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# Immature Insects

Jan Růžička

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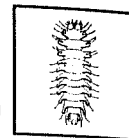
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## BEETLES\*

The Coleoptera is the largest order of insects, with more than 350,000 species worldwide and about 25,000 occurring in America north of Mexico. In the present book, they are placed in 156 families, 31 of which do not occur in the United States or Canada. Larvae of Coleoptera, unlike those of some other orders, have no one common name that can be applied to all forms, and various terms like grub, white grub, wire-worm, mealworm, rootworm, glow worm, round-headed borer, flat-headed borer, timber borer, water penny, etc. have been used for individual larval types. Most beetles are terrestrial, but a number of genera and some families are aquatic as larvae, some occur in water throughout most (or rarely all) of the life cycle, and a few are aquatic in the adult stage only. The majority of beetle larvae feed on various kinds of living and dead plant tissue (roots, stems, trunks, branches, logs, leaves, flowers, seeds), but many feed on fungi, carrion or dung, some are predaceous, and a few are parasitic. Many Coleoptera cause damage to agricultural crops, forests, or stored products, but very few are of medical importance.

## DIAGNOSIS

There is no single feature which will distinguish beetle larvae from those of other insect orders and only a few which may be considered universal within the group. The following list includes most characters considered of diagnostic value.

1. Head capsule well-developed and usually sclerotized.
2. Head usually without paired endocarinae (**adfrontal ridges**) forming a V or Y, and never with adfrontal areas formed between them and the frontal sutures or ecdysial lines; paired endocarinae, when present, very rarely extending to the anterior part of the frontoclypeal region.
3. Antennae almost always with 4 segments or fewer and with a sensorium on the penultimate segment.
4. Number of stemmata on each side always 6 or fewer.
5. Mouthparts almost always of the chewing or orthopteroid type with opposable mandibles moving in a transverse plane, and with normal palp-bearing maxillae and labium; rarely modified to form a sucking tube bearing stylets, or with immovable or non-opposable mandibles.
6. Median labial silk gland or spinneret always absent.

\*In this section a figure reference such as (Kfig. 121 p190) refers to Key fig. 121, page 190.

7. Legs usually with 5 or 6 segments (coxa, trochanter, femur, tibia, and either tarsungulus or tarsus and pretarsus, the latter consisting of one or two claws) or absent; occasionally with reduced segmentation.
8. Abdomen usually with 10 segments (occasionally fewer), without articulated appendages (cerci) on segment 10.
9. Paired abdominal prolegs almost always absent; asperity-bearing prolegs occasionally present on sterna 2-4, 3-4 or 2-5; simple prolegs rarely present on sterna 1-8; crochet-bearing prolegs rarely present on sterna 2-7 or 3-7.
10. Respiratory system usually peripneustic, without functional spiracles on metathorax; occasionally amphipneustic, metapneustic, or apneustic.
11. Spiracles often with accessory openings (annular-uniform, annular-biforous, annular-multiforous), with divided opening (biforous), or with poroid sieve-plate (cribriform); ecdysial scar, if present, never completely enclosed by sieve plate.

Because of the great diversity of form within the Coleoptera, at least some beetle larvae may be confused with immatures belonging to each of the other endopterygote orders and probably those of a few exopterygote groups as well. The triangulinids of **Strepsiptera** are said to resemble the triangulins of Meloidae and Rhipiphoridae, but they differ from them in several respects, including the absence of mandibles, antennae, and labial palps, the lack of trochanters in the legs, and the presence of a pair of long setae on the terminal 10th segment. The endoparasitic forms of Strepsiptera (larvae and adult females) are easily distinguished because of their extremely reduced body which is indistinctly segmented. The free-living last larval instar (puparium) in Mengenillidae has 5-segmented legs with 2 claws but differs from beetle larvae in the presence of compound eyes composed of numerous facets.

Larvae of **Trichoptera**, **Megaloptera**, **Raphidioptera**, and **Neuroptera** may be distinguished from most beetle larvae by the presence of 6-segmented legs, which in the Coleoptera occur only in the suborders Archostemata and Adephaga. The distinctive head of Cupedidae and Micromalthidae, with a median endocarina, well-developed mandibular molae, and a sclerotized ligula, separate them from members of the above orders, while the absence of a free labrum will distinguish adephagan larvae from those of Trichoptera, Megaloptera, and Raphidioptera. Neuroptera larvae also have the labrum fused to the head capsule, but they differ from any beetle

larvae in their distinctive feeding apparatus, consisting of a pair of sucking organs formed by the falciform or styliform mandibles and maxillae on each side, and by the complete absence of maxillary palps. The divided, blade-like mandibles of Lycidae or the perforated, sucking mandibles of Lampyridae and Phengodidae might be confused with neuropteran mouthparts, but these groups always have maxillary palps and 5-segmented legs. Six-segmented legs also occur in 2 rare families: Nannochoristidae (**Mecoptera**) and Heterobathmiidae (**Lepidoptera**); larvae of both may be distinguished from those of Coleoptera by the combination of leg segmentation and free labrum, while the former has more than 6 stemmata on each side and panorpoid spiracles (with numerous openings surrounding an ecdysial scar), and the latter has adfrontal ridges, adfrontal areas, and a median labial gland.

Larvae of **Lepidoptera** are easily confused with various beetle larvae, especially those of Chrysomelidae, but all of the former differ in having a median labial gland, which is usually developed into a protruding spinneret, almost all of them differ in having paired adfrontal ridges, with adfrontal areas formed between them and the ecdysial lines, and most of them differ in having paired, crochet-bearing prolegs on abdominal sterna 3 to 6 and 10. The median labial gland may be difficult to see in some primitive forms without distinct spinnerets (Micropterigidae), and the adfrontal ridges are absent in Micropterigidae and Agathiphagidae. A number of groups lack prolegs, while some also lack thoracic legs and may be confused with apodous Coleoptera larvae; all of these groups, however, have the typical lepidopteran head. Several beetle larvae have abdominal prolegs, but these are usually simple or asperate, without crochets, and occur on different abdominal segments than those in most Lepidoptera (1 to 9 in schizopodine Buprestidae; 2 or 3 to 7 in Hydrophilidae; 2 to 4, 3 to 4, or 2 to 5 in Oedemeridae; and 1 to 8 in Curculionidae). Crochets occur on the prolegs of some Hydrophilidae, but these larvae differ from any lepidopteran in having biforous spiracles and the labrum fused to the head capsule. Larval Micropterigidae differ from those of other Lepidoptera in having simple, more or less acute, mecopteran-like prolegs, which are not always distinct, on segments 1 to 8. The lack of lepidopteran head characters makes them particularly difficult to separate from beetle larvae; but the combination of a more or less hexagonal shape in cross-section, a retracted head, the lack of an antennal sensorium, 3-segmented legs, and a vestiture consisting of characteristic thickened setae should distinguish them.

Three-segmented thoracic legs and simple prolegs on segments 1 to 8 will also distinguish larvae of most **Mecoptera** from those of Coleoptera, and, in addition, most **Mecoptera** larvae have panorpoid spiracles, more than 6 stemmata on each side, and no distinct cardo. Larvae of Boreidae have vestigial spiracles, no prolegs, and only 3 stemmata, but they may be distinguished by their short, clawless, 3-segmented legs, which are very close together on the prothorax and widely separated on the meso- and metathorax.

Various **Hymenoptera** larvae are easily confused with those of beetles, although all possess a median labial gland (not always easy to see) and many have 2 thoracic spiracles. Larvae of Apocrita and some Symphyta (Orussidae) are lightly sclerotized and legless, with a hypognathous head, and

are most likely to be confused with some Meloidae, Rhipiphoridae, and Curculionidae; in addition to the labial gland and the presence of a 2nd thoracic spiracle (in some), the former groups have reduced maxillary and labial palps (1-segmented or absent). Larvae of most Symphyta differ from those of Coleoptera in having paired prolegs on abdominal segments 2 to 7 or 8 and usually 10 (Tenthredinidae, Argidae, Cimbicidae, Diprionidae), more than 4 antennal segments (Blasticomidae, Pamphiliidae, Xyelidae), or more than 4 plicae on most abdominal segments (Cimbicidae, Diprionidae). The only beetle larvae with prolegs on the same segments are Hydrophilidae, which have a fused labrum and biforous spiracles, never occurring in Hymenoptera, while those few beetle larvae with more than 4 antennal segments either have long, flagellate antennae, highly modified mouthparts, and a terminal respiratory chamber (Helodidae) or a median endocarina, 6-segmented legs, and mandibular molae (Cupedidae). Larvae of the last group bear a superficial resemblance to larvae of Cephidae, and both have 4 or 5 antennal segments and a median spine (suranal process) on tergum 9. Of those Symphyta larvae with fewer antennal segments, fewer plicae, and no prolegs, the Xiphydriidae and Siricidae both have vestigial legs and a suranal process, much as in larvae of Mordellidae; they differ from mordellids in having elongate-elliptical spiracles. Some surface-feeding Pergidae which lack prolegs differ from any beetle larvae in having a single large stemma on each side and the antennae reduced to dome-like structures; also there is usually a smaller, but obvious, 2nd thoracic spiracle.

The apodous larvae of **Diptera** can often be distinguished from legless beetle larvae on the basis of their incomplete head capsule and/or vertically oriented, non-opposable mandibles; in the Nematocera, however, most larvae have a well-developed head capsule and transverse, opposable mandibles, as in most Coleoptera. Except for some aquatic forms without functional spiracles (Chironomidae, Ceratopogonidae, Simuliidae), most nematoceran larvae may be distinguished from those of beetles by the type and location of their spiracles, as well as by the universal absence of a spiracular closing apparatus (present in all legless Coleoptera). The presence of spiracles on the thorax and 8th abdominal segments only (amphipneustic system, as in Tanyderidae, Psychodidae, Trichoceridae, etc.) and the presence of a single pair of spiracles on segment 8 (metapneustic system of Tipulidae, Culicidae, etc.) are conditions known among Coleoptera, but not in groups with apodous larvae. Bibionidae and a few other groups have a holopneustic system with 2 thoracic and 8 abdominal spiracles on each side, a condition unknown in Coleoptera; and the remaining Nematocera with a peripneustic system usually differ from beetles in having the thoracic and last abdominal spiracles enlarged. The spiracles of Nematocera are either of the panorpoid type, with a ring of small openings surrounding an ecdysial scar, or they have a characteristic cribriform plate with 3 openings; spiracles are never of the biforous type (as in sphaeridiine Hydrophilidae, schizopodine Buprestidae, or Eucnemidae), never have a poroid cribriform plate (as in most Buprestidae), and are never annular, annular-uniform, or annular-biforous (as in apodous Bothrideridae, Rhipiphoridae, Meloidae, Chrysomeloidea, or Curculionoidea).

Larvae of **Siphonaptera** are also legless, and they differ from apodous beetle larvae in having 2 pairs of thoracic spiracles; these spiracles are very difficult to see, however, and a more practical suite of distinguishing features consists of the fused labrum, 1-segmented but long and prominent antennae, pair of anal struts on segment 10, and transverse rows of stiff setae on the body.

A few Coleoptera larvae (cerylonine Cerylonidae and the leiodid genus *Myrmecholeva*) have the mouthparts modified to form a median tube through which the stylet-like mandibles and maxillae move; both of these larval types have a more or less hypognathous head and might be confused with certain **Homoptera**; members of the last group, however, always lack maxillary and labial palps and often have the head immovably united to the thorax. The general head structure, multisegmented antennae, mouthparts, and aquatic habits of larval Helodidae cause them to resemble the larvae (nymphs) of some **Plecoptera**, but they can be distinguished from that exopterygote group by the lack of wing pads and the structure of the leg, which has a single tarsungulus, rather than a subdivided tarsus and paired claws.

## LARVAL MORPHOLOGY

### Body Form

Beetle larvae are extremely variable in general form (figs. 34.1-6), and the body may be elongate to short and broad, parallel-sided to almost circular, and highly convex to strongly flattened. Although the body shape is best described in simple geometric terms (cylindrical, elliptical, ovoid), a number of words are commonly used, which have been derived either from Latin and Greek words describing shape or more often from the names of other arthropods having a similar shape. Beetle pupae (figs. 34.7-8) are more uniform in shape and are described later.

The term **campodeiform** (also called **lepismatoid** or **thysanuriform**) refers to a type of larva with an elongate, slightly flattened body, often somewhat tapered (at least posteriorly), and usually moderately heavily sclerotized (at least dorsally), with long, well-developed legs (fig. 34.1). This is an actively moving type of larva, usually inhabiting surfaces or relatively large **interstitial** spaces within leaf litter, and often predaceous. Campodeiform larvae occur throughout the Adephaga (with some modifications in aquatic forms), are common in the Staphylinidae, and are found in various other groups which are relatively active in the larval stage. The term also applies to the first-instars (triungulins) of Micromalthidae, Rhipiceridae, passandrine Cucujidae, ectoparasitic Bothriideridae, Meloidae, and Rhipiphoridae. The word **fusiform**, referring to a body which tapers at either end, may also be used to describe most campodeiform larvae.

An **eruciform larva** is one which is caterpillar-like, that is, more or less cylindrical with moderately well-developed legs (fig. 34.2). This type of body may be found in surface-active forms which are relatively slow moving and may be

Among the Coleoptera, many Chrysomelidae are said to have an eruciform type of larva, but the term might apply to a variety of other beetle larvae. Cylindrical larvae which are moderately to heavily and uniformly sclerotized, with short legs, are sometimes called **vermiform**, but are more commonly known as **wireworms** (fig. 34.3). This type of larva, which usually inhabits soil or rotten wood, occurs in Callirhipidae (fig. 34.3), Dryopidae, Elmidae, Elateridae, Cebrionidae, and Tenebrionidae (Alleculinae, Blaptini, Helacini). Ghilarov (1964b) restricted the word vermiform to the peculiar larvae of cardiophorine Elateridae, which are very long and narrow, lightly sclerotized, and appear to have a large number of abdominal segments, due to the transverse subdivisions of each segment. The term **orthosomatic** may be applied to any larva which is elongate and more or less parallel-sided.

An **onisciform larva** is one which is short and broad, more or less ovate, and moderately to strongly flattened; the word is derived from the name of a terrestrial isopod crustacean. The body itself is often relatively narrow and fusiform, but the onisciform appearance is caused by the presence of lateral tergal outgrowths, which may become closely adapted, so that a continuous oval or circular outline is produced, as in Psephenidae (fig. 34.4). Extremely flattened and ovoid larvae, which have the head and legs completely concealed beneath the body, are sometimes said to be **limpet-like** or **cheiloniform** (turtle-like), while the term **disc-like** is used in the larval key. Onisciform larvae are known in Carabidae (Cychrini), Micropeplidae, Scydmaenidae (*Cephenium*), Silphidae (Silphinae), Byrrhidae (*Cytilus*), Elmidae (*Phanocerus*), Psephenidae, Corylophidae (Rypobiini, *Corylophodes*), Cerylonidae (*Murmidius*, Ceryloninae), Discolomidae, Tenebrionidae (Niloninae), and Chrysomelidae (some Hispinae), but the extreme disc-like larvae occur only among the psephenids, corylophids, and discolomids, and in *Murmidius* and some hispines. This type of body has evolved for different reasons in the various groups; psephenids attach themselves to algae-covered rocks in streams and are subjected to strong currents, while the flattened hispine Chrysomelidae (Cephaloleiini, Arescini, Alurnini) live in leaf axils. The term **cyphosomatic** is used to describe a larva which is strongly convex dorsally but more or less flattened ventrally; it has been applied to larvae of some Chrysomelidae (Chrysomelinae, Criocerinae, Cassidinae).

**Scarabaeiform** is a term based on the larvae of Scarabaeoidea, which are relatively lightly sclerotized and strongly curved ventrally, forming a C or U (fig. 34.5); these larvae have also been called **grubs**, and the term **C-shaped** has been used in the key. Scarabaeiform larvae are characteristic of most scarabaeoids, some Byrrhidae, many Bostrichoidea, Bruchidae, some Chrysomelidae (Sagrinae, Cryptocephalinae, Clytrinae, Chlamisinae, Eumolpinae) and some Curculionoidea. Most of these occur in the soil, but some may be wood-borers or seed-eaters, and larvae of the cryptocephaline group are adapted for living within the confines of a faecal case. A slight ventral curvature may be found in many beetle larvae, and this may be exaggerated with preservation; but these are not considered to be scarabaeiform. In a few inter-

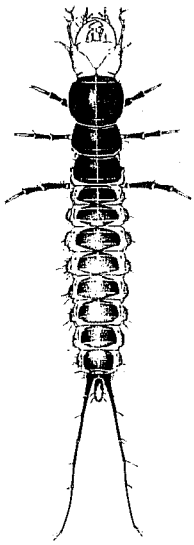


Figure 34.1

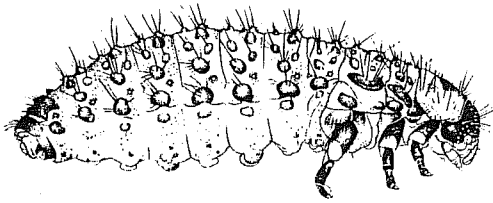


Figure 34.2

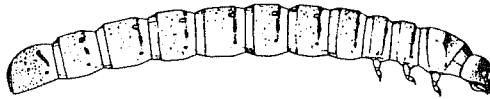


Figure 34.3

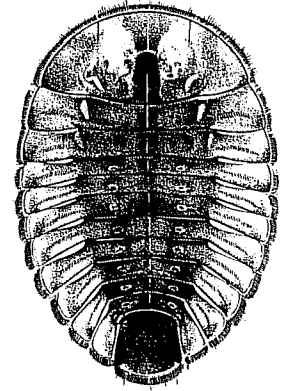


Figure 34.4

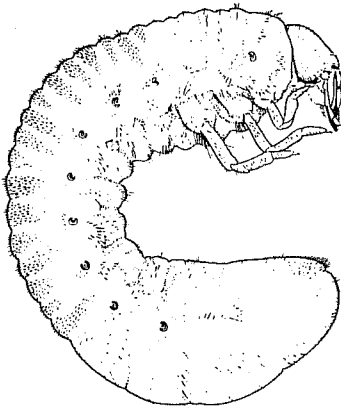


Figure 34.5

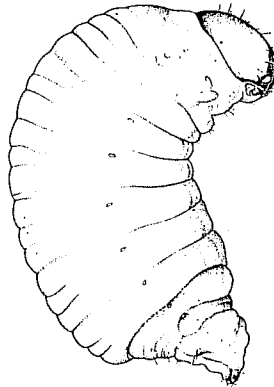


Figure 34.6

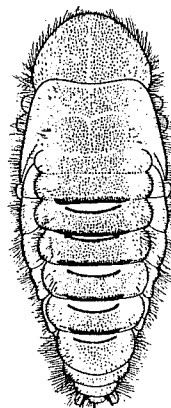


Figure 34.7

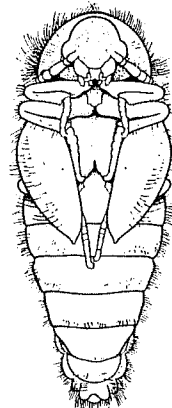


Figure 34.8

**Figure 34.1.** Campodeiform larva. *Eudalia macleayi* Bates (Carabidae: Odacanthinae). (From Britton, 1970 in *The Insects of Australia*, Melbourne University Press).

**Figure 34.2.** Eruciform larva. *Paropsisterna beata* (Newman) (Chrysomelidae: Chrysomelinae). (From Britton, 1970, in *The Insects of Australia*, Melbourne University Press).

**Figure 34.3.** Wireworm. *Zenoa picea* (Beauvois) (Callirhipidae).

**Figure 34.4.** Onisciform or platyform larva. *Sclerocyphon* sp. (Psephenidae: Eubriinae). (From Britton, 1970 in *The Insects of Australia*, Melbourne University Press).

**Figure 34.5.** Scarabaeiform larva or grub. *Anoplognathus pindarus* Carne (Scarabaeidae: Rutelinae). (From Britton, 1970, in *The Insects of Australia*, Melbourne University Press).

**Figure 34.6.** Apodous larva. *Trigonotarsus rugosus* (Beauvois) (Curculionidae: Rhynchophorinae). (From Britton, 1970, in *The Insects of Australia*, Melbourne University Press).

**Figure 34.7.** Exarate pupa. *Dermestes maculatus* De Geer (Dermestidae). dorsal view, showing median gill traps. (From Britton, 1970, in *The Insects of Australia*, Melbourne University Press).

**Figure 34.8.** Same, ventral.

of ventrally; this is known in the puffball-feeding *Pocadius* (Nitidulidae) and in species of *Leiodes* (Leiodidae), which occur in subterranean fungi.

**Apodous** or legless larvae (fig. 34.6) occur in several large groups living in dense substrates like soil, wood, seeds, etc. Most are lightly sclerotized, and many (Curculionoidea) are scarabaeiform in shape, while the wood-boring Buprestidae, Eucnemidae, and legless Cerambycidae have a straight or orthosomatic body. Most cerambycid and buprestid larvae have the thoracic region enlarged (Kfig. 121 p190) and are sometimes called **clavate** (Ghilarov, 1964b).

## Integument

The larval integument or **cuticle** is usually softer, more flexible, and more lightly pigmented than that of an adult beetle, but there is considerable variation. The term **sclerotization** is defined as the stabilization or hardening of cuticle by the addition of aromatic (phenolic and quinonoid) compounds, which cross-link proteins in a polymerization-like process called **tanning**. The formerly used synonym **chitinization** was based on the erroneous assumption that the compound **chitin**, a component of all cuticle, was responsible for the hardening process. Although tanning is usually accompanied by a darkening of the cuticle, due to the presence of

quinonoid compounds, a number of unpigmented larval cuticles (those of some "wireworms" and head capsules in many groups) may be hard and rigid, due to cuticular thickening or possibly a hardening process not involving pigmented compounds (Hackman, 1984 and personal communication). Following common usage, the word **sclerotized** will imply the presence of yellowish to black pigment. The term **hyaline** is used to describe rigid structures, like some mandibular prothecae (*see below*), which lack pigment and are more or less translucent; this is to distinguish them from truly membranous structures.

Many beetle larvae, especially those living within substrates, are very lightly sclerotized above and below, usually with a more rigid head capsule, which may or may not be more heavily pigmented than the rest of the body; examples are numerous in the Scarabaeoidea, Buprestidae, Throscidae, Cerophytidae, Bostrichoidea, Cerambycidae, eumolpine Chrysomelidae, and Curculionoidea. In other larvae, such as those of agrypnine Elateridae and various Cleroidea, the protergum and 9th abdominal tergum, as well as the head are sclerotized, but not the rest of the body. The dorsal surface is heavily sclerotized and the ventral surface either entirely membranous or with relatively small sclerotized plates separated by membrane in some Carabidae, Silphidae, Dermestidae, some Elateridae and some Tenebrionidae. Subcylindrical, uniformly sclerotized larvae (wireworms) occur in the families Callirhipidae, Dryopidae, Elateridae (especially Elaterinae), and Tenebrionidae (Alleculini, Blaptini, Helaeini, etc.). Some surface-active, soft-bodied larvae, such as those of Cantharidae, Cleridae, and Melyridae, may have red, blue, purple, or occasionally black pigment deposited in the soft cuticle, often forming patterns, while many chrysomelid larvae have a number of discrete prominences or plates which are pigmented (fig. 34.2).

In most beetle larvae, the integument is relatively smooth, and the **vestiture** consists of scattered, simple setae, which may be of fixed position within a particular taxon. In some groups, however, the sculpture is more complex and the vestiture may include modified setae of various kinds. Sometimes the entire surface or the dorsal surface is covered with fine **granules**, or these may be more sparsely distributed and form definite patterns, as in Psephenidae, priasilphine Phloeostichidae, Nitidulidae, and *Murmidius* (Cerylonidae). More prominent **setiferous tubercles** (Kfig. 3 p210) occur in a number of families, including Micropeplidae, Eucinetidae, Derodontidae, Hobartiidae, and Languriidae (Xenoscelinae, Cryptophilinae); while complex sculpture is restricted to relatively few groups, such as Erotylidae, Endomychidae, Cerylonidae (Euxestinae), Coccinellidae, and Chrysomelidae. A set of terms for cuticular prominences have been developed for Coccinellidae (Gage, 1920) and includes (from the simple to the complex): **seta**, for an articulated hair arising from a flat surface; **chalaza**, for a minute, pimple-like projection bearing a seta; **verruca**, for a small, mound-like projection bearing several setae; **struma**, for a mound-like projection bearing a few chalazae; **sentus**, for an elongate, unbranched projection bearing a few short setae along its trunk; and **parascolus** and

**scolus**, for shorter and longer, branched projections (*see section on Coccinellidae*). The word **tubercle** is sometimes used synonymously with **verruca**, but here it may apply to any simple protuberance, with or without a seta. More localized cuticular armature, including patches or rows of **asperities** or **spinules**, may occur on the thorax and abdomen of larvae which live under bark or bore into relatively solid substrates, but these are discussed in a later section.

The **seta** is the most common type of cuticular process, and it is always characterized by being articulated and by consisting of a single cell called a **trichogen**, closely associated with another type of cell, a **tormogen**, which forms the setal socket. Other articulated structures, derived from a seta, include **bristles**, **scales**, and various types of modified setae. The word **spine** refers to a multicellular, fixed, cuticular process, and terms like **spinules**, **asperities**, and **microtrichiae** have been used for those which are much smaller or more tooth-like. The word **spur** refers to an articulated, multicellular process.

Although most larvae have a relatively sparse covering of setae, a few are densely covered with long hairs; these include Scarabaeidae (Glaphyrinae), Elateridae (Tetralobini), Dermestidae, some Anobiidae and Tenebrionidae (Lagriini). In cantharid larvae, there is a dense covering of minute hairs, giving the body a velvety appearance. The most common type of modified seta is the so-called **frayed seta**, whose apex is expanded and frayed looking (Kfig. 4 p244); these are found in a number of Staphylinoidae and in several families of Cucujoidea. Some setae have numerous minute protuberances, which may be hair-like, and are called **pubescent setae** (Kfig. 5 p236). **Glandular setae** are hollow and usually have an opening at the apex; but the term has also been applied to pubescent setae. Various kinds of highly modified **scales**, which may be club-like or sometimes flattened, occur in some groups, like *Pseudomorpha* (Carabidae), Brachypsectridae, and a few Cantharidae and Coccinellidae. Setae which are covered with numerous barbs are called **spicisetae** (Kfig. 6 p230), and occur in most Dermestidae and in *Murmidius* (Cerylonidae). A more complex setal type in Dermestidae is the **hastiseta**, which has barbs along the shaft and a pair of 3-pronged structures at the apex (Kfig. 7 p230).

Other cuticular structures include the openings of defensive glands, which may be associated with reservoirs, and luminous or light-producing organs. Cuticular defensive glands are probably widespread among beetle larvae, but they have been reported for only a few groups, partly because the openings and reservoirs may be very small. Paired dorsolateral gland openings on most thoracic and abdominal terga are known in the families Staphylinidae, Cerophytidae, Phengodidae, Cantharidae, Trogossitidae (Trogossitinae), Melyridae, Coccinellidae, Tenebrionidae, and Chrysomelidae, while in Corylophidae, there are large, paired openings on abdominal segments 1 and 8 (Kfig. 138 p258) or 1-7. A single median gland opening occurs on the 8th tergum in most aleocharine Staphylinidae and on the 9th tergum in some Tenebrionidae, while head glands have been reported in Staphylinidae, Pselaphidae and Tenebrionidae (Doyen and

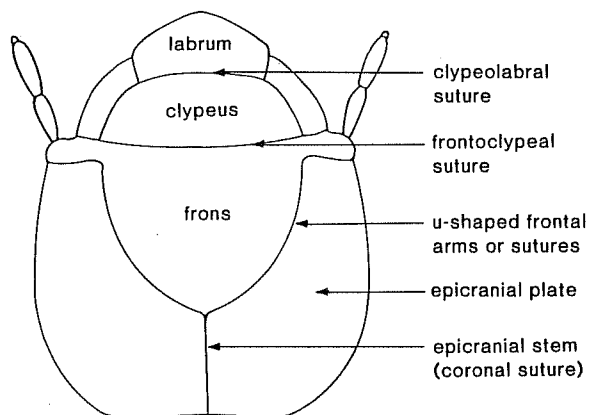


Figure 34.9. Head (Tenebrionidae), dorsal.

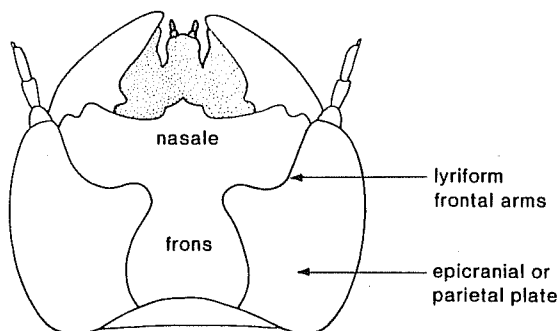


Figure 34.10. Head (Elateridae), dorsal.

Lawrence, 1979; Frank and Thomas, 1984; Kasule, 1966). Luminous or light producing organs occur on the head in Phengodidae and on the thorax and/or abdomen in Phengodidae, Lampyridae, Homalidae, and pyrophorine Elateridae (Sivinski, 1981).

### Head Capsule

The head capsule or **cranium** in beetle larvae is always distinct and usually moderately to strongly sclerotized, exceptions occurring in forms with strongly retracted heads and in the protracted heads of some Scarabaeoidea, Anobiidae, Prostomidae, Oedemeridae, Tenebrionidae, Chrysomelidae, and Curculionoidea. There are 2 large openings: the posterior **occipital foramen**, leading into the cervical region or prothorax, and the opening of the **mouth cavity** or **preoral cavity**, which may be anterior or ventral, depending upon the type of head attachment (*see below*).

Larval heads may be of 3 different types, based on the nature of their attachment to the thorax. The most common type is the **protracted and prognathous** head (Kfig. 8 p186), which is not or only slightly declined and not deeply retracted into the prothorax. A second type is also protracted but is more strongly declined or **hypognathous** (Kfig. 10 p186), so that the mouthparts are directed ventrally like those of primitive orthopteroid insects. Some strongly hypognathous heads, like those of cerylonine Cerylonidae (Kfig. 28 p200), have the mouthparts directed somewhat posteriorly; these have been called **opisthognathous**, but the term is more suitable for describing the condition in Hemiptera. The third type is prognathous but strongly **retracted** into the prothorax (Kfig. 9 p186). The protracted-prognathous head is widely distributed throughout the order, with the exception of the superfamilies Scarabaeoidea, Byrrhoidea, Bostrichoidea, Chrysomeloidea, and Curculionoidea. Distinctly hypognathous heads occur in Microsporidae, a few Staphylinidae (Ptiliidae, Silphidae), Dascillidae, all Scarabaeoidea, Byrrhidae, Dermestidae, *Endecatomus* (Bostrichidae), most Anobiidae, Ptinidae, Lymexylidae, Dermestidae, some Endomychidae, Erotylidae, some Coccinellidae, cerylonine

Cerylonidae, Mordellidae, later instars of Meloidae and Rhipiphoridae, nilonine Tenebrionidae, and most Chrysomelidae and Curculionoidea. Strongly retracted heads are characteristic of Buprestidae, most Bostrichidae, a few Anobiidae, most Cerambycidae, some Chrysomelidae (Sagrinae, leaf-mining Alticinae and Hispinae), Bruchidae, a few Anthribidae (*Bruchela*, *Euxenus*), Aglycyderidae, Oxycorynidae, Belidae, and various Curculionidae (Rhynchitini, Allocoryninae, leaf miners). In the following discussions, the head is presumed to be protracted and prognathous unless otherwise noted.

The cranium, as viewed from above, is usually divided by an **ecdysial line** called the **epicranial suture** (fig. 34.9). This "suture" may be V-shaped, U-shaped, Y-shaped, or **lyriform** (shaped like a lyre with sinuous, rather than straight or evenly curved arms, and with or without a stem). The stem, when present, is called the **epicranial stem** or **coronal suture**, while the lateral arms are called **frontal arms** or **frontal sutures**. In some Cerambycidae, the epicranial stem is located within a broad furrow for the attachment of retractor muscles (Kfig. 17 p192). The epicranial suture divides the cranium into three major areas: a **frons** (**front**) or **frontoclypeal region** in front of and between the two frontal arms, and two **epicranial plates** (**epicranial halves**) or **parietal plates**, which are behind and lateral to the frontal arms and on either side of the epicranial stem when this is present; when there is no stem, the frontal arms may be contiguous or separated at the base, so that the frons extends posteriorly to the occipital foramen, as in some Carabidae and Nitidulidae. The dorsal part of the combined epicranial plates is sometimes called the **vertex**, as in adult beetles. When complete, the frontal arms extend to the antennal insertions, but in many groups they are incomplete anteriorly, and in some the entire epicranial suture may be indistinct or absent (second instar Histeridae). In a few beetle groups (Pterogeniidae, pisenine Tetratomidae, hallomenine Melandryidae, Chalcodryidae, toxicine Tenebrionidae, anaspidine Scaptiidae), there is an additional transverse ecdysial line joining the two frontal arms near their anterior ends. In beetle larvae there are no **adfrontal areas**, which are characteristic of most Lepidoptera.

In addition to the epicranial suture, the dorsal part of the head capsule may have one or occasionally two internal ridges or cuticular thickenings called **endocarinae**, which strengthen the head and may provide additional muscle attachment surface. These are visible as dark lines, but when they are coincident with the epicranial suture, they are difficult to observe. Since the epicranial suture is a line of weakness related to molting, any section of it which appears darker or thicker is almost certainly associated with an endocarina. The most obvious type is a median endocarina extending anteriorly between the frontal arms, sometimes as a continuation of the epicranial stem (Kfig. 20 p188); this occurs in a number of families, including Cupedidae, Lucanidae, Scarabaeidae, Buprestidae, Trogossitidae, Cleridae, Phalacridae, Anthicidae, Cerambycidae, and Chrysomelidae. The type which is entirely concealed beneath the epicranial stem (Kfig. 19 p216) is more widely distributed in Scarabaeidae, and also occurs in Callirhipidae, Bostrichoidea, Lymexylidae, Languriidae (Languriinae), Melandryidae, Mordellidae, Ciidae, a few Tenebrionidae, Chrysomelidae (Clytrinae and relatives), Bruchidae, and a number of Curculionoidea. A third type of median endocarina is Y-shaped and coincident with both epicranial stem and at least the bases of the frontal arms (Kfig. 23 p220); this type is known in larvae of a few Staphylinidae (Leptochirini), Passalidae, a few Trogossitidae (Peltinae), some Melandryidae, some Zopheridae, Oedemeridae, Cephaloidea (except Stenotrachelinae), and Belidae. Paired endocarinae may occur beneath the bases of the frontal arms, when the epicranial stem is absent (Kfig. 24 p209); these are known in Buprestidae (Trachyini), Eucnemidae, Nitidulidae (*Pocadius*), Cucujidae (Laemophloeinae), Melandryidae (*Zilora*), Colydiidae (*Cicones*), Zopheridae (*Phellopsis*), Salpingidae, Inoepelidae, and a few other groups. Finally there may be paired endocarinae which are not coincident with the frontal arms but lie just mesad of them (Kfig. 25 p243), as in many Buprestidae, a few Eucnemidae, *Thymalus* (Trogossitidae), Monommidae, and Othniidae.

The frontoclypeal region may be divided by a transverse invagination called the **frontoclypeal suture** (fig. 34.9) or **epistomal suture**, represented internally by the **epistomal ridge** (see below). The large area behind the suture is called the **frons**, while the smaller area in front of it is the **clypeus**; when the frontoclypeal suture is absent, these areas may be arbitrarily delimited by an imaginary line connecting the dorsal mandibular articulations (see below). The clypeus may be further divided into a posterior, more heavily sclerotized **postclypeus** and an anterior, lightly sclerotized **anteclypeus**; the term **epistoma** has been applied by different workers to one or the other subdivision or to the clypeus as a whole. A separate sclerite, the **labrum**, is attached to the anterior edge of the clypeus (see below), and the suture between them is called the **clypeolabral suture**.

The epistomal ridge forms the dorsal part of the **mouth frame** or **peristoma** (fig. 34.12). At either end of the ridge, there is a condyle, which is the **dorsal mandibular articulation**, and this may be surrounded by a heavily sclerotized area sometimes called the **talus**. The attachments of the anterior tentorial arms, if present, may also be located at the lateral ends of the epistomal ridge (see below). The lateral portion of the peristoma on each side, between the dorsal mandibular articulation and the ventral one, is called the **pleurostoma**; the **ventral mandibular articulation** is an acetabulum into which the ventral mandibular condyle is inserted. The lower part of the frame, between the ventral articulation on each side and the median attachment to the labium, is called the **hypostoma** or **hypostomal ridge**, and it is to this that the maxilla is attached. The hypostomata may be almost transverse in larvae with **protracted ventral mouthparts** (Kfig. 214 p201), so that the maxillary and mandibular articulations are more or less at the same level; in larvae with **retracted ventral mouthparts** (fig. 34.11), however, the maxillary articulations are located well behind those of the mandibles, and the hypostomata form a ventral cavity surrounding the maxillae and labium.

In various families of beetles, the labrum has become partly or completely fused to the clypeus or frontoclypeal region; complete fusion occurs throughout the Adephaga, Hydrophiloidea, Elateroidea (except Artematopidae), and Cantharoidea (except Brachypsectridae), and in the families Scydmaenidae, Pselaphidae, Staphylinidae (Staphylininae, Paederinae, Steninae, Euaesthetinae), Rhipiceridae, Nitidulidae (Meligethinae), Phalacridae (Litochrini), Cucujidae (Passandrinae), Bothrideridae (*Sosylus*), Corylophidae, Cerylonidae (Ceryloninae), Rhipiphoridae, Meloidae (some triungulins), and Chrysomelidae (Cryptocephalinae and relatives), while partial fusion is known in Dascillidae, some Eucinetidae, Nitidulidae (Cybocephalinae), Helotidae, Cucujidae (Uleiotini), Phloeostichidae (Hymaeninae), Phalacridae (Phalacrini), Biphylidae, Byturidae (*Byturellus*), and Nemonychidae. In most groups with a completely fused labrum, the anterior part of the head forms a median projecting lobe called the **nasale** (fig. 34.10), sometimes with an additional pair of lateral lobes called **adnasalia** (sing. **adnasale**) by carabid workers (Emden, 1942b) and **paranasal lobes** by those working on elaterid larvae (Glen, 1950).

The epicranial plates extend ventrally on each side, and where they continue behind the hypostomata and ventral mouthparts they may be referred to as **postgenae**; each plate bears an **antennal fossa** and may have from 1 to 6 **stemmae** (see below). The antennal fossa is usually separated from the pleurostoma by a narrow bar of cuticle (fig. 34.12), but in some larvae (Microsporidae, some Endomychidae, Tenebrionidae: Nilioninae), the antennae are separated from the pleurostoma by a wide strip of cuticle, and in others, there is only a narrow strip of membrane between the two, and the



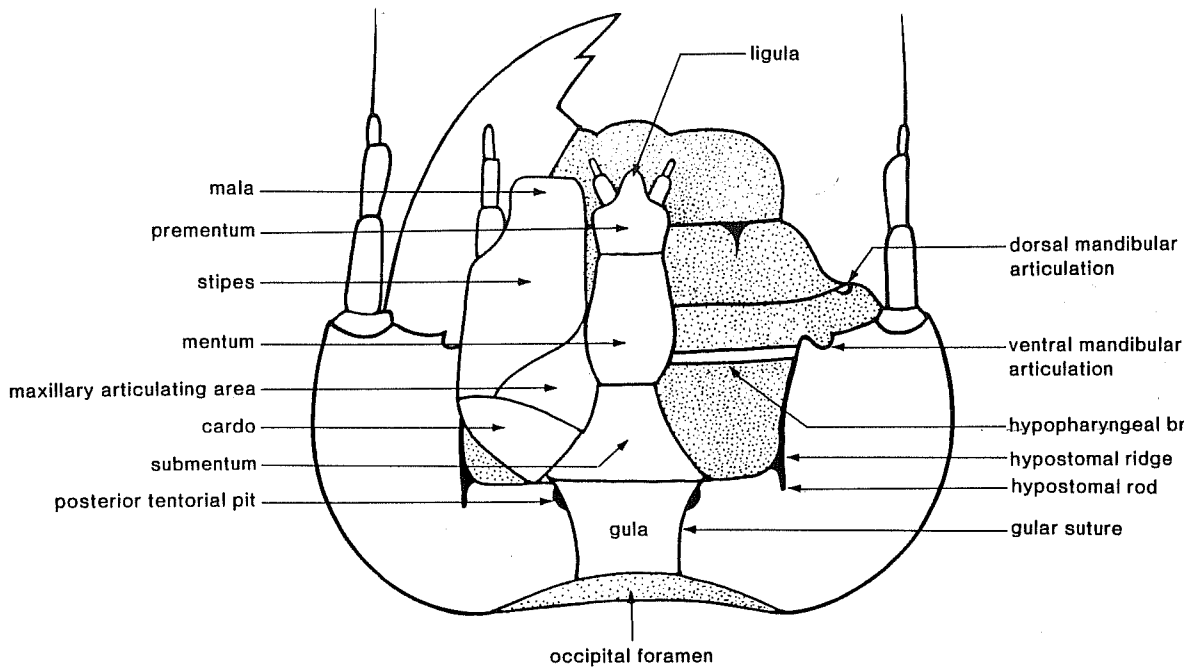


Figure 34.11. Head (composite), ventral, with left mandible and maxilla removed.

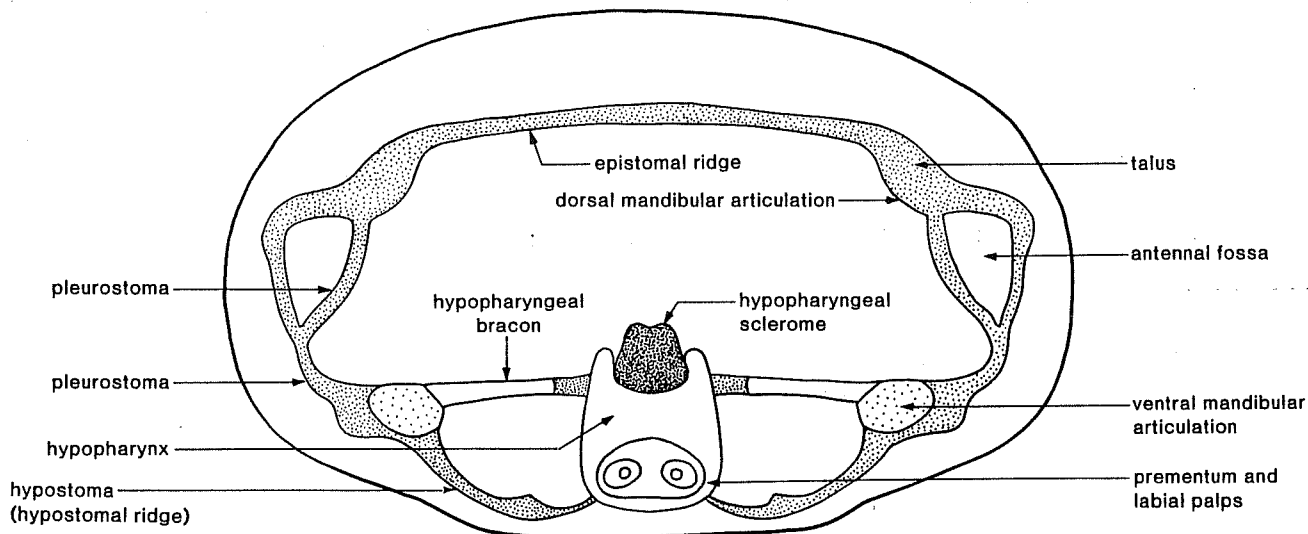


Figure 34.12. Head (Tenebrionidae), anterior, with clypeus, labrum and epipharynx, antennae, mandibles, and maxillae removed.

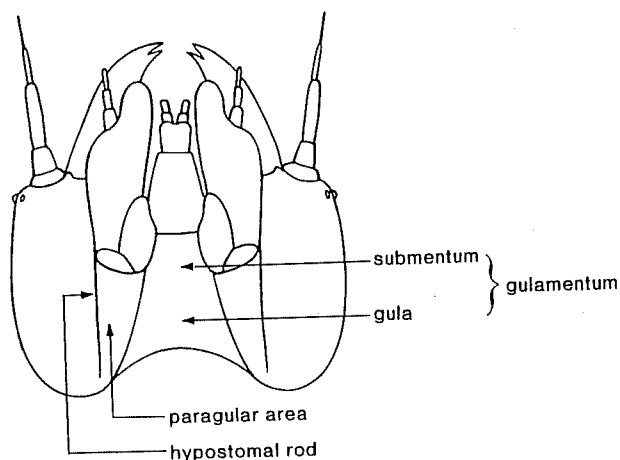


Figure 34.13. Head (Salpingidae), ventral.

antennae are usually described as being contiguous with the mandibular articulations. In some groups, a pair of distinct ridges originates just laterad of the ventral mandibular articulations and extends posteriorly, more or less parallel with the hypostomata and forming with them a housing for the ventral mouthparts (fig. 34.14); these are called **ventral epicranial ridges**, and they are well developed in Byrrhidae, most Dryopoidea, those Elateroidea having normal biting mandibles, Lymexylidae, trogossitine Trogossitidae, Derodontidae, Nosodendridae, Rhizophagidae, Languriidae (except Toraminae and Cryptophilinae), some Erotylidae, Ciidae, a few Tenebrionidae (Toxicini), Pythidae, Othniidae, cryptocephaline and related Chrysomelidae and some Anthribidae. A pair of sclerotized, cuticular thickenings, seen as dark lines, may originate on the hypostomata near the attachments of the cardines, and extend posteriorly; these are called **hypostomal rods** (figs. 34.11, 34.13) and are most conspicuous in larvae with protracted and prognathous heads. The most common type of hypostomal rods are divergent posteriorly, as in many Cucujoidea and Tenebrionoidea, but they are parallel in several cleroid families, as well as in laemophloeine Cucujidae, smicripine Nitidulidae, murmidiine Cerylonidae, Salpingidae, Inopeplidae, and some Cerambycidae. A few groups, like anaspidine Scaptiidae and Monommidae have converging hypostomal rods, and eustrophine Melandryidae have two pairs, one parallel and one diverging.

The area behind the ventral mouthparts is sometimes called the **ventral head closure**, but the terms **hypostomal region** and **gular region** have also been used. The term ventral head closure usually implies that the area is at least moderately sclerotized, so that the type of head found in Melyridae, in which this region is very lightly sclerotized, is often said to lack a ventral head closure. The **posterior tentorial pits** (fig. 34.11), representing invaginations of the **tentorium**, usually occur just behind the maxillary articulations, but they may be located well behind these in some prognathous heads

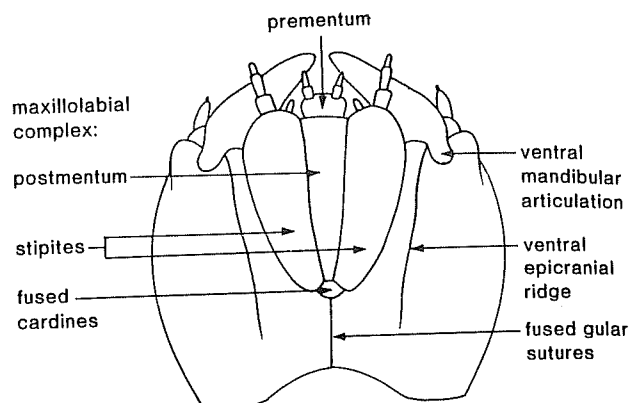


Figure 34.14. Head (Elateridae), ventral.

(Carabidae, Dytiscidae, Cleridae). Paired **gular sutures** may extend from these pits posteriorly to the occipital foramen, and the area between them is known as the **gula**. In some larvae, however, there are paired ecdysial lines, which may extend anterad of the tentorial pits or may not be associated with them at all (Hinton, 1963). It has been customary among larval taxonomists to refer to all such lines as gular sutures and the area behind the labium as the gula or **gular region**, even when the lines are absent or ill defined. Gular sutures or ecdysial lines may be fused, so that the epicranial plates meet at the ventral midline (some Carabidae), or they may be fused posteriorly, so that a triangular area, called the **pre-gula** is formed (some Hydrophilidae). In some larvae, an area is defined on either side of the gula called a **paragular area** (fig. 34.13) or **paragular plate**. The most common condition in beetle larvae is a reduced gular or hypostomal region with indistinct gular sutures, and in some groups, including Chrysomelidae and Curculionidae, this region is completely absent and the labium is attached directly to the **cervical membrane** of the neck. In most cerambycid larvae, there is an area behind the labium but well in front of the tentorial pits, which is called the **hypostomal bridge**.

The **tentorium** or cephalic **endoskeleton** usually consists of a pair of **metatentoria**, originating at the posterior tentorial pits and forming a bridge, the **corporotentorium**, a pair of **pretentoria** extending anteriorly to the epistomal ridge, and a pair of **supratentoria** extending dorsally from the pretentoria to a pair of depressions just laterad of the frontal arms on the epicranium. Reductions occur in many groups, especially with respect to the anterior and dorsal branches. The tentorium serves to strengthen the head capsule and acts as an attachment for muscles of the maxillae and labium-hypopharynx (see below). Another endoskeletal structure, the **hypopharyngeal bracon** (figs. 34.11-12), extends between the ventral mandibular articulations, passing through the hypopharynx and supporting that structure and its sclerome, when

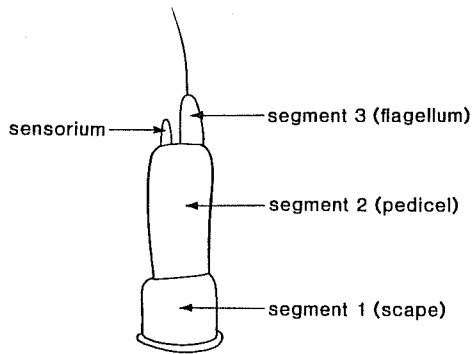


Figure 34.15. Antenna (composite).

present (*see below*). The hypopharyngeal bracon appears to be absent in Adephaga but occurs in Myxophaga and Archostemata. Within the Polyphaga, it is widely distributed, but absent in Hydrophiloidea, Dascillidae, Byrrhidae, Buprestidae, most Dryopoidea, some Cantharoidea and Elateroidea, some Bostrichoidea, and Chrysomeloidea. The presence of the bracon is one of the characters separating curculionoid larvae from those of Bruchidae and Chrysomelidae.

## Antennae

The antennae arise from a pair of **antennal fossae** or antennal cavities located on the epicranial plates near the mandibular articulations. The basic number of antennal segments in Coleoptera larvae is apparently three (fig. 34.15): a basal **scape**, which is often short and broad, a **pedicel**, which may be more elongate and which bears at or near its apex one (or occasionally more than one) hyaline vesicle called a **sensorium** (**sensory appendage, sensory appendix, sensorial appendage, supplementary joint**), and the **flagellum**, which almost always consists of a single segment with a group of sensilla and one or more setae at the apex. Four-segmented antennae occur in the primitive family Cupedidae, as well as in all Adephaga (except a few derived forms of Carabidae); that this represents a derived condition resulting from the division of the scape is suggested by the position of the sensorium on the penultimate segment and the existence of a series of larvae of *Distocupes varians* (Lea), where the early instars have 3 antennal segments, while mature larvae have 4, 5, or 6, the additional segments appearing to be divisions of the scape. Other instances of derived 4-segmented antennae occur within the polyphagan families Leiodidae (*Prionochoeta*), Scydmaenidae (*Mastigus*), Staphylinidae (Staphylininae, Paederinae, Steninae), and Scarabaeidae (Aphodiinae, Scarabaeinae, Ochodaeinae, Glaphyrinae, and all Pleurosticta). The occurrence of more than four segments is known in a few Carabidae, some Dytiscidae, Helodidae, and aphodiine Scarabaeidae, as well as in cupedids. In the case of Aphodiinae, the additional segment appears to be derived from

the scape; in Helodidae, the flagellum is divided into numerous segments (occasionally as few as 6); and in Dytiscidae, all the segments may become subdivided, except for the last, which remains reduced and lies side by side with the sensorium. Most beetle larvae have 3 antennal segments, but reductions to 2 or 1 are not uncommon. Two-segmented antennae are known in Microsporidae, Hydroscaphidae, Scydmaenidae, Pselaphidae, Passalidae, Buprestidae, Lycidae, Anobiidae, Cucujidae (Silvanini), Coccinellidae, Discolomidae, Ciidae, Tenebrionidae, Cerambycidae, Chrysomelidae, Belidae, and Aglycyderidae, while antennae consisting of a single segment are known in Rhipiceridae, Callirhipidae, Anobiidae, Ptinidae, Coccinellidae, Mordellidae, Rhipiphoridae, Meloidae, Chrysomelidae, and most families of Curculionoidea. In some groups (Amphizoidea, Buprestidae, Brachypsectridae, some Tenebrionidae), the last segment is highly reduced, so 3-segmented antennae may appear to have only 2 segments. Reduction may take place by the loss of the basal or apical segment or by the fusion of two segments. When the terminal segment is lost, the sensorium comes to lie at the antennal apex, usually accompanied by one or more setae and sensilla representing the true apical segment; **the lack of a seta at the apex of the sensorium distinguishes it from a true segment**. The fusion of apical and penultimate segments may result in the location of the sensorium near the middle of the apical segment, as in Microsporidae. In cases of extreme reduction, as in most Curculionidae, the antenna consists of a membranous dome bearing a few setae and sensilla. A most unusual situation occurs in some Phalacridae (*Phalacrus*, *Phalacropsis*), where the basal segment has been lost and the apical segment has become subdivided, resulting in a 3-segmented antenna with the sensorium at the apex of the first segment.

The size and shape of the sensorium may be useful in distinguishing certain family groups, but in some families they are extremely variable. In most larvae, the sensorium is elongate-conical or palpiform (sometimes almost setiform), and it may be very short or sometimes (Hydroscaphidae, Heteroceridae, some Cerylonidae and Endomychidae, Ciidae) longer than the terminal segment. Short, dome-like sensoria occur in a number of families, including Rhysodidae, Scydmaenidae, Scarabaeidae, Dascillidae, Lycidae, Lampyridae, Cucujidae, Erotylidae, Tenebrionidae, Pyrochroidae, and Scrautiidae. Bifurcate sensoria occur in some Pselaphidae, and tenebrionid larvae exhibit a variety of complex, dome-like sensoria, which may be C-shaped, sinuate, or broken up into several parts. In some instances, there may be more than one sensorium on the penultimate segment; multiple sensoria are known in a few Hydrophilidae, Scarabaeidae, and Elateridae, and in most Histeridae. In many Scarabaeidae, there are additional vesicles on the terminal segment; these have been called **dorsal sensory spots** by Ritcher (1966). As mentioned above, the sensorium is usually placed at the end of the penultimate segment, except in a few cases where the last two segments have become fused. An exception occurs in most

Staphylinioidea, where the apex of the penultimate segment is strongly oblique and the large sensorium is attached well before the apex and not on a line with the last segment. Some of the large, dome-like sensoria may also be subapical.

### Stemmata

The lateral eyes of larval holometabolous insects are often referred to as **ocelli** (sing. **ocellus**), but since that term has also been applied to the median and paired simple eyes of adult insects, the word **stemma** (pl. **stemmata**) is used in this book. The number of stemmata borne on each epicranial plate in Coleoptera larvae varies from 1 to 6 and many larval types lack them altogether. Each stemma may have a well-developed lens and retina, or it may be reduced so that it is little more than a pigment spot; in Carabidae: Cicindelinae, one or two of the stemmata are much larger than the others and contain numerous sensory cells (Paulus, 1979). After clearing in potassium hydroxide, stemmata are particularly difficult to see, and pigment spots may disappear; it is advisable to count the stemmata and make a sketch of their arrangement and position before clearing. A full complement of 6 stemmata occurs in most families of Adephaga, and in Agyrtidae, some Silphidae and Staphylinidae, many Hydrophilidae, Byrrhidae, several groups of Dryopoidea, Derodontidae, Dermestidae (*Dermestes*), a few Cleroidea, many cucujoid families, Cephaloidea, and several subfamilies of Chrysomelidae. The most common number in Polyphaga is 5, but it varies considerably within some families and reduction has occurred several times. Some families, like Nitidulidae and Endomychidae never have more than 4 on each side, while Coccinellidae have 3 or fewer; families of Tenebrionioidea (except some Cephaloidea) do not have more than 5, and Curculionoidea (except some Belidae) have no more than 2. In many substrate-dwelling larvae, stemmata are absent or there are only 1 or 2 pairs of pigment spots; this is the case in Scarabaeoidea, most Bostrichoidea, Bruchidae and most Curculionoidea. Some other groups, like the Elateroidea and Cantharoidea, usually have a single large stemma with a well-developed lens on each side.

Stemmata may be well separated, as in Byrrhidae or Dryopidae, or tightly clustered, as in Elmidae and Ptilodactylidae, and the arrangement may be characteristic for a group; stenine Staphylinidae, for instance, have a circular arrangement, many Carabidae have two curved rows forming an incomplete circle, and many groups have two vertical rows (3 and 3, 4 and 2, 3 and 2).

### Labrum and Epipharynx

The area on the underside (**ental** surface or that facing the inside of the mouth cavity) of the labrum is called the **epipharynx**, and the term **labrum-epipharynx** is sometimes used for the entire structure. The base of the labrum bears a pair of lateral sclerites called **tormae**, to which the lateral labral muscles are attached. Tormae vary considerably and may be useful taxonomic characters; they may be longitudinally or transversely oriented, symmetrical or asymmetrical, separate or joined mesally, and simple or complex, with

accessory processes. Various terms applied to the tormae and associated structures in Scarabaeoidea include **apotorma**, **dexiotorma**, **epitorma**, **laetotorma**, and **pternotorma**; these are defined in the glossary and are discussed and illustrated by Böving (1936), Hayes (1928), and Ritcher (1966) (see section on Scarabaeidae). In the more advanced Curculionoidea, there is another pair of labral sclerites, the **labral rods** or **epipharyngeal rods**, which are paramedian in position and extend from the apex or near the middle of the labrum-epipharynx posteriorly to the base, or beyond it into the clypeal region.

The shape of the labral apex has been used as a taxonomic character in Scarabaeoidea (Kfigs. 35 p268, 36 p273) and various other groups, while the type and distribution of labral setae is important in Tenebrionidae. The surface of the epipharynx (Kfigs. 40-41 p265) may be very complex and is taxonomically useful in some families. The anterior edge usually bears a row of setae or fine hairs, and in addition, there may be patches of setae or spines, groups of sensilla of different sorts, and sclerotized plates or small rods. A terminology for describing the epipharynx has been developed only for the Scarabaeoidea, where there may be six regions—the median **corypha**, **haptomerum**, **pedium**, and **haptolachus**, extending from front to back, and the paired lateral **paria**; other terms used for epipharyngeal structures (see glossary and references above) include **acanthoparia**, **acroparia**, **chaetoparia**, **clithrum**, **crepis**, **epizygum**, **gymnoparia**, **helus**, **nesium**, **phoba**, **plegma**, **plegmatium**, **proplegmatium**, **tylus**, and **zygum** (see section on Scarabaeidae). The area immediately behind the epipharynx forms the dorsal wall of the **cibarium** and is often provided with a complex armature, including a series of obliquely transverse **cibarial plates**, which are fringed with microtrichia and are located above the microtrichial armature at the base of the mandibles (see below).

### Mandibles

With few exceptions, Coleoptera larvae have a pair of well-developed, **opposable** mandibles, which move in a horizontal plane and articulate with the dorsal and ventral **mandibular articulations** of the head capsule by means of a **dorsal acetabulum** (figs. 34.55, 34.60) and a **ventral condyle** (figs. 34.45, 34.56-57). Each mandible is moved by a large **adductor muscle**, inserted at the inner angle (just laterad of the mola, if this is present), and a small **abductor muscle**, inserted near the outer edge; both muscles originate on the walls of the cranium, but the former occupies most of the cranial cavity and may be attached as well to an internal ridge or **endocarina**. In exceptional cases, such as mandibles of some Eucnemidae, which are not opposable, the abductor may be larger than the adductor (Ford and Spilman, 1979).

Since mandibles have been used extensively in larval taxonomy at the family level, mandibular structure and function will be dealt with in some detail. In most cases, statements on function are not based on behavioral observations, but on a combination of detailed morphological study, knowledge of food habits, examination of gut contents, and occasionally, manipulation of cleared and bleached specimens. For descriptive purposes, the mandible may be divided into four

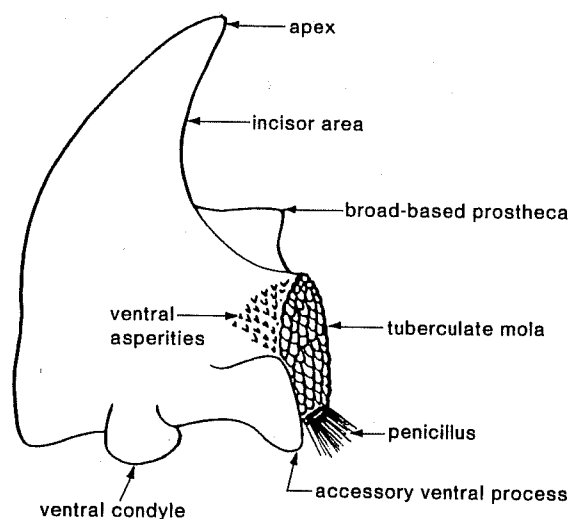


Figure 34.16. Right mandible (Languriidae), ventral.

areas (fig. 34.16): the **apex**, the **incisor area** (**scissorial area** or **cutting edge**) occupying much of the mesal surface, the **base** including the mesal surface, and the **outer edge**. The mesal portion of the mandibular base is sometimes called the **molar area**, but this term implies the presence of a definite basal structure, the **mola**, which acts in conjunction with the mola of the opposite mandible (and sometimes with a sclerome on the hypopharynx, *see* below) to process and ingest food.

Mandibular structure varies considerably, but the basic type, which is thought to represent that of an ancestral beetle larva, has a relatively wide base with a distinct mola and a narrow, relatively weak apex (figs. 34.16, 34.27, 34.39–40). There are usually two apical teeth, which are oriented obliquely to the plane of movement, sometimes an additional subapical tooth in the incisor area, and a thin, **hyaline** or translucent structure called a **prosthema** located just distal to the mola. The outer edge usually bears a pair of setae of fixed position. The surface of the mola is covered with small **tubercles** or **asperities**, which often continue onto the ventral surface, while the dorsal surface of the mandibular base has a patch of **microtrichia** arranged in oblique rows. This primitive type of mandible usually occurs in larvae which feed on small particles (spores, pollen) or very soft tissue (loose fungal hyphae, highly decayed animal or plant matter); this type of feeding is referred to as **microphagy**. The molae are symmetrical, and their surfaces meet so that the asperities or tubercles interdigitate to move small particles into the mouth cavity, while simultaneously shearing or crushing larger pieces into smaller ones, a process called **comminution**. The ventral asperities may also participate in the process, since they pass over the **hypopharyngeal sclerome** beneath them, while the oblique rows of microtrichia on the dorsal surfaces act together with the fringes on the **cibarial plates** to move small particles caught above the basal edges of the mandibles toward the molae and into the mouth cavity. The ventral part of the mandibular base has, in addition to the ventral condyle, a second, shelf-like projection, the **accessory ventral process** (also **accessory condyle**, **accessory ventral condyle**, **second**

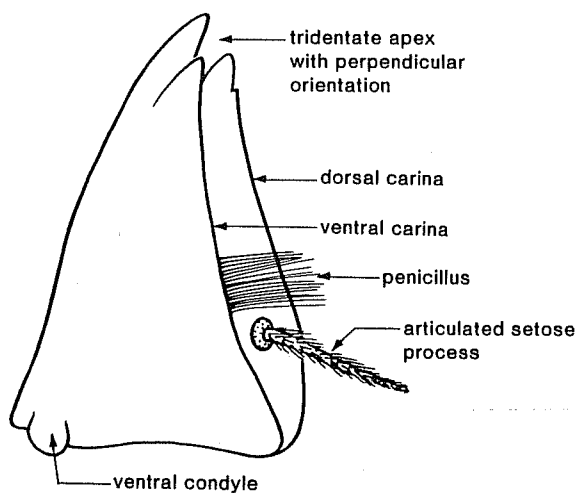


Figure 34.17. Right mandible (Elmidae), ventral.

**condyle**) (figs. 34.16, 34.51–52), located near the insertion of the adductor muscle and just laterad of the mola; this process is not a condyle, but its true function is not known. This primitive type of mandible occurs in Myxophaga, primitive Staphylinoidae, Eucinetidae, Derodontidae, and many Cucujoidea, while the same basic design with modifications in the mola or elsewhere may be found in Archostemata, Helodidae, Dascillidae, Scarabaeoidea, Lymexylidae, various Cucujoidea, many Tenebrionoidea, and a few primitive Curculionoidea.

Of the many specialized mandibles that can be derived from the primitive type, most fall into two categories: 1) the cutting, biting, gouging or scraping mandible of a **phytophagous** or **xylophagous** larva (figs. 34.29–31), and 2) the grasping, piercing mandible of a larva which is always liquid-feeding (practicing **extraoral digestion**) and usually predaceous (figs. 34.35–36, 34.38, 34.59). In both types the mola has been lost and food processing occurs at the mandibular apex, rather than at the base. Mandibles of the first group usually have a very broad base with a greater cross-sectional area and a gradually narrowed apex, which is sometimes not much narrower than the base; the gap between the mandibular apices is small and much greater force can be exerted at the apex and along the incisor edge. The second group usually includes mandibles which are narrow and **falcate** (**falciform**), with a narrower base and wide gap; these mandibles can grab and often pierce objects but cannot generate the force needed at the apex to cut through heavily reinforced plant or fungal tissue. Details of these and other specialized mandible types are covered in a later paragraph.

The mandibular apex may be simple, consisting of a single tooth (**unidentate**, Kfigs. 44, 46 p239), but more commonly there are two apical teeth (**bidentate**, Kfigs. 61 p239, 70 p262), and there may be three or more (**tridentate**, figs. 34.17, 34.31, Kfigs. 47 p193, 66 p218; **multidentate**, fig. 34.30, Kfig. 51 p187); each tooth may be acute or rounded, but this often varies with wear in a single individual. In most larvae,

the apical teeth are oriented obliquely to or almost parallel with the plane of movement (Kfigs. 51 p187, 59 p239), while in others the teeth are perpendicular to the plane of movement (Kfigs. 47 p193, 66 p218, 74 p257) and may form with the incisor area a concave scoop. Tridentate or multidentate mandibles with a flat or concave inner surface are sometimes described as **palmate** and occur in a number of Dryopoidea (figs. 34.17, 34.31). Multidentate mandibles of some Byrrhidae and Chrysomelidae have the teeth arranged in an oblique row (fig. 34.30, Kfig. 51 p187), while in some Eucinetidae and Coccinellidae (Epilachninae and Psyllorborini) there are numerous, irregularly placed teeth or spines (Kfig. 56 p227). In the unusual mandible of *Dasycerus* (Dasyceridae) (Kfig. 55 p241), there are numerous curved spines covering the entire apex. Simple, rounded, or flattened and chisel-like (Kfigs. 46 p187, 48 p234) apices occur in many substrate-inhabiting larvae, like those of Cerambycidae, Bruchidae, and Curculionoidea, while acute apices (Kfigs. 43, 44 p200) are usually found in predators. In some larvae with well-developed molae, the apex may become highly reduced, as in *Lycoperdina* (Endomychidae) (fig. 34.54) or some Lathridiidae.

The incisor area of the mandible often bears one or more subapical teeth, which may be located on a carina extending basally from the dorsalmost apical tooth (fig. 34.17), and sometimes this **dorsal carina** may be serrate. A second **ventral carina** occurs in some mandibles lacking a mola, and a concave, scoop-like area may be formed between the two carinae (fig. 34.17). An extreme form of this occurs in mandibles of certain predaceous larvae, where an open or partly closed groove is formed along the inner surface (Kfig. 44 p200); such a condition was probably prerequisite to the evolution of **perforate mandibles** to be discussed later. Another feature of the incisor area is the presence of a heavy, sclerotized tooth called a **retinaculum** (although that term is sometimes misapplied to the protheca). A single retinaculum (or occasionally more than one) is usually found on the falcate mandibles of predatory larvae (Carabidae, fig. 34.59, Hydrophilidae, Histeridae, Elateridae, fig. 34.57), but similar structures, called **scissorial teeth**, may also occur in non-predatory larvae of Dascillidae (fig. 34.52) or Scarabaeoidea.

The subapical region of the mandible may also bear a mola-like area, consisting of tubercles, teeth (Kfig. 54 p243) or fine ridges (Kfig. 52 p188); this structure is called a **pseudomola**, but that term has also been applied to a variety of basal or sub-basal molae, which are thought to have evolved secondarily in larvae which have lost the true mola.

The **mola** is the processing area at the base of many mandibles which acts in conjunction with the mola of the opposing mandible to feed small particles into the mouth cavity, to cut and shear larger particles into smaller ones, or sometimes to compact small particles into pellets to be ingested. Primitive molae are symmetrical and relatively narrow, and they extend to the basal edge of the mandible; examples may be found in many Cucujoidea (figs. 34.39, 34.42, Kfigs. 75, 78 p259), as well as in derodontids, eucinetoids, and primitive staphylinoids. From this type have evolved the slightly asymmetrical molae (Kfig. 73 p188) of Mycetophagidae or Archeocrypticidae, and the strongly asymmetrical molae (figs.

34.28, 34.41, Kfig. 74 p257) of the more advanced tenebrionoids (Prostomidae, Oedemeridae, Synchronidae, Pythidae, Pyrochroidae etc.), where each mola consists of numerous transverse or oblique ridges which meet at an angle forming multiple shearing surfaces for handling rotten wood and reinforced fungal hyphae. In most cases, the left mola is more vertical, with a flat or concave surface and often a tooth or lobe at the distal end, while the right one is inclined away from the midline and has a convex surface (figs. 34.28, 34.41, Kfigs. 73, 74 p263). In another derived type of mandible, both molae are concave, usually with smooth surfaces, as in Heteroceridae (fig. 34.32) and some Tenebrionidae (fig. 34.45); these serve to compact loose material, and may also shear larger pieces with the sharp outer edges. The tenebrionid type may act in conjunction with a concave hypopharyngeal sclerome (fig. 34.46). The concave molae in Heteroceridae are used to compact masses of wet sand or mud, which are then swallowed whole for the extraction of diatoms, algae, and other organic matter; the molae are not basal, and are considered to be pseudomolae, since heterocerids have almost certainly evolved from an ancestor lacking a mola. Another molar type, found in the endomychid *Lycoperdina* (fig. 34.54), is broad and finely tuberculate for crushing fungal spores.

The molar surface in more primitive mandibles is covered with numerous, sharp asperities or rounded tubercles, which may form transverse rows and may extend onto the ventral surface of the mandibular base (figs. 34.16, 34.40, 34.43). The molar armature is of taxonomic importance, but care should be exercised when using this character exclusively, since the surface is subject to variation caused by wear. The molar surface may be reinforced by the formation of simple, continuous ridges, which are usually transverse (fig. 34.60) but occasionally longitudinal (Dascillidae, fig. 34.52), or complex ridges, separated by deep channels (figs. 34.63–66). The ridges may become interconnected with the formation of a poroid superstructure (fig. 34.62), which may act as a fluid press, since the pores and channels communicate with the dorsal and ventral surfaces (fig. 34.61).

The dorsal surface of the mandibular base adjacent to the mola often bears a patch of fine microtrichia, which are usually arranged in oblique rows (figs. 34.39, 34.41, 34.60–61, 34.63–64). These are found in many groups having an asperate or transversely ridged mola, and they apparently act in conjunction with the fringed cibarial plates above them to move small particles toward the molar area and away from the articular areas. The ventral surface of the mandibular base may also have patches of microtrichia or asperities, but these are usually not arranged in regular rows. The ventral asperities are assumed to aid in the food processing by acting against the sclerome on the hypopharynx. In some groups of Scarabaeidae (Rutelinae, Dynastinae, Cetoniinae), there is a group of fine transverse ridges at about the middle of the mandibular base or towards the lateral edge; this is a **stridulitrum** (called **stridulatory area**), which acts in conjunction with a **pectrum** consisting of **stridulatory teeth** on the dorsal surface of the maxilla.

There are three types of accessory structures associated with the mola: a **premolar tooth**, a **submolar lobe**, and a **protheca**. The premolar tooth is a heavily sclerotized process

which is actually part of the mola. The submolar lobe is a hyaline area, usually setose, at the base of the mola in Biphylidae, Anthicidae, Euglenidae, and some Scaptiidae, but in the family Byturidae (Kfig. 76 p279), it is a flexible, setose, projecting lobe. A brush of hairs or **penicillus** may also occur at the molar base, as in some Bostrichidae (Kfig. 72 p187), *Orphilus* (Dermestidae), some cucujoids and some scarabaeoids.

The **prostheca** is a very important taxonomic character in beetle larvae, but there has been some confusion in the use of the term. In the present treatment, the word is restricted to any of the structures located just distad of the mola but not a part of it, which are almost always hyaline, at least basally, or composed of membrane or groups of hairs. The structure is not to be confused with a premolar tooth or with the retinaculum, which is heavily sclerotized, more apical in position, and almost always borne on mandibles lacking a mola. Structures similar to the prostheca may occur in mandibles without a mola, and these are discussed below. Other terms which have been used for the prostheca are **lacinia mobilis** and **lacinia mandibulæ**.

The most common type of prostheca is a fixed, hyaline process, which is relatively rigid and more or less acute at the apex; it is often said to be articulated, but rarely fulfills the requirements of an articulated appendage, as defined in the glossary. This type usually has a relatively narrow base and simple, acute apex, as in Agyrtidae, Leiodidae, or Cucujidae (figs. 34.39–40, Kfig. 78 p193), but it may be serrate (Rhizophagidae, Kfig. 82 p270) or bifid (Cryptophagidae, Kfig. 83 p270), or may have a broader base and more or less angulate apex (Languriidae, Kfig. 81 p276). More complex types of prosthecae may be composed of series of fringed membranes (Nitidulidae, fig. 34.53, Kfig. 79 p276), a brush of simple hairs associated with an acute process (Derodontidae), a group of comb-hairs (Biphylidae, fig. 34.47, Kfig. 80 p276), or a membranous lobe (some Bostrichidae, Kfig. 75 p259; some Endomychidae, fig. 34.54). Other structures which may be called prosthecae are the comb-like process in Helodidae (fig. 34.51, Kfig. 77 p273), or the hyaline area and small, articulated process in Dascillidae (fig. 34.52).

In mandibles lacking a mola, there may be a variety of structures at the base of the mesal edge, and these, like the prosthecae, are useful for identification. Commonly, there is a brush of hairs (Lampyridae; Byrrhidae, Kfig. 63 p233; Histeridae, Kfig. 53 p239); this is usually called a **penicillus**, but that term has also been restricted to a thin "pencil" of hairs. There may be an acute, rigid, hyaline process similar to the simple prostheca (and sometimes called a "retinaculum"), as in Paussini (Carabidae), Proteininae (Staphylinidae), Passandrinae (Cucujidae), *Deretaphrus* (Bothrideridae), some Coccinellidae (Kfig. 57 p224), and some Ciidae (Kfig. 58 p239), or a more complex, bifid or serrate process, usually referred to as a **lacinia mobilis** or **lacinia mandibulæ**, as in various Cleroidea (Kfig. 61 p239). A group of from 2 to 5 hyaline processes occurs in some Trogossitidae, laemphloeine Cucujidae, some Phalacridae (Kfig. 60 p239), tetratomine Tetratomidae, Perimylopidae, and Salpingidae (fig. 34.55), while a row of hyaline teeth occurs in Monommidae (fig. 34.56); these structures may represent a highly reduced

mola or prostheca or may represent independent developments. Articulated processes also occur, and they may be covered with fine hairs, as in *Araeopidius* (Ptilodactylidae) or have a brush of hairs at the apex, as in *Ptilodactyla* (fig. 34.58). Some mandibles have two types of basal structures, such as a brush and articulated, setose process in some Elmidae (fig. 34.17) or a fixed, hyaline lobe and brush of hairs in *Dermestes*. A large, fringed, membranous lobe occurs without a mola in some Erotylidae (Kfig. 64 p239), eustrophine Melandryidae, and *Endomychus* (Endomychidae).

The outer edge of the mandible in most larvae bears a pair of setae of fixed position, but in some groups, like Tenebrionidae, numerous setae may occur and some of these may be stout and spine-like. In some ground-dwelling larvae, the outer edges of the mandible are carinate and serve as wedges used in burrowing; examples are known in Cebrionidae and several groups of Tenebrionidae.

As mentioned above, mandibles lacking a mola usually fall into two groups: the broader, cutting, biting, gouging, or scraping type, and the narrower, grasping or piercing type. These, in turn, are usually associated with two different feeding strategies, namely **macrophagy**, or feeding on large particles (which are often cut or otherwise removed from an even larger food mass and then swallowed whole), and liquid-feeding or **extraoral digestion** (where digestive enzymes are ejected into a large food mass or the surrounding medium, and the breakdown products sucked back into the gut through an **oral filter**, which keeps larger particles out (see below)). Heavier mandibles and macrophagous habits almost always occur in larvae which feed on the reinforced tissue of higher plants and advanced basidiomycete fungi, while narrower, falcate mandibles and extraoral digestion usually occur in predators; exceptions are not uncommon, however, and there are a number of liquid-feeding, phytophagous Elateridae and Carabidae, as well as predaceous larvae with relatively broad and heavy mandibles.

Among the macrophagous types of larvae, wood-feeding or **xylophagous** forms are most common in the families Buprestidae, Melandryidae, Mordellidae, Cerambycidae, and Curculionidae, while those specializing on leaves and herbaceous tissue (both fresh and decomposed) occur in Byrrhidae, some dryopoid families, some Languriidae and Coccinellidae, Chrysomelidae, and some Curculionidae. Also falling into this group are those larvae which scrape algae from rock surfaces (Psephenidae, Elmidae). Larvae specializing on the tougher fruiting bodies of higher Basidiomycetes are in the families Trogossitidae (Peltinae, *Calitys*), Erotylidae, Ciidae, and Mordellidae, while seed feeders occur in Bruchidae, Anthribidae, and Curculionidae. Although there is variation in the type of apex, most mandibles in this group are the heavier type with a broad base. Exceptions occur in some Byrrhidae and Chrysomelidae (fig. 34.30), which have a somewhat flattened mandible with a multidentate apex, used to scrape tissue from a plant surface. A similar function is performed by the multispinose apex in phytophagous Coccinellidae (Kfig. 56 p227).

Narrow and falcate mandibles occur in most Adephaga, many Staphyloidea, most Hydrophiloidea, many Elateridae, all Cantharoidea, and a few cucujoid and tenebrionoid

triangulins. One of the main developments in mandibles of this type is the formation of an open groove or closed perforation, which serves to channel digestive fluids into the food mass; the internal perforation is sometimes called a **blood channel**. An open or partly closed groove occurs on the mesal surface of the mandible (Kfig. 44 p212) in larvae of some Noteridae and Dytiscidae, spercheine Hydrophilidae, Homalidae, Drilidae, Cantharidae and a few Cleridae, while **perforate mandibles** (Kfig. 43 p212) are characteristic of most Dytiscidae, Gyrinidae, Brachypsectridae, Phengodidae (fig. 34.38) and Lampyridae. A different type of perforate mandible, with a broad base and relatively large internal perforation, occurs in larvae of Haliplidae (Kfig. 49 p212), which apparently suck algal cells into the mouth through the perforation (Hickman, 1931). Another unusual type of mandible, apparently associated with liquid feeding, is that found in Lycidae (Kfig. 42 p196); each mandible is split longitudinally into two parts, which fit together to form a channel; the two mandibles are not opposable. **Styliform** mandibles are also non-opposable, but they are extremely narrow and may be capable of anteroposterior movement; they are usually enclosed, together with styliform maxillae, in a median tubular **proboscis** (Cerylonidae: Ceryloninae, Kfig. 27 p224; Leioididae: Camiarinae), but in *Cerylon* (Kfig. 28 p200) they are enclosed within the mouth cavity (**endognathous**). Non-opposable mandibles also occur in Eucnemidae, Throscidae, Cerophytidae, and cardiophorine Elateridae, but these are not associated with a proboscis. In some eucnemids, they are movable, with laterally projecting teeth; in other Eucnemidae, Throscidae, and Cardiophorinae, they are fused to the head capsule; and in Cerophytidae and *Phyllocerus* (Eucnemidae), they are styliform at the apex. All of these groups are liquid feeders, and all move through relatively compact substrates by using the mandibles, labium, or entire head capsule as a wedge.

### Ventral Mouthparts

The **ventral mouthparts** include the paired **maxillae** and unpaired **labium**, whose attachments in a prognathous head are ventrad or mesad of the mandibular articulations; they are also referred to as the **maxillolabial complex**, especially when they are closely coadapted and move as a single unit (*see below*). The ventral mouthparts are said to be strongly **protracted** when the maxillary bases (usually the points of attachment of the cardines) are at about the same level as the ventral mandibular articulations and the hypostomal margins are short and transverse (fig. 34.36, Kfigs. 92, 95 p253). This condition is characteristic of most Adephaga, a few Staphylinidae, most Hydrophiloidea, Cleridae and Chaetosomatidae, smicripine Nitidulidae, laemophloeine and pasandrine Cucujidae, Phalacridae, some Corylophidae and Lathridiidae, Prostomidae, most Cerambycidae, Bruchidae, and some Chrysomelidae. When the ventral mouthparts are **retracted**, the attachments of the cardines lie posterior to the mandibular articulations, so that the entire maxillolabial complex is recessed into the head capsule and the hypostomal margin on each side is more or less longitudinal or oblique (figs. 34.33, Kfigs. 85-90, 93 pp240,260); this is the normal

condition in beetle larvae. Intermediate situations occur in some groups, like Cantharidae (Kfig. 94 p191), ptilodactylid Ptilodactylidae (fig. 34.34), and Mycteridae, where the maxillae and labium are only slightly retracted. The points of attachment of the maxillae do not necessarily reflect the degree to which the ventral mouthparts extend forward, since the latter can be influenced by the length and orientation of the cardo and the length of the stipes. As mentioned above, a recessed housing for the ventral mouthparts may be formed between the hypostomal margins and ventral epicranial ridges (figs. 34.31, 34.33, Kfigs. 90, 93 p240).

The **maxilla** usually consists of a small basal sclerite, the **cardo** (pl. **cardines**), a larger **stipes** (pl. **stipites**), a segmented **maxillary palp** (or **palpus**), which is borne on a shelf-like projection called the **palpifer**, and a pair of **apical lobes**—the **galea** or **outer lobe** and the **lacinia** or **inner lobe**; in many larvae, there is a membranous region called the **maxillary articulating area** (**basimaxillary membrane** of Das, 1937), which lies between the junction of stipes and cardo and the base of the labium (*see below*) (fig. 34.33, Kfigs. 85 p191, 89 p197, 105, 106 p200). The cardo may be divided into two distinct sclerites, but most often it is either undivided or bisected by an internal ridge; areas mesad and distad of this ridge have been called the **proxicardo** and **disticardo**, respectively. In most larvae, the cardo is more or less transversely oriented or slightly oblique (Kfigs. 105-106 p200), but in some, including those of most Nitidulidae (Kfig. 91 p200), it is longitudinal. In some larvae with protracted mouthparts (Phalacridae, Kfig. 92 p199; Nitidulidae (Smicripinae); Cucujidae (Laemophloeinae); Histeridae), the cardo may be absent or represented by a membranous area at the maxillary base; in some other groups, like the Coccinellidae, the cardo has become fused to the stipes. The two cardines are usually widely separated, lying on either side of the labium, but in some larvae, they may be approximate, displacing the labium anteriorly (Callirhipidae, Kfig. 99 p216; Heteroceridae), contiguous, meeting behind the labium (Limnichidae, Kfig. 100 p194; some Elateridae), or fused into a single sclerite (some Elateridae, Kfig. 93 p193; Chelonariidae; Brachypsectridae, Kfig. 97 p201). In some Cerambycidae, the entire area at the base of the ventral mouthparts is lightly sclerotized, without distinct separations of the labium, cardines, and stipites.

The stipes is the main body of the maxilla, housing the muscles that operate the palp and apical lobes; it is usually longer than wide, but in some groups (Cleridae; Phalacridae, Kfig. 92 p199) it may be subquadrate or wider than long. The stipes is occasionally divided into a basal and apical section (**proxistipes** and **dististipes**, respectively), and Gilyarov (1964b) has used the term **costipes** for an anterior subdivision in Hydrophiloidea usually called the **palpifer** and here considered to be the first segment of the maxillary palp (Kfig. 102 p200). Another term, **juxtastipes**, has been used by Böving and Craighead (1931) for an area extending mesally from the base of the stipes. The dorsal surface of the stipes, near the base, in various Scarabaeoidea may have a patch or oblique row of teeth or tubercles called **stridulatory teeth**, but only in the Dynastinae, Cetoniinae, Rutelinae, and some



Melolonthinae is there an opposing stridulatory area on the ventral surface of the mandible (*see above*).

The **maxillary articulating area** is well-developed and broadly triangular in most primitive larval types, loosely joining the base of the maxilla with that of the labium, so that the 2 structures are well separated and the maxilla is capable of considerable independent movement (fig. 34.27). In many larvae, however, the articulating area extends farther forward, and may become narrowly oval, as in Ciidae or Anobiidae, so that maxillary movement is more restricted. The area is usually membranous, but in some groups it may be partly sclerotized, and occasionally it is divided into two parts. In many Ptilodactylidae, and to some degree in the Helodidae and Psephenidae, the area may be well-developed but partly or entirely concealed behind a laterally expanded labium (fig. 34.34, Kfig. 98 p230). In other groups there is no articulating area, because the maxilla and labium have become closely coadapted and more or less connate, with further restriction of independent movement. Further consolidation of the maxillolabial complex through connation and fusion is discussed at the end of this section.

The **palpifer** (or **maxillary palpiger**) is a shelf-like area located externally (laterally) near the apex of the stipes and bears the maxillary palp. There is considerable confusion about the number of palp segments in some groups, because an enlarged palpifer may be counted as an additional segment or the basal palp segment may be considered a palpifer (when the true palpifer is poorly developed or absent). **In constructing the family key, a structure with both inner and outer edges and apparently articulated at the base was always called a palp segment, while a shelf-like extension of the stipes was considered to be a palpifer; in doubtful cases, both character states were included in the matrix.** A 3-segmented maxillary palp is thought to be primitive in Coleoptera larvae, but the number varies from 1 to 5. Four-segmented palps occur in most Adephaga, some advanced Staphylinidae, most Hydrophiloidea (if the so-called palpifer is considered to be a palp segment), Helodidae, almost all Scarabaeoidea, Byrrhidae, almost all Dryopoidea, Elateroidea and Cantharoidea, Dermestidae (except Anthreninae), the bostrichid genus *Endecatomus*, and a few Anobiidae, while 5-segmented palps are restricted to a few Carabidae and some Histeridae. Reduction in the number of palp segments occurs in a number of small larvae and in many which are internal feeders. Two-segmented palps are known in the Hydroscaphidae, a few Leioididae and Scydmaenidae, *Acalyptomerus* (Clambidae), late instar Rhipiceridae, Buprestidae, *Eubrianax* (Psephenidae), some Eucnemidae, a few Phengodidae, some Bostrichidae, a few Anobiidae, rentoniine Trogossitidae, smicripine and cybocephaline Nitidulidae, passandrine Cucujidae, *Sosylus* (Bothrideridae), some Corylophidae, noviine Coccinellidae, Discolomidae, Mordellidae, first instar Rhipiphoridae, some Chrysomelidae (Sagrinae, Cassidinae, most Hispinae and some Alticinae), some Bruchidae, and most Curculionidae. Single-segmented palps occur in first instar Rhipiceridae, intermediate and late instar Rhipiphoridae, a few hispine

Chrysomelidae, some Bruchidae and some Curculionidae, while maxillary palps may be absent in coarctate Meloidae and some Eucnemidae. The apical segment of the maxillary palp has a group of sensilla at the apex (the "bouquet sensoriel" of Corbière-Tichané, 1973), and at its base there is often one or more **digitiform sensilla**, which are flattened and located in a shallow cavity, where they are appressed to the surface and difficult to see; these structures, which occur on both maxillary and labial palps in larvae and adults, apparently function as tactile mechanoreceptors (Honomichl, 1980; Zacharuk, 1962a; Zacharuk *et al.*, 1977).

It is likely that the maxilla of ancestral beetle larvae had two well-developed **apical lobes**, both relatively narrow and as long as or longer than the stipes: a basally articulated, 2-segmented **galea**, perhaps with a setose apex, and a more or less fixed, 1-segmented **lacinia** appearing as an inner apical extension of the stipes and bearing at least one tooth or spine at the apex. This combination of characters occurs in no known beetle larva, but is present in some modern Plecoptera, where both lobes are basally articulated and 2-segmented. A 2-segmented galea occurs in Carabidae, Gyrinidae, trogine Scarabaeidae, some Byrrhidae, Eulichadidae, some Ptilodactylidae, Artematopidae, various Elateridae, and a few Cantharoidea, but in most of these groups both apical lobes are small and palpiform, while in the Troginae both are falcate with apical teeth. The major evolutionary trends exhibited by the maxillary apex include: 1) the loss of the basal segment of the galea and its basal articulation, resulting in two fixed lobes (Kfigs. 109, 111 p241); 2) the reduction of both lobes, which become more or less palpiform (Kfig. 100 p203); 3) the loss of one of the lobes, usually the lacinia, resulting in a single process, often referred to as the **mala** (Kfig. 103 p205); 4) the basal fusion and then complete fusion of the galea and lacinia, resulting in a combined structure also called the **mala** (Kfigs. 105-106 p200); and 5) the loss of both apical lobes, so that only the palp arises from the apex of the stipes (Kfigs. 101-102 p194). A basally articulated galea and fixed lacinia occur in Archostemata, Micropeplidae, Dascillidae, the more primitive groups of Scarabaeoidea, Byrrhidae, most Dryopoidea and Elateroidea, some Cantharoidea, the bostrichid genus *Endecatomus*, and the Belidae, while an articulated mala or galea, without a lacinia, is characteristic of some Carabidae, Dytiscidae, Noteridae, Amphizoidae, paederine Staphylinidae, Buprestidae, Callirhipidae, some Elateridae, and most Cantharoidea. The complete loss of apical lobes occurs in Dytiscidae, Hygrobiidae, Hydrophiloidea, Eucnemidae, Rhipiphoridae, and Meloidae. Many workers consider the small, palpiform process on the first segment of the maxillary palp in Hydrophiloidea (Kfig. 102 p194) to be a galea, but this interpretation is not followed here.

A maxilla having both galea and lacinia fixed occurs in Haliplidae, the more primitive Staphylinidae, Eucinetidae, Rhipiceridae, some Scarabaeidae, Psephenidae, Derodontidae, Bostrichoidea, and a few Cucujoidea, while a single, fixed mala is known in Rhyssodidae, Dytiscidae, Haliplidae, most Staphylinidae, Clambidae, Scarabaeidae (advanced

subfamilies), some Buprestidae, Throscidae, some Cantharidae, Lymexylidae, most Cucujoidea and Tenebrionoidea, Chrysomeloidea, and Curculionoidea. Intermediate conditions occur where the apex of the mala is deeply cleft, and these have usually been coded for both character states in constructing the key.

The galea is usually broader, more rounded or truncate, and more setose than the lacinia, except in those groups where both lobes have become reduced and palpiform, but the structure varies considerably, and it may be falcate like the lacinia in Dascillidae (Kfig. 112 p208) and Scarabaeoidea. In primitive Staphylinoidea, the galea is said to be **fimbriate**, with a dense row of modified setae along the outer edge of the apex (Kfig. 111 p241), while in Helodidae, it is very broad and its apex is covered with specialized comb-hairs (fig. 34.49). The lacinia is often narrower and more falcate than the galea, and may have one or more teeth or spines at the apex; these apical teeth are usually called **unci**, but the term **uncus** has been used for a variety of lobes or teeth at the inner edge of the maxillary apex. A rounded lacinial lobe occurs in some Anobiidae, and a similar structure in the Ciidae (Kfig. 110 p239) may represent the lacinia or a secondary structure which has become reduced to a simple, spine-like process at the inner edge of the galea (Kfigs. 97a, 215 p218).

The form of the fixed mala also varies considerably, but it is usually rounded or truncate. A falciform mala (Kfig. 105 p241) occurs in some Staphylinidae, spercheine Hydrophilidae, Throscidae, Rhizophagidae, Phloeostichidae, cucujine and silvanine Cucujidae, Cryptophagidae, Languriidae, Biphyllidae, Byturidae, some Bothrididae, a few Endomychidae and Corylophidae, and donaciine and zeugophorine Chrysomelidae. In *Donacia*, there appear to be two maxillary lobes, but one of them may be a modified seta. A styliform mala (Kfig. 104 p241) occurs in the leiodid genus *Myrmecoholeva*, proteinine Staphylinidae, Cerophytidae, the eucnemid genus *Phyllocerus*, and the cerylonine Cerylonidae. In *Myrmecoholeva* and most cerylonines, these stylets and the styliform mandibles fit together with the labrum to form a piercing beak or proboscis (Kfig. 27 p224), while in *Cerophytum* they fit into lateral channels in the labial plate. In many groups with a truncate mala, there is a cleft at the apex (Kfig. 106 p249), and within this cleft there may be a **malar sclerome**; it is not certain whether the cleft represents an incomplete fusion of the galea and lacinia or a secondary subdivision of the mala. A cleft mala is most common in the Tenebrionoidea, but it also occurs in Erotylidae, Helotidae, Lymexylidae, and some staphylinoids. The malar apex sometimes has a distinct lobe at its inner angle; this structure, which occurs in Nitidulidae, Tricentotomidae, anaspidine Scaptidae and a few other groups, is usually called an **uncus**, but the term is also used for lacinial teeth and for the one or more malar teeth on the inner apical angle in many cucujoids and tenebrionoids. Other structures occurring at the malar apex include **spatulate setae**, as in the spore-feeding nitidulids of the genus *Aphenolia* (fig. 34.44) and the **pedunculate seta** (an elongate tubercle with one or more setae at the apex) found in all Cleroidea, except Phloiophilidae and primitive Trogossitidae (Crowson, 1964d). The inner edge of the mala often

bears one or more rows of spines which may continue along the edge of the stipes, and its dorsal surface may be armed with spines, setae, or a dense brush of hairs forming part of the oral filter.

The **labium** consists of two major parts: the apical **prementum** and the basal **postmentum** (fig. 34.14), but the latter is often subdivided into a basal **submentum** and a **mentum**, which lies between it and the prementum (fig. 34.11). The submentum is sometimes fused with the gula, so that a combined area called the **gulaementum** (fig. 34.13) is formed, but the limits of the submentum and gula may be arbitrarily defined by an imaginary line extending between the bases of the cardines. These terms have been used in the keys and descriptions, but they do not necessarily reflect true homologies, and various alternative terminologies have been proposed (see Anderson, 1936; Crowson, 1981; Das, 1937; Dorsey, 1943). When there are only two labial sclerites, for instance, the basal one may be called the mentum (Crowson, 1981), and when there are three, the first two have been considered subdivisions of the prementum, based on muscle insertions (Anderson, 1936). The presence of only two labial sclerites occurs throughout the order, but it is most commonly met with among the Adephaga, Dryopoidea, Elateroidea, Cantharoidea, Cleroidea, Chrysomeloidea, and Curculionoidea. In various groups (some Adephaga, Hydrophiloidea, Rhipiphoridae, some Curculionidae, etc.), there may be further reduction, so that there is a single labial plate.

The prementum represents the fusion of paired labial sclerites which are serially homologous to the maxillary stipites, and bears a pair of **palpigers** (to which the labial palps are attached), rarely a pair of **glossae**, which are homologous to the maxillary laciniae, and more often a median structure, the **ligula**, which represents fused glossae. **Paraglossae**, found in many other insect orders, may not occur in beetle larvae, although there are paired lobes on either side of the ligula in Staphylinoidea, which have been called paraglossae by Böving and Craighead (1931). In some larvae (Agyrtidae and other primitive staphylinoids, some Eucinetidae, Dascillidae), the ligula is broad and distinctly bilobed, but more often it is undivided, and in various families it is reduced or absent. In Cupedidae, Micromalthidae, and Callirhipidae, the ligula has become heavily sclerotized and wedge-like, forming a **ligular sclerome** (Kfigs. 99 p216, 117 p189).

The usual number of labial palp segments is two, but reduction often occurs, and in a few cases, there has been an increase to 3 (some Carabidae and Dytiscidae, Gyrinidae, some staphylinine Staphylinidae, some Histeridae) or 4 (some Dytiscidae). Single-segmented labial palps occur in the families Cupedidae (*Priacma* first instar), Micromalthidae, Rhyssodidae, Hydrophilidae (*Spercheus*), Clambidae (most), Rhipiceridae, Scarabaeidae (Ceratocanthinae), Buprestidae (most, but see below), Eucnemidae (many), Bostrichidae (Dinoderinae and Lyctinae), Trogossitidae (Rentoniinae), Nitidulidae, Hobartiidae, Cryptophagidae (Cryptophaginae), Rhizophagidae (Monotominae), Endomychidae (*Hyperaspis*), *Coperdina* and Merophysinae), Coccinellidae (*Hyperaspis*), Corylophidae (*Corylophodes*), Lathridiidae (many), Mycetophagidae (*Thrimolus*), Colydiidae (*Nematidium*, *Pseudendestes*), Meloidae (Tetraonycini triangulins), Mycteridae

(Lacconotinae and Hemipeplinae), Tenebrionidae (Leiochirini), Pedilidae (Cononotinae), Rhipiphoridae (Rhipidiinae), Chrysomelidae (various subfamilies), Anthribidae (some), Brentidae (few), and Curculionidae (some). In Buprestidae, the palps are represented by minute papillae or setose areas, which may not be true palps at all, and labial palps are absent in *Cerophytum*, some Eucnemidae, the coarctate instars of Meloidae, rhipiphorine Rhipiphoridae, Bruchidae, Urodon-tidae, and the anthribid genus *Euxenus*.

The mentum or postmentum is very broad in some groups, like Helodidae, Ptilodactylidae (fig. 34.34), and Psephenidae, where it may be expanded laterally to conceal the maxillary articulating area. In anchytarsine Ptilodactylidae, it is divided into three parts by longitudinal sutures (Kfig. 98 p230). In some other groups, like trogossitine Trogossitidae and Elateridae, it may be much narrower than the stipes, and in the latter group, it may be narrowed posteriorly and separated from the gular area by contiguous or fused cardines (Kfig. 100 p233).

The ental surface of the labium, posterior to the ligula, is called the **hypopharynx** (fig. 34.12). In some larvae it is a simple, membranous lobe, usually clothed with short hairs, but in others it may have a more complex structure. The hypopharynx is often supported by the **hypopharyngeal bracon** (see above) and sometimes by a pair of **hypopharyngeal rods**, extending ventrally on each side to the base of the mentum, and a **hypopharyngeal suspensorium**, consisting of one or more pairs of rods extending dorsally on either side of the cibarium and inserting in its dorsal wall. The detailed structure of the suspensorium and its variation within the order has never been investigated. The hypopharynx is simple in larvae which have the mandibular molae reduced or absent, but in those with a well-developed mola, there is usually a sclerotized bar or a cup-like or molar-like structure called the **hypopharyngeal sclerome** (figs. 34.12, 34.46, Kfig. 119 p189), which acts in conjunction with the mandibles in the processing of food. The development of this sclerome and its form may vary considerably within a family, and the structure has been used as a taxonomic character in Tenebrionidae. The sclerome is particularly well-developed in the Tenebrionoidea but is also widely distributed in the Cucujoidea and occurs in various other groups with mandibular molae. In some families, like Elateridae, there may be a bar-like sclerotization which is not associated with a mola, but its function is not clear. In Dascillidae and Scarabaeoidea, there may be two or more scleromes called **oncyli** (sing. **oncytus**), while in Dascillidae and Helodidae, the hypopharynx may also have two or more **hypopharyngeal combs** (fig. 34.48). According to Beier (1952), these combs in Helodidae are associated with the filter-feeding apparatus; fine particles are gathered by the maxillary comb-hairs (fig. 34.49), which are then brushed over the combs, where food particles are collected, moved posteromesally towards the back of the hypopharynx and compacted into a solid pellet by the hypopharyngeal sclerome and mandibular molae. The compacting function of the hypopharyngeal sclerome is also seen in the mycophagous tenebrionid *Platydemia ellipticum* (Fabricius) (figs. 34.45–46), where the larva shears masses of reinforced hyphae from the surface of a bracket fungus and compacts them between the concave molae and

the concave sclerome, probably with the aid of the setose maxillae. In addition to the sclerome, the hypopharynx may have well-defined brushes of hairs or lateral lobes, which have been called **maxillulae** by Böving and Craighead (1931). In Oedemeridae, there is a distinct columnar structure, the **pre-hypopharynx**, between the sclerome and the ligula (Rozen, 1960).

As mentioned above, the more primitive labium is more or less free from the maxillae, except basally, where they are joined by the maxillary articulating area. In several groups of beetles, there has been a consolidation of the maxillae and labium by reduction and loss of the articulating area and connation of the cardines and stipites with the postmentum or mentum. The resulting maxillolabial complex can be moved only as a single unit. This process is usually accompanied by the loss of the mandibular mola and the reduction of the apical maxillary lobes. Connation of maxillae and labium (figs. 34.32, Kfigs. 93, 100 p264) occurs mainly in Dryopoidea, Elateroidea, Cantharoidea, and Cleroidea, but it is also known in a few cucujoids and some Chrysomelidae (especially Hispinae and the clytrine-cryptocephaline group). Partial fusion is known in Dryopidae (fig. 34.31), Brachypsectridae (Kfig. 97 p201), and Lycidae, while complete fusion occurs in Cheloniidae and various Eucnemidae. This consolidation is often associated with liquid feeding, and the ental surface of the maxillolabial complex may be densely clothed with short hairs, forming with a similar brush on the epipharynx an **oral filter** (figs. 34.35–37), which serves to keep solid particles out of the gut. There are no labial silk glands in beetles, as there are in Lepidoptera, but maxillary glands, located between the bases of the maxillae and the labium, have been reported by Srivastava (1959) in Tenebrionidae, Cerambycidae and Chrysomelidae.

## Thorax and Legs

The thorax consists of three segments: **prothorax (T1)**, **mesothorax (T2)**, and **metathorax (T3)**, each of which bears a pair of articulated legs, except in specialized, internal-feeding larvae to be discussed below. In general, the prothorax is largest and most highly modified, while the meso- and metathorax are similar in structure. In larvae of most Buprestidae, some Eucnemidae, and various Chrysomeloidea and Curculionoidea, the prothorax is greatly enlarged and the legs are reduced or absent. The **cervical region** or neck is usually membranous, but sometimes there are dorsal or ventral sclerotizations, the latter of which may be confused with anterior plates of the prothoracic sternum (see below). In Cebriionidae, there is a large **cervical membrane**, lined with ridges and asperities, which is capable of being everted, displacing the head dorsally and posteriorly (Kfig. 120 p207).

The three thoracic segments and abdominal segments 1 to 7 or 8 have a similar general structure, except for thoracic modifications associated with the head and leg attachments. The **dorsum** of each segment usually consists of a large plate, called the **tergum**, and one or more pairs of smaller, lateral sclerites, the **laterotergites**. Each tergum is usually divided at the midline by a narrow **ecdysial line**, but in some forms there is a broader division, with the formation of paired, smaller

**tergites.** Paired tergites occur on all thoracic and most abdominal segments in Sphindidae and on the meso- and metathorax in some Cleridae and Trogossitidae. In some lightly sclerotized larvae (Rhysodidae, Gyrinidae, Histeridae, trogine Scarabaeidae, some Elateridae, many Cleroidea, various Chrysomeloidea and Curculionoidea) only the prothorax bears a tergal plate. Spiracles are usually located between the tergum and laterotergites on each side, but sometimes they are on a laterotergite or on the tergum. The **pleuron** is somewhat reduced, except on the thorax, where it consists of sclerites partly surrounding the leg articulations, while the **venter** usually consists of a single plate, except on the thorax, where complex and poorly understood subdivisions may occur (see below).

The structure of the **protergum** is usually simple, consisting of no more than a sclerotized plate, but in some Ly-mexylidae, Buprestidae, Oedemeridae, and Cerambycidae, there are patches of asperities, in belid larvae there may be a prominent protergal carina, in Platypodidae there is a transverse row of ring-like sclerites, and in some Eucnemidae and Bostrichidae, there are rod-like sclerotizations. Transverse carinae or rows or patches of asperities occur more commonly on the meso- and metatergum, and usually on the anterior abdominal terga as well. Examples of larvae with patches of asperities on the meta- or meso- and metatergum may be found in the families Scarabaeidae, Lucanidae, Anobiidae, Colydiidae (Pycnomerini), Synchronidae, Zopheridae, and Cephaloidea (Stenotrachelinae); while rows of asperities on these segments are known in Rhysodidae, Dascillidae (forming serrulate carinae), Scarabaeidae (Troginae), Colydiidae (*Lasconotus*), Zopheridae, and Cephaloidea (Stenotrachelinae). In some soft-bodied larvae, there may be a folding of the tergal region, so that 2 to 4 **plicae** or folds can be seen from above, while other subdivisions are visible laterally. When the tergum is divided transversely into 2 parts, as on the thorax, the anterior division is sometimes called the **prescutum** and the posterior one the **postscutum**; when 3 folds are present, they may be referred to as the prescutum, **scutum**, and **scutellum**. The thoracic spiracle is usually located in a laterotergite, sometimes called a **spiracular sclerite** (fig. 34.18) or **alar area**, lying between the prothorax and mesothorax; but in some groups the spiracle is on the mesotergum or protergum.

The thoracic pleuron (fig. 34.18) is divided by a short **pleural suture**, extending dorsally or laterally from the coxal articulation and representing an internal apodeme called the **pleural apophysis**. This suture divides the pleuron into an anterior **episternum** (= **prehypopleurum**) and a posterior **epimeron** (= **posthypopleurum**); sometimes there are two additional pleural sclerites, the **precoxale** in front of the episternum, and the **postcoxale** behind the epimeron, but these are often fused with the episternum and epimeron or with adjacent sternal elements. In some Tenebrionidae, the postcoxale on each side is enlarged and extends mesally to fuse with the **sternellum**, forming a crescent-shaped sclerite behind the coxae; this may be called the **postcoxal bridge**, although that term has also been used as a synonym of postcoxale.

The ventral region of the thorax (fig. 34.18) is more lightly sclerotized and its subdivisions usually are neither clearly defined nor clearly separated from the pleural sclerites. In some larvae, there are 2 **sternal pits** lying in the middle of the sternum between the coxal bases. These represent the invaginations of the **sternal apophyses**, and they may be joined by a transverse suture, the **sternacostal suture**, which divides the sternum into an anterior **basisternum** and a posterior **sternellum**; in the absence of a suture or pits, these terms are still used for the sternal areas in front of and behind the coxae. The basisternum may be further subdivided, but the nomenclature concerning these anterior and anterolateral sclerites is confused, and different terms are used by workers dealing with different taxa. There is often a large, sclerotized area on the prothorax, which is set off from the basisternum and extends to the anterior edge; this has been called the **pre-sternum** or **prosternum**, and it may be variously subdivided or joined laterally to the precoxalia. In addition, there may be a smaller, mesal sclerite, which may be folded beneath the head and is thought to be part of the cervical region; this has been called **cervicosternum** by Watt (1970), but the same structure was considered by St. George (1939) to be the pre-sternum. Other terms applied to these sclerites, such as **eusternum**, **preeusternum**, and **articulating area**, are in the glossary and are defined, discussed, or illustrated by Böving and Craighead (1931), Hyslop and Böving (1935), Glen (1950), St. George (1924, 1939), Wade and St. George (1923), and Watt (1970, 1974b). Sometimes there is a small sclerite lying between the sternellum and the following segment; this is called an **intersternite** by Watt (1970), but was known to earlier workers as a **poststernellum**. Various special structures of the thoracic sterna include patches of asperities on the prothorax in Cupedidae and most Buprestidae, and paired, sclerotized prosternal rods in Throscidae, Cerophytidae, and Eucnemidae.

The basic number of leg segments in larvae of Adepaga and Archostemata (figs. 34.19-20) is 6, including, from base to apex, **coxa**, **trochanter**, **femur**, **tibia**, **tarsus**, and **pretarsus**, the last consisting of paired claws or a single claw (**ungulus**). In Myxophaga and Polyphaga (fig. 34.21), the basic number is 5, including coxa, trochanter, femur, tibia, and **tarsungulus** (also referred to as the **claw**). Peterson (1951) and some other authors exclude the claw in counting leg segments, and thus consider the adepagan leg to be 5-segmented and the polyphagan leg 4-segmented. The homologies of the last 2 or 3 segments in the leg have been the subject of much controversy. Jeannel (1949) considered the apical segment in both leg types to be a tarsus; the penultimate segment was called the tibia in both groups, and the adepagan leg was said to have an extra segment, the **medius**, located between the femur and tibia. Emden (1942b) thought that the apical segment in both groups was a part of the **pretarsus** called an **ungulus** or claw, and that the penultimate segment in the polyphagan leg was a **tibiotarsus**, representing the fusion of the tibia and tarsus. Böving and Craighead (1931) and Crowson (1955, 1964d) considered the apical segment in Polyphaga to represent a fusion of the tarsus and ungulus (thus tarsungulus), and this interpretation is followed here.

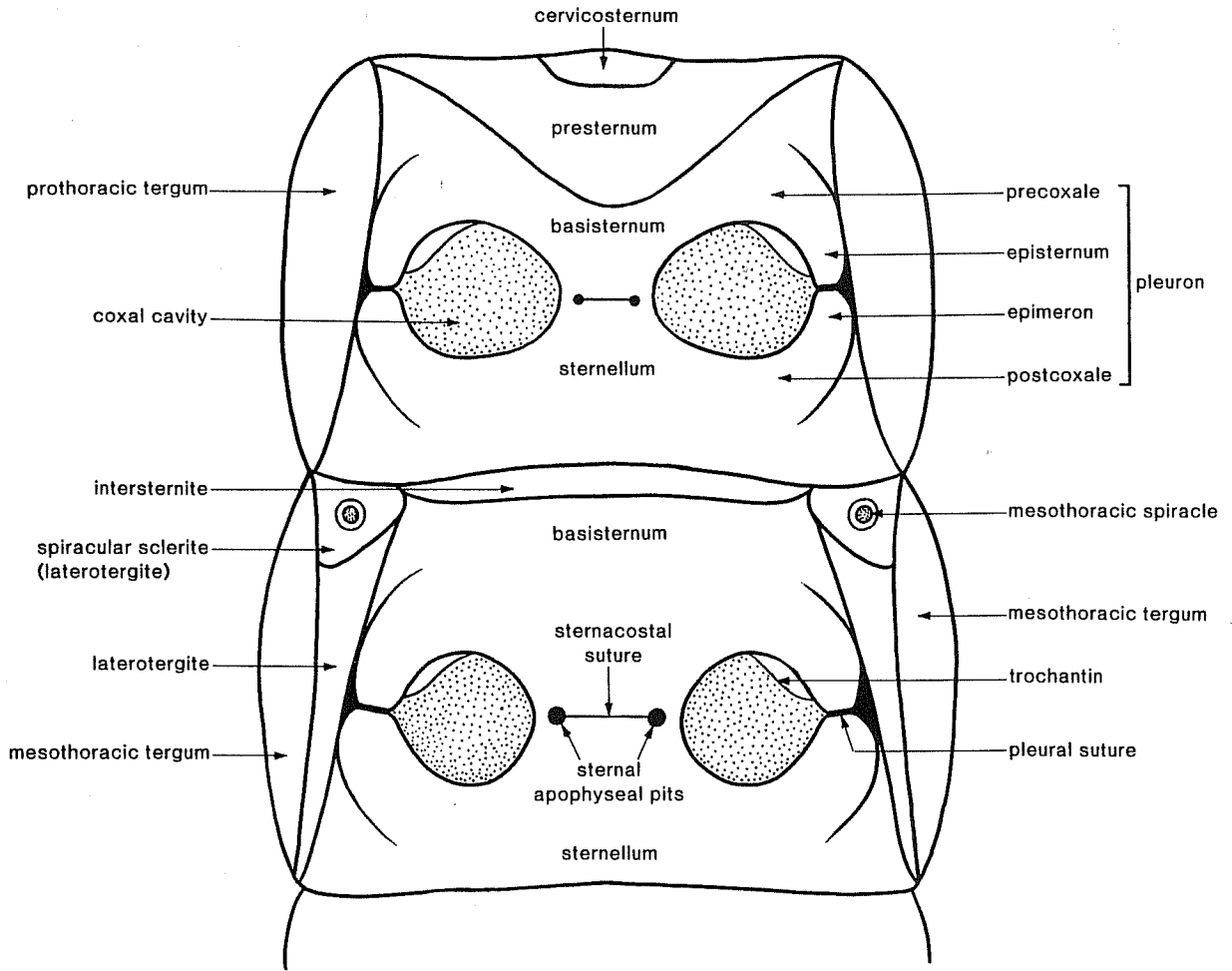


Figure 34.18. Prothorax and mesothorax (composite), ventral, with legs removed.

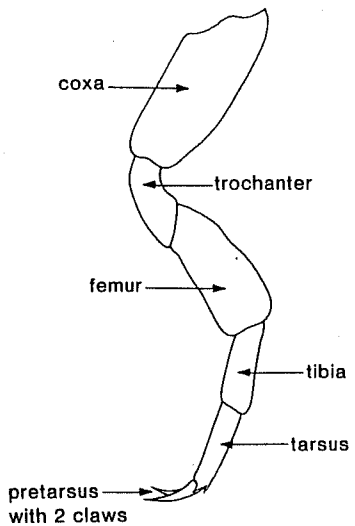


Figure 34.19

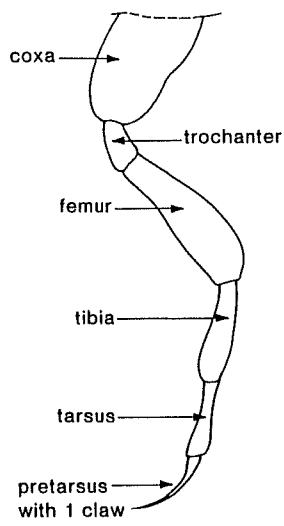


Figure 34.20

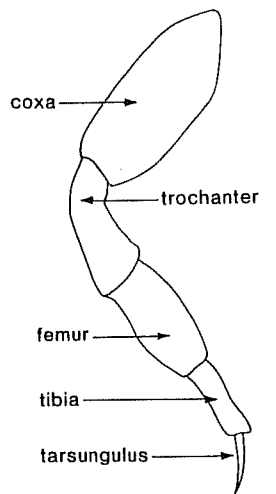


Figure 34.21

Figure 34.19. Mesothoracic leg (Carabidae).

Figure 34.20. Mesothoracic leg (Dytiscidae).

Figure 34.21. Mesothoracic leg (composite polyphagan).

Six-segmented legs occur in all Archostemata and Adephaga, with the exception of the legless forms of Micromalthidae, the myrmecophilous Carabidae: Paussini (3 segments), and the ectoparasitic Carabidae: Lebiini and Brachinini (4 segments). Five-segmented legs are characteristic of all Myxophaga and many Polyphaga, but reduction in the number of segments has occurred throughout the latter group. Four-segmented legs are found in the polyphagan families Micropeplidae, Hydrophilidae (most Sphaeridiinae), Scarabaeidae (some Geotrupinae), Callirhipidae (few), Eucnemidae (few), Cucujidae (Passandrinae), Rhipiphoridae (late instars), Cerambycidae, Bruchidae (Pachymerinae), and Chrysomelidae (Hispiinae, Donaciinae, Megalopodinae). Reduction to 2 or 3 segments has occurred in Georyssidae, Rhipiceridae, Scarabaeidae (Scarabaeinae, Geotrupinae), Mordellidae, Meloidae, Cerambycidae, Bruchidae, Anthribidae, Brentidae, and Ithyceridae. Larvae having single-segmented legs are known in rare Buprestidae and Eucnemidae, and in a few Cerambycidae, Chrysomelidae (leaf-mining Hispiinae), Nemonychidae, Anthribidae, and the genus *Cylas* (Curculionidae). Legless larvae occur in a number of Polyphaga which are internal feeders (sphaeridiine Hydrophilidae, most Buprestidae and Eucnemidae, a few Anobiidae, some Cerambycidae, a few Bruchidae and Chrysomelidae, and most Curculionoidea) or ectoparasites (most Bothripteridae, some Rhipiphoridae and Meloidae). In some of these, there are paired thoracic protuberances called **pedal lobes**, which are thought to represent leg remnants.

In many substrate-inhabiting larvae, the prothoracic legs are enlarged and variously modified for digging; examples may be found among the Tenebrionidae (Alleculinae, Tentyriinae, Helaeini, Blaptini) or in the Cebriionidae and Cerophytidae. Prehensile prothoracic legs are formed by the opposition of the femur (Noteridae) or the tibia (Haliplidae, Dytiscidae: Matini) to the apical leg segments. In several groups of Scarabaeoidea, **stridulatory organs** are formed by the meso- and metathoracic legs (Kfigs. 129, 130 p267) (Lucanidae, Passalidae, and geotrupine, pleocomine, and ceratocanthine Scarabaeidae) or pro- and mesothoracic legs (hybosorine Scarabaeidae). Sound is produced by a **plectrum**, consisting of a carina or row of tubercles located on the trochanter, femur, or apex of the posterior leg, rasping against a **stridulitrum** (also called a **pars stridens**), consisting of a variable group of tubercles or ridges located on the coxa of the anterior leg. In Passalidae (Kfig. 131 p258) and some geotrupine scarabs, the metathoracic leg is highly reduced and functions only as a plectrum.

The tarsungulus is usually somewhat claw-like, but in larvae with reduced legs, it may be rounded, reduced, or absent. Long tarsunguli occur in some triungulins, and in those of some Meloidae, the claw is **spatulate** (Kfig. 132 p203) with 2 large setae at its base, so that it appears to be 3 claws. The prothoracic tarsungulus may be divided into a lightly sclerotized basal portion and a heavily sclerotized, apical digging claw in some Tenebrionidae, while in Cerophytidae (Kfig. 133 p192), it is enlarged, heavily sclerotized, and bifurcate. There are usually 2 setae at the base of the tarsungulus, and these are usually placed side by side, but may be in a line, with one distal to the other in certain groups. Plurisetose tarsunguli

occur in the families Staphylinidae (some Staphylininae), Hydrophilidae (Spercheinae), Dascillidae, Scarabaeidae, Eulichadidae, Cantharidae, Anobiidae, and Lymexyllidae, while in various groups with reduced legs, these setae may be absent. Reduction from 2 tarsungular setae to 1 has occurred a number of times in beetle larvae, and is characteristic of all Myxophaga, almost all Dryopoidea, all Cleroidea, and a large and probably monophyletic group of Cucujoidea including Biphylidae, Byturidae, Bothripteridae, and the "cerylonid series" of Crowson (1955). Some surface-active larvae may have special structures at the leg apices for adhering to surfaces; these include the basal tarsungular tooth in some Chrysomelidae (Chlamisinae), the **adhesive setae** at the tibial apex in Coccinellidae or on the tarsungulus in meligethine and cybocephaline Nitidulidae, and the **pulvillus** (or **paronychial appendix**) at the base of the tarsungulus in some Chrysomelidae.

### Abdomen

The abdomen of a beetle larva usually consists of 10 segments, with the first 7 or 8 more or less similar in form, the 9th and sometimes the 8th variously modified, and the 10th often reduced. In cardiophorine Elateridae, the abdomen is very long, with each segment transversely subdivided, so that it appears to have more than 10 segments. The general structure of an abdominal segment was discussed briefly above. Snodgrass (1935) pointed out that the major lateral line of demarcation on the abdomen is the **dorsopleural line**, which separates the **dorsum** from the **pleuron** and **venter** and continues onto the thorax just above the episternum and epimeron; the abdominal pleuron is that area, just below this line, which corresponds to the plates around the bases of the thoracic legs and which may or may not be separated from the venter by a **pleuroventral line**. In most beetle larvae, there is no abdominal pleuron, so the major lateral line is actually a **tergosternal fold**. Specialists on beetle larvae have used various terms for the lateral lines or folds of the abdomen, and the terminology is confusing. Böving and Craighead (1931) used the term **ventrolateral suture** for the dorsopleural line, while Thomas (1957) used **pleural fold** for the same line in bark beetle larvae. Other terms applying to lateral folds include **ventropleural line** (Thomas) and **hypopleural fold** (Parkin, 1933), both corresponding to the pleuroventral line, and **dorsolateral suture** (Böving and Craighead) (= **dorso-pleural line** of Thomas), which lies on the dorsum and separates the spiracular area from the laterotergite.

The dorsum usually consists of a large, median plate, the **tergum** (or **tergal plate**), a pair of **spiracles**, and one or more pairs of **laterotergites**, or a more vaguely defined **epipleurum**. The word tergum may be used for the entire dorsum, especially when this is not clearly subdivided, but some authors use the term **tergite** or **mediotergite** for the main plate when laterotergites are present. The abdominal terga of many beetle larvae bear special kinds of armature used to gain leverage while burrowing into soil or wood or beneath bark; these have proven useful in larval identification. Patches of asperities or spinules (Kfigs. 141-143 pp293,274,295) occur in various groups, including Histeridae, many Scarabaeoidea, lissomine and oestodine Elateridae, most Anobiidae, Lymex-

ylidae, Synchronidae, most Oedemeridae, some Cerambycidae, and rhynchitine Curculionidae. In other larvae, there may be rows of tergal asperities (Kfigs. 144–148 pp251,249,214,296,213), which sometimes form incomplete circles; examples are known in the families Rhysodidae, Cucujidae (Laemophloeinae), Phalacridae (*Litochrus*), Phloeostichidae (Hymaenidae), Monommidae, and Mycteridae. In stenotracheline Cephaloidea, there are both patches and rows of asperities, while in Trictenotomidae there are peculiar patterns formed by longitudinal ridges. Another type of structure serving a similar function is the **ampulla** (Kfig. 149 p262) (also called **ambulacral wart**, **ambulatory wart**, **scansorial wart**), a hump-like projection sometimes armed at the apex with asperities; these occur in Cupedidae, Micro-malthidae, Histeridae, Trogossitidae (Trogossitinae), Cleridae, Melandryidae (Melandryinae), Mordellidae, Oedemeridae, and some Curculionoidea. In tiger beetle larvae (Carabidae: Cicindelinae) (Kfig. 135 p214) there is a large protuberance bearing 2 or 3 pairs of hooks on the 5th tergum, while in *Sphallomorpha* (Carabidae: Pseudomorphinae) (Kfig. 137 p214), there are rows of stout spines on terga 5–7. In some Eucnemidae (*Fornax*), the abdominal terga (also sterna) have well-defined areas called **matte patches**, which are covered with minute asperities (Gardner, 1935b).

In many soft-bodied larvae, the abdominal terga are transversely divided into 2 to 4 folds or **plicae** (Kfig. 136 p217), which may extend along the sides as well, and the names applied to these vary with the taxon studied (Scarabaeoidea, Ritcher, 1966; Anobiidae, Böving, 1954, Parkin, 1933; Curculionoidea, Anderson, 1952, Thomas, 1957). When there are two plicae, the anterior one may be called **prescutum**, **pro-dorsal fold**, or **prenotal fold**, and the posterior one the **scutum**, **postdorsal fold**, or **postnotal fold**. Three folds in Scarabaeoidea are called **prescutum**, **scutum**, and **scutellum**, with another fold, the **postscutellum**, behind the scutellum, but visible mainly from the side, and a lateral area, the **subscutum**, wedged between the scutum and scutellum. In Curculionoidea, the folds may be numbered, but the numbering has not been consistent (May, 1967). The area around the spiracle has been called the **alar area**, **parascutal area**, **paradorsal area**, or **spiracular sclerite**. Other terms applied to laterotergites or laterotergal areas include: **epipleurite**, **epipleural area**, **dorsopleural lobe**, **pleural lobe**, **paratergum**, and **paratergite**. Most of the paired lateral processes occurring in beetle larvae are extensions of the laterotergites, and are not pleural in origin. The true abdominal pleuron, which lies immediately below the dorsopleural line, has been called **pleurum**, **hypopleurum**, and **ventropleural lobe** by various authors. In many groups, it is absent or represented by a narrow membranous region, but distinct pleural sclerites occur in some groups, including Carabidae and various families of Dryopoidea, Elateroidea, and Cantharoidea.

The abdominal venter often consists of a single **sternum** or **sternal plate**, but this may be divided transversely or longitudinally. The mesal sclerite of a longitudinally divided venter is sometimes called the **mediosternite**, and the lateral plates are **laterosternites**, but have also been called **laterosternal folds**, **pedal areas**, or **coxal lobes**. When the venter is

transversely divided, the main plate is the **basisternum** and that posterior to it is the **sternellum**, but as in the thorax, the term **eusternum** has been used inconsistently as synonymous with the basisternum or entire sternum. In Curculionoidea, the terms **mediosternal fold** and **transverse fold** have been used for the two areas, while in Carabidae, there may be a main **ventrite**, with **preventrites** and **postventrites** in front of and behind it. Ambulatory modifications of the sterna are more or less similar to those on the terga, and include patches or rows of asperities, ampullae, plicae, and matte patches. In some larvae, there are distinct **prolegs**, similar to those found in Lepidoptera, but usually without apical hooks or **crochets**. Prolegs with simple or setose apices occur on segments 1 to 7 or 8 in larvae of various Chrysomelidae (Criocerinae, Eumolpinae, Alticinae) and Curculionidae (*Cionus*, Hyperinae), while most Oedemeridae have asperity-bearing prolegs on segments 2 to 3, 4, or 5. Some hydrophilid larvae have prolegs with crochets at the apex on sterna 3–7 (*Enochrus*) or 2–7 (genus near *Coelostoma*). In some larvae the sternal regions are very narrow and may be absent posteriorly; examples of this occur throughout the Dryopoidea.

### Abdominal Apex

The last two or three abdominal segments in beetle larvae usually differ from those anterior to them because of special adaptations involving locomotion, defense, or respiration. A type of larval abdomen which may have been ancestral in Coleoptera is characterized by having an unmodified, subterminal 9th segment and a terminal 10th segment, with distinct tergum and sternum bordering a transverse anal opening; this type of apex occurs in some Dascillidae, Scarabaeidae, and Byrrhidae, and with slight modifications in various other families. The major changes which have taken place in the abdominal apex include the following: 1) transformation of segment 10 into a cylindrical or conical **pygopod**, sometimes with hooks, asperities, or eversible holdfast organs at the apex; 2) development of a ventral pygopod (sternum 10) below the anus (Limnichidae and Heteroceridae); 3) posterior production of tergum 10 forming a median process and resulting in the ventral position of the anal region (some Haliplidae); 4) development of **articulated**, terminal or subterminal **urogomphi** on the posterior portion of tergum 9; 5) formation of lobes, pads, setose areas, or sclerites around the anus in soft-bodied, internal feeding larvae; 6) reduction of segment 9 and concealment of its sternum, with retention of a well-developed terminal 10th segment (some Cucujidae); 7) ventral movement of the anal region, so that tergum 9 becomes terminal, extending partly onto the ventral surface, and segment 10 becomes ventrally or posteroventrally oriented; 8) sclerotization of tergum 9 and development of various kinds of armature, including paired, **fixed urogomphi**; 9) transformation of tergum 9 into a hinged sclerotized plate articulating with tergum 8 (often accompanied by the partial enclosure of sternum 9 within an emargination of sternum 8, or sometimes concealment of sternum 9), in flat, subcortical larvae; 10) fusion of tergum and sternum 9, forming a complete sclerotized ring; 11) development of paired **pygopods**,



sometimes armed with hooks or asperities, from sternum 10; 12) formation of a dorsally-hinged **operculum** (tergum 9) articulating with tergum 8 and concealing sternum 9 and the anal region; 13) formation of a ventrally-hinged operculum (sternum 10) articulating with the ventral portion of segment 9 and concealing the anal region, in various aquatic and riparian larvae; 14) complete concealment of segment 10 between the edges of tergum and sternum 9; 15) reduction of segments 9 and 10 and movement of tergum 8 into a terminal position, with accompanying modifications; 16) formation of dorsal, posteriorly oriented spiracular process on tergum 8; 17) formation of a terminal **respiratory chamber** from portions of segments 8 and 9; 18) development of gill tufts or osmoregulatory papillae in the anal region. The above transformations represent a series of complex and interrelated evolutionary events. Most of them will be treated further in discussions on variation in each of the segments involved, while the last three will be covered in the section on special respiratory adaptations. Segment 8 in most larvae is not differentiated from the anterior abdominal segments, although it may have sclerotized areas or carinae associated with locomotory adaptations of the segments posterior to it. In certain cases, however, tergum 8 may become terminal, while the last two segments are reduced. Larvae of cassidine Chrysomelidae, for instance, have reduced 9th and 10th segments, and tergum 8 bears a large forked process (Kfig. 155 p221), which accumulates exuviae and other debris, thus concealing the surface-active larvae from predators. Another feature of the 8th tergum is the median defense gland in aleocharine Staphylinidae; these glands are particularly prominent in the Division Bolitocharinea (Seevers, 1978), but they occur in other groups as well (Frank and Thomas, 1984). In the adaphagan families Hygrobiidae, Amphizoidae, Noteridae, and Dytiscidae, the 8th segment is more or less terminal and lies above the reduced 9th and 10th segments, the former of which bears a pair of articulated urogomphi (*see below*). In the last three groups, tergum 8 bears a pair of large spiracles at the posterior end (often at the apex of a median process), but in Hygrobiidae, which lacks abdominal spiracles, it forms a long narrow process, similar in structure to the urogomphi. A terminal, spiracle-bearing process on tergum 8 has also evolved in the family Nosodendridae, where segments 9 and 10 are reduced and form a pair of ventrally located anal pads. Other modifications associated with the 8th pair of spiracles are discussed in the next section.

The simplest type of modification of tergum 9 involves its sclerotization, which is often greater than that of preceding abdominal terga; in some Cleridae, Corylophidae, and Chrysomelidae, there may be a distinct tergal plate similar to that on the prothorax; this plate is sometimes referred to as the **pygidium**, especially when it is clearly set off from the rest of tergum 9 (*see below*). The most obvious and consistent feature of the 9th tergum in many larvae is the presence of paired **urogomphi** (sing. **urogomphus**), which may be articulated or fixed at the base and may consist of from 1 to several segments. The term urogomphi has been used for almost any paired prominences on tergum 9, with the exception of setae or articulated spines, and those structures so designated are not necessarily homologous. The term **cerci** (sing. **cercus**) has also been used but is more properly restricted to the ap-

pendages of segment 10 in primitive insects. Other terms which have been applied to the urogomphi are **pseudocerci** and **corniculi**. In most active campodeiform larvae, which inhabit surfaces or interstitial spaces (leaf litter, etc.), the urogomphi are relatively long and narrow, project posteriorly or posterodorsally, have relatively little curvature, and bear a number of setae. These are basally articulated and/or segmented (Kfigs. 154–155 pp213,221, 162–163 p195) in some Carabidae (supertribes Nebriitae, Callistitae, Odacanthitae, Lebiitae, etc.), and most Hydradephaga, Staphyloidea, and Hydrophiloidea, and they appear to be tactile in function. In those larvae which inhabit narrower spaces beneath bark or bore into substrates like rotten wood or fungi, the urogomphi are more solidly built, never articulated or segmented, and often recurved, so that the apex points anteriorly (Kfig. 171 p196); these serve to fix the larva within its burrow and assist in locomotion.

Although most types of urogomphi are simple or at most tuberculate, some may be bifurcate or have a number of accessory branches or spines. Bifurcate urogomphi (Kfigs. 169 p201, 175, 177 p293, 183–184 pp275,249) occur in a number of families, including Elateridae (Athoinae), Melyridae, Nitidulidae, Tetratomidae, Pedilidae, and Salpingidae, while more complex forms (Kfigs. 179, 181 p275) characterize some Trogossitidae (*Calitys*, *Thymalus*), Nitidulidae (*Epuraea*, *Cryptarcha*), Languriidae (Xenoscelinae, Cryptophilinae), Cerylonidae (Euxestinae), Pythidae, Othniidae, and Inopelidae. Sometimes urogomphi may be accompanied by tubercles or teeth which extend onto the surface of the tergum (Kfig. 174 p295) or by smaller, paired processes called **pregomphi** (Kfig. 168 p255). Urogomphi may be approximate or widely separated, and in some cases there may be a median process (Kfig. 172 p215), a pit or cavity (Kfigs. 173–174 pp279,295), or 2 such pits (Kfig. 175 p293) between them.

In some larval types, tergum 9 bears a single median process, which may be spine-like and posteriorly projecting (Kfig. 159 p261), as in Archostemata, Elateridae (Elaterinae), Erotylidae (*Microsternus*), Colydiidae (*Cicones*), and Mordellidae, rounded and posteriorly projecting, as in Melandryidae (Osphyinae) and some Chrysomelidae (Alticinae), or hooked like a typical urogomphus, as in some Dryopidae and Ciidae. A forked median process occurs in some Cucujidae (*Pediacus*, *Platysus*). In scraptide Scraptideae, tergum 9 bears a large, rounded, lightly sclerotized, setose process (Kfig. 158 p261), which is deciduous, so that these larvae are often recognizable, not by the presence of the process, but by the truncate tergal apex from which the process has been removed.

Another distinctive type of 9th tergum is that bearing a concave disc or pygidium, often surrounded by teeth or serrations (Kfig. 160 p261). This feature is known in some Byrrhidae (Syncalyptinae), Lymexylidae, Tenebrionidae (Amarygmini), and Ciidae, and appears to be an adaptation for blocking the larval burrow to prevent the entrance of predators (Lawrence, 1974b). A more complex pygidium, lined with various kinds of teeth or spines, occurs in larvae of strongyliine Tenebrionidae and the pythid genus *Priognathus*. In paussine Carabidae, the 9th tergum forms a complex, multilobed disc of unknown function. In various flattened larvae living under bark (cucujine and laemophloeine Cu-



cujidae; Phalacridae (*Litochrus*), Prostomidae, Mycteridae, Pyrochroidae, techmessine Pythidae, the entire 9th tergum forms a hinged plate, sometimes called a **urogomphal plate** (Young, 1975) (Kfigs. 164–165 pp255,247, 176, 178 p275, 185 p277), articulated to segment 8 and apparently used to wedge the larva between layers of bark or wood. In the Brachypsectridae, the tergum forms an articulated spine, which is capable of extending anteriorly over the back and assists in prey capture (Crowson, 1973b). Another type of tergal plate in Callirhipidae forms a dorsally-hinged operculum, which encloses the anal region (Kfig. 186 p219).

The 9th sternum is usually relatively simple, but in various Tenebrionioidea, there are teeth or asperities variously distributed along the base (anterior edge) or occasionally at the apex. In the Hallomeninae (Melandryidae), Synchronidae, Salpingidae, *Aglenus* (Othniidae), and *Pedilus* (Pedilidae), there is a single tooth at each basal (anterolateral) angle (Kfigs. 183–184 pp275,249), while in the genus *Calopus* (Oedemeridae) and various members of the families Pythidae, Tricentenotomidae, Pedilidae, Pyrochroidae, Othniidae, and Inopeplidae, there may be from 2 to several asperities on each side of the anterior edge, sometimes forming a complete basal row (Kfigs. 178–182 p275). Two posteromesal asperities occur in the known larva of Eurygeniinae (Pedilidae) (Kfig. 177 p275), while in *Sphindocis* (Ciidae) and Prostomidae (Kfig. 176 p275), there is an apical (posterior) row of asperities. The 9th sternum is often partly enclosed within an emargination of sternum 8 in those larvae with a hinged tergal plate, but an extreme condition is known in Boridae and Mycteridae (Kfig. 185 p277), where the 9th sternum is deeply set into the 8th, and is U-shaped, almost completely enclosing segment 10 and bearing 2 or more teeth at the posterior edge; a similar condition occurs in some Elateridae (Pleonomini, Semiotini). In some larval types, sternum 9 is reduced, and it may be concealed by sternum 8, as in some Phalacridae (Kfig. 164 p255) or silvanine Cucujidae (Kfig. 167 p271). As mentioned above, the tergum is usually separated from the pleuron or combined pleuron and sternum on each side by a distinct dorsopleural line or fold; in some groups, including many Dryopoidea, however, tergum 9 is completely fused to the pleurosternal region, so that a continuous sclerotized ring is formed.

Modifications of the 10th segment are particularly striking in those larvae using this segment as an ambulatory device (pygopod or paired pygopods) and in those soft-bodied larvae in which the abdominal apex assists locomotion within substrates. In some active larvae with a terminal pygopod, such as those of various Carabidae, Staphylinioidea, and Lampyridae, there is an anal **holdfast organ** composed of a number of eversible, asperated tubes (Kfig. 191 p205) (Brass, 1914; Kemner, 1918). Paired lobes or **pygopods** (fig. 34.22), one on either side of the anal opening, occur in a number of groups. They may be simple (Archostemata, first instar brachinine Carabidae, cardiophorine Elateridae and some Tenebrionidae) or armed with 1 (Byrrhidae) or several (Ptilodactylidae, Kfig. 189 p229; Lymexylidae; Tenebrionidae) asperities, teeth, or hooks. Paired hooks may also occur in larvae without paired pygopods. In Hydroscaphidae (Kfig. 161 p209), Ptiliidae, Hydraenidae (Kfig. 163 p195), some Clambidae, Limnichidae, and some Elateridae, there is a

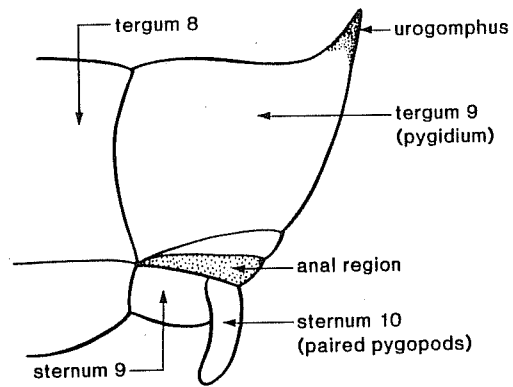


Figure 34.22. Abdominal segments 9 and 10 (Tenebrionidae), lateral.

single hook on each side of the single pygopod; gyrid larvae have 2 pairs of long hooks (Kfig. 157 p213); microsporids have 3 hooks on each side; and larvae of the elaterid genus *Semiotus* have a ring of teeth surrounding segment 10.

The anal region may be surrounded by 2 or more membranous lobes, which do not project as pygopods, and in various soft-bodied larvae there are a variety of supporting structures in the vicinity of the anus. In Bostrichidae, Anobiidae, and Ptinidae there is usually a longitudinal groove lying below the anal opening and separating a pair of oval pads or cushions; this structure has been called the **nates** by Böving (1954), who used the term **bow** for the curved sclerite below this. In most Scarabaeoidea, the anal opening may be transverse, Y-shaped, or longitudinal, and is surrounded by a dorsal **anal lobe** and 1 or 2 ventral anal lobes, or a pair of lateral anal lobes; the terms used for these lobes vary even among scarab workers (Ritcher, 1966). In most Lucanidae, the dorsal lobe is usually absent (or highly reduced), and the lateral lobes each may bear a glabrous area surrounded by a fine sclerotized line; this area is called an **anal pad**. In Scarabaeinae and Geotrupinae, the area below the anus may be subdivided forming several ventral lobes. The sternal area immediately anterior to the anal region in Scarabaeoidea often bears a group of hairs, bristles, or hooked setae, which is called a **raster** and is used extensively in the identification of scarab grubs. The raster may consist of a pair of **palidia**, each of which consists of a row of heavy spines or **palli**, surrounding a bare area called the **septula** and sometimes bordered laterally on each side by a **tegillum**, which is a continuous patch of shorter setae; in some cases, there is a single **palidium**, which is curved with the pali facing towards the anus, or the pallidium may be replaced by a **teges**, which is a continuous patch of short, straight or hooked setae. Other associated features include the **campus**, a bare area between the raster and the anterior edge of sternum 10, and a **barbula**, which is a tuft of hairs or short setae at the side of the abdomen near the anus. In the Australian genus *Cephalodesmius* (Scarabaeinae: Scarabaeini), the 10th sternum bears a coarsely striate, longitudinal ridge, which acts as a **pectrum** by rubbing against a finely striate **stridulitrum** on the gular region (Monteith and Storey, 1981).

Other modifications of the anal region include the paired spine-like processes on either side of the vertical anal slit in agriline Buprestidae (Kfig. 190 p191) and the complex lobes

and sclerotized plates found in larvae of eumolpine Chrysomelidae and various members of the weevil subfamilies Brachyicerinae and Tanymecinae (Ghilarov and Medvedev, 1964; Arnoldi and Byzova, 1964). In some aquatic or semiaquatic larvae, gill tufts or osmoregulatory papillae also arise from the membrane around the anus, but these are discussed in more detail in the next section.

Concealment of the anal region may be accomplished in several ways. In some Elateridae and Cebriionidae, the 10th segment is very small, circular, and located near the base of the undivided 9th segment, where it may be partly concealed beneath the apex of sternum 8. In some Tenebrionidae, the entire 10th segment may be concealed beneath the dorsally-hinged operculum formed by the 9th tergum. In a number of dryopoid larvae (araeopidiine Ptilodactylidae, Chelonariidae, Dryopidae, Lutrochidae, Elmidae, eubriine and psephenoidine Psephenidae), a ventrally-hinged **operculum** (Kfigs. 150, 187, 188 pp237,238) is formed from the 10th sternum, which articulates with the ventral part of the 9th segment. The operculum is operated by 1 or 2 sets of muscles, and it may be equipped with hooks (Dryopidae, Lutrochidae, Elmidae) or not. In Elmidae and Psephenidae, the operculum conceals retractable gills, but in the other groups gills are absent. Both the 10th segment and 9th sternum are reduced and at least partly concealed in larvae of some cucujine and laemophloeine Cucujidae, Phalacridae, Brachypsectridae, Nosodendridae, and various Hydradephaga and Hydrophilidae with apical respiratory structures (*see below*).

### Spiracles and Special Respiratory Structures

The normal type of respiratory system in beetle larvae is a **peripneustic** one, with functional spiracles on the mesothorax and abdominal segments 1 to 8, but a few larval types (Eulichadidae, Silphidae) have non-functional spiracular remnants on the metathorax. Hinton (1947) has shown that there is considerable variation in the number and position of functional spiracles, and this is complicated by the fact that the final instars of some aquatic larvae differ in this respect from earlier instars. A **hemipneustic** system, with spiracles on the mesothorax and abdominal segments 1-7, is present in the final instars of Hygrobiidae, Haliplidae, and some aquatic Lampyridae, as well as in the coarctate phase of the parasitic nemognathine Meloidae. An **amphipneustic** respiratory system, with metathoracic and 8th abdominal spiracles only, occurs in all instars of the gill-bearing psephenine and eubrianacine Psephenidae, while a **metapneustic** system, with a single pair of functional spiracles on abdominal segment 8, is known in Helodidae, *Araeopidius* (Ptilodactylidae), eubriine Psephenidae, and early and intermediate instars of Noteridae, Amphizoidae, Dytiscidae, and donaciine Chrysomelidae. An **apneustic** system, with no functional spiracles, is characteristic of earlier instars of Gyrinidae, Hygrobiidae, Haliplidae, berosine Hydrophilidae, Elmidae, Lutrochidae, some Ptilodactylidae and some eubriine Psephenidae, and all instars of *Psephenoides* (Psephenidae). In a few beetle groups, the type of larval respiratory system differs from any of those

mentioned; examples are final instar Noteridae and all instars of Microsporidae and Torridincolidae, with 8 abdominal spiracles and none on the thorax, Hydrosaphidae with spiracles on the mesothorax and 1st and 8th abdominal segments, last instar Gyrinidae with spiracles on the first 3 abdominal segments, and triungulins of *Tetraonyx* (Meloidae), with an enlarged pair on abdominal segment 1 and minute pairs on 2-5 (Hinton, 1947, 1967a; MacSwain, 1956; Parker and Böving, 1914).

The simplest type of spiracle is an **annular** or **uniform** type (fig. 34.24), which consists of a circular or oval opening, the edge of which is called the **peritreme**, a spiracular chamber or **atrium**, and a **spiracular closing apparatus**, lying between the atrium and the end of the tracheal trunk and consisting of a sclerotized ring and apodeme to which a muscle attaches. The inside of the atrium may be variously modified with internally projecting hairs or plates, these sometimes forming a filter. The peritreme may be simple or crenulate. During **ecdysis**, the old spiracle is pulled out through the opening of the newly formed one. The term **bilabiate** has been used by Schiödte (1862-1883), Roberts (1930), and others for a type of annular or uniform spiracle which is elongate-oval or elliptical, as in many Cerambycidae; the term is an unfortunate one, since it can be easily confused with biforous and bicameral (*see below*). An annular type of spiracle with a closing apparatus is thought to be the primitive condition in Coleoptera and occurs in all Archostemata, Adephaga, and Myxophaga; within the Polyphaga, however, it may have been secondarily derived several times from the annular-biforous type mentioned below. Annular spiracles are characteristic of most Staphylinidae, all Eucinetidae, Brachypsectridae, most Bostrichoidea, some Cleridae, all Melyridae and many Cucujoidea, Tenebrionoidea, Chrysomeloidea, and Curculionoidea. The distribution of the spiracular closing apparatus in the Coleoptera has been of interest in phylogenetic studies; this structure is widespread throughout the order, but is absent in Dascillidae, Scarabaeidae (with the exception of Troginae and Glaphyrinae), Byrrhidae, Dryopoidea, Armatopidae, Elateridae, Cebriionidae, and Cantharoidea (except Brachypsectridae).

In some types of spiracles, there are one or more **accessory openings** (**accessory chambers**, **lateral air tubes**, **secondary chambers**) connected to the main opening (fig. 34.25). The terms **annular-uniform**, **annular-biforous** (also **bicameral**), and **annular-multiforous** are used for those with 1, 2, or more than 2 accessory openings (Crowson, 1981; Roberts, 1930; Steinke, 1919). Annular-uniform spiracles are known in only a few groups of Polyphaga, including some Bostrichidae and Anobiidae, Phalacridae (*Phalacrus*), a few Melandryidae, and Aglycyderidae. Annular-multiforous spiracles occur in Lymexylidae, a few Anobiidae, several groups of Tenebrionidae, *Calopus* (Oedemeridae), Mycteridae, and some Cerambycidae. The accessory openings are usually distributed around the peritreme, but in Mycteridae they are clustered at one end.

The annular-biforous spiracle may represent the ancestral condition in Polyphaga, since it occurs in a number of primitive groups, like Agyrtidae, Leioididae, Derodontidae, Nosodendridae, and Phloiophilidae, and is common and

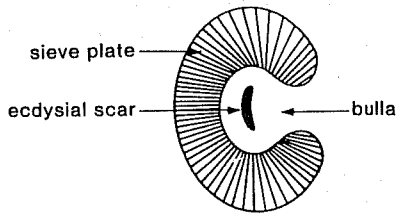


Figure 34.23

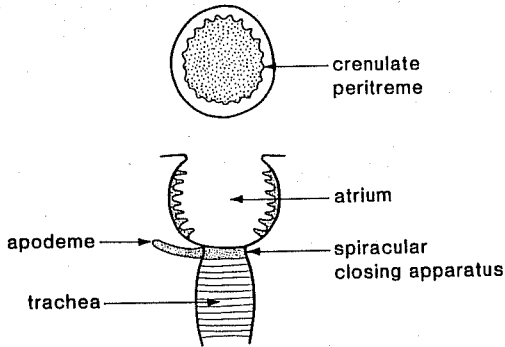


Figure 34.24

Figure 34.23. Cribriform spiracle (Scarabaeidae).

Figure 34.24. Annular spiracle (composite) and cross-section.

widespread in all cucujiform superfamilies. In some cases, the accessory openings are very small, so that the spiracle looks like the annular type, and in others the main opening is very small and the accessory openings long, so that it resembles the biforous type, but lacks an ecdysial scar (*see* below). In descriptions, these are usually called biforous. In Cerambycidae and Curculionidae, the early instars may have annular-biforous spiracles, while later instars have the annular or annular-multiforous type (Duffy, 1953; Gardner, 1925, 1927; Roberts, 1936).

The **biforous spiracle** has its opening blocked by a median septum, with a narrow, slit-like opening on either side of it (figs. 34.26, 34.50). These two openings are accompanied by an **ecdysial scar** (or **stigmatic scar**), which represents the opening through which the old spiracle is pulled during molting. This specialized type of molting has been called by Hinton (1947) the **elateroid ecdysial process** and is also associated with the cribriform spiracle. Biforous spiracles occur in Hydrophiloidea, late instar Rhipiceridae, *Trox* (Scarabaeidae: Troginae), *Eucanthus* (Scarabaeidae: Geotrupinae), Byrrhidae, *Schizopus* (Buprestidae), all Dryopoidea with functional spiracles, all Elateroidea, and Cantharoidea (except Brachypsectridae).

The **cribriform spiracle** (fig. 34.23) also has the main opening blocked, though not by a single division but by a **sieve plate** (respiratory plate, cribriform plate) bearing numerous

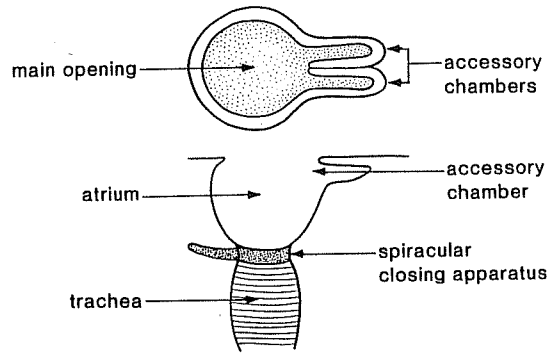


Figure 34.25

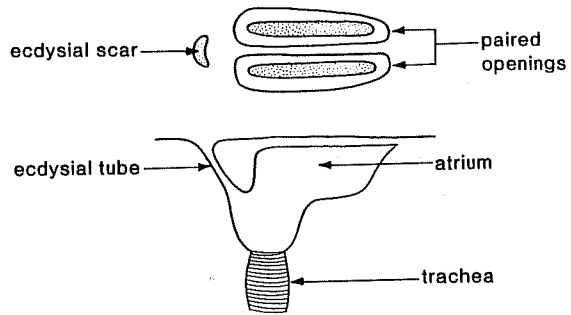


Figure 34.26

Figure 34.25. Annular-biforous spiracle (composite) and cross-section.

Figure 34.26. Biforous spiracle (composite) and cross-section.

perforations. The cuticular area immediately adjoining the sieve plate and usually partly or almost completely surrounded by it is called the **bulla**, and it is here that the **ecdysial scar** is located. Cribriform spiracles with a typical kidney-shaped or **reniform** sieve plate (Kfigs. 205–206, 208 p265) occur in Dascillidae and almost all Scarabaeoidea and Buprestidae, while Heteroceridae have a different type (Kfig. 207 p265). The **undulate spiracle** (Kfig. 209 p281) found in Chelonariidae is of a biforous type with undulated openings which may be partly blocked by cross pieces, forming a transition to the cribriform spiracle. A different sort of cribriform spiracle also occurs on the 8th segment in some eubrine Psephenidae (Hinton, 1955).

The normal location of the thoracic spiracle is on a mesosternal laterotergite that is wedged in between the protergum and mesotergum, but in some soft-bodied larvae (lyctine Bostrichidae, Ptinidae) it may be on the prothorax. The abdominal spiracles vary in size and position, and sometimes the first and last differ in position from those in between. The abdominal spiracles are usually situated on laterotergites or lateral extensions of a single tergal plate.

Many aquatic larvae, as well as those living in wet terrestrial environments subjected to flooding or in wet, sappy areas in wood or under bark, have mechanisms for allowing at least some spiracles access to free air. These include: 1) placement of some or all spiracles at the ends of *spiracular*

tubes (Kfig. 210 p281) so that they are raised above the surface of the integument; 2) dorsal placement of some spiracles (usually thoracic and 1st and 8th abdominal); 3) dorsal or posterior location of 8th spiracles; 4) placement of the 8th spiracles at the end of a posteriorly projecting, median process; and 5) formation of a terminal **respiratory chamber**. The thoracic spiracles are placed on tubes in some subcortical Tenebrionoidea, like Prostomidae and Inopeplidae, while abdominal spiracular tubes occur in many groups, including Hydraenidae (*Tympanogaster*), Chelonariidae, Derodontidae, Nosodendridae, various Cucujoidea, and some cassidine and hispine Chrysomelidae. In Hydrosaphidae, some Nitidulidae, and Biphyllidae, the 8th spiracles are each placed at the end of a tube which is located at the posterior end of the segment and faces posteriorly (Kfigs. 161 p261, 168 p255), while in *Donacia* (Chrysomelidae), the 8th spiracles are enclosed within spine-like structures (Kfig. 156 p231), which are used to puncture the stems of aquatic plants in order to tap the air supply. Dorsal placement of thoracic spiracles occurs in Hydrosaphidae, *Tympanogaster* (Hydraenidae), and some Nosodendridae; and in the first and last groups, the 1st abdominal spiracles may also be dorsally situated. The dorsal and posterior movement of the 8th spiracles, which may come to lie close to one another near the midline, is known in some Psephenidae, *Araeopidius* (Ptilodactylidae) (Kfig. 187 p238), some Chelonariidae, and Dryopidae, while their placement at the apex of a median process occurs in Dytiscidae (Kfig. 154 p213), Noteridae, Amphizoidae (Kfig. 153 p213), and Nosodendridae.

The **respiratory chamber** (also called **stigmatic atrium** or **breathing pocket**) of advanced Hydrophilidae is comprised of the 8th and 9th terga and encloses a large, posteriorly projecting pair of spiracles; this chamber may be complexly lobed, and its floor (9th tergum) may have as many as 3 pairs of urogomphus-like processes—the **mesocerci**, **paracerci**, and **acrocerci**. The mesocerci are usually the most prominent within the chamber, while the acrocerci lie at its posterior edge and are often visible when the chamber is closed. A pair of **procerci** may also be present at the lateral edges of the 8th tergum, above the spiracles. The 10th segment is ventrally oriented, and lies below the floor of the respiratory chamber. A terminal respiratory chamber also occurs in larvae of Helodidae, but it is simpler in structure and also encloses the anal region.

In aquatic, semi-aquatic, and riparian larvae there may be, in addition to or instead of spiracles, a variety of structures which allow oxygen to pass into the tracheal system or directly into the haemocoel when the cuticle is entirely submerged in water. The general term **gill** is used for these structures, and the term **plastron** refers to a specific situation in which a gas layer is held in position by hydrofuge structures which prevent the entry of water under pressure. Most gills are thin-walled processes which project from the venter, the lateral portions of thorax and abdomen, or the anal region.

Almost all gills in Coleoptera are **tracheal gills**, that is they contain **tracheae** or **tracheoles**, but at least in Hygrobiidae, the larval gill lacks tracheae and is called a **blood gill**. Gills associated with the spiracular openings are called **spiracular gills**. Thin-walled papillae in the anal region of some larvae have been called either **anal gills** or **anal papillae**, since it is thought that at least some have an osmoregulatory function. Typical gills, here referred to as **gill tufts**, consist of a number of fine branches radiating from a single stem.

Paired lateral or dorsolateral processes, which are usually thin-walled and unbranched (sometimes fringed with fine processes), occur on abdominal or sometimes thoracic and abdominal segments in some Dytiscidae (*Coptotomus*), some Haliplidae (*Peltodytes*), Gyridae (Kfig. 157 p213), Hydrophilidae (*Spercheus*, *Crenitis*, *Hydrophilus*, various Berosinae), and aquatic Lampyridae. Branched gill tufts (Kfig. 151 p231) occur ventrally on all thoracic segments and the first 3 abdominal segments in Hygrobiidae, and on A1–7 in Eulichadidae, A1–4 in Eubrianacinae (Psephenidae), and A2–6 in Psepheninae (Psephenidae). Three finely-branched **anal gills** occur in larvae of *Hyphalus* (Limnichidae), Lutrochidae, Elmidae (Kfig. 188 p223), and Eubriinae (Psephenidae), and in the last group they are accompanied by a pair of **anal papillae**. In Helodidae, there are 5 larger, unbranched anal gills. In many anchytarsine Ptilodactylidae, the anal region bears a single conical papilla above the anus and 2 smaller papillae associated with each pygopod, but in *Anchytarsus* (Kfig. 189 p229) there is, in addition, a cluster of 9 gills on each side of the anal region.

Spiracular gills are of 3 types: segmented, as in Torridincolidae (Kfig. 152 p257); vesicular, as in Microsporidae and most Hydrosaphidae (Kfig. 211 p208); and tufted, as described by Reichardt (1974) for the hydrosaphid genus *Scaphydra* (Kfig. 212 p208). The first type consists of a 2- or 3-segmented process, with the spiracular opening at the end of segment 1 or 2 and the apical portion of the gill covered with a plastron mesh. A **vesicular gill** consists of a thin-walled extension of the peritreme to form a balloon-like structure with the opening at the apex. The last type looks like a minute gill tuft extending from the peritreme.

The ptilodactylid *Araeopidius monachus* (LeConte) has a very peculiar type of respiratory structure. The thoracic spiracles and abdominal spiracles 1–7 are atrophied and each is partly surrounded by a plate-like structure (Kfig. 213 p251) that contains a fine mesh and whose surface is covered with minute pores (.05–.13 microns); this is called a **plastron plate** and apparently functions as a respiratory organ during periods of submergence in much the same way as the plastron of a housefly egg (Hinton, 1967b). Some aquatic larvae are probably capable of breathing directly through portions of the cuticle with tracheae near the surface. In some Haliplidae, tracheoles actually penetrate minute cuticular processes that have been called **microtracheal gills** (Seeger, 1971).

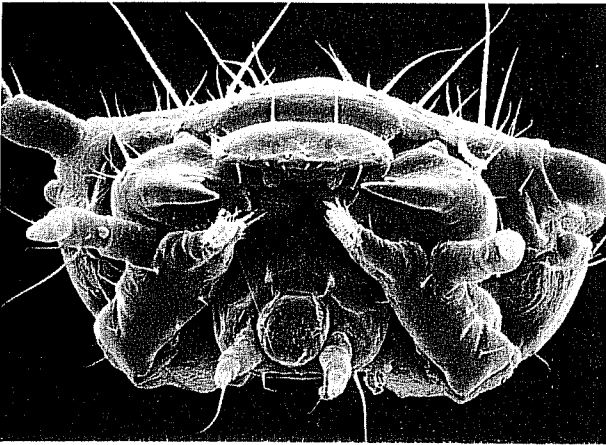


Figure 34.27. *Anisotoma blanchardi* Horn (Leiodidae). Passaconaway, New Hampshire. Head, anterior, showing symmetrical, asperate molae and highly flexible maxillae with fimbriate apices.

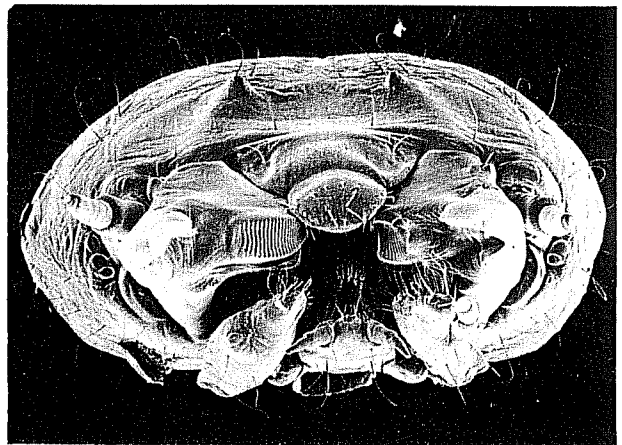


Figure 34.28. *Bolitotherus cornutus* (Panzer) (Tenebrionidae). Frederick, Maryland. Head, anterior, showing asymmetrical, transversely ridged molae.

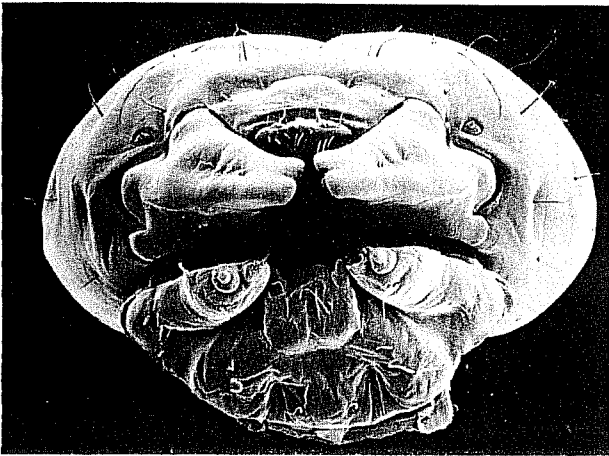


Figure 34.29. *Curculio* sp. (Curculionidae). Ontario. Head, anterior, showing heavy, broad-based, phytophagous mandibles without molae.

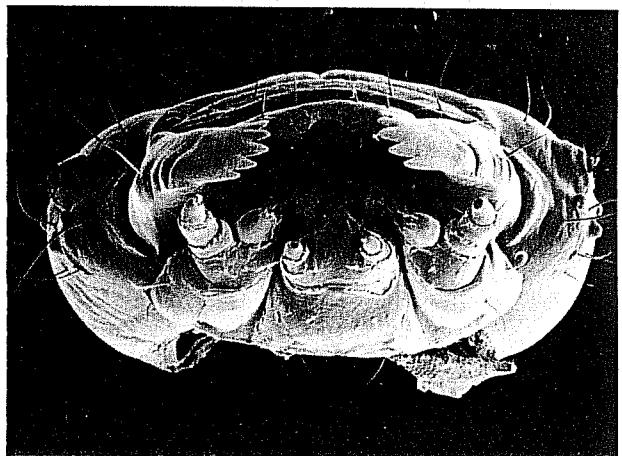


Figure 34.30. *Leptinotarsa lineolata* (Stål) (Chrysomelidae). Gardner Canyon, Arizona. Head, anterior, showing phytophagous mandibles with multidentate apices and no molae.

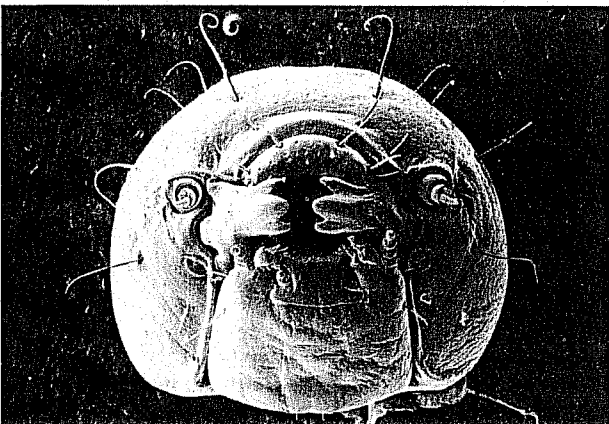


Figure 34.31. *Dryops* sp. (Dryopidae). Barro Colorado Island, Panama. Head, anterior, showing phytophagous type mandibles with tridentate, palmate apices and no molae, and maxillae fused to labium.

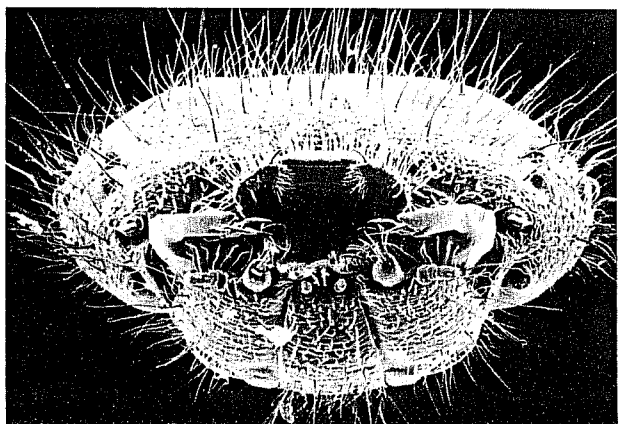


Figure 34.32. *Lanternarius gemmatus* (Horn) (Heteroceridae). Del Norte Co., California. Head, anterior, showing mandibles with concave pseudomolae and consolidated maxillolabial complex.

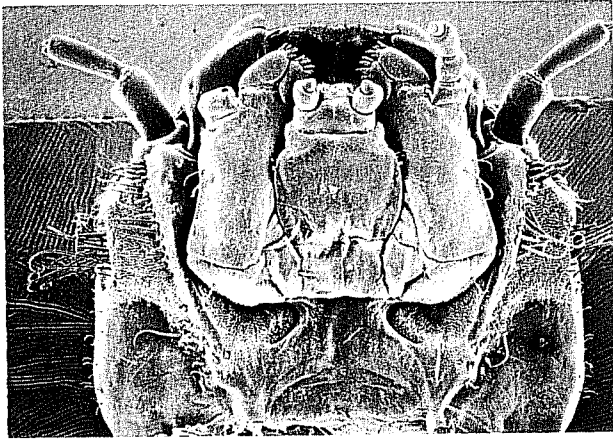


Figure 34.33. *Stenocolus scutellaris* LeConte (Eulichadidae). Richardson Springs, California. Head, ventral, showing ventral epicranial ridges, well-developed maxillary articulating area, and articulated, digitiform galea and lacinia.

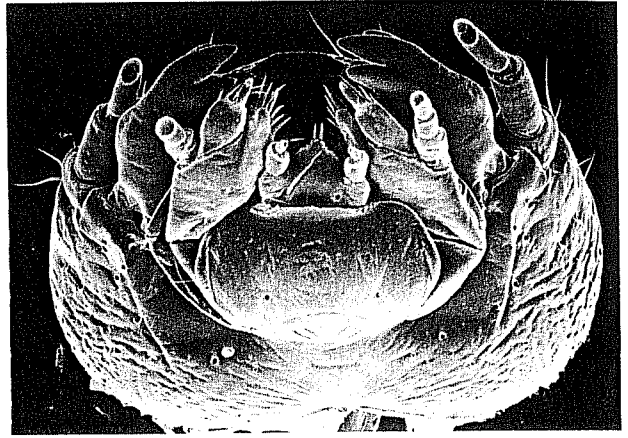


Figure 34.34. *Ptilodactyla* sp. (Ptilodactylidae). 8 mi. S Gatlinburg, Tennessee. Head, anteroventral, showing expanded mentum and concealed maxillary articulating area.

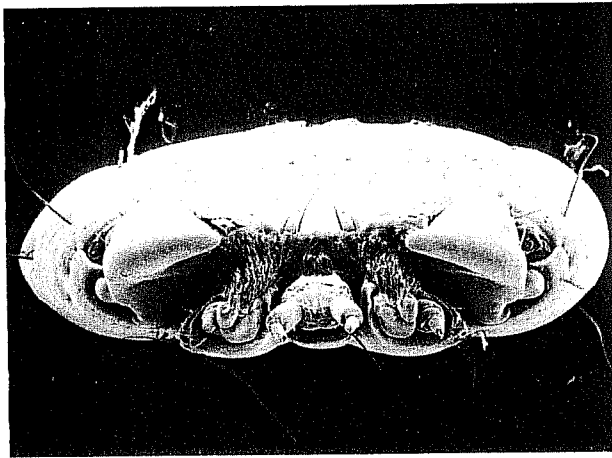


Figure 34.35. *Athous* sp. (Elateridae). Peddler Hill, California. Head, anterior, showing unidentate mandibles without molae and liquid-feeding mouthparts with oral filter blocking mouth cavity.

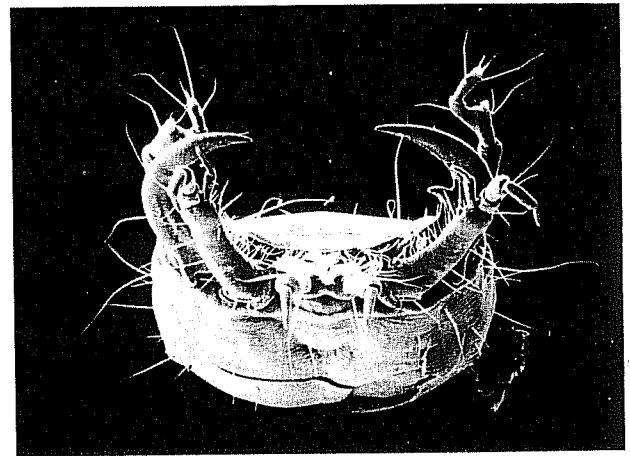


Figure 34.36. *Agonum* sp. (Carabidae). Concord, Massachusetts. Head, anterior, showing falcate mandibles with retinacula, strongly protracted ventral mouthparts, articulated, 2-segmented maxillary mala, and oral filter.

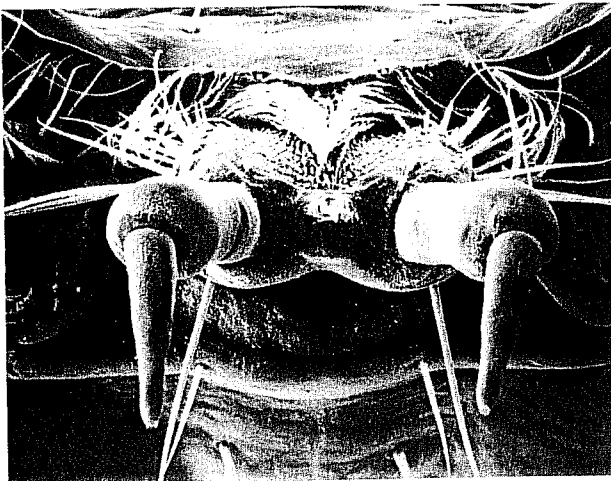


Figure 34.37. *Agonum* sp. Same data. Oral filter at higher magnification, showing barbed hairs.

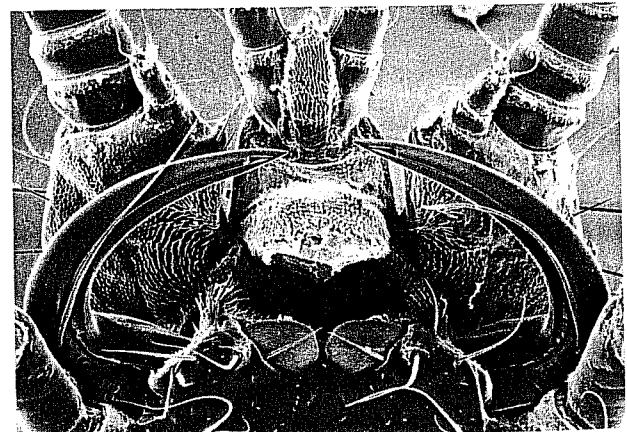


Figure 34.38. *Phengodes* sp. (Phengodidae). Rose Lake, Clinton Co., Michigan. Anterior part of head, anterodorsal view, showing nasale and falcate, perforate mandibles.



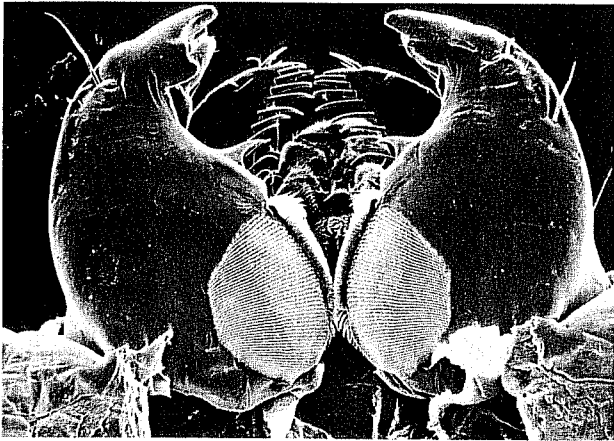


Figure 34.39. *Cucujus clavipes* Fabricius (Cucujidae). 6 mi. E Mineral, California. Anterior part of head, dorsal with frontoclypeal region and labrum-epipharynx removed, showing mandibles in closed position with molar asperities interdigitating, dorsal microtrichial patches, acute prostheca, and falcate, spinose maxillary malae.

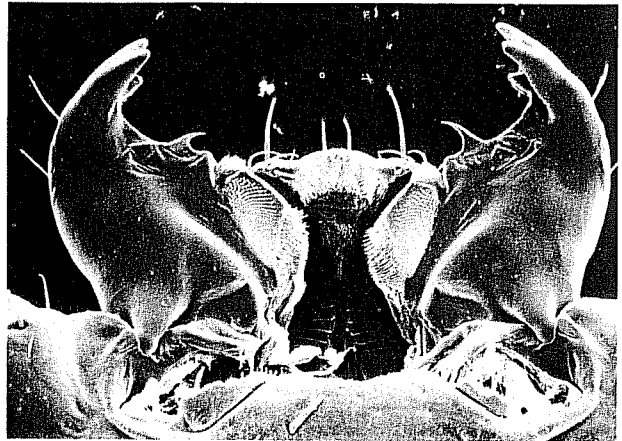


Figure 34.40. *Cucujus clavipes*. Same data. Anterior part of head, ventral with maxillae and labium removed, showing mandibles in open position, ventral condyle, accessory ventral process, asperities on ventral surface of mandibular base, epipharynx, and cibarial plates.

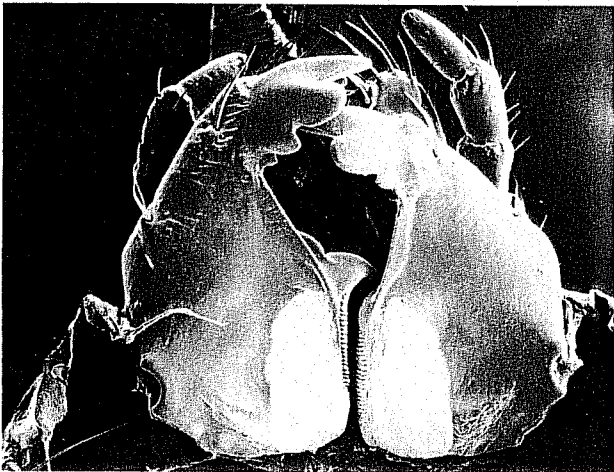


Figure 34.41. *Dendroides* sp. (Pyrochroidae). Phoenix Lake, Marin Co., California. Anterior part of head, dorsal, with frontoclypeal region and labrum-epipharynx removed, showing large, concave/convex, strongly asymmetrical, multiple-shearing molae, premolar tooth on left mola, and dorsal microtrichial patches.

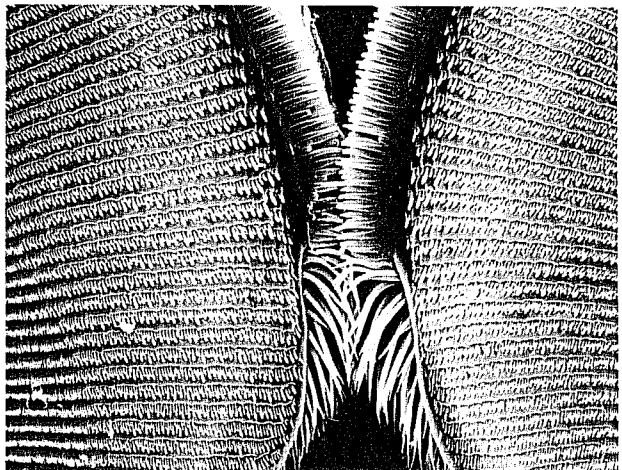


Figure 34.42. *Cucujus clavipes*. Same data as fig. 39. Mandibular bases, dorsal, at higher magnification, showing details of molar surfaces and dorsal rows of microtrichia.

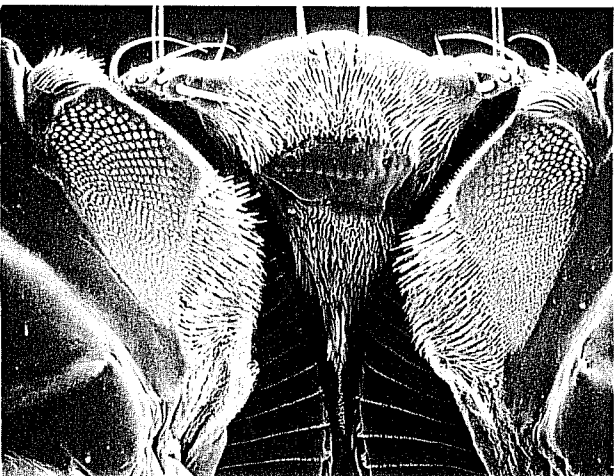


Figure 34.43. *Cucujus clavipes*. Same data as fig. 39. Mandibular bases, ventral, at higher magnification, showing details of ventral asperities, epipharynx, and cibarial plates.

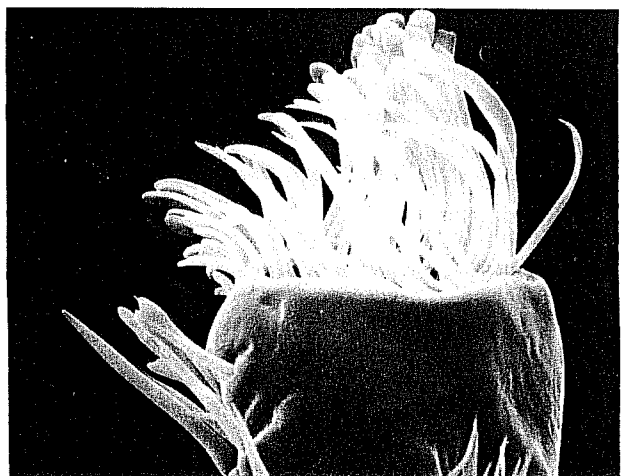


Figure 34.44. *Aphenolia monogama* (Crotch) (Nitidulidae). Wasco Co., Oregon. Apex of right mala, dorsal, showing spatulate setae.

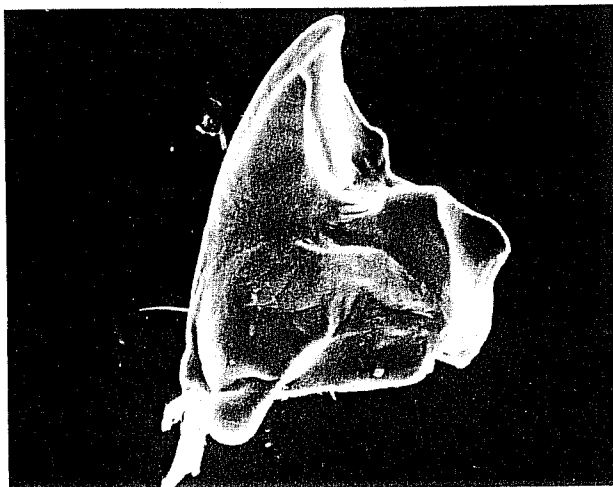


Figure 34.45. *Platydemus ellipticus* (Fabricius) (Tenebrionidae). Wakulla Springs, Florida. Right mandible, ventral, showing simple, concave mola, ventral condyle, and dorsal carina with single, weak tooth.

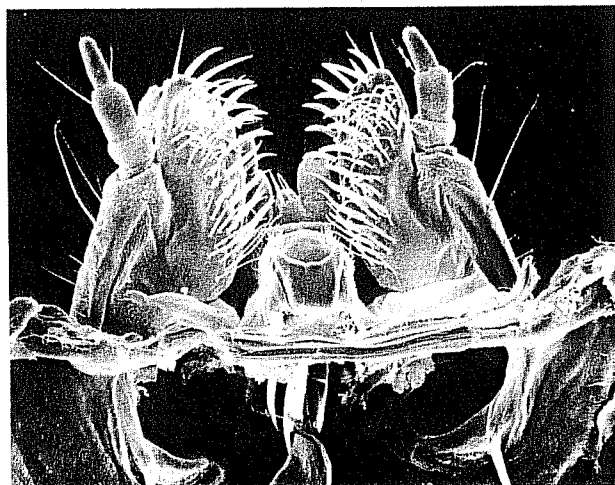


Figure 34.46. *Platydemus ellipticus*. Same data. Anterior part of head, dorsal, with frontoclypeal region, labrum-epipharynx, and mandibles removed, showing truncate maxillary mala with setose-spinose inner edge and dorsal surface, hypopharyngeal bracon, and hypopharyngeal sclerome.



Figure 34.47. *Anchorius lineatus* Casey (Biphylidae). 1 mi. NW Arivaca, Arizona. Mandibular prosthema, ventral, showing comb-hairs.

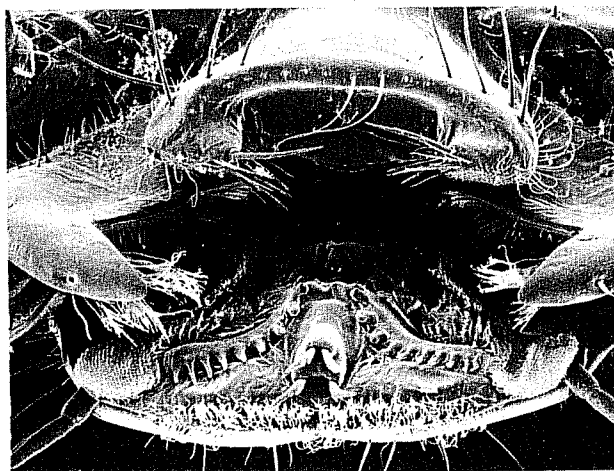


Figure 34.48. *Prionocyphon* sp. (Helodidae). Bedford, Massachusetts. Anterior part of head, with maxillae laterally displaced, showing labrum-epipharynx, mandibular apices, and hypopharynx with series of combs, spines, and setae.



Figure 34.49. *Prionocyphon* sp. Same data. Apex of maxilla, showing comb-hairs.



Figure 34.50. *Dryops* sp. (Dryopidae). Barro Colorado Island, Panama. Biforous spiracle on abdominal segment 8, showing 2 openings and ecdysial scar.





Figure 34.51

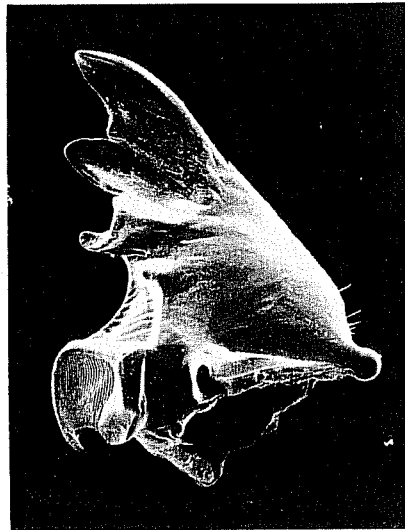


Figure 34.52

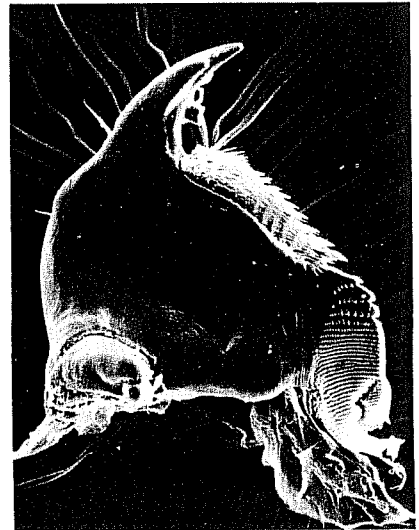


Figure 34.53

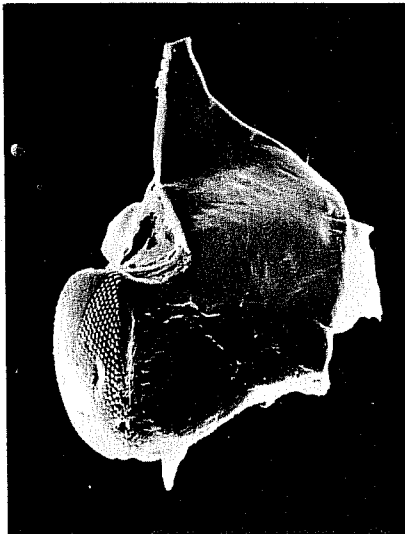


Figure 34.54

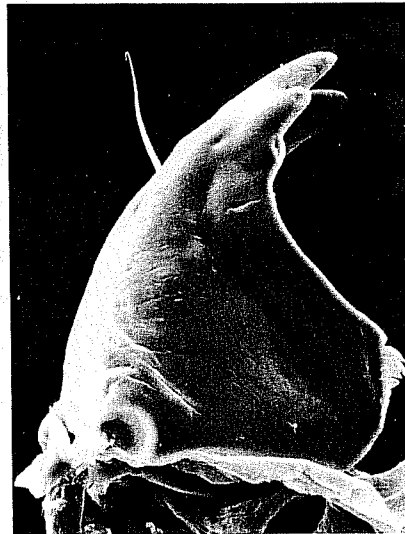


Figure 34.55

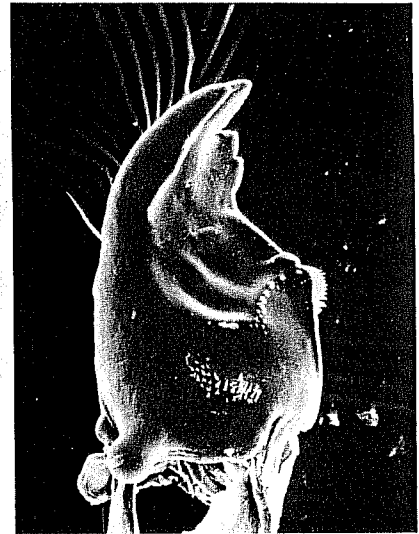


Figure 34.56

**Figure 34.51.** *Prionocyphon* sp. Same data as fig. 48. Right mandible, ventral, showing transversely ridged mola, comb-like prostheca, small ventral condyle, and accessory ventral process.

**Figure 34.52.** *Dascillus davidsoni* LeConte (Dascillidae). Novato, California. Left mandible, ventral, showing longitudinally ridged mola, large accessory ventral process, small, articulated prostheca, hyaline area (appearing wrinkled), and large scissorial teeth.

**Figure 34.53.** *Glischrochilus* sp. (Nitidulidae). Great Smoky Mts. Nat. Park, Tennessee. Right mandible, ventral, showing enlarged ventral condyle, ventral asperities, and prostheca consisting of fringed membranes.

**Figure 34.54.** *Lycoperdina ferruginea* LeConte (Endomychidae). Great Smoky Mts. Nat. Park, Tennessee. Right mandible, meso-dorsal view, showing reduced apex and large, finely tuberculate mola (worn in middle) (prostheca has been damaged).

**Figure 34.55.** *Rhinosimus* sp. (Salpingidae). Great Smoky Mts. Nat. Park, Tennessee. Left mandible, dorsal, showing dorsal acetabulum and group of hyaline processes at mandibular base.

**Figure 34.56.** *Hyporhagus gilensis* Horn (Monommidae). Vail, Arizona. Right mandible, ventral, showing dorsal carina with 2 weak teeth and ring of asperities representing reduced mola.

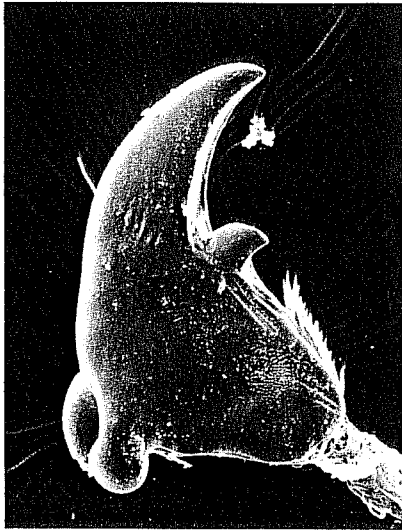


Figure 34.57

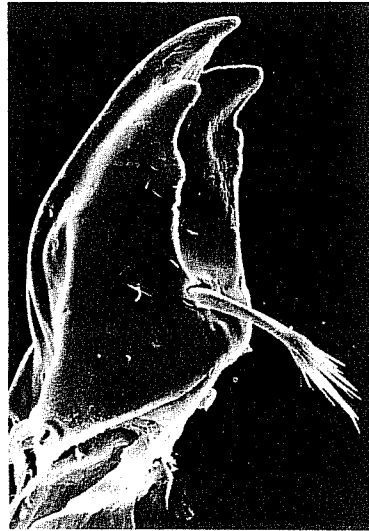


Figure 34.58



Figure 34.59

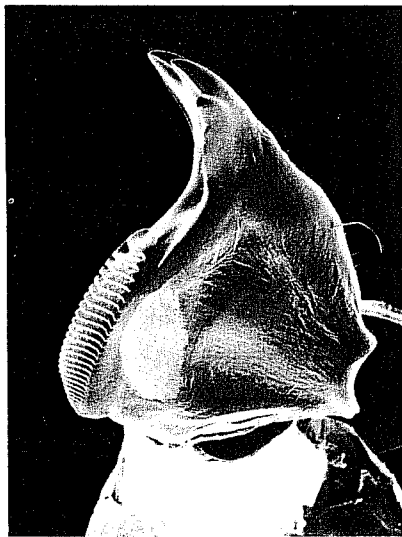


Figure 34.60

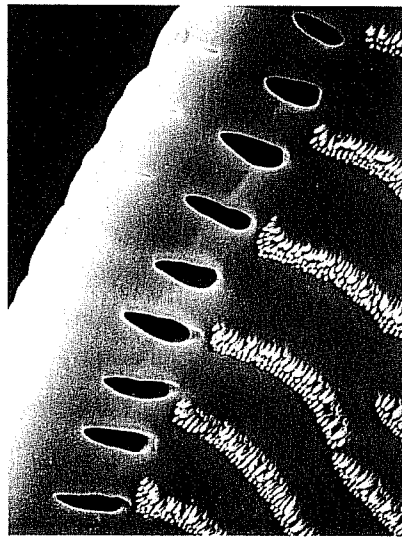


Figure 34.61



Figure 34.62

**Figure 34.57.** *Athous* sp. (Elateridae). Peddler Hill, California. Right mandible, ventral, showing fairly broad base with penicillus, retinaculum, and unidentate apex.

**Figure 34.58.** *Ptilodactyla* sp. 8 mi. S Gatlinburg, Tennessee. Right mandible, ventral, showing tridentate apex, concave incisor area, and articulated process with setose apex at mandibular base.

**Figure 34.59.** *Agonum* sp. (Carabidae). Concord, Massachusetts. Right mandible, ventral, showing narrow base, fine penicillus, retinaculum, unidentate apex, and serrate incisor edge.

**Figure 34.60.** *Ditylus* sp. (Oedemeridae). Vernon, British Columbia. Right mandible, dorsal, showing dorsal acetabulum (in profile), dorsal microtrichial patch, and mola consisting of simple, transverse ridges.

**Figure 34.61.** *Pterogenius nietneri* Candeze (Pterogeniidae). Haggala, Sri Lanka. Part of mesal edge of mandible, dorsal, showing reinforced mola, openings to channels beneath mola, and rows of microtrichia.

**Figure 34.62.** *Pterogenius nietneri* Candeze. Same data. Surface of mandibular mola, showing ridges and pores.

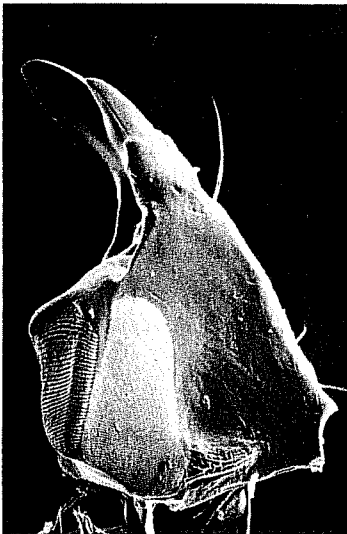


Figure 34.63

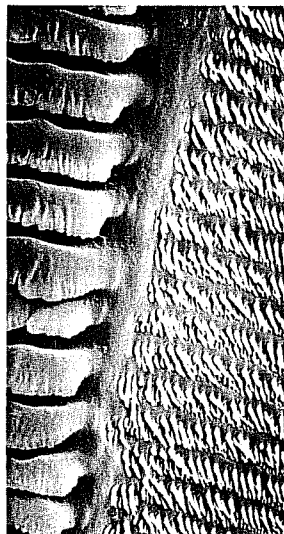


Figure 34.64

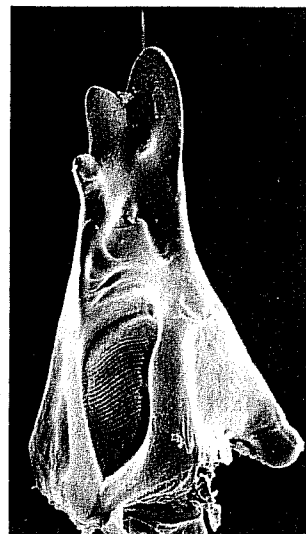


Figure 34.65

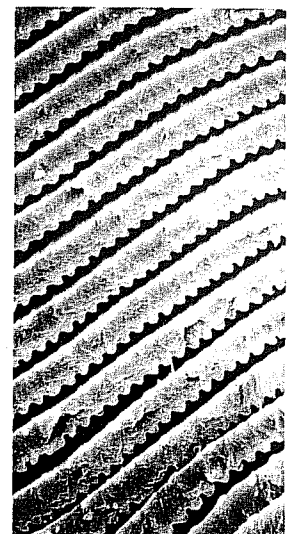


Figure 34.66

**Figure 34.63.** *Synchroa punctata* Newman (Synchroidae). Bear Mountain, New York. Right mandible, dorsal, showing dorsal microtrichial patch and concave mola with complex, transverse ridges separated by deep grooves.

**Figure 34.64.** *Synchroa punctata*. Same data. Part of mandibular base, dorsal, showing molar ridges and dorsal microtrichia.

**Figure 34.65.** *Synchroa punctata*. Same data. Left mandible, mesal view, showing complex mola and transverse ridges.

**Figure 34.66.** *Synchroa punctata*. Same data. Part of molar surface, showing complex ridges and deep grooves.

## BIOLOGY AND ECOLOGY

Beetles are holometabolous insects, with a life cycle consisting basically of an egg, larva, pupa, and adult or imago; there are some cases, however, where the egg or pupal stage has been eliminated (*see below*). Truly **viviparous** species, which have eliminated the egg stage, are rare among the Coleoptera, examples occurring in the archostematan genus *Micromalthus* and the termitophilous *Corotoca* (Staphylinidae: Aleocharinae). **Ovoviviparous** forms, in which eggs hatch immediately before or during deposition, are known in some aleocharine Staphylinidae and chrysomeline Chrysomelidae. In some cave-dwelling Leiodidae, such as *Leptodirus*, the eggs are very large and the larva upon hatching is almost fully developed. The size of beetle eggs and the number of eggs produced by a single female vary considerably (*see Table 2* in Hinton, 1981). Very small beetles, such as Myxophaga, Ptiliidae or Clambidae, produce only 1 or 2 eggs at a time, while very large numbers of small eggs may be found in some Meloidae and Lymexylidae. The morphology of beetle eggs has been covered in detail by Hinton (1981); those with a hard, sculptured **chorion** are rare in the group, but they have been reported in Cupedidae (*Cupes*, *Priacma*). Eggs are usually deposited singly, but in several groups, such as Coccinellidae and Chrysomelidae, they form characteristic clusters. **Oöthecae** or egg cases occur in several families. Members of the Hydrophilidae and some Hydraenidae enclose their eggs, singly or in batches, within silken cocoons produced by the **colleterial glands**. A number of Chrysomelidae produce oöthecae which may be composed of faeces (**scatoshells**), colleterial gland secretions, or both; these have been reported in

Cassidinae and in the so-called Camptosomata (Clytrinae, Cryptocephalinae, Chlamisinae, and Lamprosomatinae), but they also occur in some Australian Sagrinae and Eumolpinae. In the Clytrinae and related groups, the larval and pupal stages are also spent within a faecal case. Parental care, which includes mass provisioning and the guarding of eggs and sometimes larvae, has been reported in a number of beetles, including some Carabidae (*Abax*, *Molon*, *Mormolyce*), Silphidae, Staphylinidae (*Platystethus*, *Bledius*), Scarabaeidae (Geotrupinae, Scarabaeinae), Heteroceridae, Chrysomelidae (Cassidinae), Platypodidae and Scolytidae.

A common feature of newly hatched larvae is the presence of **egg bursters** (also known as **hatching spines**), which are small teeth or spines used to break the chorion upon hatching. Egg bursters appear to be absent in Archostemata and Myxophaga, while those in Adepaga occur on the frontal region. Frontal egg bursters are also known in the polyphagan families Hydraenidae, Hydrophilidae, and Derodontidae (*Laricobius*). More common among Polyphaga are thoraco-abdominal egg bursters, which occur in pairs on some thoracic and abdominal terga; these are known in Staphylinidae, Histeridae, Lucanidae, Passalidae, Scarabaeidae, Rhipiceridae, Byrrhidae, Bostrichidae, Ptinidae, Nitidulidae, Coccinellidae, Tenebrionidae, Pyrochroidae, Melandryidae, Cerambycidae, Chrysomelidae, and Curculionidae, and will probably be discovered in other families as well.

The number of larval instars in Coleoptera varies from 1 to almost 30, but is normally 3 to 5. In Adepaga, Staphylinoidae, and Scarabaeoidea, the number is usually 3, while in Dermestidae it is usually 6 or 7 but may be much higher.

Beetles with only 2 larval instars are relatively rare, occurring in Histeridae and some Leiodidae, and a single instar is known only in some highly evolved cave forms (Leiodidae: Bathysciinae).

First instars differ from later instars in many groups, and sometimes these differences are striking. Differences between first and later instars may be in general form, tergal pigmentation and armature (Sphaerosomatidae, teredine Bothrideridae), form of the 9th tergum (Lymexylidae, Tenebrionidae), or number of antennal segments (Cupedidae, Dytiscidae, Helodidae). Differences may also occur among later instars, especially that immediately preceding the pupal stage, which is often called the **prepupa**. Extreme differences among larval instars, often connected with differences in habits, is called **hypermetamorphosis**. A common type of hypermetamorphosis involves a campodeiform type of first instar, which is involved in active or passive dispersal; this type of larva is usually called a **triungulin** (based on the apparently 3-clawed first instars of some Meloidae). These active larval types are usually found in beetles which are parasitic, and they may seek out the host themselves (Carabidae, Staphylinidae, Rhipiceridae, Drilidae, Cucujidae, Bothrideridae) or attach themselves to flying adults, in order to be passively transported to the host larvae (Meloidae, Rhipiphoridae). Among non-parasitic groups, active first instars may be found in some groups where eggs are laid on or near the surface of the soil and larvae must seek out subsurface food sources, like roots (schizopodine Buprestidae, vesperine Cerambycidae); but in *Micromalthus*, the triungulin, known as a **caraboid larva**, apparently seeks out wood in the proper state of decay. A unique situation occurs in some Cantharidae, where the first instar is an inactive form called a **prolarva**; this has been termed **foetometamorphosis**. Another type of hypermetamorphosis involves only the last instar or prepupa. In some Eucnemidae, for instance, the prepupa is buprestid-like, with an enlarged prothorax, while earlier instars are elongate and flattened. The most complex types of hypermetamorphosis may involve more than two larval types; these occur in Micromalthidae, Rhipiphoridae, and Meloidae, and are discussed in the sections dealing with those families.

Beetle pupae (figs. 34.7-8) are always **adecticous** (without functional mandibles) and almost always **exarate** (with free appendages). **Obtect** pupae, which are usually more heavily sclerotized, with the appendages more or less fixed to the body, have evolved 5 or more times in the Coleoptera, occurring in Ptiliidae, staphylinine Staphylinidae, Clambidae, Coccinellidae, and Chrysomelidae (especially Hispinae and Cassidinae). Many pupae develop within substrates or in pupal cells of various kinds, but others occur on surfaces, partly enclosed within the last larval exuviae, which may be armed with modified setae, spines, or glandular reservoirs. There is considerable variation in the number of functional pupal spiracles; there are usually 6 in Adephaga, 8 in Cantharoidea and some Elateroidea, 7 in numerous groups, and fewer in some specialized forms. Pupal spiracles have a closing apparatus, even when one is lacking in the larva. Modifications of the pupal prothorax are usually precursors

of the same structures of the adult (horns in male scarabaeoids and tenebrionids), but in Pterogeniidae (Lawrence, 1977c), the pupal pronotum bears a spiny, club-like anterior process not found in the adult. Defensive structures on the pupa include long setae or spines, glands (Cantharidae), and pinching devices known as **gin traps** (Hinton, 1946a). Gin traps are formed by sclerotized and often armed portions of two adjacent sclerites, and may involve 2 to 7 abdominal segments. Median, unpaired gin traps are known in Dryopidae, Ptilodactylidae, and Dermestidae; paramedian, paired ones occur in Scarabaeidae (Dynastinae and some Rutelinae), Psephenidae (some Eubriinae), Cucujidae (Passandrinae), and Cerambycidae (some Prioninae); and lateral gin traps are found in a number of Tenebrionidae and a few lamiine Cerambycidae. Most aquatic beetles have terrestrial pupae, but aquatic pupae with plastron-bearing gills are known in Torridincolidae and Psephenidae (Psephenoidinae). Loss of the pupal stage occurs in those beetles which have completely larviform females (Phengodidae and a few Lycidae).

### Habitats

Although beetle larvae may be found in almost any type of situation, there are some habitats, like leaf litter, rotten wood, bracket fungi, and the rotten cambial layer beneath the bark of logs or standing dead trees, which are particularly fruitful for collecting. In the following sections, lists are given of the families likely to be found in some major habitat types. Some of these families are not commonly collected and may be dependent upon particular conditions of the microhabitat. Some litter inhabitants, like Ptilodactylidae or Dryopidae, for instance, are restricted to wetter, riparian conditions, while others (Dermestidae, Melyridae) turn up more often in dry litter samples. A subcortical region undergoing bacterial or yeast fermentation will harbor a different fauna than one which has been excavated by bark beetles or one which is relatively dry or covered with a bloom of fungal conidia. The litter and soil habitats are combined, since they grade into one another, and the subcortical habitat is treated together with dead wood for the same reason. Notes have been added on those forms which are more or less restricted to one or another. It is also possible to find inhabitants of bark and wood turning up in "leaf litter" samples, especially when the latter includes sticks and debris under logs, as in most forest areas. Some families, of course, are geographically restricted, and the family composition of samples from the southeastern United States may differ somewhat from that of samples collected in boreal forests. Exotic groups have been marked with an asterisk.

**Marine Riparian. Beaches, Mudflats, Intertidal Rocks:** Carabidae, Staphylinidae, Limnichidae (Hyphalinae,\* Cephalobryrrhinae, Thaumastodinae\*), Phycosecidae,\* Melyridae, Tenebrionidae (Coniointini, Phaleriini, Opatrini), Salpingidae (Aegialitinae).

**Freshwater Riparian:** Cyathoceridae,\* Microsporidae, Carabidae, Hydraenidae, Staphylinidae (*Bledius*, etc.), Georyssidae, Hydrophilidae, Helodidae, Ptilodactylidae, Chelonariidae, Heteroceridae, Limnichidae, Dryopidae, Curculionidae.

**Freshwater Lotic:** Amphizoidae, Hydraenidae, Eulichadidae, Ptilodactylidae, Lutrochidae, Elmidae, Psephenidae.

**Freshwater Hydropetric:** Torridincolidae,\* Hydrosca-phidae, Hydraenidae (some\*), Psephenidae.

**Freshwater Lentic:** Haliplidae, Hygrobiidae,\* Noter-idae, Dytiscidae, Gyrinidae, Hydrophilidae, Helodidae, Chrysomelidae (Donaciinae), Curculionidae.

**Leaf Litter and Soil:** Carabidae, Ptiliidae, Leiodidae, Scydmaenidae, Scaphidiidae, Staphylinidae, Pselaphidae, Hydrophilidae (Sphaeridiinae), Histeridae, Eucinetidae, Clambidae, Dascillidae, Rhipiceridae, Scarabaeidae, Byrrhidae, Buprestidae, Ptilodactylidae, Chelonariidae, Dry-opidae, Limnichidae, Elateridae, Cebrionidae, Throscidae, Eucnemidae (*Phyllocerus*),\* Lycidae, Phengodidae, Lam-pyridae, Cantharidae, Dermestidae, Cleridae, Melyridae, Nitidulidae (*Eपुरaea*, *Haptoncus*, *Stelidota*, *Lasiodactylus*, etc.), Rhizophagidae, Phloeostichidae (Priasilphinae),\* Phalacridae, Cucujidae (Silvaninae), Cryptophagidae, Languriidae (Cryptophilinae, Toraminae), Cerylonidae, Dis-colomidae,\* Endomychidae, Corylophidae, Lathridiidae, Archeocrypticidae, Colydiidae, Tenebrionidae, Meloidae, Anthicidae, Euglenidae, Scaptiidae, Cerambycidae, Chry-somelidae (Clytrinae, Cryptocephalinae, Eumolpinae, Gal-erucinae, Alticinae), Ithyceridae, Curculionidae.

Most of the groups mentioned above live in leaf litter or in the upper layers of the soil, and some represent groups living elsewhere as larvae and dropping into the litter and soil for pupation. Specialized soil-dwelling larvae, grubs and wire-worms of various kinds which feed on humus, plant roots, or other soil inhabitants, occur in the families Dascillidae, Rhip-iceridae, Scarabaeidae, Buprestidae (Schizopodinae, Julodinae, Stigmoderini), Elateridae, Cebrionidae, Throscidae, Eucnemidae (*Phyllocerus*), Tenebrionidae (Tentyriinae, Phaleriini, Helaeini, Blaptini, Eleodini, Opatrini, Alleculini), Cerambycidae (Vesperinae, Anoploderminae, Lepturinae, etc.), Chrysomelidae (Eumolpinae, Galerucinae, Alticinae), Ithyceridae, Curculionidae (many). Some leiodids and niti-dulids are found in the vicinity of subterranean fungi.

**Under Bark and in Dead Wood:** Cupedidae, Micromal-thidae, Rhysodidae, Carabidae, Ptiliidae, Leiodidae, Scyd-maenidae, Scaphidiidae, Staphylinidae, Pselaphidae, Hydrophilidae (Sphaeridiinae), Sphaeritidae, Synteliidae, Histeridae, Eucinetidae, Clambidae, Lucanidae, Passalidae, Scarabaeidae (Ceratocanthinae, Aphodiinae, Rutelinae, Dynastinae, Cetoniinae), Buprestidae, Callirhipidae, Ptilodac-tylidae, Cerophytidae, Throscidae, Eucnemidae, Elateridae, Brachypsectridae, Lycidae, Derodontidae, Nosodendridae, Dermestidae, Bostrichidae, Anobiidae, Lymexylidae, Tro-gossitidae, Chaetosomatidae,\* Cleridae, Melyridae, Sphin-didae, Nitidulidae, Rhizophagidae, Phloeostichidae (Hymaeinae),\* Cucujidae, Phalacridae, Helotidae,\* Cryp-tophagidae, Languriidae (some Xenoscelinae), Erotylidae, Biphylidae, Bothrideridae, Cerylonidae, Discolomidae,\* En-domychidae, Coccinellidae, Corylophidae, Lathridiidae, My-cetophagidae, Ciidae, Tetratomidae, Melandryidae, Mordellidae, Rhipiphoridae, Colydiidae, Monommidae,

Prostomidae, Synchronidae, Zopheridae, Tenebrionidae, Ce-phaloidae, Oedemeridae, Mycteridae, Boridae, Tricentotom-idae,\* Pythidae, Pyrochroidae, Pedilidae, Othniidae, Salpingidae, Inopeplidae, Anthicidae, Euglenidae, Scapti-idae, Cerambycidae, Anthribidae, Belidae,\* Aglycyder-idae,\* Brentidae, Curculionidae, Scolytidae, Platypodidae.

Most of the above groups are collected under the bark of rotten logs and stumps or in rotten wood which is fairly damp and soft; others are found in the vicinity of fungus fruiting bodies on which they feed. Those families with flat-tened larvae specialized for living in subcortical spaces in-clude Staphylinidae (Piestinae, Osoriinae, Oxytelinae), Buprestidae, Nitidulidae (some), Phloeostichidae (Hym-aeinae), Cucujidae (Cucujinae, Laemophloeinae), Phala-cridae (some), Tenebrionidae (few), Mycteridae, Boridae, Pythidae (most), Pyrochroidae, Pedilidae (some), Othniidae, Salpingidae, Inopeplidae and Cerambycidae. Larvae of Hy-drophilidae (Sphaeridiinae), Sphaeritidae, Synteliidae, Histeridae, Nosodendridae, Nitidulidae (many Carpophilinae and Cryptarchinae, some Nitidulinae) Rhizophagidae (Rhizo-phaginae), Helotidae, and Biphylidae, are usually associated with sap flows, slime fluxes, or fermenting areas under bark (some as predators of fly larvae). Others, like Brachypsec-tridae and some Coccinellidae, represent predators which may occur under loose bark. The flattened larvae of Prostomidae live in pockets of red rotten wood, where they feed in between wood layers, while flattened eucnemid larvae may move be-tween fibers of wood which may be rotten to fairly solid. Those more cylindrical or grub-like larvae which bore through rotten wood are included in the families Cupedidae, Micromal-thidae, Rhysodidae, Staphylinidae (Osoriinae), Lucanidae, Passalidae, Scarabaeidae, Callirhipidae, Cerophytidae, Throscidae, Elateridae, Lymexylidae, Melandryidae, Mor-dellidae, Zopheridae, Tenebrionidae (Phrenapatini, Tene-brionini, Amarygmini, Ulomini, Coelometopini, Cnodalonini, Strongyliini, Alleculini, Helopini, etc.), Cephaloidae, Oede-meridae, Tricentotomidae, Pythidae (*Priognathus*), Ceram-bycidae and Curculionoidea. Some groups are restricted to relatively sound wood or that which is undergoing dry rot; they often occur in branches and small twigs. These include Buprestidae, Eucnemidae, Dermestidae (Orphilinae), Bos-trichidae, Anobiidae, Ciidae, Melandryidae, Mordellidae, Colydiidae, Salpingidae, Cerambycidae, and many Curcu-lionoidea.

**Dung:** Ptiliidae, Leiodidae, Staphylinidae, Hydrophil-idae (Sphaeridiinae), Histeridae, Scarabaeidae (few Geotru-pinae, Hybosorinae, Scarabaeinae, Aphodiinae), Ptinidae.

**Carriion:** Leiodidae, Silphidae, Staphylinidae, Hister-idae, Scarabaeidae (Troginae, few Scarabaeinae), Dermest-idae (*Dermestes*), Cleridae (some Corynetinae), Phyco-secidae,\* Melyridae, Nitidulidae (*Omosita*, *Nitidula*).

**Fruiting Bodies of Slime Molds (Myxomycetes):** Leiod-idae (many Anisotomini), Scaphidiidae (*Baeocera*), Staphy-linidae, Eucinetidae, Clambidae, Sphindidae, Lathridiidae (most *Enicmus*).

**Fruiting Bodies of Pyrenomycetes (Xylariales, etc.):** Rhizophagidae (Monotominae), Cucujidae (Laemophloeinae), Phalacridae (*Litochropus*, *Acylomus*), Cryptophagidae (some *Cryptophagus*), Biphyllidae, Lathridiidae (some *Enicmus*), Colydiidae (*Bitoma*, *Cicones*, etc), Mycetophagidae (*Litargus*), Anthribidae.

**Fruiting Bodies of Macrofungi (especially Polyporales):** Carabidae (especially Lebiini), Ptiliidae (especially Nanosellini), Leioididae, Eucinetidae, Derodontidae (*Derodontus*), Dermestidae (*Orphilus*), Bostrichidae (*Endecatomus*), Anobiidae (Dorcatominae), Trogossitidae, Cleridae (Thaneroclerinae), Nitidulidae, Hobartiidae,\* Cryptophagidae, Lamingtoniidae,\* Languriidae (*Cryptophilus*), Erotylidae, Sphaerosomatidae,\* Discolomidae,\* Endomychidae, Corylophidae, Lathridiidae, Mycetophagidae, Pterogeniidae,\* Archeocrypticidae, Ciidae, Tetratomidae, Melandryidae (Hallomeninae, Eustrophinae, Orchesiini), Mordellidae (*Mordella*), Colydiidae, Zopheridae, Tenebrionidae (Bolitophagini, Toxicini, Diaperini), Anthribidae (*Euparius*).

**Epigeal Gasteromycetes (Puffballs etc.):** Leioididae (*Creagrophorus*, *Nargomorphus*), Nitidulidae (*Pocadius*), Cryptophagidae (some *Cryptophagus*), Endomychidae (*Lycoperdina*).

**Hypogean Fungi (Hemenogastrales, Tuberales, etc.):** Leioididae (Hydnobiini, Leiodini, Catopocerinae, Coloninae), Scarabaeidae (some Geotrupinae), Nitidulidae (*Thalycra*).

**Mosses and Liverworts:** Pselaphidae, Byrrhidae, Artematopidae (Macropogoninae), Elateridae, Cantharidae, Tenebrionidae (Leiochrini\*).

**Surfaces of Leaves:** Phalacridae (*Acylomus*, *Stilbus*), Coccinellidae, Corylophidae (*Corylophodes*), Lathridiidae (Corticariinae), Chrysomelidae (Criocerinae, Chrysomelinae, Cassidinae, Chlamisinae), Curculionidae (Attelabinae, Gonipterinae, etc.).

**Mining in Leaves:** Buprestidae (Trachyinae), Nitidulidae (*Xenostrogylus*,\* *Anister*\*), Chrysomelidae (Zeugophorinae, some Hispinae and Alticinae), Curculionidae (*Orchestes*, *Prionomerus*,\* *Rhamphus*,\* *Cionus*,\* etc).

**Flowers, Flower Heads, Male Cones:** Nitidulidae (Carteretinae, Meligethinae, some Nitidulinae), Phalacridae (*Olibrus*), Languriidae (some Xenoscelinae on cycads), Byturidae, Meloidae (triungulins), Rhipiphoridae (triungulins), Nemonychidae (on gymnosperms), Oxycorynidae (Hydnoraceae),\* Curculionidae (Allocoryninae and Antliarhininae on cycads, many groups on angiosperms).

**Seeds, Seed Pods:** Nitidulidae, Bruchidae, Urodontidae, Anthribidae, Curculionidae.

## TECHNIQUES

Techniques for collecting and preserving larval Coleoptera and preparing them for study are covered in Volume 1 and in a number of general texts or manuals, such as Borror, DeLong and Triplehorn (1981), Cogan and Smith (1974), Emden (1942a), Martin (1977), Oldroyd (1958), Peterson (1951, 1959), Upton and Norris (1980) and Walsh and Dibb (1975), and will not be treated in detail here. Although many larvae are easily collected by hand or with an aspirator, mass

collecting techniques are very useful in obtaining specimens which are very small or which live in habitats where they are difficult to observe. When specimens are widely scattered among leaf litter and other debris, it is necessary to first concentrate them and then remove them from the concentrate into preservative or rearing containers. Concentration is accomplished by a **sifter (concentrator or extraction sieve)**. This consists of a long cloth cylinder, narrowed at one end, where it is tied off, and with a metal hoop (with a handle) holding the other end open; a second metal hoop (also with a handle) to which an 8 or 10 mm metal sieve is soldered, is sewn into the cloth at some distance from the open hoop. When leaf litter, humus, sticks, bits of wood and bark, etc. are placed between the open hoop and the sieve and vigorously shaken, fine debris passing through the sieve accumulates at the narrow, tied end, and is eventually poured into cloth bags for further processing.

Extraction devices using heat to drive living organisms out of the sample and into preserving fluid are usually called **Berlese funnels** or **Tulgren funnels**, depending upon construction details and heat source; the most common type uses electric light bulbs for a heat source and alcohol as a preserving fluid. Noxious chemicals may be used instead of heat, and alcohol may be replaced by wet towels if living samples are desired. A **Winkler apparatus** is based on the same principle but the concentrate is kept in small, gauze bags, which are allowed to dry over a funnel.

Another collecting device is the **pitfall trap**, which consists of an open container set into the ground, usually covered with a rain roof and filled with a non-volatile liquid, which kills the insects and retards fungal and bacterial decay until the sample can be placed in a more permanent preservative. A mixture of propylene glycol and propylene phenoxetol has a useful combination of fungicidal, bactericidal, humectant, and narcotic properties.

The **elutriator** is a useful device for mass collecting aquatic, littoral or interstitial organisms from sand, gravel, or bottom debris. It consists of a cylindrical container open at one end, with several small openings near the other end, through which air and water are pumped; when the substrate is placed in the container, light organic matter and living organisms float to the top and spill over the edge of the container to be caught in a fine mesh screen (Kingsbury and Beveridge, 1977). Many other special collecting techniques exist for aquatic insects, and these are discussed in some detail in Merritt and Cummins (1984).

Although the above methods will result in large collections of larval Coleoptera, many of which can be identified by comparison with previously determined specimens, it is essential to associate as many larvae as possible with adults to insure correct identifications at the species level. This may be accomplished by 1) collecting larvae alive and attempting to rear them through to the adult stage in the laboratory, 2) collecting pupae associated with larval exuviae, and allowing the pupae to eclose in the laboratory, or 3) collecting living adults and allowing them to produce eggs and larvae in the laboratory. Techniques involved in rearing larvae are numerous, and some are covered in Peterson (1959), or in other chapters of this book.

**Errors in counting palp segments** almost always arise from confusion between the basal palp segment and the palpifer or palpiger from which it arises. In the key and in subsequent family coverage, a palpifer (or maxillary palpiger) or palpiger (labial palpiger) is a shelf-like extension of the apicolateral portion of the stipes or prementum, respectively, which is not separated by a distinct line of demarcation and does not have a distinct inner edge. There are some instances where an intermediate condition exists, and these usually have been coded for both character states. **Difficulties in counting leg segments** cannot be avoided in groups with reduced legs, like Cerambycidae or Mordellidae, and these larvae are usually coded for several states. In some larvae, the coxa is not clearly separated from the pleural region, while in others the tarsungulus may appear to be divided. As mentioned above, the pretarsus is considered to be a separate segment consisting of either paired claws or a single claw; thus most Archostemata and Adepaga have 6 leg segments. The polyphagan leg may be 5-segmented or less, and the last segment or tarsungulus may or may not be claw-like. This terminology conflicts with that used by Peterson (1951) where the terminal claws are not counted as leg segments.

**Mandibular characters** are extremely useful and cannot be avoided in a family key, but they do **require the removal of one or both mandibles**; sometimes it is possible to examine the mandibles in place in well-cleared specimens, but the superimposition of the maxillae may create artifacts. Mandibular characters are discussed in detail in the morphology section above, and only a few comments are needed here. A mandibular **mola** is an enlargement and modification of the

mandibular base which meets a similar structure on the opposing mandible for the purpose of ingesting, compacting, or breaking down food material; it is often asperate, tuberculate, or ridged. In some larvae (various Carabidae, Histeridae or Hydrophilidae), the mandibles are slightly enlarged at the base but have no structure which can be called a mola. A **prostheca** is any structure just distad of the mola that is not a sclerotized tooth attached to the mola (premolar lobe), and it may be membranous, hyaline, or partly sclerotized, or may consist of a group of hyaline processes or a brush of hairs. A mandible without a mola cannot have a prostheca, as defined here, and similar structures at the mandibular base are called processes, lobes, or brushes, or are sometimes referred to collectively as a lacinia mobilis in the key or family diagnoses. The term **pseudomola** has been used for a food processing area of the mandible which may be, but is usually not, basal, and which is thought to have evolved secondarily in a mandible type which has lost the true basal mola. Needless to say, this term has little practical value in a key, but it has been used for some subapical, mola-like structures which cannot be confused with a basal mola. A **retinaculum** is a heavily sclerotized tooth on the incisor edge of a mandible lacking a mola. Heavy incisor lobes or teeth in mola-bearing mandibles of dascillids and scarabaeoids are called scissorial teeth.

**Urogomphi** are paired processes on the 9th tergum; there is usually a single or dominant pair. They are not regarded as homologous structures but as numerous parallel developments, and they vary considerably throughout the order, being simple or complex, fixed or articulated, and of various shapes and orientations. When a second, smaller pair of processes occurs in front of the urogomphi, they are called **pregomphi**.

## KEY

### —IMPORTANT

- A. For ease of use: Read the introduction to this key (p. 184).
  - B. If the head is partially embedded in the thorax, it *must* be dissected so the rear of the head, cranial sutures and related structures are clearly visible.
  - C. The presence or absence of a mola can usually be determined without removing the mandibles by cutting on both sides of the head between the mandible and maxilla so the maxillo-labial complex can be pried downward, revealing the inner bases of the mandibles.
  - D. Key Figures: Some figures are duplicated many places in the key. They are usually placed in numerical sequence (e.g. 8, 23, 96, 150, etc.) on the page or facing page where they are used. If the figure is not present, it will be on the previous (←) or following (→) two pages. Check the bottom corners for its location.
- 
1. Thoracic legs absent or represented by non-articulated and non-segmented protuberances (pedal lobes), which are broader than long. All forms lightly sclerotized, except some Eucnemidae, which have the head modified forming a wedge-like plate. Mandibular mola usually absent ..... 4
  - 1'. Thoracic legs present and articulated at base (or if basal articulation not well defined, then legs segmented or narrow and longer than wide) ..... 2



- 196(195). Apex of mala or galea rounded or truncate (figs. 88, 109, 110) ..... 197
- 196'. Apex of mala or galea falciform (figs. 89, 105, 111) or stylet-like (fig. 104);  
urogomphi usually articulated at base (figs. 162, 163) (see 3rd choice) ..... 205
- 196<sup>2</sup>. Apex of mala trilobed (fig. 107); urogomphi articulated at base (fig. 162);  
labrum more or less fused to clypeus, but with vague indication of  
clypeolabral suture (fig. 14). In rotten mushrooms ..... (*Oxyporus*) (*Oxyporinae*) *Staphylinidae* p. 341
- 197(196). Antennal segments 1 or 2; body elongate and subcylindrical, lightly sclerotized;  
head moderately to strongly declined (hypognathous) (fig. 10) ..... 198
- 197'. Antennal segments 3 (see 3rd choice) ..... 199
- 197<sup>2</sup>. Antennal segments 4; urogomphi articulated at base (fig. 162). In leaf litter,  
rotten wood, carrion, dung, under bark ..... (part) *Staphylinidae* p. 341
- 198(197). Segments in T2 leg 3 or 4, the segments indistinctly separated (fig. 128);  
ventral epicranial ridges absent; antennal sensorium not or only slightly  
longer than terminal antennal segment. In rotten wood, stems, fungus  
fruiting bodies ..... (part) *Mordellidae* p. 508

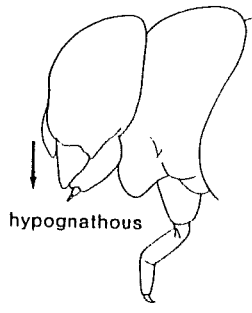


Figure 10

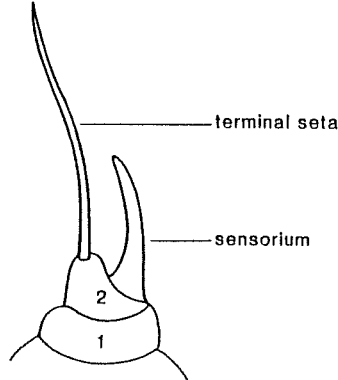


Figure 32

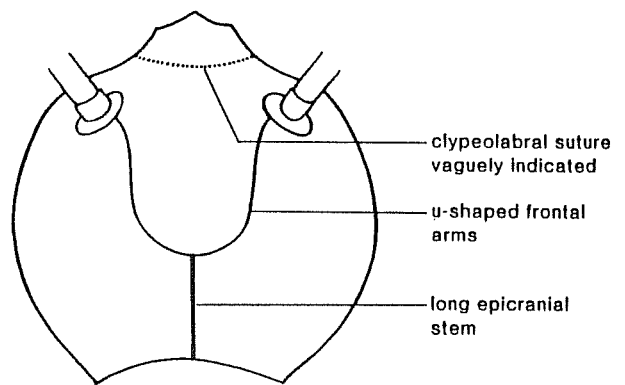


Figure 14

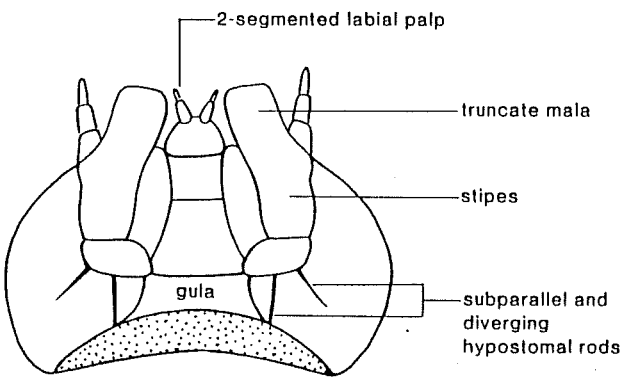
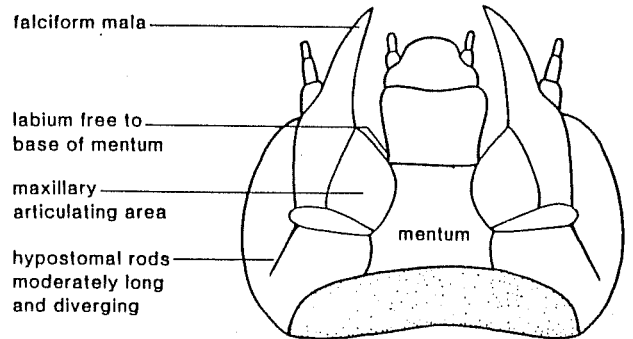
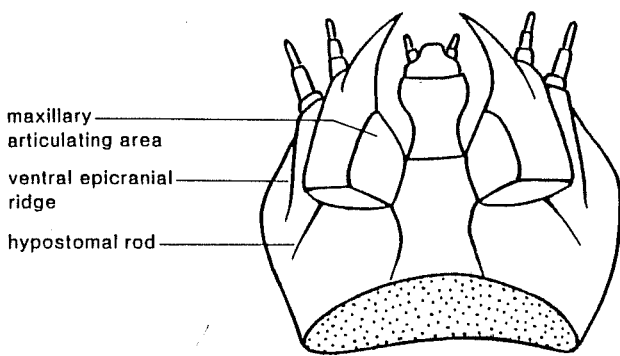


Figure 88



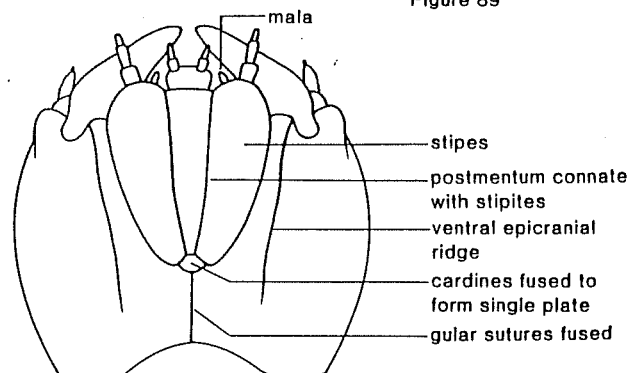
Mouthparts Retracted

Figure 89



Mouthparts Retracted

Figure 90



Mouthparts Retracted

Figure 93



- 198'. Segments in T2 leg 5 including tarsungulus (fig. 126); ventral epicranial ridges present (figs. 90, 93); antennal sensorium much longer than terminal (2nd) antennal segment (fig. 32). In fungus fruiting bodies ..... (Ciinae part) *Ciidae* p. 502
- 199(197'). Maxilla with single mala (figs. 88, 89) ..... 200
- 199'. Maxilla with separate galea and lacinia (figs. 109, 111) ..... 204
- 200(199). Apex of mandible truncate and lined with rows of spines (fig. 55); body somewhat flattened and lightly sclerotized; urogomphi fixed at base. On fungus covered logs ..... *Dasyceridae* p. 335
- 200'. Apex of mandible not truncate or lined with rows of spines ..... 201

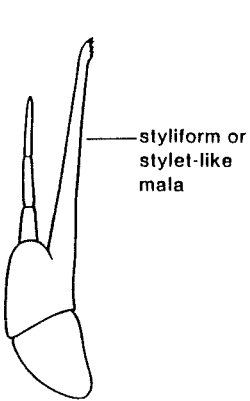


Figure 104

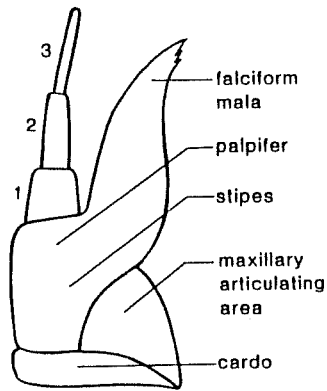


Figure 105

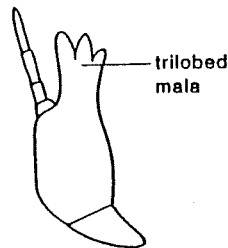


Figure 107

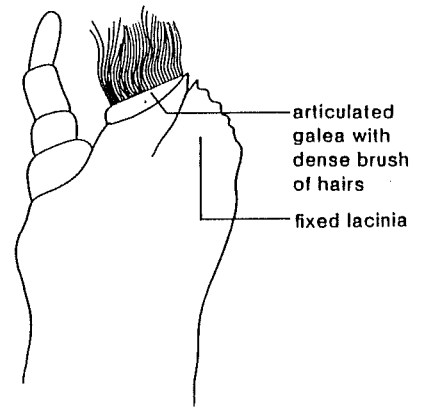


Figure 109

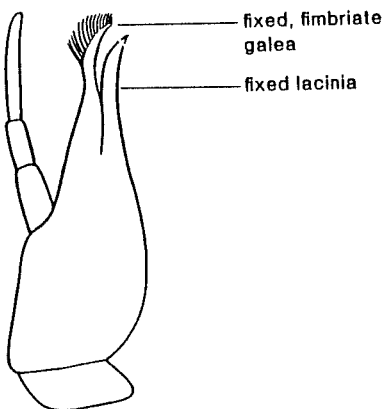


Figure 111

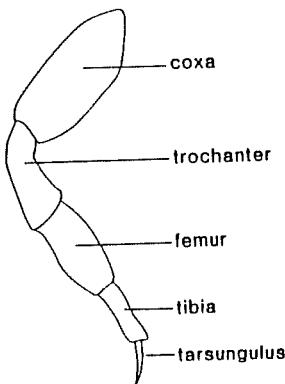


Figure 126

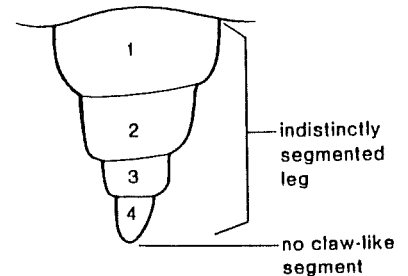


Figure 128

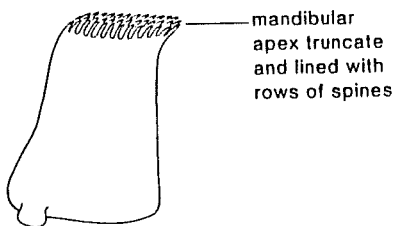


Figure 55

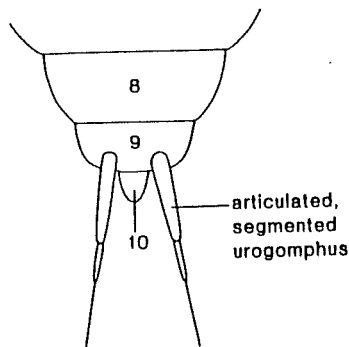


Figure 162

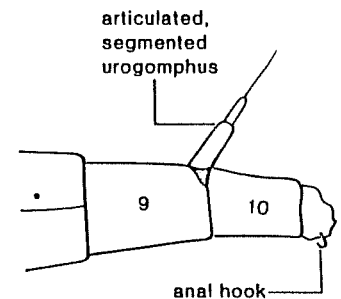


Figure 163

- 201(200'). Apex of antennal segment 2 oblique, so that sensorium arises proximad of segment 3 (fig. 30); frontoclypeal suture absent; hypostomal rods absent; segment A10 distinct and usually visible from above (fig. 162); urogomphi often articulated at base (fig. 162); abdominal terga usually bearing distinct plates, which are set off from those on sterna and are never asperate. In leaf litter, rotten wood, carrion, dung, under bark ..... (part) *Staphylinidae* p. 341
- 201'. Apex of antennal segment 2 truncate, so that sensorium and segment 3 arise together (fig. 29); frontoclypeal suture (figs. 13, 19) and hypostomal rods (fig. 89) present, OR abdominal terga with patches or rows of asperities; segment A10 reduced, not visible from above; urogomphi fixed at base; abdominal terga and sterna not forming distinct plates ..... 202.
- 202(201'). Head moderately to strongly declined (hypognathous) (fig. 10); gular region absent (labium contiguous with thoracic membrane) (fig. 96); segments in T2 leg 3 or 4, the segments indistinctly separated (fig. 128); body elongate and cylindrical, lightly sclerotized. In rotten wood, stems, fungus fruiting bodies ..... (part) *Mordellidae* p. 508

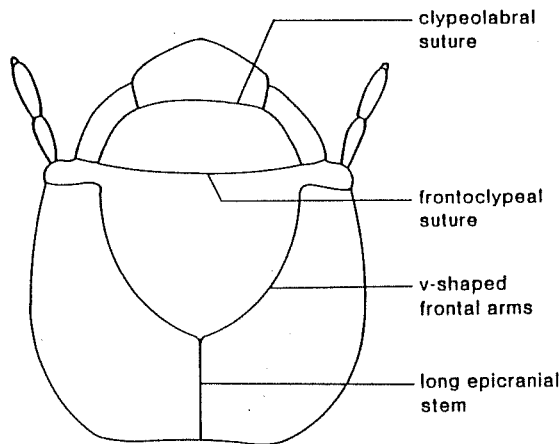


Figure 13

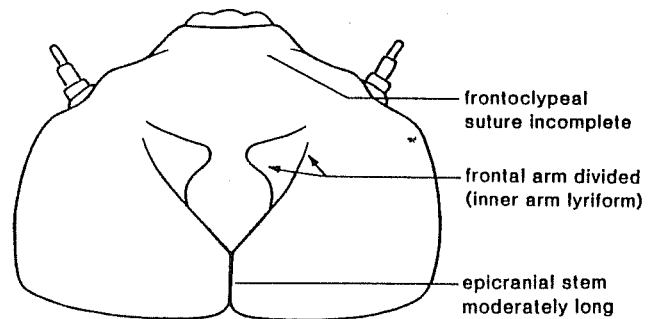


Figure 18

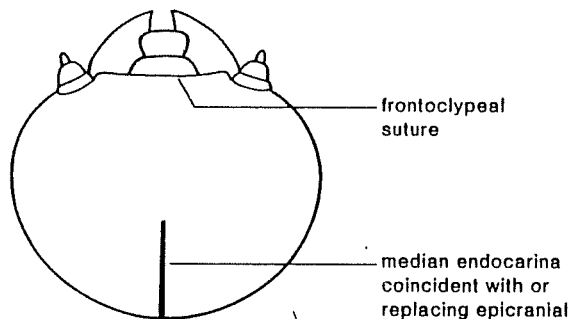


Figure 19

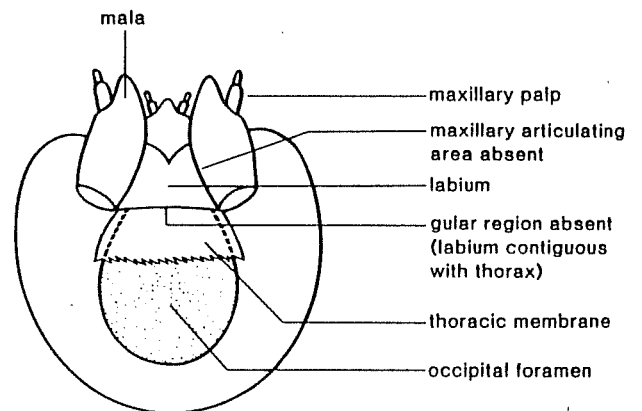


Figure 96

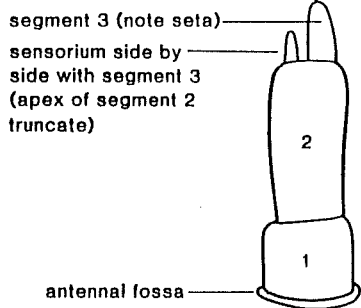


Figure 29

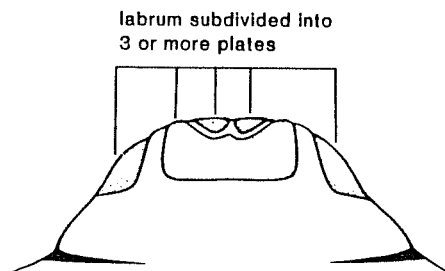


Figure 39

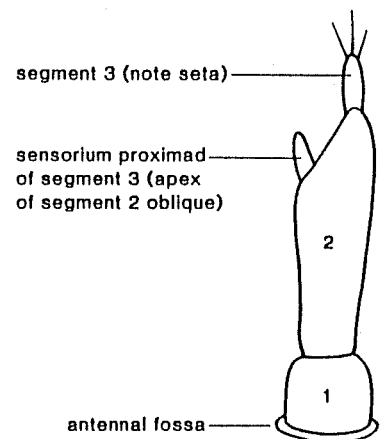


Figure 30

- 202'. Head prognathous or slightly declined; gular region present (separating labium from thorax) (fig. 85); segments in T2 leg 5, including tarsungulus (fig. 126) ..... 203
- 203(202'). Frontoclypeal suture present (figs. 13, 19); hypostomal rods almost always present (fig. 89); mesocoxae almost always separated by more than 2 coxal diameters; dorsal surfaces very lightly pigmented and without asperities. In rotten wood, fungus fruiting bodies ..... (Melandryinae part) *Melandryidae* p. 505
- 203'. Frontoclypeal suture absent (fig. 18); hypostomal rods absent; mesocoxae separated by 1 to 2 coxal diameters; dorsal surfaces with pigmented maculae and rows or patches of asperities. Under bark, in soft fungi ..... (Penthe part) (Penthinae) *Tetratomidae* p. 504
- 204(199'). Epicranial stem absent or very short; mandibles broad at base, not falcate; labrum not subdivided; abdominal segments without lateral plates or spine-like processes; galea without large, dense brush of hairs, but often fimbriate (with fringe of setae) (fig. 111). In leaf litter, carrion, fungi ..... (part) *Leiodidae* p. 327
- 204'. Epicranial stem moderately long (fig. 14); mandibles narrow and falcate (fig. 44); labrum subdivided into 3 or more sclerites (fig. 39); abdominal segments produced laterally forming tergal plates or spine-like processes; galea with large, dense brush of hairs (fig. 109). In carrion, decaying vegetation ..... *Silphidae* p. 339
- 205(196'). Epicranial stem absent or very short; maxilla with separate galea and lacinia (fig. 111) ..... 206
- 205'. Epicranial stem moderately long (fig. 14); maxilla with single mala (fig. 105) ..... 207
- 206(205). Head prognathous or slightly declined; segments in T2 leg 5 including tarsungulus (fig. 126); urogomphi articulated at base (fig. 162); dorsal surfaces generally smooth; thoracic and abdominal segments without lateral tergal processes; mandible without subapical pseudomola. In leaf litter, carrion, fungi ..... (part) *Leiodidae* p. 327
- 206'. Head moderately to strongly declined (hypognathous) (fig. 10); segments in T2 leg 3 or 4; urogomphi fixed at base; dorsal surfaces generally spinose or complexly sculptured; thoracic and abdominal segments each with 1 or 2 pairs of lateral tergal processes; mandible with subapical pseudomola consisting of several spines or teeth (fig. 54). In decaying vegetation ..... *Micropeplidae* p. 334

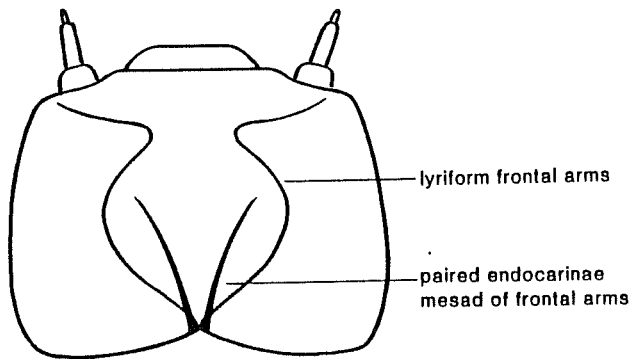


Figure 25

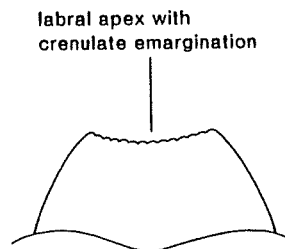


Figure 37

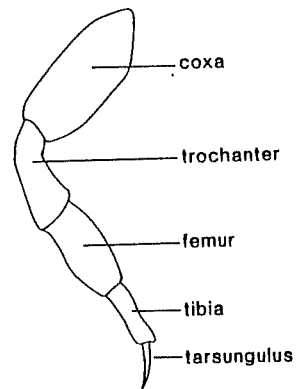


Figure 126

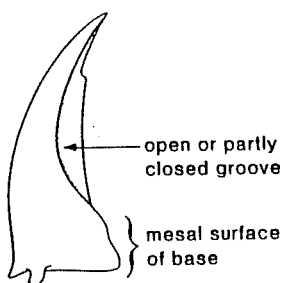


Figure 44

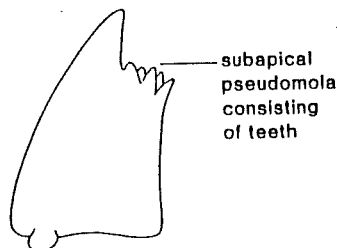


Figure 54

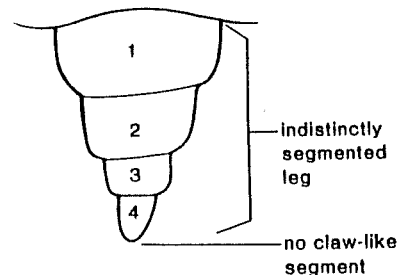


Figure 128

- 207(205'). Labrum with crenulate emargination (fig. 37). On surfaces of fungi and bark, in leaf litter ..... *Scaphidiidae* p. 337
- 207'. Labrum without crenulate emargination. In leaf litter, rotten wood, carrion, dung, under bark ..... (part) *Staphylinidae* p. 341
- 208(195'). Mentum or postmentum not divided longitudinally; paired endocarinae located mesad of frontal arms (fig. 25); maxilla with single mala (fig. 88); segments in maxillary palp 3; ventral epicranial ridges absent; maxillary articulating area exposed (fig. 85); anal region without hooks or papillae. Under bark, in rotting stems ..... (part) *Monommiidae* p. 514
- 208'. Mentum or postmentum divided longitudinally into 3 parts (fig. 98); paired endocarinae absent; maxilla with separate galea and lacinia (fig. 98); segments in maxillary palp 4; ventral epicranial ridges present (fig. 93); maxillary articulating area concealed behind expanded mentum (fig. 98); anal region with several pairs of hooks and 1 or more papillae (fig. 189). In plant debris in or near streams ..... (*Anchytarsinae* part) *Ptilodactylidae* p. 391

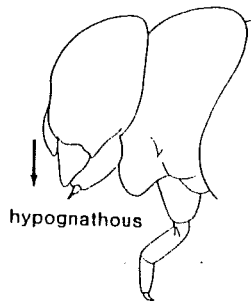


Figure 10



Figure 4

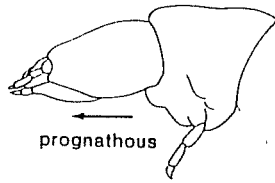


Figure 8

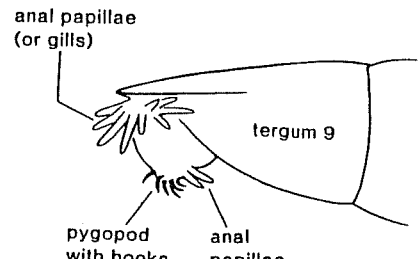


Figure 189

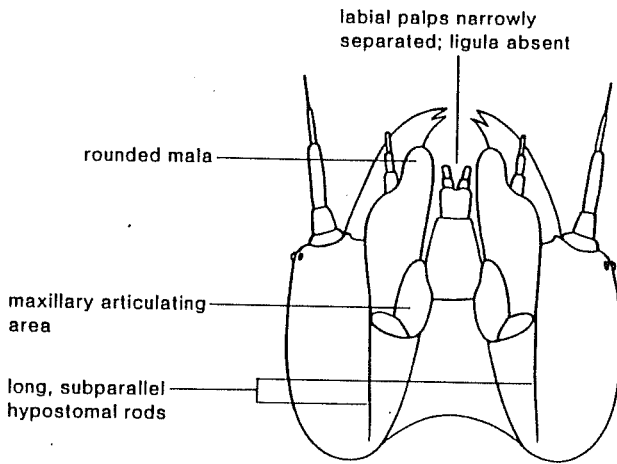
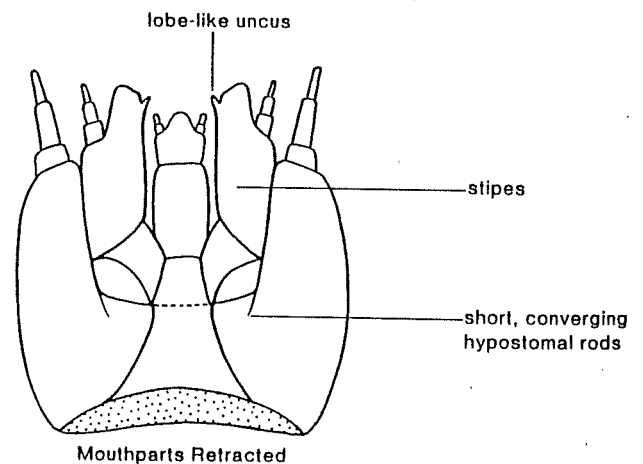


Figure 86



Mouthparts Retracted

Figure 87

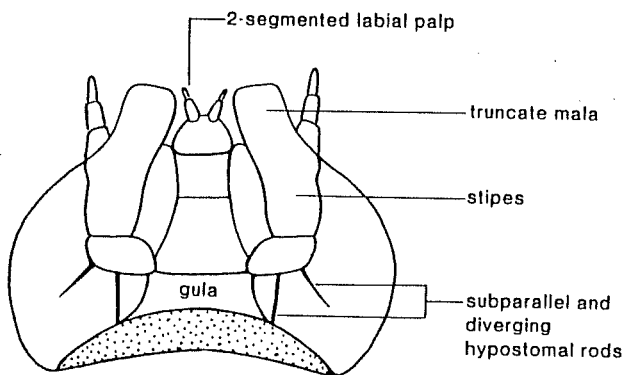
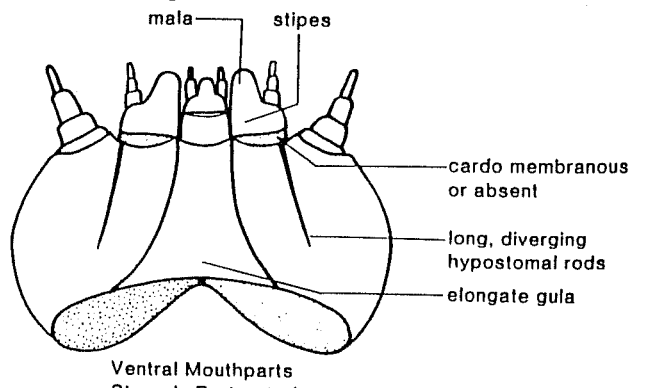


Figure 88



Ventral Mouthparts Strongly Protracted

Figure 92