

General characteristics of insects. Relationship with other Arthropods, splitting up into different evolutionary lines, Reasons for success of the insects in diverse environments.

Hard Parts: General segmentation, tagmatosis and organization.

Cuticle: Detailed structure along with its biochemistry. Epidermal layer; its structure and function. Basement membrane. Colors of insects. cuticular outgrowths and appendages sclerotization.

Head: cephalization, sclerites, modifications.

Antennae: Different modes of ingestion and types of mouth parts.

Neck: Sclerites.

Thorax: Sclerites: legs, their different modifications and functions.

Wings: Origin; Different regions. Development and basal attachments, main veins and their branches (generalized insects), wing coupling.

Abdomen: Secondary appendages and external genitalia, Flight; types of flight. Aerodynamics, fuels, endoskeleton; head, thorax and abdomen.

Soft Parts: Muscular system; basic structure, types of muscles; muscle contraction and its energetics, comparative structure of all the systems, e.g., digestive, excretory, respiratory, incubatory, and nervous system and their physiology.

Sense organs: sound and light producing organs.

Nutritive requirements: Fat body, exocrine and endocrine glands including pheromones and their functions.

Reproduction: Reproductive organs and different types of reproduction in insects, egg fertilization and maturation

Development: Embryology up to dorsal closure, different types of metamorphosis, apolysis and ecdysis and the role of endocrine secretions.

Practical

Preparation of permanent slides. All the hard parts (antennae, mouth parts, wings, legs, terminal segments and genitalia). Different systems, especially digestive, reproductive of the following insects. American cockroach, Gryllus, grasshopper, housefly, butterfly, mosquito, any common beetle. Red cotton bug. Wasp and honey bee. Sympathetic nervous system of cockroach and gryllus. Salivary glands of cockroach, red cotton bug and honey bee

Recommended Books:

1. RICHARDS, O. W. and DAVIES, R. G. Imm's General Textbook of Entomology. Vol. 1, 10th Edition. 1977. Chapman & Hall, London,
 2. Chapman, R.F. The Insects: Structure and Function, 2000. Blackwell Science Inc., London.
 3. Wigglesworth, V. B. Insect Physiology 8th Edition. 1984, Springer Publisher.
 4. Robert L. Patton. W. B. Insect Physiology. 1963. Saunders Co., Philadelphia.
 5. Price, W. INSECT ECOLOGY. 1997. John Wiley & Sons.
 6. Krebs, C. J. Ecology: The Experimental Analysis Abundance. 5th Edition. 2000. Benjamin-Cummings Publishing Company.
 7. Tembhare, Db. Modern Entomology. 2002. Himalaya Publishing House. India.
 8. Southood, T.R.E. Ecological Methods. 1978. Chapman and Hall, London.
- Yazdani, S.S., and Agarwal, M.L. Elements of Insect Ecology. 1997. Narosa Publishing House. India.

EVOLUTIONARY RELATIONSHIPS

supposedly ancestral Uniramian stock. On this view, the Trilobites, Chelicerata and Crustacea seem to be only rather distantly related to one another and to the Uniramia, and their origins are obscure. An older interpretation of Arthropod relationships, but one which is still defended by modern authorities such as Siewing, Hennig, Lauterbach and Weygoldt, holds that the Arthropoda is a natural, monophyletic assemblage, among which the major evolutionary lines are related as is depicted in Fig. 99.

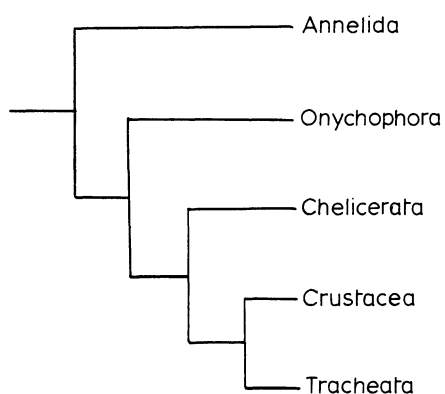


Fig. 99 Probable relationships of some major Arthropodan groups

There is little convincing palaeontological evidence enabling a decision to be made between these alternative interpretations. Already in the Lower Cambrian Burgess Shale deposits of N. America there is an abundant and diverse Arthropod fauna composed of trilobites and some 30 genera of non-trilobitic Arthropods which cannot be placed satisfactorily in any higher taxa and which shed no light on the possibly polyphyletic nature of the group. Probably the most interesting of the Burgess Shale fossils is *Aysheaia pedunculata* which, although marine and differing in some respects from *Peripatus* and its Recent allies, seems to be close to the ancestors of the Onychophora and confirms the archaic character of this group.

THE ANCESTRY OF INSECTS

Both the alternative views of Arthropod phylogeny outlined above concur in associating the insects with the Myriapods rather than the Trilobita, Chelicerata or Crustacea, but they do not agree in the further details of the phylogeny which they offer. For Manton and others who accept the likelihood of widespread convergent evolution, the different groups of Myriapods and most, if not all, of the major groups of Apterygote insects evolved separately from primitive Onychophora-

THE ANCESTRY OF INSECTS

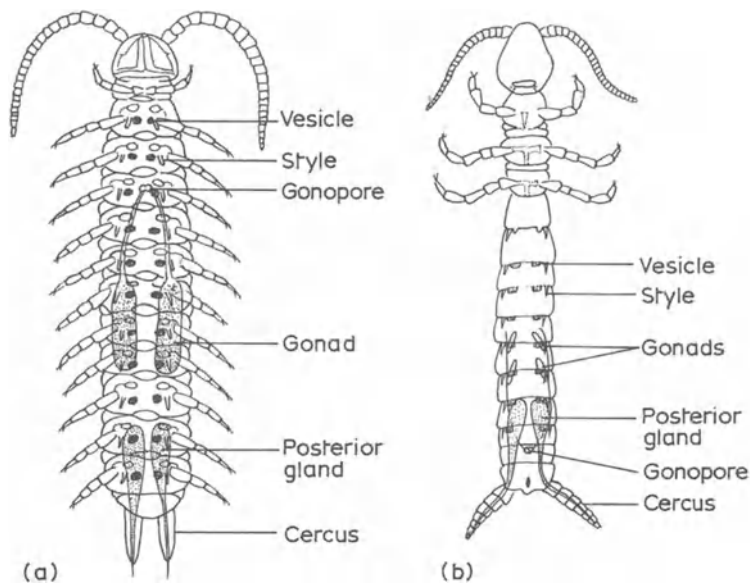


Fig. 100 Structural features of (a) Symphyla and (b) Diplura

like Uniramia with a soft cuticle, unsegmented lobopodial appendages, and little specialization of head-segments. The alternative hypothesis regards the Myriapods and insects as together making up a monophyletic group, the Tracheata, whose synapomorphies include the loss of the second pair of antennae and mandibular palps (found in Crustacea) and the acquisition of tracheae and Malpighian tubules. Neither phylogenetic hypothesis seems to be very firmly based, though the monophyletic character of the Tracheata is better supported by cladistic arguments. Even so, the precise nature of the cladistic relationships among the various groups of Myriapods and between them and the insects remain unsettled. The insects (in the sense of all groups of hexapod arthropods) are now increasingly regarded as a monophyletic entity because of an impressive array of synapomorphic characters. Although some of these have been modified in the course of insect evolution, the ground-plan of the insects entails: a three-segmented thorax; three pairs of walking legs; head incorporating three gnathal segments (mandibular, maxillary and labial); abdomen of 11 segments plus a terminal non-segmented telson; legs composed of six basic segments (coxa, trochanter, femur, tibia, tarsus and pretarsus); and probably also a characteristic arrangement of $9 + 9 + 2$ microtubules in the sperm flagellum. It is not improbable that the insects' closest allies among the Myriapoda are to be found in the Symphyla, though the arguments for this depend heavily on symplesiomorphic resemblances between the Symphyla and the Diplura and therefore need to be re-

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evaluated (Fig. 100). Again, palaeontology has contributed little to the solution of this problem. Myriapod fossils are few and uninformative, while the earliest known insect, *Rhyniella praecursor* from the Rhynie chert of Scotland (Lower Devonian), is a Collembolan and sheds little light on the origin of the class.

APTERYGOTE RELATIONSHIPS

Comparative structural data suggest that the primary evolutionary division among the insects is into a group of Entognathan orders (the Diplura, Protura and Collembola) on the one hand, and all remaining insects on the other. The argument for the monophyly of the Entognatha depends largely on the characteristic way in which the mouthparts are partly or entirely sunk into a gnathal pouch, formed through overgrowth of cephalic folds and from which the tips of the mandibles and maxillae can be protruded for feeding. Manton, it is true, has shown that the Diplura and Collembola have rather different forms of entognathy, but this does not prove that the condition was acquired independently, and the Entognatha also show two other synapomorphies: the compound eyes and the Malpighian tubules, assumed to have been present in primitive insects, are reduced or absent. Within the Entognatha the Diplura show more primitive features than do the Protura and Collembola. These last two orders probably form a monophyletic group since they share several specialized features such as the absence of cerci and abdominal spiracles; the more deeply sunk mouthparts; a groove, the linea ventralis, on the underside of the head; and the reduction or loss of one of the pretarsal claws.

The sister-group of the Entognatha consists of all the remaining insects and can be referred to as the Ectognatha. There is little doubt that it is a monophyletic complex, as it shows a large number of synapomorphies: the second antennal segment (pedicel) contains Johnston's organ; the flagellar segments of the antennae have lost their intrinsic musculature; posterior tentorial arms have been acquired; the tarsi are divided into non-musculated subsegments (tarsomeres); the first abdominal segment has lost its paired appendages; an appendicular ovipositor is derived from the eighth and ninth abdominal segments; and the developing embryo is enclosed in an amniotic cavity. The dominant group of Ectognathan insects is, of course, the Pterygota (winged insects and their secondarily apterous descendants), whose monophyletic character is established by the common possession in their ground-plan of wings and associated thoracic modifications. However, the Ectognatha also includes the primitively wingless insects formerly regarded as a single order and called the Thysanura. There is now little doubt that these form two monophyletic taxa, the orders

unrecognized and/or undescribed (“novel”) taxa. Obviously any expectation of an even spread of novel species is unrealistic, since some groups and regions of the world are poorly known compared to others. However, amongst the minor (less species-rich) orders there is little or no scope for dramatically increased, unrecognized species richness. Very high levels of novelty, if they exist, realistically could only be amongst the Coleoptera, drab-colored Lepidoptera, phytophagous Diptera, and parasitic Hymenoptera.

Some (but not all) recent re-analyses tend towards lower estimates derived from taxonomists’ calculations and extrapolations from regional sampling rather than those derived from ecological scaling: a figure of between four and six million species of insects appears realistic.

1.3.3 The location of insect species richness

The regions in which additional undescribed insect species might occur (i.e. up to an order of magnitude greater number of novel species than described) cannot be in the northern hemisphere, where such hidden diversity in the well-studied faunas is unlikely. For example, the British Isles inventory of about 22,500 species of insects is likely to be within 5% of being complete and the 30,000 or so described from Canada must represent over half of the total species. Any hidden diversity is not in the Arctic, with some 3000 species present in the American Arctic, nor in Antarctica, the southern polar mass, which supports a bare handful of insects. Evidently, just as species-richness patterns are uneven across groups, so too is their geographic distribution.

Despite the lack of necessary local species inventories to prove it, tropical species richness appears to be much higher than that of temperate areas. For example, a single tree surveyed in Peru produced 26 genera and 43 species of ants: a tally that equals the total ant diversity from all habitats in Britain. Our inability to be certain about finer details of geographical patterns stems in part from the inverse relationship between the distribution of entomologists interested in biodiversity issues (the temperate northern hemisphere) and the centers of richness of the insects themselves (the tropics and southern hemisphere).

Studies in tropical American rainforests suggest much undescribed novelty in insects comes from the beetles, which provided the basis for the original high

richness estimate. Although beetle dominance may be true in places such as the Neotropics, this might be an artifact of the collection and research biases of entomologists. In some well-studied temperate regions such as Britain and Canada, species of true flies (Diptera) appear to outnumber beetles. Studies of canopy insects of the tropical island of Borneo have shown that both Hymenoptera and Diptera can be more species rich at particular sites than the Coleoptera. Comprehensive regional inventories or credible estimates of insect faunal diversity may eventually tell us which order of insects is globally most diverse.

Whether we estimate 30–80 million species or an order of magnitude less, insects constitute at least half of global species diversity (Fig. 1.1). If we consider only life on land, insects comprise an even greater proportion of extant species, since the radiation of insects is a predominantly terrestrial phenomenon. The relative contribution of insects to global diversity will be somewhat lessened if marine diversity, to which insects make a negligible contribution, actually is higher than currently understood.

1.3.4 Some reasons for insect species richness

Whatever the global estimate is, insects surely are remarkably speciose. This high species richness has been attributed to several factors. The small size of insects, a limitation imposed by their method of gas exchange via tracheae, is an important determinant. Many more niches exist in any given environment for small organisms than for large organisms. Thus, a single acacia tree, that provides one meal to a giraffe, may support the complete life cycle of dozens of insect species; a lycaenid butterfly larva chews the leaves, a bug sucks the stem sap, a longicorn beetle bores into the wood, a midge galls the flower buds, a bruchid beetle destroys the seeds, a mealybug sucks the root sap, and several wasp species parasitize each host-specific phytophage. An adjacent acacia of a different species feeds the same giraffe but may have a very different suite of phytophagous insects. The environment can be said to be more fine-grained from an insect perspective compared to that of a mammal or bird.

Small size alone is insufficient to allow exploitation of this environmental heterogeneity, since organisms must be capable of recognizing and responding to environmental differences. Insects have highly organized

6 The importance, diversity, and conservation of insects

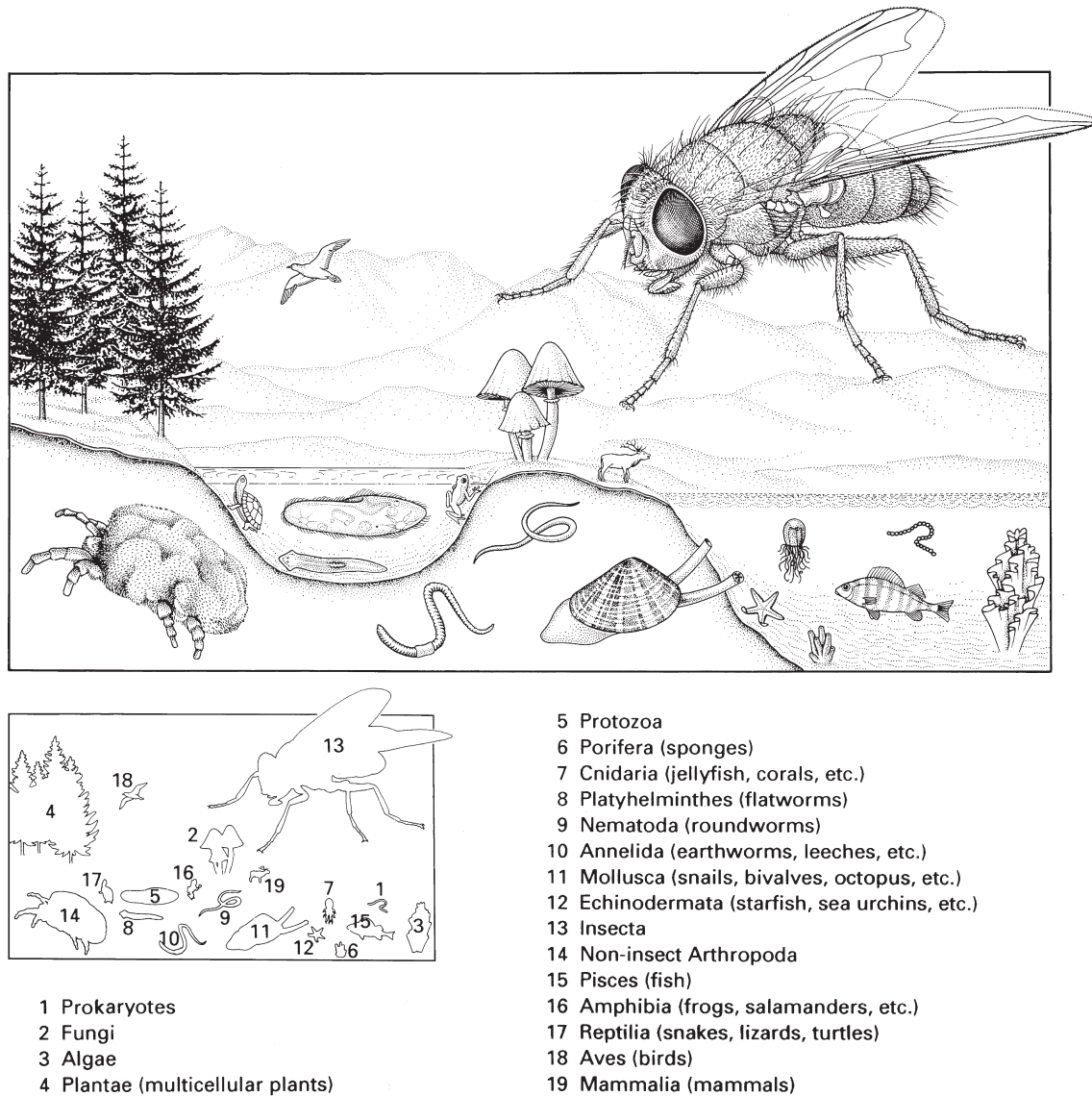


Fig. 1.1 Speciescape, in which the size of individual organisms is approximately proportional to the number of described species in the higher taxon that it represents. (After Wheeler 1990.)

sensory and neuro-motor systems more comparable to those of vertebrate animals than other invertebrates. However, insects differ from vertebrates both in size and in how they respond to environmental change. Generally, vertebrate animals are longer lived than insects and individuals can adapt to change by some degree of learning. Insects, on the other hand, normally

respond to, or cope with, altered conditions (e.g. the application of insecticides to their host plant) by genetic change between generations (e.g. leading to insecticide-resistant insects). High genetic heterogeneity or elasticity within insect species allows persistence in the face of environmental change. Persistence exposes species to processes that promote speciation, predominantly

involving phases of range expansion and/or subsequent fragmentation. Stochastic processes (genetic drift) and/or selection pressures provide the genetic alterations that may become fixed in spatially or temporally isolated populations.

Insects possess characteristics that expose them to other potential diversifying influences that enhance their species richness. Interactions between certain groups of insects and other organisms, such as plants in the case of herbivorous insects, or hosts for parasitic insects, may promote the genetic diversification of eater and eaten. These interactions are often called coevolutionary and are discussed in more detail in Chapters 11 and 13. The reciprocal nature of such interactions may speed up evolutionary change in one or both partners or sets of partners, perhaps even leading to major radiations in certain groups. Such a scenario involves increasing specialization of insects at least on plant hosts. Evidence from phylogenetic studies suggests that this has happened – but also that generalists may arise from within a specialist radiation, perhaps after some plant chemical barrier has been overcome. Waves of specialization followed by breakthrough and radiation must have been a major factor in promoting the high species richness of phytophagous insects.

Another explanation for the high species numbers of insects is the role of sexual selection in the diversification of many insects. The propensity of insects to become isolated in small populations (because of the fine scale of their activities) in combination with sexual selection (section 5.3) may lead to rapid alteration in intra-specific communication. When (or if) the isolated population rejoins the larger parental population, altered sexual signaling deters hybridization and the identity of each population (incipient species) is maintained in sympatry. This mechanism is seen to be much more rapid than genetic drift or other forms of selection, and need involve little if any differentiation in terms of ecology or non-sexual morphology and behavior.

Comparisons amongst and between insects and their close relatives suggest reasons for insect diversity. We can ask what are the shared characteristics of the most speciose insect orders, the Coleoptera, Hymenoptera, Diptera, and Lepidoptera? Which features of insects do other arthropods, such as arachnids (spiders, mites, scorpions, and their allies) lack? No simple explanation emerges from such comparisons; probably design features, flexible life-cycle patterns and feeding habits play a part (some of these factors are explored in Chapter 8). In contrast to the most speciose insect groups, arach-

nids lack winged flight, complete transformation of body form during development (metamorphosis) and dependence on specific food organisms, and are not phytophagous. Exceptionally, mites, the most diverse and abundant of arachnids, have many very specific associations with other living organisms.

High persistence of species or lineages or the numerical abundance of individual species are considered as indicators of insect success. However, insects differ from vertebrates by at least one popular measure of success: body size. Miniaturization is the insect success story: most insects have body lengths of 1–10 mm, with a body length around 0.3 mm of mymarid wasps (parasitic on eggs of insects) being unexceptional. At the other extreme, the greatest wingspan of a living insect belongs to the tropical American owlet moth, *Thysania agrippina* (Noctuidae), with a span of up to 30 cm, although fossils show that some insects were appreciably larger than their extant relatives. For example, an Upper Carboniferous silverfish, *Ramsdeldion schusteri* (Zygentoma), had a body length of 6 cm compared to a modern maximum of less than 2 cm. The wingspans of many Carboniferous insects exceeded 45 cm, and a Permian dragonfly, *Meganeuropsis americana* (Protodonata), had a wingspan of 71 cm. Notably amongst these large insects, the great size comes predominantly with a narrow, elongate body, although one of the heaviest extant insects, the 16 cm long hercules beetle *Dynastes hercules* (Scarabaeidae), is an exception in having a bulky body.

Barriers to large size include the inability of the tracheal system to diffuse gases across extended distances from active muscles to and from the external environment (Box 3.2). Further elaborations of the tracheal system would jeopardize water balance in a large insect. Most large insects are narrow and have not greatly extended the maximum distance between the external oxygen source and the muscular site of gaseous exchange, compared with smaller insects. A possible explanation for the gigantism of some Palaeozoic insects is considered in section 8.2.1.

In summary, many insect radiations probably depended upon (a) the small size of individuals, combined with (b) short generation time, (c) sensory and neuro-motor sophistication, (d) evolutionary interactions with plants and other organisms, (e) metamorphosis, and (f) mobile winged adults. The substantial time since the origin of each major insect group has allowed many opportunities for lineage diversification (Chapter 8). Present-day species diversity results from

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either higher rates of speciation (for which there is limited evidence) and/or lower rates of species extinction (higher persistence) than other organisms. The high species richness seen in some (but not all) groups in the tropics may result from the combination of higher rates of species formation with high accumulation in equable climates.

1.4 NAMING AND CLASSIFICATION OF INSECTS

The formal naming of insects follows the rules of nomenclature developed for all animals (plants have a slightly different system). Formal scientific names are required for unambiguous communication between all scientists, no matter what their native language. Vernacular (common) names do not fulfill this need: the same insects even may have different vernacular names amongst peoples that speak the same language. For instance, the British refer to “ladybirds”, whereas the same coccinellid beetles are “ladybugs” to many people in the USA. Many insects have no vernacular name, or one common name is given to many species as if only one is involved. These difficulties are addressed by the Linnaean system, which provides every described species with two given names (a binomen). The first is the generic (genus) name, used for a usually broader grouping than the second name, which is the specific (species) name. These latinized names are always used together and are italicized, as in this book. The combination of generic and specific names provides each organism with a unique name. Thus, the name *Aedes aegypti* is recognized by any medical entomologist, anywhere, whatever the local name (and there are many) for this disease-transmitting mosquito. Ideally, all taxa should have such a latinized binomen, but in practice some alternatives may be used prior to naming formally (section 17.3.2).

In scientific publications, the species name often is followed by the name of the original describer of the species and perhaps the year in which the name first was published legally. In this textbook, we do not follow this practice but, in discussion of particular insects, we give the order and family names to which the species belongs. In publications, after the first citation of the combination of generic and species names in the text, it is common practice in subsequent citations to abbreviate the genus to the initial letter only (e.g. *A. aegypti*). However, where this might be ambiguous,

Table 1.1 Taxonomic categories (obligatory categories are shown in bold).

Taxon category	Standard suffix	Example
Order		Hymenoptera
Suborder		Apocrita
Superfamily	-oidea	Apoidea
Family	-idae	Apidae
Subfamily	-inae	Apinae
Tribe	-ini	Apini
Genus		<i>Apis</i>
Subgenus		
Species		<i>A. mellifera</i>
Subspecies		<i>A. m. mellifera</i>

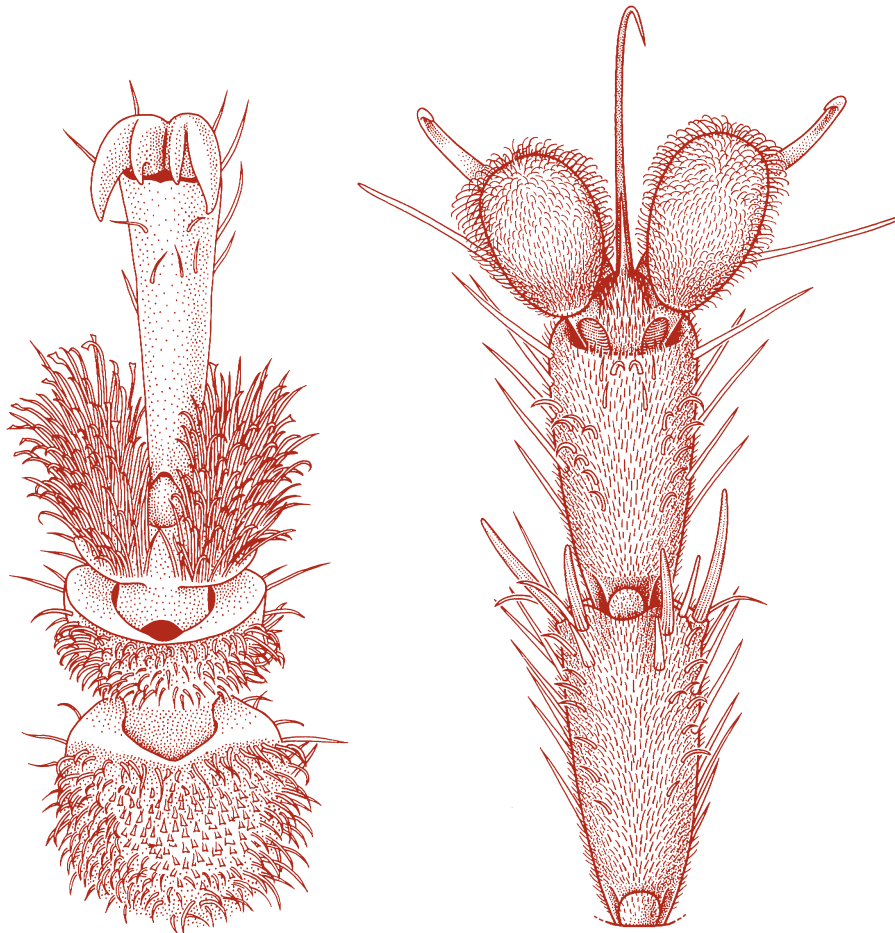
such as for the two mosquito genera *Aedes* and *Anopheles*, the initial two letters *Ae.* and *An.* are used, as in Chapter 15.

Various taxonomically defined groups, also called **taxa** (singular **taxon**), are recognized amongst the insects. As for all other organisms, the basic biological taxon, lying above the individual and population, is the species, which is both the fundamental nomenclatural unit in taxonomy and, arguably, a unit of evolution. Multi-species studies allow recognition of genera, which are discrete higher groups. In a similar manner, genera can be grouped into tribes, tribes into subfamilies, and subfamilies into families. The families of insects are placed in relatively large but easily recognized groups called orders. This hierarchy of ranks (or categories) thus extends from the species level through a series of “higher” levels of greater and greater inclusivity until all true insects are included in one class, the Insecta. There are standard suffixes for certain ranks in the taxonomic hierarchy, so that the rank of some group names can be recognized by inspection of the ending (Table 1.1).

Depending on the classification system used, some 30 orders of Insecta are recognized. Differences arise principally because there are no fixed rules for deciding the taxonomic ranks referred to above – only general agreement that groups should be monophyletic, comprising all the descendants of a common ancestor (Chapter 7). Orders have been recognized rather arbitrarily in the past two centuries, and the most that can be said is that presently constituted orders contain

Chapter 2

EXTERNAL ANATOMY



"Feet" of leaf beetle (left) and bush fly (right). (From scanning electron micrographs by C.A.M. Reid & A.C. Stewart.)

22 External anatomy

Insects are segmented invertebrates that possess the articulated external skeleton (exoskeleton) characteristic of all arthropods. Groups are differentiated by various modifications of the exoskeleton and the appendages – for example, the Hexapoda to which the Insecta belong (section 7.2) is characterized by having six-legged adults. Many anatomical features of the appendages, especially of the mouthparts, legs, wings, and abdominal apex, are important in recognizing the higher groups within the hexapods, including insect orders, families, and genera. Differences between species frequently are indicated by less obvious anatomical differences. Furthermore, the biomechanical analysis of morphology (e.g. studying how insects fly or feed) depends on a thorough knowledge of structural features. Clearly, an understanding of external anatomy is necessary to interpret and appreciate the functions of the various insect designs and to allow identification of insects and their hexapod relatives. In this chapter we describe and discuss the cuticle, body segmentation, and the structure of the head, thorax, and abdomen and their appendages.

First some basic classification and terminology needs to be explained. Adult insects normally have wings (most of the Pterygota), the structure of which may diagnose orders, but there is a group of primitively wingless insects (the “apterygotes”) (see section 7.4.1 and Box 9.3 for defining features). Within the Insecta, three major patterns of development can be recognized (section 6.2). Apterygotes (and non-insect hexapods) develop to adulthood with little change in body form (**ametaboly**), except for sexual maturation through development of gonads and genitalia. All other insects either have a gradual change in body form (**hemimetaboly**) with external wing buds getting larger at each molt, or an abrupt change from a wingless immature insect to winged adult stage via a pupal stage (**holometaboly**). Immature stages of hemimetabolous insects are generally called **nymphs**, whereas those of holometabolous insects are referred to as **larvae**.

Anatomical structures of different taxa are **homologous** if they share an evolutionary origin, i.e. if the genetic basis is inherited from an ancestor common to them both. For instance, the wings of all insects are believed to be homologous; this means that wings (but not necessarily flight; see section 8.4) originated once. Homology of structures generally is inferred by comparison of similarity in **ontogeny** (development from egg to adult), composition (size and detailed appearance), and position (on the same segment and same

relative location on that segment). The homology of insect wings is demonstrated by similarities in venation and articulation – the wings of all insects can be derived from the same basic pattern or groundplan (as explained in section 2.4.2). Sometimes association with other structures of known homologies is helpful in establishing the homology of a structure of uncertain origin. Another sort of homology, called **serial homology**, refers to corresponding structures on different segments of an individual insect. Thus, the appendages of each body segment are serially homologous, although in living insects those on the head (antennae and mouthparts) are very different in appearance from those on the thorax (walking legs) and abdomen (genitalia and cerci). The way in which molecular developmental studies are confirming these serial homologies is described in Box 6.1.

2.1 THE CUTICLE

The cuticle is a key contributor to the success of the Insecta. This inert layer provides the strong **exoskeleton** of body and limbs, the **apodemes** (internal supports and muscle attachments), and wings, and acts as a barrier between living tissues and the environment. Internally, cuticle lines the tracheal tubes (section 3.5), some gland ducts and the foregut and midgut of the digestive tract. Cuticle may range from rigid and armor-like, as in most adult beetles, to thin and flexible, as in many larvae. Restriction of water loss is a critical function of cuticle vital to the success of insects on land.

The cuticle is thin but its structure is complex and still the subject of some controversy. A single layer of cells, the **epidermis**, lies beneath and secretes the cuticle, which consists of a thicker **procuticle** overlaid with thin **epicuticle** (Fig. 2.1). The epidermis and cuticle together form an **integument** – the outer covering of the living tissues of an insect.

The epicuticle ranges from 3 μm down to 0.1 μm in thickness, and usually consists of three layers: an **inner epicuticle**, an **outer epicuticle**, and a **superficial layer**. The superficial layer (probably a glycoprotein) in many insects is covered by a lipid or wax layer, sometimes called a free-wax layer, with a variably discrete cement layer external to this. The chemistry of the epicuticle and its outer layers is vital in preventing dehydration, a function derived from water-repelling (hydrophobic) lipids, especially hydrocarbons. These

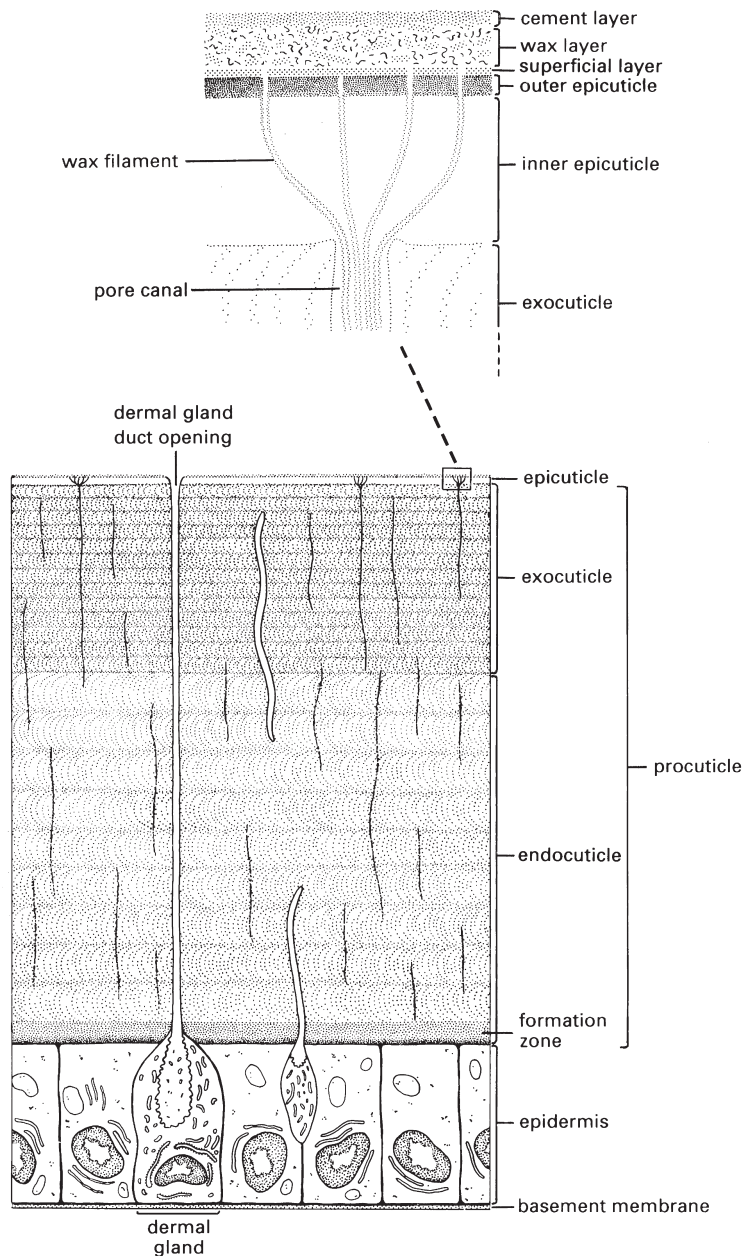


Fig. 2.1 The general structure of insect cuticle; the enlargement above shows details of the epicuticle. (After Hepburn 1985; Hadley 1986; Binnington 1993.)

compounds include free and protein-bound lipids, and the outermost waxy coatings give a bloom to the external surface of some insects. Other cuticular patterns, such as light reflectivity, are produced by various kinds of epicuticular surface microsculpturing, such as close-

packed, regular or irregular tubercles, ridges, or tiny hairs. Lipid composition can vary and waxiness can increase seasonally or under dry conditions. Besides being water retentive, surface waxes may deter predation, provide patterns for mimicry or camouflage, repel

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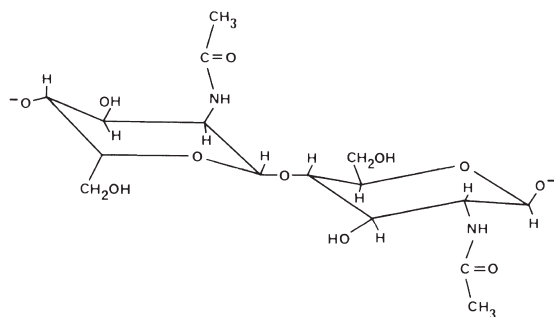


Fig. 2.2 Structure of part of a chitin chain, showing two linked units of *N*-acetyl-*D*-glucosamine. (After Cohen 1991.)

excess rainwater, reflect solar and ultraviolet radiation, or give species-specific olfactory cues.

The epicuticle is inextensible and unsupportive. Instead, support is given by the underlying chitinous cuticle known as procuticle when it is first secreted. This differentiates into a thicker **endocuticle** covered by a thinner **exocuticle**, due to **sclerotization** of the latter. The procuticle is from 10 μm to 0.5 mm thick and consists primarily of chitin complexed with protein. This contrasts with the overlying epicuticle which lacks chitin.

Chitin is found as a supporting element in fungal cell walls and arthropod exoskeletons, and is especially important in insect extracellular structures. It is an unbranched polymer of high molecular weight – an amino-sugar polysaccharide predominantly composed of β -(1–4)-linked units of *N*-acetyl-*D*-glucosamine (Fig. 2.2).

Chitin molecules are grouped into bundles and assembled into flexible microfibrils that are embedded in, and intimately linked to, a protein matrix, giving great tensile strength. The commonest arrangement of chitin microfibrils is in a sheet, in which the microfibrils are in parallel. In the exocuticle, each successive sheet lies in the same plane but may be orientated at a slight angle relative to the previous sheet, such that a thickness of many sheets produces a helicoid arrangement, which in sectioned cuticle appears as alternating light and dark bands (lamellae). Thus the parabolic patterns and lamellar arrangement, visible so clearly in sectioned cuticle, represent an optical artifact resulting from microfibrillar orientation (Fig. 2.3). In the endocuticle, alternate stacked or helicoid arrangements of microfibrillar sheets may occur, often giving rise to

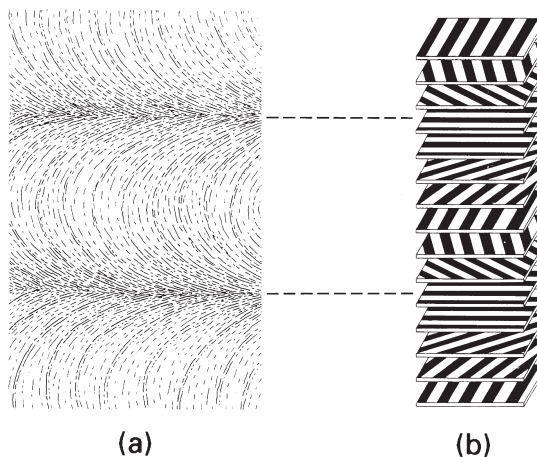


Fig. 2.3 The ultrastructure of cuticle (from a transmission electron micrograph). (a) The arrangement of chitin microfibrils in a helicoid array produces characteristic (though artifactual) parabolic patterns. (b) Diagram of how the rotation of microfibrils produces a lamellar effect owing to microfibrils being either aligned or non-aligned to the plane of sectioning. (After Filshie 1982.)

thicker lamellae than in the exocuticle. Different arrangements may be laid down during darkness compared with daylight, allowing precise age determination in many adult insects.

Much of the strength of cuticle comes from extensive hydrogen bonding of adjacent chitin chains. Additional stiffening comes from **sclerotization**, an irreversible process that darkens the exocuticle and results in the proteins becoming water-insoluble. Sclerotization may result from linkages of adjacent protein chains by phenolic bridges (quinone tanning), or from controlled dehydration of the chains, or both. Only exocuticle becomes sclerotized. The deposition of pigment in the cuticle, including deposition of melanin, may be associated with quinones, but is additional to sclerotization and not necessarily associated with it.

In contrast to the solid cuticle typical of sclerites and mouthparts such as mandibles, softer, plastic, highly flexible or truly elastic cuticles occur in insects in varying locations and proportions. Where elastic or spring-like movement occurs, such as in wing ligaments or for the jump of a flea, **resilin** – a “rubber-like” protein – is present. The coiled polypeptide chains of this protein function as a mechanical spring under tension or compression, or in bending.

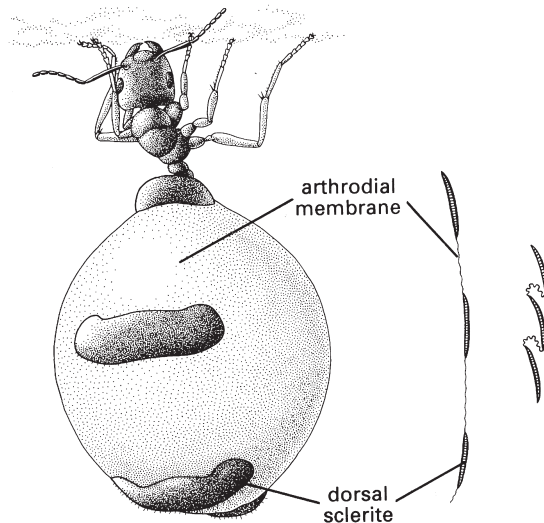


Fig. 2.4 A specialized worker, or replete, of the honeypot ant, *Camponotus inflatus* (Hymenoptera: Formicidae), which holds honey in its distensible abdomen and acts as a food store for the colony. The arthrodial membrane between tergal plates is depicted to the right in its unfolded and folded conditions. (After Hadley 1986; Devitt 1989.)

In soft-bodied larvae and in the membranes between segments, the cuticle must be tough, but also flexible and capable of extension. This “soft” cuticle, sometimes termed **arthrodial membrane**, is evident in gravid females, for example in the ovipositing migratory locust, *Locusta migratoria* (Orthoptera: Acrididae), in which intersegmental membranes may be expanded up to 20-fold for oviposition. Similarly, the gross abdominal dilation of gravid queen bees, termites, and ants is possible through expansion of the unsclerotized cuticle. In these insects, the overlying unstretchable epicuticle expands by unfolding from an originally highly folded state, and some new epicuticle is formed. An extreme example of the distensibility of arthrodial membrane is seen in honeypot ants (Fig. 2.4; see also section 12.2.3). In *Rhodnius* nymphs (Hemiptera: Reduviidae), changes in molecular structure of the cuticle allow actual stretching of the abdominal membrane to occur in response to intake of a large fluid volume during feeding.

Cuticular structural components, waxes, cements, pheromones (Chapter 4), and defensive and other compounds are products of the epidermis, which is a near-continuous, single-celled layer beneath the cuticle.

Many of these compounds are secreted to the outside of the insect epicuticle. Numerous fine **pore canals** traverse the procuticle and then branch into numerous finer **wax canals** (containing **wax filaments**) within the epicuticle (enlargement in Fig. 2.1); this system transports lipids (waxes) from the epidermis to the epicuticular surface. The wax canals may also have a structural role within the epicuticle. **Dermal glands**, part of the epidermis, produce cement and/or wax, which is transported via larger ducts to the cuticular surface. Wax-secreting glands are particularly well developed in mealybugs and other scale insects (Fig. 2.5). The epidermis is closely associated with molting – the events and processes leading up to and including **ecdysis** (eclosion), i.e. the shedding of the old cuticle (section 6.3).

Insects are well endowed with cuticular extensions, varying from fine and hair-like to robust and spine-like. Four basic types of protuberance (Fig. 2.6), all with sclerotized cuticle, can be recognized on morphological, functional, and developmental grounds:

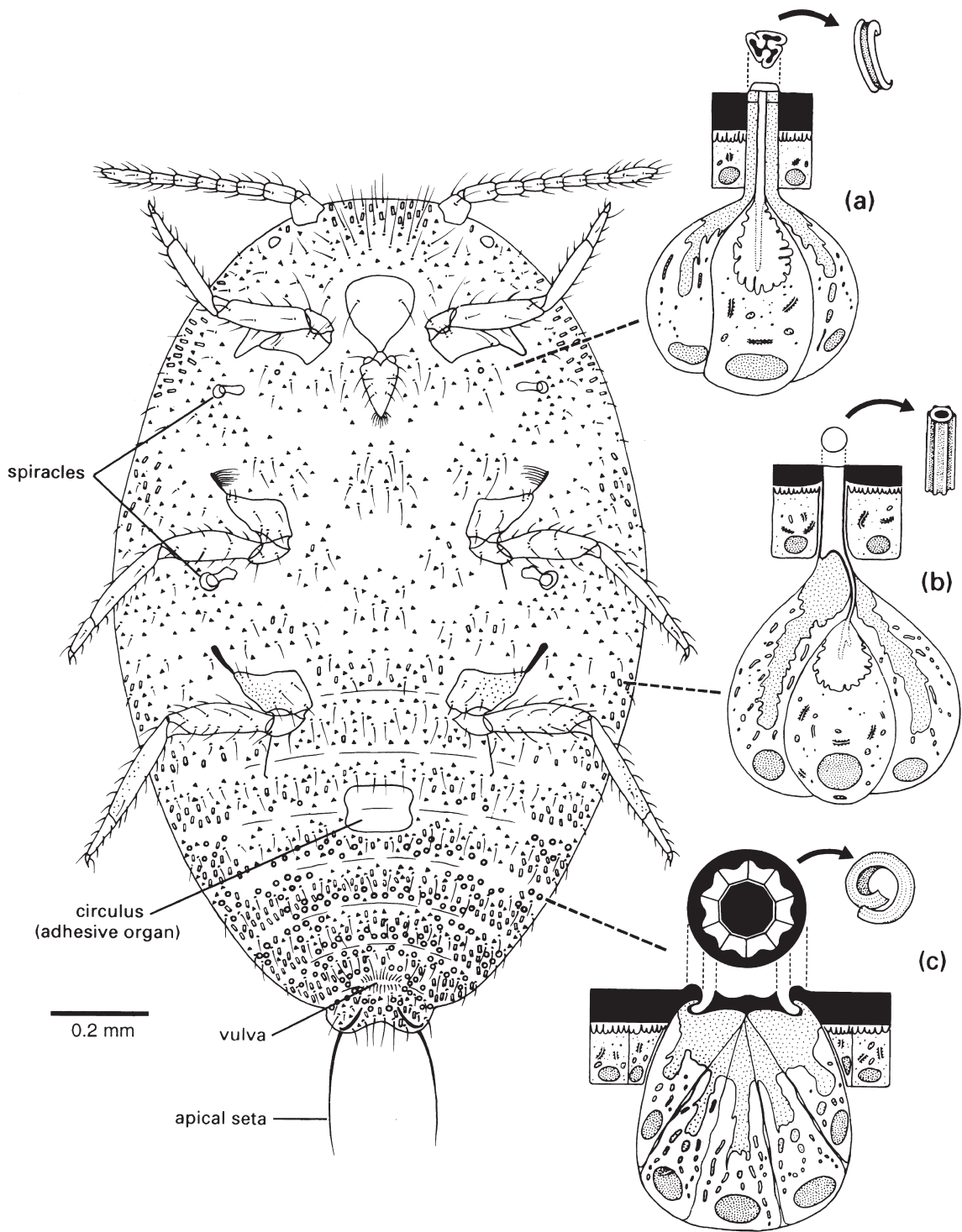
- 1 **spines** are multicellular with undifferentiated epidermal cells;
- 2 **setae**, also called **hairs**, **macrotrichia**, or **trichoid sensilla**, are multicellular with specialized cells;
- 3 **acanthae** are unicellular in origin;
- 4 **microtrichia** are subcellular, with several to many extensions per cell.

Setae sense much of the insect’s tactile environment. Large setae may be called bristles or chaetae, with the most modified being **scales**, the flattened setae found on butterflies and moths (Lepidoptera) and sporadically elsewhere. Three separate cells form each seta, one for hair formation (**trichogen** cell), one for socket formation (**tormogen** cell), and one sensory cell (Fig. 4.1).

There is no such cellular differentiation in multicellular spines, unicellular acanthae, and subcellular microtrichia. The functions of these types of protuberances are diverse and sometimes debatable, but their sensory function appears limited. The production of pattern, including color, may be significant for some of the microscopic projections. Spines are immovable, but if they are articulated, then they are called **spurs**. Both spines and spurs may bear unicellular or subcellular processes.

2.1.1 Color production

The diverse colors of insects are produced by the interaction of light with cuticle and/or underlying cells or



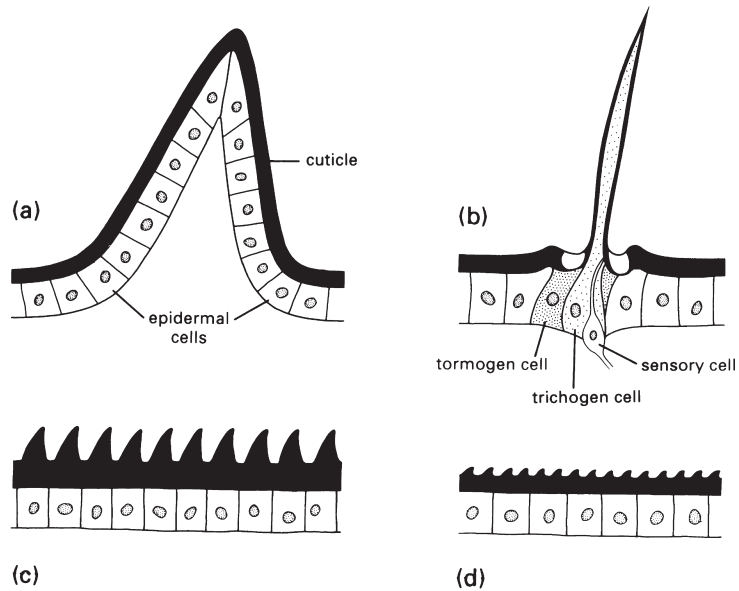


Fig. 2.6 The four basic types of cuticular protuberances: (a) a multicellular spine; (b) a seta, or trichoid sensillum; (c) acanthae; and (d) microtrichia. (After Richards & Richards 1979.)

fluid by two different mechanisms. Physical (structural) colors result from light scattering, interference, and diffraction, whereas pigmentary colors are due to the absorption of visible light by a range of chemicals. Often both mechanisms occur together to produce a color different from either alone.

All physical colors derive from the cuticle and its protuberances. **Interference** colors, such as iridescence and ultraviolet, are produced by refraction from varying spaced, close reflective layers produced by microfibrillar orientation within the exocuticle, or, in some beetles, the epicuticle, and by diffraction from regularly textured surfaces such as on many scales. Colors produced by light **scattering** depend on the size of surface irregularities relative to the wavelength of

light. Thus, whites are produced by structures larger than the wavelength of light, such that all light is reflected, whereas blues are produced by irregularities that reflect only short wavelengths.

Insect pigments are produced in three ways:

- 1 by the insect's own metabolism;
- 2 by sequestering from a plant source;
- 3 rarely, by microbial endosymbionts.

Pigments may be located in the cuticle, epidermis, hemolymph, or fat body. Cuticular darkening is the most ubiquitous insect color. This may be due to either sclerotization (unrelated to pigmentation) or the exocuticular deposition of melanins, a heterogeneous group of polymers that may give a black, brown, yellow, or red color. Carotenoids, ommochromes, papiliochromes, and pteridines (pterins) mostly produce yellows to reds, flavonoids give yellow, and tetrapyrroles (including breakdown products of porphyrins such as chlorophyll and hemoglobin) create reds, blues, and greens. Quinone pigments occur in scale insects as red and yellow anthraquinones (e.g. carmine from cochineal insects), and in aphids as yellow to red to dark blue-green aphins.

Colors have an array of functions in addition to the obvious roles of color patterns in sexual and defensive display. For example, the ommochromes are the main visual pigments of insect eyes, whereas black melanin, an effective screen for possibly harmful light rays, can

Fig. 2.5 (opposite) The cuticular pores and ducts on the venter of an adult female of the citrus mealybug, *Planococcus citri* (Hemiptera: Pseudococcidae). Enlargements depict the ultrastructure of the wax glands and the various wax secretions (arrowed) associated with three types of cuticular structure: (a) a trilocular pore; (b) a tubular duct; and (c) a multilocular pore. Curled filaments of wax from the trilocular pores form a protective body-covering and prevent contamination with their own sugary excreta, or honeydew; long, hollow, and shorter curled filaments from the tubular ducts and multilocular pores, respectively, form the ovisac. (After Foldi 1983; Cox 1987.)

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convert light energy into heat, and may act as a sink for free radicals that could otherwise damage cells. The red hemoglobins which are widespread respiratory pigments in vertebrates occur in a few insects, notably in some midge larvae and a few aquatic bugs, in which they have a similar respiratory function.

2.2 SEGMENTATION AND TAGMOSIS

Metameric segmentation, so distinctive in annelids, is visible only in some unsclerotized larvae (Fig. 2.7a). The segmentation seen in the sclerotized adult or nymphal insect is not directly homologous with that of larval insects, as sclerotization extends beyond each primary segment (Fig. 2.7b,c). Each apparent segment represents an area of sclerotization that commences in front of the fold that demarcates the primary segment and extends almost to the rear of that segment, leaving an unsclerotized area of the primary segment, the **conjunctival** or **intersegmental membrane**. This **secondary** segmentation means that the muscles, which are always inserted on the folds, are attached to solid rather than to soft cuticle. The apparent segments of adult insects, such as on the abdomen, are secondary in origin, but we refer to them simply as segments throughout this text.

In adult and nymphal insects, and hexapods in general, one of the most striking external features is the amalgamation of segments into functional units. This process of **tagmosis** has given rise to the familiar **tagmata** (regions) of **head**, **thorax**, and **abdomen**. In this process the 20 original segments have been divided into an embryologically detectable six-segmented head, three-segmented thorax, and 11-segmented abdomen (plus primitively the telson), although varying degrees of fusion mean that the full complement is never visible.

Before discussing the external morphology in more detail, some indication of orientation is required. The bilaterally symmetrical body may be described according to three axes:

- 1 **longitudinal**, or **anterior** to **posterior**, also termed **cephalic** (head) to **caudal** (tail);
- 2 **dorsoventral**, or **dorsal** (upper) to **ventral** (lower);
- 3 **transverse**, or **lateral** (outer) through the longitudinal axis to the opposite lateral (Fig. 2.8).

For appendages, such as legs or wings, **proximal** or **basal** refers to near the body, whereas **distal** or **apical** means distant from the body. In addition, structures

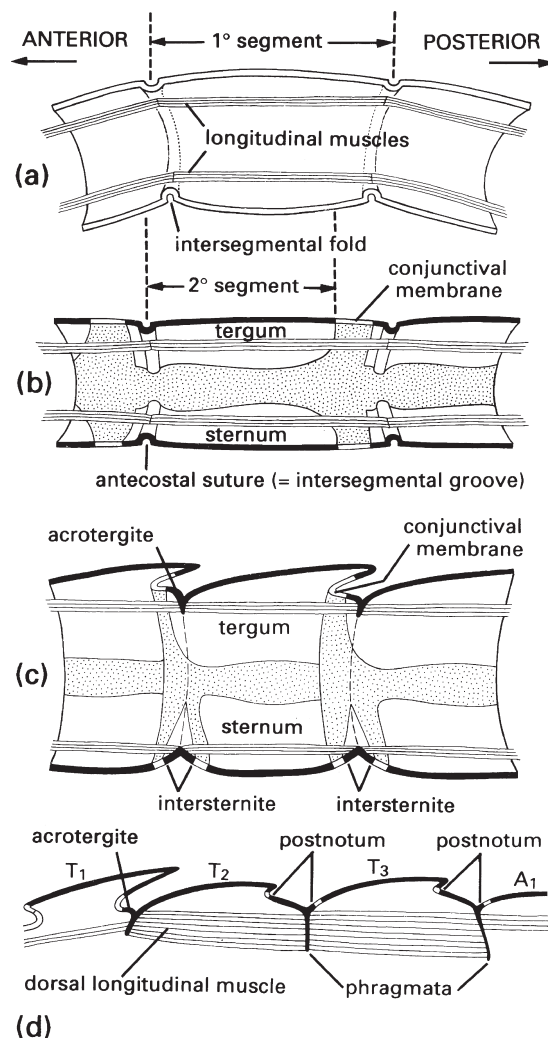


Fig. 2.7 Types of body segmentation. (a) Primary segmentation, as seen in soft-bodied larvae of some insects. (b) Simple secondary segmentation. (c) More derived secondary segmentation. (d) Longitudinal section of dorsum of the thorax of winged insects, in which the acrotergites of the second and third segments have enlarged to become the postnota. (After Snodgrass 1935.)

are **mesal**, or **medial**, if they are nearer to the **midline** (**median line**), or **lateral** if closer to the body margin, relative to other structures.

Four principal regions of the body surface can be recognized: the **dorsum** or upper surface; the **venter** or lower surface; and the two lateral **pleura** (singular:

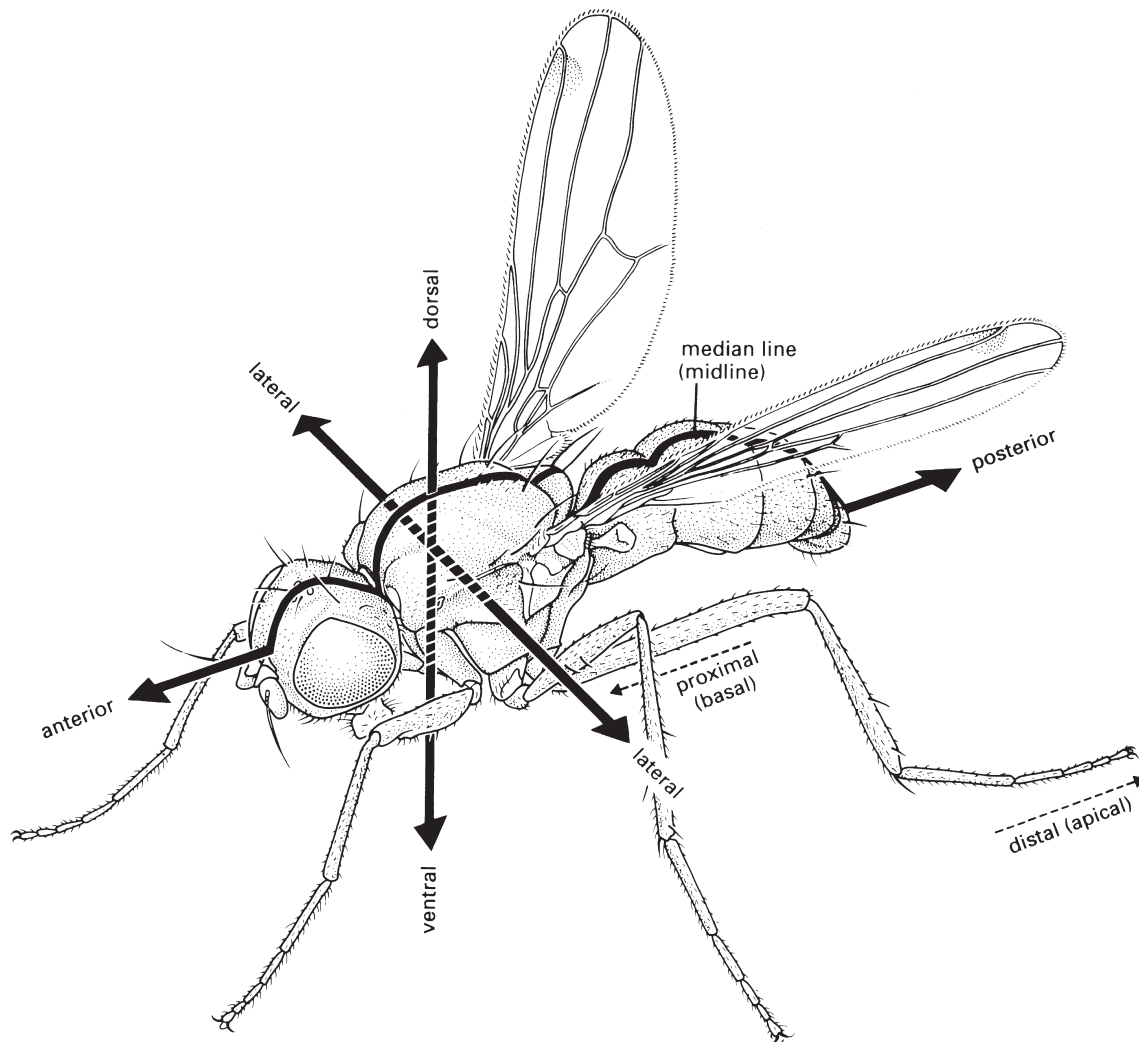


Fig. 2.8 The major body axes and the relationship of parts of the appendages to the body, shown for a sepsid fly. (After McAlpine 1987.)

pleuron), separating the dorsum from the venter and bearing limb bases, if these are present. Sclerotization that takes place in defined areas gives rise to plates called **sclerites**. The major segmental sclerites are the **tergum** (the dorsal plate; plural: **terga**), the **sternum** (the ventral plate; plural: **sterna**), and the pleuron (the side plate). If a sclerite is a subdivision of the tergum, sternum, or pleuron, the diminutive terms **tergite**, **sternite**, and **pleurite** may be applied.

The abdominal pleura are often at least partly mem-

branous, but on the thorax they are sclerotized and usually linked to the tergum and sternum of each segment. This fusion forms a box, which contains the leg muscle insertions and, in winged insects, the flight muscles. With the exception of some larvae, the head sclerites are fused into a rigid capsule. In larvae (but not nymphs) the thorax and abdomen may remain membranous and tagmosis may be less apparent (such as in most wasp larvae and fly maggots) and the terga, sterna, and pleura are rarely distinct.

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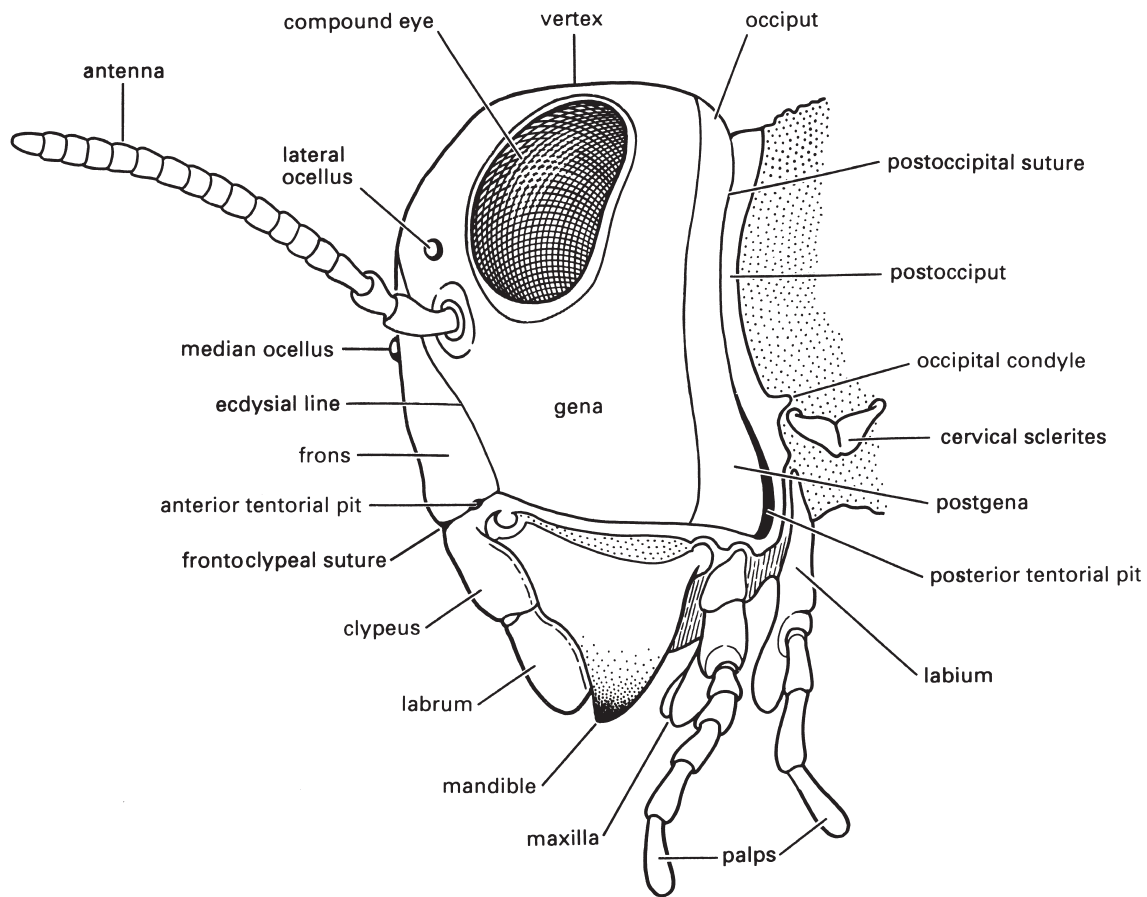


Fig. 2.9 Lateral view of the head of a generalized pterygote insect. (After Snodgrass 1935.)

2.3 THE HEAD

The rigid cranial capsule has two openings, one posteriorly through the **occipital foramen** to the prothorax, the other to the mouthparts. Typically the mouthparts are directed ventrally (**hypognathous**), although sometimes anteriorly (**prognathous**) as in many beetles, or posteriorly (**opisthognathous**) as in, for example, aphids, cicadas, and leafhoppers. Several regions can be recognized on the head (Fig. 2.9): the posterior horse-shoe-shaped **posterior cranium** (dorsally the **occiput**) contacts the **vertex** dorsally and the **genae** (singular: **gena**) laterally; the vertex abuts the **frons** anteriorly and more anteriorly lies the **clypeus**, both of which may be fused into a **frontoclypeus**. In adult and nymphal

insects, paired **compound eyes** lie more or less dorso-laterally between the vertex and genae, with a pair of sensory **antennae** placed more medially. In many insects, three light-sensitive “simple” eyes, or **ocelli**, are situated on the anterior vertex, typically arranged in a triangle, and many larvae have stemmatal eyes.

The head regions are often somewhat weakly delimited, with some indications of their extent coming from **sutures** (external grooves or lines on the head). Three sorts may be recognized:

1 remnants of original segmentation, generally restricted to the **postoccipital suture**;

2 **ecdysial lines** of weakness where the head capsule of the immature insect splits at molting (section 6.3), including an often prominent inverted “Y”, or **epi-**

cranial suture, on the vertex (Fig. 2.10); the frons is delimited by the arms (also called **frontal sutures**) of this “Y”;

3 grooves that reflect the underlying internal skeletal ridges, such as the **frontoclypeal** or **epistomal** suture, which often delimits the frons from the more anterior clypeus.

The head endoskeleton consists of several invaginated ridges and arms (**apophyses**, or elongate apodemes), the most important of which are the two pairs of **tentorial arms**, one pair being posterior, the other anterior, sometimes with an additional dorsal component. Some of these arms may be absent or, in pterygotes, fused to form the **tentorium**, an endoskeletal strut. Pits are discernible on the surface of the cranium at the points where the tentorial arms invaginate. These pits and the sutures may provide prominent landmarks on the head but usually they bear little or no association with the segments.

The segmental origin of the head is most clearly demonstrated by the mouthparts (section 2.3.1). From anterior to posterior, there are six fused head segments:

- 1** labral;
- 2** antennal, with each antenna equivalent to an entire leg;
- 3** postantennal, fused with the antennal segment;
- 4** mandibular;
- 5** maxillary;
- 6** labial.

The neck is mainly derived from the first part of the thorax and is not a segment.

2.3.1 Mouthparts

The mouthparts are formed from appendages of all head segments except the second. In omnivorous insects, such as cockroaches, crickets, and earwigs, the mouthparts are of a biting and chewing type (**mandibulate**) and resemble the probable basic design of ancestral pterygote insects more closely than the mouthparts of the majority of modern insects. Extreme modifications of basic mouthpart structure, correlated with feeding specializations, occur in most Lepidoptera, Diptera, Hymenoptera, Hemiptera, and a number of the smaller orders. Here we first discuss basic mandibulate mouthparts, as exemplified by the European earwig, *Forficula auricularia* (Dermaptera: Forficulidae) (Fig. 2.10), and then describe some of the more common modifications associated with more specialized diets.

There are five basic components of the mouthparts:

- 1 labrum**, or “upper lip”, with a ventral surface called the **epipharynx**;
- 2 hypopharynx**, a tongue-like structure;
- 3 mandibles**, or jaws;
- 4 maxillae** (singular: **maxilla**);
- 5 labium**, or “lower lip” (Fig. 2.10).

The labrum forms the roof of the preoral cavity and mouth (Fig. 3.14) and covers the base of the mandibles; it may be formed from fusion of parts of a pair of ancestral appendages. Projecting forwards from the back of the preoral cavity is the hypopharynx, a lobe of probable composite origin; in apterygotes, earwigs, and nymphal mayflies the hypopharynx bears a pair of lateral lobes, the **superlinguae** (singular: **superlingua**) (Fig. 2.10). It divides the cavity into a dorsal food pouch, or **cibarium**, and a ventral **salivarium** into which the salivary duct opens (Fig. 3.14). The mandibles, maxillae, and labium are the paired appendages of segments 4–6 and are highly variable in structure among insect orders; their serial homology with walking legs is more apparent than for the labrum and hypopharynx.

The mandibles cut and crush food and may be used for defense; generally they have an apical cutting edge and the more basal molar area grinds the food. They can be extremely hard (approximately 3 on Moh’s scale of mineral hardness, or an indentation hardness of about 30 kg mm⁻²) and thus many termites and beetles have no physical difficulty in boring through foils made from such common metals as copper, lead, tin, and zinc. Behind the mandibles lie the maxillae, each consisting of a basal part composed of the proximal **cardo** and the more distal **stipes** and, attached to the stipes, two lobes – the mesal **lacinia** and the lateral **galea** – and a lateral, segmented **maxillary palp**, or **palpus** (plural: **palps** or **palpi**). Functionally, the maxillae assist the mandibles in processing food; the pointed and sclerotized laciniae hold and macerate the food, whereas the galeae and palps bear sensory setae (mechanoreceptors) and chemoreceptors which sample items before ingestion. The appendages of the sixth segment of the head are fused with the sternum to form the labium, which is believed to be homologous to the second maxillae of Crustacea. In prognathous insects, such as the earwig, the labium attaches to the ventral surface of the head via a ventromedial sclerotized plate called the **gula** (Fig. 2.10). There are two main parts to the labium: the proximal **postmentum**, closely connected to the posteroventral surface of the

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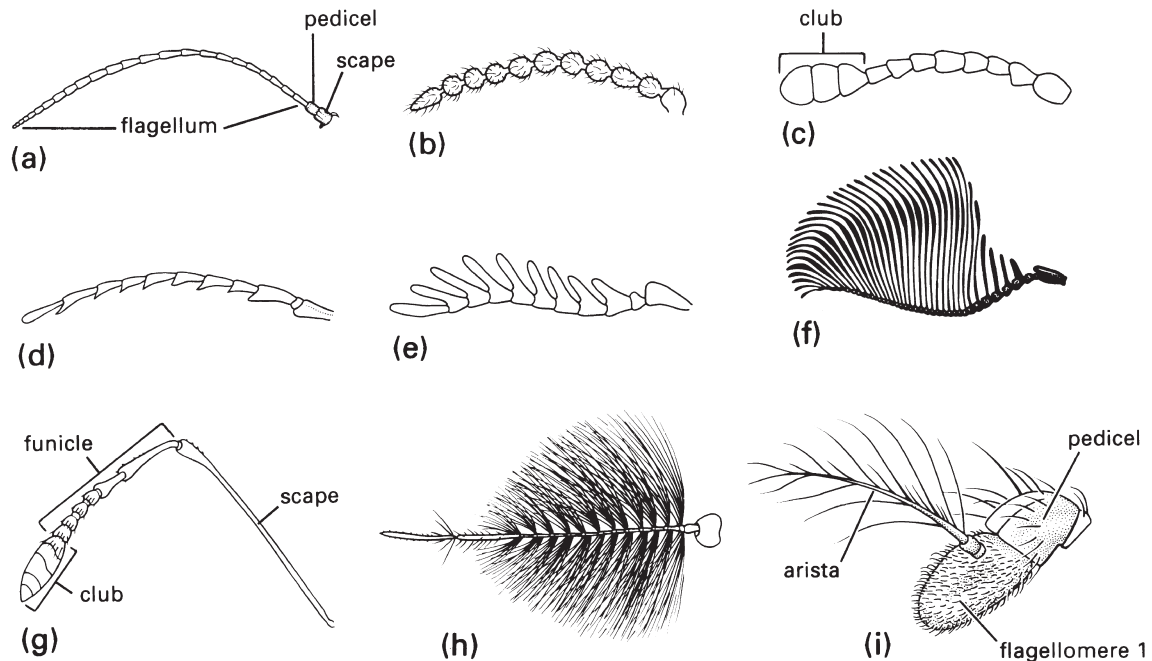


Fig. 2.17 Some types of insect antennae: (a) filiform – linear and slender; (b) moniliform – like a string of beads; (c) clavate or capitate – distinctly clubbed; (d) serrate – saw-like; (e) pectinate – comb-like; (f) flabellate – fan-shaped; (g) geniculate – elbowed; (h) plumose – bearing whorls of setae; and (i) aristate – with enlarged third segment bearing a bristle.

antenna typically has three main divisions (Fig. 2.17a): the first segment, or **scape**, generally is larger than the other segments and is the basal stalk; the second segment, or **pedicel**, nearly always contains a sensory organ known as **Johnston's organ**, which responds to movement of the distal part of the antenna relative to the pedicel; the remainder of the antenna, called the **flagellum**, is often filamentous and multisegmented (with many **flagellomeres**), but may be reduced or variously modified (Fig. 2.17b–i). The antennae are reduced or almost absent in some larval insects.

Numerous sensory organs, or **sensilla** (singular: **sensillum**), in the form of hairs, pegs, pits, or cones, occur on antennae and function as chemoreceptors, mechanoreceptors, thermoreceptors, and hygrometers (Chapter 4). Antennae of male insects may be more elaborate than those of the corresponding females, increasing the surface area available for detecting female sex pheromones (section 4.3.2).

The mouthparts, other than the mandibles, are well endowed with chemoreceptors and tactile setae. These sensilla are described in detail in Chapter 4.

2.4 THE THORAX

The thorax is composed of three segments: the first or **prothorax**, the second or **mesothorax**, and the third or **metathorax**. Primitively, and in apterygotes (bristletails and silverfish) and immature insects, these segments are similar in size and structural complexity. In most winged insects the mesothorax and metathorax are enlarged relative to the prothorax and form a **pterothorax**, bearing the wings and associated musculature. Wings occur only on the second and third segments in extant insects although some fossils have prothoracic winglets (Fig. 8.2) and homeotic mutants may develop prothoracic wings or wing buds. Almost all nymphal and adult insects have three pairs of thoracic legs – one pair per segment. Typically the legs are used for walking, although various other functions and associated modifications occur (section 2.4.1). Openings (**spiracles**) of the gas-exchange, or tracheal, system (section 3.5) are present laterally on the second and third thoracic segments at most with one pair per segment. However, a secondary condition in some

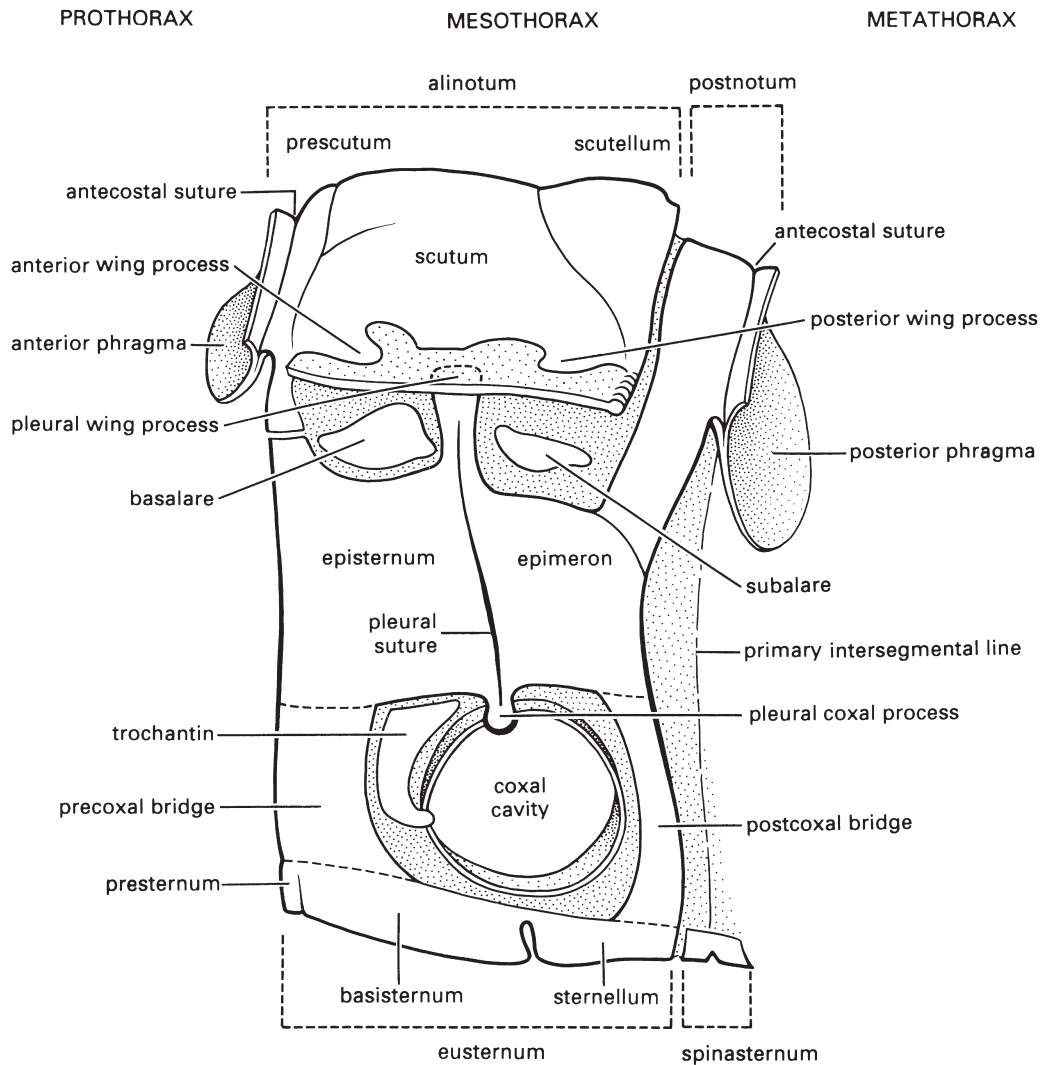


Fig. 2.18 Diagrammatic lateral view of a wing-bearing thoracic segment, showing the typical sclerites and their subdivisions. (After Snodgrass 1935.)

insects is for the mesothoracic spiracles to open on the prothorax.

The tergal plates of the thorax are simple structures in apterygotes and in many immature insects, but are variously modified in winged adults. Thoracic terga are called **nota** (singular: **notum**), to distinguish them from the abdominal terga. The **pronotum** of the prothorax may be simple in structure and small in comparison with the other nota, but in beetles, mantids, many

bugs, and some Orthoptera the pronotum is expanded and in cockroaches it forms a shield that covers part of the head and mesothorax. The pterothoracic nota each have two main divisions – the anterior wing-bearing **alinothum** and the posterior phragma-bearing **postnotum** (Fig. 2.18). **Phragmata** (singular: **phragma**) are plate-like apodemes that extend inwards below the **antecostal sutures**, marking the primary intersegmental folds between segments; phragmata provide

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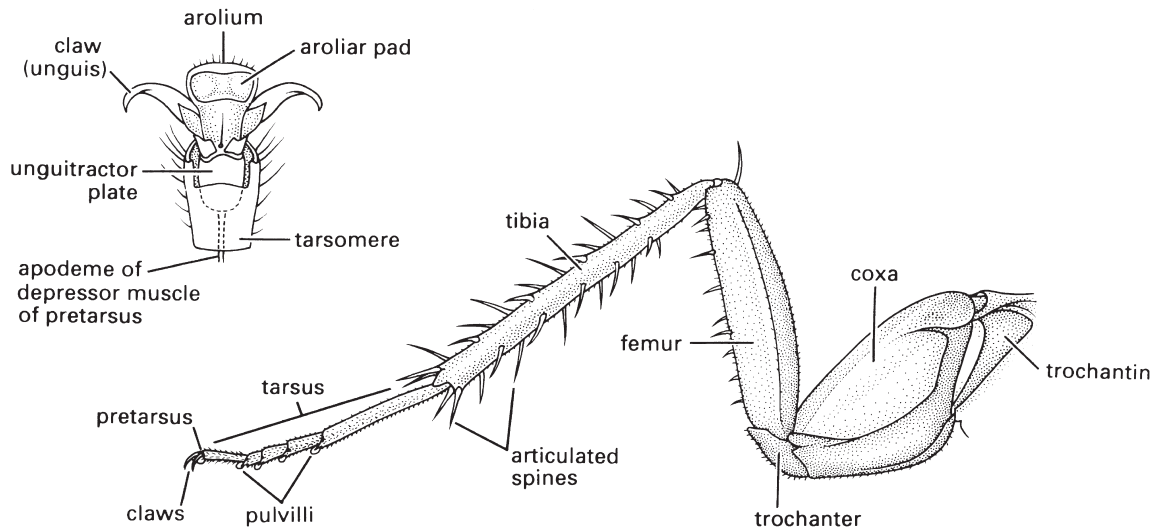


Fig. 2.19 The hind leg of a cockroach, *Periplaneta americana* (Blattodea: Blattidae), with enlargement of ventral surface of pretarsus and last tarsomere. (After Cornwell 1968; enlargement after Snodgrass 1935.)

attachment for the longitudinal flight muscles (Fig. 2.7d). Each alinotum (sometimes confusingly referred to as a “notum”) may be traversed by sutures that mark the position of internal strengthening ridges and commonly divide the plate into three areas – the anterior **prescutum**, the **scutum**, and the smaller posterior **scutellum**.

The lateral pleural sclerites are believed to be derived from the subcoxal segment of the ancestral insect leg (Fig. 8.4a). These sclerites may be separate, as in silverfish, or fused into an almost continuous sclerotic area, as in most winged insects. In the pterothorax, the pleuron is divided into two main areas – the anterior **episternum** and the posterior **epimeron** – by an internal **pleural ridge**, which is visible externally as the **pleural suture** (Fig. 2.18); the ridge runs from the **pleural coxal process** (which articulates with the coxa) to the **pleural wing process** (which articulates with the wing), providing reinforcement for these articulation points. The **epipleurites** are small sclerites beneath the wing and consist of the **basalaria** anterior to the pleural wing process and the posterior **subalaria**, but often reduced to just one basalare and one subalare, which are attachment points for some direct flight muscles. The **trochantin** is the small sclerite anterior to the coxa.

The degree of ventral sclerotization on the thorax varies greatly in different insects. Sternal plates, if pre-

sent, are typically two per segment: the **eusternum** and the following intersegmental sclerite or **interster-nite** (Fig. 2.7c), commonly called the **spinasternum** (Fig. 2.18) because it usually has an internal apodeme called the **spina** (except for the metasternum which never has a spinasternum). The eusterna of the prothorax and mesothorax may fuse with the spinasterna of their segment. Each eusternum may be simple or divided into separate sclerites – typically the **prester-num**, **basisternum**, and **sternellum**. The eusternum may be fused laterally with one of the pleural sclerites and is then called the **laterosternite**. Fusion of the sternal and pleural plates may form **precoxal** and **postcoxal bridges** (Fig. 2.18).

2.4.1 Legs

In most adult and nymphal insects, segmented **fore**, **mid**, and **hind legs** occur on the prothorax, mesothorax, and metathorax, respectively. Typically, each leg has six segments (Fig. 2.19) and these are, from proximal to distal: **coxa**, **trochanter**, **femur**, **tibia**, **tarsus**, and **pretarsus** (or more correctly **post-tarsus**) with claws. Additional segments – the prefemur, patella, and basitarsus (Fig. 8.4a) – are recognized in some fossil insects and other arthropods, such as arachnids, and one or more of these segments are evident in some

(in most prognathous heads) through the extension ventrally and anteriorly of a ventral cervical sclerite to form the *gula*. At the same time the basal segment of the labium may also become elongated (Figure 3.4A).

3.2. Head Appendages

3.2.1. Antennae

A pair of antennae are found on the head of the pterygote insects and the apterygote groups with the exception of the Protura. However, in the larvae of many higher Hymenoptera and Diptera they are reduced to a slight swelling or disc.

In a typical antenna (Figure 3.6) there are three principal components: the basal *scape* by which the antenna is attached to the head, the *pedicel* containing Johnston's organ (Chapter 12, Section 3.1), and the *flagellum*, which is usually long and annulated. According to Kukulová-Peck (1992), the scape, pedicel, and flagellum are homologous with the subcoxa, coxa, and remaining segments, respectively, of the ancestral leg (Figure 3.21A). The annuli on the flagellum do not correspond with the ancestral leg joints; that is, the annuli are constrictions, not sutures. The scape is set in a membranous socket and surrounded by the antennal sclerite on which a single articulation may occur. In the majority of insects movement of the whole antenna is effected by muscles inserted on the scape and attached to the cranium or tentorium. However, in Collembola there is no Johnston's organ and each antennal segment is moved by a muscle inserted in the previous segment.

Although retaining the basic structure outlined above, the antennae take on a wide variety of forms (Figure 3.7) related to their varied functions. Generally, it is the flagellum that is modified. For example, in some male moths and beetles the flagellum is plumose and flabellate, respectively, providing a large surface area for the numerous chemosensilla that give these insects their remarkable sense of smell (see Chapter 12, Section 4). By contrast, the plumose nature of the antennae of male mosquitoes makes them highly sensitive to the sounds generated by the beating of the female's wings (Chapter 12, Section 3.1). Other functions of antennae include touching, temperature and humidity perception, grasping prey, and holding on to the female during mating (Schneider, 1964; Zacharuk, 1985). For taxonomists, this variety of form may be an important diagnostic feature.

3.2.2. Mouthparts

The mouthparts consist of the labrum, a pair of mandibles, a pair of maxillae, the labium, and the hypopharynx. In Collembola, Protura, and Diplura the mouthparts are

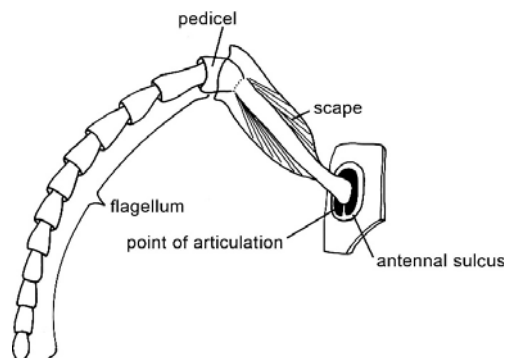


FIGURE 3.6. Structure of an antenna. [From R. E. Snodgrass, *Principles of Insect Morphology*. Copyright 1935 by McGraw-Hill, Inc. Used with permission of McGraw-Hill Book Company.]

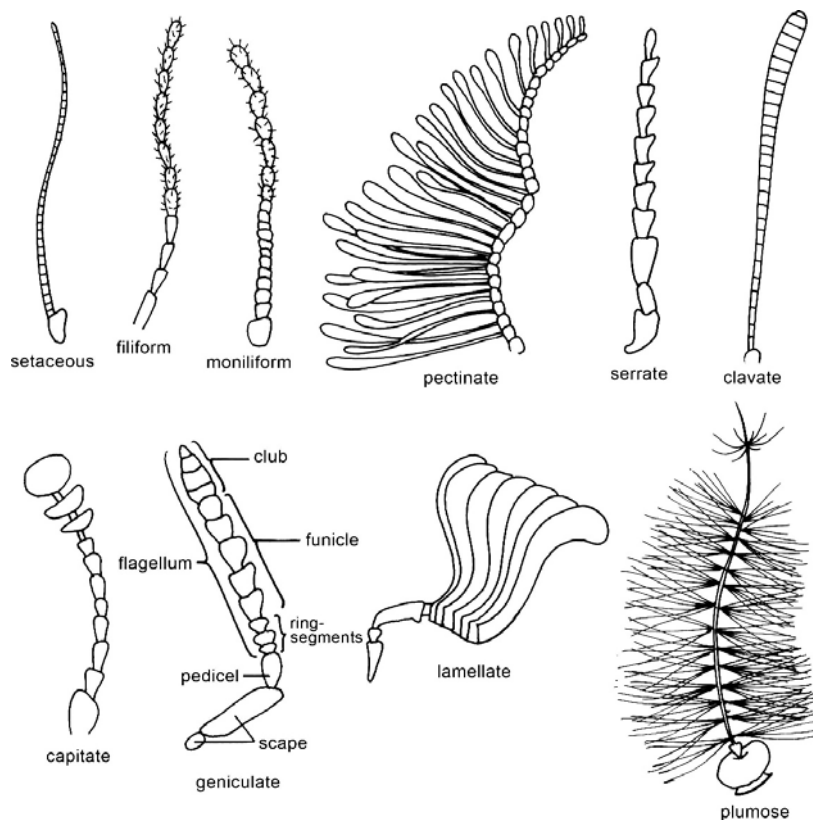


FIGURE 3.7. Types of antennae. [After A. D. Imms, 1957, *A General Textbook of Entomology*, 9th ed. (revised by O. W. Richards and R. G. Davies), Methuen and Co.]

enclosed within a cavity formed by the ventrolateral extension of the genae, which fuse in the midline (the *entognathous* condition). In Microcoryphia, Zygentoma, and Pterygota the mouthparts project freely from the head capsule, a condition described as *ectognathous*. The form of the mouthparts is extremely varied (see below), and it is appropriate to describe first their structure in the more primitive chewing condition.

Typical Chewing Mouthparts. In a typical chewing insect the labrum (Figure 3.3A) is a broadly flattened plate hinged to the clypeus. Its ventral (inner) surface is usually membranous and forms the lobe-like epipharynx, which bears mechano- and chemosensilla.

The mandible (Figure 3.8A) is a heavily sclerotized, rather compact structure having almost always a dicondylic articulation with the subgena. Its functional area varies according to the diet of the insect. In herbivorous forms there are both cutting edges and grinding surfaces on the mandible. The cutting edges are typically strengthened by the addition of zinc, manganese or, rarely, iron, in amounts up to about 4% of the dry weight. In carnivorous species the mandible possesses sharply pointed “teeth” for cutting and tearing. In Microcoryphia the mandible has a single articulation with the cranium and, as a result, much greater freedom of movement.

Of all of the mouthparts the maxilla (Figure 3.8B) retains most closely the structure of the primitive insectan limb. The basal segment is divided by a transverse line of flexure into two subsegments, a proximal *cardo* and a distal *stipes*. The cardo carries the single condyle with which the maxilla articulates with the head. Both the cardo and stipes are, however, attached on their entire inner surface to the membranous head pleuron. The stipes

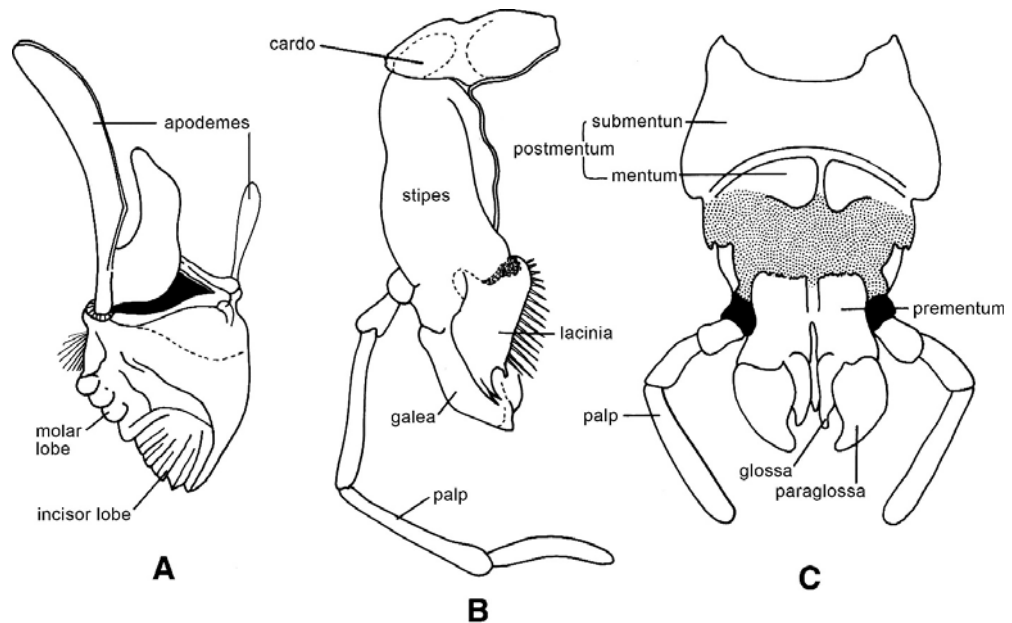


FIGURE 3.8. Structure of (A) mandible, (B) maxilla, and (C) labium of a typical chewing insect. [From R. E. Snodgrass, *Principles of Insect Morphology*. Copyright 1935 by McGraw-Hill, Inc. Used with permission of McGraw-Hill Book Company.]

bears an inner *lacinia* and outer *galea*, and a *maxillary palp*. This basic structure is found in both apterygotes and the majority of chewing pterygotes, although in some forms reduction or loss of the lacinia, galea, or palp occurs. In Kukalová-Peck's (1991) view the cardo and stipes correspond to the subcoxa and coxa + trochanter, respectively, of the ancestral appendage; the lacinia and the galea to the coxal and trochanteral endites, respectively; and the palp to the remaining segments. The laciniae assist in holding and masticating the food, while the galeae and palps are equipped with a variety of mechano- and chemosensilla.

The labium (Figure 3.8C) is formed by the medial fusion of the primitive appendages of the postmaxillary segment, together with, in its basal region, a small part of the sternum of that segment. The labium is divided into two primary regions, a proximal *postmentum* corresponding to the maxillary cardines plus the sternal component, and a distal *prementum* homologous with the maxillary stipites. The postmentum is usually subdivided into *submentum* and *mentum* regions. The prementum bears a pair of inner *glossae* and a pair of outer *paraglossae*, homologous with the maxillary laciniae and galeae, respectively, and a pair of *labial palps*. When the glossae and paraglossae are fused they form a single structure termed the *ligula*.

Arising as a median, mainly membranous, lobe from the floor of the head capsule and projecting ventrally into the preoral cavity is the hypopharynx (Figures 3.3D and 3.9). It is frequently fused to the labium. In a few insects (bristletails and mayfly larvae) a pair of lobes, the *superlinguae*, which arise embryonically in the mandibular segment, become associated with the hypopharynx. The hypopharynx divides the preoral cavity into anterior and posterior spaces, the upper parts of which are the *cibarium* (leading to the mouth) and *salivarium* (into which the salivary duct opens), respectively.

Mouthpart Modifications. The typical chewing mouthparts described above can be found with minor modifications in Odonata, Plecoptera, the orthopteroids and blattoids,

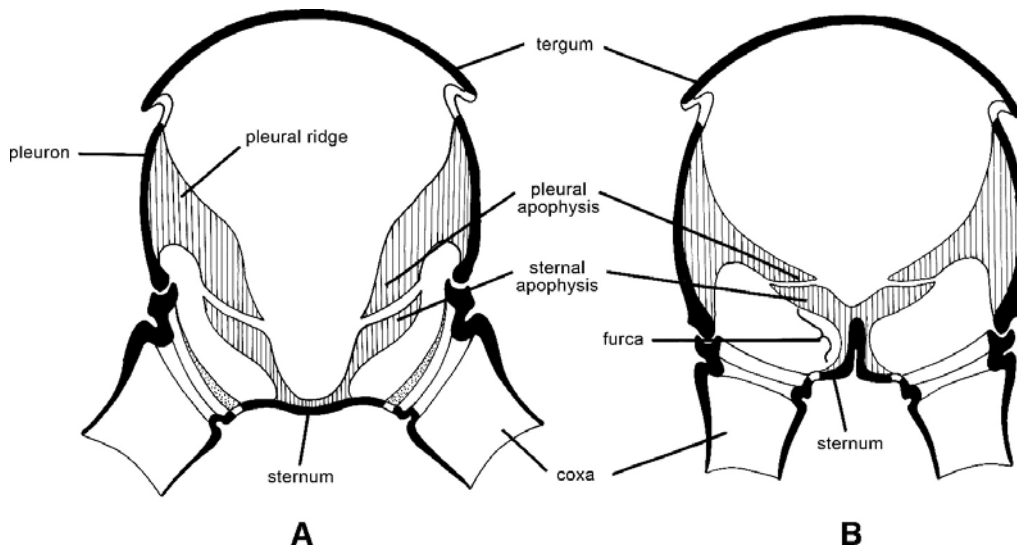


FIGURE 3.19. Diagrammatic cross-sections of the thorax to show the endoskeleton. (A) Normal condition; and (B) condition when furca present. [From R. E. Snodgrass, *Principles of Insect Morphology*. Copyright 1935 by McGraw-Hill, Inc. Used with permission of McGraw-Hill Book Company.]

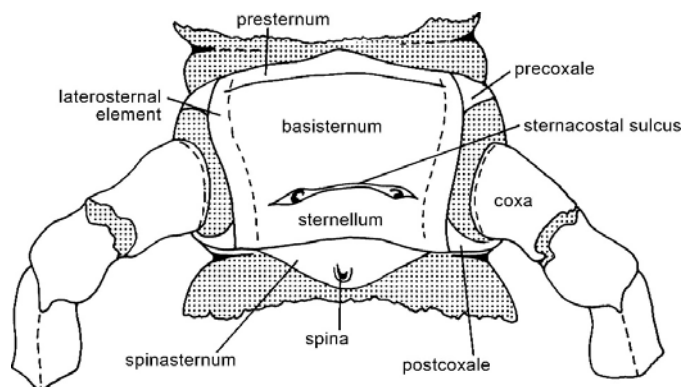


FIGURE 3.20. Ventral view of a generalized thoracic sternum. [From R. E. Snodgrass, *Principles of Insect Morphology*. Copyright 1935 by McGraw-Hill, Inc. Used with permission of McGraw-Hill Book Company.]

of the neck region. The *pronotum* especially is different, lacking the antecostal region and phragma through neck membranization. In some groups (e.g., Orthoptera, Hemiptera, and Coleoptera) the pronotum is greatly enlarged; in others it is reduced to a narrow band between the head and mesothorax. In those orders whose members have a single pair of functional wings, the tergal plates of the segment from which the wings are absent are usually reduced in size.

4.3. Thoracic Appendages

4.3.1. Legs

In the vast majority of insects each thoracic segment bears a pair of legs. In the cases where legs are absent, for example, in all dipteran, and many coleopteran and hymenopteran larvae, the condition is secondary. Typically, the legs are concerned with walking and running, but they may be specialized for a range of other physical functions, some of which are described below. In addition, for many insects they are important organs of taste

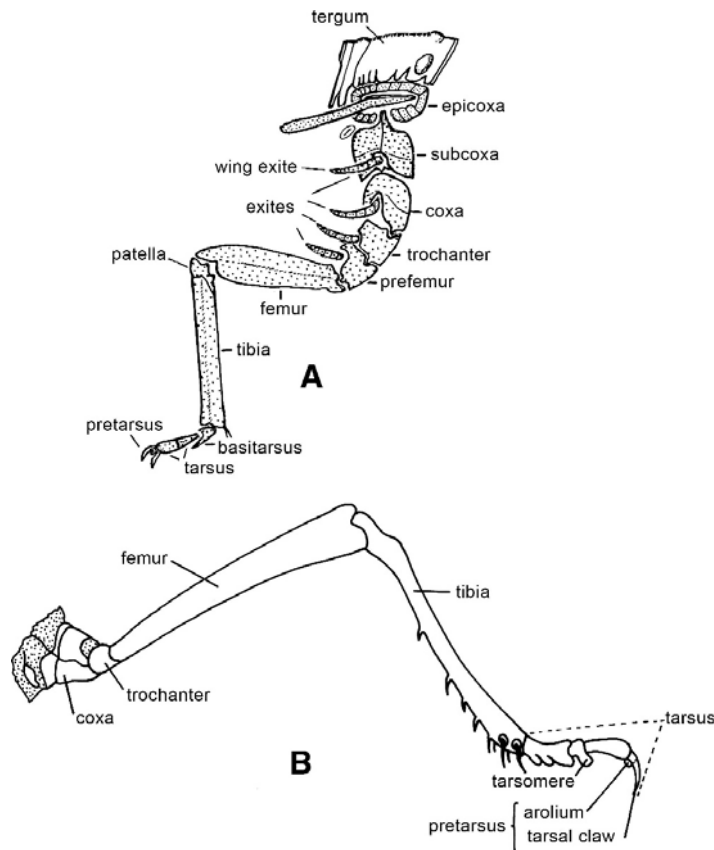


FIGURE 3.21. (A) Hypothetical ground plan of leg podites in ancestral insect; and (B) typical leg of a modern insect. [A, after J. Kukalová-Peck, 1987, New Carboniferous Diplura, Monura, and Thysanura, the hexapod ground plan, and the role of thoracic side lobes in the origin of wings (Insecta), *Can. J. Zool.* **65**:2327–2345. By permission of the National Research Council of Canada and the author. B, from R. E. Snodgrass, *Principles of Insect Morphology*. Copyright 1935 by McGraw-Hill, Inc. Used with permission of McGraw-Hill Book Company.]

(see Chapter 12, Section 4.1). As noted earlier, Kukalová-Peck (1987) suggested that the ancestral limb included 11 podites, as well as exites and endites (Figure 3.21A). Because of fusion of podites with the pleuron or with adjacent podites the full complement of podites in the leg is never seen, though in many fossils and a few extant Ephemeroptera and Odonata as many as eight podites can be identified.

Typical Walking Leg. The leg consists of six podites, the coxa, trochanter, femur, tibia, tarsus, and pretarsus (Figure 3.21B). Between adjacent parts are a narrow, annulated membrane, the *corium*, and usually a mono- or dicondylic articulation.

The coxa is a short, thick segment strengthened at its proximal end by an internal ridge, the *basicosta* (Figure 3.22). The coxa usually has a dicondylic articulation with the pleuron. In some orders the *basicostal sulcus* is U- or V-shaped over the posterior half of the coxa (Figure 3.22). The sclerite thus demarcated becomes thickened and is known as the *meron*. The trochanter is a small segment. It always has a dicondylic articulation with the coxa but is usually firmly fixed to the femur, which is generally the largest leg segment. Following the slender tibia is the tarsus, a segment that is usually subdivided into between two and five *tarsomeres* and a pretarsus. The pretarsus, in most insects, takes the form of a pair of *tarsal claws* and a median lobe, the *arolium* (Figure 3.23).

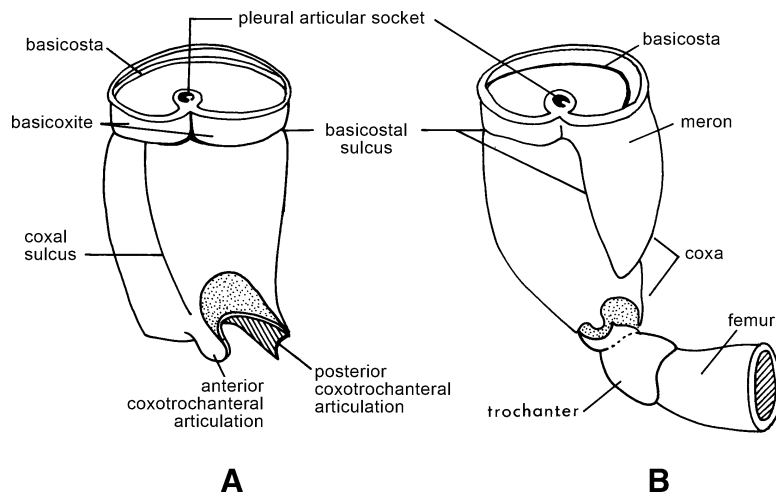


FIGURE 3.22. Structure of the coxa. (A) Lateral view; and (B) coxa with a well-developed meron. [From R. E. Snodgrass, *Principles of Insect Morphology*. Copyright 1935 by McGraw-Hill, Inc. Used with permission of McGraw-Hill Book Company.]

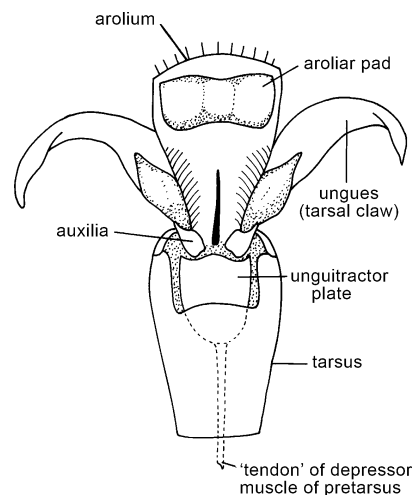


FIGURE 3.23. Distal part of a leg showing the arolium and claws. [From R. E. Snodgrass, *Principles of Insect Morphology*. Copyright 1935 by McGraw-Hill, Inc. Used with permission of McGraw-Hill Book Company.]

Leg Modifications. The functions for which the legs have become modified include jumping, swimming, grasping, digging, sound production, and cleaning.

In Orthoptera and a few Coleoptera (e.g., flea beetles) the femur on the hindleg is greatly enlarged to accommodate the extensor muscles of the tibia used in jumping. In swimming insects, the tibia and tarsus of the hindlegs (occasionally also the middle legs) are flattened and bear rigid hairs around the periphery (Figure 3.24A). Legs modified for grasping are found in predaceous insects such as the mantis and giant water bug, in ectoparasitic lice, and in males of various species where they are used for hanging onto the female during mating. In the mantis, the tibia and femur of the foreleg are equipped with spines and operate together as pincers (Figure 3.24B). The foreleg of a louse is short and thick and has at its tip a single, large tarsal claw that folds back against the tibial process (Figure 3.24C). Suctorial pads have been developed on the fore limbs in males of many beetle species. In *Dytiscus*, for example, the first three tarsomeres are flattened and possess large numbers of cuticular

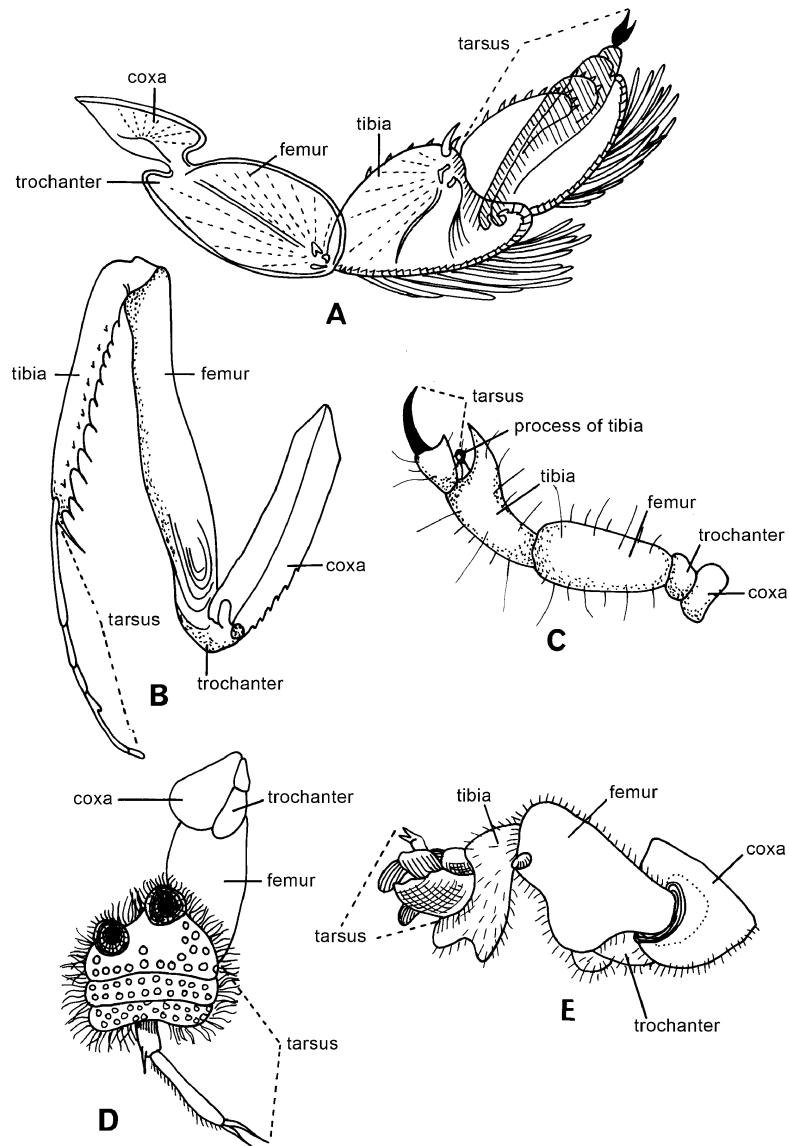


FIGURE 3.24. Leg modifications. (A) Hindleg of *Gyrinus* (swimming); (B) foreleg of a mantis (grasping prey); (C) foreleg of a louse (attachment to host); (D) foreleg of *Dytiscus* (holding onto female); and (E) foreleg of a mole cricket (digging). [A, after L. C. Miall, 1922, *The Natural History of Aquatic Insects*, published by Macmillan Ltd. B, D, E, after J. W. Folsom, 1906, *Entomology: With Special Reference to Its Biological and Economic Aspects*.]

cups, two of which are extremely enlarged (Figure 3.24D). The forelegs of soil-dwelling insects such as the mole cricket (Figure 3.24E), cicadas, and various beetles are modified for digging. The legs are large, heavily sclerotized, and possess stout claws. The tarsomeres are reduced in number or may disappear entirely in some forms. In many Orthoptera sounds are produced when the hind femora, which have a row of cuticular pegs on their inner surface, are rubbed against ridged veins on the fore wing. Modifications to the forelegs for cleaning purposes are found in many insects. In certain Coleoptera and Hymenoptera, for example, the honey bee (Figure 3.25A), a notch lined with hairs occurs on the metatarsus

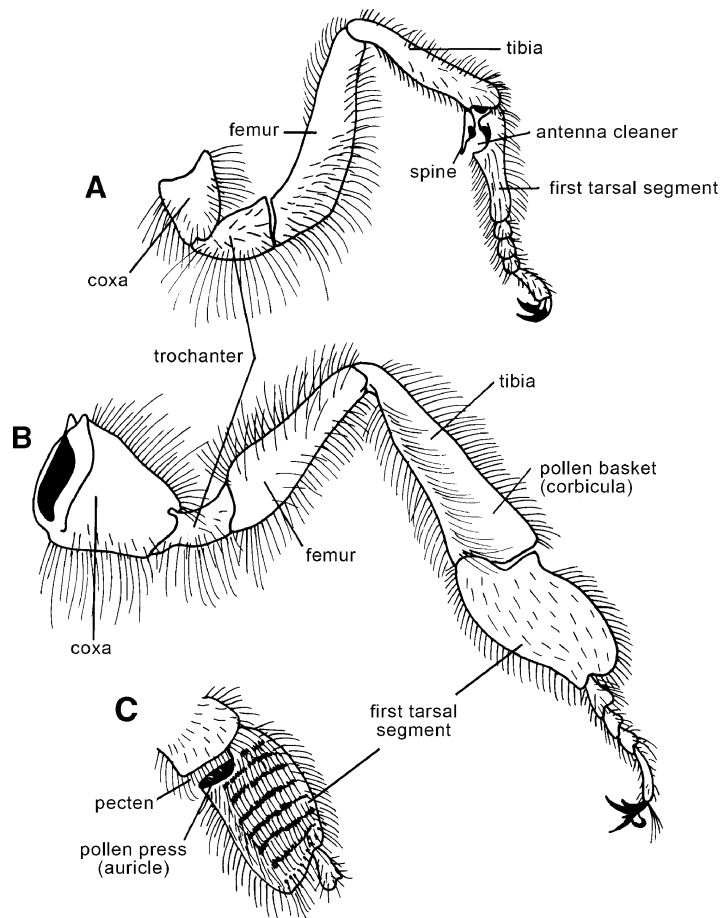


FIGURE 3.25. Leg modifications in the worker honey bee. (A) Foreleg showing the cleaning notch, (B) outer surface of hindleg showing the pollen basket, and (C) inner surface of hind tarsus and tip of hind tibia showing rake and pollen press. [After R. E. Snodgrass, 1925. *Anatomy and Physiology of the Honey bee*, McGraw-Hill Book Company.]

of the foreleg through which the antenna can be drawn and cleaned. The hindlegs of the bee are modified for pollen collection (Figure 3.25B). Rows of hairs, the *comb*, on the inner side of the first tarsomere scrape pollen off the abdomen. The *rake*, a fringe of hairs at the distal end of the tibia, then collects the pollen from the comb on the opposite leg and transfers it to the pollen *press*. When the press is closed, the pollen is pushed up into the pollen *basket*, where it is stored until the bee returns to its nest.

4.3.2. Wings

The majority of adult Pterygota have one or two pairs of functional wings. The complete absence of wings is a secondary condition, associated with the habits of the group concerned, for example, soil-dwelling or endoparasitism. The wings may be modified for a variety of purposes other than flight.

Development and General Structure. Regardless of its evolutionary origin (Chapter 2, Section 3.1) a wing contains the usual integumental elements (cuticle, epidermis, and

(in most prognathous heads) through the extension ventrally and anteriorly of a ventral cervical sclerite to form the *gula*. At the same time the basal segment of the labium may also become elongated (Figure 3.4A).

3.2. Head Appendages

3.2.1. Antennae

A pair of antennae are found on the head of the pterygote insects and the apterygote groups with the exception of the Protura. However, in the larvae of many higher Hymenoptera and Diptera they are reduced to a slight swelling or disc.

In a typical antenna (Figure 3.6) there are three principal components: the basal *scape* by which the antenna is attached to the head, the *pedicel* containing Johnston's organ (Chapter 12, Section 3.1), and the *flagellum*, which is usually long and annulated. According to Kukulová-Peck (1992), the scape, pedicel, and flagellum are homologous with the subcoxa, coxa, and remaining segments, respectively, of the ancestral leg (Figure 3.21A). The annuli on the flagellum do not correspond with the ancestral leg joints; that is, the annuli are constrictions, not sutures. The scape is set in a membranous socket and surrounded by the antennal sclerite on which a single articulation may occur. In the majority of insects movement of the whole antenna is effected by muscles inserted on the scape and attached to the cranium or tentorium. However, in Collembola there is no Johnston's organ and each antennal segment is moved by a muscle inserted in the previous segment.

Although retaining the basic structure outlined above, the antennae take on a wide variety of forms (Figure 3.7) related to their varied functions. Generally, it is the flagellum that is modified. For example, in some male moths and beetles the flagellum is plumose and flabellate, respectively, providing a large surface area for the numerous chemosensilla that give these insects their remarkable sense of smell (see Chapter 12, Section 4). By contrast, the plumose nature of the antennae of male mosquitoes makes them highly sensitive to the sounds generated by the beating of the female's wings (Chapter 12, Section 3.1). Other functions of antennae include touching, temperature and humidity perception, grasping prey, and holding on to the female during mating (Schneider, 1964; Zacharuk, 1985). For taxonomists, this variety of form may be an important diagnostic feature.

3.2.2. Mouthparts

The mouthparts consist of the labrum, a pair of mandibles, a pair of maxillae, the labium, and the hypopharynx. In Collembola, Protura, and Diplura the mouthparts are

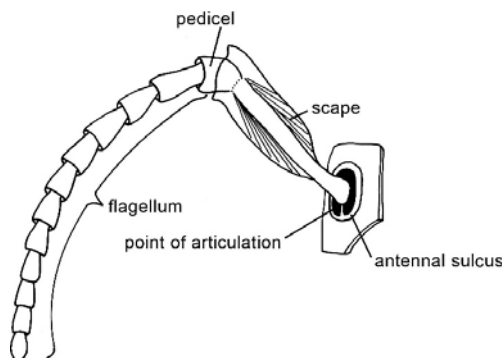


FIGURE 3.6. Structure of an antenna. [From R. E. Snodgrass, *Principles of Insect Morphology*. Copyright 1935 by McGraw-Hill, Inc. Used with permission of McGraw-Hill Book Company.]

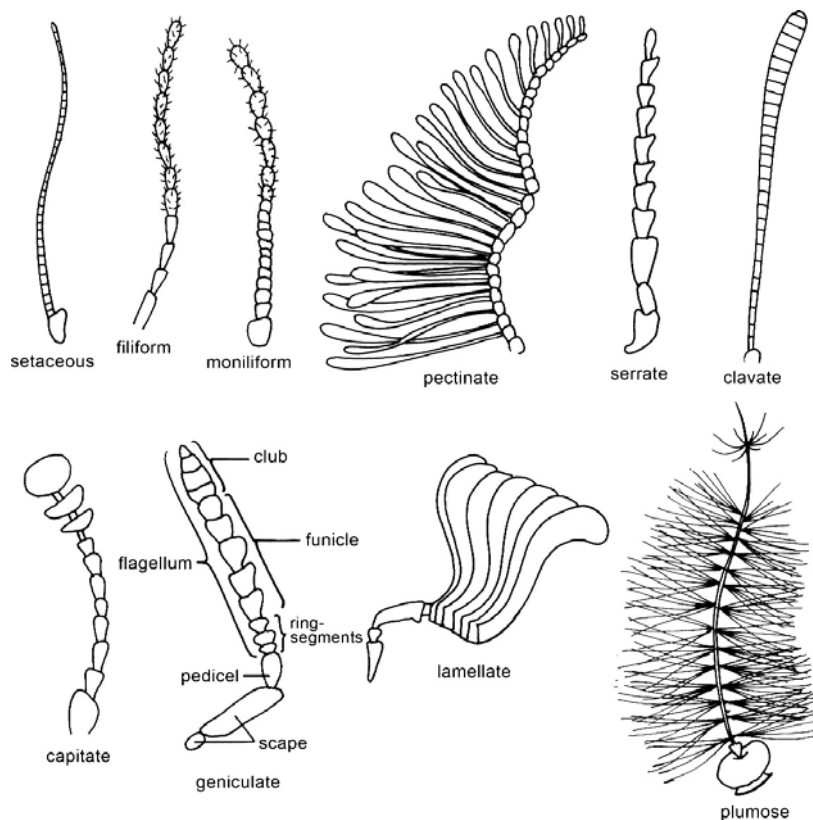


FIGURE 3.7. Types of antennae. [After A. D. Imms, 1957, *A General Textbook of Entomology*, 9th ed. (revised by O. W. Richards and R. G. Davies), Methuen and Co.]

enclosed within a cavity formed by the ventrolateral extension of the genae, which fuse in the midline (the *entognathous* condition). In Microcoryphia, Zygentoma, and Pterygota the mouthparts project freely from the head capsule, a condition described as *ectognathous*. The form of the mouthparts is extremely varied (see below), and it is appropriate to describe first their structure in the more primitive chewing condition.

Typical Chewing Mouthparts. In a typical chewing insect the labrum (Figure 3.3A) is a broadly flattened plate hinged to the clypeus. Its ventral (inner) surface is usually membranous and forms the lobe-like epipharynx, which bears mechano- and chemosensilla.

The mandible (Figure 3.8A) is a heavily sclerotized, rather compact structure having almost always a dicondylic articulation with the subgena. Its functional area varies according to the diet of the insect. In herbivorous forms there are both cutting edges and grinding surfaces on the mandible. The cutting edges are typically strengthened by the addition of zinc, manganese or, rarely, iron, in amounts up to about 4% of the dry weight. In carnivorous species the mandible possesses sharply pointed “teeth” for cutting and tearing. In Microcoryphia the mandible has a single articulation with the cranium and, as a result, much greater freedom of movement.

Of all of the mouthparts the maxilla (Figure 3.8B) retains most closely the structure of the primitive insectan limb. The basal segment is divided by a transverse line of flexure into two subsegments, a proximal *cardo* and a distal *stipes*. The cardo carries the single condyle with which the maxilla articulates with the head. Both the cardo and stipes are, however, attached on their entire inner surface to the membranous head pleuron. The stipes

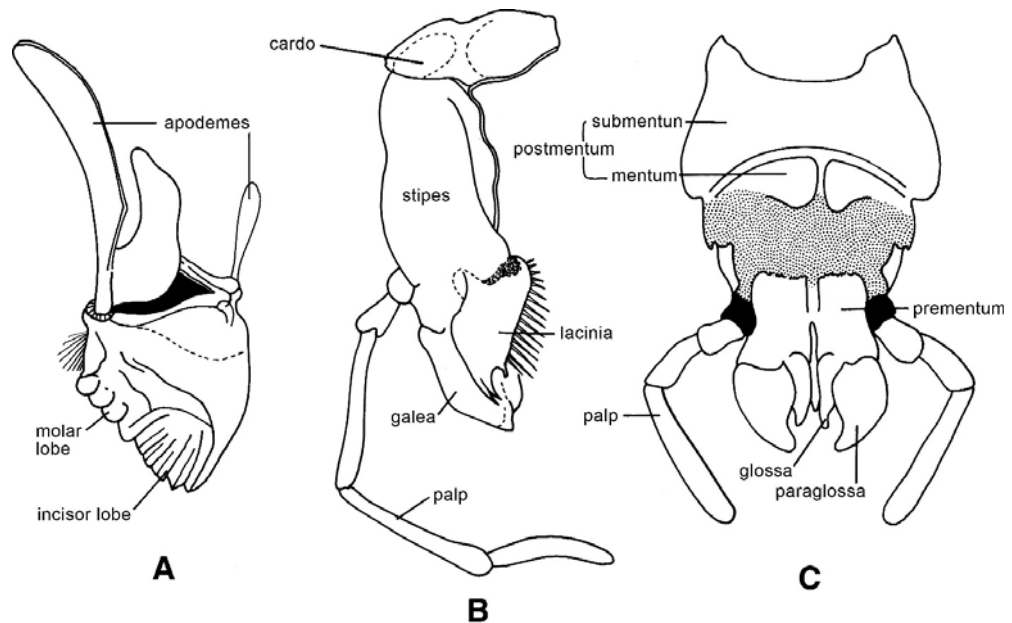


FIGURE 3.8. Structure of (A) mandible, (B) maxilla, and (C) labium of a typical chewing insect. [From R. E. Snodgrass, *Principles of Insect Morphology*. Copyright 1935 by McGraw-Hill, Inc. Used with permission of McGraw-Hill Book Company.]

bears an inner *lacinia* and outer *galea*, and a *maxillary palp*. This basic structure is found in both apterygotes and the majority of chewing pterygotes, although in some forms reduction or loss of the lacinia, galea, or palp occurs. In Kukalová-Peck's (1991) view the cardo and stipes correspond to the subcoxa and coxa + trochanter, respectively, of the ancestral appendage; the lacinia and the galea to the coxal and trochanteral endites, respectively; and the palp to the remaining segments. The laciniae assist in holding and masticating the food, while the galeae and palps are equipped with a variety of mechano- and chemosensilla.

The labium (Figure 3.8C) is formed by the medial fusion of the primitive appendages of the postmaxillary segment, together with, in its basal region, a small part of the sternum of that segment. The labium is divided into two primary regions, a proximal *postmentum* corresponding to the maxillary cardines plus the sternal component, and a distal *prementum* homologous with the maxillary stipites. The postmentum is usually subdivided into *submentum* and *mentum* regions. The prementum bears a pair of inner *glossae* and a pair of outer *paraglossae*, homologous with the maxillary laciniae and galeae, respectively, and a pair of *labial palps*. When the glossae and paraglossae are fused they form a single structure termed the *ligula*.

Arising as a median, mainly membranous, lobe from the floor of the head capsule and projecting ventrally into the preoral cavity is the hypopharynx (Figures 3.3D and 3.9). It is frequently fused to the labium. In a few insects (bristletails and mayfly larvae) a pair of lobes, the *superlinguae*, which arise embryonically in the mandibular segment, become associated with the hypopharynx. The hypopharynx divides the preoral cavity into anterior and posterior spaces, the upper parts of which are the *cibarium* (leading to the mouth) and *salivarium* (into which the salivary duct opens), respectively.

Mouthpart Modifications. The typical chewing mouthparts described above can be found with minor modifications in Odonata, Plecoptera, the orthopteroids and blattoids,

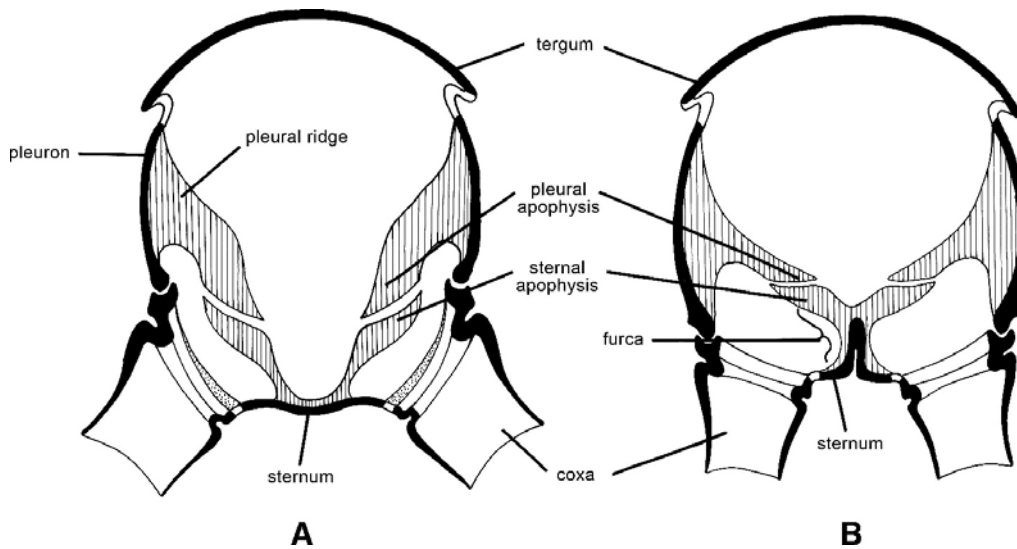


FIGURE 3.19. Diagrammatic cross-sections of the thorax to show the endoskeleton. (A) Normal condition; and (B) condition when furca present. [From R. E. Snodgrass, *Principles of Insect Morphology*. Copyright 1935 by McGraw-Hill, Inc. Used with permission of McGraw-Hill Book Company.]

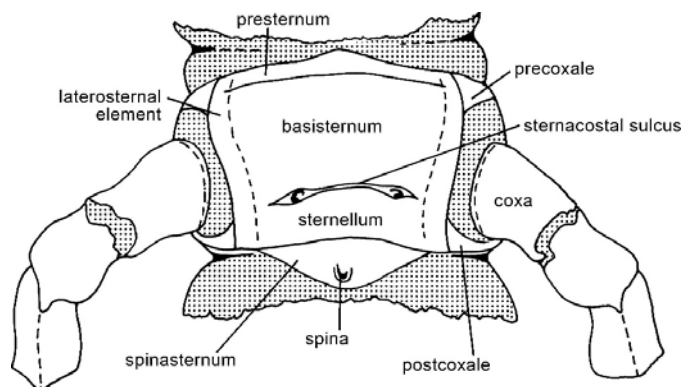


FIGURE 3.20. Ventral view of a generalized thoracic sternum. [From R. E. Snodgrass, *Principles of Insect Morphology*. Copyright 1935 by McGraw-Hill, Inc. Used with permission of McGraw-Hill Book Company.]

of the neck region. The *pronotum* especially is different, lacking the antecostal region and phragma through neck membranization. In some groups (e.g., Orthoptera, Hemiptera, and Coleoptera) the pronotum is greatly enlarged; in others it is reduced to a narrow band between the head and mesothorax. In those orders whose members have a single pair of functional wings, the tergal plates of the segment from which the wings are absent are usually reduced in size.

4.3. Thoracic Appendages

4.3.1. Legs

In the vast majority of insects each thoracic segment bears a pair of legs. In the cases where legs are absent, for example, in all dipteran, and many coleopteran and hymenopteran larvae, the condition is secondary. Typically, the legs are concerned with walking and running, but they may be specialized for a range of other physical functions, some of which are described below. In addition, for many insects they are important organs of taste

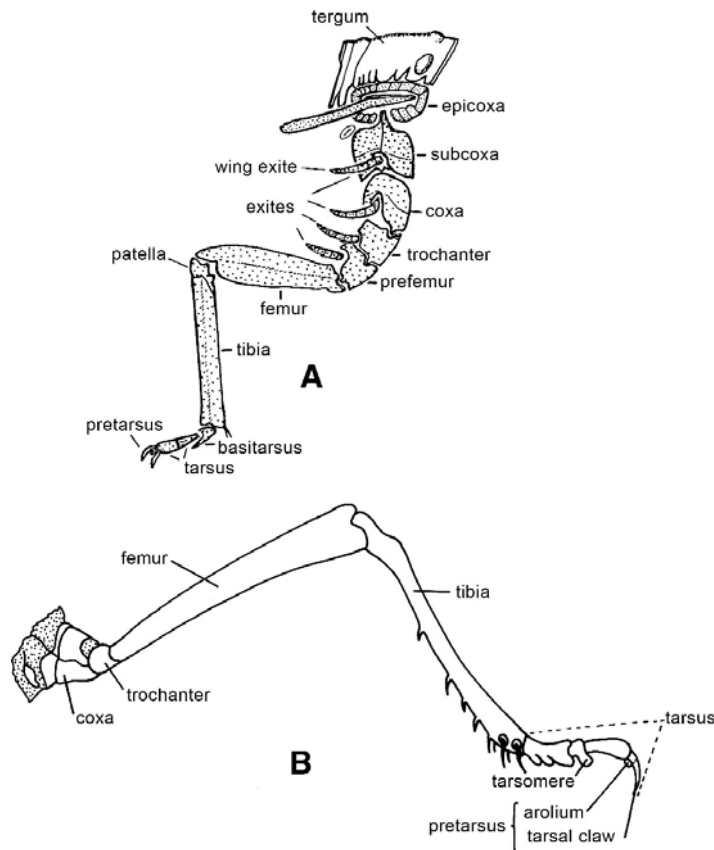


FIGURE 3.21. (A) Hypothetical ground plan of leg podites in ancestral insect; and (B) typical leg of a modern insect. [A, after J. Kukalová-Peck, 1987, New Carboniferous Diplura, Monura, and Thysanura, the hexapod ground plan, and the role of thoracic side lobes in the origin of wings (Insecta), *Can. J. Zool.* **65**:2327–2345. By permission of the National Research Council of Canada and the author. B, from R. E. Snodgrass, *Principles of Insect Morphology*. Copyright 1935 by McGraw-Hill, Inc. Used with permission of McGraw-Hill Book Company.]

(see Chapter 12, Section 4.1). As noted earlier, Kukalová-Peck (1987) suggested that the ancestral limb included 11 podites, as well as exites and endites (Figure 3.21A). Because of fusion of podites with the pleuron or with adjacent podites the full complement of podites in the leg is never seen, though in many fossils and a few extant Ephemeroptera and Odonata as many as eight podites can be identified.

Typical Walking Leg. The leg consists of six podites, the coxa, trochanter, femur, tibia, tarsus, and pretarsus (Figure 3.21B). Between adjacent parts are a narrow, annulated membrane, the *corium*, and usually a mono- or dicondylic articulation.

The coxa is a short, thick segment strengthened at its proximal end by an internal ridge, the *basicosta* (Figure 3.22). The coxa usually has a dicondylic articulation with the pleuron. In some orders the *basicostal sulcus* is U- or V-shaped over the posterior half of the coxa (Figure 3.22). The sclerite thus demarcated becomes thickened and is known as the *meron*. The trochanter is a small segment. It always has a dicondylic articulation with the coxa but is usually firmly fixed to the femur, which is generally the largest leg segment. Following the slender tibia is the tarsus, a segment that is usually subdivided into between two and five *tarsomeres* and a pretarsus. The pretarsus, in most insects, takes the form of a pair of *tarsal claws* and a median lobe, the *arolium* (Figure 3.23).

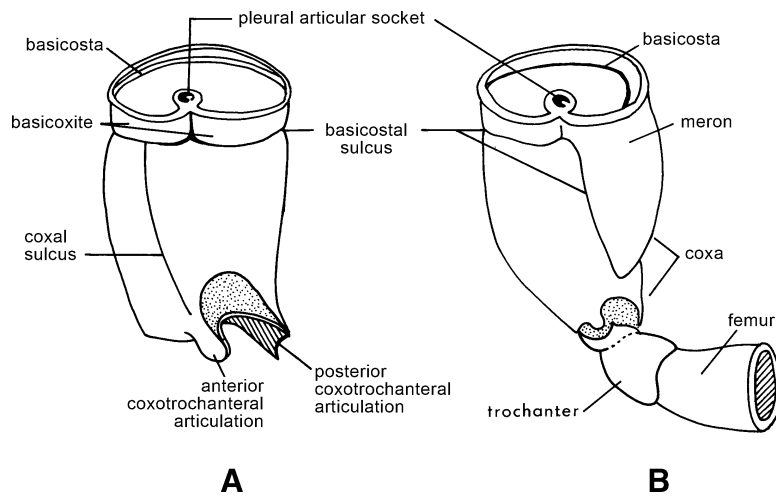


FIGURE 3.22. Structure of the coxa. (A) Lateral view; and (B) coxa with a well-developed meron. [From R. E. Snodgrass, *Principles of Insect Morphology*. Copyright 1935 by McGraw-Hill, Inc. Used with permission of McGraw-Hill Book Company.]

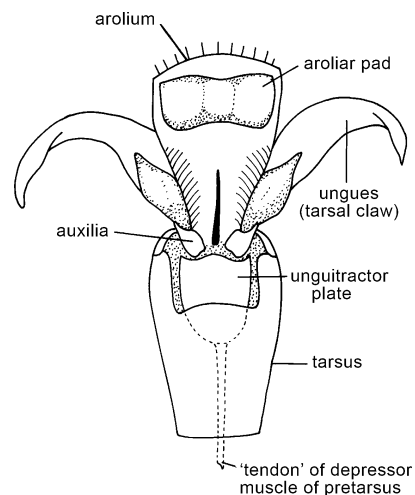


FIGURE 3.23. Distal part of a leg showing the arolium and claws. [From R. E. Snodgrass, *Principles of Insect Morphology*. Copyright 1935 by McGraw-Hill, Inc. Used with permission of McGraw-Hill Book Company.]

Leg Modifications. The functions for which the legs have become modified include jumping, swimming, grasping, digging, sound production, and cleaning.

In Orthoptera and a few Coleoptera (e.g., flea beetles) the femur on the hindleg is greatly enlarged to accommodate the extensor muscles of the tibia used in jumping. In swimming insects, the tibia and tarsus of the hindlegs (occasionally also the middle legs) are flattened and bear rigid hairs around the periphery (Figure 3.24A). Legs modified for grasping are found in predaceous insects such as the mantis and giant water bug, in ectoparasitic lice, and in males of various species where they are used for hanging onto the female during mating. In the mantis, the tibia and femur of the foreleg are equipped with spines and operate together as pincers (Figure 3.24B). The foreleg of a louse is short and thick and has at its tip a single, large tarsal claw that folds back against the tibial process (Figure 3.24C). Suctorial pads have been developed on the fore limbs in males of many beetle species. In *Dytiscus*, for example, the first three tarsomeres are flattened and possess large numbers of cuticular

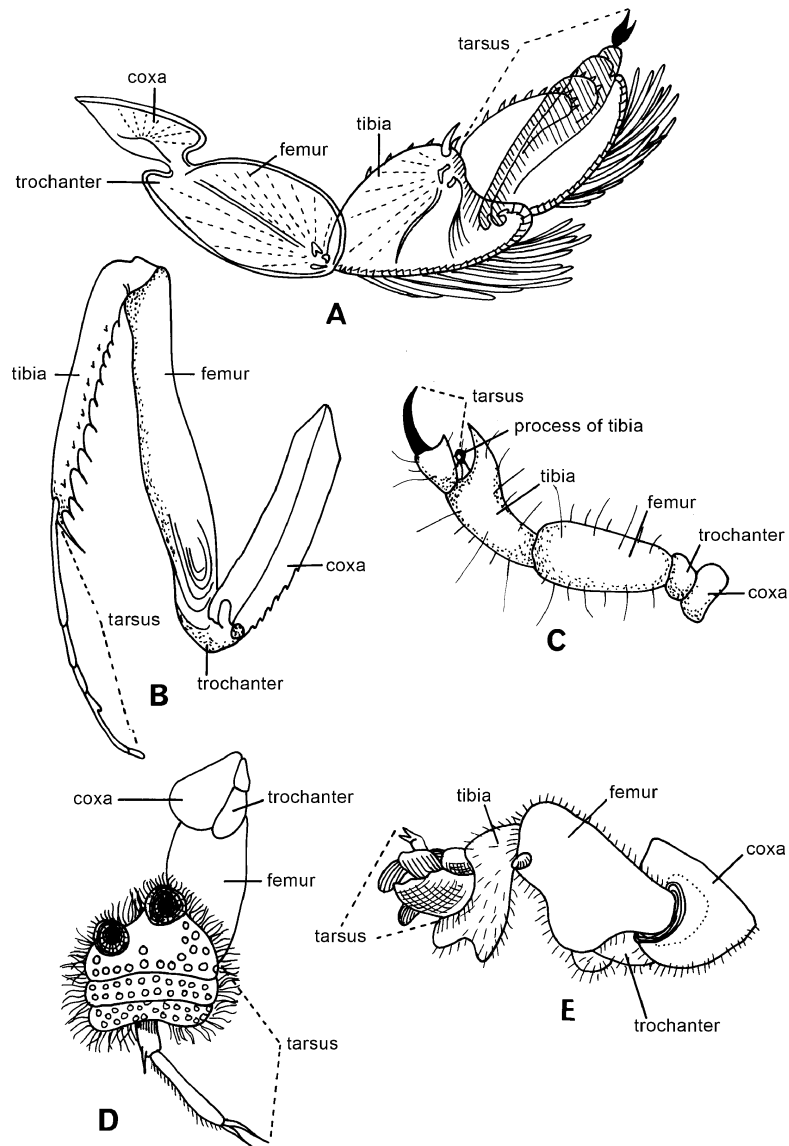


FIGURE 3.24. Leg modifications. (A) Hindleg of *Gyrinus* (swimming); (B) foreleg of a mantis (grasping prey); (C) foreleg of a louse (attachment to host); (D) foreleg of *Dytiscus* (holding onto female); and (E) foreleg of a mole cricket (digging). [A, after L. C. Miall, 1922, *The Natural History of Aquatic Insects*, published by Macmillan Ltd. B, D, E, after J. W. Folsom, 1906, *Entomology: With Special Reference to Its Biological and Economic Aspects*.]

cups, two of which are extremely enlarged (Figure 3.24D). The forelegs of soil-dwelling insects such as the mole cricket (Figure 3.24E), cicadas, and various beetles are modified for digging. The legs are large, heavily sclerotized, and possess stout claws. The tarsomeres are reduced in number or may disappear entirely in some forms. In many Orthoptera sounds are produced when the hind femora, which have a row of cuticular pegs on their inner surface, are rubbed against ridged veins on the fore wing. Modifications to the forelegs for cleaning purposes are found in many insects. In certain Coleoptera and Hymenoptera, for example, the honey bee (Figure 3.25A), a notch lined with hairs occurs on the metatarsus

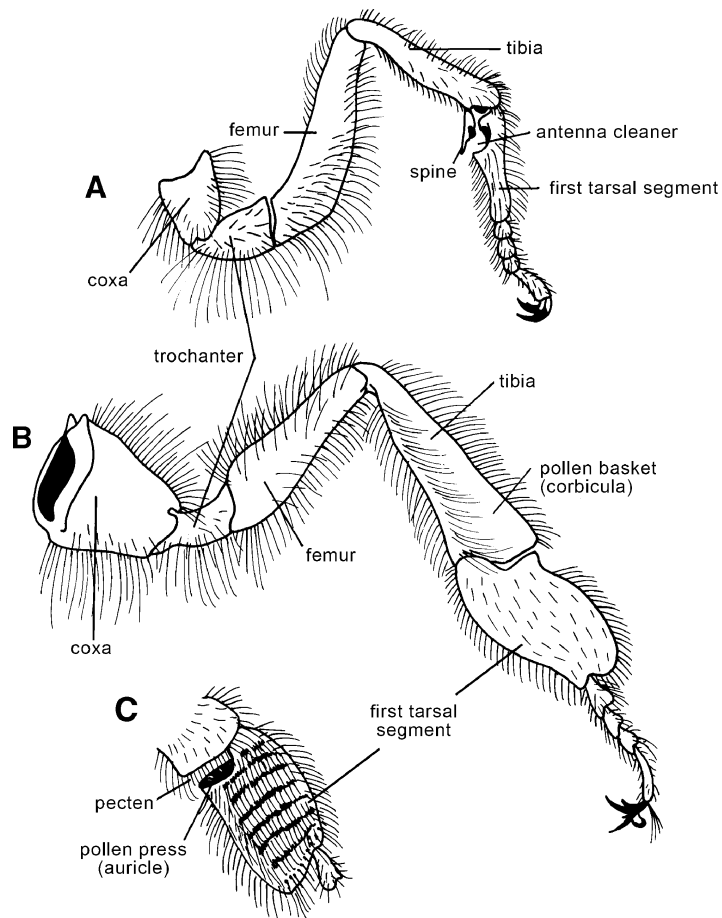


FIGURE 3.25. Leg modifications in the worker honey bee. (A) Foreleg showing the cleaning notch, (B) outer surface of hindleg showing the pollen basket, and (C) inner surface of hind tarsus and tip of hind tibia showing rake and pollen press. [After R. E. Snodgrass, 1925. *Anatomy and Physiology of the Honey bee*, McGraw-Hill Book Company.]

of the foreleg through which the antenna can be drawn and cleaned. The hindlegs of the bee are modified for pollen collection (Figure 3.25B). Rows of hairs, the *comb*, on the inner side of the first tarsomere scrape pollen off the abdomen. The *rake*, a fringe of hairs at the distal end of the tibia, then collects the pollen from the comb on the opposite leg and transfers it to the pollen *press*. When the press is closed, the pollen is pushed up into the pollen *basket*, where it is stored until the bee returns to its nest.

4.3.2. Wings

The majority of adult Pterygota have one or two pairs of functional wings. The complete absence of wings is a secondary condition, associated with the habits of the group concerned, for example, soil-dwelling or endoparasitism. The wings may be modified for a variety of purposes other than flight.

Development and General Structure. Regardless of its evolutionary origin (Chapter 2, Section 3.1) a wing contains the usual integumental elements (cuticle, epidermis, and

Ephemeroptera and Odonata. Primitively, two further segments lie proximal to the coxa and in extant insects one of these, the epicoxa, is associated with the wing articulation, or tergum, and the other, the subcoxa, with the pleuron (Fig. 8.4a).

The tarsus is subdivided into five or fewer components, giving the impression of segmentation; but, because there is only one tarsal muscle, **tarsomere** is a more appropriate term for each “pseudosegment”. The first tarsomere sometimes is called the basitarsus, but should not be confused with the segment called the basitarsus in certain fossil insects. The underside of the tarsomeres may have ventral pads, **pulvilli**, also called **euplantulae**, which assist in adhesion to surfaces. Terminally on the leg, the small pretarsus (enlargement in Fig. 2.19) bears a pair of lateral **claws** (also called **ungues**) and usually a median lobe, the **arolium**. In Diptera there may be a central spine-like or pad-like **empodium** (plural: **empodia**) which is not the same as the arolium, and a pair of lateral pulvilli (as shown for the bush fly, *Musca vetustissima*, depicted on the right side of the vignette of this chapter). These structures allow flies to walk on walls and ceilings. The pretarsus of Hemiptera may bear a variety of structures, some of which appear to be pulvilli, whereas others have been called empodia or arolia, but the homologies are uncertain. In some beetles, such as Coccinellidae, Chrysomelidae, and Curculionidae, the ventral surface of some tarsomeres is clothed with adhesive setae that facilitate climbing. The left side of the vignette for this chapter shows the underside of the tarsus of the leaf beetle *Rhyparida* (Chrysomelidae).

Generally the femur and tibia are the longest leg segments but variations in the lengths and robustness of each segment relate to their functions. For example, walking (**gressorial**) and running (**cursorial**) insects usually have well-developed femora and tibiae on all legs, whereas jumping (**saltatorial**) insects such as grasshoppers have disproportionately developed hind femora and tibiae. In aquatic beetles (Coleoptera) and bugs (Hemiptera), the tibiae and/or tarsi of one or more pairs of legs usually are modified for swimming (**natatorial**) with fringes of long, slender hairs. Many ground-dwelling insects, such as mole crickets (Orthoptera: Gryllotalpidae), nymphal cicadas (Hemiptera: Cicadidae), and scarab beetles (Scarabaeidae), have the tibiae of the fore legs enlarged and modified for digging (**fossorial**) (Fig. 9.2), whereas the fore legs of some predatory insects, such as mantispid lacewings (Neuroptera) and mantids (Mantodea), are specialized

for seizing prey (**raptorial**) (Fig. 13.3). The tibia and basal tarsomere of each hind leg of honey bees are modified for the collection and carriage of pollen (Fig. 12.4).

These “typical” thoracic legs are a distinctive feature of insects, whereas abdominal legs are confined to the immature stages of holometabolous insects. There have been conflicting views on whether (i) the legs on the immature thorax of the Holometabola are developmentally identical (serially homologous) to those of the abdomen, and/or (ii) the thoracic legs of the holometabolous immature stages are homologous with those of the adult. Detailed study of musculature and innervation shows similarity of development of thoracic legs throughout all stages of insects with ametaboly (without metamorphosis, as in silverfish) and hemimetaboly (partial metamorphosis and no pupal stage) and in adult Holometabola, having identical innervation through the lateral nerves. Moreover, the oldest known larva (from the Upper Carboniferous) has thoracic and abdominal legs/leglets each with a pair of claws, as in the legs of nymphs and adults. Although larval legs appear similar to those of adults and nymphs, the term **prolegs** is used for the larval leg. Prolegs on the abdomen, especially on caterpillars, usually are lobe-like and each bears an apical circle or band of small sclerotized hooks, or **crochets**. The thoracic prolegs may possess the same number of segments as the adult leg, but the number is more often reduced, apparently through fusion. In other cases, the thoracic prolegs, like those of the abdomen, are unsegmented outgrowths of the body wall, often bearing apical hooks.

2.4.2 Wings

Wings are developed fully only in the adult, or exceptionally in the subimago, the penultimate stage of Ephemeroptera. Typically, functional wings are flap-like cuticular projections supported by tubular, sclerotized veins. The major veins are longitudinal, running from the wing base towards the tip, and are more concentrated at the anterior margin. Additional supporting **cross-veins** are transverse struts, which join the longitudinal veins to give a more complex structure. The major veins usually contain tracheae, blood vessels, and nerve fibers, with the intervening membranous areas comprising the closely appressed dorsal and ventral cuticular surfaces. Generally, the major veins are alternately “convex” and “concave” in relation to the surface plane of the wing, especially near the

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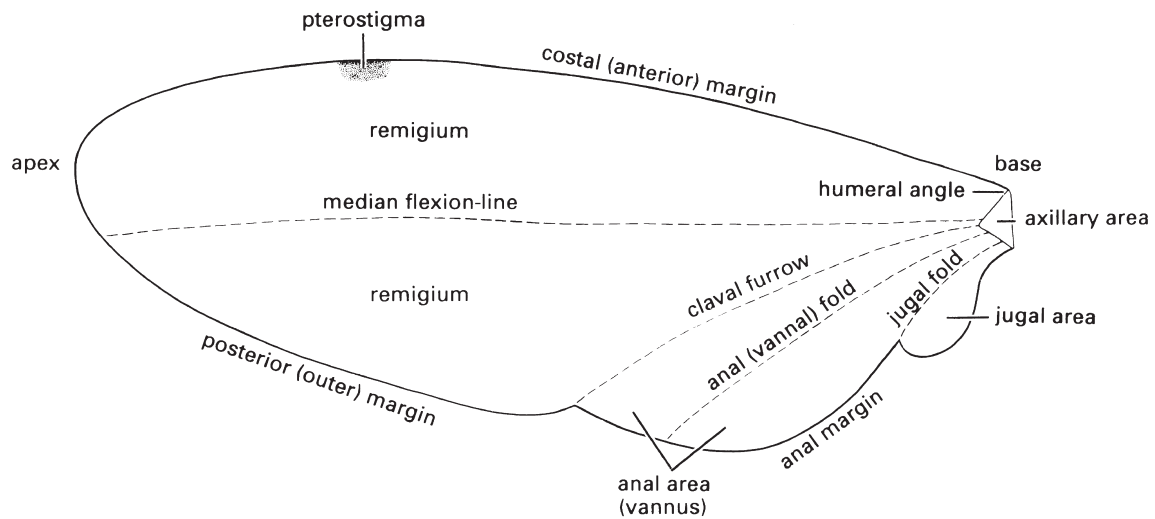


Fig. 2.20 Nomenclature for the main areas, folds, and margins of a generalized insect wing.

wing attachment; this configuration is described by plus (+) and minus (–) signs. Most veins lie in an anterior area of the wing called the **remigium** (Fig. 2.20), which, powered by the thoracic flight muscles, is responsible for most of the movements of flight. The area of wing posterior to the remigium sometimes is called the **clavus**; but more often two areas are recognized: an anterior **anal area** (or **vannus**) and a posterior **jugal area**. Wing areas are delimited and subdivided by **fold-lines**, along which the wing can be folded; and **flexion-lines**, at which the wing flexes during flight. The fundamental distinction between these two types of lines is often blurred, as fold-lines may permit some flexion and vice versa. The **claval furrow** (a flexion-line) and the **jugal fold** (or fold-line) are nearly constant in position in different insect groups, but the **median flexion-line** and the **anal** (or **vannal**) **fold** (or fold-line) form variable and unsatisfactory area boundaries. Wing folding may be very complicated; transverse folding occurs in the hind wings of Coleoptera and Dermaptera, and in some insects the enlarged anal area may be folded like a fan.

The fore and hind wings of insects in many orders are coupled together, which improves the aerodynamic efficiency of flight. The commonest coupling mechanism (seen clearly in Hymenoptera and some Trichoptera) is a row of small hooks, or **hamuli**, along the anterior margin of the hind wing that engages a fold along the posterior margin of the fore wing (**hamulate** coupling).

In some other insects (e.g. Mecoptera, Lepidoptera, and some Trichoptera), a jugal lobe of the fore wing overlaps the anterior hind wing (**jugate** coupling), or the margins of the fore and hind wing overlap broadly (**amplexiform** coupling), or one or more hind-wing bristles (the **frenulum**) hook under a retaining structure (the **retinaculum**) on the fore wing (**frenate** coupling). The mechanics of flight are described in section 3.1.4 and the evolution of wings is covered in section 8.4.

All winged insects share the same basic wing venation comprising eight veins, named from anterior to posterior of the wing as: **precosta** (PC), **costa** (C), **subcosta** (Sc), **radius** (R), **media** (M), **cubitus** (Cu), **anal** (A), and **jugal** (J). Primitively, each vein has an anterior convex (+) **sector** (a branch with all of its subdivisions) and a posterior concave (–) sector. In almost all extant insects, the precosta is fused with the costa and the jugal vein is rarely apparent. The wing nomenclatural system presented in Fig. 2.21 is that of Kukalová-Peck and is based on detailed comparative studies of fossil and living insects. This system can be applied to the venation of all insect orders, although as yet it has not been widely applied because the various schemes devised for each insect order have a long history of use and there is a reluctance to discard familiar systems. Thus in most textbooks, the same vein may be referred to by different names in different insect orders because the structural homologies were not recognized

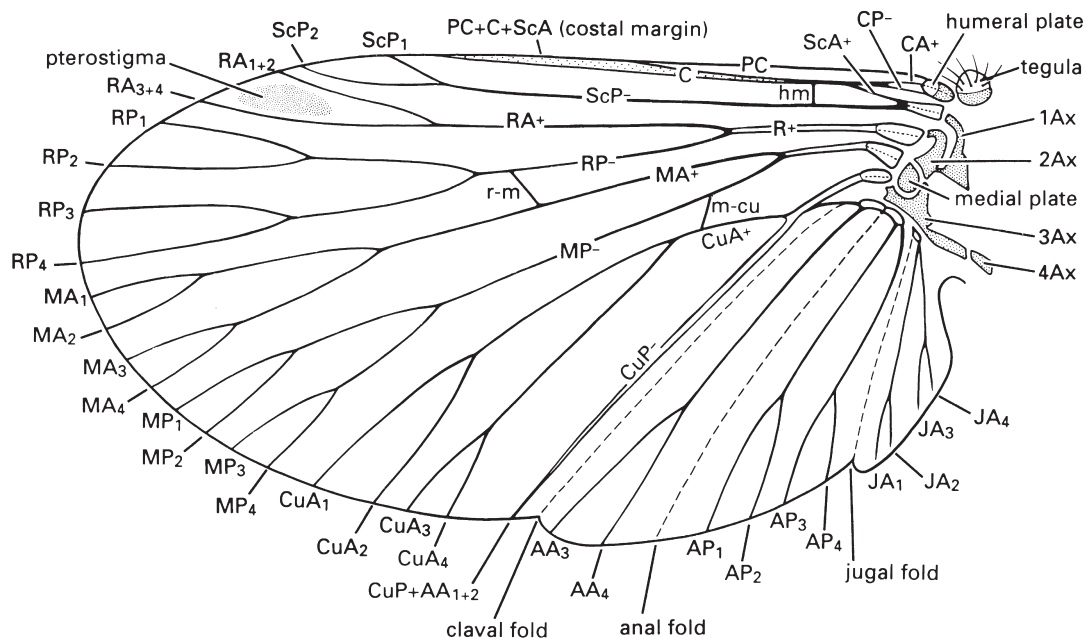


Fig. 2.21 A generalized wing of a neopteran insect (any living winged insect other than Ephemeroptera and Odonata), showing the articulation and the Kukulová-Peck nomenclatural scheme of wing venation. Notation as follows: AA, anal anterior; AP, anal posterior; Ax, axillary sclerite; C, costa; CA, costa anterior; CP, costa posterior; CuA, cubitus anterior; CuP, cubitus posterior; hm, humeral vein; JA, jugal anterior; MA, media anterior; m-cu, cross-vein between medial and cubital areas; MP, media posterior; PC, precosta; R, radius; RA, radius anterior; r-m, cross-vein between radial and median areas; RP, radius posterior; ScA, subcosta anterior; ScP, subcosta posterior. Branches of the anterior and posterior sector of each vein are numbered, e.g. CuA₁₋₄. (After CSIRO 1991.)

correctly in early studies. For example, until 1991, the venational scheme for Coleoptera labeled the radius posterior (RP) as the media (M) and the media posterior (MP) as the cubitus (Cu). Correct interpretation of venational homologies is essential for phylogenetic studies and the establishment of a single, universally applied scheme is essential.

Cells are areas of the wing delimited by veins and may be **open** (extending to the wing margin) or **closed** (surrounded by veins). They are named usually according to the longitudinal veins or vein branches that they lie behind, except that certain cells are known by special names, such as the discal cell in Lepidoptera (Fig. 2.22a) and the triangle in Odonata (Fig. 2.22b). The **pterostigma** is an opaque or pigmented spot anteriorly near the apex of the wing (Figs. 2.20 & 2.22b).

Wing venation patterns are consistent within groups (especially families and orders) but often differ between groups and, together with folds or pleats, provide major

features used in insect classification and identification. Relative to the basic scheme outlined above, venation may be greatly reduced by loss or postulated fusion of veins, or increased in complexity by numerous cross-veins or substantial terminal branching. Other features that may be diagnostic of the wings of different insect groups are pigment patterns and colors, hairs, and scales. Scales occur on the wings of Lepidoptera, many Trichoptera, and a few psocids (Psocoptera) and flies. Hairs consist of small microtrichia, either scattered or grouped, and larger macrotrichia, typically on the veins.

Usually two pairs of functional wings lie dorsolaterally as **fore wings** on the mesothorax and as **hind wings** on the metathorax; typically the wings are membranous and transparent. However, from this basic pattern are derived many other conditions, often involving variation in the relative size, shape, and degree of sclerotization of the fore and hind wings. Examples of fore-wing modification include the

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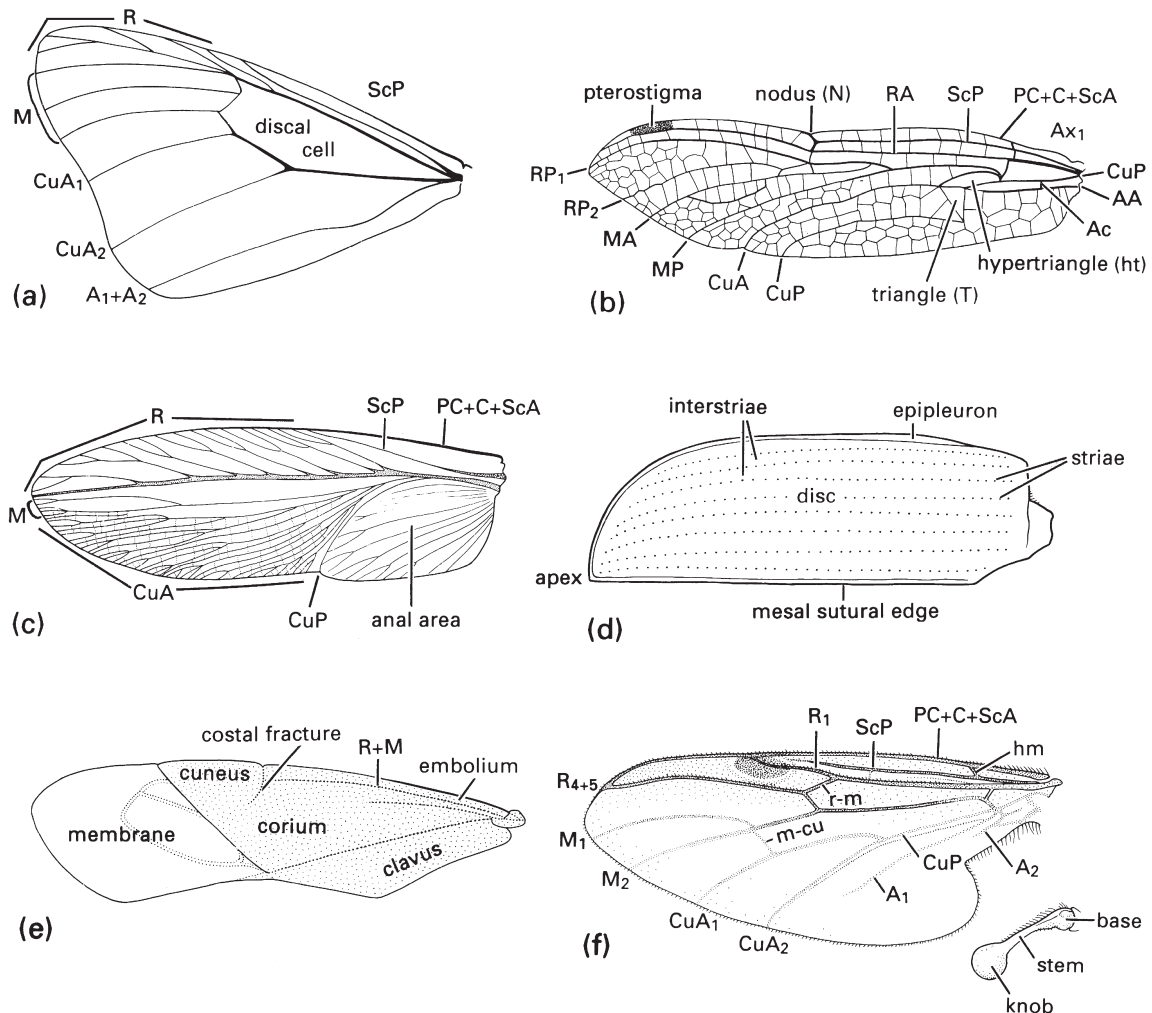


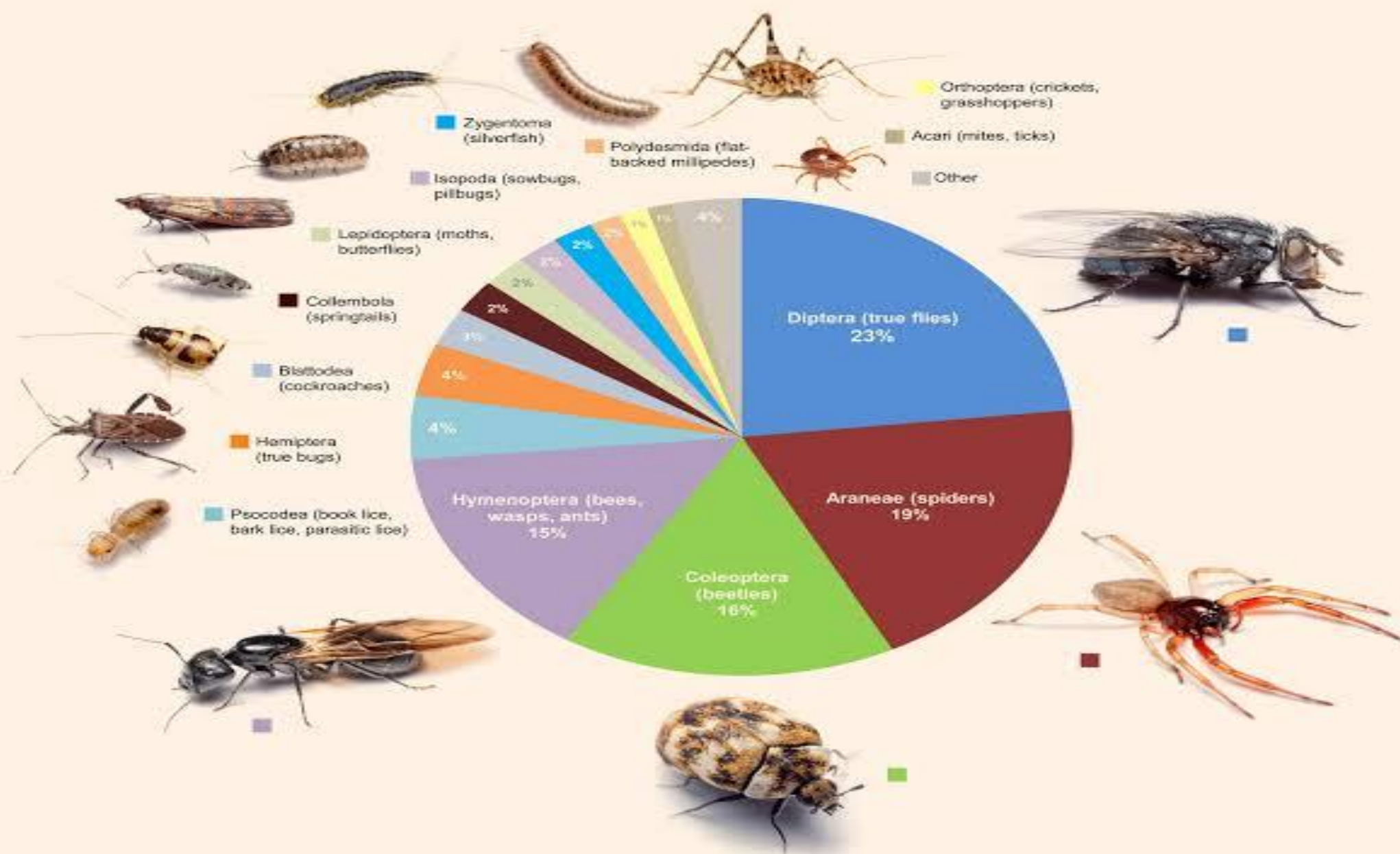
Fig. 2.22 The left wings of a range of insects showing some of the major wing modifications: (a) fore wing of a butterfly of *Danaus* (Lepidoptera: Nymphalidae); (b) fore wing of a dragonfly of *Urothemis* (Odonata: Anisoptera: Libellulidae); (c) fore wing or tegmen of a cockroach of *Periplaneta* (Blattodea: Blattidae); (d) fore wing or elytron of a beetle of *Anomala* (Coleoptera: Scarabaeidae); (e) fore wing or hemelytron of a mirid bug (Hemiptera: Heteroptera: Miridae) showing three wing areas – the membrane, corium, and clavus; (f) fore wing and haltere of a fly of *Bibio* (Diptera: Bibionidae). Nomenclatural scheme of venation consistent with that depicted in Fig. 2.21; that of (b) after J.W.H. Trueman, unpublished. ((a–d) After Youdeowei 1977; (f) after McAlpine 1981.)

thickened, leathery fore wings of Blattodea, Dermaptera, and Orthoptera, which are called **tegmina** (singular: **tegmen**; Fig. 2.22c), the hardened fore wings of Coleoptera that form protective wing cases or **elytra** (singular: **elytron**; Fig. 2.22d & Plate 1.2), and the **hemelytra** (singular: **hemelytron**) of heteropteran Hemiptera with the basal part thickened and the apical

part membranous (Fig. 2.22e). Typically, the heteropteran hemelytron is divided into three wing areas: the **membrane**, **corium**, and **clavus**. Sometimes the corium is divided further, with the **embolium** anterior to R + M, and the **cuneus** distal to a **costal fracture**. In Diptera the hind wings are modified as stabilizers (**halteres**) (Fig. 2.22f) and do not function as wings,

Success of Insects:

- ▶ **Biologically most successful group on earth.**
- ▶ **They are remarkably speciose.**
- ▶ **Arthropods species are more than all other species combined.**
- ▶ **80% of all animals are Arthropods.**
- ▶ **76% of Arthropods are insects.**



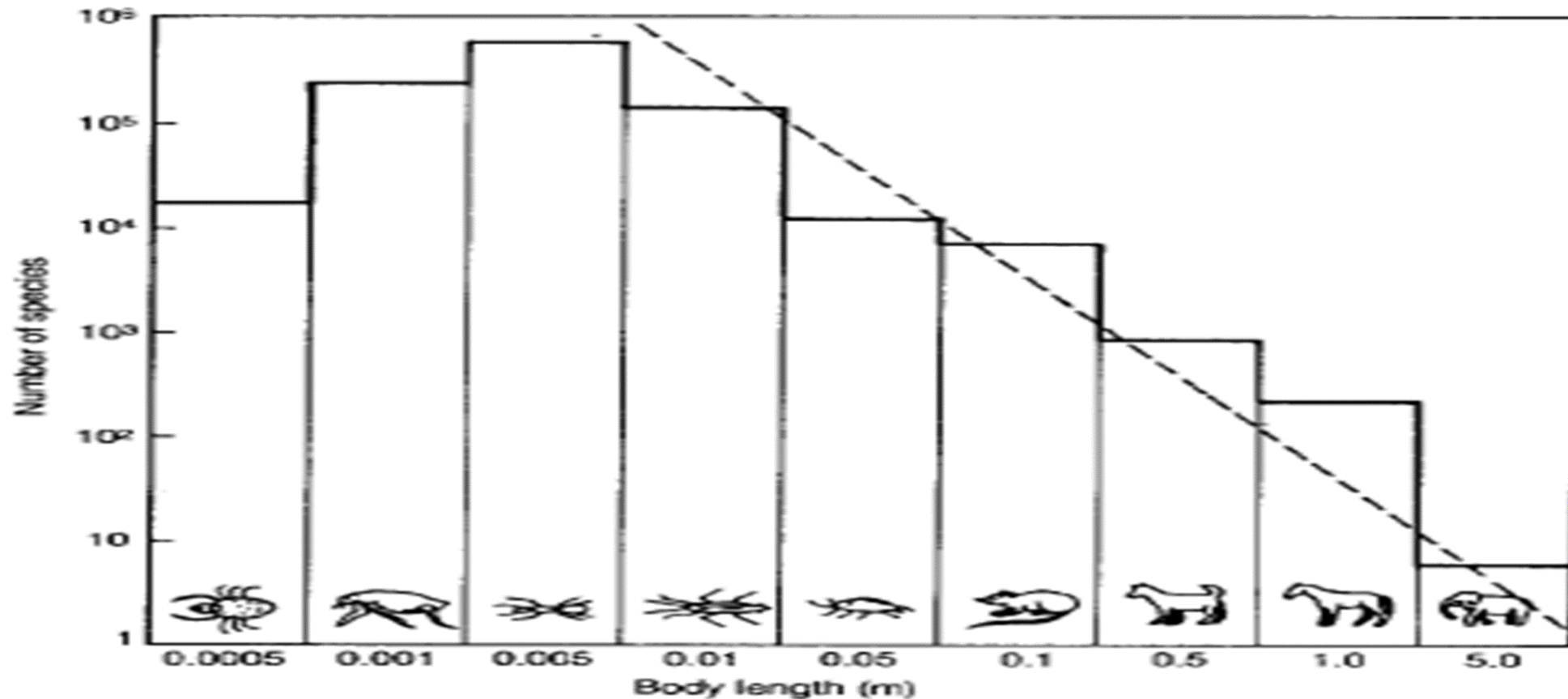
Reasons for Success:

Small Size:

- ▶ Most are 1-10 mm in length.
- ▶ Minimal resources needed for survival and reproduction.
- ▶ More niches due to small size.
- ▶ Can live entire life on single plant.
- ▶ 1 acacia tree support life cycle of dozens insects.
- ▶ Can hide in trees, flowers, grass or rocks.



- The no of species declines with body length.
Extrapolating to the left will show that many species of small organisms have not yet been discovered and described.



Exoskeleton:

- ▶ **Located outside the body.**
- ▶ **Gives shape and support.**
- ▶ **Provides protection from attack or injury.**
- ▶ **Minimizes loss of body fluids.**
- ▶ **Resists both chemical and physical attack.**

Exoskeleton

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Anthropod eye and skeleton



Sensory System:

- ▶ **Highly organized.**
- ▶ **Comparable to Vertebrates.**
- ▶ **They don't adopt to changes by learning.**
- ▶ **Show genetic changes between generations.**

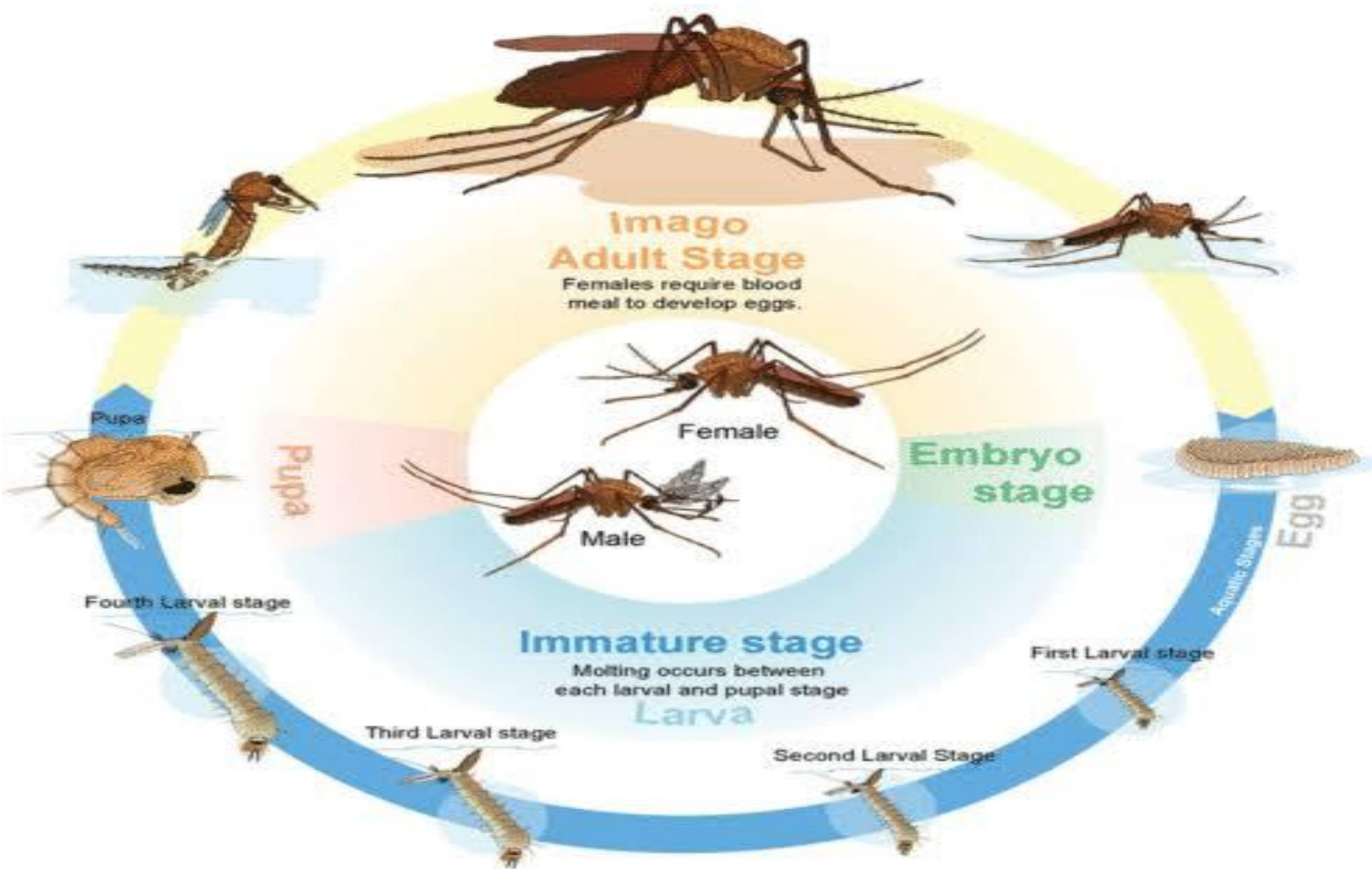
Flight:

- ▶ **Insects are only Invertebrates that can fly.**
- ▶ **Acquire that ability 300 million years ago.**
- ▶ **Can escape from predator by flying.**
- ▶ **Populations can escape quickly to new habitat.**
- ▶ **Can fly for hours without stopping.**



Metamorphosis:

- ▶ **Metamorphosis are developmental changes from immature to adult.**
- ▶ **Include physical, biochemical and behavioral changes.**
- ▶ **Promote survival dispersal and reproduction of species.**
- ▶ **Incomplete metamorphosis is slow and doesn't include all body parts.**
- ▶ **More advanced insects undergo complete metamorphosis.**
- ▶ **In complete metamorphosis larva first molts into pupa.**
- ▶ **An adult insect emerges from within exoskeleton of pupa.**



Reproductive Potential:

- ▶ **High reproductive potential.**
- ▶ **Produce large number of eggs.**
- ▶ **High fertility.**
- ▶ **Can store sperms for months or years.**
- ▶ **A single mating can fertilize all eggs.**
- ▶ **Short life cycle.**

Insect Cuticle

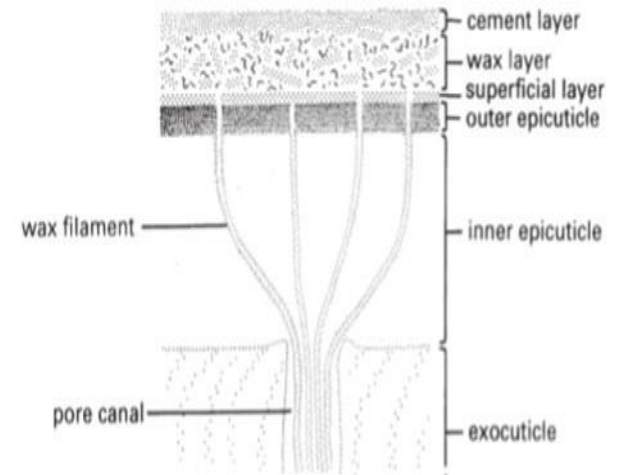
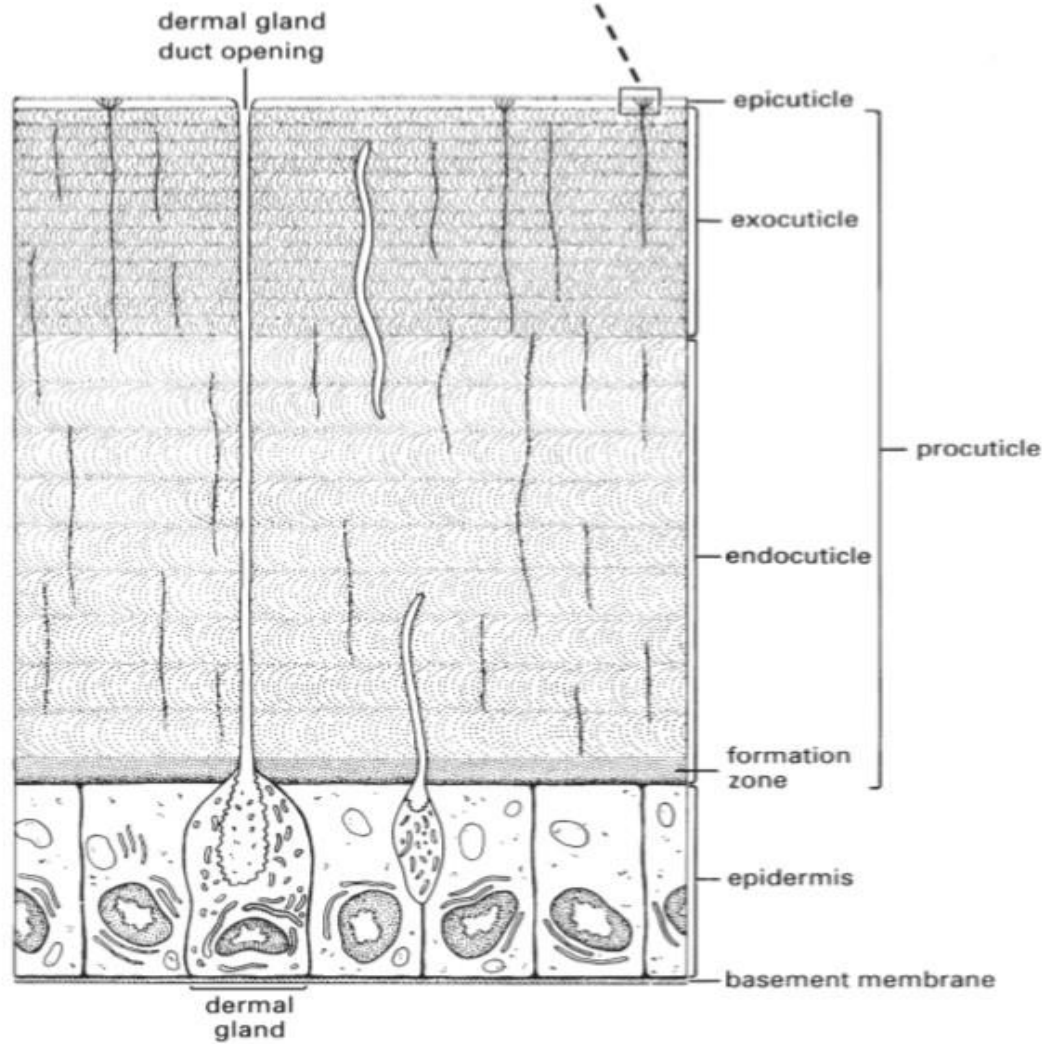
In all insects there is a thin layer of cuticle with special properties and is comprised of following layers:

- 1. Epicuticle**
- 2. Exocuticle**
- 3. Endocuticle**

- There is always an epicuticle layer and the epidermal cell layer.
- The exocuticle and endocuticle may be greatly reduced or absent in particular parts of the cuticle of the same or different insects.

The Epicuticle

- ◉ Complex and the outermost layer and probably the most important layer.
- ◉ Responsible for water proofing and general impermeability of cuticle.
- ◉ Produced by epidermis and dermal glands.



Significance of Epicuticle

1. Cement layer :

- ◉ Outermost layer, associated with wax layer.
- ◉ May serve to protect it.
- ◉ Not found in all insects.

2. Wax layer:

- Hydrocarbons constitute 90% of this layer.
- Important to insects for water loss, thus waterproofing of cuticle.

3. Outer epicuticle:

- Cuticulin is a very thin layer of protein.
- It is impregnated with lipids, some of which may be covalently bound to proteins as lipoproteins.
- First layer formed following the molt.
- It protects the new procuticle from digestion by molting enzymes.
- It is also called cuticulin layer.

4. Inner epicuticle:

- Function not that clear but it is a much thicker layer (1 μm) than the outer epicuticle.

5. Wax canal filament:

- A filament of wax that is produced by the hypodermal cells.
- Extends to the inner part of the epicuticle.

6. Pore canals:

- Tiny pores that run from the hypodermal cells to the inner part of the inner epicuticular layer.
- Pore canals are passageways from 0.1 μm to 0.15 μm diameter extending from the epidermal cells through the endo and exocuticle.

The Exocuticle

- ◉ The exocuticle contains chitin and protein.
- ◉ It lies just beneath the epicuticle .
- ◉ It is highly sclerotized and is therefore hard and rigid.
- ◉ The thickness of the exocuticle is variable and species specific.
- ◉ Adult insects generally have a thicker and more sclerotized exocuticle than larval insects.

The Endocuticle

- ◉ The Endocuticle Is continually being synthesized.
- ◉ Contains most of the chitin, which is broken-down at the molt by chitinase .
- ◉ In soft-bodied insects and regions of flexibility, this layer is well developed and not the exocuticle.

Chemical composition of the cuticle

Lipids

- Waxes: Wax blooms produced by several groups of insects.
- Cuticular hydrocarbons: used by systematists .

Carbohydrates

- Chitin-polysaccharide : with units of N-acetylglucosamine residues Chitin gives the cuticle its strength, not its hardness.

Proteins

- Arthropodin: Untanned protein that during sclerotization is crosslinked to produce sclerotin and give the cuticle its hardness.

Sclerotin

- Tanned protein that gives cuticle hardness. This is brought about by a process called sclerotization and involves eclosion hormone and bursicon , another rhormone .

Chitinase

- Enzyme involved in digestion of chitin at the molt. It is released and produced by the epidermal cells.

Proteinases

- Enzymes other than chitinase that aid in the digestion of the endocuticle at the molts.

Resilin

- Colorless rubber-like protein, Can be stretched and stores energy due to tension.

Physical properties of the Cuticle

- ◉ Hardness
- ◉ Strength
- ◉ Flexibility
- ◉ Plasticization
- ◉ Ability to heal or repair wounds
- ◉ Hydrophobicity

➤ **Hardness:**

Is due to the amount of sclerotization or tanning of the proteins that takes place.

➤ **Strength:**

Is due to the presence of chitin in the endocuticle.


➤ **Flexibility:**


It is due to less proteins being sclerotized and is usually due to more endocuticle being present than exocuticle. Also certain proteins, such as resilin provide flexibility.



COLORATION:

- Color production is due to interaction of light with:
 - i. Cuticle or underlying cells.
 - ii. Fluids
- **Physical** (structural) colors are due to:
 - i. Scattering of light
 - ii. Interference
 - iii. Diffraction

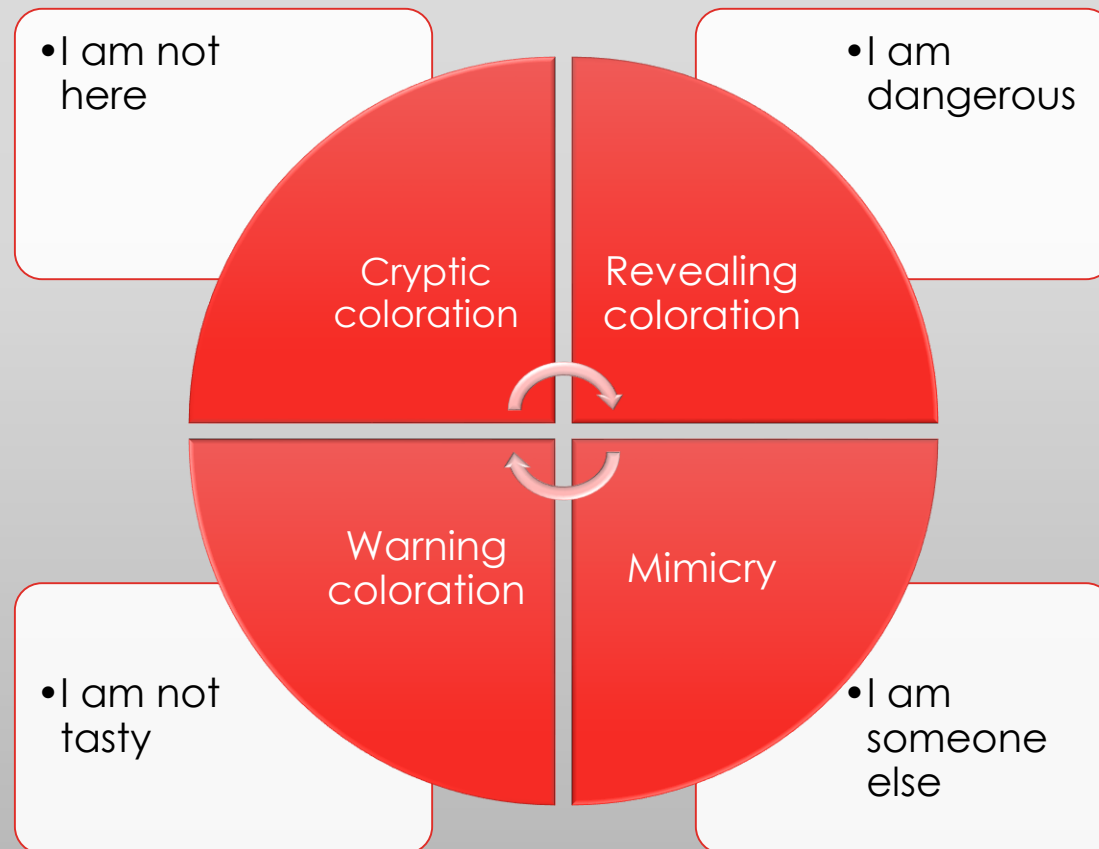
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- **Pigmentary** colors are due to:
 - i. Absorption of light by chemicals.
 - ii. All physical colors are derived from cutical and its protuberances.
 - **Interference** colors are produced by interference from reflective layers produced by microfibrillar orientation within exocuticle.
 - In some **beetles**, by deflection from some regularly textured surfaces such as on many scales.

- 
- Colors produced by **scattering** depend on:
 - i. Size surface irregularities relative to wavelength of light.
 - **Whites** are produced by structures larger than wavelength of light.
 - **Blues** are produced by irregularities that reflect only short wavelength.

Pigment production:

- Pigments are produced in **three** ways:
 - i. By insects own metabolism.
 - ii. By sequestering from a plant source.
 - iii. Rarely, by microbial endosymbionts.

COLORATION DEFENSE



CRYPISIS

- Coloration that makes insects difficult to distinguish against their background.
- There are **three** types of crypsis:
 - a. Homochromism
 - b. Homomorphism
 - c. Homotypism



HOMOCHROMISM

- Similarity of insect to the color of inanimate objects.
- These insects are often the same color as the leaves or twigs on which they rest.



HOMOMORPHISM:

- Similarity of insect to the **form** of inanimate object.
- These insects are often the same **form** as the leaves or twigs on which they rest.



HOMOTYPISM

- Similarity of animals to the color & form of inanimate objects.
- Same colour & form as the leaves or twigs on which they rest



REVEALING COLORATION

- Any pattern of threatening or startling behavior such as:
 - Suddenly displaying conspicuous eye spots to scare off or momentarily distract a predator thus giving the prey animal an opportunity to escape.



WARNING COLORATION

- The correlation between conspicuous signals, such as bright coloration and prey unprofitability.



MIMICRY

- Resemblance of one species to another.
- I am someone else.
- Related to Camouflage
 - Defense
 - Aggressive
 - Auto/self



DEFENSIVE MIMICRY

- It takes place when organisms are able to avoid an encounter that would be harmful to them by deceiving an enemy into treating them as something else.



AGGRESSIVE MIMICRY

- Predators or parasites which share characteristics with a species harmless to their prey, allowing them to **avoid detection** by the latter.
- Mimic may resemble the prey or host itself.

Aggressive mimicry:





AUTOMIMICRY

- Occurs **within a single species** one case being where one part of an organism's body resembles another part.
- Mimic imitates other morphs within the same species.

AUTOMIMICRY

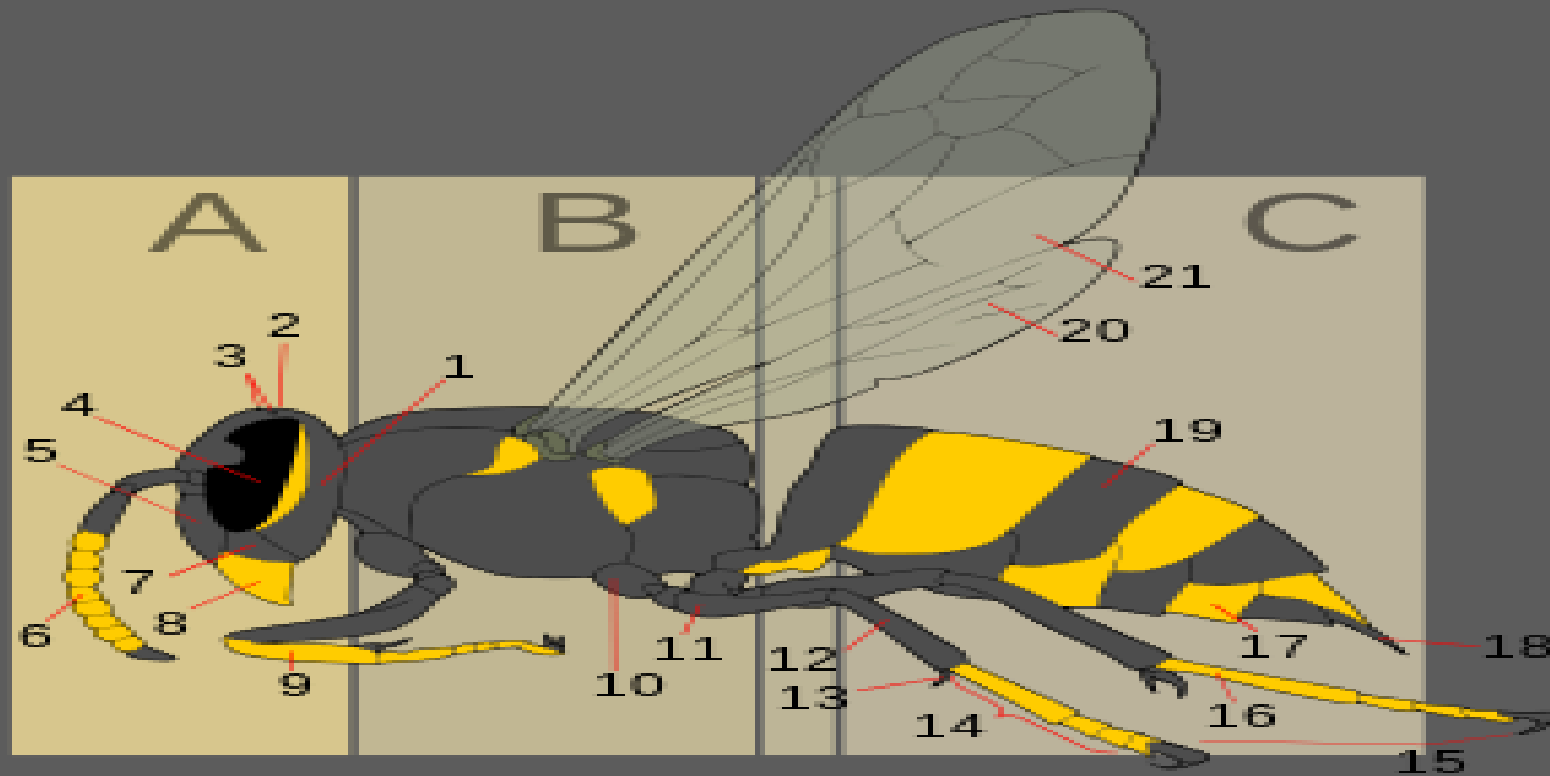




INTRODUCTION

- Most striking external feature.
- Amalgamation of segments into functional units.
- Tagmosis gives rise to tagmata of head ,thorax and abdomen.

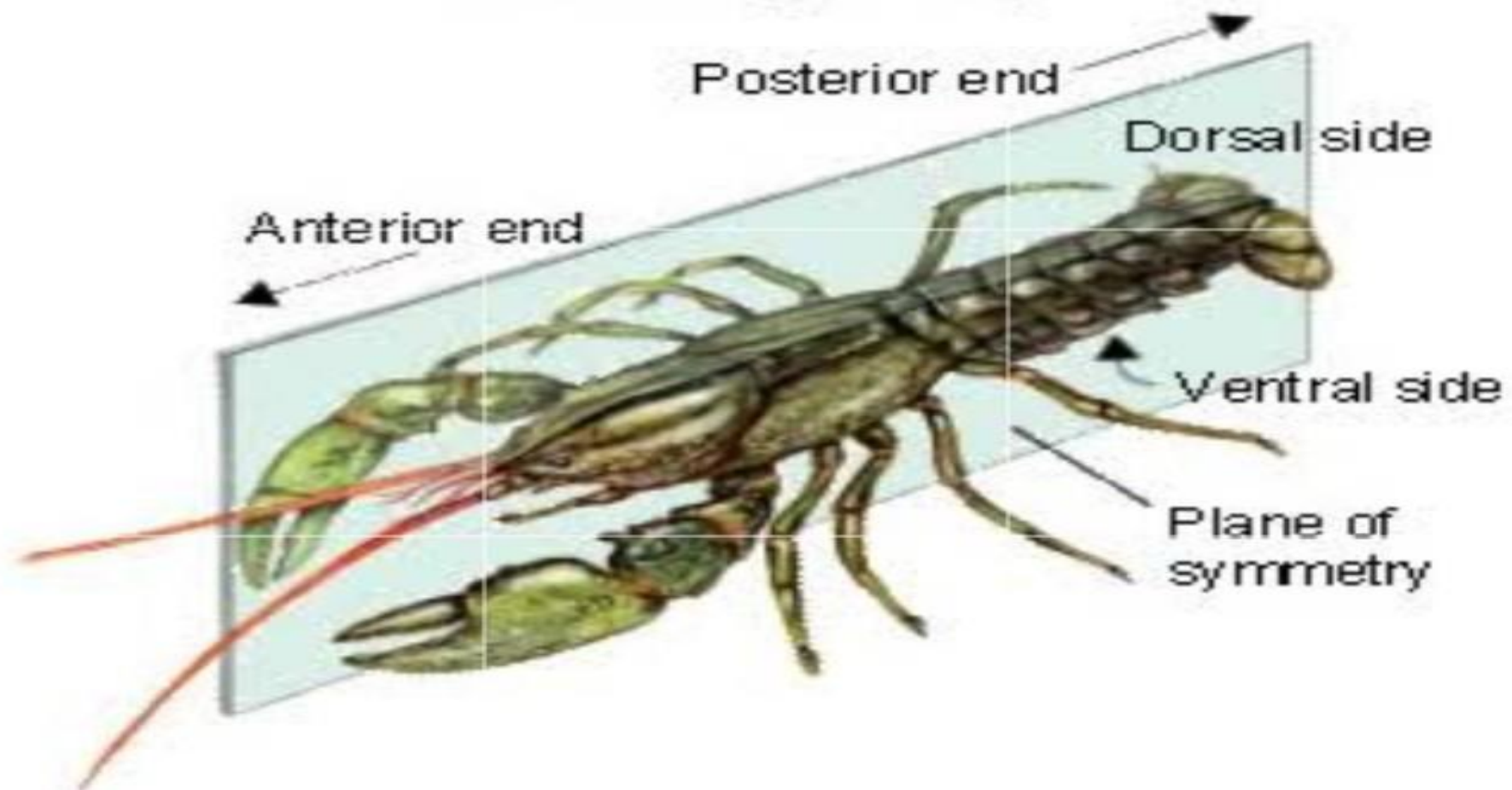
- 21 original segments have divided into six segmented head, three segmented thorax and eleven segmented abdomen.



BODY SYMMETRY

- The bilaterally symmetrical body may be described according to three axes:
 - 1 **Longitudinal**, or anterior to posterior, also termed cephalic(head) to caudal(tail).
 - 2 **Dorsoventral**, or dorsal(upper) to ventral(lower).
 - 3 **Transverse**, or lateral (outer) through the longitudinal axis to the opposite lateral.

Bilateral Symmetry

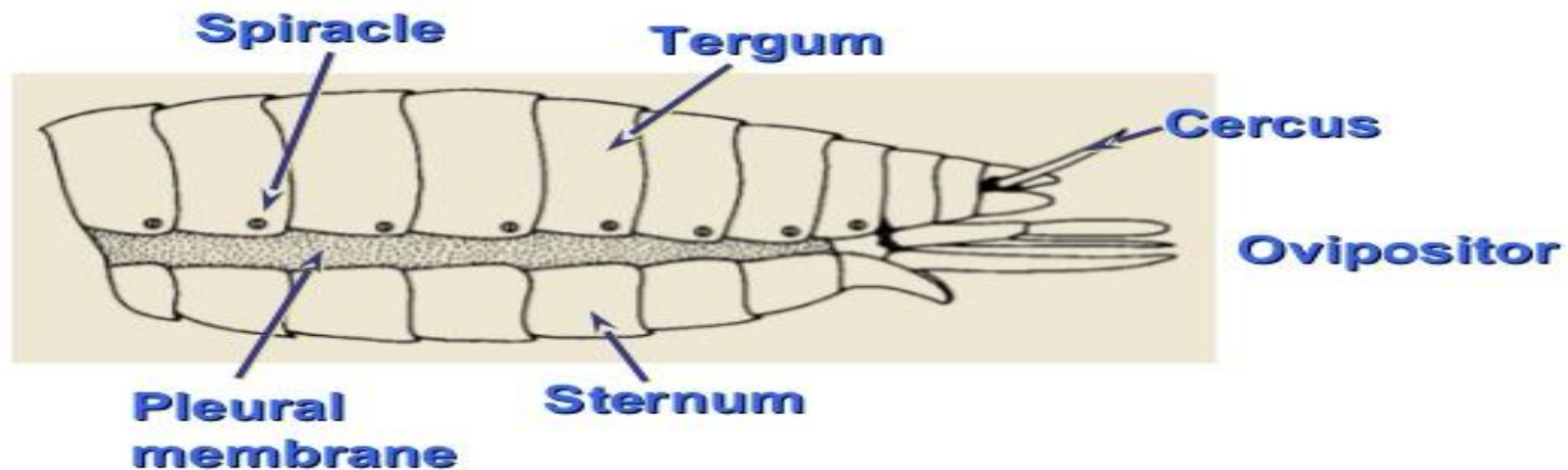


BODY SURFACE

- Four principal regions of the body surface
 1. The dorsum or upper surface.
 2. The venter or lower surface; and
 3. The two lateral pleura(singular.
- Sclerotization gives rise to plates called **sclerites**.

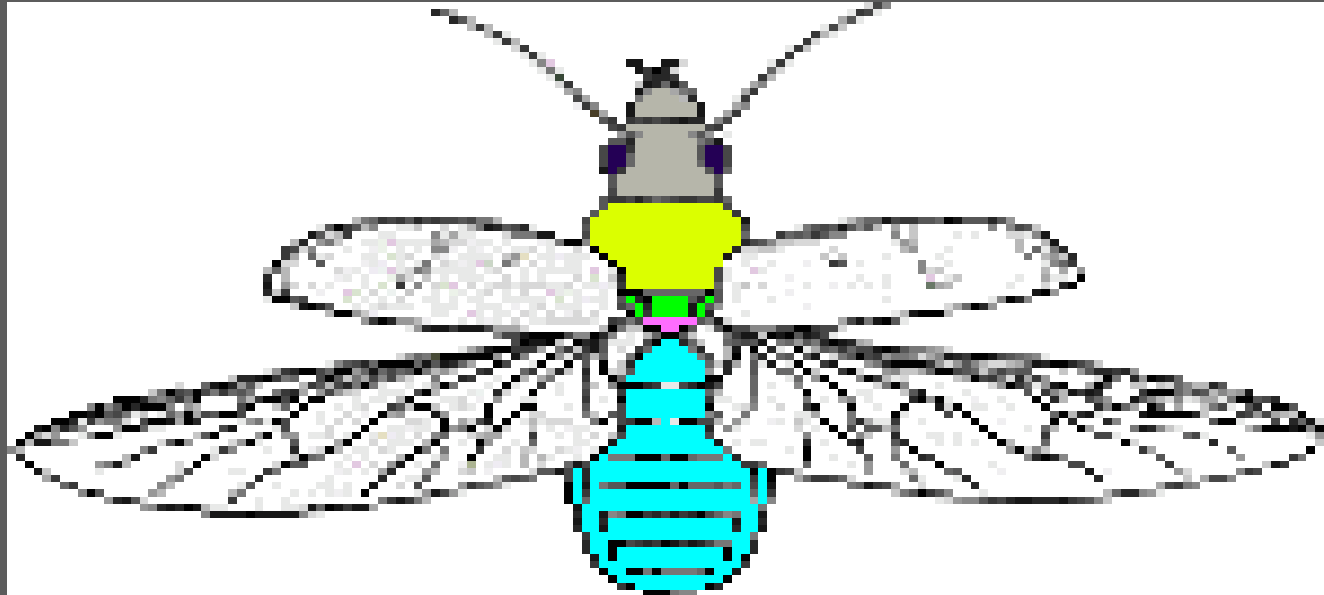
- Major segmental sclerites are:
Tergum (the dorsal plate; plural: terga),
The sternum (the ventral plate; plural: sterna),
The pleuron (the side plate).

Insect abdomen



INSECT BODY PARTS

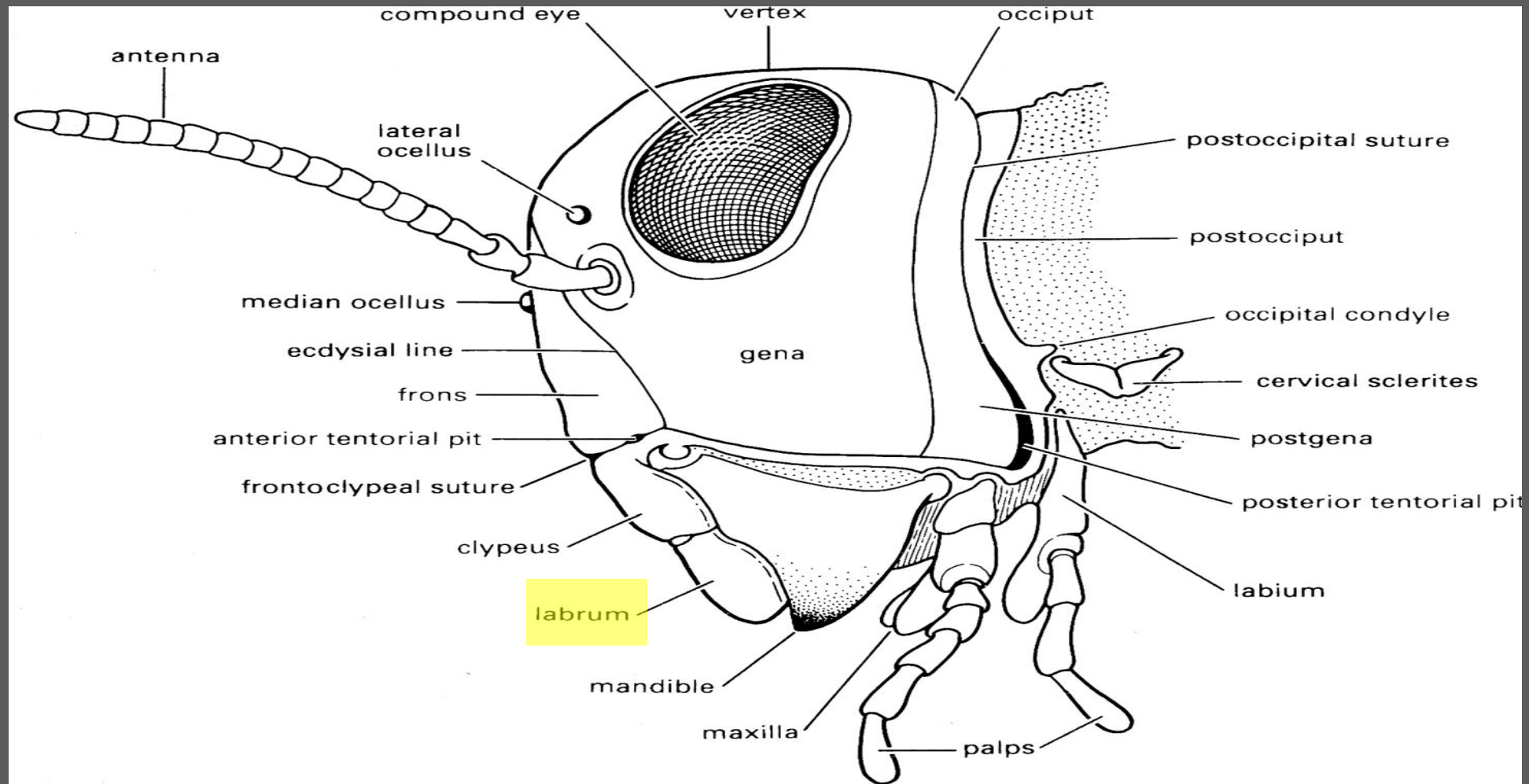
- A brief guide to the main external features of insects and the terminology used to describe the various body-parts.



BODY PARTS

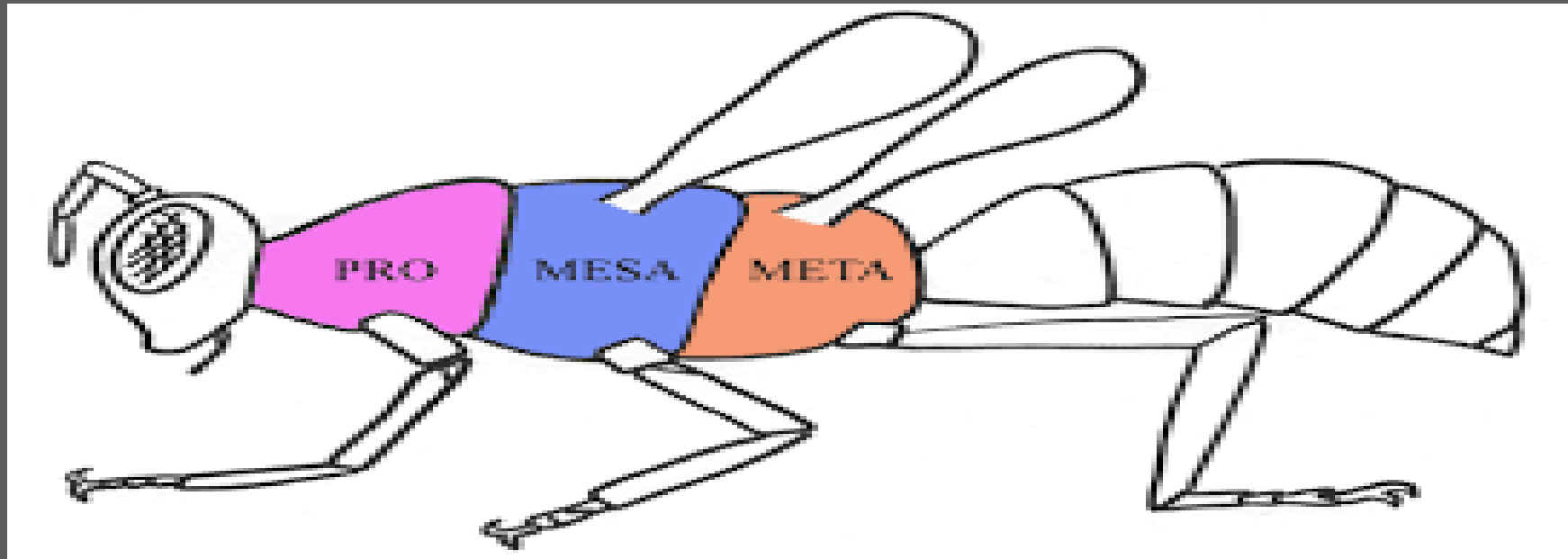
- The insect body is divided into three main parts
- **head**,
- **thorax** and
- **abdomen** - as shown above.
- The head bears the mouthparts, the eyes and a pair of antennae.
- Many of these insects also have two or more small, single-faceted eyes, called **simple eyes** or **ocelli** (singular: **ocellus**).

HEAD SEGMENTATION

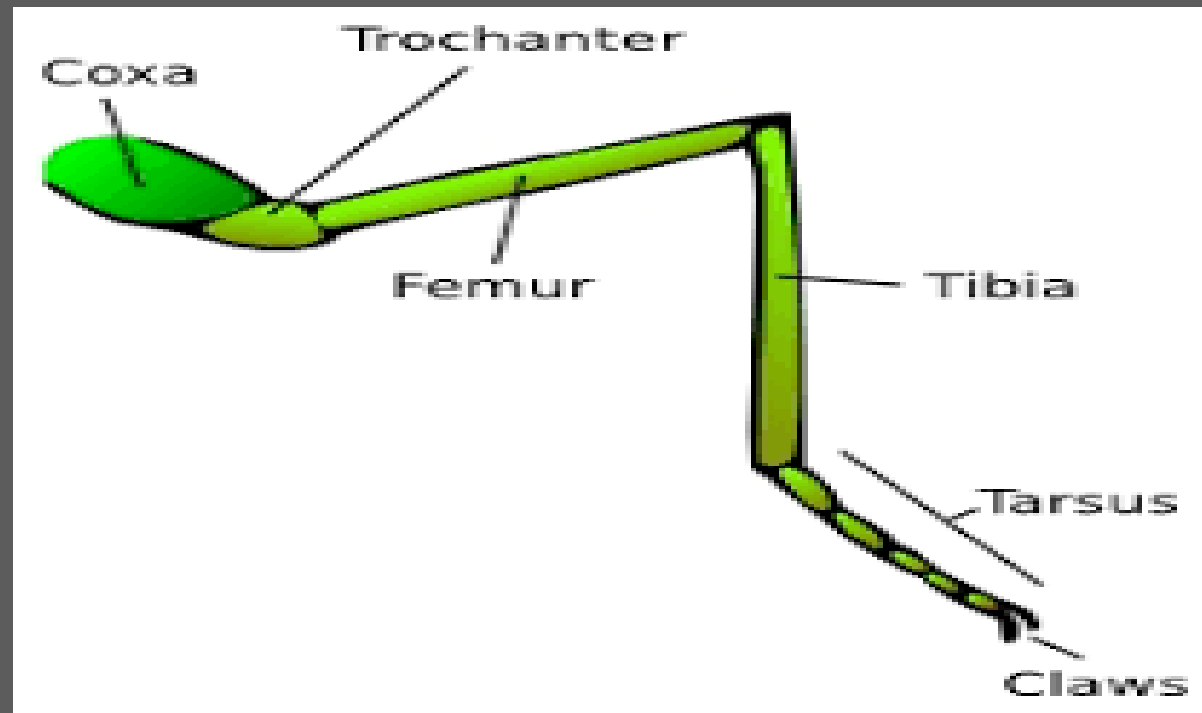


THORAX:

- The thorax consists of three segments
 1. The **prothorax** (front),
 2. The **mesothorax** (middle)
 3. The **metathorax** (back).



- Segment bears a pair of **jointed legs**.
 - Each leg consists of four main parts
 - The **coxa**
 - The **femur**
 - The **tibia**
 - The **tarsus** (plural: **tarsi**)
- Small joints on tarsus ,carrying a pair of terminal **claws**.



TERMINAL SEGMENTS OF THE TARSUS

- In winged insects, the meso and metathoracic segments each bear a pair of wings

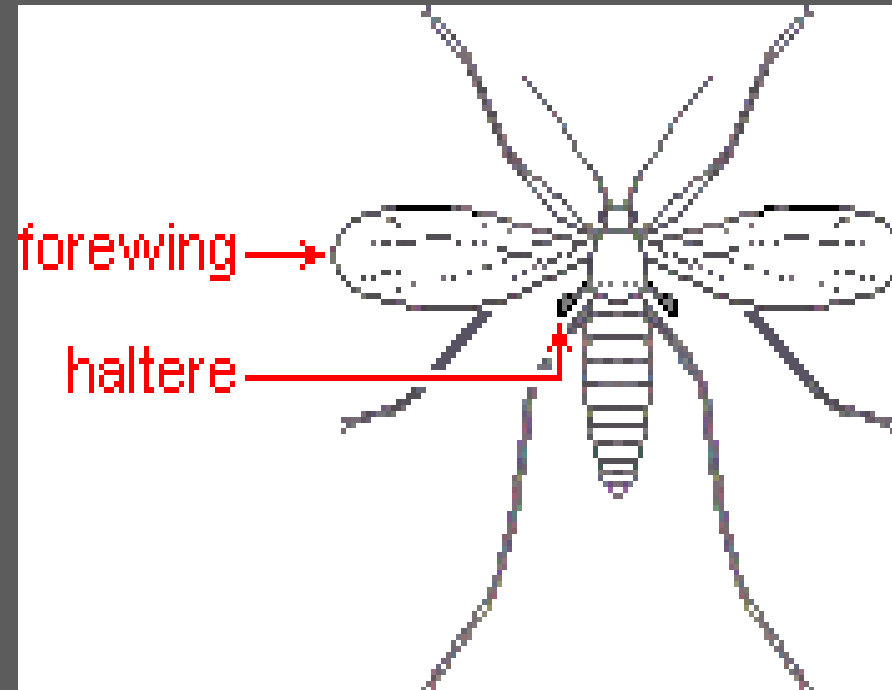
1. The **forewings**

2. The **hindwings**

- Although in many insects one or both pairs of wings have been lost, or modified into other structures.
- Special wing modifications include the structures called **halteres** found in the Diptera (true flies), and the structures called **elytra** (singular: **elytron**) found in the Coleoptera (beetles) and Dermaptera (earwigs).

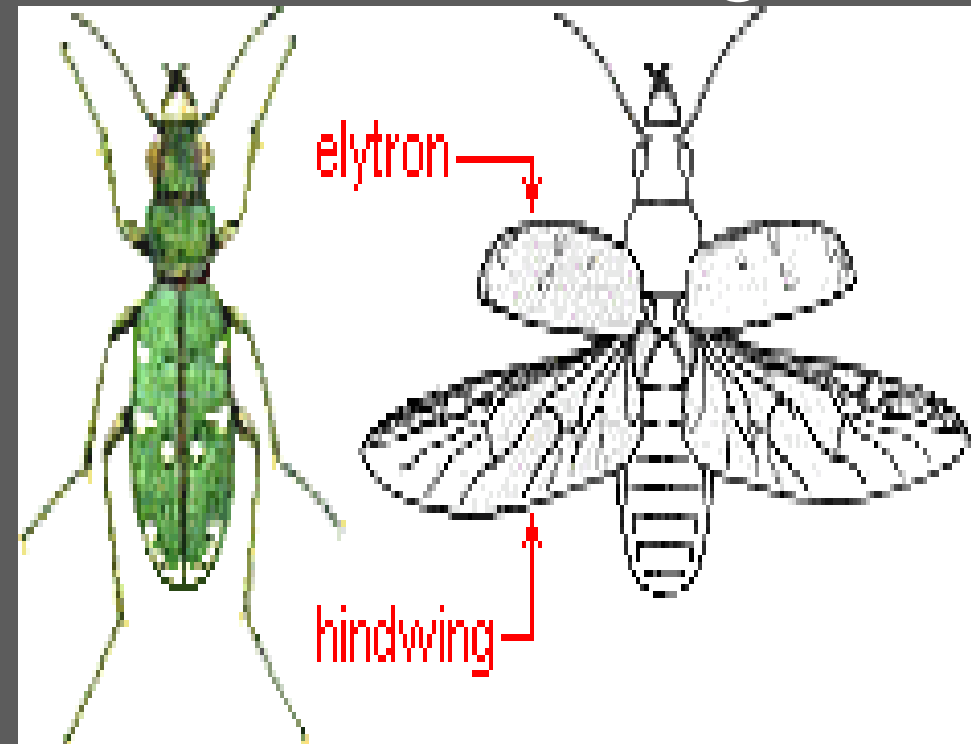
HALTERES

- Small, club-shaped organs of balance found in Diptera (flies) on each side of the thorax just behind the forewings.



ELYTRA

- The hard leathery forewings of Coleoptera and Dermaptera that serve as protective covering or wing case for hind wings.



ABDOMEN

- The abdomen is made up of similar segments.
- Often bears a pair of jointed, terminal appendages called the **cerci** (singular: **cercus**). Typical cerci are illustrated in(a) below,
- Although in some insects they consist of many more joints than in the example shown.

- **Abdominal Appendages of Adult Insects**

Typical cerci



Cerci and tail filament



Cerci modified as forceps e.g. earwigs



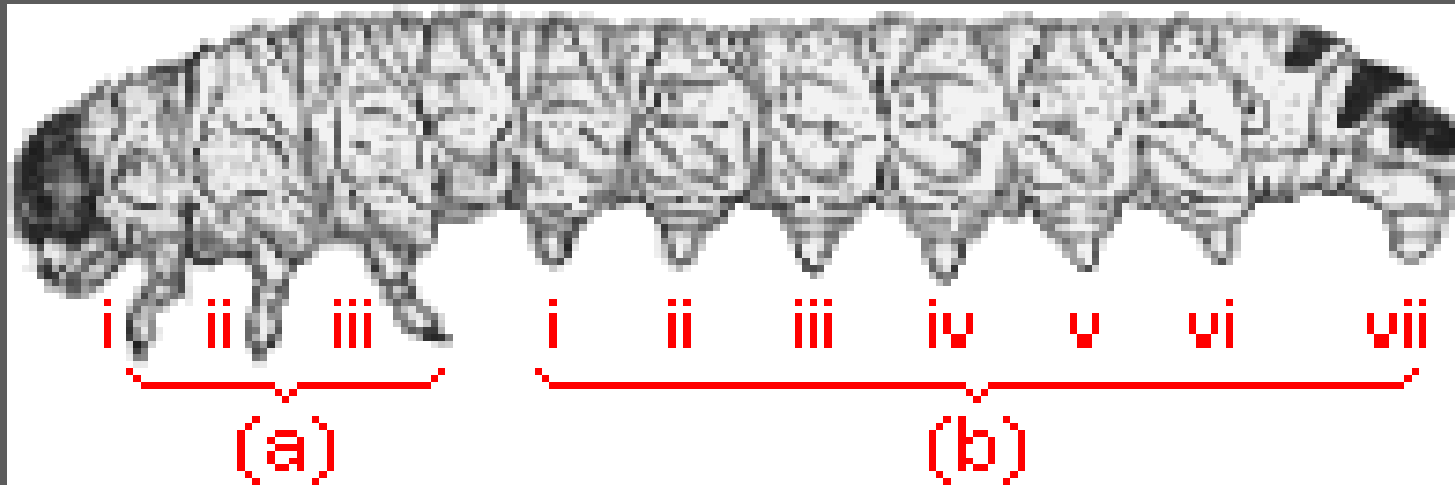
Paired cornicles
e.g. some aphids



- In the larvae stages of some Endopterygota eg, those of many butterflies and moths, the abdomen carries several pairs of appendages called **false-legs** or **prolegs**.
- These are unjointed, fleshy structures.
- Larvae with prolegs are commonly called caterpillars.



- Caterpillar of a Sawfly showing (a) jointed legs (i-iii) of the thorax and (b) the fleshy pro-legs (i- vii) of the abdomen.
- There are always three pairs of thoracic legs.
- Number of pro-legs may vary depending on the species.



STRUCTURE OF HEAD

CAPSULE:-

The rigid cranial capsule has two openings, one posteriorly through the occipital foramen to the prothorax, the other to the mouthparts.

MOUTHPARTS:-

Typically the mouthparts are directed ventrally (hypognathous), although sometimes anteriorly (prognathous) as in many beetles, or posteriorly (opisthognathous) as in, for example, aphids, cicadas, and leafhoppers.

STRUCTURE OF HEAD

REGIONS IN HEAD:-

The posterior horseshoe-shaped posterior cranium(dorsally the occiput) contacts the vertex dorsally and the genae (singular: gena) laterally; the vertex abuts the frons anteriorly and more anteriorly lies the clypeus, both of which may be fused into a frontoclypeus.

COMPOUND EYES:-

In adult and nymphal insects, paired compound eyes lie more or less dorsolateral between the vertex and genae, with a pair of sensory antennae placed more medially. In many insects, three light-sensitive “simple” eyes, or ocelli, are situated on the anterior vertex, typically arranged in a triangle, and many larvae have stemmatal eyes.

STRUCTURE OF HEAD

SUTURES:-

- 1) remnants of original segmentation, generally restricted to the postoccipital suture.
- 2) ecdysial lines of weakness where the head capsule of the immature insect splits at molting, including an often prominent inverted “Y”, or epicranial suture, on the vertex ; the frons is delimited by the arms (also called frontal sutures) of this “Y”
- 3) grooves that reflect the underlying internal skeletal ridges, such as the frontoclypeal or epistomal suture, which often delimits the frons from the more anterior clypeus.

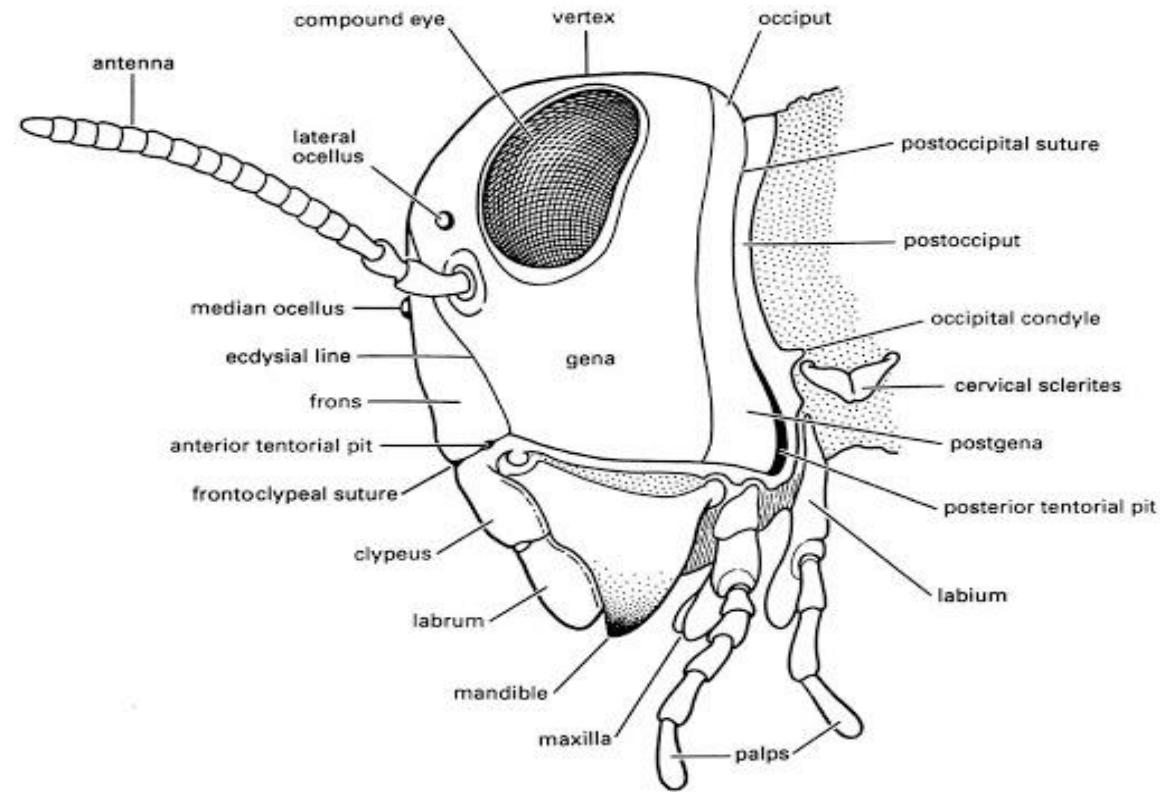
ENDOSKELETON OF HEAD

The head endoskeleton consists of several invaginated ridges and arms (apophyses, or elongate apodemes), the most important of which are the two pairs of tentorial arms, one pair being posterior, the other anterior, sometimes with an additional dorsal component.

HEAD SEGMENTS:-

1. Labral
2. antennal, with each antenna equivalent to an entire leg
3. post antennal, fused with the antennal segment
4. Mandibular
5. Maxillary
6. labial.

Head of insect



STRUCTURE OF THORAX

SEGMENTS:-

The thorax is composed of 3 segments:-

1. Prothorax
2. Mesothorax
3. Metathorax

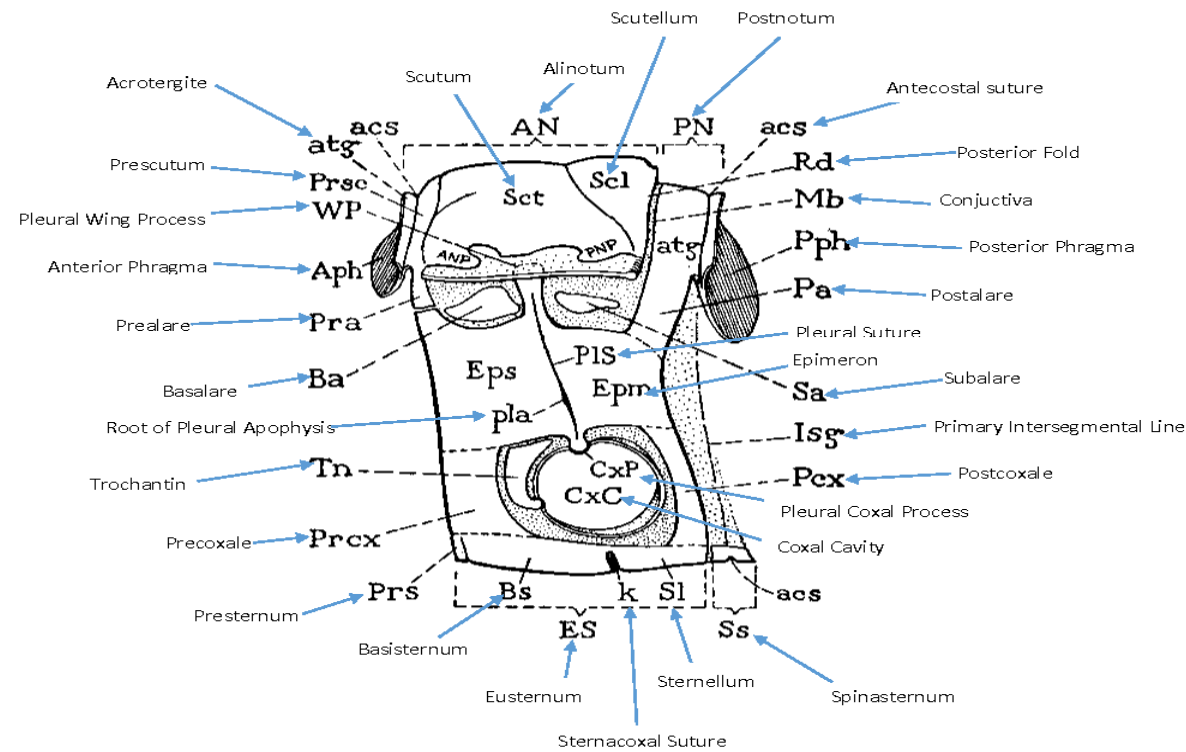
In apterygotes and immature insects, these segments are smaller in size and structurally complex. In winged insects mesothorax and metathorax are enlarged than prothorax. Wings occur only in second and third segment.

STRUCTURE OF THORAX

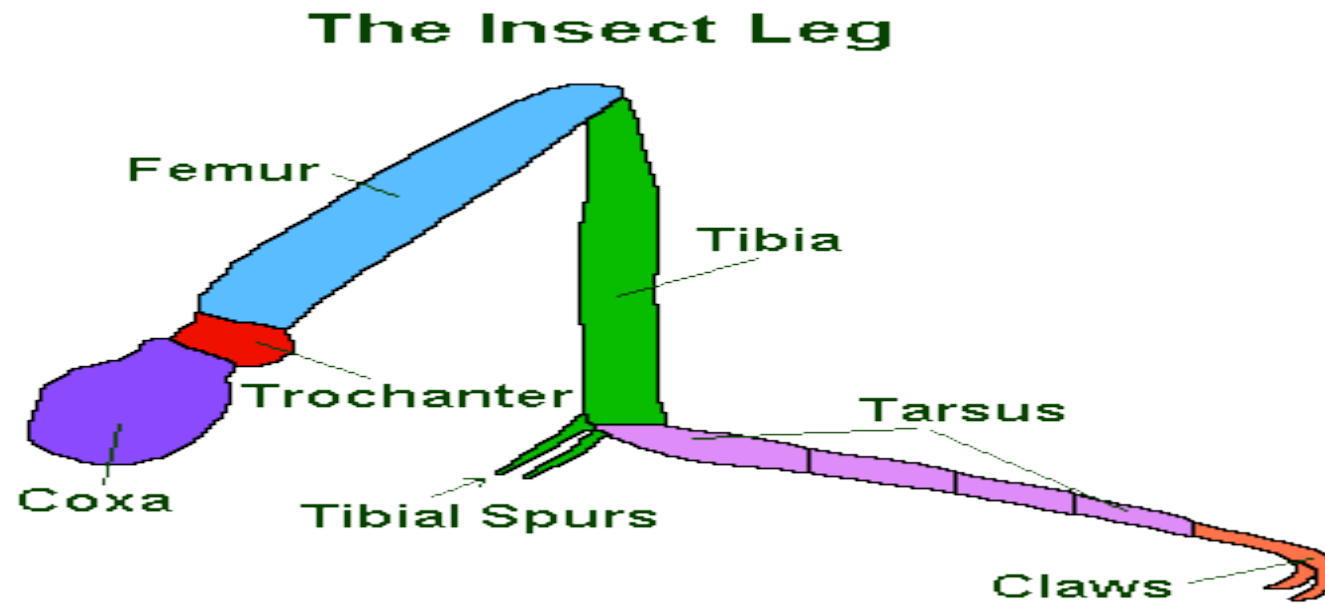
FEATURE:-

- It has 3 pairs of legs. One pair in each segment. Legs are used to walk and various functions.
- Spiracles are used in gaseous exchange and are present on the thorax segment at most with one pair per segment.
- Tergal plates are simple in immature insects but are modified in winged insects.
- Thoracic terga are called nota to distinguish them from abdominal terga.

STRUCTURE OF THORAX



INSECT LEG



Insect legs

All the three thoracic segments of insect possess a pair of legs as locomotory organs giving the hexapods and the class insecta as hexapods.

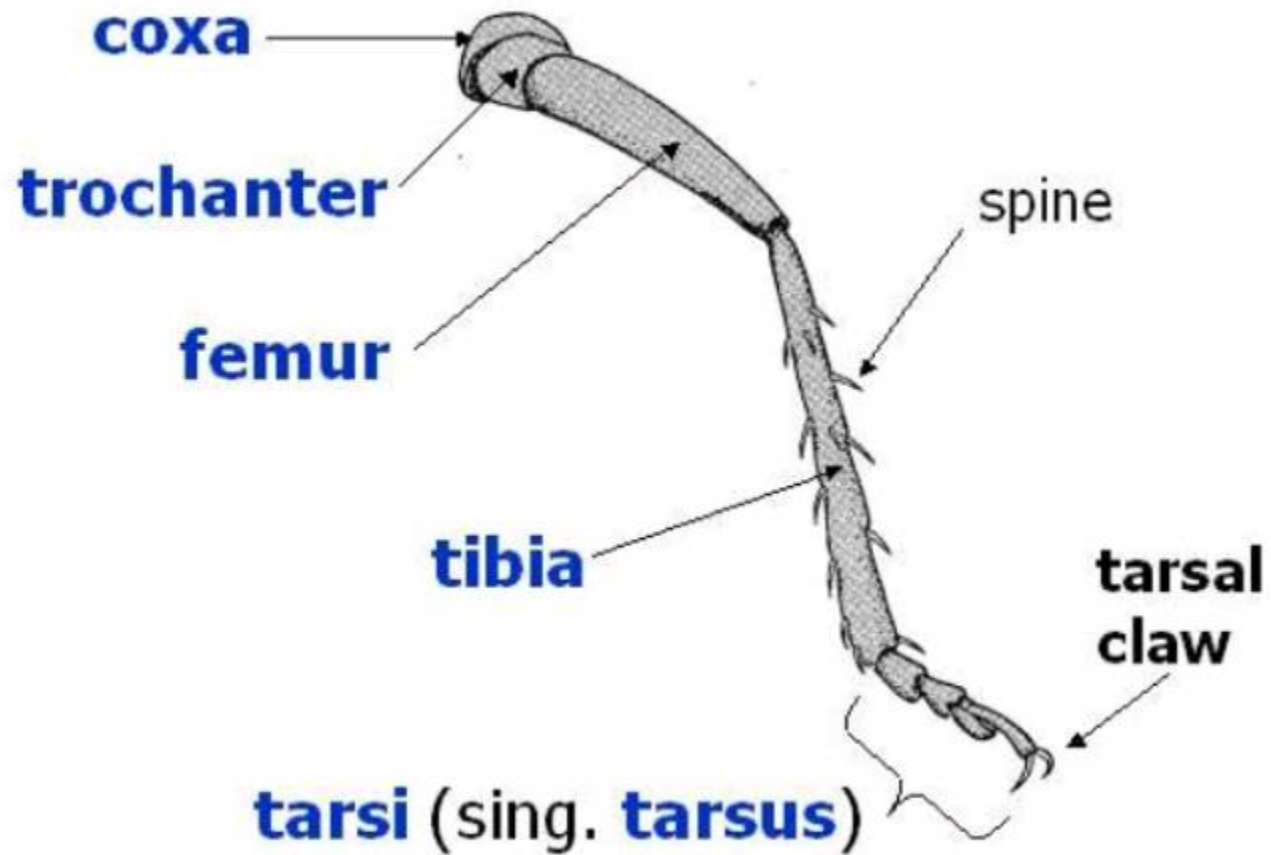
- Fore-legs are located on the prothorax
- Mid-legs on the mesothorax
- Hind legs on the metathorax

Insect leg mainly consists of five parts

1. Coxa
2. Trochanter
3. Femur
4. Tibia
5. Tarsus

Structure of legs

- **Coxa:** It is functional basal segment and it is rigidly fixed to thorax or weakly articulated.
- **Trochanter:** It is very small and the second segment. It is articulated with coxa and more or less to femur.
- **Femur:** It is the largest, strongest segment and is articulated with the tibia
- **Tibia:** It is equal or more than the length of femur, articulated with tarsus.
- **Tarsus:** It is the largest segment of legs and usually divided into sub segments tarsomeres.



Legs modification

- Saltatorial -jumping
- Raptorial - seizing
- Fossorial - digging
- Natatorial - swimming
- Cursorial -running
- Ambulatory-walking

1. Ambulatory legs

- Ambulatory legs are used for walking.
- The structure is similar to cursorial (running) legs.
- Examples: Bugs (order Hemiptera), leaf beetles beetles (Corder oleoptera).



2. Saltatorial legs

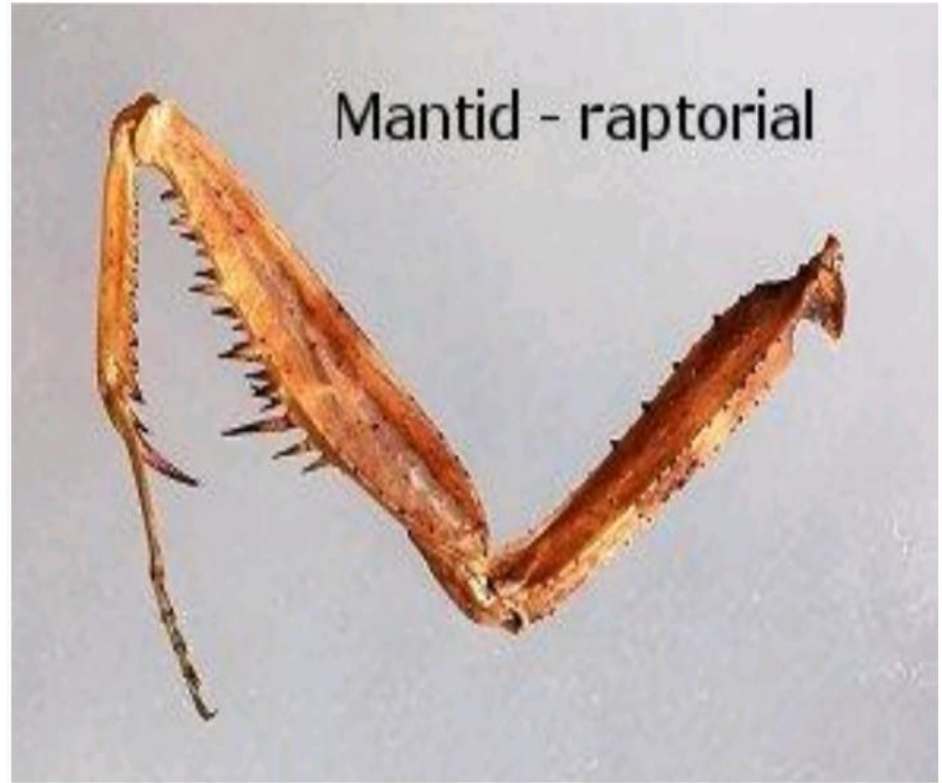
- Saltatorial hind legs adapted for jumping.
- These legs are characterized by an elongated femur and tibia.
- Examples:
Grasshoppers, crickets and katydids (order Orthoptera).



3. Raptorial legs

➤ Raptorial fore legs modified for grasping (catching prey).

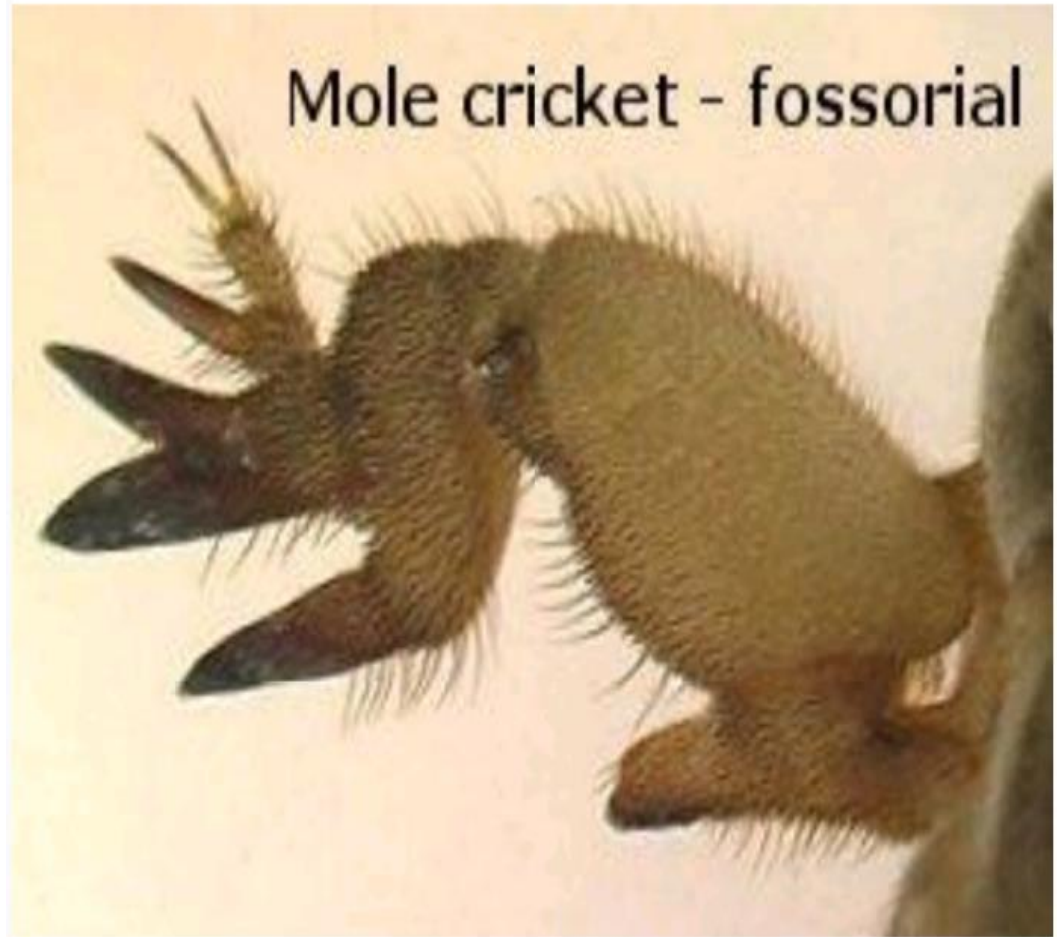
➤ Examples: Mantids (order Mantodea), ambush bugs, giant water bugs and water scorpions (order Hemiptera).



4. Fossorial legs

➤ Fossorial fore legs are modified for digging.

➤ Examples: Ground dwelling insects; mole crickets (order Orthoptera) and cicada nymphs (order Hemiptera).



5. Natatorial legs

- Natatorial legs are modified for swimming.
- These legs have long setae on the tarsi.
- Examples:
Aquatic beetes (order Coleoptera) and bugs (order Hemiptera).



6. Cursorial legs

➤ Cursorial legs are modified for running.

➤ The long, thin leg segments.

➤ Examples: Cockroaches (order Blattaria), ground and tiger beetles (order Coleoptera).



Cockroach - cursorial

WINGS

- Wings are fully developed only in adult.
- Exceptionally present in subimago, the penultimate stage of Ephemeroptera.
- Functional wings are flap-like cuticular projections supported by tubular, sclerotized veins.



MAJOR VEINS OF WINGS

- The major veins are longitudinal, running from the wing base towards the tip, and are more concentrated at the anterior margin.
- Additional supporting cross-veins are transverse struts, which join the longitudinal veins to give more complex structure.
- The major veins usually contain tracheae, blood vessels, and nerve fibers, with the intervening membranous areas comprising the closely appressed dorsal and ventral cuticular surfaces.
- The major veins are alternately “convex” and “concave” in relation to the surface plane of the wing, especially near the wing attachment; this configuration is described by plus(+) and minus(-) signs.



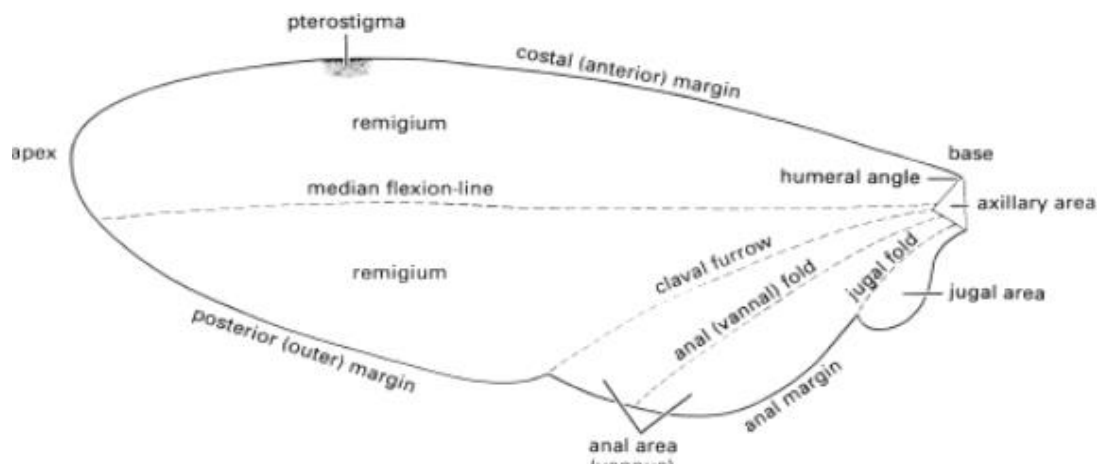
AREAS OF WINGS

- Most veins lie in the anterior area of the wing called **remigium**.
- The remigium powered by the thoracic flight muscles, is responsible for most of the movements of flight.
- The area of the wing posterior to the remigium sometimes is called the **clavus**.
- More often two areas are recognized: an anterior anal area(or vannus) and posterior jugal area.
- Wing areas are delimited.



FOLD-LINES OF WINGS

- Wings are delimited and subdivided by fold-lines, along which the wings can be folded.
- Flexion-lines, at which the wing flexes during flight.
- The fundamental distinction between these two types of lines is often blurred, as fold lines may permit some flexion.
- The claval furrow(a flexion line) and the jugal fold(or fold line) are nearly constant in position in different insect groups, but the median flexion-line and the anal(or vannal) fold(or fld-line) form variable and unsatisfactory area boundaries.
- Wing folding may be very complicated; transverse folding occurs in the hind wings of coleoptera and Dermaptera, and in some insects the enlarged anal area folded like fan.



HIND WINGS AND FORE WINGS

- The fore wings and hind wings of insects in many orders are coupled together, which improves the aerodynamic efficiency of flight.
- The commonest coupling mechanism(seen in Hymenoptera and trichoptera) is a row of small hooks, or hamuli, along the anterior margin of the hind wing that engages a fold along the posterior margin of the fore wing(hamulate coupling).
- In some other insects (Mecoptera, Lepidoptera and some Trichoptera), a jugal lobe of the fore wing overlaps the anterior hind wing(jugate coupling), or the margins of the fore and hind wing overlap broadly(amplexiform coupling), or one or more hind wing bristles(the frenulum) hook under a retaining structure (the retinaculum) or the fore wing (frenate coupling).



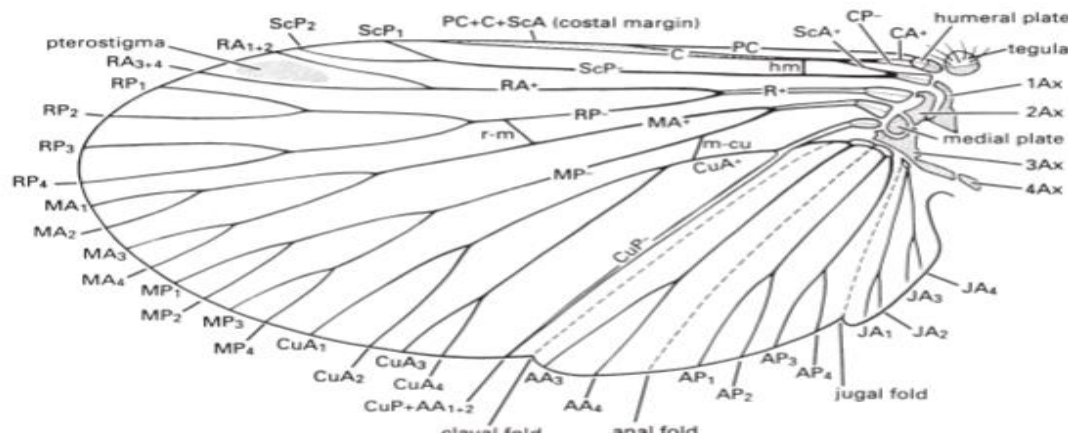
WINGS VENATION

- All winged insects share the same basic wing venation comprising of eight veins, named from anterior to posterior of the wing .
 1. Precosta(PC)
 2. Costa(C)
 3. Subcosta (Sc)
 4. Radius (R)
 5. Media (M)
 6. Cubitus(Cu)
 7. Anal(A)
 8. Jugal (J)
- Each vein has anterior convex(+) sector(a branch with all of its subdivisions), and a posterior concave(-) sector
- In almost all extant insects, the precosta is fused with costa and the jugal vein is rarely apparent.



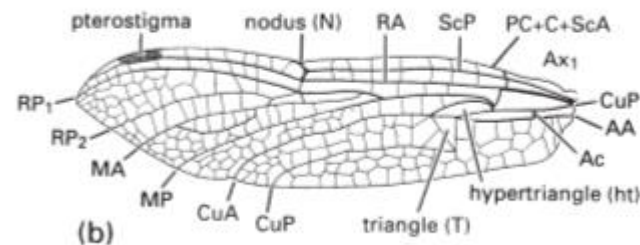
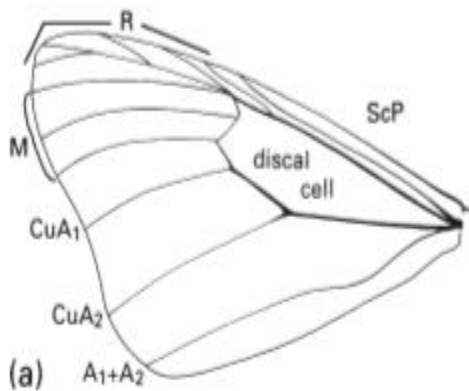
WING NOMENCLATURAL SYSTEM

- The wing nomenclatural system is that of Kukalova-Peck and is based on comparative studies of fossils and living insects.
- This system can be applied to the venation of all insects orders, but not applied widely because each insect order have a long history of use.
- The same vein may be referred to by different names in different insect orders because the structural homologies were not recognized correctly in early studies.
- For example, until 1991, the venational scheme for coleoptera labeled the radius posterior(RP) as the media(M) and the media posterior(MP) as cubitus(Cu).
- Correct interpretation of venational homologies is essential for phylogenetic studies.



CELLS OF WINGS

- Cells are areas of the wing delimited by veins and may be open(extending to the wing margin) or closed(surrounded by veins).
- They are named according to the longitudinal veins or vein branches, that they lie behind, except that certain cells are known by special name, such as the discal cell in lepidopter and the triangle in odonata.
- The pterostigma is an opaque or pigmented spot interiorly near the apex of the veins.



WING VENATION PATTERNS

- Wing venation patterns are consistent within groups (especially families and orders) but often differ between groups and, together with folds or pleats, provide major features used in insects classification and identification.
- Venation maybe greatly reduced by loss or postulated fusion of veins, or increased in complexity by numerous cross veins or substantial terminal branching .
- Other features that maybe diagnostic of the wings of different insects group are pigment pattern and colors, hairs, and scales.
- Scales occurs on the wings of lepidoptera, many Trichoptera, and few psocids (psocoptera) and flies.
- Hairs consists of small microtrichia, either scattered or grouped, and larger mactrichia, typically on the veins.
- Typically two pairs of functional wings on the mesothorax and as hind wings on the metathorax; typically the wings are membranous and transparent.
- However , from this pattern many other conditions are derived, involving variation in size, shape, and degree of sclertization of the fore and hind wings.

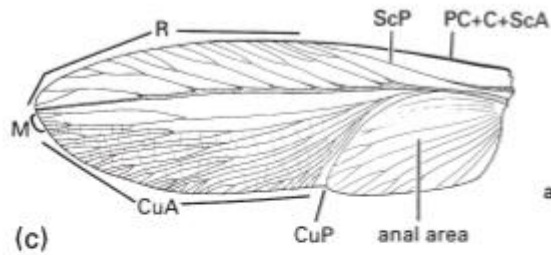


MODIFICATION OF FORE WING

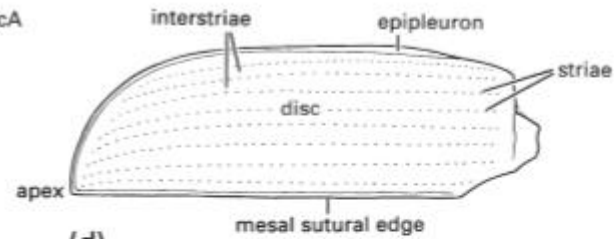
- The modification of fore wing include the thickened, leathery fore wings of Blattoda, Dermaptera, and orthoptera, which are called **tegmina** (**singular tegmen fig c**), the hardened fore wings of coleoptera that form protective wing cases or elytra (**singular; elytron fig d**), and the **hemelytra** (**singular; hemelytron**) of heteropteran.
- Hemiptera with the basal part thickened and the apical part membranous.(e)
- Typically, the heteropteran **hemelytron** is divided into three wing areas:
 1. **The membrane**
 2. **Corium**
 3. **Clavus**
- Sometimes the corium is further divided, with the embolium anterior to R+M, and the cuneus distal to a costal fracture.
- In Diptera the hind wings are modified as stabilizers (**halteres fig f**) and do not function as wings.



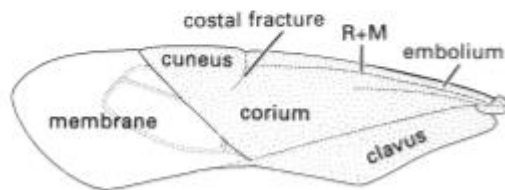
MODIFICATION OF FORE WING



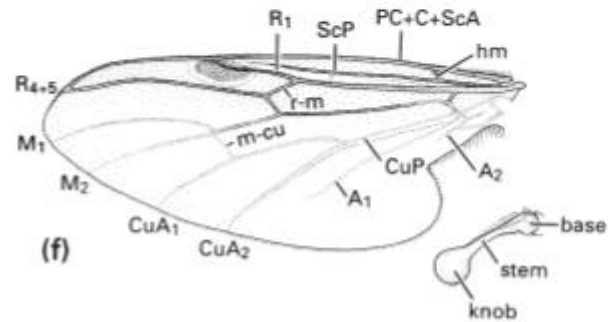
(c)



(d)



(e)



(f)



NAME: -----ROLL No.-----

Department of Zoology ..The Islamia University of Bahawalpur

Exam	Title Paper	Class/Subject	Time	Marks
Mid-term Spring 2020	Introduction to Entomology	BS/Zoology 6th Semester	12 Min	6

Q # 1 (a). Mark each statement as True or False. Write true statement if false. (0.5x6=3 Marks)

1. Remnants of original segmentation, generally restricted to the postoccipital suture.

2. .

3. .

4. .

5. .

6. .

Q # 1 (b): Choose the right word for each statement.

(0.5x6=3 Marks)

1. There are orders of insecta.

(A)	10	(B)	20	(C)	25	(D)	30
-----	----	-----	----	-----	----	-----	----

2. .

(A)		(B)		(C)		(D)	
-----	--	-----	--	-----	--	-----	--

3. Tick the statement/statements which is/are WRONG.

(A)	Cuticle lines the tracheal tube.
(B)	Apterygotes do not change from larvae to adults.
(C)	Metamerism is visible in Annelids.
(D)	Insects have two major body parts.

4. .

(A)		(B)		(C)		(D)	
-----	--	-----	--	-----	--	-----	--

5. .

(A)		(B)		(C)		(D)	
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6. .

(A)		(B)		(C)		(D)	
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Exam	Title Paper	Class/Subject	Time	Marks
Mid-term Spring 2020	Introduction to Entomology	BS/Zoology 6th Semester	50 Min	6

Q. 2: Answer following short questions.

(0.5x10=5 Marks)

1. Define Tagmosis?
2. Write down four principal regions of the body surface of insects?
3. .
4. .
5. .
6. .
7. .
8. .
9. .
- 10.

Q. 3: Write a note on Metamorphosis in insects.

1