extensible or some partially compressible tracheae or from air sacs. Coordinated opening and closing of the spiracles usually accompanies ventilatory movements and provides the basis for the unidirectional airflow that occurs in the main tracheae of larger insects. Anterior spiracles open during inspiration and posterior ones open during expiration. The presence of air sacs, especially if large or extensive, facilitates ventilation by increasing the volume of tidal air that can be changed as a result of ventilatory movements. If the main tracheal branches are strongly ventilated, diffusion appears sufficient to oxygenate even the most actively respiring tissues, such as flight muscles. However, the design of the gas exchange system of insects places an upper limit on size because, if oxygen has to diffuse over a considerable distance, the requirements of a very large and active insect either could not be met, even with ventilatory movements and compression and expansion of tracheae, or would result in substantial loss of water through the spiracles. Interestingly, many large insects are long and thin, thereby minimizing the diffusion distance from the spiracle along the trachea to any internal organ.

3.6 THE GUT, DIGESTION, AND NUTRITION

Insects of different groups consume an astonishing variety of foods, including watery xylem sap (e.g. nymphs of spittle bugs and cicadas), vertebrate blood (e.g. bed bugs and female mosquitoes), dry wood (e.g. some termites), bacteria and algae (e.g. black fly and many caddisfly larvae), and the internal tissues of other insects (e.g. endoparasitic wasp larvae). The diverse range of mouthpart types (section 2.3.1) correlates with the diets of different insects, but gut structure and function also reflect the mechanical properties and the nutrient composition of the food eaten. Four major feeding specializations can be identified depending on whether the food is solid or liquid or of plant or animal origin (Fig. 3.12). Some insect species clearly fall into a single category, but others with generalized diets may fall between two or more of them, and most endopterygotes will occupy different categories at different stages of their life (e.g. moths and butterflies switch from solid-plant as larvae to liquid-plant as adults). Gut morphology and physiology relate to these dietary differences in the following ways. Insects that take solid food typically have a wide, straight, short gut with strong musculature and obvious protection from abrasion (especially in the midgut, which has no cuticular lining). These features are most obvious in solid-feeders with rapid throughput of food as in plant-feeding caterpillars. In contrast, insects feeding on blood, sap, or nectar usually have long, narrow, convoluted guts to allow maximal contact with the liquid food; here, protection from abrasion is unnecessary. The most obvious gut specialization of liquid-feeders is a mechanism for removing excess water to concentrate nutrient substances prior to digestion, as seen in hemipterans (Box 3.3). From a nutritional viewpoint, most plant-feeding insects need to process large amounts of food because nutrient levels in leaves and stems are often low. The gut is usually short and without storage areas, as food is available continuously. By comparison, a diet of animal tissue is nutrient-rich and, at least for predators, well balanced. However, the food may be available only intermittently (such as when a predator captures prey or a blood meal is obtained) and the gut normally has large storage capacity.

3.6.1 Structure of the gut

There are three main regions to the insect gut (or alimentary canal), with sphincters (valves) controlling food/fluid movement between regions (Fig. 3.13). The **foregut** (**stomodeum**) is concerned with ingestion, storage, grinding, and transport of food to the next region, the **midgut** (**mesenteron**). Here digestive enzymes are produced and secreted and absorption of the products of digestion occurs. The material remaining in the gut lumen together with urine from the Malpighian tubules then enters the **hindgut** (**proctodeum**), where absorption of water, salts, and other valuable molecules occurs prior to elimination of the feces through the anus. The gut epithelium is one cell layer thick throughout the length of the canal and rests on a basement membrane surrounded by a variably developed muscle layer. Both the foregut and hindgut have a cuticular lining, whereas the midgut does not.

Each region of the gut displays several local specializations, which are variously developed in different insects, depending on diet. Typically the foregut is subdivided into a **pharynx**, an **oesophagus** (esophagus), and a **crop** (food storage area), and in insects that ingest solid food there is often a grinding organ, the

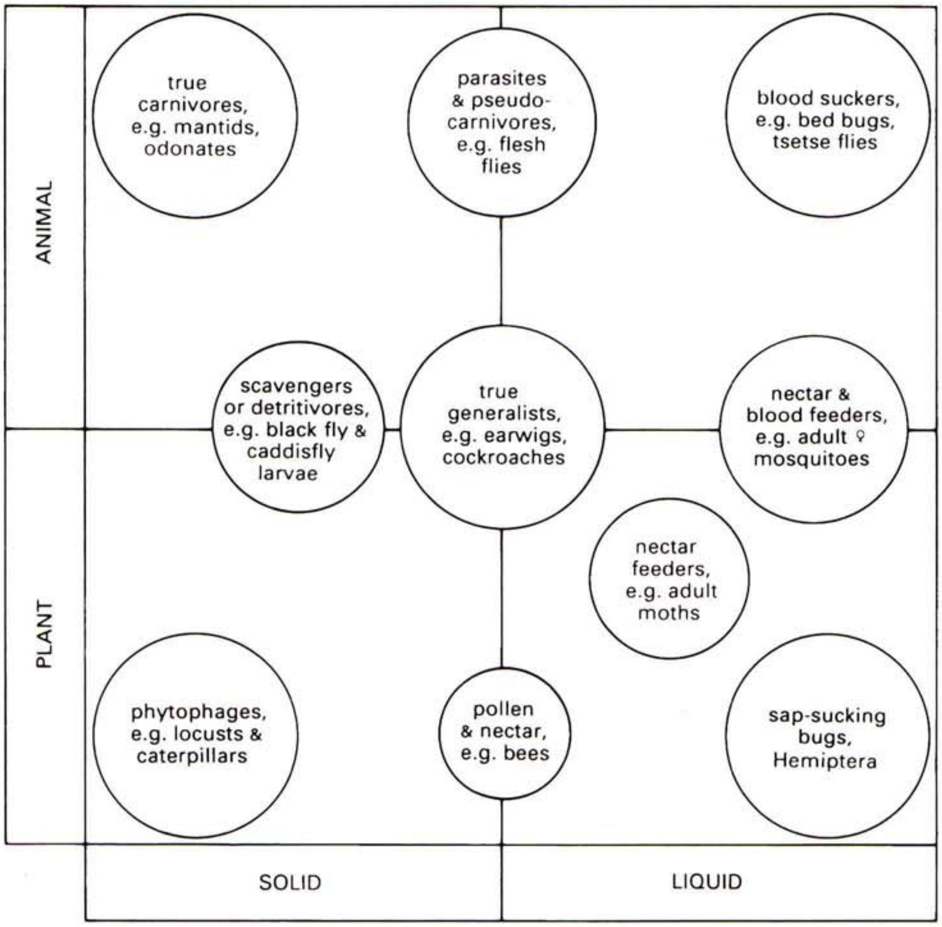


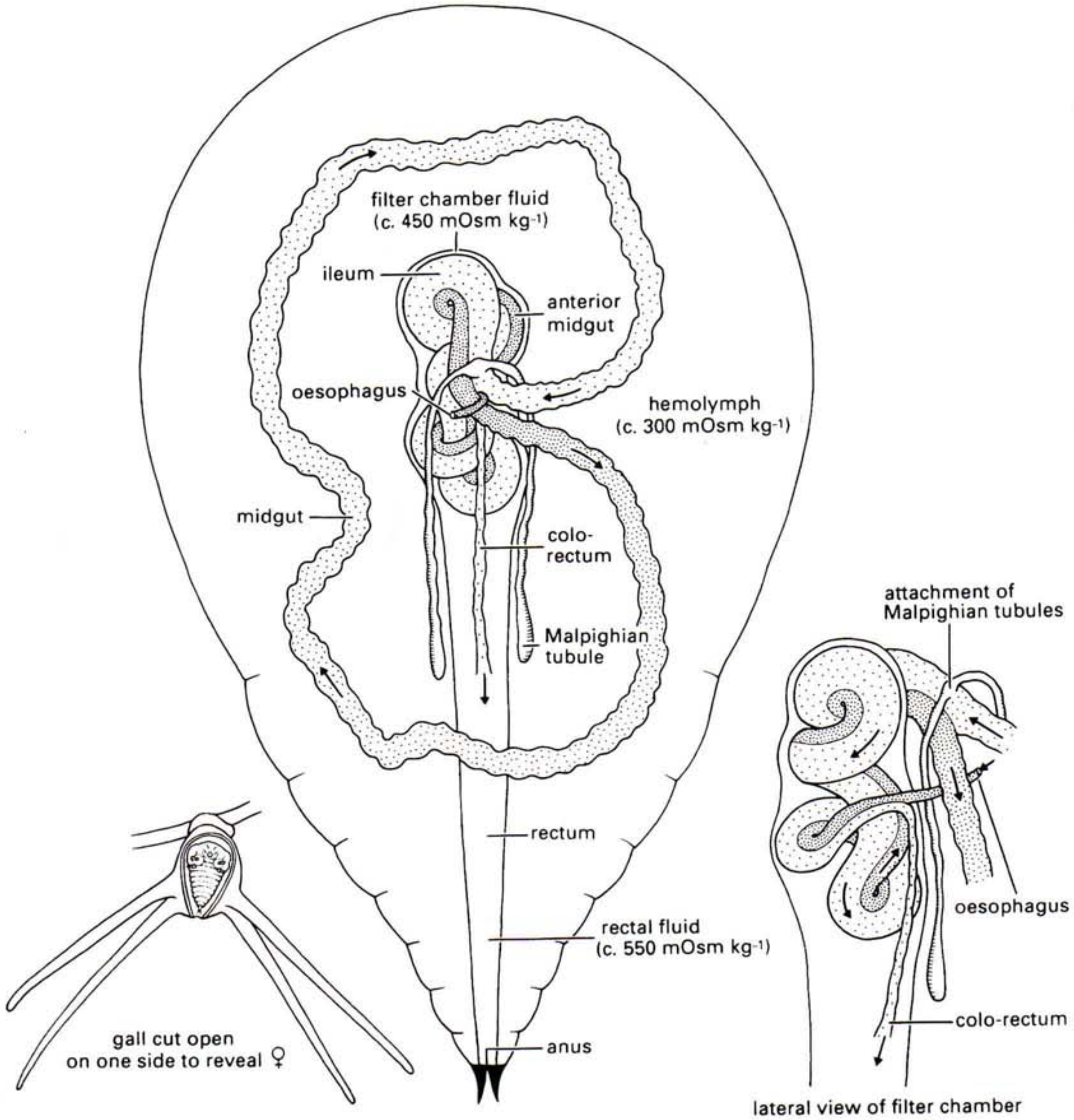
Fig. 3.12 The four major categories of insect feeding specialization. Many insects are typical of one category, but others cross two categories (or more, as in generalist cockroaches). (After Dow 1986.)

proventriculus (or gizzard). The proventriculus is especially well developed in orthopteroid insects, such as cockroaches, crickets, and termites, in which the epithelium is folded longitudinally to form ridges on which the cuticle is armed with spines or teeth. At the anterior end of the foregut the mouth opens into a preoral cavity bounded by the bases of the mouthparts and often divided into an upper area, or **cibarium**, and a lower part, or **salivarium** (Fig. 3.14a). The paired **labial** or **salivary glands** vary in size and arrangement from simple elongated tubes to complex branched or lobed structures.

Complicated glands occur in many Hemiptera that produce two types of saliva (see section 3.6.2). In Lepidoptera, the labial glands produce silk, whereas mandibular glands secrete the saliva. Several types of secretory cell may occur in the salivary glands of one insect. The secretions from these cells are transported along cuticular ducts and emptied into the ventral part of the preoral cavity. In insects that store meals in their foregut, the crop may take up the greater portion of the food and often is capable of extreme distension, with a posterior sphincter controlling food retention. The crop may be an enlargement of part of the tubular gut (Fig. 3.7) or a lateral diverticulum.

The generalized midgut has two main areas: the tubular **ventriculus** and blind-ending lateral diverticula called **caeca** (ceca). Most cells of the midgut are

Box 3.3 The filter chamber of Hemiptera



Most Hemiptera have an unusual arrangement of the midgut which is related to their habit of feeding on plant fluids. An anterior and a posterior part of the gut (typically involving the midgut) are in intimate contact to allow concentration of the liquid food. This filter chamber allows excess water and relatively small molecules, such as simple sugars, to be passed quickly and directly from the anterior gut to the hindgut, thereby short-circuiting the main absorptive portion of the midgut. Thus, the digestive region is not diluted by water nor congested by superabundant food molecules. Well-developed filter chambers are characteristic of cicadas and spittle bugs, which feed on xylem (sap that is rich in ions, low in organic compounds, and with low osmotic pressure), and leafhoppers and coccoids, which feed on phloem (sap that is rich in nutrients, especially sugars, and with high osmotic pressure). The gut physiology of such sap-suckers has been rather poorly studied because accurate recording of gut fluid composition and osmotic pressure depends on the technically difficult task of taking readings from an intact gut.

Adult female coccoids of gall-inducing *Apiomorpha* species (Eriococcidae) (section 11.2.5) tap the vascular tissue of the gall wall to obtain phloem sap. Some species have a highly developed filter chamber formed from loops of the anterior midgut and anterior hindgut enclosed within the membranous rectum. Depicted here is the gut of an adult female of *A. munita* viewed from the ventral side of the body. The thread-like sucking mouthparts (Fig. 11.4c) in series with the cibarial pump connect to a short oesophagus, which can be seen here in both the main drawing and the enlarged lateral view of the filter chamber. The oesophagus terminates at the anterior midgut, which coils upon itself as three loops of the filter chamber. It emerges ventrally and forms a large midgut loop lying free in the hemolymph. Absorption of nutrients occurs in this free loop. The Malpighian tubules enter the gut at the commencement of the ileum, before the ileum enters the filter chamber where it is closely apposed to the much narrower anterior midgut. Within the irregular spiral of the filter chamber, the fluids in the two tubes move in opposite directions (as indicated by the arrows).

The filter chamber of these coccoids apparently transports sugar (perhaps by active pumps) and water (passively) from the anterior midgut to the ileum and then via the narrow colo-rectum to the rectum, from which it is eliminated as honeydew. In *A. munita*, other than water, the honeydew is mostly sugar (accounting for 80% of the total osmotic pressure of about 550 mOsm kg^{-1*}). Remarkably, the osmotic pressure of the hemolymph (about 300 mOsm kg^{-1}) is much lower than that within the filter chamber (about 450 mOsm kg^{-1}) and rectum. Maintenance of this large osmotic difference may be facilitated by the impermeability of the rectal wall.

*Osmolarity values are from the unpublished data of P.D. Cooper & A.T. Marshall.

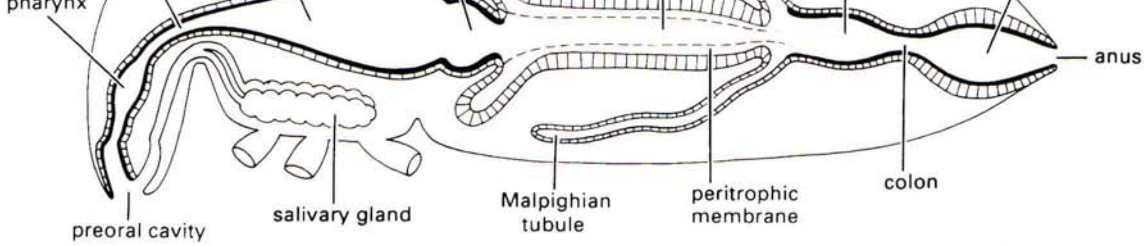


Fig. 3.13 Generalized insect alimentary canal showing division into three regions. The cuticular lining of the foregut and hindgut are indicated by thicker black lines. (After Dow 1986.)

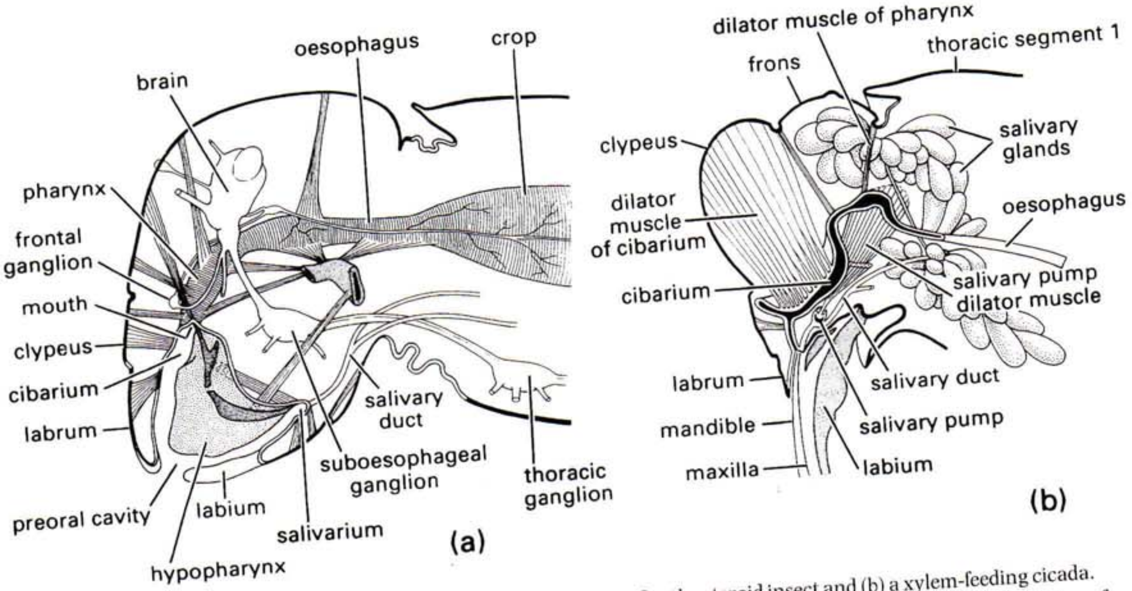


Fig. 3.14 Preoral and anterior foregut morphology in (a) a generalized orthopteroid insect and (b) a xylem-feeding cicada. Musculature of the mouthparts and the (a) pharyngeal or (b) cibarial pump are indicated but not fully labeled. Contraction of the respective dilator muscles causes dilation of the pharynx or cibarium and fluid is drawn into the pump chamber. Relaxation of these muscles results in elastic return of the pharynx or cibarial walls and expels food upwards into the oesophagus. (After Snodgrass 1935.)

structurally similar, being columnar with microvilli (finger-like protrusions) covering the inner surface. The distinction between the almost indiscernible foregut epithelium and the thickened epithelium of the midgut usually is visible in histological sections (Fig. 3.15). The midgut epithelium mostly is separated from the food by a thin sheath called the **peritrophic membrane**, consisting of a network of chitin fibrils in a protein–glycoprotein matrix. These proteins, called peritrophins, may have evolved from gastrointestinal mucus proteins by acquiring the ability to bind chitin. The peritrophic membrane either is delaminated from the whole midgut or produced by cells in the anterior region of the midgut. Exceptionally Hemiptera and Thysanoptera lack a peritrophic membrane, as do just the adults of several other orders.

Typically, the beginning of the hindgut is defined by the entry point of the Malpighian tubules, often into a distinct **pylorus** forming a muscular pyloric sphincter, followed by the ileum, colon, and rectum. The main functions of the hindgut are the absorption of water, salts, and other useful substances from the feces and urine; a detailed discussion of structure and function is presented in section 3.7.1.

3.6.2 Saliva and food ingestion

Salivary secretions dilute the ingested food and adjust its pH and ionic content. The saliva often contains digestive enzymes and, in blood-feeding insects, anticoagulants and thinning agents are present. In insects with extra-intestinal digestion, such as predatory Hemiptera, digestive enzymes are exported into the food and the resulting liquid is ingested. Most Hemiptera produce an alkaline watery saliva that is a vehicle for enzymes (either digestive or lytic), and a proteinaceous solidifying saliva that either forms a complete sheath around the mouthparts (stylets) as they pierce and penetrate the food or just a securing flange at the point of entry (section 11.2.4, Fig. 11.4c). Stylet-sheath feeding is characteristic of phloem- and xylem-feeding Hemiptera, such as aphids, scale insects (coccoids), and spittle bugs, which leave visible tracks formed of exuded solidifying saliva in the plant tissue on which they have fed. The sheath may function to guide the stylets, prevent loss of fluid from damaged cells, and/or absorb necrosis-inducing compounds to reduce defensive reaction by the plant. By comparison, a macerate-and-flush strategy is typical of Heteroptera,

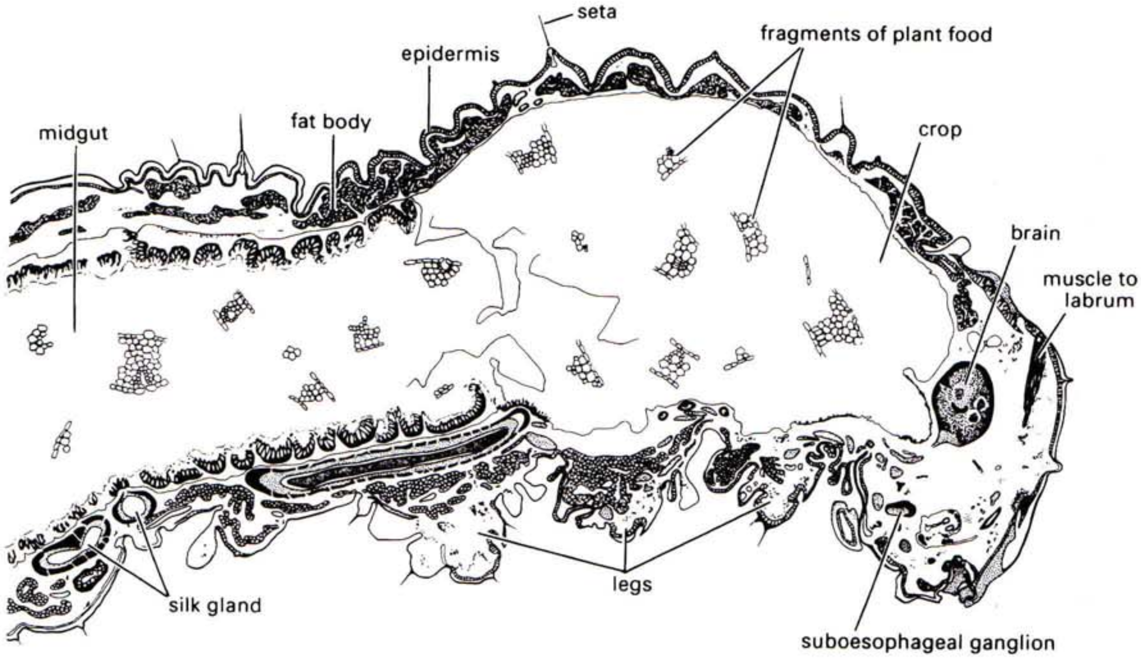


Fig. 3.15 Longitudinal section through the anterior body of a caterpillar of the small white, small cabbage white, or cabbage white butterfly, *Pieris rapae* (Lepidoptera: Pieridae). Note the thickened epidermal layer lining the midgut.

such as mirids and coreids. These insects disrupt the tissues of plants or other insects by thrusting of the stylets and/or by addition of salivary enzymes. The macerated and/or partly digested food is "flushed out" with saliva and ingested by sucking.

In fluid-feeding insects, prominent dilator muscles attach to the walls of the pharynx and/or the preoral cavity (**cibarium**) to form a pump (Fig. 3.14b), although most other insects have some sort of pharyngeal pump (Fig. 3.14a) for drinking and air intake to facilitate cuticle expansion during a molt.

3.6.3 Digestion of food

Most digestion occurs in the midgut, where the epithelial cells produce and secrete digestive enzymes and also absorb the resultant food breakdown products. Insect food consists principally of polymers of carbohydrates and proteins, which are digested by enzymatically breaking these large molecules into small monomers. The midgut pH usually is 6.0–7.5, although very alkaline values (pH 9–12) occur in many plant-feeding insects that extract hemicelluloses from plant cell walls, and very low pH values occur in many Diptera. High pH may prevent or reduce the binding of dietary tannins to food proteins, thereby increasing the digestibility of ingested plants, although the significance of this mechanism *in vivo* is unclear. In some insects, gut lumenal surfactants (detergents) may have an important role in preventing the formation of tannin–protein complexes, particularly in insects with near-neutral gut pH.

In most insects, the midgut epithelium is separated from the food bolus by the peritrophic membrane, which constitutes a very efficient high-flux sieve. It is perforated by pores, which allow passage of small molecules while restricting large molecules, bacteria, and food particles from directly accessing the midgut cells. The peritrophic membrane also may protect herbivorous insects from ingested allelochemicals such as tannins (section 11.2). In some insects, all or most midgut digestion occurs inside the peritrophic membrane in the **endoperitrophic space**. In others,

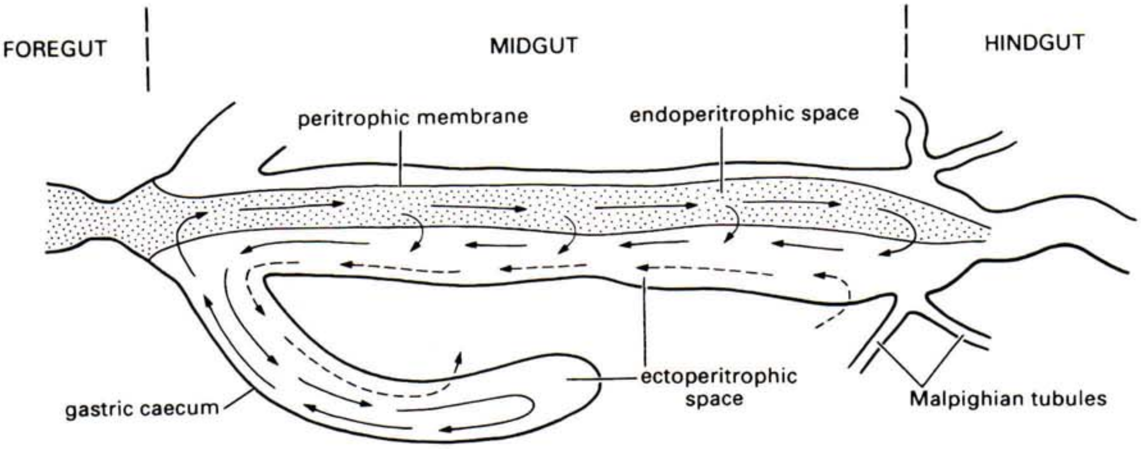


Fig. 3.16 Generalized scheme of the endo–ectoperitrophic circulation of digestive enzymes in the midgut. (After Terra & Ferreira 1981.)

only initial digestion occurs there and smaller food molecules then diffuse out into the **ectoperitrophic space**, where further digestion takes place (Fig. 3.16). A final phase of digestion usually occurs on the surface of the midgut microvilli, where certain enzymes are either trapped in a mucopolysaccharide coating or bound to the cell membrane. Thus the peritrophic membrane forms a permeability barrier and helps to compartmentalize the phases of digestion, in addition to providing mechanical protection of the midgut cells, which was once believed to be its principal function. Fluid containing partially digested food molecules and digestive enzymes is thought to circulate through the midgut in a posterior direction in the endoperitrophic space and forwards in the ectoperitrophic space, as indicated in Fig. 3.16. This endo–ectoperitrophic circulation may facilitate digestion by moving food molecules to sites of final digestion and absorption and/or by conserving digestive enzymes, which are removed from the food bolus before it passes to the hindgut.

Unusually, both Hemiptera and Thysanoptera (but not Psocodea), which lack a peritrophic membrane, have an extracellular lipoprotein membrane, the **perimicrovillar membrane** (PPM), ensheathing the microvilli of the midgut cells and forming a closed space. The PPM and associated perimicrovillar space may function to improve absorption of organic molecules, such as amino acids, by generating a concentration gradient between the liquid contents of the gut lumen and the fluid in the perimicrovillar space adjacent to the midgut cells. The PPM has membrane-bound α-glucosidase which breaks down sucrose in the ingested plant sap.

3.6.4 The fat body

In many insects, especially the larvae of holometabolous groups, fat body tissue is a conspicuous component of the internal anatomy (Figs 3.7 & 3.15). Typically, it forms a white or yellow tissue formed of loose sheets, ribbons, or lobes of cells lying in the hemocoel. The structure of this organ is ill-defined and taxonomically variable, but often caterpillars and other larvae have a peripheral layer of fat body beneath the cuticle and a central layer around the gut. The fat body is an organ of multiple metabolic functions, including the metabolism of carbohydrates, lipids, and nitrogenous compounds; the storage of glycogen, fat, and protein; the synthesis and regulation of blood sugar; and the synthesis of major hemolymph proteins (such as hemoglobins, vitellogenins for yolk formation, and storage proteins). Fat body cells can switch their activities in response to nutritional and hormonal signals to supply the requirements of insect growth, metamorphosis, and reproduction. For example, specific storage proteins are synthesized by the fat body during the final larval instar of holometabolous insects and accumulate in the hemolymph to be used during metamorphosis as

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a source of amino acids for the synthesis of proteins during pupation. **Calliphorin**, a hemolymph storage protein synthesized in the fat body of larval blow flies (Diptera: Calliphoridae: *Calliphora*), may form about 75% of the hemolymph protein of a late-instar maggot, or about 7 mg; the amount of calliphorin falls to around 3 mg at the time of pupariation and to 0.03 mg after emergence of the adult fly. The production and deposition of proteins specifically for amino acid storage is a feature that insects share with seed plants but not with vertebrates. Humans, for example, excrete any dietary amino acids that are in excess of immediate needs.

The principal cell type found in the fat body is the **trophocyte** (or **adipocyte**), which is responsible for most of the above metabolic and storage functions. Visible differences in the extent of the fat body in different individuals of the same insect species reflect the amount of material stored in the trophocytes; little body fat indicates either active tissue construction or starvation. Two other cell types – urocytes and mycetocytes (also called bacteriocytes) – may occur in the fat body of some insect groups. **Urocytes** temporarily store spherules of urates, including uric acid, one of the nitrogenous wastes of insects. Amongst studied cockroaches, rather than being permanent stores of excreted waste uric acid (storage excretion), urocytes recycle urate nitrogen, perhaps with assistance of mycetocyte bacteria. **Mycetocytes** (**bacteriocytes**) contain symbiotic microorganisms and are scattered through the fat body of cockroaches or contained within special organs, sometimes surrounded by fat body. These bacteria-like symbionts appear important in insect nutrition.

3.6.5 Nutrition and microorganisms

Broadly defined, nutrition concerns the nature and processing of foods needed to meet the requirements for growth and development, involving feeding behavior (Chapter 2) and digestion. Insects often have unusual or restricted diets. Sometimes, although only one or a few foods are eaten, the diet provides a complete range of the chemicals essential to metabolism. In these cases, monophagy is a specialization without nutritional limitations. In others, a restricted diet may require utilization of microorganisms in digesting or supplementing the directly available nutrients. In particular, insects cannot synthesize sterols (required for molting hormone) and carotenoids (used in visual pigments), which must come from the diet or microorganisms.

Insects may harbor extracellular or intracellular microorganisms, referred to as **symbionts** because they are dependent on their insect hosts. These microorganisms contribute to the nutrition of their hosts by functioning in sterol, vitamin, carbohydrate, or amino acid synthesis and/or metabolism. Symbiotic microorganisms may be bacteria or bacteroids, yeasts or other unicellular fungi, or protists. Studies on their function historically were hampered by difficulties in removing them (e.g. with antibiotics, to produce aposymbionts) without harming the host insect, and also in culturing the microorganisms outside the host. The diets of their hosts provided some clues as to the functions of these microorganisms. Insect hosts include many sap-sucking hemipterans (such as aphids, psyllids, whiteflies, scale insects, thrips, leafhoppers, and cicadas) and sap- and blood-sucking heteropterans (Hemiptera), parasitic lice (Psocodea), some wood-feeding insects (such as termites and some longicorn beetles and weevils), many seed- or grain-feeding insects (certain beetles), and some omnivorous insects (such as cockroaches, some termites, and some ants). Predatory insects never seem to contain such symbionts. That microorganisms are required by insects on suboptimal diets has been confirmed by modern studies showing, for example, that critical dietary shortfall in certain essential amino acids in aposymbiotic aphids is compensated for by production by *Buchnera* symbionts (Gammaproteobacteria). Similarly, the nutritionally poor xylem sap diet of sharpshooters (Hemiptera: Cicadellidae) is augmented by the biosyntheses of its two main symbionts: *Sulcia muelleri* (Bacteroidetes), which has genes for the synthesis of essential amino acids, and *Baumannia cicadellinicola* (Gammaproteobacteria) that provides its host with a number of cofactors including B vitamins. In some termites, spirochete bacteria provide much of a colony's nitrogen, carbon and energy requirements via acetogenesis and nitrogen fixation. Although insects once were presumed to lack cellulases, they are present at least in termite guts, and their role in cellulose digestion relative to that of their symbionts is under active study.

Extracellular symbionts may be free in the gut lumen or housed in diverticula or pockets of the midgut or hindgut. For example, termite hindguts contain a veritable fermenter comprising many bacteria, fungi, and protists, including flagellates, which assist in the degradation of the otherwise refractory dietary lignocellulose, and in the fixation of atmospheric nitrogen. The process involves generation of methane, and calculations suggest that tropical termites' symbiont-assisted cellulose digestion produces a significant proportion of the world's methane (a greenhouse gas) production.

Transmission of extracellular symbionts from an individual insect to another involves one of two main methods, depending upon where the symbionts are located within the insect. The first mode of transmission, by oral uptake by the offspring, is appropriate for insects with gut symbionts. Microorganisms may be acquired from the anus or the excreta of other individuals or eaten at a specific time, as in some bugs, in which the newly hatched young eat the contents of special symbiont-containing capsules deposited with the eggs.

Intracellular symbionts (**endosymbionts**) may occur in as many as 70% of all insect species. Endosymbionts probably mostly have a mutualistic association with their host insect, but some are best referred to as "guest microbes" because they appear parasitic on their host. Examples of the latter include *Wolbachia* (section 5.10.4), *Spiroplasma*, and microsporidia. Endosymbionts may be housed in the gut epithelium, as in lygaeid bugs and some weevils; however, most insects with intracellular microorganisms house them in symbiont-containing cells called mycetocytes or bacteriocytes, according to the identity of the symbiont. These cells are in the body cavity, usually associated with the fat body or the gonads, and often in special aggregations of mycetocytes, forming an organ called a **mycetome** or **bacteriome**. In such insects, the symbionts are transferred to the ovary and then to the eggs or embryos prior to oviposition or parturition: a process referred to as **vertical** or **transovarial transmission**. Lacking evidence for lateral transfer (to an unrelated host), this method of transmission found in many Hemiptera and cockroaches indicates a very close association or coevolution of the insects and their microorganisms. Evidence for benefits of endosymbionts to hosts is accruing rapidly due to genome sequencing and studies of gene expression. For example, as mentioned above, the provision of the otherwise dietarily scarce essential amino acids to aphids by their bacteriocyte-associated *Buchnera* symbiont is well substantiated. Of interest for further research is the suggestion that aphid biotypes with *Buchnera* bacteriocytes show enhanced ability to transmit certain plant viruses of the genus *Luteovirus* relative to antibiotic-treated, symbiont-free individuals. The relationship between bacteriocyte endosymbionts and their phloem-feeding host insects is a very tight phylogenetic association (see also *Wolbachia* infections, section 5.10.4), suggesting a very old association with co-diversification.

Some insects that maintain fungi essential to their diet cultivate them external to their body as a means of converting woody substances to an assimilable form. Examples are the fungus gardens of some ants (Formicidae) and termites (Termitidae) (sections 9.5.2 & 9.5.3) and the fungi transmitted by certain timber pests, namely, wood wasps (Hymenoptera: Siricidae) and ambrosia beetles (Coleoptera: Scolytinae).

3.7 THE EXCRETORY SYSTEM AND WASTE DISPOSAL

Excretion – the removal from the body of waste products of metabolism, especially nitrogenous compounds – is essential. It differs from defecation in that excretory wastes have been metabolized in cells of the body rather than simply passing directly from the mouth to the anus (sometimes essentially unchanged chemically). Of course, insect feces, either in liquid form or packaged in pellets and known as **frass**, contain both undigested food and metabolic excretions. Aquatic insects eliminate dilute wastes from their anus directly into water, and so their fecal material is flushed away. In comparison, terrestrial insects generally must conserve water. This requires efficient waste disposal in a concentrated or even dry form while simultaneously avoiding the potentially toxic effects of nitrogen. Furthermore, both terrestrial and aquatic insects must conserve ions, such as sodium (Na^+), potassium (K^+), and chloride (Cl^-), that may be limiting in their food or, in aquatic insects, lost into the water by diffusion. Production of insect urine or frass therefore results from two intimately related processes: excretion and **osmoregulation**, the maintenance of a favorable body fluid composition (osmotic and ionic homeostasis). The system responsible for excretion and osmoregulation is referred to loosely as the excretory system, and its activities are performed largely by the Malpighian tubules and hindgut as outlined below. However, in freshwater insects, hemolymph composition must be regulated in response to constant loss of salts (as ions) to the surrounding water, and ionic regulation involves both the typical excretory system and special cells, called **chloride cells**, which usually are associated

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with the hindgut. Chloride cells are capable of absorbing inorganic ions from very dilute solutions and are best studied in larval dragonflies and damselflies.

3.7.1 The Malpighian tubules and rectum

The main organs of excretion and osmoregulation in insects are the Malpighian tubules acting in concert with the rectum and/or ileum (Fig. 3.17). Malpighian tubules are outgrowths of the alimentary canal and consist of long thin tubules (Fig. 3.1) formed of a single layer of cells surrounding a blind-ending lumen. They range in number from as few as two in most scale insects (coccoids) to over 200 in large locusts. Generally they are free, waving around in the hemolymph, where they filter out solutes. Only aphids lack Malpighian tubules. The vignette for this chapter shows the gut of *Locusta*, but with only a few of the many Malpighian tubules depicted. Similar structures are believed to have arisen convergently in different arthropod groups, such as myriapods and arachnids, in response to the physiological stresses of life on dry land. Traditionally, insect Malpighian tubules are considered to belong to the hindgut and be ectodermal in origin. Their position marks the junction of the midgut and the cuticle-lined hindgut.

The anterior hindgut is called the **ileum**, the generally narrower middle portion is the **colon**, and the expanded posterior section is the **rectum** (Fig. 3.13). In many terrestrial insects the rectum is the only site of water and solute resorption from the excreta, but in other insects, for example the desert locust *Schistocerca gregaria* (Orthoptera: Acrididae), the ileum makes some contribution to osmoregulation. In a few insects, such as the cockroach *Periplaneta americana* (Blattodea: Blattidae), even the colon may be a potential site of some fluid absorption. The resorptive role of the rectum

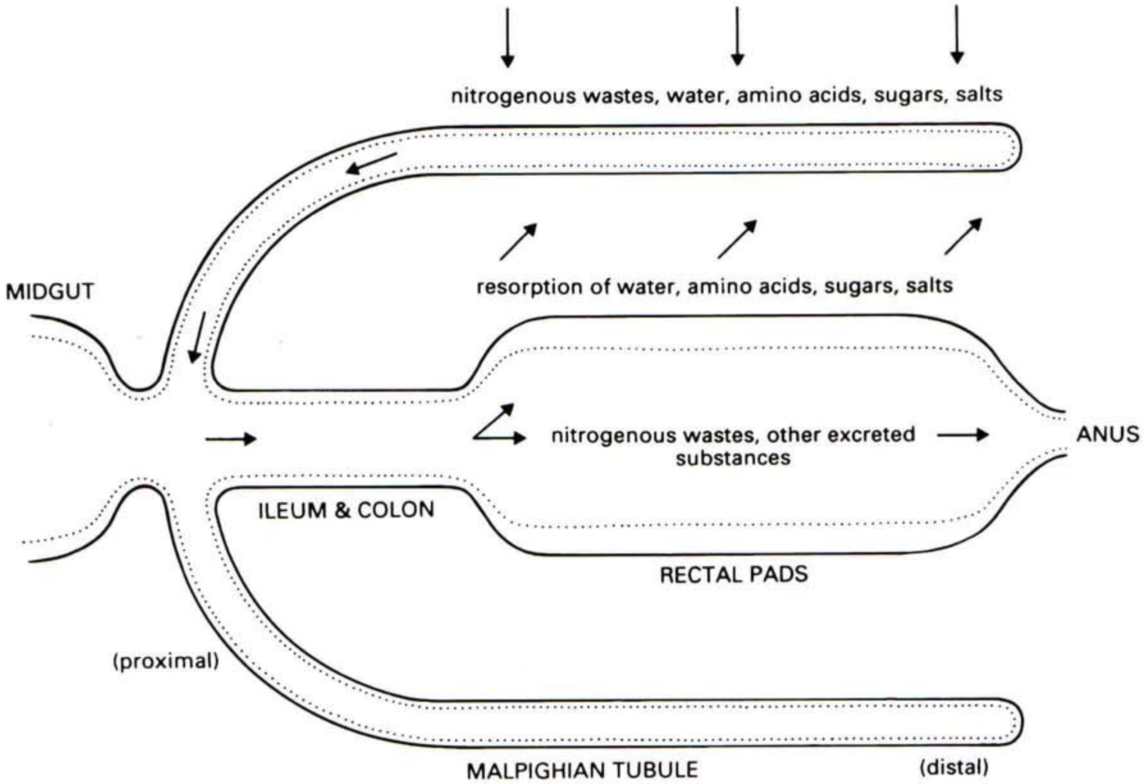

Fig. 3.17 Schematic diagram of a generalized excretory system showing the path of elimination of wastes. (After Daly et al. 1978.)

(and sometimes the anterior hindgut) is indicated by its anatomy. In most insects, specific parts of the rectal epithelium are thickened to form **rectal pads** or papillae composed of aggregations of columnar cells; typically there are six pads arranged longitudinally, but there may be fewer pads or many papillate ones.

The general picture of insect excretory processes outlined here is applicable to most freshwater species and to the adults of many terrestrial species. The Malpighian tubules produce a filtrate (the primary urine) which is isosmotic but ionically dissimilar to the hemolymph, and then the hindgut, especially the rectum, selectively reabsorbs water and certain solutes but eliminates others (Fig. 3.17). Details of Malpighian tubule and rectal structure and of filtration and absorption mechanisms differ between taxa, in relation to both taxonomic position and dietary composition (Box 3.4 gives an example of one type of specialization: cryptonephric systems), but the excretory system of the desert locust *S. gregaria* (Fig. 3.18) exemplifies the general structure and principles of insect excretion. The Malpighian tubules of the locust produce an isosmotic filtrate of the hemolymph, which is high in K^+ and low in Na^+, and has Cl^- as the major anion. The active transport of ions, especially K^+, into the tubule lumen generates an osmotic pressure gradient so that water passively follows (Fig. 3.18a). Sugars and most amino acids also are filtered passively from the hemolymph (probably via junctions between the tubule cells), whereas the amino acid proline (later used as an energy source by the rectal cells) and non-metabolizable and toxic organic compounds are transported actively into the tubule lumen. Sugars, such as sucrose and trehalose, are resorbed from the lumen and returned to the hemolymph. The continuous secretory activity of each Malpighian tubule leads to a flow of primary urine from its lumen towards and into the gut. In the rectum, the urine is modified by removal of solutes and water to maintain fluid and ionic homeostasis of the locust's body (Fig. 3.18b). Specialized cells in the rectal pads carry out active recovery of Cl^- under hormonal stimulation. This pumping of Cl^- generates electrical and osmotic gradients that lead to some resorption of other ions, water, amino acids, and acetate.

3.7.2 Nitrogen excretion

Many predatory, blood-feeding and even plant-feeding insects ingest nitrogen, particularly certain amino acids, far in excess of requirements. Most insects excrete nitrogenous metabolic wastes at some or all stages of their life, although some nitrogen is stored in the fat body or as proteins in the hemolymph in some insects. Many aquatic insects and some flesh-feeding flies excrete large amounts of ammonia, whereas in terrestrial insects wastes generally consist of **uric acid** and/or certain of its salts (**urates**), often in combination with urea, pteridines, certain amino acids, and/or relatives of uric acid, such as hypoxanthine, allantoin, and allantoic acid. Amongst these waste compounds, ammonia is relatively toxic and usually must be excreted as a dilute solution, or else rapidly volatilized from the cuticle or feces (as in cockroaches). Urea is less toxic but more soluble, requiring much water for its elimination. Uric acid and urates require less water for synthesis than either ammonia or urea (Fig. 3.19), are non-toxic and, having low solubility in water (at least in acidic conditions), can be excreted essentially dry, without causing osmotic problems. Waste dilution can be achieved easily by aquatic insects, but water conservation is essential for terrestrial insects and uric acid excretion (**uricotelism**) is highly advantageous.

Deposition of urates in specific cells of the fat body (section 3.6.4) was viewed as "excretion" by storage of uric acid. However, it might constitute a metabolic store for recycling by the insect, perhaps with the assistance of symbiotic microorganisms, as in cockroaches that house bacteria in their fat body. These cockroaches, including *P. americana*, do not excrete uric acid in the feces even if fed a high-nitrogen diet but do produce large quantities of internally stored urates.

By-products of feeding and metabolism need not be excreted as waste: for example, the antifeedant defensive compounds of plants may be sequestered directly or may form the biochemical base for synthesis of chemicals used in communication (Chapter 4) including warning and defense. White-pigmented uric acid derivatives color the epidermis of some insects and provide the white in the wing scales of certain butterflies (Lepidoptera: Pieridae).

3.8 REPRODUCTIVE ORGANS

The reproductive organs of insects exhibit an incredible variety of forms, but there is a basic design and function to each component so that even the most aberrant reproductive system can be understood in terms of a generalized plan. Individual components of the

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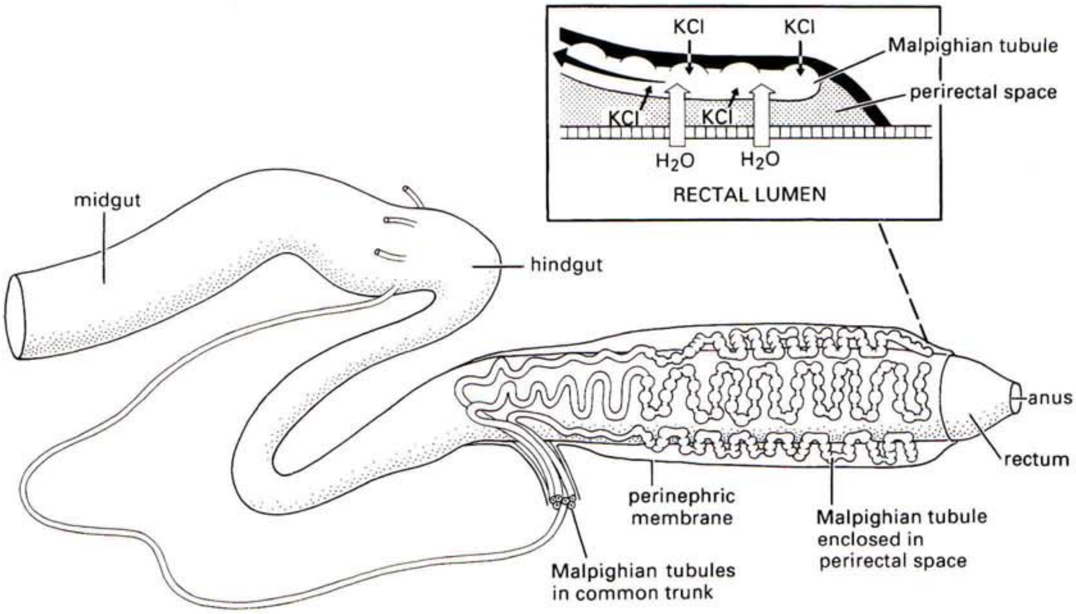
Box 3.4 Cryptonephric systems*

Many larval and adult Coleoptera, larval Lepidoptera, and some larval Symphyta have a modified arrangement of the excretory system that is concerned either with efficient dehydration of feces before their elimination (in beetles) or ionic regulation (in plant-feeding caterpillars). These insects have a **cryptonephric system** in which the distal ends of the Malpighian tubules are held in contact with the rectal wall by the perinephric membrane. Such an arrangement allows some beetles that live on a very dry diet, such as stored grain or dry carcasses, to be extraordinarily efficient in their conservation of water. Water even may be extracted from the humid air in the rectum. In the cryptonephric system of the mealworm, *Tenebrio molitor* (Coleoptera: Tenebrionidae), shown here, ions (principally of potassium chloride, KCl) are transported into and concentrated in the six Malpighian tubules, creating an osmotic gradient that draws water from the surrounding perirectal space and the rectal lumen. The tubule fluid is then transported forwards to the free portion of each tubule, from which it is passed to the hemolymph or recycled in the rectum.



*After Grimstone et al. 1968; Bradley 1985.

reproductive system can vary in shape (e.g. of gonads and accessory glands), position (e.g. of the attachment of accessory glands), and number (e.g. of ovarian or testicular tubes, or sperm storage organs) between different insect groups, and sometimes even between different species in a genus. Knowledge of the homology of the components assists in interpreting structure and function in different insects. Generalized male and female systems are depicted in Fig. 3.20, and a comparison of the corresponding reproductive structures of male and female insects is provided in Table 3.2. Many other aspects of reproduction, including copulation and regulation of physiological processes, are discussed in detail in Chapter 5.

system, the warmth of cones harms the plant because it leads to seed herbivory.

4.2.2 Thermoregulation

Insects are poikilothermic; that is, they lack the means to maintain homeothermy, a constant temperature independent of fluctuations in ambient (surrounding) conditions. Although the temperature of an inactive insect tends to track the ambient temperature, many insects can alter their temperature, both upwards and downwards, even if only for a short time. The temperature of an insect can be varied from ambient either behaviorally using external heat (ectothermy) or by physiological mechanisms (endothermy). Endothermy relies on internally generated heat, predominantly from metabolism associated with flight. As some 94% of flight energy is generated as heat (only 6% directed to mechanical force on the wings), flight is not only very energetically demanding but also produces much heat.

Understanding thermoregulation requires some appreciation of the relationship between heat and mass (or volume). The small size of insects in general means that any heat generated is rapidly dissipated. In an environment at 10°C a 100 g bumble bee with a body temperature of 40°C experiences a temperature drop of 1°C per second in the absence of any further heat generation. The larger the body the slower is this heat loss, which is one factor enabling larger organisms to be homeothermic, with the greater mass buffering against heat loss. However, a consequence of the mass/heat relationship is that a small insect can warm up quickly from an external heat source, even one as restricted as a light fleck. Clearly, with insects showing a 500,000-fold variation in mass and 1000-fold variation in metabolic rate, there is scope for a range of variants on thermoregulatory physiologies and behaviors. We review the conventional range of thermoregulatory strategies below, but refer elsewhere to tolerance of extreme temperature (section 6.6.2).

Behavioral thermoregulation (ectothermy)

The extent to which radiant energy (either solar or substrate) influences body temperature is related to the aspect that a diurnal insect adopts. Basking, by which many insects maximize heat uptake, involves both posture and orientation relative to the source of heat. The setae of some "furry" caterpillars, such as gypsy moth larvae (Lymantriidae), serve to insulate the body against convective heat loss while not impairing radiant heat uptake. Wing position and orientation may enhance heat absorption or, alternatively, provide shading from excessive solar radiation. Cooling may include shade-seeking behavior, such as seeking cooler environmental microhabitats or altered orientation on plants. Many desert insects avoid temperature extremes by burrowing. Some insects living in exposed places may avoid excessive heating by "stilting"; that is, raising themselves on extended legs to elevate most of the body out of the narrow boundary layer close to the ground. Conduction of heat from the substrate is reduced, and convection is enhanced in the cooler moving air above the boundary layer.

There is a complex (and disputed) relationship between temperature regulation and insect color and surface sculpturing. Amongst some desert beetles (Tenebrionidae), black species become active earlier in the day at lower ambient temperatures than do pale ones, which in turn can remain active longer during hotter times. The application of white paint to black tenebrionid beetles results in substantial body temperature changes: black beetles warm up more rapidly at a given ambient temperature and overheat more quickly compared with white ones, which have greater reflectivity to heat. These physiological differences correlate with certain observed differences in thermal ecology between dark and pale species. Further evidence of the role of color comes from a beclouded cicada (Hemiptera: *Cacama valvata*) in which basking involves directing the dark dorsal surface towards the sun, in contrast to cooling, when the pale ventral surface only is exposed.

For aquatic insects, in which body temperature must follow water temperature, there is little or no ability to regulate body temperature beyond seeking microclimatic differences within a water body.

Physiological thermoregulation (endothermy)

Some insects can be endothermic because the thoracic flight muscles have a very high metabolic rate and produce much heat. The thorax can be maintained at a relatively constant high temperature during flight. Temperature regulation may involve clothing the thorax with insulating scales or hairs, but insulation must be balanced with the need to dissipate any excess heat generated during flight. Some butterflies and locusts alternate heat-producing flight with gliding, which allows cooling, but many insects must fly continuously and cannot glide. Bees and many moths prevent thoracic overheating in flight by increasing the heart rate and circulating hemolymph from the thorax to the poorly insulated abdomen where radiation and convection dissipate heat. At least in some bumble bees (*Bombus*) and carpenter bees (*Xylocopa*) a counter-current system that normally prevents heat loss is bypassed during flight to augment abdominal heat loss.

The insects that produce elevated temperatures during flight often require a warm thorax before they can take off. When ambient temperatures are low, these insects use the flight muscles to generate heat prior to switching them for use in flight. Mechanisms differ according to whether the flight muscles are synchronous or asynchronous (section 3.1.4). Insects with synchronous flight muscles warm up by contracting antagonistic muscle pairs synchronously and/or synergistic muscles alternately. This activity generally produces some wing vibration, as seen for example in odonates. Asynchronous flight muscles are warmed by operating the flight muscles whilst the wings are uncoupled, or the thoracic box is held rigid by accessory muscles to prevent wing movement. Usually no wing movement is seen, although ventilatory pumping movements of the abdomen may be visible. When the thorax is warm but the insect is sedentary (e.g. whilst feeding), many insects maintain temperature by shivering, which may be prolonged. In contrast, foraging honey bees may cool off during rest, and must then warm up before take-off.

4.3 CHEMICAL STIMULI

In comparison with vertebrates, insects show a more profound use of chemicals in communication, particularly with other individuals of their own species. Insects produce chemicals for many purposes. Their perception in the external environment is through specific chemoreceptors.

4.3.1 Chemoreception

The chemical senses may be divided into **taste**, for detection of aqueous chemicals, and **smell**, for airborne ones, but the distinction is relative. Alternative terms are contact (taste, gustatory) and distant (smell, olfactory) chemoreception. For aquatic insects, all chemicals sensed are in aqueous solution, and strictly all chemoreception should be termed "taste". However, if an aquatic insect has a chemoreceptor that is structurally and functionally equivalent to one in a terrestrial insect that is olfactory, then the aquatic insect is said to "smell" the chemical.

Chemosensors trap chemical molecules, which are transferred to a site for recognition, where they specifically depolarize a membrane and stimulate a nerve impulse. Effective trapping involves localization of the chemoreceptors. Thus, many contact (taste) receptors occur on the mouthparts, such as the labella of higher Diptera (Fig. 2.14a) where salt and sugar receptors occur, and on the ovipositor, to assist with identification of suitable oviposition sites. The antennae, which often are forward-directed and prominent, are first to encounter sensory stimuli and are endowed with many distant chemoreceptors, some contact chemoreceptors, and many mechanoreceptors. The legs, particularly the tarsi which are in contact with the substrate, also have many chemoreceptors. In butterflies, stimulation of the tarsi by sugar solutions evokes an automatic extension of the proboscis. In blow flies, a complex sequence of stereotyped feeding behaviors is induced when a tarsal chemoreceptor is stimulated with sucrose. The proboscis starts to extend and, following sucrose stimulation of the chemoreceptors on the labellum, further proboscis extension occurs and the labellar lobes open. With more sugar stimulus, the source is sucked until stimulation of the mouthparts ceases. When this happens, a predictable pattern of search for further food follows.

Insect chemoreceptors are sensilla with one or more pores (holes). Two classes of sensilla can be defined based on their ultrastructure: **uniporous**, with one pore, and **multiporous**, with several to many pores. Uniporous sensilla range in appearance from hairs to pegs, plates, or simply pores in a cuticular depression, but all have relatively thick walls and a simple permeable pore, which may be apical or central. The hair or peg contains a chamber, which is in basal contact with a dendritic chamber that lies beneath the cuticle. The outer chamber may extrude a viscous liquid, presumed to assist in the entrapment and transfer of chemicals to the dendrites. It is assumed that these uniporous chemoreceptors predominantly detect chemicals by contact, although there is evidence for some olfactory function. Gustatory (contact) neurons are classified and JH plays a role in termination of diapause. Resumption of ecdysteroid secretion from the prothoracic glands appears essential for the termination of pupal diapause. JH is important in diapause regulation in adult insects but, as with the immature stages, may not be the only regulator. In larvae, pupae, and adults of *Bombyx mori*, complex antagonistic interactions occur between a **diapause hormone**, originating from paired neurosecretory cells in the suboesophageal ganglion, and JH from the corpora allata. The adult female produces diapause eggs when the ovariole is under the influence of diapause hormone, whereas in the absence of this hormone and in the presence of juvenile hormone, non-diapause eggs are produced.

6.6 DEALING WITH ENVIRONMENTAL EXTREMES

The most obvious environmental variables that confront an insect are seasonal fluctuations in temperature and humidity. The extremes of temperatures and humidities experienced by insects in their natural environments span the range of conditions encountered by terrestrial organisms. For reasons of human interest in cryobiology (revivable preservation), responses to extremes of cold and desiccation have been studied better than those to high temperatures alone.

The options available for evading extremes are behavioral avoidance, such as by burrowing into soil of a more equable temperature, migration (section 6.7), diapause (section 6.5), and *in situ* tolerance/survival in a highly altered physiological condition, the topic of the following sections.

6.6.1 Cold

Biologists have long been interested in the occurrence of insects at the extremes of the Earth, in surprising diversity and sometimes in large numbers. Holometabolous insects are abundant in refugial sites within 3° of the North Pole. Fewer insects, notably a chironomid midge and some penguin and seal lice, are found on the Antarctic proper. Freezing, high elevations, including glaciers, sustain resident insects, such as the Himalayan *Diamesa* glacier midge (Diptera: Chironomidae), which sets a record for cold activity, being active at an air temperature of −16°C. Snowfields also support seasonally cold-active insects such as grylloblattids, and *Chionea* (Diptera: Tipulidae) and *Boreus* (Mecoptera), the snow "fleas". Low-temperature environments pose physiological problems that resemble dehydration in the reduction of available water, but clearly also include the need to avoid freezing of body fluids. Expansion and ice-crystal formation typically kill mammalian cells and tissues, but perhaps some insect cells can tolerate freezing. Insects may possess one or several of a suite of mechanisms – collectively termed **cryoprotection** – that allows survival of cold extremes. These mechanisms may apply in any life-history stage, from resistant eggs to adults. Although they form a continuum, the following categories can aid understanding.

Freeze tolerance

Freeze-tolerant insects include some of the most cold-hardy species, mainly occurring in Arctic, sub-Arctic, and Antarctic locations that experience the most extreme winter temperatures (e.g. −40 to −80°C). Protection is provided by seasonal production of icenucleating agents (or INAs) under the induction of falling temperatures and prior to onset of severe cold. These proteins, lipoproteins, and/or endogenous crystalline substances such as urates, act as sites where (safe) freezing is encouraged outside cells, such as in the hemolymph, gut, or Malpighian tubules. Controlled and gentle extracellular ice formation acts also to gradually dehydrate cell contents, and thus avoid freezing. In addition, substances such as glycerol and/or related polyols, and sugars including sorbitol and trehalose, allow **supercooling** (remaining liquid at subzero temperature without ice formation) and also protect tissues and cells prior to full ice-nucleating agent activation and after freezing. Antifreeze proteins may also be produced; these fulfill some of the same protective roles, especially during freezing conditions in fall and during the spring thaw, outside the core deep-winter freeze. Onset of internal freezing often requires body contact with external ice to trigger ice nucleation, and may take place with little or no internal supercooling. Freeze tolerance does not guarantee survival, which depends not only on the actual minimum temperature experienced but also upon acclimation before cold onset, the rapidity of onset of extreme cold, and perhaps also the range and fluctuation in temperatures experienced during thawing. In the well-studied galling tephritid fly *Eurosta solidaginis*, all these

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mechanisms have been demonstrated, plus tolerance of cell freezing, at least in fat body cells.

Freeze avoidance

Freeze avoidance describes both a survival strategy and a species' physiological ability to survive low temperatures without internal freezing. In this definition, insects that avoid freezing by supercooling can survive extended periods in the supercooled state and show high mortality below the supercooling point, but little above it, and are freeze avoiders. Mechanisms for encouraging supercooling include evacuation of the digestive system to remove the promoters of ice nucleation, plus pre-winter synthesis of polyols and antifreeze agents. In these insects cold hardiness (potential to survive cold) can be calculated readily by comparison of the supercooling point (below which death occurs) and the lowest temperature experienced by the insect. Freeze avoidance has been studied in the autumnal moth, *Epirrita autumnata*, and goldenrod gall moth, *Epiblema scudderiana*.

Chill tolerance

Chill-tolerant species occur mainly from temperate areas polewards, where insects survive frequent encounters with subzero temperatures. This category contains species with extensive supercooling ability (see above) and cold tolerance, but is distinguished from these by mortality that is dependent on duration of cold exposure and low temperature (above the supercooling point). That is, the longer and the colder the freezing spell, the more deaths are attributable to freezing-induced cellular and tissue damage. A notable ecological grouping that demonstrates high chill tolerance are species that survive extreme cold (lower than supercooling point) by relying on snow cover, which provides "milder" conditions where chill tolerance permits survival. Examples of studied chill-tolerant species include the beech weevil, *Rhynchaenus fagi*, in Britain, and the bertha armyworm, *Mamestra configurata*, in Canada.

Chill susceptibility

Chill-susceptible species lack cold hardiness, and although they may supercool, death is rapid on exposure to subzero temperatures. Such temperate insects tend to vary in summer abundances according to the severity of the preceding winter. Thus, several studied European pest aphids (*Myzus persicae*, *Sitobion avenae*, and *Rhopalosiphum padi*) can supercool to −24°C (adults) or −27°C (nymphs) yet show high mortality when held at subzero temperatures for just a minute or two. Eggs show much greater cold hardiness than nymphs or adults. As overwintering eggs are produced only by sexual (**holocyclic**) species or clones, aphids with this life cycle predominate at increasingly high latitudes in comparison with those in which overwintering is in a nymphal or adult stage (**anholocyclic** species or clones).

Opportunistic survival

Opportunistic survival is observed in insects living in stable, warm climates in which cold hardiness is little developed. Even though supercooling is possible, in species that lack avoidance of cold through diapause or quiescence (section 6.5) mortality occurs when an irreversible lower threshold for metabolism is reached. Survival of predictable or sporadic cold episodes for these species depends upon exploitation of favorable sites, for example by migration (section 6.7) or by local opportunistic selection of appropriate microhabitats.

Clearly, low-temperature tolerance is acquired convergently, with a range of different mechanisms and chemistries involved in different groups. A unifying feature may be that the mechanisms for cryoprotection are rather similar to those shown for avoidance of dehydration, which may be preadaptive for cold tolerance. Although each of the above categories contains a few unrelated species, amongst the terrestrial bembidiine Carabidae (Coleoptera) the Arctic and sub-Arctic regions contain a radiation of cold-tolerant species. A preadaptation to aptery (wing loss) has been suggested for these beetles, as it is too cold to warm flight muscles. Nonetheless, the summer Arctic is plagued by actively flying (and human-biting) flies that warm themselves by their resting orientation towards the sun.

6.6.2 Heat

The hottest inhabited terrestrial environment – vents in thermally active areas – support a few specialist insects. For example, the hottest waters in thermal springs of Yellowstone National Park are too hot to touch, but by selection of slightly cooler microhabitats amongst the cyanobacteria/blue-green algal mats, a brine fly, *Ephydra bruesi* (Ephydridae), can survive at 43°C. At least some other species of ephydrids, stratiomyiids, and chironomid larvae (all Diptera) tolerate nearly 50°C in Iceland, New Zealand, South America, and perhaps other sites where volcanism provides hot-water springs. The other aquatic temperature-tolerant taxa are found principally amongst the Odonata and Coleoptera.

High temperatures tend to kill cells by denaturing proteins, altering membrane and enzyme structures and properties, and by loss of water (dehydration). Inherently, the stability of non-covalent bonds that determine the complex structure of proteins determines the upper limits, but below this threshold there are many different but interrelated temperature-dependent biochemical reactions. Exactly how insects tolerant of high temperature cope biochemically is little known. **Acclimation**, in which a gradual exposure to increasing (or decreasing) temperatures takes place, certainly provides a greater disposition to survival at extreme temperatures compared with instantaneous exposure. Acclimation conditioning should be considered when comparing effects of temperature on insects.

Options of dealing with high air temperatures include behaviors such as use of a burrow during the hottest times. This activity takes advantage of the buffering of soils, including desert sands, against temperature extremes so that near-stable temperatures occur within a few centimeters of the fluctuations of the exposed surface. Overwintering pupation of temperate insects frequently takes place in a burrow made by a late-instar larva, and in hot, arid areas night-active insects such as predatory carabid beetles may pass the extremes of the day in burrows. Arid-zone ants, including Saharan *Cataglyphis*, Australian *Melophorus*, and Namibian *Ocymyrmex*, show several behavioral features to maximize their ability to use some of the hottest places on Earth. Long legs hold the body in cooler air above the substrate, they can run as fast as 1 m s^{-1}, and are good navigators to allow rapid return to the burrow. Tolerance of high temperature is an advantage to *Cataglyphis* because they scavenge upon insects that have died from heat stress. However, *Cataglyphis bombycina* suffers predation from a lizard that also has a high temperature tolerance, and predator avoidance restricts the above-ground activity of *Cataglyphis* to a very narrow temperature band, between that at which the lizard ceases activity and its own upper lethal thermal threshold. *Cataglyphis* minimizes exposure to high temperatures using the strategies outlined above, and adds thermal respite activity; climbing and pausing on grass stems above the desert substrate, which may exceed 46°C. Physiologically, *Cataglyphis* may be amongst the most thermally tolerant land animals because they can accumulate high levels of heat-shock proteins in advance of their departure to forage from their (cool) burrow to the ambient external heat. The few minutes' duration of the foraging frenzy is too short for synthesis of these protective proteins after exposure to the heat.

The proteins once termed heat-shock proteins (abbreviated as HSP) may be best termed stress-induced proteins when they are involved in temperature-related activities, as at least some of the suite can be induced also by desiccation and cold. Their function at higher temperatures appears to be to act as molecular chaperones assisting in protein folding. In cold conditions, protein folding is not the problem, but rather it is loss of membrane fluidity, which can be restored by fatty acid changes and by denaturing of membrane phospholipids, perhaps also under some control of stress proteins.

The most remarkable specialization involves a larval chironomid midge, *Polypedilum vanderplanki*, which lives in West Africa on granite outcrops in temporary pools, such as those that form in depressions made by native people when grinding grain. The larvae do not form cocoons when the pools dry, but their bodies lose water until they are almost completely dehydrated. In this condition of **cryptobiosis** (alive but with all metabolism ceased), the larvae can tolerate temperature extremes, including artificially imposed temperatures in dry air from more than 100°C down to −27°C. On wetting, the larvae revive rapidly, feed and continue development until the onset of another cycle of desiccation or until pupation and emergence.

6.6.3 Aridity

In terrestrial environments, temperature and humidity are intimately linked, and responses to high temperatures are inseparable from concomitant water stress. Although free water may be unavailable in the arid tropics for long periods, many insects are active year-round in places such as the Namib Desert, an essentially rain-free desert in southwestern Africa. This desert has provided a research environment for the study of water relations in arid-zone insects ever since the discovery of "fog basking" amongst some tenebrionid beetles. The cold oceanic current that abuts the hot Namib Desert produces daily fog that sweeps inland. This provides a source of aerial moisture that can be precipitated onto the bodies of beetles that present a head-down stance on the slip face of sand dunes, facing the fog-laden wind. The precipitated moisture then runs to the mouth of the beetle. Such atmospheric water gathering is just one from a range of insect behaviors and morphologies that allow survival under these stressful conditions. Two different strategies exemplified by different beetles can be compared and contrasted: detritivorous tenebrionids and predaceous carabids, both of which have many aridity-tolerant species.

The greatest water loss by most insects occurs via evaporation from the cuticle, with lesser amounts lost through respiratory gas exchange at the spiracles and through excretion. Some arid-zone beetles have reduced their water loss 100-fold by one or more strategies including extreme reduction in evaporative water loss through the cuticle (section 2.1), reduction in spiracular water loss, reduction in metabolism, and extreme reduction of excretory loss. In the studied arid-zone species of tenebrionids and carabids, cuticular water permeability is reduced to almost zero such that water loss is virtually a function of metabolic rate alone; that is, loss is by the gas-exchange pathway, predominantly related to variation in the local humidity around the spiracles. Enclosure of the spiracles in a humid subelytral space is an important mechanism for reduction of such losses. Observation of unusually low levels of sodium in the hemolymph of studied tenebrionids compared with levels in arid-zone carabids (and most other insects) implies reduced sodium pump activity, reduced sodium gradient across cell membranes, a concomitantly inferred reduction in metabolic rate, and reduced respiratory water loss. Uric acid precipitation when water is reabsorbed from the rectum allows the excretion of virtually dry urine (section 3.7.2), which, with retention of free amino acids, minimizes loss of everything except the nitrogenous wastes. All these mechanisms allow the survival of a tenebrionid beetle in an arid environment with seasonal food and water shortage. In contrast, desert carabids include species that maintain a high sodium pump activity and sodium gradient across cell membranes, implying a high metabolic rate. They also excrete more dilute urine, and appear less able to conserve free amino acids. Behaviorally, carabids are active predators, needing a high metabolic rate for pursuit, which would incur greater rates of water loss. This may be compensated for by the higher water content of their prey, compared with the desiccated detritus that forms the tenebrionid diet.

To test whether these distinctions are different "adaptive" strategies, or if tenebrionids differ more generally from carabids in their physiology, irrespective of any aridity tolerance, will require wider sampling of taxa, and some appropriate tests to determine whether the observed physiological differences are correlated with taxonomic relationships (i.e. are preadaptive for life in low-humidity environments) or ecology of the species. Such tests have not been undertaken.

6.7 MIGRATION

Diapause, as described above, allows an insect to track its resources in time: when conditions become inclement, development ceases until diapause breaks. An alternative to shutdown is to track resources in space by directed movement. The term **migration** once was restricted to the to-and-fro major movements of vertebrates, such as wildebeest, salmonid fish, and migratory birds including swallows, shorebirds, and maritime terns. However, there are good reasons to expand this to include organisms that fulfill some or all of the following criteria, in and around specific phases of movement:

- persistent movement away from an original home range;
- relatively straight movement in comparison with station-tending or zig-zagging within a home range;
- undistracted by (unresponsive to) stimuli from home range;
- distinctive pre- and post-movement behaviors;
- reallocation of energy within the body.

All migrations in this wider sense are attempts to provide a homogeneous suitable environment despite temporal fluctuations in a single home range. Criteria such as length of distance traveled, geographical area in which migration occurs, and whether or not the outward-bound individual undertakes a return are unimportant to this definition. Furthermore, thinning out of a population (dispersal) or advance across a similar habitat (range extension) is not migration.

According to this definition, seasonal movements from the upper mountain slopes of the Sierra Nevada down to California's Central Valley by the convergent ladybird beetle (*Hippodamia convergens*) is as much a migratory activity as is a transcontinental movement of a monarch butterfly (*Danaus plexippus*). Pre-migration behaviors in insects include redirecting metabolism to energy storage, cessation of reproduction, and production of wings in polymorphic species in which winged and wingless forms coexist (polyphenism; section 6.8.2). Feeding and reproduction are resumed post-migration. Some responses are under hormonal control, whereas others are environmentally induced. Evidently, pre-migration changes must anticipate the altered environmental conditions that migration has evolved to avoid. As with induction of diapause (above), the principal cue is change in day length (photoperiod). A strong linkage exists between the several cues for onset and termination of reproductive diapause and induction and cessation of migratory response in studied species, including monarch butterflies and milkweed bugs (*Oncopeltus fasciatus*). Individuals of both species migrate south from their extensive range associated with North American host milkweed plants (Asclepiadaceae). At least in this migrant generation of monarchs, a magnetic compass complements solar navigation in deriving the bearings towards the overwintering site. Shortening day length induces a reproductive diapause in which flight inhibition is removed and energy is transferred to flight instead of reproduction. The overwintering generation of both species is in diapause, which ends with a two- (or more) stage migration from south to north that essentially tracks the sequential development of subtropical to temperate annual milkweeds as far as southern Canada. The first flight in early spring from the overwintering area is short, with both reproduction and flight effort occurring during short-length days, but the next generation extends far northwards in longer days, either as individuals or by consecutive generations. Few if any of the returning individuals are the original outward migrants. In the milkweed bugs there is a circadian rhythm (Box 4.4) with oviposition and migration temporally segregated in the middle of the day, and mating and feeding concentrated at the end of the daylight period. Both milkweed bugs and monarch butterflies have non-migratory multivoltine relatives that remain in the tropics. Thus it seems that the ability to diapause and thus escape south in the autumn has allowed just these two species to invade summer milkweed stands of the temperate region.

It is a common observation that insects living in "temporary" habitats of limited duration have a higher proportion of flighted species, and within polymorphic taxa, more flighted individuals. In longer-lasting habitats loss of flight ability, either permanently or temporarily, is more common. Thus, amongst European water-striders (Hemiptera: Gerridae) species associated with small ephemeral water bodies are winged and regularly migrate to seek new water bodies; those associated with large lakes tend to winglessness and sedentary life histories. Evidently, flightedness relates to the tendency (and ability) to migrate in locusts, as exemplified in *Chortoicetes terminifera* (the Australian migratory locust) and *Locusta migratoria*, which demonstrate adaptive migration to exploit transient favorable conditions in arid regions (see section 6.10.5 for *L. migratoria* behavior).

Although such massed movements described above are very conspicuous, even the "passive dispersal" of small and lightweight insects can fulfill many of the criteria of migration. Thus, even reliance upon wind (or water) currents for movement may involve the insect being capable of any or all of the following:

- changing behavior to embark, such as young scale insects crawling to a leaf apex and adopting a posture there to enhance the chances of extended aerial movement;
- being in appropriate physiological and developmental condition for the journey, as in the flighted stage of otherwise apterous aphids;
- sensing appropriate environmental cues to depart, such as seasonal failure of the host plant of many aphids;
- recognizing environmental cues on arrival, such as odors or colors of a new host plant, and making controlled departure from the current.

Naturally, embarkation on such journeys does not always bring success and there are many strandings of migratory insects in unsuitable habitat, such as icefields and in open oceans. Nonetheless, clearly some fecund insects make use of predictable meteorological conditions to make long journeys in a consistent direction, depart from the air current and establish in a suitable, novel habitat. Aphids are a prime example, but certain thrips and scale insects and other agriculturally damaging pests can locate new host plants in this way.

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