

As we have mentioned previously the mouthparts are homologous with the insectan legs. The main evidence we have to support this comes from comparing the musculature of both the legs and the mouthparts, and by comparing the appendages from different arthropods.

- * So, before we get to the mouthparts we need to briefly discuss the generalized arthropod leg. We will discuss the arthropod legs in much greater detail later in the semester. The generalized arthropod leg can be divided into 2 basic regions: the **COXOPODITE** and the **TELOPODITE**.
- * The primitive telopodite was composed of the following leg segments: the **TROCHANTER(S)**, **FEMUR**, **PATELLA**, **TIBIA**, **TARSI**, and **PRETARSA**.
- * The primitive coxopodite consisted of 2 segments: the **SUBCOXA** and the **COXA**. The subcoxa is not always present in more advanced forms. The subcoxa is stationary, immovable, and incorporated into the pleural wall of the body segment where it becomes, according to Snodgrass, the pleuron, the sclerotization of the pleural wall. The coxa, is now the movable limb basis.
- * Inherent in this view is the fact that the insect coxa does not contain elements of the subcoxa. Snodgrass repeated this view in 1950. He further stated that the mandibles were homologous with the coxa; thus, the mandibles have no subcoxal component.
- * So, now lets look at the mouthparts.

LABRUM

- * The labrum or upper lip is an integral part of the chewing mechanism although unlike the three gnathal mouthparts, it was not modified from appendages. This ovoid sclerite probably represents a portion of the old prostomium overhanging the mouth. It is a broad lobe suspended from the **clypeus** and forms the upper lip. In other words, the labrum simply serves as an upper lip for the preoral cavity, connected with the head capsule only along its proximal margin and freely articulating with the clypeus. Its ental surface may be membranous, and may be produced into a median lobe, called the **epipharynx**. There may also be a mass of sensory pits and setae on its ental surface. Two sets of muscles control the movement of the labrum (see fig. 2.2A in Chapman). One set connects with the anterior margin and moves the labrum away from the mandibles. The other set connects on the posterolateral margins on a couple of small sclerites called **tormae** (sing. **torma**); these move the labrum closer to the mandibles.

MANDIBLES

- * The mandibles are the first gnathal segments. The corresponding appendages in the Chelicerata are the pedipalps (the chelicerae are evidence of the intercalary segment, and not homologous with any appendages in present day insects). The mandibles are the paired, hollow, but heavily sclerotized, unsegmented jaws arising directly behind the labrum. The shape and structure of the mandibles can vary greatly; for example, in some insects (such as the grasshoppers and crickets) the mandibles are short and stout, and possess both cutting and grinding ridges, while in others (such as predaceous beetles) they are long and sicklelike.
- * In the Crustacea, a great diversity of mandibular form is evident. A well-developed **telopodite** is often present (e.g. *Anaspides tasmaniae*). In this case, a broad **basendite** is present that is entirely movable upon the coxopodite, and which is formed into an **incisor** and **molar region**. The coxopodite has both subcoxal and coxal components.
- * In the Diplopoda, the mandible consists of a large basal portion, the coxopodite, which shows a subdivision into subcoxal and coxal portions. Snodgrass recognized the subcoxal portion as the **cardo** and the coxal portion as the **stipes**. There is a distal lobe which is apparently a **basendite**, homologous with the **lacinia** of the insect maxilla.

- * The mandibles of the Chilopoda are similar to those of the Diplopoda but the coxopodite is not subdivided. But it does have subcoxal and coxal components. An articulated basendite is present, again homologous with the **lacinia**.
- * In the Apterygota, the primitively wingless insects, the mandibles are similar to the Chilopoda and the simpler Crustacea in all groups except the Lepismatidae (Thysanura). The Lepismatidae (silverfish & firebrats) are more closely allied with the Pterygota. In the entognathous groups (Protura & Collembola) and the Archeognatha (Microcoryphia), the mandibles are relatively long and slender and have a single point of articulation (see fig. 2.3 in Chapman). This is called **monocondylic articulation**. The question of whether the mandible of Apterygota is subdivided into the subcoxa and coxa is not addressed by Snodgrass on p. 136, but if we assume that there is homology between the ambulatory limb and the mandible, then we should assume that the mandible of Apterygota is homologous with the coxa of the limb. The subcoxal element will have migrated into the wall of the head capsule. The musculature, having both dorsal and ventral muscles, suggests that the mandibles evolved from the basis of a leg-like appendage provided with the usual tergal and sternal promotor and remotor muscles.
- * A different view is given by Matsuda (1965) based upon supposed homologies of the maxillary and mandibular muscles. In a nutshell, this author claims that the insect mandible has subcoxal components because the maxilla has, in his opinion, a subcoxal component (the cardo). Snodgrass holds that the cardo and stipes together represent the coxa. The cardo is subcoxal in origin for Matsuda and Chaudonneret (1950). So, the muscles of the mandible and maxilla can be homologized, therefore, because the maxilla possesses subcoxal components, the mandible does as well.
- * The mandibles of the Pterygota and the Lepismatidae differ from those we've seen so far in that they possess 2, not 1, articulations (called **dicondylic articulation**) with the head capsule (see fig. 2.2b in Chapman). The primary (or primitive) point of articulation is accomplished by means of a knob situated on the posterior angle of the mandible, called the **posterior condyle**, which fits into a pocket provided by the ventral margin of the **postgena**. The **anterior mandibular articulation** is a much less prominent projection which is accommodated by a notch in the lateral margins of the **postclypeus** (Chapman says this articulation is with the **subgena**). These mandibles tend to be shorter and more heavily sclerotized, and the cuticle of the cusps is often hardened by the presence of zinc or manganese.
- * Two apodemes accommodate the movement of the mandible. The **anterior rotator muscle** and the **posterior rotator muscle** in the Apterygota have become the **adductor** and **abductor** (**note:** abductor muscles move the distal part of an appendage away from the midline of the body, while adductor muscles move the distal part of an appendage towards the body) muscles in the Pterygota. The **adductor tendon** is a broad apodeme connecting the mesal margin of the mandible with a set of powerful muscles. These **adductor muscles** close the jaws in the cutting or grinding function. Opening the jaws is accomplished by a comparatively weak set of **abductor muscles** attached to the **adductor tendon** which operates on the outer angle of the mandible. The mandibles, then, are rocked forward with a powerful stroke and backward on a horizontal plane by 2 opposing sets of muscles, while the 2 points of articulation serve as a hinge.

MAXILLA

- * The maxillae are paired structures arising directly behind the mandibles, they are broadly united with and articulate with the ventral margin of the postgena; they are segmented and each maxilla bears a feelerlike organ, the **palp**. The basal segment of the maxilla is the **cardo** (pl. = **cardines**), the second segment is the **stipes** (plural = **stipites**). In many insects (including the Orthoptera) the cardo is actually composed of 2 segments. The proximal extremity of the cardo fits into a notch or **maxillary articulation** in the posterior margin of the postgena. The segmented (5 segments in the Orthoptera) palp arises from a lobe on the stipes called the **palpifer** (the apparent first segment or basal attachment of the first maxillary palpus). Distally, the stipes bears 2 lobelike structures: the medial elongate jawlike structure is called the **lacinia**, and the lateral lobelike structure is called the **galea**, either or both may be absent. The palp and the galea are

probably sensory in function, while the lacinia probably functions as another cutting and grinding structure similar to the mandibles. Articulation of the opposing maxillae is on the same horizontal plane as the mandibles.

- * Anterior and posterior rotator muscles connect to the cardo; ventral adductor muscles connect the tentorium with both the cardo and stipes. Flexor muscles are contained within the maxillae, connecting from the stipes to both the lacinia and the galea; also, there is a lacinial flexor muscle connecting to the cranium. Neither the lacinia nor the galea have extensor muscles. The palp has elevator and depressor muscles, and each segment has an intrasegmental muscle which causes the next segment to flex.
- * The maxilla of the lower Pterygota is more generalized than the 2 other gnathal appendages. Snodgrass considered the cardo and stipes collectively to be the coxa. Matsuda and others claim the cardo is the subcoxa. No good embryological evidence supports this but paleontological evidence does. The palpus is the telopodite. The lacinia and galea are the basendites. There is no evidence for the palpifer to be considered a segment homologous to any limb segment.

LABIUM

- * The labium is a single structure, but evolved from 2 maxilla-like structures, and lies behind the maxillae. The labium represents the paired 3rd gnathal appendages that have fused together, and they are sometimes called the 2nd maxillae of the insects.
- * The basal part of the labium (equivalent to the maxillary cardines) is called the **postmentum**. The postmentum may be subdivided into a proximal **submentum** and a distal **mentum**. Distal to the postmentum (equivalent to the maxillary stipites) is the **prementum**. The prementum functions similarly to the labrum, it is the posterior lip that closes the mouth opening. The prementum distally bears four lobes, collectively called the **ligula**; the two inner lobes are called the **glossae** (equivalent to the maxillary lacinia) and the two outer lobes are called the **paraglossae** (equivalent to the maxillary galea). These lobes may or may not be present, or they may be fused to form a single median lobe. The prementum also bears laterally on each side a palpus, often composed of 3-segments. The basal region from which the labial palpus arises is called the **palpiger**.
- * The distal, free-moving part of the labium including the prementum, the palps, and the terminal lobes (glossae and paraglossae) is sometimes called the **prelabium**. The proximal portion of the labium, including the postmentum (mentum + submentum), which articulates directly with the cervix, and appears to be closely associated with the postocciput as the sclerite of its origin is sometimes called the **postlabium**. The line of flexion between the prelabium and the postlabium is sometimes called the **labial suture**. All the proximal muscles of the labium are inserted on the movable prelabium.
- * The musculature of the labium is similar to the maxillae, but there are no muscles that attach to the postmentum. The ventral adductors connect the tentorium to the prementum. Glossae and paraglossae have flexor muscles, but not extensors. There are some muscles in the labium that have no equivalents in the maxillae; these are involved in regulating the flow of saliva, or to move the prementum.

HYPOPHARYNX

- * The hypopharynx is an extremely important organ which is generally neglected. It functions as the tongue and has salivary duct openings at its base. It is located below the pharynx, directly posterior to the mouth opening.
- * Most of the hypopharynx is membranous, but the **adoral** surface (surface towards the mouth opening) is sclerotized distally, and proximally contains a pair of **suspensorial sclerites**, which are hinged to a pair of **lingual sclerites**; muscles attached to the above sclerites allow the hypopharynx to be moved back and forth. The lower ends of the suspensorial sclerites bend mesad, forming a U-shaped band, called the **suspensorium**. The small lateral arms of the suspensorial sclerites are called the **loral arms**.

- * The food is passed over the hypopharynx on its way to the mouth, over the surface of the hypopharynx between the suspensorial sclerites (HS). This surface is usually depressed and is called the **sitophore**. It is the floor of the **cibarium**. Below the hypopharynx and above the inner aspect of the postlabium is formed another cavity called the **salivarium** into which the salivary duct opens.

THE MECHANISM OF INGESTION

- * 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.
- * **Constriction of the cibarium:** The sitophore has a sheet of transverse muscle fibers attached laterally on the suspensory arms (HS), and the opposing clypeal surface is likewise covered with a layer of transverse fibers which together serve to constrict the cibarium.
- * **Dilation of the cibarium:** There is a prominent set of muscles called the intraclypeal muscles (5A & 5B) serve at the same time to compress the clypeus and dilate the cibarium.
- * On its lower aspect, the cibarium is dilated by the action of the **fan-shaped muscles originating on the tentorium** (Fig. 7A).
- * A primitive sucking pump is produced when the hypopharynx is pushed against the upper surface of the cibarium and the muscles just noted act alternately to dilate and compress the cibarium. No new structure is needed to develop the sucking pump of insects like the mosquito or cicada.

HAUSTELLATE MOUTHPARTS

- * There are no fossil records or species in existence that can give us satisfactory clues to the intermediate steps that may have occurred in the evolution of the haustellate mouthparts. The feeding mechanisms for the various haustellate orders of insects (Hymenoptera, Lepidoptera, Diptera, Hemiptera-Homoptera, etc.) are not comparable, that is the elaboration of the basic mandibulate structures into a sucking tube has been different in each group. All of the mandibulate structures have been preserved in the Hymenoptera and Hemiptera, although they are very modified. But the mandibles are completely lacking in some Lepidoptera and Diptera. One structure that all of the haustellate insects do have in common is the modification of the cibarium into a pumping apparatus referred to as the **cibarial pump**.

Piercing-sucking mouthparts - Hemiptera

- * The long and conspicuous, 3 to 4-segmented **labium** (sometimes called the rostrum) is not involved in the elaboration of the actual piercing-sucking tube. It is an ovate cylinder with heavily sclerotized walls and a shallow dorsal groove or **dorsal gutter**. This is such a highly specialized structure that the elements of a typical mandibulate labium are obscure. The purpose of the labium is simply to serve as a sheath for the sucking mechanism that lies encased in its dorsal gutter while at rest. During feeding, the labium is actually withdrawn and does not enter into the tissues of a host. There is a cluster of papillae at the distal end of the labium which probably is probably sensory in function.
- * The piercing-sucking mechanism is a closely appressed bundle of 4, hair or needle-like shafts or **stylets**. An examination of the musculature at the base of these stylets leads us to believe that they were modified from typical appendicular mandibles and maxillae. In gross appearance, the stylets appear to be a single, hair-like bristle. A cross-section, however, reveals that 4 distinct heavily sclerotized and elaborately sculptured structures are involved. The outer pair are the **mandibular stylets** which are grooved to fit an inner pair of **maxillary stylets**. The mandibles are the principal piercing stylets. Note that the tips are pointed and provided with sharp cutting plates and recurved spines for anchoring the stylets in host tissue. The tips of the maxillae are also pointed, but their structure would indicate that they are secondary to the mandibles as penetrating organs.

- * The cross-sectional view illustrates the longitudinal grooves and mortising that holds the maxillary stylets together and provides longitudinal tubes. The dorsal tube or **food canal** leads to the cibarium, while the ventral tube or **salivary canal** opens into the salivarium. Mortise joints also hold the mandibular stylets firmly to the maxillae. Although the stylet bundle is securely united, each of the grooved mandibular stylets may move freely and independently upon the maxillae in a longitudinal plane. This forward and longitudinal movement of the mandibles is accomplished by **protractor muscles** arising from the **mandibular apodeme** and attached to the base of the stylet. The maxillary stylets as a unit are also protracted by muscles attached to a **maxillary apodeme** anchored on the posterior tentorium.
- * Penetration of host tissue is accomplished by the alternate and individual protraction of each mandibular stylet. When the pair of mandibular stylets have reached a maximum protraction, the pair of maxillary stylets are protracted to a position that is even with them, and the cycle is repeated. Recurved barbs on the tip of the mandibular stylets serve to hold the entire bundle in position in the host tissue during each cycle of protraction. When the stylets have reached a desirable feeding site, **saliva** is pumped down the salivary canal by means of the elaborate **salivary syringe**, and liquid food is pumped up the food canal by means of the cibarial pump.
- * The **labrum** is a sharply pointed flexible flap articulating at its base with the **anteclypeus** and lying over the dorsal gutter of the entire first basal segment of the labium. This modified labrum is more than a simple covering flap. Examination of the ental surface will reveal a deep groove which ensheathes the basal portion of the stylet bundle. This is the **labral stylet groove** which serves to hold the stylets in position before their separation in the head cavity.

Piercing-sucking mouthparts - Diptera (Mosquito)

- * **Note:** Diptera mouthparts in general - there is a wide variety of mouthpart types within the Order, but in all types, the salivary canal is within the hypopharynx, and the food canal is formed between the labrum and the other mouthparts. The mandibles and maxillae are styliform in species that suck blood from vertebrates, but they are usually lacking in other species, including the blood-sucking Cyclorrhapha. When they are present, they are the penetrating organs; when they are not present, often the labium is the penetrating organ (if it is expanded and lobe-like, it is called the **labellum**).
- * The mosquito mouthparts are also of a piercing-sucking type. Although they are similar to the Hemipteran mouthparts in some respects, they are very different in other respects.
- * The encasing sheath is still made up of the **labium**, but now there are 6 stylets rather than the 4 found in the Hemiptera. In addition to the pair of **mandibular stylets** and the pair of **maxillary stylets**, there is also a **labral stylet** and a **hypopharyngeal stylet**. The **maxillary palps** are also well-developed. The **salivary channel** is in the hypopharyngeal stylet. The **food channel** is between the grooved labral stylet and the hypopharyngeal stylet. The labium does no piercing and folds up or back as the stylets enter the tissue.
- * Other flies (such as robber flies) are similar except that there are no mandibular stylets and the principal piercing organ is the hypopharynx. There are 4 stylets: the labrum, maxillae, and hypopharynx. The salivary channel is still in the hypopharyngeal stylet, and the food channel is between the labrum and hypopharynx.
- * In still other flies (such as horn fly or stable fly) the principal piercing structure in these flies is the labium; the labrum and hypopharynx are slender and stylet-like, and lie in a dorsal groove of the labium. The labium terminates in a pair of small hard plates, the **labellum**, which are armed with teeth. The salivary channel is still in the hypopharynx, and the food channel is still between the labrum and the hypopharynx.

Sponging mouthparts - Diptera (house fly)

- * The entire proboscis resembles a stubby, foot-like organ when it is protracted for feeding. In this position, we can recognize 3 distinct regions: 1) a comparatively soft, cone-shaped basal region or **rostrum**, 2) a cylindrical

median region or **haustellum**, and 3) a distal pair of fleshly lobes forming the foot or **labella**. When at rest, the haustellum is partially retracted within the rostrum and is folded anteriorly upon it, while the ventral surface of the labella is tipped upward and posteriorly from its horizontal feeding position.

- * The base of the proboscis or the rostrum is largely membranous except for a large U-shaped anterior sclerite identified as the **clypeus**, and 2 small lateral sclerites or **maxillary plates** bearing unsegmented palps which are the **maxillary palps**. The maxillary plates may simply be a remnant of the maxillae or a palpifer.
- * The haustellum is a fleshy cylinder which is entirely membranous except for a posterior plate descriptively identified as the **thecal plate**, and a sclerotized dorsal groove or **labial gutter**. Overlying the labial gutter is the **labrum**. Note that the labrum is ovoid in cross-section and deeply grooved on its ental surface. The **hypopharynx** is stylet-like in form and underlies the labrum and lies within the gutter.
- * The **salivary gland** provided with a pumping mechanism or **syringe** empties directly into the tubular hypopharynx. The longitudinal groove of the labrum forms a short sucking tube leading from the labellum to the cibarial pump.
- * The labella are fleshy lobes forming a foot-like pad at the distal end of the proboscis. It is assumed by morphologists that these lobes are modifications of the labial palps although their resemblance to palps appears quite remote. During feeding, the labella are broadly expanded and directly contact the food source. The labella is deeply incised on its anterior margin, and the incision corresponds with the groove of the labial gutter. A V-shaped sclerite, the **discal sclerite**, margins the apex of this labellar incision.
- * Food passes directly into the food channel formed by the labrum and hypopharynx. A series of tubes transversely line the labellar lobes and empty into large **collecting channels** which parallel the discal sclerite. These tubes are referred to as the **canaliculi**, or pseudotracheae since they remotely resemble the tracheal tubes of the respiratory system. There are 5 sclerotized teeth anchored on the discal plate on the mesal margin of each labellum. These minute teeth are the **prestomal teeth**. When the labella are pressed against a surface and presumably rotated, the prestomal teeth may serve as a cutting and rasping device.

Rasping-sucking mouthparts - Thysanoptera

- * Thrips - cone shape formed by clypeus, labrum, and labium.
- * Only left mandible present - used to penetrate the plant tissue.
- * Maxillary stylets held together to form food channel.
- * There is no salivary channel - salivary duct opens in front of esophagus.

Siphoning mouthparts - Lepidoptera

- * There is considerable simplification in the formation of the sucking tube in the Lepidoptera. The long, coiled tubular structure bears a superficial resemblance to the ensheathing proboscis of the Hemiptera, but close examination reveals that the proboscis of the Lepidoptera is actually the sucking tube and that it is not a modification of the labium. In cross-section, the proboscis is composed of 2 ovoid cylinders, deeply grooved on their mesal surface, and fitted together by mortise joints so that the longitudinal grooves form a channel or **food canal**. Examination of the basal structures of each half of this proboscis gives us satisfactory clues to its origin.
- * Two articulatory sclerites can be readily identified as the **cardo** and **stipes**. Identification of the proboscis as a modification of the maxillae is assured by the inconspicuous, 2-segmented **maxillary palp** borne by the stipes on its ventral margin. The long, sucking tube must, then, be one of the maxillary endites, and each half of the tube is usually identified as the **galea**. At the base of the proboscis, the galea are divided and the food canal empties through a narrow canal into a large, bulbular **cibarial pump**. There is no salivary channel, although adult Lepidoptera do have saliva.

- * All of the other typical mandibulate mouthparts are reduced or wanting except for the conspicuous **labial palps**. These palps are usually 3-segmented. The **labium** itself is greatly reduced to a simple oblong **postmental** sclerite articulating with the **cervix**, and a plate-like **prementum** occupying the ventral aspect of the head and bearing the **labial palps**. The **mandibles** are either not present or are represented as vestiges by 2 sclerites arising at the lateral margins of the **labrum**. The **labrum** is a small flap at the base of the proboscis. A fleshy distal tip of the labrum may serve to cover the food canal as it extends into the cibarium. There appear to be no remnants of the **hypopharynx**.

Chewing-lapping mouthparts - Honeybee.

- * The **labrum** is a simple flap, and the **mandibles** are preserved as in the typical mandibulate form. Although the **mandibles** are strong **dicondylic** structures, they are no longer employed for tearing and grinding in the ingestion of food. Their function in the drone and queen is obscure, but in the worker the mandibles are employed for grasping, cleaning brood cells, shaping wax, and other duties of the hive. A sexual dimorphism is evident in the form of the mandibles. The ental surface of the worker bee mandible is a flat and apparently effective spatulate tool. The drone, of course, has little interest in the labors of the hive, and the hairy mandibles have relatively less functional form.
- * The maxillae, labium, and hypopharynx have been greatly modified into a sucking tube. The head of the honeybee is hypognathous and the **postmentum** is a very small triangular sclerite in comparison with the greatly expanded **prementum**. The **prementum** is a completely sclerotized half-cylinder. This cylindrical structure is completed by the membranous **hypopharynx** on its dorsal surface. There is a **salivary gland** and a small **salivarium** which empties at the apex of the hypopharynx between 2 suspensory rods or **ligular arms**. At the apex of the prementum is a small triangular plate described as the **distal plate of the prementum**, but which may be the **ligula**.
- * Two pair of appendages and a median tube complete the labium. The large, segmented outer pair are the **labial palps**. Note that the basal 2 segments are elongated, flat and L-shaped in cross-section. The distal 2 segments of the labial palps are small and typically **palpiform**. A median pair of spoon-shaped appendages are the **paraglossae**. The salivary duct opens at the base of the paraglossae, and when the paraglossae are drawn together they close ventrally over the base of the median glossa. Although the median tube is referred to as the **glossa**, it is an unpaired structure and is only remotely homologous with the glossae of chewing insects. At the tip of the glossa is a spoon-shaped segment given the descriptive but anatomically incorrect name of **flabellum**.
- * The maxillae are readily identified as the flat appendages on either side of the labium. The cardo articulates directly with the postmentum by means of a V-shaped sclerite or yoke described as the **lorum**, and with the postgena by means of an articular flange. The **stipes** bear a greatly reduced 2-segmented maxillary palp, a weakly sclerotized and lobular **lacinia**, and an elongated and flattened **galea**.

Antennae - review antennal parts and types from text books. You should know the basic parts: scape, pedicel, and flagellum. And you should know the various types of antennae (e.g., moniliform, clavate, labellate, etc.)

Eyes - we will discuss eyes later in the course when we discuss sensory structures.