The Insects
Structure and Function

4th edition

R. F. Chapman

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1 Head

Insects and other arthropods are built up on a segmental plan and their characteristic feature is a hard, jointed exoskeleton. The cuticle, which forms the exoskeleton, is continuous over the whole of the outside of the body and consists of a series of hard plates, the sclerites, joined to each other by flexible membranes, which are also cuticular. Sometimes the sclerites are articulated together so as to give precise movement of one on the next. Each segment of the body primitively has a dorsal sclerite, the tergum, joined to a ventral sclerite, the sternum, by lateral membranous areas, the pleura. Arising from the sternopleural region on each side is a jointed appendage.

In insects, the segments are grouped into three units, the head, thorax and abdomen, in which the various basic parts of the segments may be lost or greatly modified. Typical walking legs are only retained on the three thoracic segments. In the head, the appendages are modified for sensory and feeding purposes and in the abdomen they are lost, except that some may be modified as the genitalia and in Apterygota some pregenital appendages are retained.

1.1 HEAD

The insect head is a strongly sclerotized capsule joined to the thorax by a flexible membranous neck. It bears the mouthparts, comprising the labrum, mandibles, maxillae and labium, and also important sense organs, the antennae, compound eyes and ocelli. On the outside it is marked by grooves most of which indicate ridges on the inside, and some of these inflexions extend deep into the head, fusing with each other to form an internal skeleton. These structures serve to strengthen the head and provide attachments for muscles as well as supporting and protecting the brain and foregut.

The head is derived from the primitive pre-oral archecerebrum and a number of primitively post-oral segments. Molecular studies of *Drosophila* suggest that there are seven postoral segments: labral, ocular, antennal, intercalary, mandibular, maxillary and labial (Schmidt-Ott *et al.*, 1994). The last three segments are often called the gnathal segments because their appendages form the mouthparts of the insect.

Reviews: Bitsch, 1973; Denis & Bitsch, 1973; DuPorte, 1957; Matsuda, 1965; Snodgrass, 1935, 1960

1.1.1 Orientation

The orientation of the head with respect to the rest of the body varies (Fig. 1.1). The hypognathous condition, with the mouthparts in a continuous series with the legs, is probably primitive. This orientation occurs most commonly in phytophagous species living in open habitats. In the prognathous condition the mouthparts point forwards and this is found in predaceous species that actively pursue their prey, and in larvae, particularly of Coleoptera, which use their mandibles in burrowing. In Hemiptera, the elongate proboscis slopes backwards between the forelegs. This is the opisthorhynchous condition.

The mouthparts enclose a cavity, the pre-oral cavity, with the mouth at its inner end (Fig. 1.2). The part of the pre-oral cavity enclosed by the proximal part of the hypopharynx and the clypeus is known as the cibarium. Between the hypopharynx and the labium is a smaller cavity known as the salivarium, into which the salivary duct opens.

1.1.2 Rigidity

The head is a continuously sclerotized capsule with no outward appearance of segmentation, but it is marked by a number of grooves. Most of these grooves are sulci (singular: sulcus), marking lines along which the cuticle is inflected to give increased rigidity. The term suture should be retained for grooves marking the line of fusion of two formerly distinct plates. The groove which ends between the points of attachment of maxillae and labium at the back of the head is generally believed to represent the line of fusion of the maxillary and labial segments and it is therefore known as the postoccipital suture.

Since the sulci are functional mechanical developments to resist the various strains imposed on the head capsule, they are variable in position in different species and any one of them may be completely absent. However, the needs

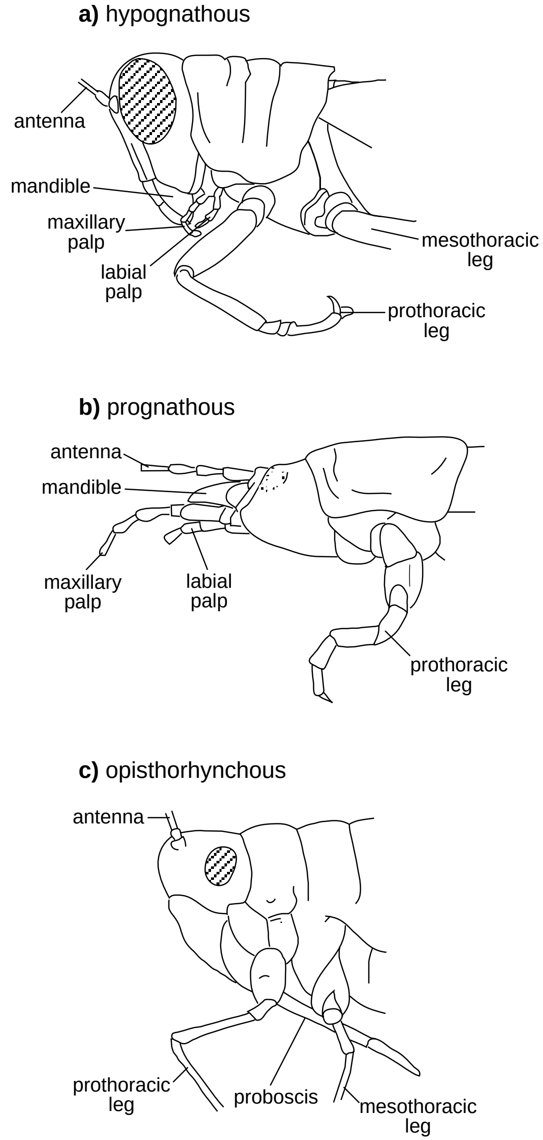

Fig. 1.1. Orientation of the head. **(a)** Hypognathous – mouthparts ventral, in a continuous series with the legs (grasshopper). **(b)** Prognathous – mouthparts in an anterior position (beetle larva). **(c)** Opisthorhynchous – sucking mouthparts with the proboscis extending back between the front legs (aphid).

for strengthening the head wall are similar in the majority of insects, so some of the sulci are fairly constant in occurrence and position (Fig. 1.3). The most constant is the epistomal (frontoclypeal) sulcus, which acts as a brace

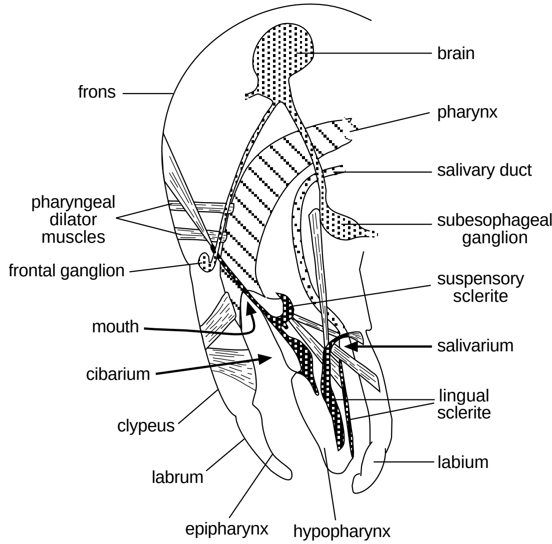

Fig. 1.2. Pre-oral cavity and some musculature. Diagrammatic vertical section through the head of an insect with biting and chewing mouthparts. Sclerites associated with the hypopharynx are black with white spots. Muscles attached to these sclerites move the hypopharynx (after Snodgrass, 1947).

between the anterior mandibular articulations. At each end of this sulcus is a pit, the anterior tentorial pit, which marks the position of a deep invagination to form the anterior arm of the tentorium. The lateral margins of the head above the mandibular articulations are strengthened by a horizontal inflexion indicated externally by the subgenal sulcus. This sulcus is generally a continuation of the epistomal sulcus to the postoccipital suture. The part of the subgenal sulcus above the mandible is called the pleurostomal sulcus, the part behind the mandible is the hypostomal sulcus. Another commonly occurring groove is the circumocular sulcus, which strengthens the rim of the eye and may develop into a deep flange protecting the inner side of the eye. Sometimes this sulcus is connected to the subgenal sulcus by a vertical subocular sulcus; the inflexions associated with these sulci act as a brace against the pull of the muscles associated with feeding. The circumantennal ridge, marked by a sulcus externally, strengthens the head at the point of insertion of the antenna, while running across the back of the head, behind the compound eyes, is the occipital sulcus.

The areas of the head defined by the sulci are given names for descriptive purposes, but they do not represent primitive sclerites. Since the sulci are variable in position, so

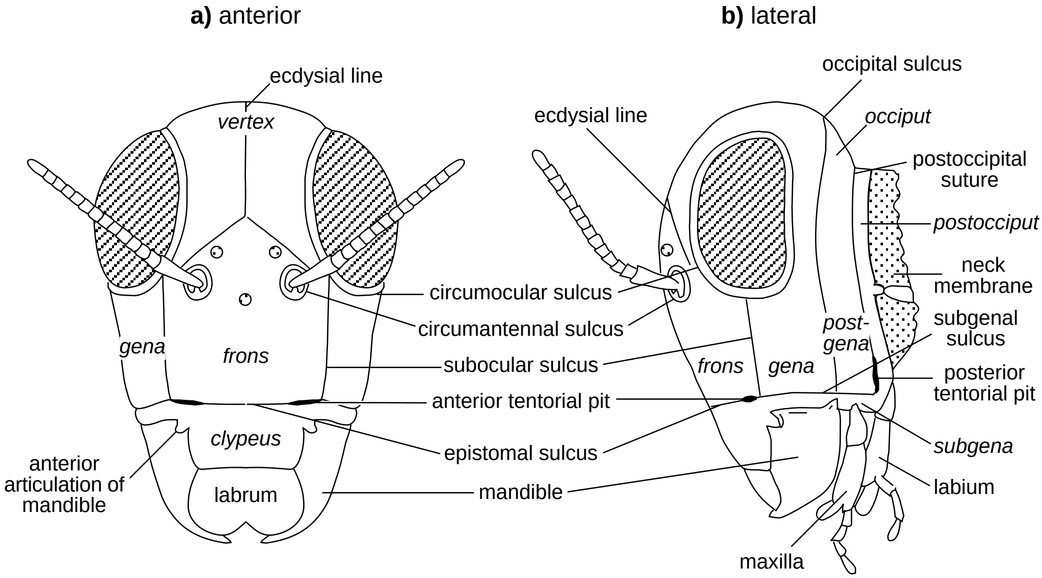

Fig. 1.3. Common lines or grooves on the insect head and the areas which they define (italicized) (modified after Snodgrass, 1960).

too are the areas which they delimit. The front of the head, the frontoclypeal area, is divided by the epistomal sulcus into the frons above and the clypeus below (Fig. 1.3). It is common to regard the arms of the ecdysial cleavage line as delimiting the frons dorsally, but this is not necessarily so (Snodgrass, 1960). From the frons, muscles run to the pharynx, the labrum and the hypopharynx; from the clypeus arise the dilators of the cibarium. The two groups of muscles are always separated by the frontal ganglion and its connectives to the brain (Fig. 1.2). Dorsally the frons continues into the vertex and posteriorly this is separated from the occiput by the occipital sulcus. The occiput is divided from the postocciput behind it by the postoccipital suture, while at the back of the head, where it joins the neck, is an opening, the occipital foramen, through which the alimentary canal, nerve cord and some muscles pass into the thorax.

The lateral area of the head beneath the eyes is called the gena, from which the subgena is cut off below by the subgenal sulcus, and the postgena behind by the occipital sulcus. The region of the subgena above the mandible is called the pleurostoma and that part behind the mandible is the hypostoma.

In hypognathous insects with a thick neck, the posterior ventral part of the head capsule is membranous. The postmentum of the labium is contiguous with this membrane, articulating with the subgena on either side. The hypostomal sulci bend upwards posteriorly and are continuous with the postoccipital suture (Fig. 1.4a). In insects with a narrow neck, permitting greater mobility of the head, and in prognathous insects, the cuticle of the head below the occipital foramen is sclerotized. This region has different origins. In Diptera, the hypostomata of the two sides meet in the midline below the occipital foramen to form a hypostomal bridge which is continuous with the postocciput (Fig. 1.4b). In other cases, Hymenoptera and the water bugs *Notonecta* and *Naucoris*, a similar bridge is formed by the postgenae, but the bridge is separated from the postocciput by the postoccipital suture (Fig. 1.4c). Where the head is held in the prognathous position, the lower ends of the postocciput fuse and extend forwards to form a median ventral plate, the gula (Fig. 1.4d), which may be a continuous sclerotization with the labium. Often the gula is reduced to a narrow strip by enlargement of the postgenae and sometimes the postgenae meet in the midline, so that the gula is obliterated. The median ventral suture which is thus formed at the point of contact of the postgenae is called the gular suture.

In all insects, the rigidity of the head is increased by four deep cuticular invaginations, known as apodemes, which usually meet internally to form a brace for the head

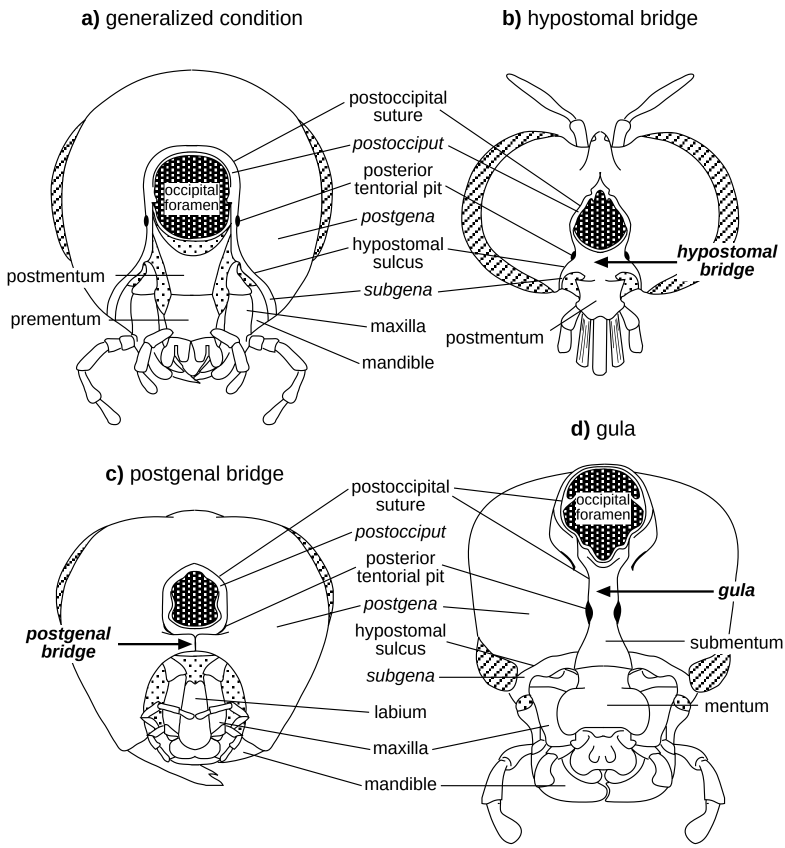

Fig. 1.4. Sclerotization at the back of the head. Notice the position of the bridge below the occipital foramen with reference to the posterior tentorial pit. Membranous areas stippled, compound eyes cross-hatched. The names of areas defined by sulci are italicized (after Snodgrass, 1960). **(a)** Generalized condition, no ventral sclerotization; **(b)** hypostomal bridge (*Deromyia*, Diptera); **(c)** postgenal bridge (*Vespula*, Hymenoptera); **(d)** gular bridge formed from the postoccipital sclerites (*Epicauta*, Coleoptera).

and for the attachment of muscles. The structure formed by these invaginations is called the tentorium (Fig. 1.5). Its two anterior arms arise from the anterior tentorial pits, which in Apterygota and Ephemeroptera are ventral and medial to the mandibles. In Odonata, Plecoptera and Dermaptera the pits are lateral to the mandibles, while in most higher insects they are facial at either end of the epistomal sulcus. The posterior arms arise from pits at the ventral ends of the postoccipital suture and they unite to form a bridge running across the head from one side to the other. In Pterygota the anterior arms also join up with the bridge, but the development of the tentorium as a whole is very variable. Sometimes a pair of dorsal arms arise from the anterior arms and they may be attached to the dorsal wall of the head by short muscles. In Machilidae (Archaeognatha) the posterior bridge is present, but the anterior arms do not reach it, while in Lepismatidae (Thysanura) the anterior arms unite to form a central plate near the bridge and are joined to it by very short muscles.

1.1.3 Molting

Immature insects nearly always have a line along the dorsal midline of the head dividing into two lines on the face so as to form an inverted Y (Fig. 1.3). There is no groove or ridge along this line, and it is simply a line of weakness, continuous with that on the thorax, along which the cuticle splits when the insect molts (see Fig. 16.11). It is therefore called the ecdysial cleavage line, but has commonly been termed the epicranial suture. The anterior arms of this line are very variable in their development and position and, in Apterygota, they are reduced or absent. The ecdysial cleavage line may persist in the adult insect and sometimes the cranium is inflected along this line to form a true sulcus. Other ecdysial lines may be present on the ventral surface of the head of larval insects (Hinton, 1963).

1.2 NECK

The neck or cervix is a membranous region which gives freedom of movement to the head. It extends from the postocciput at the back of the head to the prothorax, and possibly

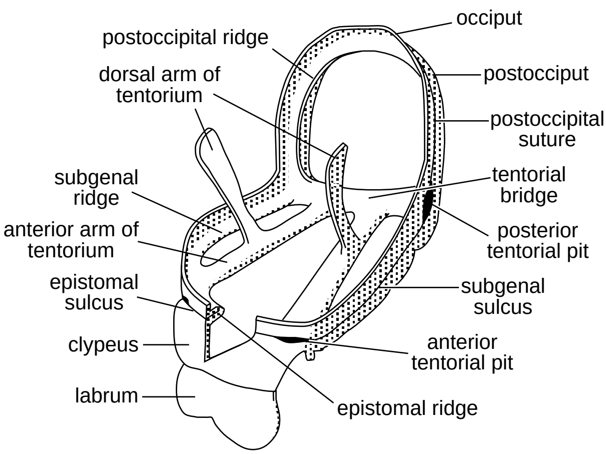

Fig. 1.5. Tentorium. Cutaway of the head capsule to show the tentorium and its relationship with the grooves and ridges of the head (after Snodgrass, 1935).

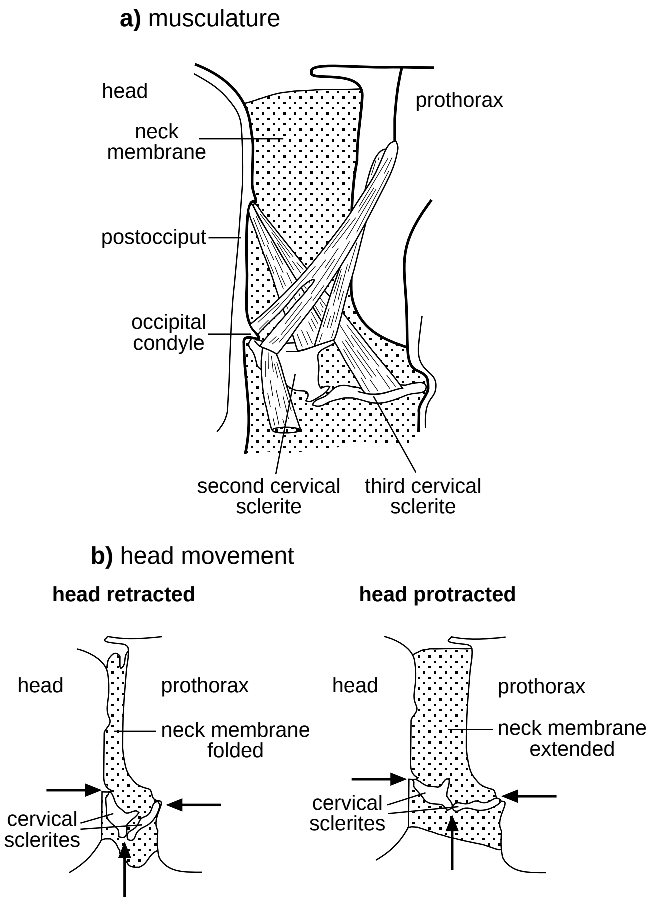

Fig. 1.6. Neck and cervical sclerites of a grasshopper. **(a)** Seen from the inside to show the muscles (after Imms, 1957). **(b)** Diagrams showing how a change in the angle between the second and third cervical sclerites retracts or protracts the head. (The first cervical sclerite is small and is not shown). Arrows indicate points of articulation.

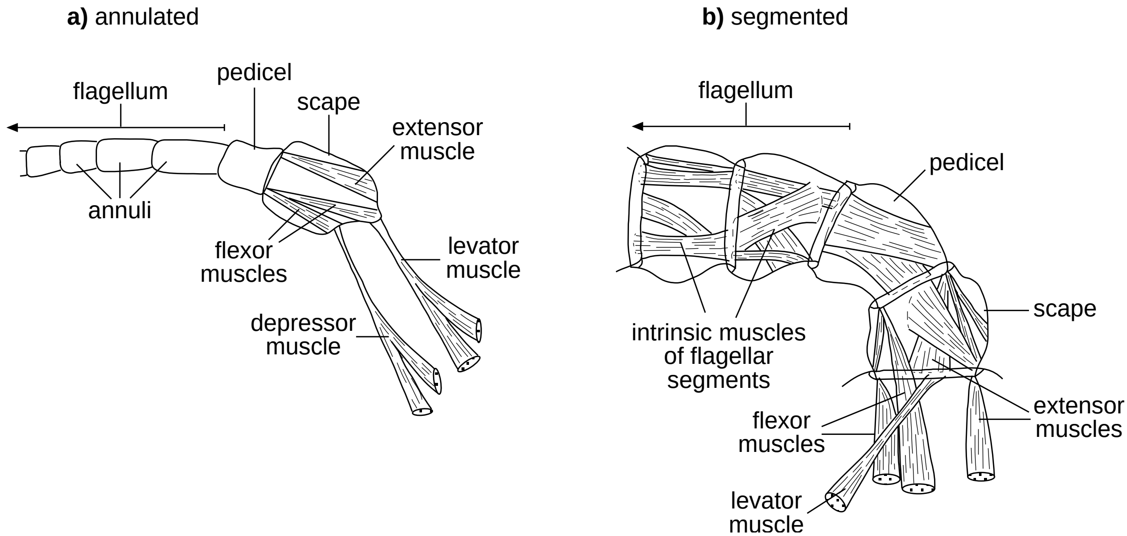

Fig. 1.7. Antenna. Proximal region showing the musculature. **(a)** Typical insect annulated antenna. There are no muscles in the flagellum (*Locusta*, Orthoptera). **(b)** Segmented antenna of a non-insect hexapod (*Japyx*, Diplura) (after Imms, 1940).

represents the posterior part of the labial segment together with the anterior part of the prothoracic segment. Laterally in the neck membrane are the cervical sclerites. Sometimes there is only one, as in Ephemeroptera, but there may be two or three. In *Schistocerca* (Orthoptera) the first lateral cervical sclerite, which articulates with the occipital condyle at the back of the head, is very small. The second sclerite articulates with it by a ball and socket joint allowing movement in all planes. Posteriorly it meets the third (posterior) cervical sclerite and movement at this joint is restricted to the vertical plane. The third cervical sclerite connects with the prothoracic episternum, relative to which it can move in all planes.

Muscles arising from the postocciput and the pronotum are inserted on the cervical sclerites (Fig. 1.6a) and their contraction increases the angle between the sclerites so that the head is pushed forwards (Fig. 1.6b). A muscle arising ventrally and inserted on to the second cervical sclerite may aid in retraction or lateral movements of the head. Running through the neck are longitudinal muscles, dorsal muscles from the antecostal ridge of the mesothorax to the postoccipital ridge, and ventral muscles from the sternal apophyses of the prothorax to the postoccipital ridge or the tentorium. These muscles serve to retract the head on to the prothorax, while their differential contraction will cause lateral movements of the head. *Schistocerca* has 16 muscles on each side of the neck, each of which is innervated by several axons, often including an inhibitory fiber. This polyneuronal innervation, together with the versatility of the cervical articulations and the complexity of the musculature, permits movement of the head in a highly versatile and accurately controlled manner.

1.3 ANTENNAE

All insects possess a pair of antennae, but they may be greatly reduced, especially in larval forms. Amongst the non-insectan Hexapoda, Collembola and Diplura have antennae, but Protura do not.

1.3.1 Antennal structure

The antenna consists of a basal scape, a pedicel and a flagellum. The scape is inserted into a membranous region of the head wall and pivoted on a single marginal point, the antennifer (Fig. 1.8a), so it is free to move in all directions. Frequently the flagellum is divided into a number of similar annuli joined to each other by membranes so that the flagellum as a whole is flexible. The term segmented should be avoided with reference to the flagellum of insects since the annuli are not regarded as equivalent to leg segments.

The antennae of insects are moved by levator and depressor muscles arising on the anterior tentorial arms and inserted into the scape, and by flexor and extensor muscles arising in the scape and inserted into the pedicel (Fig. 1.7a). There are no muscles in the flagellum, and the nerve which

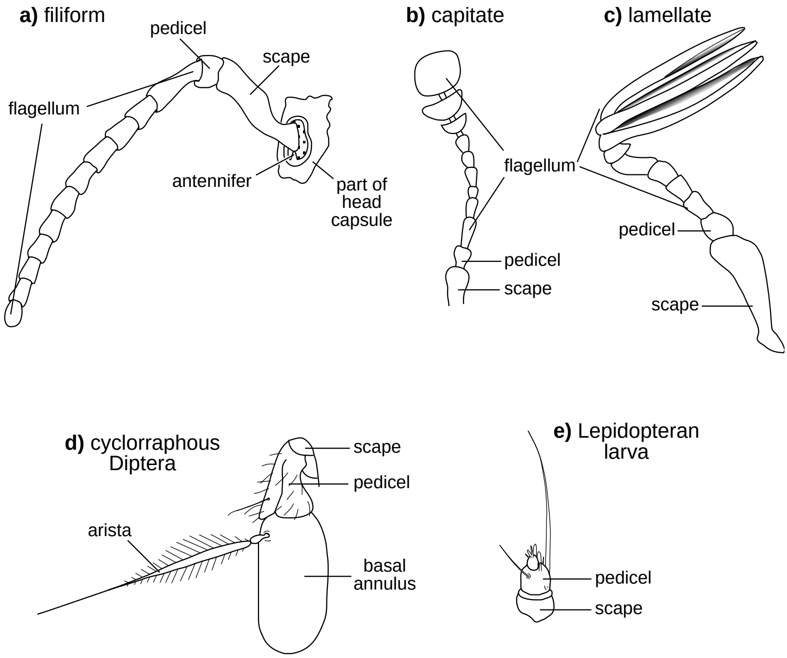

Fig. 1.8. Antennae. Different forms occurring in different insects. Not all to same scale.

traverses the flagellum is purely sensory. This is the annulated type of antenna. In Collembola and Diplura the musculature at the base of the antenna is similar to that in insects, but, in addition, there is an intrinsic musculature in each unit of the flagellum (Fig. 1.7b), and, consequently, these units are regarded as true segments.

The number of annuli is very variable between species. Adult Odonata, for example, have five or fewer annuli while adult *Periplaneta* have over 150, increasing from about 48 in the first stage larva.

The form of the antenna varies considerably depending on its precise function (Fig. 1.8). Sometimes the modification produces an increase in surface area allowing a large number of sensilla to be accommodated on the antenna (Fig. 1.9) and, in the case of the plumose antennae of some male moths, enabling them to sample a large volume of air. Sexual dimorphism in the antennae is common, those of the male often being more complex than those of the female. This often occurs where the male is attracted to or recognizes the female by her scent. Conversely, in chalcids scent plays an important part in host-finding by the female and in this case the female's antennae are more specialized than the male's.

The antennae of larval hemimetabolous insects are similar to those of the adult, but with fewer annuli. The number increases at each molt (see Fig. 15.10). In *Periplaneta*, for example, there are only 48 annuli in the first stage larva compared with over 150 in the adult. The antennae of larval holometabolous insects are usually considerably different from those of the adult. The larval antennae of Neuroptera and Megaloptera have a number of annuli, but in larval Coleoptera and Lepidoptera the antennae are reduced to three simple segments. In some larval Diptera and Hymenoptera the antennae are very small and may be no more than swellings of the head wall.

1.3.2 Sensilla on the antennae

The antennae are primarily sensory structures and they are richly endowed with sensilla in most insects. It is characteristic of insects that the pedicel contains a chordotonal organ, Johnston's organ, which responds to movement of the flagellum with respect to the pedicel (see section 23.2.3.2). In addition, the scape and pedicel often have hair plates and groups of campaniform sensilla that provide information on the positions of the basal segments with respect to the head and to each other. Scattered mechanosensory hairs are also often present on these segments.

The principal sensilla on the flagellum of most insects are olfactory, and these have a variety of forms (see section 24.1.1). It is common for contact chemoreceptors, mechanoreceptors

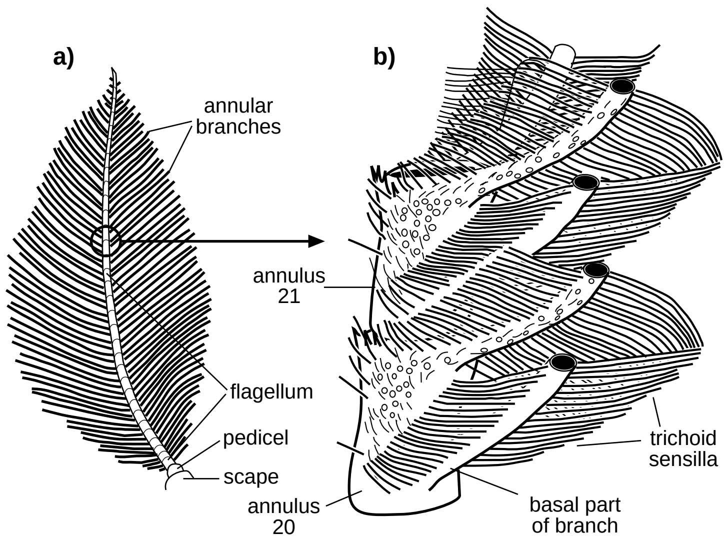

Fig. 1.9. Antenna. Plumose form providing space for large numbers of sensilla (male of the moth *Telea polyphemus*) (after Boeckh, Kaissling & Schneider, 1960). **(a)** The whole antenna seen from above. Two slender branches arise on opposite sides of each annulus. **(b)** Detail of two annuli from the side showing the bases of the branches and arrangement of long trichoid olfactory sensilla along the branches.

and thermohygroreceptors also to be present. Where the flagellum is made up of a series of similar annuli, successive annuli often have a similar arrangement of sensilla, but the sensilla are often concentrated in particular regions. In *Melanoplus* (Orthoptera), for instance, there are no basiconic or coeloconic pegs on the proximal annuli; most of these sensilla are found on the annuli in the middle of the flagellum (Fig. 1.10). In Pieridae (Lepidoptera), most of the antennal sensilla are aggregated on the terminal club. The terminal annulus often has a group of contact chemoreceptors at its tip. The total numbers of sensilla on an antenna are often very large. Adult male *Periplaneta*, for instance, have about 250 000 sensilla on each antenna and male corn borer moths, *Ostrinia*, about 8000. When the antennae are sexually dimorphic, as in many Lepidoptera, the more complex antenna bears a much larger number of sensilla. For example, male *Telea* have over 65 000 sensilla on one antenna, while the female has only about 13 000.

Review: Zacharuk, 1985

1.3.3 Functions of antennae

The antennae function primarily as sense organs and they are the primary olfactory receptors of all insects (see section 24.1.1). They also have a tactile function by virtue of the large number of mechanosensitive sensilla that are often present. Very long antennae, such as occur in the cockroach, are possibly associated with their use as feelers. Johnston's organ is important in the regulation of airspeed in flying insects (see Fig. 9.36) and in some insects, male mosquitoes, female *Drosophila* and worker honeybees, for example, it is concerned in the perception of near-field sounds (see Fig. 23.11).

Sometimes the antennae have other functions. The adult water beetle *Hydrophilus* submerges with a film of air over its ventral surface which it renews at intervals when it comes to the surface. At the water surface the body is inclined to one side and a funnel of air, connecting the ventral air bubble to the outside air, appears between the head, the prothorax and the distal annuli of the antenna, which is held along the side of the head. The four terminal annuli of the antenna are enlarged and are clothed with hydrofuge hairs

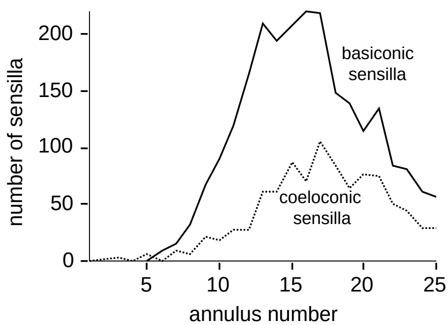

Fig. 1.10. Distribution of sensilla along the flagellum of a male grasshopper. Only olfactory sensilla are shown. 1 = most proximal annulus, adjacent to the pedicel; 25 = most distal annulus (*Melanoplus*) (data from Slifer *et al.*, 1959).

which facilitate the formation of the air funnel. In the newly hatched larva of *Hydrophilus* the antennae assist the mandibles in masticating the prey. This is facilitated by a number of sharp spines on the inside of the antennae.

In fleas and Collembola the antennae are used in mating. Male fleas use the antennae to clasp the female from below and the inner surfaces bear large numbers of adhesive discs. These discs, about 5 μm in diameter, are set on stalks above the general surface of the cuticle and within each one there is a gland, presumably secreting an adhesive material. Species with sessile or semi-sessile females lack these organs (Rothschild and Hinton, 1968). In many Collembola the males have prehensile antennae with which they hold on to the antennae of the female and, in *Sminthurides aquaticus*, the male may be carried about by the female, holding on to her antennae, for several days.

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