

Manual of medical entomology

Fourth edition

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Preface

With the fourth edition of the *Manual of Medical Entomology*, we have expanded the taxonomic keys to encompass a broader geographic scope of arthropods of medical or veterinary importance. This manual had its beginning as an assemblage of mimeographed keys used by students in the medical entomology course at the University of California, Berkeley. For that reason the early editions emphasized the fauna of California. In addition to including more of the common medically important species of North America, with this edition we have expanded coverage to include genera of mosquitoes of the Western Hemisphere and genera of the kissing bugs of the world.

Users of earlier editions will recognize many of the illustrations used here, but nearly all have been redrawn, and more than 200 new ones have been added to augment new key sections or to illustrate poorly understood characters.

The improved quality of this revision is due in large measure to generous contributions and constructive suggestions made by colleagues and specialists of the various arthropod groups. We acknowledge this help with sincere gratitude. Our special thanks go to Roger D. Akre, Richard F. Darsie, K. C. Emerson, Stephanie Clark Gil, K. C. Kim, Robert W. Lake, John F. MacDonald, Thomas N. Mather, Bernard C. Nelson, Harold E. Stark, William J. Turner, George Uetz, and Robert K. Washino.

Finally our appreciation goes to those former students in our classes of medical entomology at the University of California, Berkeley, at the University of Delaware, and at Washington State University, who through their questions and suggestions have helped in a grand way to improve this, our latest effort. It is to them and to the students yet to come that we dedicate this manual.

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Introduction

Medical entomology is a biological science dealing with arthropods that affect the health of humans or other vertebrate animals, through their ability to transmit causal agents of disease, through their direct attacks, or as a result of the harmful effects produced by contact. This defines medical entomology in the broad sense to include both public health and veterinary entomology.

This manual is primarily a teaching tool to familiarize students with the use of taxonomic keys for identifying medically important arthropods and with those characters of taxonomic value for each of the diverse groups of arthropods. Accurate identification is essential to any definitive diagnosis of an arthropod infestation and hence to valid recommendations for its control. The second purpose of this manual is to serve as a concise reference collection of keys for the medical entomologist as the first step in identification of medically important arthropods before more specific keys are employed. These exercises then are largely in the form of taxonomic keys which, with the help of illustrations, are designed as studies in diagnosis and not in systematic entomology. Additional techniques are described for the study of arthropods.

Initial study is made of a generalized arthropod, followed by brief, intensive consideration of several lines of development undergone by arthropod mouthparts, inasmuch as structural variations from the generalized types not only provide guideposts to identification, but also serve as important clues to function of the organ and habits of the organism. Techniques of rearing, collecting, preserving, and mounting arthropods for study are covered. Proper dissection of arthropods and methods of identifying a blood pathogen and the source of a blood meal are described.

In using the syllabus it is necessary that the student read the exercise before reporting to the laboratory, correlating with it information gained from the textbook and collateral reading in reference works. Very few drawings are required because most of the more difficult key characters have been illustrated. However, the conscientious student should add labeled sketches of his own whenever questionable characters appear with the specimens provided. In this way structures can be clarified that otherwise might be misinterpreted if based only upon a description.

In addition to the formal laboratory exercises each student should prepare one or more special reports detailing the life history of these subject arthropods. If possible such arthropods should be collected from their natural habitats and reared so that preserved, mounted, and labeled specimens will serve as part of the report. The report also may include literature research of the original taxonomic description of the arthropod to emphasize those specific characters that distinguish it from all other species. The student may need to prepare his own original descriptions for life stages that have no published descriptions.

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1 Insect morphology

The vast majority of all known kinds of animals (72%) are insects. Each kind, or species, of insect has its own ecological niche requirements, and no two species have the same set either of requirements or of behavioral traits. These differences translate into an array of morphological modifications that better adapt a species to its niche. Such morphological differences can be used to distinguish one species from another. The correct identification of a medically important insect or other arthropod is the primary step in accomplishing its control or elimination.

Identification of the myriad insects and other arthropods that are of medical importance requires that students be able to compare and visually discriminate among a wide range of structural characteristics that differ among species. By the use of dichotomous keys, comparisons are made sequentially to lead a student or researcher through a series of correct descriptive choices that best matches the specimen at hand.

In order to use the keys, the student or researcher must be familiar with the structural terminology that describes the generalized insect. Many such terms are used throughout the keys in this manual regardless of the group being studied. In addition, there are a few terms used only for structures peculiar to certain groups of insects (e.g., ectospermalege in Cimicidae; trumpet and air tube in mosquito pupae and larvae, respectively). The student must learn these peculiarities in order to become familiar with the use of keys for various groups important to the medical entomologist.

As a starting point, this exercise will introduce terms for structures that make up any insect. This knowledge will equip you, the student, to practice using dichotomous keys as an aid to identifying unknown, medically important insects. This knowledge also will prepare you to make comparative judgments of insect morphology – that is, a functional interpretation of advantages or disadvantages of structural modifications or specializations in medically important insects.

A generalized insect: the cockroach

Study the cockroach – any house-frequenting species will do – as an example of a generalized insect of minor medical importance. Cockroaches are modestly specialized with respect to their running capabilities, or cursorial habits, and their structure has changed little in the last 350 million years. Using the following description and Figure 1.1 as a guide, locate those structures that are visible on your cockroach specimen.

The adult insect body is divided into three functional regions: **head** (the nerve and sensory control center and the food-ingesting unit), **thorax** (the locomotor unit), and **abdomen** (the food-digesting, food-assimilating, and reproductive unit).

Head

The head bears the mouthparts (with their associated appendages as palpi), one pair of antennae, the ocelli (if present), and the compound eyes. Chewing-type mouthparts, as in the cockroach, are considered to represent a relatively primitive or generalized type. Other insects demonstrate more specialized types: piercing-sucking and sponging. Mouthparts will be considered in more detail in Exercise 2.

The six segments that make up the head are largely fused with each other, so there are few external morphological landmarks that give clues to the limits of distinct segments. Thus most subdivisions of the head are designated as regions or areas. The clypeal region of the head is the area to which the labrum or front “lip” is appended. The occipital head region is the back of the head capsule, and the ocellar, or vertex, region is between the eyes. The genal regions are the sides of the head and the cervical region is the neck. The stomal, or oral, region includes the mouthparts and the supporting margins of the head capsule.

Thorax

The thorax is composed of three segments. Proceeding from front to rear (anterior to posterior, or cephalad to caudad), they are the **prothorax**, **mesothorax**, and **metathorax**. Each of these segments bears

one pair of legs. The legs are divided into distinct sections, as the name **arthropod** (jointed leg) implies. The small, proximal segment – that one attached to the body – is the **coxa**. Moving distally (toward the extremity of the leg), the segments in order are **trochanter** (also a small segment), **femur**, **tibia**, and **tarsus**, the larger leg segments. The tarsus is usually subdivided into a number of tarsal segments, characteristically five, and terminates in a **pretarsus**. The pretarsus (Figure 1.2) consists of a central **arolium**, typically padlike; a pair of **claws** (ungues); and an **unguitractor plate**. The arolium may be modified into a spinelike process, the **empodium**, and under each claw there may be a straplike or padlike **pulvillus**.

The meso- and metathorax each possesses a pair of wings except for very primitive insects or specialized insects that have secondarily lost their wings during the course of evolutionary changes. The **wings** are formed from membranous expansions of the thoracic body wall that are reinforced or strengthened by tubular thickenings called **veins**. The form and location of specific veins are important characters for identification of many flying insects.

Many groups of insects (orders) possess both pairs of wings, which function in the characteristic mode of lift surfaces moved in flight. In some groups, wings also may be modified for other functions such as shields to protect the fragile flight wings (e.g., cockroaches and beetles) or as gyroscopic balances used in flight (e.g., flies).

The meso- and metathorax also each typically bears a pair of lateral spiracles (respiratory apertures).

Thoracic segments are made up of a number of hardened plates, or **sclerites**. The dorsal sclerite is called the **notum**, the ventral sclerite is the **sternum**, and the lateral sclerites are **pleura**. A pleuron may be subdivided into smaller units with names such as **mesepimeron**, **metepisternum**, **hypopleuron**, and **meron**. These details will be treated more fully in those exercises where pleurites are used as key characters.

Abdomen

The abdomen of more primitive insects usually is composed of 11 segments, but in higher groups normally only 9 or 10 are visible. The terminal segments may coalesce or telescope so that only 3 or 4 can be seen without manipulating the specimen. The dorsal sclerite of each segment is the **tergum** (or tergite) and the ventral sclerite the **sternum** (sternite). If distinct lateral plates are present, as in the sucking lice, they are called **pleura**, or pleurites. Each pleurite, or the pleural region of the tergite, usually surrounds the external respiratory opening, the **spiracle**.

The caudal (posterior) region of the abdomen typically bears the external **genitalia** and associated structures and terminates with the **anus**. Male genitalia tend to be more elaborate and conspicuous, taking the form of claspers, rods, and an intromittent apparatus. Female genitalia are simpler, often valvelike or slitlike, and may be telescoped to be quite hidden. In a few groups the female ovipositor is elongated into a conspicuous structure for subsurface egg depositing or as a defensive weapon (e.g., bees, wasps).

Comparison of cockroach with a higher insect

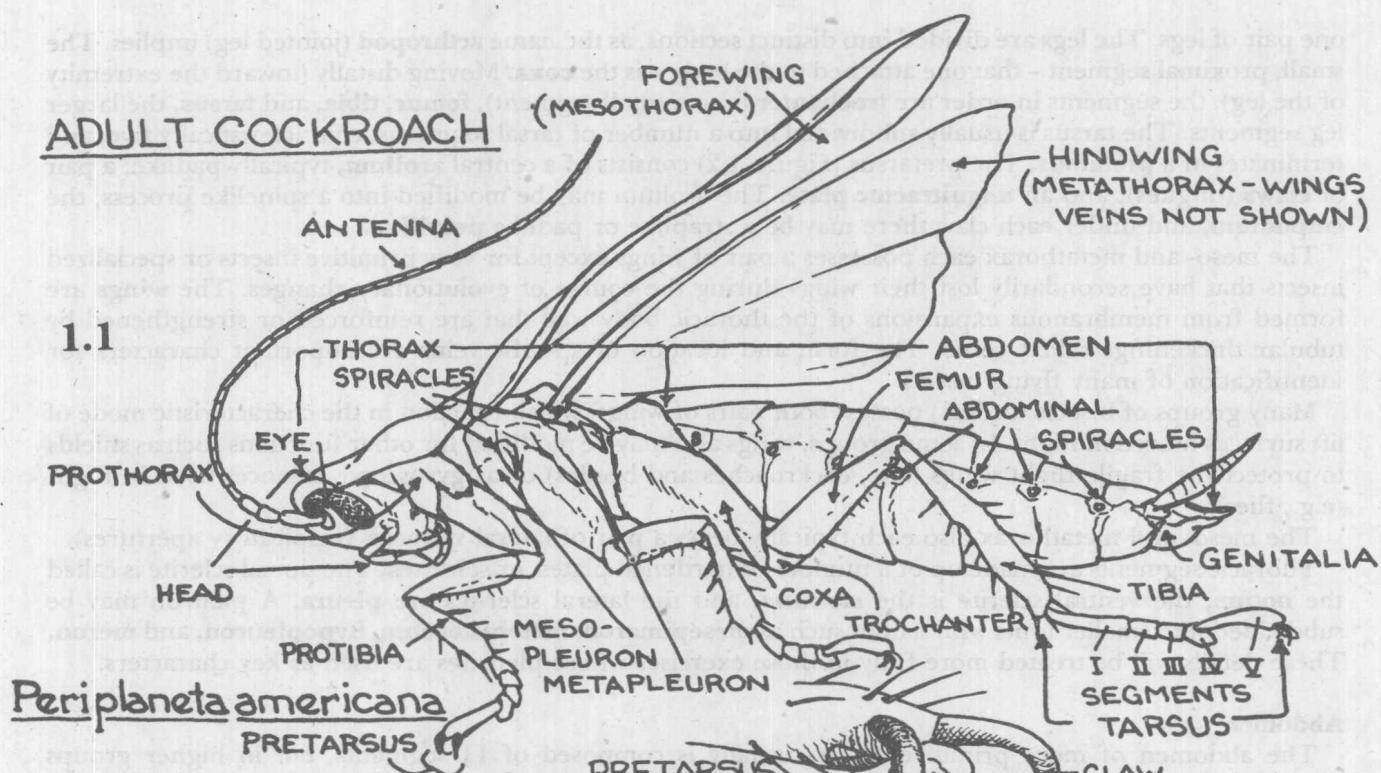
After completing study of the cockroach, examine a higher insect (such as a blow fly or a house fly) and locate the structures homologous to those of the cockroach that occur on that insect. Use Figure 1.3 to aid in making this comparison. Note the exaggerated morphological dominance of the mesothorax, reflecting the more highly developed capabilities of flight in flies.

If time is available, further detailed comparisons of sclerite homologies can be made within the Diptera using the thorax of the mosquito, horse fly, or house fly.

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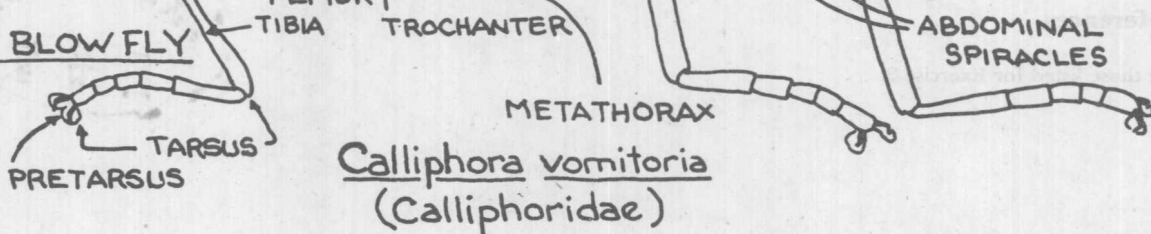
See those listed for Exercise 2.

ADULT COCKROACH



ADULT BLOW FLY

1.3



Calliphora vomitoria
(Calliphoridae)

2 Mouthparts

Insect mouthparts may be divided into two general categories: (1) chewing or mandibulate, as found in the cockroach, beetle, and bird louse; and (2) sucking or haustellate, as found in the bed bug, mosquito, house fly, flea, and butterfly. Sucking mouthparts can be subdivided further into (a) piercing, as in the mosquito, body louse, bed bug, and flea; and (b) nonpiercing, as in the blow fly and house fly.

The basic preoral (before the true mouth) structures of all insects have evolved from the type used in a generalized chewing function, with the **mandibles** as the principal tearing and probing structures. Sucking mouthparts are modified greatly from the chewing type, often with the elongated **maxillae**, **mandibles**, and variously modified **labium** as the principal structures. Most medically important insects belong to the category with sucking mouthparts.

Chewing insects typically feed on solid substrates, as opposed to sucking insects, which feed on various fluids. As vectors of pathogens, chewing insects are of far less importance than sucking insects to the medical entomologist, but study of chewing insects' mouthparts is needed as reference for understanding the origin and functioning of those highly modified structures seen in sucking insects. Chewing insects can serve as intermediate hosts of helminth parasites of vertebrates and as mechanical vectors of disease agents, but they do not introduce pathogenic agents into deeper tissues while feeding. Sucking insects, however, are able to introduce pathogens into subsurface tissues, including the bloodstream, and thus are of major importance as vectors of disease-causing agents.

Basically, insect mouthparts consist of upper (**labrum**) and lower (**labium**) lips separated by two pairs of lateral jaws (**mandibles** and **maxillae**), which embrace a central tonguelike structure (**hypopharynx**). The proximal anterior surface of the hypopharynx closes the back of the **true mouth**, and its posterior surface marks the location of the salivary pore. The front of the true mouth is closed by the posterior wall of the labrum, the **epipharynx**. Among different groups of insects, different oral structures are modified or exaggerated to be used as principal food-getting mouthparts. The labrum (or labroepipharynx) and hypopharynx are integral outgrowths of the cranial wall, whereas the mandibles, maxillae, and labium evolved from segmented appendages of the fused cephalic segments and are homologous to the thoracic legs.

Basic chewing-type mouthparts (Figure 2.1A-F)

Chewing mouthparts occur in cockroaches, locusts, crickets, beetles, and immatures of most holometabolous insects. Examine the head of a cockroach, and locate and manipulate the oral structures identified in Figure 2.1A-F. Dissect the mouthparts free from the head beginning with the labrum and proceeding to the labium while referring to the following description of preoral structures.

Labrum

This is a flaplike, sensory dorsal lip; there are gustatory areas on the ventral, or epipharyngeal, surface. The labrum is bounded above by the **clypeus**, but hangs free below. The labrum functions to keep food in the preoral cavity and to protect the basal articulations of the mandibles.

Mandibles

These are paired, darkly pigmented jawlike structures exposed upon removal of the labrum. They are toothed on the inner, or mesal, aspect and serve as the main scratching, grasping, cutting, and masticating structures. They articulate in a transverse plane, pivoting at two points located on the rim of the cranium. The cutting areas are distal, whereas the molar areas are proximal; these areas may be used separately or simultaneously. The basal mandibular brushes help align food.

Maxillae

Removal of the mandibles reveals the paired maxillae. Each is a complex of three distal units (**galea**, **lacinia**, and a segmented **palpus**) supported basally by the **cardo** and **stipes**. The lateral flaplike galea partly covers the outer face of the mandible and functions as a lateral lip closing the sides of the preoral cavity. The lacinia is distally toothed (maxadentes) and manipulates all food pieces cut by the mandibles. The maxillae open and close and rock back and forth simultaneously (on a single point of articulation on the cardo) in opposite phase to the mandibles. They push cut pieces of food into the preoral cavity for mastication in mandibular molar areas; they are used for secondary mastication of soft foods and serve to hold the food bolus in the preoral cavity from below. The lacinarasta (brushes) are probably tactile. The paired maxillary palpi function as sensory structures to locate food near the head and drum on food and feeding surface. The palpi determine food alignment (but do not manipulate food) in the preoral cavity and possess gustatory areas.

Hypopharynx

This is a fleshy lobe or tonguelike structure protruding into the preoral cavity between the bases of the maxillae. The salivary duct opens at its ventral base. The hypopharynx helps mix salivary secretions with the food bolus in the preoral cavity. It is mainly gustatory in function. Retraction of the hypopharynx helps draw the bolus from the preoral cavity through the **true mouth** and into the pharynx.

Labium

This is a complex, hinged flap that acts as the lower lip and resembles a pair of medially fused maxillae. The labium forms the floor, or back, of the preoral cavity and consists of a **mentum** base subdivided into smaller units, paired segmented **palpi**, and distal lobes, the **glossae** and **paraglossae**. The labium is a sensory structure, seldom functioning to align food. The paraglossae are displaced laterally during feeding as the labium pushes its salivary wetted anterior surface against the food bolus.

Observation of chewing operation

Operation of chewing mouthparts can be observed in the following way.

Starve and withhold water from a cockroach for 24 hours, and fasten the live specimen, belly up, in a dish of warm paraffin. Hold the insect in place until the paraffin cools and hardens. Under a stereoscopic microscope offer the immobilized insect small amounts of banana, honey, or a sweet fluid (e.g., soft drink) on the tip of an applicator stick. Watch the movement and sequence of feeding by the battery of preoral structures. The feeding action can be summarized as follows: cutting and tearing pieces of food by mandibles; manipulation, and some mastication, by the maxilla; transport into the pharynx from the preoral cavity by the hypopharynx; the labrum, mandibles, galea, and paraglossae all functioning to confine the food to the preoral cavity. Even though chewing and sucking appear to describe distinct modes of ingestion, preoral structures of both types must also function in the common role of drinking or imbibing fluids.

Understanding the progressive transition and modification of piercing-sucking mouthparts from the basic chewing function is not as illogical or difficult as one might assume. The following types and subtypes are described to represent this transition, using arthropods of some medical importance.

Modified chewing-type mouthparts, mallophagan type (Figure 2.2)

The mouthparts of the more primitive bird lice (Mallophaga, Amblycera) show essentially the same arrangement of preoral structures as seen in the cockroach. The small size and depressed head form of the chewing louse require that the mouthparts be examined on a cleared, slide-mounted specimen. Study the mouthparts of an amblyceran under a compound microscope and locate those structures illustrated in the accompanying figures. The opposable **mandibles** are dark and heavily sclerotized. Exceptional differences from the basic chewing-type mouthparts are the picklike development of the **lacinial lobe** of the maxilla and the coordinated development and working of epipharynx and hypopharynx into a "crest" and "sitophore" to help shuttle feather barbules, or skin scrapings, into the pharynx (Buckup, 1959). The **galeal lobe** of the maxilla operates in a jawlike movement, but the lacinial lobe acts independently. The lacinia has

a set of simple protractor retractor muscles to allow an in-and-out probing action by the thornlike lacinial tip.

Piercing mouthparts, hemipteran type (Figure 2.3)

The piercing-sucking apparatus of the hemipteran, or true bug, type is characterized by a fascicle of four, much elongated, thin, piercing stylets homologous with the mandibles and maxillae of the basic chewing mouthparts. These stylets are ensheathed in the large protective labium when not in use. Both labrum and hypopharynx are small and inconspicuous; they appear to have little direct function in feeding. Examine the proboscis or rostrum of an assassin bug (*Reduviidae*), and locate the structures shown in Figure 2.3.

In feeding by the triatomine, *Rhodnius prolixus*, the protracted labium makes contact with the feeding surface and usually ejects fluid from its tip, which quickly hardens to form a supporting feeding collar, or cone. The **labium** is shortened by telescoping and bending to give greater exposure to the stylets. The barbed mandibles probe with rapid alternating movements to draw and anchor the fascicle in the feeding surface. The **maxillae** are interlocked to form the dorsal food canal and salivary duct; they slide back and forth on each other to make deeper sampling thrusts and withdrawals (as deep as 1.5 mm) until a suitable blood vessel is penetrated near the entry site. In bed bugs the proboscis (labium and the contained stylets) is swung forward to about a 90° angle, and the body is flexed to produce a hump at the thorax; the bed bug rocks back and forth as the fascicle is thrust in and out of the feeding surface (Usinger, 1966).

Piercing mouthparts, anopluran type (Figure 2.4)

Anopluran mouthparts represent one extreme modification of the basic structures for a piercing function. In the Anoplura, the styletlike mouthparts are largely retracted internally into a ventrally located cephalic sac when not in use. Usually the labrum is the only visible mouthpart externally; it forms part of a short, eversible, snoutlike tube known as the haustellum, or mouth cone. Partial eversion of the haustellum exposes the buccal teeth, which are used to penetrate the outer, or horny, layer of host skin with a rapid action described as like a "rotary saw" (Lavoipierre, 1967). The completely embedded haustellum is then fully everted so that the buccal teeth anchor the head to the substrate.

The three piercing stylets, formed as a single bundle, are forced by muscle contraction from the cephalic sac out through the haustellum to probe for a capillary. Stylets usually probe 50–100 μm into tissues beyond the haustellum, but they are capable of extension triple that distance. The probing stylet bundle can be flexed from one side to the other as much as 45° and can be withdrawn very rapidly. The haustellum remains embedded for some time following withdrawal of the stylets.

The dorsal stylet is believed to be maxillary in origin, the median stylet is formed from the salivary duct, and the ventral stylet with serrated tips is formed from fused apical elements of the labium. There is no vestige of the mandibles remaining (Stojanovich, 1945). Another unique feature of the anopluran head is the **obturaculum**, an elastic, cupulate plug that separates the head cavity from the thorax. Retractable muscles originating on the obturaculum are inserted on the proximal arms of the piercing stylets (Stojanovich, 1945).

Piercing-sucking mouthparts, dipteran types

Mouthparts of flies are basically suctorial in nature, with both piercing and nonpiercing types represented. There is generally a wide diversity of mouthpart structures among Diptera. Internally, the preoral area is developed into a strong sucking diaphragm pump, the **cibarial pump**. Externally, the elongated piercing stylets are sheathed by the conspicuous labium except where the labium itself is the principal piercing structure. In some families mouthparts are reduced, or vestigial, and nonfunctional in the adult flies (e.g., Gasterophilidae and many Oestridae).

Three subtypes characterize adult dipteran mouthparts: the horse fly-mosquito subtype, the house fly subtype, and the stable fly subtype. These subtypes are described below. Study fresh or slide-mounted specimens representing each subtype.

Horse fly subtype (Figure 2.6)

This is the generalized subtype, which is both piercing and sponging in function and represents the mouthparts of hematophagous lower Diptera (e.g., mosquitoes, black flies, punkies, sand flies, snipe flies, and horse flies). Visualize the basic elements of the chewing-type mouthparts as being elongated to form a proboscis; the finer elements are ensheathed in a prominent labium. When this type of proboscis is examined in cross section, the similarity of mouthparts arrangement to that of the chewing type is made clearer.

The **labrum** is an elongated passive structure that closes the roof of the food canal. Immediately behind the labrum are the **mandibles**. In most groups of blood-sucking lower Diptera the mandibles operate in a transverse plane much as do those of the basic chewing-type insect. However, their operation is more analogous to the shearlike snipping of scissors because of the contiguous interaction of the flattened mandibular blades. The scissoring movement permits the mandibles to slide between the apposed labrum and **hypopharynx**.

In mosquitoes (Figure 2.5) the mandibles move within a vertical, or probing, plane resulting from a change in position of mandibular musculature (Hudson, 1970). They move vertically adjacent to the labrum and apposed hypopharynx. In this case the mandibles do not appear to play a major role in probing entry, but serve to shield the maxillary teeth during withdrawal of the stylets.

The **hypopharynx** is a single median stylet traversed by the salivary duct and connected basally to the **salivary pump**. It generally forms the floor of the food canal by more-or-less close adherence to the exposed **epipharyngeal groove** of the labrum. In mosquitoes, however, the labrum and hypopharynx form a rather tight seal to produce the food canal.

The **maxilla** is developed from the maxillary lacinia of chewing-type mouthparts. The paired maxillae are the principal probing and anchoring structures of the piercing stylets. They lie ventrolaterad to the labrum and move alternately to pull the stylets into the feeding substrate through the anchoring and cutting action of their distal, posteriorly directed teeth (Figure 2.5).

The **labium** is the largest of the mouthparts and is homologous to the chewing-type prementum. It is unpaired, and the dorsal gutter receives the slender piercing stylets when in repose. During blood feeding the labium is elbowed back to expose the biting stylets. At the apex of the labium is a pair of flexible lobes, the **labella**, which represents the paraglossa of more generalized mouthparts. In the act of blood feeding, the labella serve to support the piercing stylets at the point of skin entry. In many flies the labellar surface is traversed by closely set, fine channels (**canaliculi**) directed toward the embraced stylets. Canaliculi direct surfacing blood to the food canal to be sucked up during feeding.

A pair of internal head pumps produces the suction needed to draw blood from the feeding substrate (Figure 2.6). The **cibarial pump**, the larger of these, contracts alternately with the **pharyngeal pump** to shuttle blood into the **esophagus**. Cibarial pump muscles originate on the clypeus and insert on the anterior wall of the pump. Both pumps are of a simple diaphragm-type structure with a rigid wall and a flexible wall. The flexible wall is drawn by muscle action to open the lumen of the pump, and relaxation causes the wall to close the lumen by inherent elasticity. A similarly constructed, third, internal head pump, the **salivary pump**, lies posterior to the rigid wall of the cibarial pump. Muscles to operate the salivary pump originate on the rigid wall of the cibarial pump. Action of the salivary pump forces secretions through the hypopharynx to be released at the tip of the stylets (Bonhag, 1951).

Make a parasagittal cut and dissection of the head of a freshly killed or preserved horse fly. The three pumps can be located and their action determined. Only females have well-developed mandibles in this type of mouthparts, and only females will pierce tissue to suck blood.

House fly subtype (Figure 2.7)

The majority of Diptera possess the nonpiercing, sponging type of mouthparts exemplified by the house fly and blow fly. In this subtype both males and females have similar oral structures with small differences. The large fleshy proboscis, formed by the **labium**, is most prominent. The labium terminates in a pair of sponging or rasping organs, the **labella** (like that seen in the horse fly subtype). Minute grooves in the labellar surface function like canaliculi of the horse fly labium, but are called **pseudotracheae**.

With the exception of the **maxillary palpi**, both mandibles and maxillae are inconspicuous, having been incorporated into basal elements of the labium and preoral area. Lying on top of the grooved labium is the short, spadelike **labrum-epipharynx**. The **hypopharynx** is pressed close posteriorly to the labrum and thus forms the **food canal** with the deeply grooved epipharynx.

Internally there are only two pumps: the enlarged, heavily muscled cibarial pump and a smaller salivary

pump. Make a parasagittal section of the head of an adult blow fly or flesh fly and compare the internal structures with those of the horse fly subtype.

Stable fly subtype (Figure 2.8)

This subtype of dipteran mouthparts is found in the stable fly, horn fly, tsetse fly, and the ked, or louse fly, and its relatives. This subtype is specialized for piercing only and consists of a rigid proboscis formed from the **labium**, **labrum**, and **hypopharynx**; it has the same elements as the house fly subtype, but the labium is the principal piercing structure. The small **labellar lobes** at the tip of the labium are armed with rasping denticles, **prestomal teeth**, which cut into the substrate and anchor the proboscis during blood feeding. The food canal is formed by the ventral groove of the labrum-epipharynx in close apposition to the labial gutter. As with other subtypes, the hypopharynx is traversed in length by the salivary duct. **Maxillary palps** are located at the base of the proboscis, but maxillae and mandibles have been incorporated into basal elements of the labium.

In the louse fly (Figure 2.9) and related bat flies (Streblidae and Nycteribiidae), this rigid type of proboscis is retracted as a single unit into a deep internal pouch in the ventral head region and is protracted for feeding.

Piercing mouthparts, siphonapteran type (Figure 2.11)

The general appearance of the mouthparts of fleas belies the close phylogenetic relationship of the Siphonaptera to the Diptera. The labrum is rudimentary, and the piercing stylets are formed from the **maxillary laciniae** and the elongated **epipharynx**. Both sexes of adult fleas are obligate blood feeders, and both possess piercing-type mouthparts.

The epipharynx is an unpaired stylet rigidly fixed to the prestomal area. Its proximal loop with a flexible anterior wall forms the frame and diaphragm for the cibarial pump (Snodgrass, 1946). The floor of this pump is closed by the short **hypopharynx**. The epipharynx is blunt apically and is grooved behind to form the food canal with the closely appressed concaved laciniae. In addition to the bladelike toothed laciniae, the maxillae include a pair of large, palpus-bearing **lateral lobes** (wrongly termed "mandibles" by some). Mandibles are absent in the adult flea. Salivary secretions released from the tip of the short hypopharynx are conducted along the stylets by a pair of microscopic lacinial grooves.

The simple labium with its conspicuous terminal, segmented palpi serves as a protective sheath for the stylets in repose. In the act of feeding, the labium is bent forward, and its palpi are elbowed back so that the penetrating stylets are cradled in the notch of the labial prementum (Figure 2.11). As in the horse fly subtype of dipteran sucking apparatus, a second internal pump, the pharyngeal pump, is developed posterior to the true mouth at the proximal end of the cibarial pump.

Piercing-sucking mouthparts, lepidopteran type (Figure 2.10)

There are very few known skin-piercing or blood-sucking species of the large order Lepidoptera. That some moths may suck blood or habitually pierce the skin of mammal hosts was reported in convincing detail by Banziger (1968, 1970). The piercing mouthparts of the blood-sucking species have been modified from those of a larger group of fruit-piercing moths. Unlike other mouthpart types described, the fascicle in these moths is formed from only one pair of basic oral elements, the maxillae. The piercing stylet, a long flexible proboscis coiled in repose, consists of the opposed concaved surfaces of the hollow maxillary galeae. The appressed galeae form the food canal, but there is no independent salivary duct as in other mouthpart types. These moths lack a hypopharynx.

Extension of the proboscis (paired galeae) into a protracted feeding and probing attitude (Figure 2.10) is accomplished largely by internal fluid pressure in each hollow galea body. Penetration is made by rapid spindlelike flexing of the extended tip of the proboscis pressed against the feeding substrate. This produces superficial tearing at the entry site by the apical hooks of the paired galeae. Probing is made by combined rotating action of the head and basal maxillary sclerites so that the galeae slide against each other alternately. They are pulled deeper into tissue by anchoring action of their erectile lateral barbs. This is similar to lacinial penetration in the dipteran and siphonapteran types. During feeding the moth draws the entire

proboscis up and down in the wound to produce continual blood flow with the galeal rasping spines. Salivary secretions are introduced through the food canal or by free flow down the outside of the proboscis (Banziger, 1970).

Piercing-sucking mouthparts, Acari, Ixodida type (Figure 2.12)

Although mites and ticks are not insects, they are of great importance to medical entomology and possess basic mouthparts that cannot be homologized with those of insects. Acarines, like other arachnids, imbibe only fluids.

Solids must be liquefied externally by salivary secretion on the substrate, or in the preoral cavity, for ingestion. The mouthpart-bearing section of the acarine is known as the **gnathosoma** or **capitulum**. Essentially the capitulum consists of a sclerotized ringlike collar bearing a pair of segmented palpi (or pedipalps) laterally and a medial pair of protractible toothed, cylindrical shafts (chelicerae). The basis capituli is composed largely of the fused coxae of the palpi. The preoral cavity is closed dorsally by the **epistome** and ventrally by the **hypostome**. In ticks the hypostome is enlarged and elongated with prominent teeth ventrally that anchor the mouthparts in the feeding substrate.

According to Gregson (1960) the process of feeding by *Dermacentor andersoni* may be subdivided into three periods: attaching, feeding, and detaching.

Attaching involves the secretion of a milky fluid that hardens quickly into a latex-like material forming a papilla that molds the exterior oral structures to the feeding substrate. Feeding is done by intermittent probing and cutting of subdermal tissues by the digits. Clear salivary fluid is introduced into the wound during this stage and acts as an anticoagulant or changes capillary permeability. Detaching results when the chelicerae are withdrawn, thus decreasing pressure by other mouthparts against the molded papilla and allowing the tick to back away.

Salivary secretions are introduced directly into the preoral cavity or through a pair of long slender **salivary stylets** located between the palpi and hypostome. The chelicerae are terminated by one movable and one immovable toothed digit (**chela**) and are protracted to tear and probe by internal fluid pressure. Retraction of the chelicerae is by muscle action.

The adult ixodid tick can be examined as a large, easily obtained example of the generalized parasitiform acarine mouthparts.

Maggot mouthparts, larvae of cyclorrhaphous Diptera (Figure 2.13)

In general the mouthparts of those immature insects with gradual metamorphosis are smaller replicas of adult chewing or piercing mouthparts. Immature insects having complete metamorphosis generally have chewing-type mouthparts regardless of the type found in adults. However, maggots, the larvae of cyclorrhaphous or higher flies, possess peculiar, more modified oral structures – the cephalopharyngeal skeleton and mouth-hooks. These oral structures are so changed from a basic chewing function that their homologies are difficult to recognize. Because many maggots also are agents of myiasis, their uniquely adapted oral structures warrant closer examination.

Larvae of cyclorrhaphous Diptera typically have only a paired set of **mouth-hooks** as externally visible oral structures. These mouth-hooks articulate internally with the H-shaped **labial-hypopharyngeal sclerite** which embraces a pair of median **malar sclerites** (cardo) anteriorly and joins with the ventroanterior arms of the **paraclypeal phragmata** posteriorly. The phragmata, with its rigid ventral wall and strongly muscled and flexible dorsal wall, functions as a diaphragm pump much as does the cibarial pump of adult Diptera (Figure 2.6). The salivary duct opens close to the labial-hypopharyngeal sclerite. Scratching, probing, and tearing by the mouth-hooks (formed mostly from the maxillae) moves food particles in a fluid medium of salivary secretions into the **oral atrium**. Sucking action by the cibarial pump draws the liquid diet into the anterior digestive tract (Menees, 1962). Mouth-hooks also function for anchoring the maggot in soft substrate or as grappling hooks for creeping locomotion. Examine the larval cephalopharyngeal structures and mouth-hooks of representative higher Diptera (e.g., late-stage larvae of Calliphoridae, Sarcophagidae, Muscidae, Gasterophilidae, or Cuterebridae).

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2.1 BASIC CHEWING-TYPE MOUTHPARTS

Blattella germanica (Blattellidae)

