THE MOUTHPARTS OF INSECTS.

C. L. METCALF, UNIVERSITY OF ILLINOIS[1].

The mouthparts of insects are derived from the original paired appendages of the fourth, fifth and sixth somities, with certain adventitious median processes that develop at an early embryonic stage, as unpaired lobes in close conjunction with the mouth opening (Figure 1).

In the modern insects there are eight, separate, and more or less independent parts, that go to make up the trophi (Table I). The paired appendages of the fourth somite are distinct in the majority of insects as the *mandibles*, and their homologues on the fifth segment as the *maxillae*. The pair on the sixth segment in all insects has fused to form a single organ, the lower lip, called the *labium*. An unpaired median sclerite (Fig. 1, Lm)

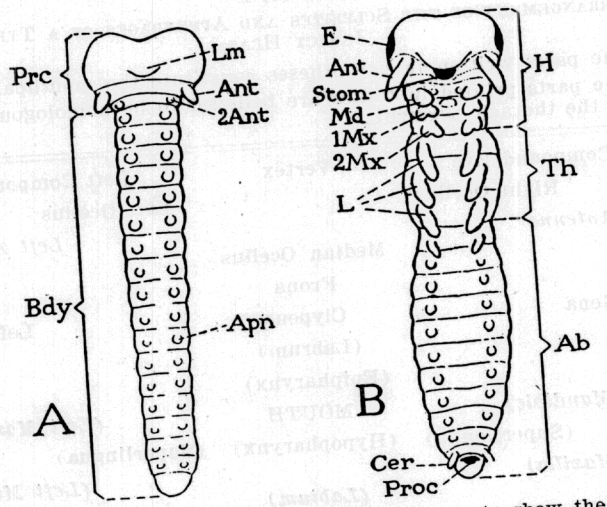

FIG. 1.—Insect embryos at two different stages, to show the origin of the mouthparts, in part as paired appendages of the head segment (**Md, 1 Mx, 2Mx**), homologous with antennae (**Ant.**) and legs (**L.**); and in parts as unpaired, median lobes above and below the mouth opening.

Ab, abdomen; **Ant,** antennae; **2 Ant,** rudimentary second antennae; **Apn,** ventral paired appendages of early embryo, common to head, thoracic and abdominal segments; **Bdy,** body of early embryo embracing three head segments, three thoracic segments and twelve abdominal segments; **Cer,** cercus; **E,** compound eye; **H,** head as constituted in adult; **L,** appendages which form the legs; **Lm,** median appendage of first segment which forms the labrum; **Md,** appendages which form the maxillae; **2Mx,** appendages which unite to form the labium or lower lip; **Prc,** procephalon or embryonic head of three segments; **Proc,** the anus; **Stom,** the mouth; **Th,** thorax. Between the **Md.** and **1Mx** are shown the three appendages which unite to form the hypopharynx with its superlinguae. (**From Snodgrass in Smithsonian Report for 1925.**)

[1] Contribution from the Entomological Laboratories of the University of Illinois, No. 126.

arises on the embryonic insect head just in front of the mouth and develops into the upper lip, called the labrum. In many insects the prolongation and differentiation of a part of the roof of the mouth forms the *epipharynx* and a similar prolongation from the floor of the mouth is called the *hypopharynx*. According to Snodgrass the latter organ arises from three embryonic lobes, (Fig. 1), which grow together; thus accounting for the trilobed condition sometimes found in the Thysanura, Collembola, Orthoptera, Coleoptera, Dermaptera and Corrodentia. The lateral lobes are called superlinguae and are said by Crampton to be homologous with the paragnaths of the Crustacea.

The arrangement of the mouthparts of an insect, with reference to the mouth opening and other head structures, is indicated in Table I, which is plotted to show the position of the parts as the insect would face the reader.

TABLE I.

ARRANGEMENT OF THE SCLERITES AND APPENDAGES OF A TYPICAL INSECT HEAD.

The parts written in parentheses constitute the mouthparts.
The parts printed in italics are believed to be homologous to the legs of the thoracic segments.

Right Compound Eye	Vertex	Left Compound Eye
Right Ocellus		Left Ocellus
Right Antenna		*Left Antenna*
	Median Ocellus	
	Frons	
Right Gena	Clypeus	Left Gena
	(Labrum)	
	(Epipharynx)	
(Right Mandible)	MOUTH	*(Left Mandible)*
(Superlingua)	(Hypopharynx)	(Superlingua)
(Right Maxilla)		*(Left Maxilla)*
	(Labium)	

Probably no group of structures in the animal kingdom exhibits a better example of the adaptive modification of originally similar, serially arranged organs to very different-looking structures and to diverse functions. Of the appendages shown in figure 1, A, (*Apn* and *Ant*) the latter develop into the antennae and the remainder diversify to form the mouthparts, the legs, the cerci and genitalia, while many of those on the basal segments of the abdomen disappear during ontogenetic development.

In this paper attention is directed only to the modification of the eight parts which constitute the trophi. It will be seen that these structures diversify to such an extent that their homologies would never be suspected; and can be recognized, if at all, only by the most judicious study of their embryonic and postembryonic development. Their structures and uses become so varied in the different orders of insects as to constitute at least twelve different functional types and subtypes, which are discussed below.

The usual classification of mouthparts has been into "biting" and "sucking". This is so totally inadequate that one is surprised that it sufficed so long. Herms[1] advanced a classification that reveals the fundamental differences between many of the so-called "sucking mouthparts." Patton and Cragg[2] have given an excellent exposition of the structure and function of the blood-sucking species. On the work of these and many other authors in this particular phase of insect morphology, the following scheme of classification is founded. The known mouthparts of insects are here grouped into eight functional types. One of these types is subdivided into five sub-types, which are allied chiefly by function, being very diverse in structure. The two series, mandibulate and haustellate, merge into each other.

TABLE II.

TYPES OF INSECT MOUTHPARTS ARRANGED ACCORDING TO FUNCTION.

I. Mandibulate Series

A. The Chewing Type.
B. The Predator Type.
C. The Acuminate Type.

II. Haustellate Series

D. The Chewing-lapping Type.
E. The Rasping-sucking Type.
F. The Piercing-sucking Type.
   (a) The Bug or Hemipterous Sub-type.
   (b) The Common Biting-fly or Dipterous Sub-type.
   (c) The Special Biting-fly or Muscid Sub-type.
   (d) The Flea or Siphonapterous Sub-type.
   (e) The Louse or Anoplurous Sub-type.
G. The Sponging Type.
H. The Siphoning Type.

[1] Herms, W. B., **Medical and Veterinary Entomology**, The MacMillan Company, 1915.

[2] Patton, W. S., and F. W. Cragg, **A Textbook of Medical Entomology**, Christian Literature Society for India, London, 1913.

I. Mandibulate Series.

A. The Chewing Type. This type of mouthparts, which is the only form adequately described in most text books of zoology and entomology, is too well known to require detailed description here. The nature and arrangement of the parts is well illustrated by figure 2, which shows the parts *in situ* in the central drawing and more fully exposed in the surrounding figures. The characteristics of this type are two pairs of tooth-like or jaw-like structures, adapted to work together transversely; two pairs of jointed palpi; and two, more or less lip-like structures, one above the mouth and one beneath it.

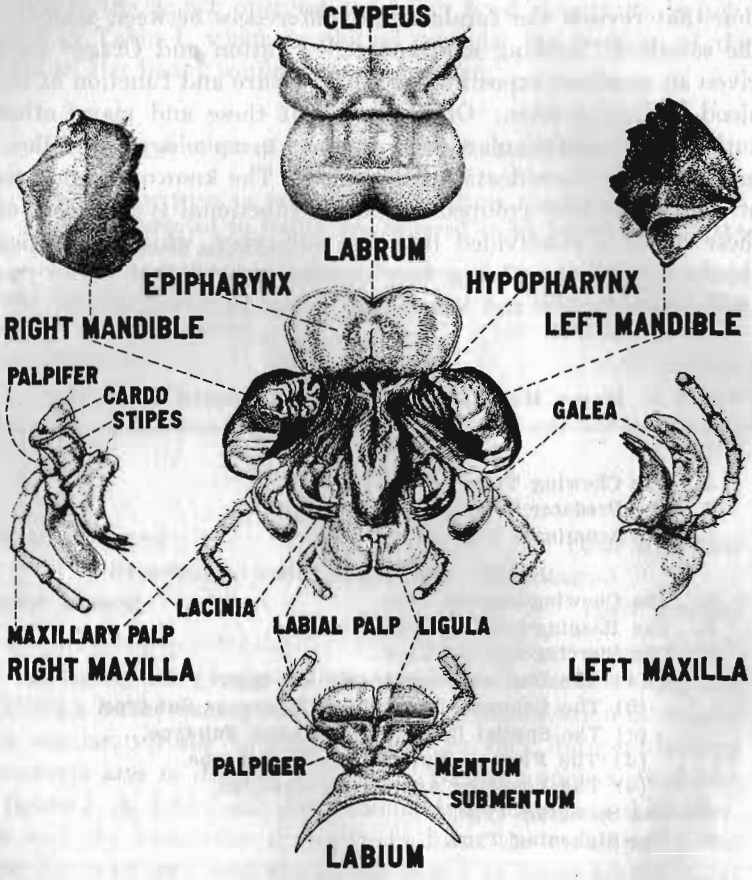

FIG. 2.—Mouthparts of the chewing type, as found in the grasshopper. The eight fundamental parts are widespread, in situ, in the central figure, and fully exposed to show the separate parts, in the surrounding figures.
(Drawings by Antonio M. Paterno.)

This is believed to be the primitive, fundamental and generalized type from which all the other types have been derived. It is found in the nymphs and adults of the orders Thysanura, Orthoptera, Dermaptera, Isoptera and Mallophaga; in the larvae and adults of Coleoptera, Neuroptera, Trichoptera, and some Hymenoptera; and in the larvae of Lepidoptera and some Diptera, besides many other insects that are less well known. There are many modifications from the fundamental type figured, some of which are indicated by the footnotes to Table III. In-

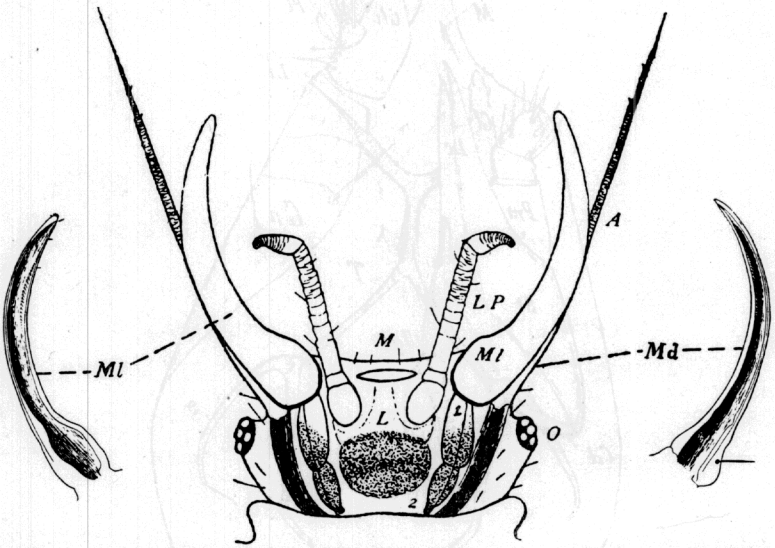

FIG. 3.—Mouthparts of the predatory type, as found in the larva of an aphid lion, **Chrysopa oculata.** At center a ventral view of the head, showing: **A,** the antenna, **L,** the labium, **LP,** the labial palpus, **M,** the true mouth opened by dissection, **Md,** the mandible, lying above, **Ml,** the maxilla, **O,** the compound eye. 1 and 2 are probably basal segments of the maxilla. At the right is shown the left mandible, ventral view, exposed to show the groove which, fitted against a similar groove in the maxilla, forms the food channel. At the left is shown the left maxilla, dorsal view, showing groove which complements that of the mandible.

(Modified from Smith, Cornell University Memoir 58.)

stead of serving for chewing plant tissues, they may be specialized for catching and devouring small animals, for fighting or clasping, for carrying or molding wax, for sifting food, or for brushing off pollen grains. All of these modifications are placed in this type, provided they readily conform to the characteristics given above.

B. *The Predatory Type.*—Some of the predaceous insects have departed so far from the chewing form of mouthparts as to be referable there no longer. The condition in the larvae of

the Chrysopidae and some other Neuropteroid larvae constitutes a distinct type. In these insects (Fig. 3) the true mouth opening has become closed. Two adventitous mouths open, one at the base of each mandible. The mandibles (Fig. 3, Md.) are greatly elongated, sickle-shaped, grooved full length along the under side. Over this groove fits the maxilla (Ml) of the same side, which conforms to the shape of the mandible and bears a flange, interlocking it to the mandible. In this way a tube is

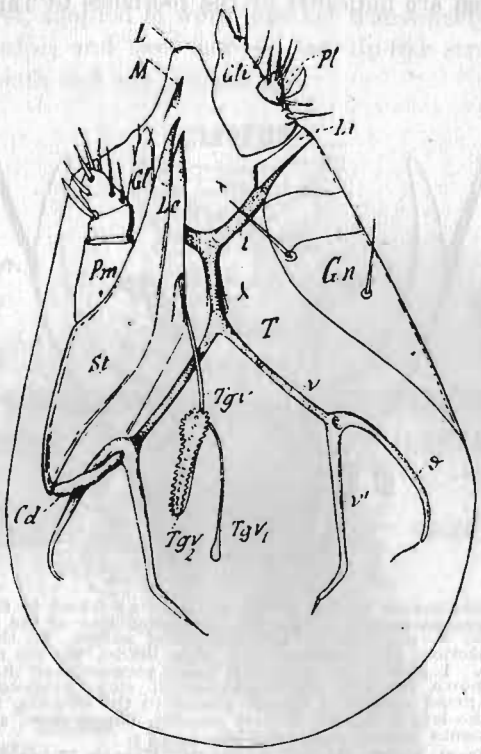

FIG. 4.—Mandibulate mouthparts of the acuminate type, as found in the Proturan, Acerentulus tiarneus. Note the elongation of the mandible (M), the galea (Gl), and lacinia (Lc).

Cd, cardo; Gn, gena; L, labrum; Li, basal sclerite of labium; Pl, labial palp; Pm, maxillary palp; St, stipes. (After Imms, from Berlese, Redia, 1909)

formed leading from the sharp tip of this compound organ into the provisional mouth of that side. Small, soft-bodied animals are speared with one or both of these organs and their fluid contents sucked into the stomach.

C. *The Acuminate Type.* The mandibulate series also exhibits certain forms specialized for imbiding plant juices. The *Protura* (Fig. 4) may serve as an example. Here the parts are

elongated and very sharp, the mandibles, galeae, and laciniae all being styliform and withdrawn into the head. This type together with the Chewing-lapping Type and the Rasping-sucking Type, placed arbitrarily in the haustellate series, make a fair gradation from the Chewing Type to the Piercing-sucking Type.

D. *The Chewing-Lapping Type.* This type is significant as connecting the mandibulate and haustellate series. The labrum, epipharynx, and mandibles have retained the form found in chewing insects altho the latter are modified to the industrial demands of the bee-community life and used for portage and for molding the wax cells.

The maxillae and labium on the other hand (Fig. 5) are elongated and highly specialized for lapping up nectar. Both pairs of palpi are present, the labial pair (Lb Plp) long and conspicuous, but the maxillary palpi (Mx Plp) very small. Between the labial palpi are the short paraglossae (*Pgl*) and a long, slender, hairy, grooved tongue, the fused glossae (*Gls*) with a specialized, spoon-shaped labellum *(Lbl)* at the end. The galeae (*Ga*) of the maxillae are also elongate and lie parallel to the tongue. According to Snodgrass a temporary *food channel* is formed by the concave inner surfaces of the galeae, roofing over the glossae and fitting snugly lengthwise against the labial palpi which in turn lie tightly against the sides of the glossae. Through such a complexly formed tube ("held, like a straw in one's mouth, by the mandibles grasping the bases of the galeae while the epipharynx plugs the gap where the ends of the galeae diverge toward the head") a drop of honey may be sucked up.

According to George E. King, in securing nectar from the open nectaries of flowers the bee thrusts out the glossa or tongue and licks the nectar with the tip of it. The glossa, thus smeared with nectar, is retracted between the labial palpi and galeae, and the nectar is squeezed off the tongue by the galeae and deposited so as to accumulate in the small cavity formed by the paraglossa at the base of the glossa. Then by bending the labium upward near mid-length the base of the glossa is brought into close apposition to the mouth opening and its accumulated nectar passes into the pharynx. The nectar thus gathered serves as food for the bees and the surplus is stored as honey. The inner channel (*l*) or the ventral channel (*Lum*) of the glossa, or both, may serve as a salivary groove to conduct saliva to the

tip of the tongue where it may be used to dissolve solids such as sugar, preparatory to swallowing. The mandibles are used for carrying things and, in the honeybee, for molding wax into cells.

The parts when not in use are folded up, out of the way by means of a hinge or joint between the mentum and submentum and cardo and stipes.

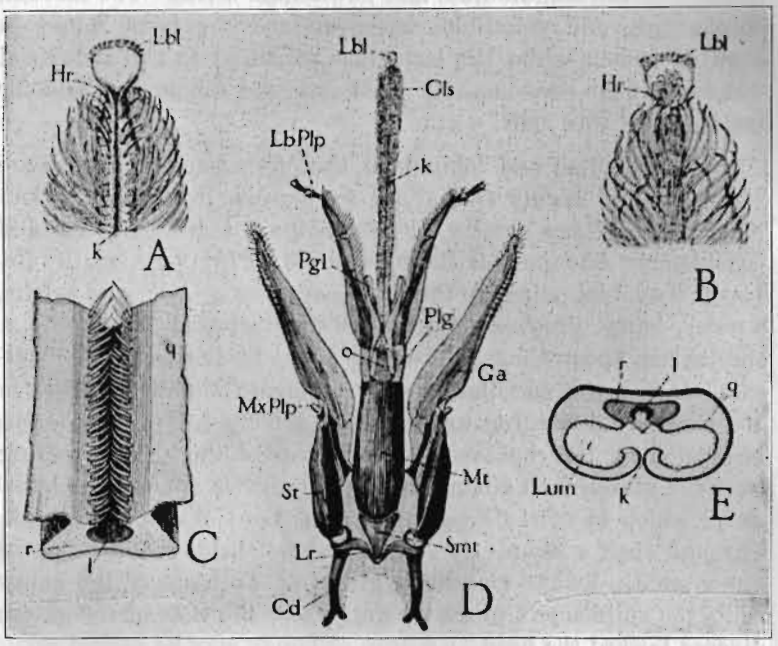

FIG. 5.—Chewing-lapping type of mouthparts, from the honeybee. The mandibles, labrum and epipharynx, which are not figured, are much as in Figure 2. The labium and maxillae, shown here are elongated to form a lapping tongue.

A, tip of glossa or tongue, from beneath, showing labellum (Lbl), the ventral groove to inner cavity **(k),** and the guard hairs **(Hr)** at its end. **B,** the same from above.

C, a small piece of glossal rod **(r)** dissected out of the glossal canal **(E, Lum)** with adjoining walls **(q)** attached and showing inner channel of the rod **(l)** guarded by rows of hairs.

D, ventral view of the maxillae and labium with parts spread: The following are parts of the maxilla: **Cd,** cardo; **Ga,** galea; **MxPlp,** maxillary palp; **St,** stipes. The following are parts of the labium: **Gls,** glossa; **k,** ventral groove of glossa; **Lbl,** labellum; **LbPlp,** labial palp; **Mt,** mentum; **Smt,** submentum; **Pgl,** paraglossae; **Plg,** palpiger; **Smt,** submentum.

E, cross section of glossa, showing its principal canal **(Lum)** opening through the ventral groove **(k),** with its lining walls **(q)** and the glossal rod **(r)** with its inner channel (l). **(After Snodgrass, Anatomy of the Honeybee.)**

II. Haustellate Series.

E. *The Rasping-Sucking Type.* In some respects this type is transitional between the chewing type and the piercing-sucking type. The mouthparts, including the lower part of the head, are asymmetrical (Fig. 6). The labrum (*l*) and parts of the maxillae (*g*) and labium (*j*) form a mouth-cone with the mouth

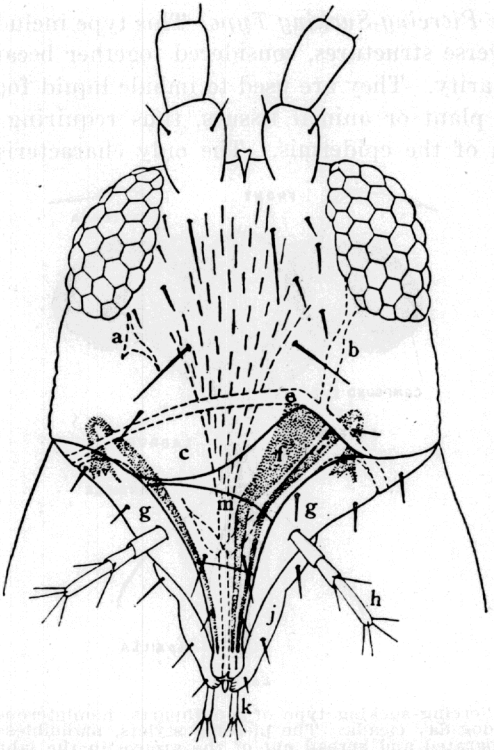

FIG. 6.—Rasping-sucking type of mouthparts, from the thrips, **Euthrips tritici.** Note the asymmentry of the parts especially **a, b, e,** and **f.**

a, b, e, chitinous band on wall of head; **c,** clypeus; **f,** mandible; **g,** maxilla; **h,** maxillary palp; **i,** maxillary stylet of left side; **j,** labium; **l,** labrum; **m,** hypopharynx. **(After Borden, Journal Econ. Entomo., 1915.)**

at its apex. The right mandible is reduced. The left mandible (*f*) the two maxillae (*i*) and the hypopharynx (*m*) are elongate, styliform, and completely retracted within the cavity of the head or mouth-cone. In operation they are protruded thru the mouth-cone and, by movements of the head, used to lacerate the epidermis of plants, when the juices are sucked up by the mouth-cone. This type is well characterized and distinguished from

both the chewing type and the piercing-sucking type by the following characteristics: (a) The labium is not prolongated as a beak beyond the rest of the mouthparts; (b) there are two pairs of palpi; (c) the stylets are completely withdrawn into the head; and (d) the asymmetrical condition.

Such mouthparts are found in nymphal and adult thrips, Order Thysanoptera.

F. *The Piercing-Sucking Type.* This type includes a variety of very diverse structures, considered together because of functional similarity. They are used to imbide liquid foods from the interior of plant or animal tissues, thus requiring piercing or penetration of the epidermis. The only characteristic common

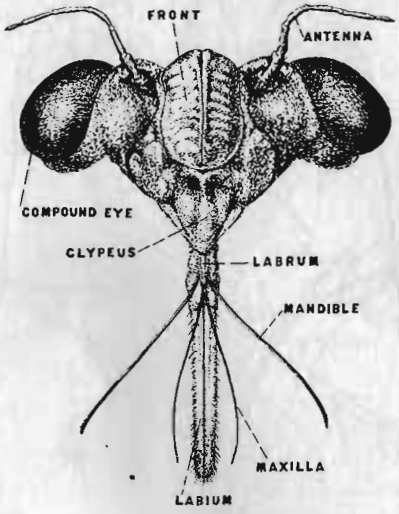

FIG. 7.—Piercing-sucking type of mouthparts, hemipterous sub-type, as found in the dog-day cicada. The piercing stylets, mandibles and maxillae, have been separated and spread out of the groove in the labium. See also figure 8. (Drawing by Antonio M. Paterno.)

to all of the subtypes placed in this division is the presence of a group of slender stylets apposed or interlocked to form a food channel. Usually the stylets serve as piercing organs and they are usually protected when not in use by the prolongated, subcylindrical labium. It should be emphasized that the conspicuous outer tube or labium is, with the exception of the special dipterous subtype, simply a protective, ensheathing structure that has nothing to do with piercing the tissues or drawing up the liquid food. Except in the fleas there is a single pair of palpi.

(a) *The Bug or Hemipterous Sub-type.* The simplest of the piercing-sucking forms to understand is that found in the squash bug, cicada, aphids, scale insects and all other Hemiptera and Homoptera (Figs. 7 *and* 8). The labium is long, nearly cylindri-

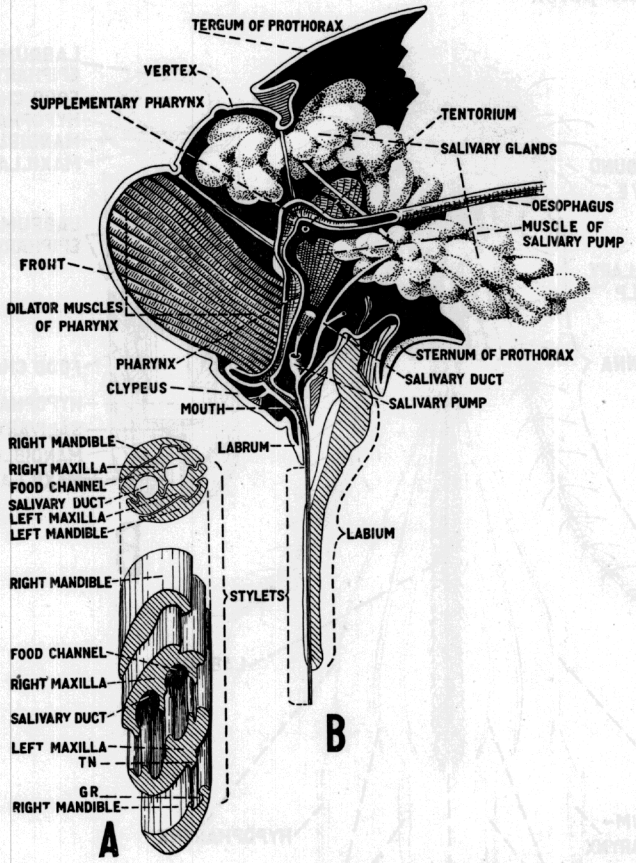

FIG. 8.—Piercing-sucking mouthparts of the periodical cicada, hemipterous sub-type. A, cross-section and isometric projection of a short piece of the stylets, greatly magnified to show how the maxillae and the mandibles are locked together, and how the food channel and salivary duct are formed by grooves in the mesal face of the latter. B, sagittal section of the head and mouthparts of the cicada showing how the liquid food is drawn from the stylets into the mouth and oesophagus by the action of the dilator muscles of the pharynx; also the salivary glands, ducts and pump and the ensheathing labium. See also figure 7.

(B, modified after Snodgrass, Proc. Ent. Soc. Wash., 1921.)

Figure 8. **(Drawings by Antonio M. Paterno.)**

cal, jointed, without apical labella, and deeply grooved along its dorsal surface for the reception and protection of the delicate stylets. The stylets are four in number, two mandibles and two maxillae. The latter (Fig. 8, A) are doubly channeled on mesal

faces to form, by apposition, a dorsal food channel and a ventral salivary duct. All four stylets are closely interlocked by tongues and grooves to form a single, hair-like structure, which alone enters the wound. This is the only piercing type that has a beak and no palpi.

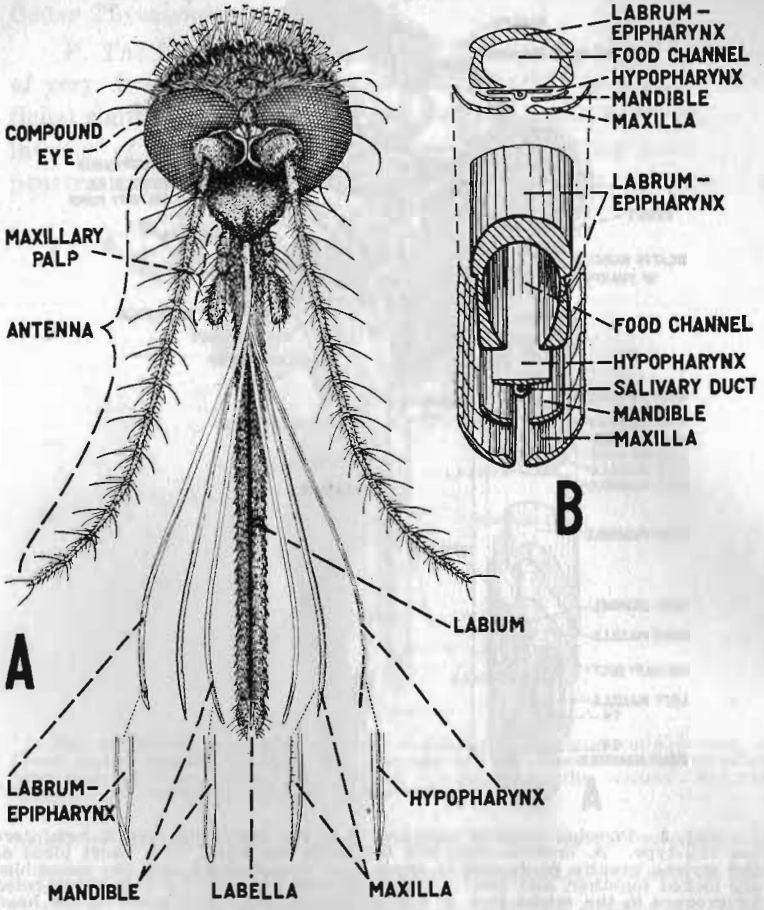

FIG. 9.—Piercing-sucking mouthparts of a mosquito, common biting-fly subtype. A, dorsal view with the stylets separated and their apices greatly magnified; B, cross-section and isometric projection of the six stylets showing how the food channel and salivary duct are formed. (Drawings by Antonio M. Paterno.)

Morphologists are not in agreement as to the homology of the parts labeled labrum, clypeus and front.

(b) *The Common Biting-fly or Dipterous Sub-type.* This form (Fig. 9) is found, with minor variances, in several families

of flies such as mosquitoes, black flies and horse flies, that suck the blood of man and other animals. The labium is cylindrical and grooved dorsally, but unjointed except for the differentiation of a pair of labella at its apex. These are probably only sensory pads in the mosquitoes but in the horse flies are en-

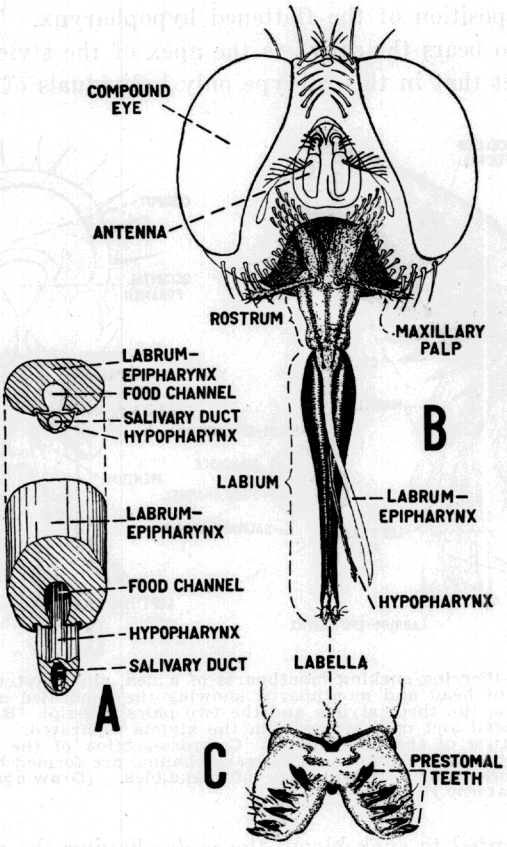

FIG. 10.—Piercing-sucking mouthparts of the stable fly, special biting-fly subtype. **A**, cross-section and isometric projection of the two stylets showing composition of food-channel and salivary duct. **B**, dorsal view of head and mouthparts with stylets separated from labial groove. **C**, the labella greatly magnified to show the prestomal teeth with which piercing is accomplished. **(Drawings in part by Antonio M. Paterno.)**

larged and provided with nearly closed channels (*pseudotracheae*), radiating over their surface, that serve to sponge up exposed liquids by capillary attraction, in the manner further explained under the sponging type, below. This type differs from the hemipterous subtype in three other significant respects.

There is a single pair of palpi, the maxillary. There are six stylets: in addition to the two mandibles and two maxillae the labrum-epipharynx and the hypopharynx are elongate, slender, styliform. The mandibles and maxillae are not interlocked (Fig. 9, B) but the food channel is formed by a deep groove in the ventral side of the labrum-epipharynx which is closed, for sucking, by apposition of the flattened hypopharynx. The hypopharynx also bears the saliva to the apex of the stylets. It is a curious fact that in this subtype only individuals of the female

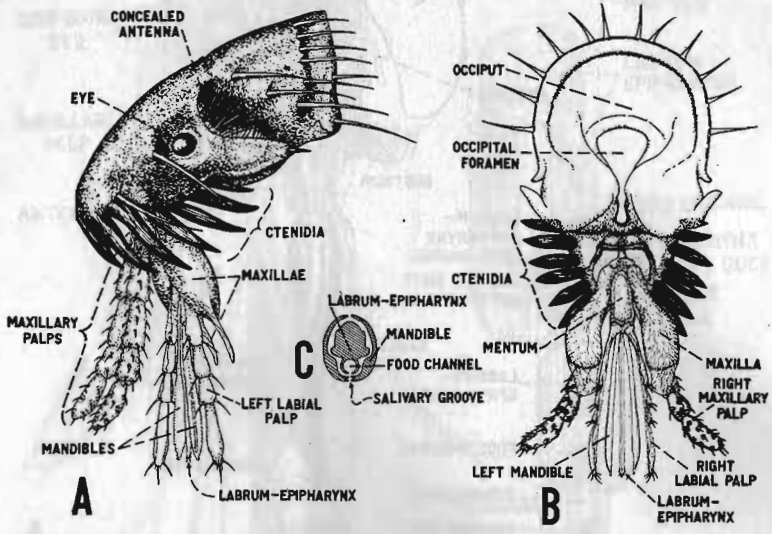

FIG. 11.—Piercing-sucking mouthparts of a flea, siphonapterous subtype. A, side view of head and mouthparts, showing the concealed antennae, the broad maxillae, the three stylets and the two pairs of palpi. B, ventro-caudal view of head and mouthparts with the stylets separated. Note the ensheathing nature of the labial palpi. C, cross-section of the three stylets showing how the food channel and salivary channel are formed by grooves in labrum-epipharynx and ventral edge of mandibles. (Drawings in part by Antonio M. Paterno.)

sex are adapted to suck blood, the males having the mouthparts reduced and impotent.

(c) *The Special Biting-fly or Muscid Sub-type.* This type (Fig. 10) is known only in such Muscidae as suck the blood of animals: the stable fly, horn fly, tsetse flies and others. Its derivation has been traced by Patton and Cragg (l. c.) through certain intermediate forms from the sponging type described below. Structurally it is closely allied to the sponging type, but differs in having the labella reduced in size, without pseudo-

tracheal channels, and provided with sharp prestomal teeth (Fig. 10, C). According to Patton and Cragg, the skin of the host animal is punctured by the rapid protraction and retraction of the membrane bearing these teeth; and the attenuated labium follows the cutting labella into the wound. The food channel and salivary duct (Fig. 10, A) are formed in the same way as in the common biting-fly type by the labrum-epipharynx and the hypopharynx and there is a pair of maxillary palpi.

It is interesting to note that the only stylets developed here are the ones lacking in the hemipterous subtype; the labrum-epipharynx and hypopharynx being styliform, the mandibles and maxillae wanting.

(d) *The Flea or Siphonapterous Sub-type.* Still another combination of these homologous units is made (Fig. 11) in the adults of the order Siphonaptera or fleas, to serve the same functions of piercing the skin and sucking the blood. This is the only piercing-sucking type in which both pairs of palpi are clearly represented. The labium is not prolongated as a grooved beak, but the labial palpi are each flattened on the mesal surface and serve to ensheath the stylets loosely. The maxillae are not developed as piercing stylets but are broad plates much flattened apically and said to serve as fulcra to steady the head and mouthparts in the act of feeding. There are three stylets: a pair of blade-like serrated mandibles and an unpaired structure believed to be the labrum-epipharynx. It is grooved ventrally somewhat as in subtypes (b) and (c) but, in the absence of the hypopharynx, this groove is closed by apposition to the ventral edge of the mandibles (Fig. 11, C). A unique method of conveying saliva into the wound beyond the short hypopharynx is through a minute channel formed by the apposed, grooved, ventral edges of the mandibles (Fig. 11, C).

(e) *The Louse or Anoplurous Sub-type.* Allied to the others of the piercing-sucking type, functionally, this form is, structurally, very different and. superficially, more nearly analogous to the rasping-sucking type. There is no prolonged beak. A very short haustellum (Fig. 12, *h*) bears a circlet of denticles (*d*) probably of use in anchoring the head in place in the act of feeding. There are no palpi. The piercing structures are a complicated set of chitinous stylets which are, when at rest, with-

* Peacock, A. D., **The Structure of the Mouthparts and Mechanism of Feeding in Pediculus humanus,** Parasitology, Vol. XI, pp. 98-117, 1919.

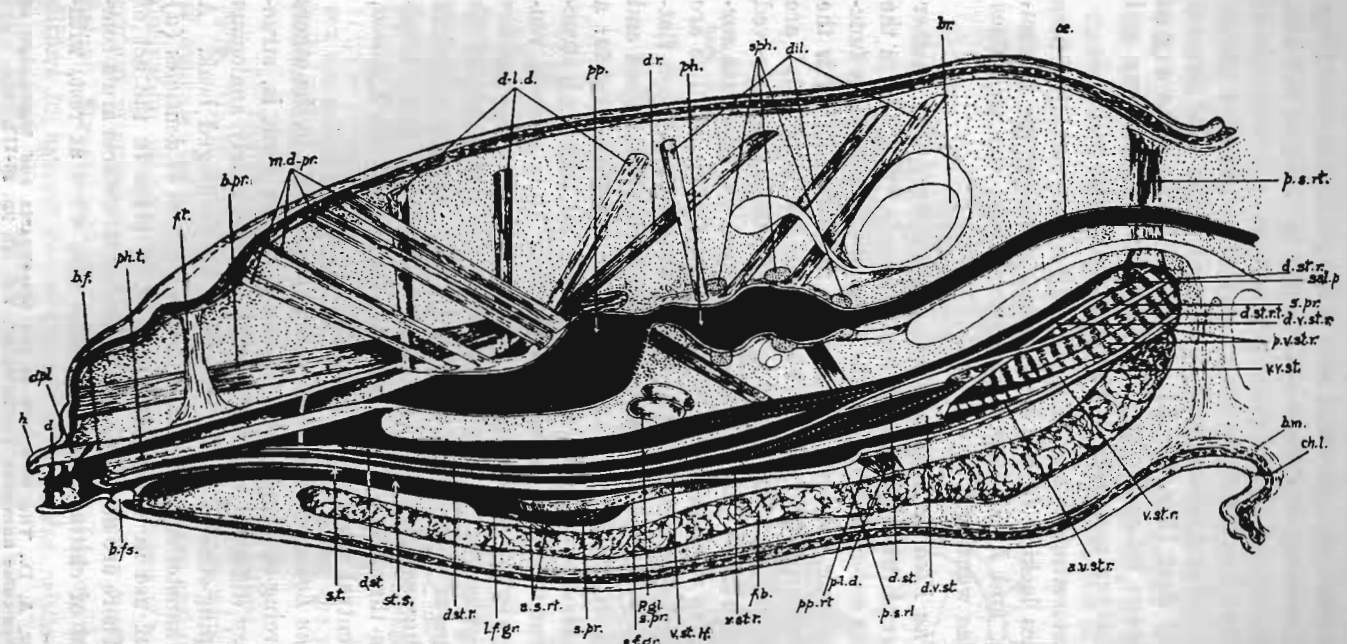

FIG. 12.—Piercing-sucking mouthparts of the human louse, anoplurous subtype; sagittal section, showing structures of the right half of the head. p. f., buccal funnel; br., brain; d, denticles; d. st., dorsal stabber or stylet; h, haustellum or rostrum; ph, pharynx; ph. t., pharyngeal tube; pp., pumping pharynx; st., sac tube; st. s., stylet sac; v. st. r. and v. st. lf., ventral stabber or stylet. Compare Figure 13. (From Peacock, in Parasitology, Vol. XI.)

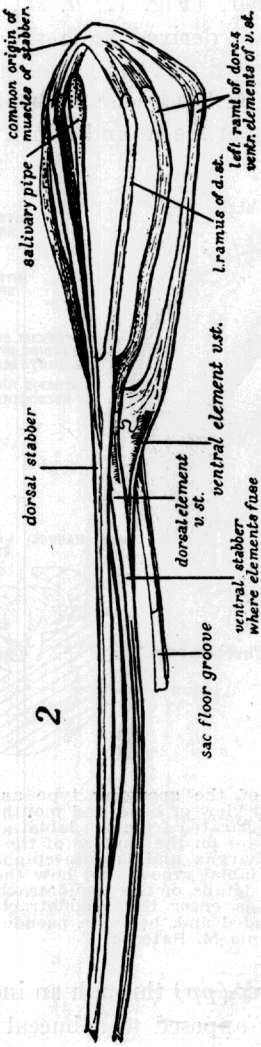

FIG. 13.—The stylets or tabbers of the human louse, exposed from the stylet sac in which they lie when not in use. Compare figure 12. (From Peacock, in Parasitology, Vol. XI.)

drawn into a blind diverticulum of the pharynx (*st. s*) lying in the head beneath the pharynx and oesophagus. As described and figured by Peacock,* they may be resolved into a dorsal and ventral stylet or stabber, (Fig. 12, *d. st.*, *v. st.* and Fig. 13) which Tillyard says are derived from the hypopharynx. The parts are very complicated and the homologies exceedingly difficult to understand. The head cone probably serves to suck up the blood as it oozes from the wound and it is there transferred

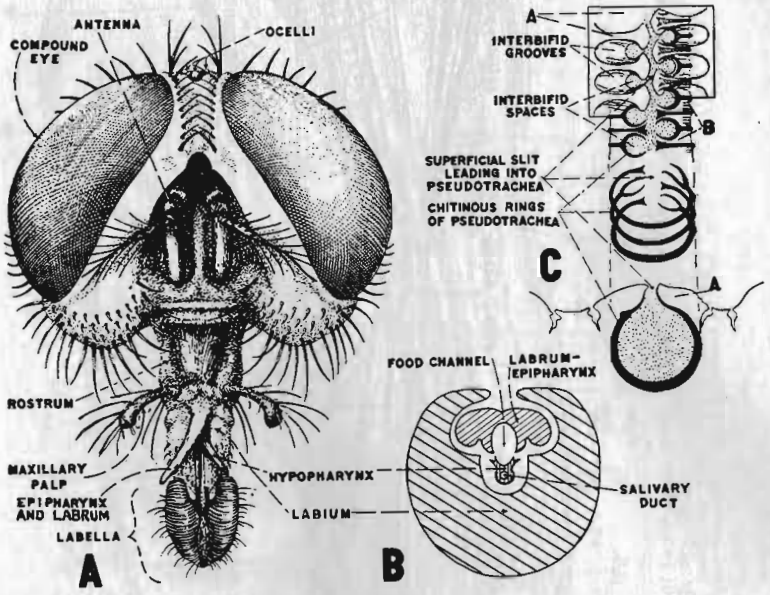

FIG. 14.—Mouthparts of the sponging type as found in the common house fly. A, antero-dorsal view of head and mouthparts with the proboscis extended and the stylets separated from the labial groove. Note the radiating channels (pseudotracheae) on the surface of the labella. B, a cross-section of the labium, hypopharynx and labrum-epipharynx showing how the latter are sheltered in the labial groove and how the food channel and salivary duct are formed. C, details of the pseudotracheae showing the nature of the slit by which liquids enter the pseudotrachea, the chitinous rings which keep its walls distended and, below, a pseudotrachea in cross-section. (Drawings in part by Antonio M. Paterno.)

to the pumping pharynx *(pp)* through an incomplete pharyngeal tube (*ph. t.*) which is apposed to a buccal funnel lying dorsal to it.

G. *The Sponging Type.* This type of mouthparts is well illustrated by the condition in the common house fly (Fig. 14) and many other Diptera of the sub-order Cyclorrhapha. The structures are very complicated and have been described in de-

tail by Graham-Smith,* and Hewitt.† There is a prominent, elbowed proboscis. The proximal portion, known as the rostrum (Fig. 14, A), is formed in part by the head capsule. It is retractile and bears near its apex the maxillary palpi. The labial palpi are wanting, unless, as some writers contend, they are rep-

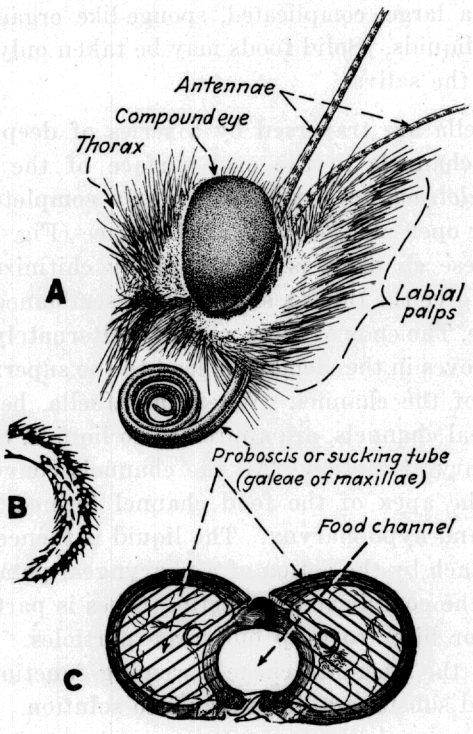

FIG. 15.—Siphoning mouthparts of a moth or butterfly.

A. side view of the head with the galeae of the maxillae, constituting the proboscis, partially uncoiled, below the head; the hair-covered labial palps, in front; and the bases of the antennae, above.

B. the tip of the proboscis of the cotton moth, a very exceptional condition in which the proboscis is provided with spines and capable of lacerating ripe fruits to get the sap (after Comstock.)

C. a cross-section of the proboscis **(after Comstock)** showing how right and left galea interlock to form the food channel.

resented by the labella. The distal portion of the proboscis, called the haustellum, is formed largely of the labium. It is grooved on its dorsal aspect as in the piercing-sucking forms. In this groove are sheltered two, short, non-piercing stylets, the

* Graham-Smith, **Flies and Disease: Non-blood-sucking Flies.** Cambridge, 1913.

† Hewitt, C. G., **The House Fly.** Cambridge, 1914.

labrum-epipharynx and the hypopharynx. They form a food channel exactly as in the common and special biting-fly sub-types described above (Fig. 14, B). Mandibular and maxillary stylets are wanting.

The most significant structures in this type are the labella which form a large, complicated, sponge-like organ for imbiding exposed liquids. Solid foods may be taken only by dissolving them in the saliva.

The labella are traversed by a series of deep cylindrical furrows or channels in the oral surface of the membranes (called *pseudotracheae*) which are nearly complete tubes but are narrowly open along the exposed surface (Fig. 14, C.) The lumen of these channels is kept open by chitinized loops or rings, which give the tubes a superficial resemblance to respiratory tracheae. The ends of these rings are alternately single and bifid and grooves in the membrane lead to the superficial, longitudinal slit of the channel. When the labella, bearing these pseudotracheal channels, are appressed to liquids, the channels fill by capillary attraction. All the channels converge at one point near the apex of the food channel formed by labrum-epipharynx and hypopharynx. The liquid is thence sucked up into the stomach by the action of a pharyngeal pump. The significance of the complicated collecting tubes is partly to serve as a screen or filter to keep out large particles. Some have attributed to the pseudotracheae a rasping function of use in bringing solid substances like sugar into solution.

H. The Siphoning Type. A very highly specialized condition of the mouthparts is found in adult moths and butterflies. The specialization is largely by reduction; but parts of the maxillae, believed to be the galeae, are greatly elongated, grooved mesally, and interlocked to form a slender, hollow, sucking tube used chiefly to draw up the nectar from flowers with long tubular corollas (Fig. 15, A and C). These stylets are not capable of piercing plant or animal tissues except in rare instances. Sometimes stiff spines at its apex (Fig. 15, B) are used to lacerate the ripe skins of fruits and so tap the sap-wells of plants. The proboscis which may reach a length several times that of the body is protected by coiling it up like a watch spring

under the head, where it does not impede flight. The labial palpi are well developed. All the other parts are small, inconspicuous or wanting.

Tables III, IV, and V show the nature of the several mouthparts in the mandibulate and haustellate series and Tables VI and VII the division of labor in the several haustellate types.

TABLE III.—MANDIBULATE SERIES.

TYPE OF MOUTHPARTS AND INSECT REPRESENTATIVES	LABRUM	EPIPHARYNX	MANDIBLES	MAXILLAE			HYPO-PHARYNX	LABIUM		
				Galea	Lacinia	Palpi		Glossae	Para-glossae	Palpi
Typical Chewing Mouthparts of Thysanura, Orthoptera Dermaptera, Odonata, Isoptera, Corrodentia Mallophaga, Coleoptera, larval Lepidoptera, some Hymenoptera, and other orders. (1)	Typical, hinged, upper lip; apical margin sometimes incised at middle. (2)	Soft, sensory, (tactile and gustatory). Covers ventral surface of labrum.	Strongly chitinized; pyrimidal; variously denticulated. Usually a single sclerite. Work transversely. (3)	Typically helmet-like; often two-segmented.	Typically tooth-like; sometimes with a claw-like terminal digitus. (4)	Usually 5-segmented; hairy; bear taste-buds; homologue of crustacean endopodite.	A tongue-like swelling from floor of mouth cavity; bears the opening of salivary duct. (5)	Median pair of lobes; homologous with the laciniae. Often variously united to form a ligula. (6)	Submedian pair of lobes; homologous with the galeae. (6)	Usually 3-segmented; hairy; gustatory and tactile.
Predatory Type Mouthparts of Chrysopidae larvae and other Neuroptera. (7)	Reduced	Reduced	Elongate, sickle-shaped. Grooved on ventral surface to tip.	Elongate, conform to shape of the mandibles; flange locks with groove of mandibles to make a pair of sucking tubes.		Generally absent.	Reduced	Reduced.	Reduced.	Variable, often large.
Acuminate Type Mouthparts of Protura and certain Collembola	Elongate; forms upper part of sucking beak.		Styliform, sharp, withdrawn into the head.	Slender	Slender, styliform, sharp.	Variously segmented.		Elongate; form the lower part of the sucking beak.		Variously segmented.

NOTES:
(1) Parts similar but greatly elongated in the order Mecoptera.
(2) Sometimes wanting as in the Rhyncophora and Strepsiptera.
(3) Sometimes greatly enlarged and specialized, as in soldier termites and male Lucanidae; may be specialized for grinding, cutting, crushing, grasping, sifting or carrying.
(4) Specialized as elongate, chisel-like rods in the Corrodentia; ensheathed by the galeae, but not articulated to the rest of the maxillae.
(5) Side pieces, called superlinguae, homologous to the paragnaths of the Crustacea, are developed in Thysanura, Collembola, Orthoptera, Dermaptera, Corrodentia, Coleoptera, etc.
(6) Wanting in the Strepsiptera.
(7) The true mouth opening is closed and non-functional. An adventitious mouth at the base of each mandible.

TABLE IV—HAUSTELLATE SERIES.

TYPE OF MOUTHPARTS AND INSECT REPRESENTATIVES	LABRUM	EPIPHARYNX	MANDIBLES	MAXILLAE			HYPO-PHARYNX	LABIUM		
				Galea	Lacinia	Palpi		Ligula: Glossa	Ligula: Paraglossa	Palpi
PIERCING-SUCKING TYPE: Hemipterous Sub-type. Homoptera and Hemiptera, Nymphs and Adults.	Very small and narrow.		Elongate, slender stylets, barbed distally. Interlocked by tongue and groove to sides of maxillae.	Elongate, slender stylets and plates on the sides of the head. Right and left stylets doubly grooved mesally and fused to form a dorsal food-channel and a ventral salivary channel.		Wanting	Small, chitinized organ between bases of the maxillae.	Elongate, usually 4- or 3-segmented. Deeply grooved on dorsal surface to form a protective sheathe for stylets.		Wanting.
PIERCING-SUCKING TYPE: Common Dipterous Sub-type. Mosquitoes, Horseflies, and Black Flies. Adult females only.	Well-chitinized; fused with dorsum of epipharynx.	Well-chitinized; fused with venter of labrum.	Piercing, needle-like or blade-like stylets.	Form a pair of piercing stylets.		1 to 4 segments.	Lanceolate, flattened. Is apposed to labrum-epipharynx to form the food channel. Traversed by salivary duct.	Elongate, cylindrical, grooved dorsally to form a sheath for stylets.		Wanting or modified into the labella.
	Grooved ventrally, U-shaped in cross-section. Apposed to hypopharynx to form the food channel.							Labella may be fleshy and provided with microscopic food channels called pseudotracheae.		
SPONGING TYPE: House Fly and many other Cyclorrhaphous Diptera. Adult males and females.	A portion of the head capsule is prolongated ventrally as the truncated, cone-shaped, proximal segment of the proboscis, called the **rostrum**. The distal segment of the proboscis, called the **haustellum**, is formed chiefly of the mouthparts. Labella with pseudotracheal channels, forming a very complex sponging organ.									
	Stylet-like, fused; borne on the dorsal face of the **haustellum**; non-piercing.		Wanting	Wanting.		Usually one-segmented.	Stylet-like, borne on the dorsal face of the haustellum; non-piercing.	Form a 1-segmented haustellum which ensheaths the stylets.		Wanting or modified into labella.

TABLE IV—HAUSTELLATE SERIES—*Continued.*

TYPE OF MOUTHPARTS AND INSECT REPRESENTATIVES	LABRUM	EPIPHARYNX	MANDIBLES	MAXILLAE			HYPO-PHARYNX	LABIUM		
				Galea	Lacinia	Palpi		Ligula		
								Glossa	Paraglossa	Palpi
PIERCING-SUCKING TYPE: Special Dipterous Sub-type. Stable Fly, Horn Fly, Tse-tse Flies and others. Adult males and females.	Rostrum reduced in size. Haustellum elongate, slender, rigid and horny. Labella provided on their antero-dorsal membrane with chitinous prestomal teeth used for cutting. No pseudotracheal channels.									
	Stylet-like, fused; too short for piercing.		Wanting	Wanting.		One-segmented.	Stylet-like, but too short for piercing.	Form a 1-segmented hanstellum which ensheaths the stylets.		Wanting or modified into labella.
PIERCING-SUCKING TYPE: Siphonapterous Sub-type. Fleas. Adult males and females.	Elongate, grooved ventrally to form the food channel by apposition to the ventral edge of the mandibles.		Elongate, blade-like, serrated stylets. Ventral edges grooved to form salivary channel.	Broad blades, much flattened dorso-ventrally; said to serve as fulcra for other parts while feeding.		Large, four-segmented.	Short, concave ventrally; extends distad a short way between labrum-epipharynx and mandibles.	Not recognizable.		Elongate, concave mesally; ensheathing stylets. Usually 5-segmented (2 to 17)
PIERCING-SUCKING TYPE: Anoplurous Sub-type. Blood-sucking Lice. Adults and Nymphs.	Not recognizable.	Not recognizable.	Not recognizable.	Not recognizable.		Wanting.	Forms two, unpaired stylets for piercing.	Not recognizable.		Wanting.
RASPING-SUCKING TYPE: Thrips. Adults and Nymphs.	Asymmetrical; forms dorsal part of mouth cone.	Not recognizable.	Left one styliform; right one aborted.	Asymmetrical		2 to 8 segmented.	Styliform.	Forms ventral part of mouth cone.		Small, 1- to 4-segments.
				Forms the side walls of the mouth cone.	Styliform.					

TABLE IV—HAUSTELLATE SERIES—*Concluded.*

TYPE OF MOUTHPARTS AND INSECT REPRESENTATIVES	LABRUM	EPIPHARYNX	MANDIBLES	MAXILLAE			HYPO-PHARYNX	LABIUM		
				Galea	Lacinia	Palpi		Ligula: Glossa	Ligula: Paraglossa	Palpi
SIPHONING TYPE: Moths and Butterflies. Adult males and females.	Usually an inconspicuous, short transverse plate.		Usually entirely wanting.	Right and left grooved mesally and fused to form the food channel. Very long.	Wanting.	Usually wanting.	Present on floor of the mouth.	A small plate on the ventral aspect of the head.		Wanting.
CHEWING-LAPPING TYPE: Long-tongued Bees. Adult males and females.	As in the chewing type.	Sensory area on ventral surface of labrum.	As in chewing type; but industrial rather than trophic.	Greatly elongated, blade-like.	Reduced.	Greatly reduced.	Wanting.	Fused and greatly elongated as a tongue; with a labellum at apex.	As in the chewing type.	Greatly elongated, ensheathing the tongue.

TABLE V.

DIVISION OF LABOR IN VARIOUS HAUSTELLATE INSECT MOUTHPARTS.

EXAMPLES.	CUTTING APPARATUS.	FOOD CHANNEL.	SALIVARY CHANNEL.	HOW STYLETS ARE PROTECTED.	REMARKS.
Hemiptera and Homoptera. males and females	2 mandibles and 2 maxillae.	Apposed, mesal grooves in the maxillae (dorsal).	Apposed, mesal grooves in the maxillae (ventral).	Longitudinal groove in dorsal face of labium, and a short labrum at base.	Four stylets: the two mandibles and two maxillae. Labrum and hypopharynx short. No palpi. No labella.
Mosquitoes, Horse Flies, Black Flies. Females only	2 mandibles and 2 maxillae.	Labrum-epipharynx grooved ventrally and closed by apposition to the hypopharynx.	Salivary duct traverses the hypopharynx.	Longitudinal groove in dorsal face of the labium.	Six stylets: the two mandibles, two maxillae, labrum-epipharynx and hypopharynx. Maxillary palpi (one pair). Labella; sometimes provided with pseudotracheal channels.
Blood sucking Muscidae: Stable Fly, Horn Fly, Tse-tse Flies. males and females	Chitinous, prestomal teeth on the antero-dorsal membrane of the labella.	Labrum-epipharynx grooved ventrally and closed by apposition to the hypopharynx.	Salivary duct traverses the hypopharynx.	Longitudinal groove in dorsal face of the labium.	Two stylets: the labrum-epipharynx and hypopharynx; too short for piercing. Mandibular and maxillary stylets wanting. Maxillary palpi (one pair). Labella without pseudotracheal channels. The only piercing insects in which the labium enters the wound.
Non-blood-sucking Muscidae and other cyclorrhaphous Diptera. males and females	None.	Labrum-epipharynx grooved ventrally and closed by apposition to the hypopharynx.	Salivary duct traverses the hypopharynx.	Longitudinal groove in dorsal face of the labium.	Two stylets: the labrum-epipharynx and hypopharynx; not piercing. Mandibular and maxillary stylets wanting. Maxillary palpi (one pair). Labella very highly specialized with pseudotracheal channels for sponging up exposed liquids.

TABLE V.

DIVISION OF LABOR IN VARIOUS HAUSTELLATE INSECT MOUTHPARTS—*Concluded.*

EXAMPLES.	CUTTING APPARATUS.	FOOD CHANNEL.	SALIVARY CHANNEL.	HOW STYLETS ARE PROTECTED.	REMARKS.
Siphonaptera: Fleas. males and females	2 mandibles.	Labrum-epipharynx grooved ventrally and closed by apposition to the ventral edges of the mandibles.	Apposed, mesal grooves in ventral edges of the mandibles.	By the ensheathing, concave, mesal faces of the labial palpi.	Three stylets: the labrum-epipharynx and the two mandibles. The maxillae are broad, flat blades that do not enter the wound. Hypopharynx wanting. Two pairs of palpi, well developed.
Anoplura: Blood-sucking Lice. males and females	2, stabber-like stylets; formed from hypopharynx?	Head cone and internal pharyngeal structures.	Associated with and traverses the dorsal stabber.	Completely withdrawn into the head when not in use.	Two median stylets: retracted into a sac beneath the pharynx when not in use. Mandibles and maxillae unrecognizable. No palpi. No protruding beak (labium). A circlet of teeth about the mouth.
Thysanoptera: Thrips. males and females	Left mandible, 2 maxillae, and hypopharynx?	Head cone formed by labrum, galeae and labium.	Ducts open at apex of mouth cone.	Withdrawn into the head when not in use.	Four stylets: the left mandible, the two maxillae and the hypopharynx. Two pairs of palpi. Head and mouthparts asymmetrical.
Lepidoptera: Moths and Butterflies. males and females	None: Very rarely spines on apex of the galeae.	Right and left galea each grooved mesally and apposed to form a sucking tube.	Wanting.	Coiled like a watch spring, close under the head when not in use.	Two, greatly-elongated, non-piercing stylets, closely interlocked. Labrum, mandibles and maxillary palpi wanting. Labial palpi (one pair).
Long-tongued Hymenoptera. males and females	None.	Temporary tube formed by apposition, lengthwise, of the glossae, labial palps and galeae.	Ventral channel on the glossa.	Hinged, folded back beneath the head when not in use.	No piercing stylets. Two pairs of palpi. Mandibles and labrum of chewing type. Maxillae and labium elongated.