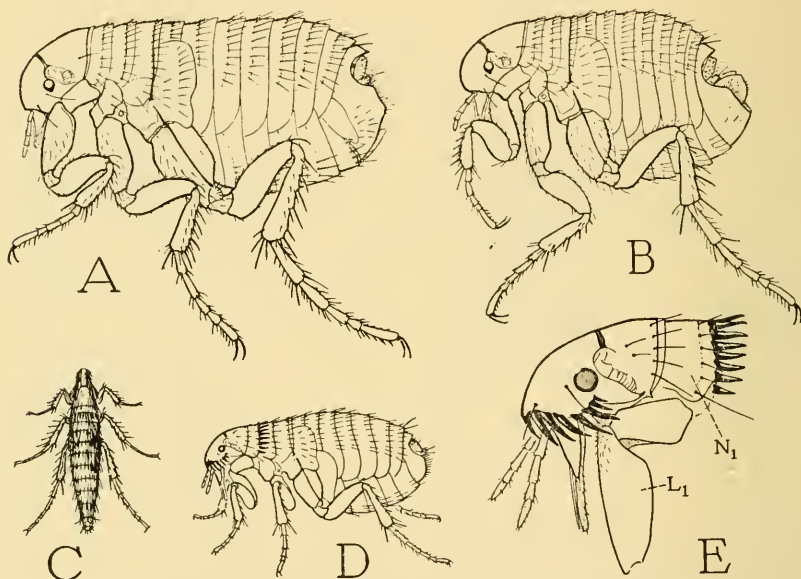


FIG. 33.—Examples of fleas. Order Siphonaptera.

A, the human flea, *Pulex irritans* L., female (length a little over 2 mm.). B, same, male (length $1\frac{3}{4}$ mm.). C, the dog flea, *Ctenocephalides canis* (Curtis), in natural position of repose, dorsal view. D, same, lateral view, more enlarged, female (length about 2 mm.). E, head, pronotum (N_1), and base of first leg (L_1) of female dog flea; note combs (ctenidia) of strong spines on lower edge of head and on margin of pronotum.

(C, D, E), the cat flea, and the rat flea, but the names have little significance since these fleas are promiscuous with regard to hosts.

Entomologists have much discussed the theoretical question of the relation of fleas to other insects, without arriving at any consensus; the fleas remain an independent order of obscure origin. Their feeding apparatus has features found in diverse groups of insects, but the combination of characters is peculiar to the fleas.

The head of a typical flea (fig. 34 A) is flattened from side to side, rounded above, and strongly declivous or angulated anteriorly. On each side is a deep depression containing a short, segmented antenna

(*Ant*), and in some species, just before the antennal cavity, is a small round eye (*O*). So closely is the head joined to the thorax that the flea practically has no neck, and the way the pleura of the prothoracic segment are turned forward beneath the head makes it appear that the head is supported on the bases of the front legs (fig. 33). From the anterior part of the head depend the mouth parts, which are relatively large and fully exposed (fig. 34 A). They include a pair of broad maxillary lobes (*MxL*) bearing long palpi (*MxPlp*), two paired stylets (*Lc*) commonly regarded as the mandibles, a slender labium with parallel palpi (*LbPlp*), and a median unpaired stylet (*Hphy*), the nature of which will be discussed later. The mouth parts are attached on an oval membranous area at the anterior end of the head within the completely sclerotized peristomal margin of the cranium. The ventral arc of the peristome is the edge of the *hypostome*, which forms the lower wall of the head. The following descriptions of the feeding apparatus refer to *Pulex irritans* L.

The maxillary lobes are the largest members of the flea mouth parts. They are most unusual in their position, since they lie laterad of the other organs in the group, attached on the peristomal margin of the cranium in the usual position of the mandibles (fig. 34 A, *MxL*), and furthermore, so closely approximated dorsally (B) that the mesal angles of their bases all but meet at the median line in front of the other mouth parts. Each appendage (F) has the form of a three-sided pyramid, except that the wide anterior face has a broadly rounded distal margin (B) and thins down to a delicate, transparent apical lamella. The four-segmented palpus (F, *Plp*) arises within the median basal angle of the maxillary lobe and ordinarily projects downward. Only the presence of the palpus attests that the maxillary lobe is not a mandible.

The paired stylets (fig. 34 A, B, *Lc*) lie between the maxillae, and in the natural position are mostly concealed by the labium. They have the form of a pair of long parallel blades, concave on their opposed surfaces, armed with rows of minute teeth on their outer surfaces (G). The base of each appendage is turned backward at right angles to the blade, and is thickened to form a strong lever arm (G, *lvr*) implanted in the supporting membrane mesad of the corresponding maxillary lobe. The two basal arms (C) of these stylets lie at the sides of a small, median, peglike sclerite (C, *b*) projecting upward from the hypostomal margin of the peristome (*a*), which supports the labium but apparently has no functional relation to the associated stylets. The lever arms of the stylets articulate on the

posterior basal angles of the maxillary lobes (D), and have retractor and protractor muscles, which by their action on the arms impart a back-and-forth movement to the blades.

Nearly all writers have called the paired stylets of the flea the "mandibles," regardless of the fact that their basal arms have neither of the two usual mandibular articulations with the head, and, because of their position between the maxillae, have no connection whatever with the cranial margin. Moreover, each arm is closely associated with the base of the corresponding maxillary lobe (fig. 34 D), and by its free end articulates with the latter. The retractor muscle (32) of the lever arm arises on the lateral wall of the cranium, *the protractor (41) arises within the maxillary lobe*. The paired stylets of the flea, therefore, are the *maxillary laciniae*, detached and operating independently, as in Corrodentia, Mallophaga, Thysanoptera, and Hemiptera. This fact was noted 40 years ago by Börner (1904), but has not been accepted by subsequent writers because Heymons (1899) claimed that the mouth parts of the flea pupa are formed within the corresponding parts of the larva, and that the mandibular rudiments of the pupa go over directly into the paired stylets of the adult. Sharif (1937) appears to have verified Heymons' statements concerning the relation of the pupal organs to those of the larva, though he does not follow the development into the imago. The anatomy of the adult flea is in accord with Börner's interpretation; the facts of development must be reinvestigated. Börner's idea that the basal arm, or lever, of the lacinial blade is the "cardo" of the maxilla, however, is not tenable because in other insects the lacinia has no connection with the cardo, and the cardo has no muscles arising in any other part of the maxilla (see figure 4 B). The maxillary lobe of the flea must be largely the stipes, since it bears the palpus and contains the palpus muscles in addition to the lacinial muscle. The galea is either absent or indistinguishably united with the stipes.

The labium of the flea (fig. 34 J) is a relatively simple appendage supported at its base on the small peglike sclerite (*b*) above mentioned projecting upward from the hypostomal margin between the lacinial levers (C). The labium consists of an elongate basal lobe, and of two slender distal palpi held close together. In *Pulex irritans* the labial palpi are three-segmented, in other species they may have from two to five segments. The basal part of the labium is deeply grooved on its anterior surface for the reception of the median and paired stylets; the tips of the palpi extend slightly beyond the latter.

The unpaired stylet of the flea's mouth parts is a slender, slightly sinuous rod (fig. 34 I), armed along its anterior edge with a row

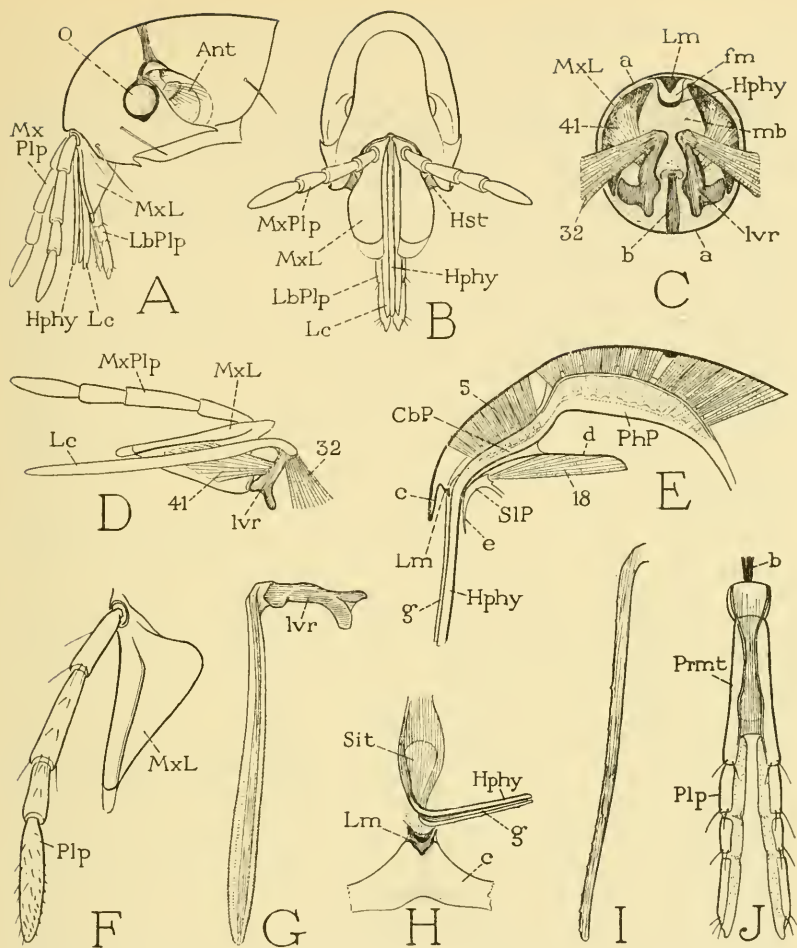


FIG. 34.—The head and feeding organs of a flea, *Pulex irritans* L. Order Siphonaptera.

A, head and mouth parts, left side. B, same, anterior view, more enlarged. C, membranous area of the peristome, and bases of mouth parts implanted in it, as seen from inside the head. D, right maxilla, mesal view, showing relation of lacinia to maxillary lobe. E, median sectional view of anterior part of head showing sucking and salivary-ejection apparatus. F, maxillary lobe and palpus. G, maxillary lacinia. H, inner view of labrum and floor of sucking pump (*Sit*), with base of hypopharynx turned to one side. I, exposed part of hypopharynx, lateral. J, labium, anterior.

a, margin of peristome; *Ant*, antenna; *b*, sclerite supporting labium on hypostomal margin of peristome; *c*, infolded distal margin of clypeus; *CbP*, cibarial pump; *d*, hypopharyngeal plate giving attachment to muscles of salivary pump; *e*, tapering process behind base of hypopharynx, apparently containing exit of salivary pump; *fm*, food meatus; *g*, groove of hypopharynx; *Hphy*, hypopharynx; *Hst*, hypostoma; *LbPlp*, labial palpus; *Lc*, lacinia; *Lm*, labrum; *lvr*, lacinial lever; *mb*, peristomal membrane; *MxL*, maxillary lobe (stipes); *MxPlp*, maxillary palpus; *O*, ocellus; *PhP*, pharyngeal pump; *Prmt*, prementum; *Sit*, sitophore; *SIP*, salivary pump.

Muscles.—5, dilators of cibarial pump; 18, dilator of salivary pump; 32, retractor of lacinia; 41, protractor of lacinia.

of small, widely spaced nodules. In nearly all entomological texts and in papers on fleas this stylet is called the "labrum," "labrum-epipharynx," or "epipharynx." Ewing (1929) labels it "hypopharynx," as do also Riley and Johannsen (1938) in their figure of a flea's head taken from Ewing. Heymons (1899) asserted that the unpaired stylet is developed within the labrum of the larval flea, and is therefore the "labrum."

Repeated dissections of the head of *Pulex irritans* show that the median stylet has no connection with the front wall of the head, and is therefore *not* the labrum. At its base it turns backward within the head and expands into a shallow oval basin (fig. 34 H, *Sit*), which is the floor of the cibarial pump (E, *CbP*); the latter is directly continued into the floor of a much larger pharyngeal pump (*PhP*). The unpaired stylet of the flea is thus seen to be the *hypopharynx*. The basinlike expansion (sitophore) of its base narrows anteriorly to a groove (E, H, *g*) running out on the anterior surface of the stylet. (Published figures of other species always show the groove on the posterior surface of the stylet.) Normally the hypopharynx is closely embraced by the lacinial blades, and the three stylets are held in the channel of the labium.

The true labrum of the flea is difficult to demonstrate. The facial wall of the cranium ends with a thin, slightly bilobed margin above the bases of the maxillae (fig. 34 B), but from this margin there is inflected a triangular inner lamella (E, H, *c*) that culminates in a small, recurved, triangular cusp (*Lm*) turned downward against the base of the hypopharynx. Evidently this reflected lamella, or at least its apical cusp (*Lm*), represents the labrum. The posterior wall of the cusp is continuous with the dorsal wall of the cibarial pump (E).

The method by which the flea bites is not sufficiently known from observation on the insects during feeding. Since the lacinial blades are the only members of the mouth parts that are independently movable in a lengthwise direction, it is generally thought that they are the principal piercing organs. The exuding blood is probably drawn up through the channel of the hypopharynx. The sucking apparatus of the fleas is highly developed and resembles that of the biting nematoceros Diptera insofar as it consists of a cibarial pump (fig. 34 E, *CbP*) and a pharyngeal pump (*PhP*), but the same double structure occurs also in the Anoplura and in some other sucking insects. The cibarial pump is flat and bellowslike, its floor being the shallow sitophore expansion of the base of the hypopharynx (H, *Sit*); on the thin dorsal wall are attached the dilator muscles (E, 5) arising

on the clypeal region of the head. The pharyngeal pump (E, *Php*) is much larger than the cibarial pump; it has high but relatively weak lateral walls, and a deeply inflected dorsal wall on which are attached a long row of frontal dilator muscles.

The fleas have a small salivary ejection pump resembling that of Diptera, Thysanoptera, and Hemiptera, lying beneath the cibarial pump (fig. 34 E, *SIP*). Its dilator muscles (*18*) arise from a horizontal plate (*d*) above it that appears to spring from the base of the hypopharynx. The exit canal is shown in sections by Weber (1933) and others to enter a minute tapering process (*e*) beneath the hypopharynx (regarded by most writers as the "hypopharynx") and to discharge into the canal between the laciniae ("mandibles"). The salivary canal of the fleas thus apparently does not traverse the hypopharynx as in Diptera, but opens in the more usual position between the hypopharynx and the labium.

Fleas in themselves are not agreeable associates either for animals or for man, and their promiscuous habit of going from one host to another makes them particularly obnoxious, since the human members of a family are always liable to infestations of fleas from their dogs or cats, or even from rats living in the house or adjacent structures. Aside from their physical annoyance, however, fleas are undesirable visitors also because they are transmitters of at least two diseases affecting man, endemic typhus and plague, and are probably more important vectors of the dog tapeworm than is the biting dog louse. In the case of the fleas the eggs of the tapeworm are ingested by the larval flea, which is not parasitic, and the larval worms go over through the pupa into the adult stage of the flea. Human subjects become infested by accidentally swallowing an infested flea. Typhus fever is one of the *Rickettsia* diseases ordinarily transmitted from man to man by the sucking lice, but the endemic form is supposed to be resident in rats, from which it is transmitted to human beings by fleas.

Plague is primarily a disease of rodents, caused by a bacterium, *Pasteurella pestis* (L. and N.), but it is one to which man also is highly susceptible and nonresistant. In human subjects the disease assumes three forms distinguished as bubonic, pneumonic, and septicemic, and may be transmitted by hypodermic inoculation, by inhalation, or by ingestion. The first form is that which ordinarily results from the bite of an infected flea.

Fleas become infected with the plague organism by ingestion of blood from a diseased host. In the alimentary canal of the insect the bacteria multiply in great numbers, and some of them are ejected

in a virulent condition with the feces, but they do not invade the body cavity of the flea or get into the salivary glands. It was formerly supposed, therefore, that transmission is not by the bite of the flea, but results from the rubbing or scratching of infected fecal material into the puncture or some other abrasion of the skin. Experiments have shown that inoculation can be brought about in this way; but it is now well established that the bite alone of an infected flea produces infection of the victim and is undoubtedly the usual way by which the disease is transmitted to human beings, either from a rodent (generally a rat) or from another person. There is no evidence that fleas carry the plague bacteria on their mouth parts, and a normal flea does not ordinarily discharge blood from the mouth. The discovery was made by Bacot and Martin (1914), however, that regurgitation does take place with plague-infected fleas in which the entrance to the stomach has been blocked by a mass of bacteria, and that it is by such fleas that the disease is spread. More recent investigations, as those by Eskey (1938) in California, have fully substantiated the observations of Bacot and Martin made in India.

The alimentary canal of the flea (fig. 35 A) has no crop, but there is a small, oval proventriculus (*Prvnt*) interpolated, as in the cockroach, just before the stomach. The inner wall of this organ is armed with consecutive rings of long, slender spines curving inward and backward (B), the ends of which project into the stomach mouth when the proventriculus is contracted. The function of these spines is not known. It has been suggested that they act normally as a barrier to regurgitation from the stomach, but the long, tubular stomodaeal valve (*Stlv*) projecting into the stomach should serve this purpose. In plague-infected fleas, however, the proventricular spines become clogged with the multiplying bacteria (C) and may soon accumulate such a mass of them that the entrance to the stomach is partially or completely blocked (D, E). Fleas in the latter condition are unable to utilize the food drawn into the oesophagus, and, because of resulting hunger, they repeatedly attempt to feed, with the result that the oesophagus is filled to repletion with still more blood. The tension thus created produces a regurgitation with each new attempt at feeding, and the contaminated blood of the oesophagus is thus injected into the puncture.

All rodent fleas are not susceptible in the same degree to blockage of the stomach, and hence different species are not equally dangerous as spreaders of plague. The highest incidence of transmitted infection obtained experimentally is always with the Old World rat flea, *Xenopsylla cheopis* (Roths.). This species is now widely distributed,

particularly in warmer regions; it occurs in most of the coastal ports of the United States, and has been found in a number of inland States where formerly the climate was supposed to be too severe for it (see Ewing and Fox, 1943).

Plague is probably endemic in many localities among wild rodents, but human infection from such sources is rare. In a study of plague

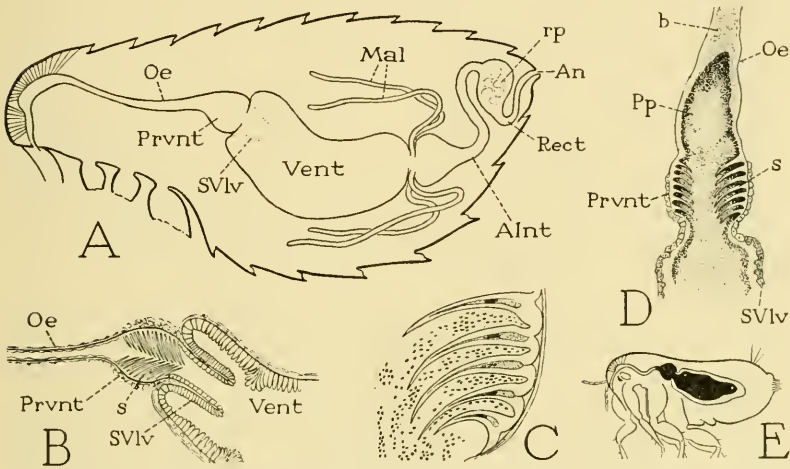


FIG. 35.—The alimentary canal of a flea, and its stoppage with plague bacteria. (A-C, from Faasch, 1935; D, E, from Bacot and Martin, 1914.)

A, outline of a flea and the alimentary canal, left side. B, section of proventriculus and anterior end of ventriculus, showing proventricular spines and stomodaeal valve. C, spines of proventriculus, with plague bacteria, *Pasteurella pestis*, lodged among them. D, lengthwise section of oesophagus, proventriculus and anterior end of ventriculus from a rat flea, *Nosopsyllus fasciatus* (Bosc.), with stomach entrance blocked by a plug of plague bacteria. E, a flea having the proventriculus and stomach entirely filled with mass of plague bacteria.

Alnt, anterior intestine; *An*, anus; *b*, blood in oesophagus; *Mal*, Malpighian tubules; *Oe*, oesophagus; *Pp*, mass of *Pasteurella pestis* in proventriculus; *Prvnt*, proventriculus; *Rect*, rectum; *rp*, rectal papillae; *s*, proventricular spines; *SVlv*, stomodaeal valve; *Vent*, ventriculus (stomach).

among California ground squirrels Eskey (1938) points out that the native fleas of these rodents are relatively inefficient vectors of the disease as compared with the fleas of domestic rats, and do not readily transmit plague when feeding, even though they themselves may be infected. Eskey suggests that the biting and swallowing of fleas is probably an important means of spreading the disease among animals.

VII. THE THIRPS. ORDER THYSANOPTERA

The thrips are small or minute piercing-and-sucking insects, which derive their ordinal name from the fact that their slender wings are

fringed with long hairs. Some species, however, have no wings, and members of the same species may be either winged or wingless. The thrips feed for the most part on the sap of plants, including fungi, but some attack other soft-bodied insects. Occasionally, also, they become an annoyance to man, particularly at places in the country or at bathing resorts where there happens to be a large infestation on neighboring host plants, from which swarms of the tiny insects may settle on exposed parts of the body, giving an unpleasant tickling feeling or a pricking sensation. Certain species, moreover, have been found not only to "bite" human subjects, but even to suck blood. The evidence against the thrips on this score is reviewed by Bailey (1936). The Thysanoptera are here introduced not because of their occasional role as human pests, but because the structure of their feeding organs will serve as an introduction to that in the next order, the Hemiptera, which, studied alone, is difficult to understand.

The head of an ordinary thrips ("thrips" is singular and used also in the plural) is elongate with the face strongly receding and ending below in a small conical beak directed downward (fig. 36 A). The beak is composed of the labrum in front (*Lm*), the maxillae on the sides, and the labium behind (*Lb*). Enclosed by these parts are a median hypopharynx (*Hphy*), and three stylets not shown in the figure. The space between the hypopharynx and the inner wall of the labrum is the food meatus (*fm*), which leads up into a strong sucking pump (*CbP*) with its dilator muscles (5) arising on the extensive clypeal area of the head (*Clp*). Between the base of the hypopharynx and the labium the salivary duct opens into a narrow salivary pocket (*Slv*). The relations of the labrum, the hypopharynx, the cibarium (sucking pump), the salivary orifice, and the labium in the thrips are thus seen to be the same as in the cockroach (fig. 7 A). The special features of the thrips are in the structure of the mandibles and maxillae, though all parts of the feeding organs are subject to irregularities of form and an asymmetry that make their study somewhat confusing.

The mandibles of the thrips are not exposed externally; they are retracted into the head between the labrum and the maxilla and are contained in pouches of the head wall. Only the left mandible is functionally developed, the right being either greatly reduced in size, or absent. The persisting left mandible has the form of a stylet with an enlarged base (fig. 36 B), and is the piercing organ of the thrips. According to Reyne (1927) the mandible has retractor but no protractor muscles; in some forms, however, it is protractile by reason of a leverlike connection with the movable labrum. The mandible is

said to be used as a pick or punch operated by tapping movements of the head.

The maxillae consist each of an external lobe and a mesal stylet (fig. 36 C). The outer lobe (*MxL*), as above noted, lies in the side of the conical beak; it presents a broad basal region (*St*), evidently the stipes, bearing a small segmented palpus (*Plp*) and a tapering terminal part (*Ga*), which may be taken for the galea. The slender

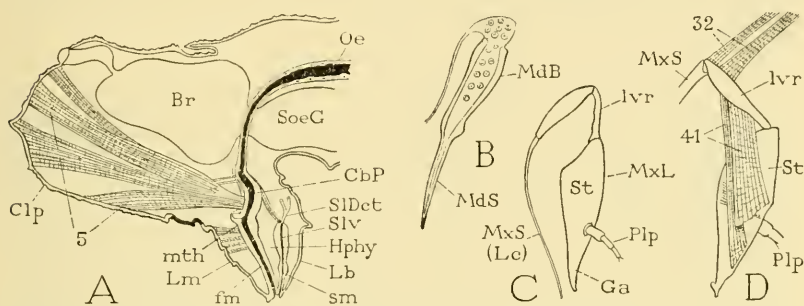


FIG. 36.—Feeding apparatus of a thrips. Order Thysanoptera. (A, B, C, from Peterson, 1915; D from Reyne, 1927.)

A, vertical section of head and beak of *Hercinothrips femoralis* (Reuter), showing sucking pump and its dilator muscles. B, mandible of same. C, maxilla of *Frankliniella tritici* (Fitch). D, maxilla with muscles of the stylet of *Heliothrips haemorrhoidalis* (Bouché).

Br, brain; *Cbp*, cibarial pump; *Clp*, clypeus; *fm*, food meatus; *Ga*, perhaps the galea; *Hphy*, hypopharynx; *Lb*, labium; *Lc*, lacinia; *Lm*, labrum; *lvr*, lacinal lever; *MdB*, base of mandible; *MdS*, mandibular stylet; *mth*, mouth of cibarial pump; *MxL*, maxillary lobe; *MxS*, maxillary stylet (lacinia); *Oe*, oesophagus; *Plp*, palpus; *SIDet*, salivary duct; *Slv*, salivarium; *sm*, salivary meatus; *SoeG*, suboesophageal ganglion; *St*, stipes.

Muscles.—5, dilators of cibarial pump; 32, retractor of lacinia; 41, protractor of lacinia.

stylet (*MxS*) is in some forms connected with the base of the stipes by a lever arm (*lvr*), and is protractile and retractile within the proboscis. The retractor muscles (D, 32) arise on the head wall and are inserted on the stylet and the lever; the protractors arise in the stipes and have their insertions on the lever. The structure and mechanism of the thrips maxilla, therefore, is practically the same as that of the flea (fig. 34 D), the principal differences being in the position of the palpus and in the presence of a joint between the stylet and the lever in the thrips. It has been shown by Reyne (1927) that the maxillary stylet of the Thysanoptera is developed from a secondarily detached part of the maxilla; the musculature leaves little doubt that it represents the lacinia, and a reference to the cockroach (fig. 4 B) shows how readily the lacinia (*Lc*) with its muscles (32, 41) might become an independent part by separation

from the body of the maxilla. The lever evidently belongs to the lacinia ; in the fleas it is merely the angulated basal part of the lacinia (fig. 34 G), in the Corrodentia a lever is not differentiated (fig. 10 G). The connection of the stylet with the lever and the insertion of the stipital muscles on it in the fleas and thrips shows that the lever is not the cardo as some writers have supposed it to be. The same maxillary structure will be encountered again in the Hemiptera, but in this order the stipital lobe has become united with the lateral wall of the head, and the maxillary palpus is suppressed.

VIII. THE SUCKING BUGS. ORDER HEMIPTERA

This order consists of the insects that entomologists regard as true bugs ; its most unpopular member is the bed bug. The Hemiptera are predominantly *beaked insects*, the proboscis of other sucking insects being seldom such a rigid structure as that of the bugs, or, if it is beaklike, it is never in other groups a characteristic feature of the entire order. According to the structure of the wings, though wings are not present in all species, the Hemiptera are divided into two suborders, one called the Homoptera because the fore and hind wings are of similar structure, the other the Heteroptera because the wings are usually different. The name Hemiptera is used by some entomologists for the Heteroptera alone, but by priority it includes both suborders.

Only a few of the bugs are bloodsucking insects, but the blood-feeders include the widely known bed bug, and some others termed conenoses, or assassin bugs, all of which belong to the Heteroptera. Most of the species feed either on other insects or on the juices of plants, and among the latter are many destructive pests of cultivated vegetables, flowers, and fruit trees, such as the leafhoppers, the aphids, the scale insects, the mealy bugs, the whiteflies, the red bugs, and the squash bugs. In their feeding apparatus the Hemiptera are the most specialized of all the insects, but since they have an "incomplete" metamorphosis they do not rank with the flies, the fleas, the beetles, the butterflies, or the wasps and the bees. Though our present interest in the order centers in the bloodsucking species, the feeding apparatus is of essentially the same structure in all. For a preliminary study, therefore, we may select one of the larger and better-known plant-feeding forms such as the cicada, a member of the Homoptera.

GENERAL STRUCTURE OF THE HEMIPTEROUS FEEDING APPARATUS

The head of a cicada (fig. 37 A) is conical with the apex downward. The prominent compound eyes (*E*) cap the lateral angles,

the long, strong beak projects ventrally and posteriorly from the lower end. On the face below the antennae is a large, bulging striated plate (*Clp*), which is the upper part of the clypeal region and hence named the postclypeus; below it is a smaller anteclypeus (*Aclp*). On each side of the head beneath the eye the head wall is produced downward in a prominent lobe (*MxL*) ending against the base of the beak. From developmental studies made on other Homoptera this lobe is known to be derived from the maxilla, and, from evidence that will presently appear, it is specifically the stipes. This lobe, in fact, corresponds with the maxillary lobe of the flea (fig. 34 A, *MxL*) and with the body of the maxilla in the thrips (fig. 36 C); in the Hemiptera it has been incorporated into the head wall, and the maxillary palpus has been suppressed. Between the maxillary lobe and the clypeus in the cicada is a narrow lateral sclerite known as the *lorum* (fig. 37 A, *Lor*).

The structure of the head and the beak can be studied best in a freshly emerged cicada, because at this stage the skin is soft and the various parts can be readily separated. With such a specimen (fig. 37 B) it is to be seen that a narrow tapering labrum (*Lm*) extends downward from the lower end of the anteclypeus, and normally (A) fits close against the base of the beak. Also now fully exposed on each side is a small, soft appendage (B, *Ga*) hanging from the lower edge of the maxillary lobe, and therefore suggestive of a much-reduced galea; in the natural condition (A) this appendage closes laterally the cleft between the labrum and the base of the labium. The beak itself dissociates into a cylindrical labium (B, *Lb*) and four very slender, bristlelike stylets. The labium is three-segmented and has no palpi; its anterior surface is deeply excavated by a groove in which normally are lodged the stylets, one pair of which is lateral, the other median. The lateral stylets (*MdS*) are extensions of the mandibles, the median pair (*MxS*) belong to the maxillae, their basal parts being concealed in pouches of the ventral head wall. Exposed before the stylets is a small, median, conical hypopharyngeal lobe (*HL*), and it is now to be seen that the loral plate (*Lor*) on each side of the head is an upward extension from the hypopharynx interpolated between the postclypeus and the maxillary lobe. Anterior to the hypopharynx is an opening, the food meatus (*fm*), leading into a large cavity, which is the lumen of the sucking pump.

Some writers have contended that the loral plates of the Hemiptera are parts of the clypeus, but the contention is entirely disproved by the fact that the clypeus and the lora are separated by deep inflections

of their adjacent margins that extend clear through the head; in other words, the respective lamellae of the internal folds are continuous from one side to the other. Laterally the lamellae are united, but medially they separate to form the lumen of the sucking pump, the clypeal lamella becoming here the anterior wall, or roof, of the pump, the loral lamella the floor of the pump (fig. 37 D). The clypeal lamella, therefore, is the "epipharyngeal" wall of the preoral food cavity, the loral lamella belongs to the hypopharynx, as do also the loral plates from which it is inflected.

A dissection of the head will reveal the basal structures of the mandibular and maxillary stylets, the internal elaboration of the hypopharynx, the composition of the sucking pump, and the salivary ejection pump. The stylets arise from the membranous walls of the containing pouches in the lower part of the head behind the lobe of the hypopharynx and mesad of the maxillary lobes. The hypopharynx has not been fully understood by most students of Hemiptera because it is complicated in an unusual manner.

To understand the nature of the hemipterous mandible, we must imagine that the appendage has been sunken into the head behind the loral plate of the hypopharynx, and that its apex has grown out into a long bristlelike stylet. The base of the stylet thus concealed is enlarged and gives off two arms (fig. 37 D). One arm (*ra*) goes upward in the wall of the containing pouch and gives attachment to a group of retractor muscle fibers (*28*) arising on the dorsal wall of the head; the other arm (*pa*) slants laterally with its outer edge exposed in the membranous fold of the head wall between the lorum and the maxillary lobe, and gives attachment to the protractor muscles (*29*) arising on the inner surface of the lorum. A third muscle (*27*) arising in the side of the head is inserted between the two mandibular arms, and is also a retractor. The two retractor muscles of the cicada mandible would appear to represent the cranial abductor and adductor of the jaw in a generalized insect (fig. 3 E, G, *27*, *28*). The loral muscle can be no other than the hypopharyngeal muscle of the mandible (*29*), since the loral plate is a lateral extension of the hypopharynx; this muscle in the cicada has become reversed in position by the dorsal retraction of the mandible and thus functionally converted into a protractor.

The maxillary stylet also is enlarged at its base (fig. 37 E), and it is connected with the maxillary lobe (*MxL*) on the side of the head by a lever sclerite (*lvr*). Retractor muscles (*32*) arising on the dorsal wall of the cranium are inserted directly on the base of the stylet, and protractor muscles (*41*) arising in the maxillary

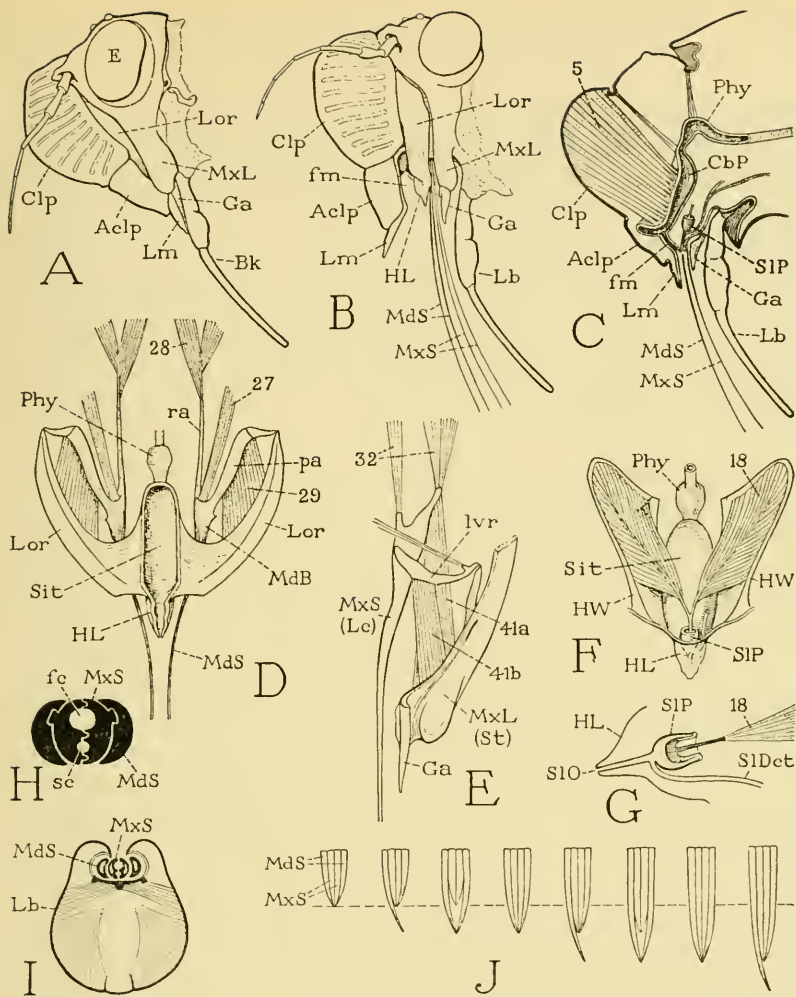


FIG. 37.—Structure and mechanism of the feeding organs of Hemiptera as exemplified in the Homoptera.

A, head of a seventeen-year cicada, *Magicicada septendecim* (L.), side view. B, same of newly emerged specimen with lower parts of head separated. C, median vertical section of cicada's head showing sucking pump and salivary ejection pump. D, hypopharynx and bases of mandibles of cicada, anterior view, diagrammatic. E, right maxilla of cicada, posterior view. F, hypopharynx of cicada, posterior view, showing wing plates, floor of sucking pump, and salivary pump with its muscles. G, diagram of salivary pump in vertical section. H, diagrammatic cross section of stylet fascicle. I, cross section of beak of cicada, showing stylet fascicle in groove of labium. J, diagrams illustrating penetration of the stylets according to Weber (1928, 1930).

Aclp, anteclypeus; *Bk*, beak; *CbP*, cibarial pump; *Clp*, clypeus; *fc*, food canal of beak; *fm*, food meatus; *Ga*, galea; *HL*, free lobe of hypopharynx; *HW*, posterior wing plates of hypopharynx; *Lb*, labium; *Lc*, lacinia (maxillary stylet); *Lm*, labrum; *Lor*, lorum; *MdS*, mandibular stylet; *MxL*, maxillary lobe (united with side of head); *MxS*, maxillary stylet (lacinia); *pa*, protractor arm of mandible; *Phy*, pharynx; *ra*, retractor arm of mandible; *sc*, salivary canal; *Sit*, sitophore; *SIP*, salivary pump.

Muscles.—5, dilators of cibarial pump; 18, dilator of salivary pump; 27, 28, retractors of mandible; 29, protractor of mandible; 32, retractors of maxillary stylet (lacinia); 41a, 41b, protractors of maxillary stylet.

lobe are inserted on both the stylet base and the lever. Here, therefore, we find again the same maxillary structure and mechanism as was seen in the fleas (fig. 34 D) and the thrips (fig. 36 D). The detached lacinia becomes an independently movable stylet of the piercing apparatus, supported on the maxillary lobe by a basal lever. The origin of the protractor muscles of the lacinia on the maxillary lobe of the head shows that the latter is the *stipes*, which, since the entire active function of the maxilla is now taken over by the lacinia alone, has become united with the cranial wall, giving a firmer support to the lacinia and better resistance to the pull of the protractor muscles of the latter.

The hypopharynx of the cicada comprises not only the small conical lobe projecting from the lower wall of the head in the usual hypopharyngeal position between the other mouth parts (fig. 37 B, *HL*), but includes also the floor of the sucking pump (D, *Sit*), the loral plates (*Lor*), and a pair of large, posterior winglike plates (F, *HW*) lying in the walls of the stylet pouches. The anterior surface of the free lobe (D, *HL*) contains a narrow food channel, and is continued up into the head where the channel widens into the deeply concave floor of the sucking pump (*Sit*). The lateral walls of the lobe, as already observed, are extended upward into the loral plates (*Lor*) exposed on the sides of the head (A, B), on which the protractor muscles of the mandibles (D, 29) take their origin. The loral plates of the Homoptera, therefore, evidently represent, greatly expanded, the small loral arms of the suspensory apparatus of the cockroach hypopharynx (fig. 6 B, *x*) on which the hypopharyngeal muscles of the mandibles (A, 29) are attached. In the Heteroptera the loral plates are usually small, and may be completely concealed beneath the edges of the maxillary lobes. The hemipterous hypopharynx is further complicated by an extension from its posterior surface of the pair of large winglike plates (fig. 37 F, *HW*) that form the posterior walls of the stylet pouches, and give attachment on their internal surfaces to the muscles of the salivary pump (18).

The sucking pump of the cicada is a large, capsulelike structure standing almost vertical in the lower part of the head (fig. 37 C, *CbP*). Its strongly sclerotized posterior wall is a deep oval basin corresponding with the sitophore depression on the base of the hypopharynx in the cockroach (fig. 6 A, *Sit*). The flexible anterior wall is invaginated into the concavity of the posterior wall, and on its midline are inserted huge bundles of dilator muscle fibers arising on the bulging postclypeus (fig. 37 C, 5). The compression stroke of the pump results from the elasticity of the anterior wall, which

springs back automatically when the dilator muscles relax, its anterior end coming down first drives the food liquid on toward the rear exit. The lateral margins of the pump are supported on the pair of plates formed, as above noted, by the united lamellae of the folds inflected between the edges of the clypeus and the lora. In figure 37 D the clypeal, or "epipharyngeal," lamella, including the roof of the pump, is supposed to have been removed, leaving only the loral (hypopharyngeal) lamella with the sitophore.

Following the cibarial pump in the cicada is a small pharyngeal sack (fig. 37 C, D, F, *Phy*), but since it has no particular development of its dilator muscles, it is probably not so important a pumping organ as in the lice, the nematoceros flies, and the fleas.

A salivary ejection pump is well developed in all Hemiptera. It is usually a short cup-shaped chamber turned backward from the end of the salivary duct (fig. 37 C, G, *SIP*), lying within the hypopharyngeal lobe and discharging through an exit duct opening at the apex of the latter (G, *SIO*). The plunger of the pump is a pistonlike invagination of the blind end of the chamber with an axial stalk on which are attached a pair of large convergent muscles (F, *18*) arising on the internal surfaces of the wing plates of the hypopharynx. The muscles retract the plunger, and saliva is drawn into the pump chamber from the salivary duct; expulsion of the liquid results from the elastic spring-back of the plunger when the muscles relax. Valves have been noted in some forms guarding the entrance and exit apertures of the pump.

When the parts of the hemipterous beak are all together in the natural functional position, the mandibular and maxillary stylets issuing from their pouches are entirely concealed within the groove of the labium (fig. 37 I). The maxillary stylets lie between the mandibular stylets with their inner surfaces in contact. The opposing walls are doubly grooved (H) and the grooves fit over each other so as to form two lengthwise, tubular channels. The anterior channel is the food canal of the beak (*fc*), the posterior channel the salivary canal (*sc*). Where the stylets diverge at their bases against the tip of the hypopharynx, the food canal opens into the groove on the anterior surface of the hypopharyngeal lobe (D) that leads back into the cibarial pump; the halves of the salivary canal embrace the tip of the hypopharynx so that the channel between them is in position to receive the ejected saliva. By this arrangement the saliva may be conveyed to the tip of the beak while the food liquid is ascending in the opposite direction through the food canal.

The piercing mechanism of the Hemiptera is fairly simple. The

only movements the stylets are capable of making are those of protraction and retraction, and the movement in each direction is very short because it can be no greater than the contraction length of the operating muscle. At each outward thrust, therefore, a stylet penetrates the food tissue by only a small fraction of its length; many repeated thrusts are necessary to gain an effective depth. The stylets, therefore, must retain their hold in the tissue with each successive penetration, otherwise the retractor muscles would simply undo the work of the protractors. In some species the stylets are anchored in the wound by barbs on their extremities, in others they are held in place by a muscular clamp in the base of the labium; in either case the force of the contracting retractor muscles, instead of drawing the stylets back, pulls the head down toward the feeding surface. Thus, when the stylets are first inserted, the head is held high, while feeding is in progress the head is low and the body tilted up behind. The labium does not in any case enter the feeding puncture. As the stylets sink deeper and deeper, the labium either is pushed back at its base into the membrane of the neck, or it bends back angularly at its joints.

In order to assure coherence of the four stylets in the fascicle during the penetration of a food tissue, the stylets in some forms are held together by dovetailed grooves and ridges on their opposed surfaces (fig. 37 H). The stylets can thus slide freely on one another, but are prevented from coming apart. Studies made by Weber (1928) on certain species of Homoptera show the procedure of the stylets in operation. The mandibles appear to be the effective piercing organs, and they work alternately; first one mandibular stylet (fig. 37 J) is thrust out and held in position, then the tip of the other comes down and meets it. The two maxillary stylets, enclosing the food and salivary conduits, are now pushed out together between the mandibles, after which the whole operation is repeated. The successive movements are very rapid, and gradually the stylet fascicle penetrates the food plant until a sap vein is tapped, when the stylets cease their action and the sucking pump begins its work.

More detailed descriptions of the hemipterous feeding apparatus, and comparative studies of its structure and mechanism in the Homoptera and Heteroptera are given by Weber (1928, 1930, 1933), Snodgrass (1935), and Butt (1943).

BED BUGS. FAMILY CIMICIDAE

The family of the bed bug belongs to the suborder Heteroptera, and includes a small number of species pertaining to several genera.

The common bed bug, pestiferous to man everywhere in temperate regions, and which will attack also household animals and poultry, is *Cimex lectularius* L. (fig. 38 A). Other species of *Cimex* that feed on human blood are limited to tropical and subtropical parts of Asia, Africa, and America. The rest of the family consists of species that live parasitically on bats and birds, or in birds' nests, one of these being a serious pest of poultry in the southwestern part of the United States and in Mexico. Insects of a possibly related family, the Polyctenidae, are exclusively bat parasites. Bed bugs are not known to be involved in the spread of disease, though it has been shown that they may themselves become infected with the agents of certain human diseases.

The bed bug appears to be specially adapted by its flat form for getting into the crevices of beds, but of course it existed long before beds were invented, and it might as well be said that beds were made to accommodate the bugs. The bed bug is not entirely a wingless insect; it has a pair of flaps on the mesothorax (fig. 38 A, W_2) that evidently are remnants of wings possessed by its remote progenitors. The broad abdomen has only eight exposed segments, but since the true first segment is suppressed, those that are visible are segments II to IX.

The head of the bed bug is broad as seen from above or below (fig. 38 B, C), and is set deeply into the prothorax between the large flanges projecting from the sides of the latter; in side view (H) the head appears to be conical, with the beak ordinarily turned downward and backward from the anterior end. On the dorsal surface (B, H) is a broad, spatulate anteclypeus (*Aclp*) projecting over the base of the beak; the postclypeal area is not defined by a suture, but it must include the extensive part of the dorsal head wall (L, *Clp*) on which the dilator muscles of the sucking pump (5a, 5b) are attached. A pale line on the head of an immature bug (B) does not appear to be a true frontoclypeal sulcus. Turning downward from the edge of the anteclypeus is a broad triangular labrum (C, H, *Lm*) covering the base of the beak anteriorly. At the sides of the beak and uniting below it are two flat projections of the head wall (C, H, *MxL*) that give attachment to the protractor muscles of the maxillary stylets (H, 41), and hence represent the maxillary lobes of the cicada (fig. 37 A, *MxL*). Loral plates are not distinct in the bed bug, but the area of the head wall on each side in the angle between the anteclypeus and the maxillary lobe (H, *Lor*) represents the lorum of Homoptera because it runs down beneath the maxillary lobe directly into the

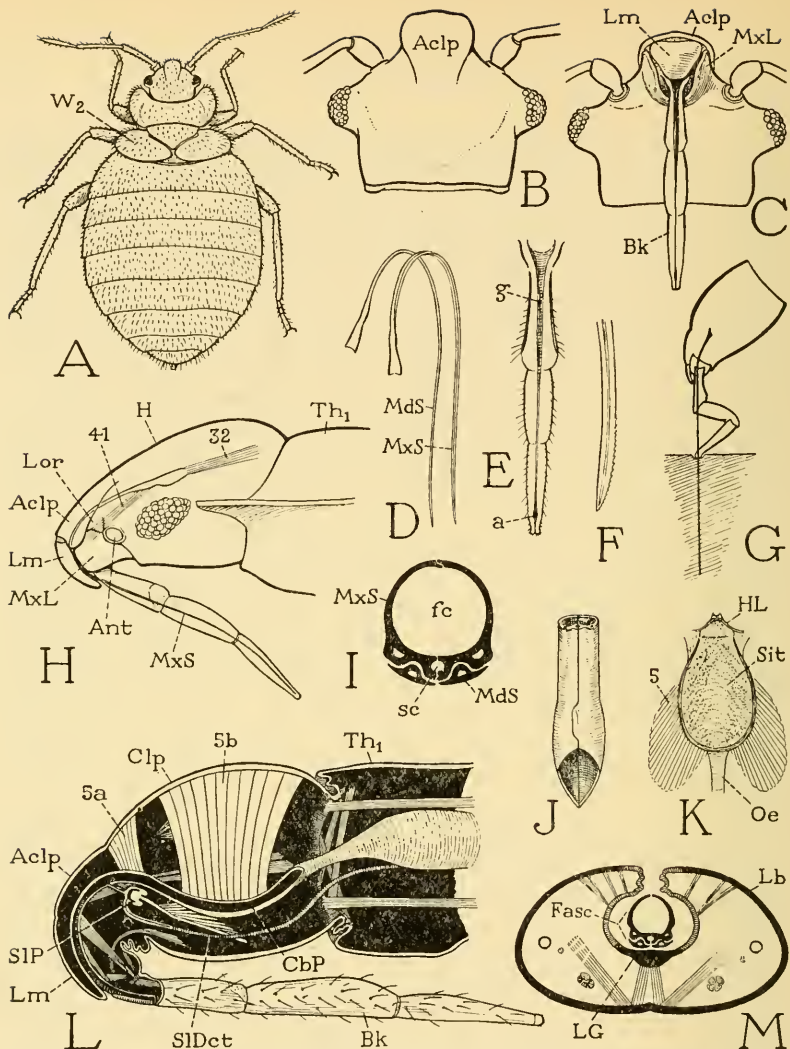


FIG. 38.—The common bed bug of Temperate regions, *Cimex lectularius* L., and its feeding organs. Order Hemiptera, family Cimicidae. (G, I, J, L, M, from Kemper, 1932.)

A, female bed bug (length 6 mm.). B, head, dorsal. C, same, ventral, showing beak. D, mandibular and maxillary stylets of one side. E, labium, anterior (ventral in flexed position). F, distal part of a mandibular stylet. G, position of head and beak with stylets deeply inserted during feeding. H, head and prothorax, left side, showing position and muscles of maxillary stylet. I, cross section of stylet fascicle. J, distal part of interlocked maxillary stylets. K, upper wall of hypopharyngeal lobe and floor of sucking pump, ventral, with dilator muscles attached on dorsal wall. L, lengthwise section of head showing sucking apparatus and salivary pump. M, cross section of beak through distal part of third labial segment.

a, subapical aperture of labial groove; *Aclp*, anteclypeus (tylus); *Ant*, base of antenna (removed); *Bk*, beak; *CbP*, cibarial pump; *Fasc*, fascicle of stylets in labial groove; *fc*, food canal; *g*, labial groove; *H*, head; *HL*, free lobe of hypopharynx; *Lb*, labium; *Lm*, labrum; *Lor.*, lorium; *MdS*, mandibular stylet; *MxL*, maxillary lobe; *MxS*, maxillary stylet; *Oe*, oesophagus; *sc*, salivary canal; *Sit*, sitophore (floor of sucking pump); *SID*, salivary duct; *SIP*, salivary pump; *Th₁*, prothorax; *W₂*, reduced wing.

Muscles.—*5a*, *5b*, dilators of cibarial pump; *32*, retractor of maxillary stylet; *41*, protractor of maxillary stylet.

side of the hypopharynx, and gives attachment to the protractor muscles of the mandibular stylet.

The beak of the bed bug is considerably longer than the head and when not in use is turned backward at its base with its distal part between the front legs (fig. 38 C, H). The outer part of the organ is the labium, which has four segments (E), but the short first segment is mostly concealed by the labrum and the maxillary lobes. On its anterior (or under) surface is a deep groove (*g*), which contains the fascicle of the stylets (M, *Fasc*). Near the tip of the last segment the lips of the groove diverge to leave a small aperture (E, *a*). The narrowed distal part of the labium ends with two small swellings bearing minute papillae, which are probably sensory organs.

The mandibular and maxillary stylets are held together in a fascicle within the groove of the labium (fig. 38 M). The mandibular stylets are much slenderer than the maxillary stylets and lie against the posterior surfaces of the former (I). Between the maxillary stylets is the relatively large food canal (*fc*) and a minute salivary canal (*sc*). At the base of the beak the stylets turn backward into the head pouches and on their enlarged bases are inserted the protractor and retractor muscles, there being no lever arm connected with either the mandibular or the maxillary stylet in the bed bug. The retractor muscles arise posteriorly on the head wall; the protractors of the mandibles arise on the loral extensions of the hypopharynx, those of the maxillae (H, 4I) on the maxillary lobes of the head.

The hypopharynx is a small, flat, triangular lobe (fig. 38 K, *HL*). Its dorsal surface is continued back into a large, oval deeply concave, basinlike sitophore (*Sit*) with strong lateral margins, which is the floor of the sucking pump (L, *CbP*). The thin dorsal wall of the pump when not in action is completely collapsed into the cavity of the ventral wall. The dilator muscles (L, 5a, 5b) consist of two huge lateral bundles of fibers (K), arising on nearly the whole upper wall of the head. There is no differentiated pharynx, the cibarial pump discharges directly into the tubular oesophagus. Within the hypopharynx is a small salivary ejection pump of the usual type of structure (L, *SIP*). The relation of the stylets to the hypopharynx and to the food meatus is the same as that described in the cicada.

When the bed bug feeds and the stylets are being driven into the flesh of the victim, the labium, as shown by Kemper (1932), accommodates the lowering of the head in part by a telescoping of the basal segments, but principally by a backward bending of the third and fourth segments in a sharp elbow (fig. 38 G). The stylet fascicle, however, maintains a direct course from the end of the second

segment to the subterminal aperture of the fourth (E, *a*), and is held at the puncture between the sensory apical lobes. The mandibular stylets would appear to be the effective cutting and piercing organs, since their distal parts are finely toothed (F); the closely adhering maxillary stylets are cut off obliquely at their tips (J), giving an opening into the food canal like that of a hypodermic needle. The irritation often produced by the bed bug's bite is supposedly due to the saliva injected into the puncture at the time of feeding. The bed bug feeds only on vertebrate blood, but it can survive a long time without food. A fully engorged bug becomes much altered in appearance, the ordinarily flat abdomen taking on a plump, oval form.

ASSASSIN BUGS. FAMILY REDUVIIDAE

Most of the common species of Reduviidae, known as assassin bugs or conenoses, are fairly large insects (fig. 39 A, B, C). They are predaceous in their feeding habits, and have a strong, three-segmented beak. While most of them attack other insects, some have developed a liking for the blood of mammals, and do not hesitate to attack man, particularly if he can be taken while asleep. Various species, however, including those illustrated at A and C of figure 39, will "bite" in self-defense if carelessly handled, and the resulting pain from such species is perhaps the most severe inflicted by any insect. On the other hand, certain species that attack sleeping human subjects are said to pierce the face or even the lips of their victims so gently that the latter may not even be awakened.

The head of an assassin bug is relatively small compared with the size of the body (fig. 39 C), but it is strongly constructed and has an elongate form (E). From its anterior end the thick beak curves downward and backward when not in use, with its tip lodged in a groove of the prosternum. The mandibular and maxillary stylets arise far back in the head behind the compound eyes (E, only the maxillary stylet shown); their protractor muscles (*4I*), therefore, are unusually long. In the flexed position of the beak the stylets follow the anterior curvature of the labium as they issue from the head, and their tips lie in the labial groove at the apex of the terminal segment. The labium has little flexibility at its joints and is not capable of making an elbow bend as in the bed bug and many other Heteroptera, but it is freely hinged to the head by its thick base, and is provided with strong muscles by which it can be turned vertically or directed anteriorly (E). When the beak swings forward the anterior side of the labial base folds into the head; the distance from the head to the

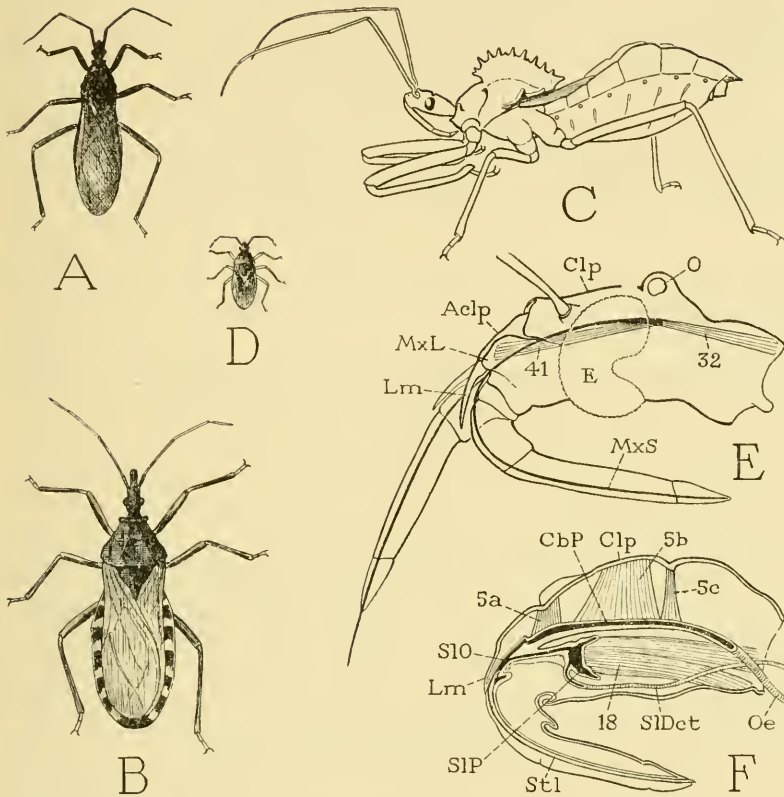


FIG. 39.—Assassin bugs, family Reduviidae, and a bloodsucker of the family Lygaeidae. Order Hemiptera. (A, B, C, D, one-third larger than natural size.)

A, *Reduvius personatus* (L.), a common, painfully biting assassin bug of Europe and North America. B, *Triatoma infestans* (Klug), a South American vector of Chagas' disease. C, the wheel bug, *Arilus cristatus* (L.). D, *Clerada apicicornis* Sign., a South American blood-feeding member of the Lygaeidae. E, head of *Reduvius personatus*, showing beak in positions of flexion and extension, and automatic protraction of stylets. F, section of head of same, showing sucking pump and salivary ejection pump (simplified from Weber, 1930).

Aclp, anteclypeus; *CbP*, cibarial pump; *Clp*, clypeus; *E*, compound eye; *Lm*, labrum; *MxL*, maxillary lobe; *MxS*, maxillary stylet; *O*, ocellus; *Oe*, oesophagus; *SIDet*, salivary duct; *SIO*, salivary orifice; *SIP*, salivary pump; *Stl*, fascicle of stylets.

Muscles.—*5a*, *5b*, *5c*, dilators of cibarial pump; *18*, dilator of salivary pump; *32*, retractor of maxillary stylet; *41*, protractor of maxillary stylet.

tip of the beak is thereby shortened, and the stylets automatically protrude from the apex of the beak. With the beak fully extended the stylets are thus protracted a distance equal to the length of the terminal segment of the labium (as shown in the extended beak of figure 39 E). The stylets can now be still farther pushed out by the contraction of the long protractor muscles. Considering the size of the bloodsucking species, these bugs are thus able to penetrate the skin of their victims; smaller species feed on soft-bodied insects.

The sucking pump of the Reduviidae is long and slender (fig. 39 F, *CbP*); it lies horizontally in the head and is amply provided with dilator muscles (5). Because of the length of the pump, the clypeal area of the head wall, which accommodates the pump muscles, is extended far back on the upper surface of the head (E, F, *Clp*). The salivary pump is unusually large in the species figured (F, *SIP*), which is a painful biter, and evidently is equipped for injecting a large dose of its toxic saliva into the wound made by the stylets.

Assassin bugs that habitually feed on human blood are vectors of at least one serious human malady, that known as Chagas' disease, or Brazilian trypanosomiasis, occurring in South America and Panama, but particularly prevalent in Brazil. The causative agent of the disease is a protozoan blood parasite of mammals, *Trypanosoma cruzi* Chagas, which evidently is more widely spread among wild animals than cases of the disease in human subjects would indicate, since the organism has been found in native wood rats of southern California. The insect vectors become infected from the blood of an infected person or that of any of the various wild animals that form a perpetual source, or "reservoir," of the disease in nature. The trypanosomes undergo a metamorphosis and development in the alimentary canal of the bug, and it is by means of the feces of the latter, ejected at the time of feeding, that the disease is spread. The bugs attack exposed parts of sleeping persons, usually the face or the lips, and inoculation results from scratching the infected feces into an abrasion of the skin, or from penetration of the trypanosomes into the mucous membrane of the mouth. Fully 20 species of reduviid bugs are known to be vectors of the disease agent, of which one is shown at B of figure 39.

Various other species of predaceous Heteroptera are likely to "bite" when handled or to attack man under unusual conditions (see Myers, 1929; Lent 1939). In the family Lygaeidae, however, members of the genus *Clerada*, widely distributed in the Tropics, said by Myers to be known as the "squirrel bug" in India, are true blood-suckers that will feed on man, though they usually inhabit the nests

of animals. Ferreira and Deane (1938) give a report of investigations on the American species *Clerada apicicornis* Sign. (fig. 39 D) in Brazil, where the insect was found to be abundant in human habitations. The bloodsucking and domiciliary habits of this species, therefore, make it another possible transmitter of Brazilian trypanosomiasis (see Lent, 1939).

The digestion of hemoglobin in the alimentary canal, and the distribution of its disintegration products in the body tissues of a reduviid and other bloodsucking insects is discussed in a recent paper by Wigglesworth (1943).

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