Chapter 1

The Importance and Diversity of Arthropod Ectoparasites

1.1 INTRODUCTION

The arthropods are a bewilderingly diverse assemblage of invertebrates, containing over 80% of all known animal species and occupying almost every known habitat. They include such familiar animals as flies, crabs, centipedes and spiders as well as a plethora of small and little known groups.

There are more species of arthropod than all other animals on earth combined; over a million species have been described and millions more may be awaiting description or discovery. Dazzlingly beautiful, behaviourally complex and ecologically essential, they play fundamental roles in almost all biological communities and ecosystems.

Among the great variety of species of arthropod and lifestyles that they display, a relatively small number have developed the ability to live directly at the expense of other animals, known as **hosts**. This relationship is to the detriment of the host but does not usually kill the host immediately. This is described as **parasitism**. The degree of harm caused by the parasite may vary considerably, and may only be evident at certain times, such as when the host is in poor condition or the parasite density is high. It is important to stress that the parasite lives at the expense of the host and to distinguish parasitic from commensal relationships, in which the host neither benefits nor is harmed. Harm may be defined in practical, proximate terms, as a reduction in factors such as condition, mobility or growth of the host, or in ultimate, evolutionary terms as a reduction in the ability of the host to pass on its genes to the next generation.

Arthropods parasitise a wide range of hosts, including other arthropods. This book is concerned specifically with the economically important arthropods which spend all or some portion of their lives parasitising livestock, poultry or companion animals. These parasites, with a few exceptions, live on or burrow into the surface of their host's epidermis and are generally described as **ectoparasites**.

1.2 ECTOPARASITE HOST RELATIONSHIPS

Within the broad definition of parasitism given above, the association between arthropod ectoparasite and vertebrate host may take a variety of forms. In some cases the parasite may be totally dependent on the host, in which case the parasitism is described as **obligatory**. Alternatively, the parasite may feed or live only occasionally on the host, without being dependent on it, in which case the parasitism is described as **facultative**.

The host provides a number of important resources for the ectoparasite. Most vitally, the host supplies a source of food, which may be blood, lymph, tears or sweat or the debris of skin, hair or feathers. The host's body also provides the environment in which many ectoparasites live, generating warmth, moisture and, within the skin or hair, a degree of protection from the external environment. The host may also provide transportation from place to place for the parasite, a site at which to mate and, in many cases, the means of transmission from host to host.

Despite the benefits of a close association with the host, there is considerable variation in the amount of time spent on the host by various species of ectoparasite. Some ectoparasites, such as many of the species of lice for example, live in continuous association with their host throughout their life-cycle and are therefore highly dependent on the host. The majority of ectoparasites, however, have only intermittent contact with their host, and are free-living for the major portion of their life-cycles. In some cases ectoparasites, such as many of the species of mite, are highly host-specific; only one host species is exploited and, in some instances, the parasite can exist only on one defined area of the host's body. Other species are able to exploit a wider range of hosts.

Whether a pest is an obligatory or facultative ectoparasite, lives in continuous or intermittent association with its host, or is host specific or a generalist, is of interest from a biological perspective and has major implications for both the control of ectoparasites and the treatment of ectoparasite-associated disease.

1.3 ECTOPARASITE DAMAGE

As a result of their activity, arthropod ectoparasites may have a variety of direct and indirect effects on their hosts. Direct harm caused may be due to:

- Blood loss: although each individual ectoparasite only removes a small volume of blood from a host, in large numbers the blood removed by feeding may be directly debilitating and anaemia is common in heavily infested hosts. In one study in the USA it was estimated that over 90 kg of blood was removed by ticks from a cow over a single season. Similarly, the feeding of horse flies may be responsible for the loss of up to 0.5 litres of blood per day from cattle. Two hundred fleas feeding on a kitten may be capable of removing up to 10% of the animal's blood over a period of several days.
- Myiasis: the infestation of the living tissues with fly larvae causes direct damage to carcasses or skin.
- Skin inflammation and pruritus: various skin infestations caused by arthropod activity cause pruritus (itching), often accompanied by hair and wool loss (alopecia) and occasionally by skin thickening (lichenification). The presence of ectoparasites on or burrowing into the skin can stimulate keratinocytes to release cytokines (e.g. IL-1) which leads to epidermal hyperplasia and cutaneous inflammation. The antigens produced by ectoparasites (e.g. salivary and faecal) can in some individuals stimulate an immune response leading to hypersensitivity. *Sarcoptes scabiei* infestation in the dog, for example, leads to an IgE-mediated type I hypersensitivity which is manifested in severe cutaneous inflammation and pruritus.
- Toxic and allergic responses: caused by antigens and anticoagulants in the saliva of blood-feeding arthropods.

The behaviour of ectoparasites also may cause harm indirectly, again particularly when they are present at high density, causing:

- Disturbance: the irritation caused, particularly by flies as they attempt to feed or oviposit, commonly results in a variety of behaviours such as head shaking, stamping, skin twitching, tail switching or scratching. Cattle under persistent attack from flies may congregate in a group with their heads facing the centre. Sheep under attack from nasal bot flies may be seen pressing their nostrils to the ground before running short distances and repeating the action. These activities may result in reduced growth and loss of condition because the time spent in avoidance behaviour is lost from grazing or resting. Different individuals of a host population usually vary considerably in the level of parasitism and this may be associated with their behavioural responses. For example, in cattle the more passive individuals and tolerant individuals tend to be most heavily attacked by blood-feeding flies.
- Self-wounding: the activity of particular ectoparasites, such as warble flies, may cause dramatic avoidance responses in the intended host, known as gadding. The stampeding

animal may inflict serious self-injury following collision with fences and other objects.

- Social nuisance: large populations of flies may breed in animal dung, particularly in and around intensive husbandry units. The activity of flies may result in considerable social and legal problems, especially where suburban developments have encroached on previously rural areas. Adult flies and their faeces may also decrease the aesthetic appearance and value of farm facilities and produce, such as hens' eggs, and cause irritation and annoyance to employees.

In addition to direct effects, one of the most important roles of ectoparasites is in their action as **vectors** of pathogens. These pathogens include protozoa, bacteria, viruses, cestodes (tapeworms) and nematodes (round worms). Pathogens such as bacteria and viruses may be transmitted directly to new hosts, the ectoparasite acting as a mechanical vector. These pathogens may be picked up on the body, feet or mouthparts when the ectoparasites feed. Mechanical transmission usually has to occur within a few hours of the original contact with the infected host, because the survival of most pathogens is relatively limited when exposed outside their host.

Alternatively, for many protozoa, tapeworms and nematodes, the pathogens need to go through specific stages of their life-cycle in the body of the arthropod ectoparasite. In these cases the arthropod serves as an intermediate host and is known as a biological vector. Again the vector acquires the pathogen from an infected animal when it feeds. After development of the pathogen in the vector, the vector becomes infective and can transmit the pathogen when it next feeds. In contrast to mechanical transmission, biological transmission requires a period of time between acquisition of the pathogen and the maturation of infection. The vector may then remain infective for the remainder of its life. The effects of pathogens on the vector are largely unknown and this may be a fruitful area for future research; those studies which have been possible suggest that there may be measurable costs to the vector for carrying a heavy infection.

A pathogen may reside and multiply in alternative vertebrate hosts which are immune or only mildly infected by it. For example, the bacterium *Yersinia pestis*, which causes bubonic plague known as 'the black death', is endemic in wild rodent populations. However, in domestic rats and humans, to which it is transmitted by fleas, it is highly pathogenic. Such alternate hosts are known as **reservoirs** of disease.

The direct damage caused by most ectoparasites is directly proportional to their abundance. This is not the case, however, for disease vectors, where even very low numbers of infected vectors may cause considerable economic and welfare problems.

Although relatively few in number, through their direct and indirect effects on their hosts, the various species of arthropod ectoparasite have had, and continue to exert, a major impact on the history of humans and their domesticated animals.

1.4 THE EVOLUTION OF ECTOPARASITE–HOST RELATIONSHIPS

Insects and related arthropods probably arose at least 500 million years ago, 300 million years before warm-blooded vertebrates. Unfortunately, the poor geological record for insects gives us little direct evidence of how parasitism evolved. Nevertheless, it would appear likely that, over time, as the terrestrial vertebrates appeared on earth several species of arthropod were able to exploit the new resource and opportunities created.

Parasitism probably evolved at least twice, and possibly several times, independently in different arthropod groups, depending on the relationship between the ectoparasite and its host. One route may have involved arthropods which were pre-adapted to living with vertebrates. These arthropods initially may have fed on general organic matter, and then moved to scavenging detritus, such as skin or hair, present in a vertebrate lair or nest. From here, coupled with the generalised feeding habits, it is only a short evolutionary step for the ectoparasite to move on to the host to feed on skin and hair and, in some cases, to facultative and obligate blood-feeding.

The second route to ectoparasitism may have involved arthropods which had existing adaptations which allowed them to feed on vertebrates. These arthropods may have had mouthparts already adapted for biting, rasping or sucking. They were perhaps liquid feeders, which occasionally opportunistically fed on blood in wounds, or they may have been active predators, in the adult or pre-adult stages, perhaps of other arthropods. Again, from taking the occasional meal from a vertebrate some subsequently may have switched to depending on blood as a food source.

These two evolutionary pathways involve similar adaptations, but they have led to very different relationships with the host. The generally accepted viewpoint throughout most of the twentieth century has been that commensalism or very mild parasitism is the inevitable eventual evolutionary end product of host–parasite co-evolution. It was thought that parasites would be selected to minimise the damage that they did to the host and that virulent (damaging) parasites were more recently evolved and were poorly adapted. This was because more virulent parasites might quickly weaken and damage the host and, if the host were to die, either as a direct result of the parasitism or perhaps because the weakened host might succumb to disease or predation, the ectoparasite would lose the benefits of a predictable food supply, protection from the external environment and its means of dispersal. However, more recent work has shown that there may be good evolutionary reasons to expect a wide range of levels of pathogenicity and damage caused by different parasites, depending on the particular behaviour and ecology of both the parasite and host, and the way in which these two animals interact.

Ectoparasites, such as many of the lice or mites, which live in relatively permanent association with their hosts, are usually small, with relatively low mobility. The risks and uncertainties associated with living without their host and having to find another meal are sufficiently high that for these animals excessive virulence, leading to the death or debilitation of the host, might result in their own death and failure to reproduce. Hence, these ectoparasites have become obligate, host-specific specialists, in normal circumstances, doing minimal damage and, in some cases, existing almost as commensals, e.g. species of *Demodex* mites. In many cases these arthropods may well have followed the first evolutionary route to ectoparasitism; even before becoming ectoparasites they were pre-adapted to living in close association with vertebrates and their survival and dispersal depended on the continued existence and health of the vertebrate with which they were associated.

In contrast, an ectoparasite that (a) was relatively mobile, so that it could find a new host quickly and efficiently, (b) was relatively resistant to the adverse effects of climate, so that it could survive without its host and (c) had a broad range of relatively abundant hosts on which it could feed, might be expected to evolve higher levels of virulence to maximise the amount that could be 'extracted' from a host as quickly as possible. For such an ectoparasite, the death of the host would be of little importance since it could survive well independently and find a new host quickly when needed. Arthropods with these characteristics, which inflict relatively high levels of damage, such as many of the blood-feeding flies and ticks, may have followed the second evolutionary route to parasitism, starting off as free-living scavengers or predators which subsequently became opportunistic feeders on vertebrates.

Of course, varying degrees of virulence between the extremes described will have evolved, depending on the precise interactions between the ectoparasite and host. The associations seen today between ectoparasites and hosts are also the outcome of the response of the host to the ectoparasite. From the perspective of the host, the attention of any parasites is, by definition, unwelcome. As arthropods evolved new ways of exploiting their hosts more effectively, the hosts also evolved strategies to combat the activities of the ectoparasites. These range from immune responses to behaviours such as grooming, periodic changing of nest sites or bedding, or even seasonal mass migrations to avoid areas of high parasite density. Hosts that were better able to tolerate their ectoparasites, minimised the damage caused or developed ways of ridding themselves of ectoparasites, survived longer and produced more offspring than other hosts. However, over time ectoparasites have also been selected to try to get round or exploit these host responses. Hence, over the millions of years, a constant evolutionary battle has been waged, in which arthropods have been evolving to exploit vertebrate hosts and in which hosts have been co-evolving to mitigate the effects of parasites on their fitness.

However, in relatively recent history, the associations between ectoparasites and their hosts have been subjected to a number of dramatic changes, mediated by human activity, which have resulted in a substantial shift in the nature of many parasite–host relationships.

1.5 A MODERN AND GROWING PROBLEM?

During the late mesolithic and early neolithic periods, 10 000–20 000 years ago, livestock and companion animals were first domesticated and farmed by humans (Fig. 1.1). This development has continued to the present day and has been combined with rapidly growing human populations, expansion and settlement in new areas, increased rates of human movement worldwide and increasing urbanisation.

Fig. 1.1 Detail from Tomb 3, Beni Hasan, Egypt (from Newberry, 1893).

- The massive increase in human populations has necessitated a growing intensification of animal husbandry, not only to meet the immediate demands for food and animal products such as wool and leather, but also to provide draught animals and fulfil the multitude of roles that animals play in human society. More and more animals have been reared using more intensive husbandry practices. This presents ectoparasites with a superabundance of hosts. The higher host density increases the potential for ectoparasite transmission and allows ectoparasites, adapted to experience huge mortalities associated with finding a new host, to build up massive population densities in very short periods of time.
- The artificial selection of livestock, poultry and companion animals for domestication and high productivity has been associated in many cases with a reduction in resistance to ectoparasite damage and the exaggeration of features which confer greater susceptibility to ectoparasite infestation. For example, the outer coat of primitive sheep is stiff and hairy and covers a woolly undercoat which only grows in winter. The outer hairs are known as kemps. In highly domesticated sheep, these kemps are absent and the fleece consists entirely of the woolly undercoat which grows all year round. Selection for a longer, thick fleece has increased the susceptibility of sheep to various types of disease and ectoparasite, particularly blowfly myiasis.
- With the increasing global movement of human populations, domestic animals have been transported into new areas of the world where they are attacked by endemic ectoparasites to which they have little or no resistance. This has been the case particularly with the introduction of domestic cattle, *Bos taurus*, into areas where they are attacked by a wide variety of ectoparasites and ectoparasite-borne diseases, which previously existed only on indigenous Bovidae or other Artiodactyla. The movement of humans and domestic animals has also allowed the introduction of ectoparasites into areas in which they were previously absent, such as sucking lice (Anoplura)

introduced into Australia with sheep. In the near future, the majority of the world population will live in urban areas. This growing urbanisation of humans and their associated companion animals provides arthropods and arthropod-borne diseases with a large, concentrated pool of potential hosts and enables ectoparasites to transfer between individual hosts more readily. In addition, in houses, which they frequently share with their companion animals, humans have created conditions in which many species of arthropod pest survive and flourish, often in areas of the world where they would otherwise perish. This is especially the case for fleas and mites, where modern houses can provide them with carefully controlled temperature, humidity and lighting, a protective microhabitat and a regular supply of hosts.

1.6 AN INTRODUCTION TO ARTHROPOD STRUCTURE AND FUNCTION

To those unfamiliar with invertebrate morphology and physiology, arthropods can seem dauntingly complex. They have many anatomical features which are often analogous to those of vertebrates but which are totally dissimilar in structure and function. In the following sections, a brief overview of a range of key arthropod features is presented, with specific reference to the ectoparasites of veterinary interest. This is by no means a comprehensive examination of the subject. A huge range of variation exists in the morphology and physiology of this diverse phylum and for a more detailed treatment the reader is referred to more specialist texts at the end of the chapter.

1.6.1 Arthropod segmentation

Arthropods are metameric, that is they are divided into segments. However, within a number of arthropod classes, particularly the arachnids and the insects, there has been a tendency for segmentation to become reduced and, in many of the mites for example, it has almost disappeared. Reduction in segmentation has occurred through loss, fusion or the tendency for segments to become dramatically changed in structure to fulfil specific functions, often associated with feeding, oviposition or mating. However, even in those arthropods that have almost lost their segmentation, it can usually still be seen in the embryo.

A characteristic feature of many arthropod groups is the division of the body into clusters of segments, such as the head, thorax and abdomen (Fig. 1.2). This is known as tagmatisation. Each **tagma** contains a specific set of segments and is specialised for functions different from those of the other tagmata.

1.6.2 The arthropod exoskeleton

The **exoskeleton** is the outer covering which provides support and protection to the living tissues of arthropods. In many respects it is one of the keys to the success of the phylum, but it also imposes many limitations.

The exoskeleton is non-cellular. Instead it is composed of a number of layers of **cuticle** which are secreted by a single outer cell layer of the body known as the **epidermis** (Fig. 1.3). The outer layer of cuticle, the **epicuticle**, is composed largely of proteins and, in many arthropods, is covered by a waxy layer. The next two layers are the outer **exocuticle** and the inner **endocuticle**. Both are composed of a protein and a polysaccharide called **chitin**, which has long, fibrous molecules containing nitrogen. The chitin molecules are bundled into microfibrils which are aligned parallel to each other. The parallel microfibrils are only loosely bound side by side to each other in sheets, so they are flexible across their axis but are very resistant to stretching – like a rope. Protein chains run between the microfibril bundles, to form a stable, complex glycoprotein. In this state, therefore, cuticle is naturally pale-coloured and flexible. For extra strength the exocuticle may be tanned, or **sclerotised.** This is where the proteins, interwoven between the chitin bundles, become

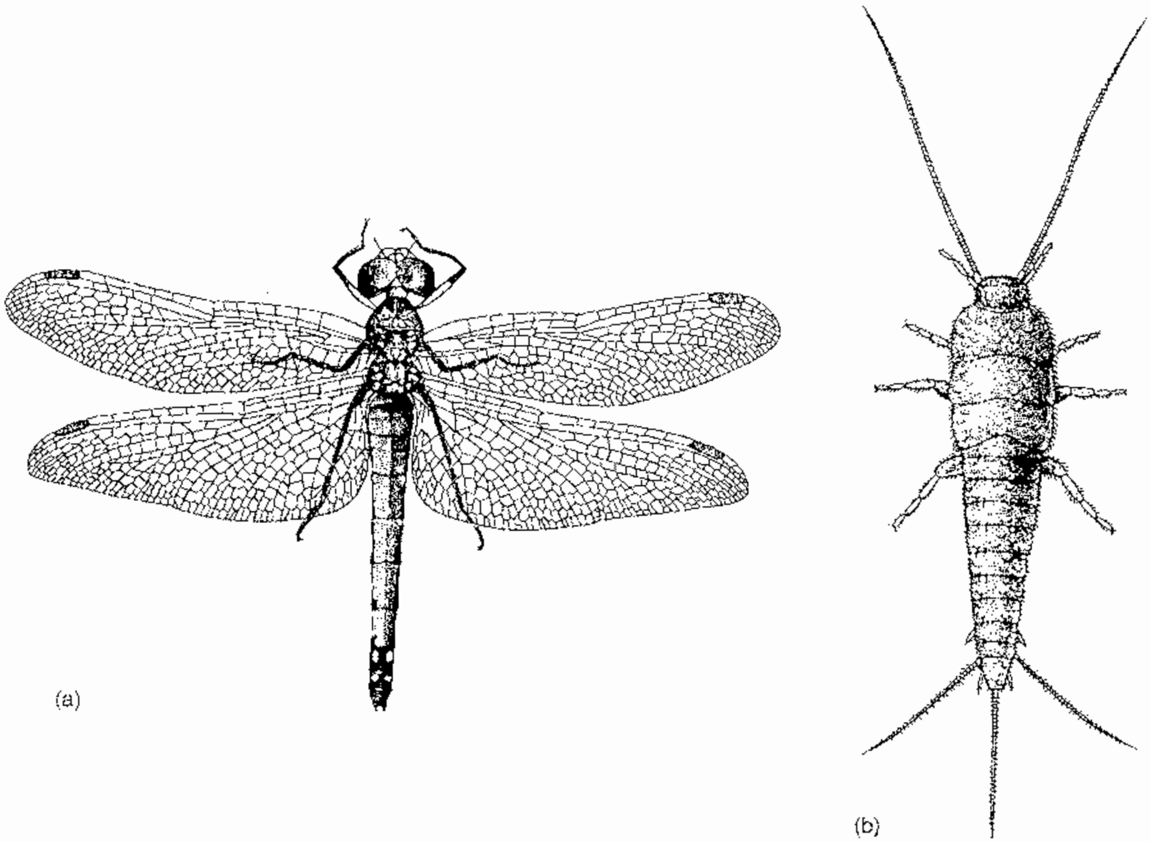

Fig. 1.2 A winged damselfly (a) and primitively flightless silverfish (b), showing division of the body into head, thoracic and abdominal segments (reproduced from Gulian & Cranston, 1994).

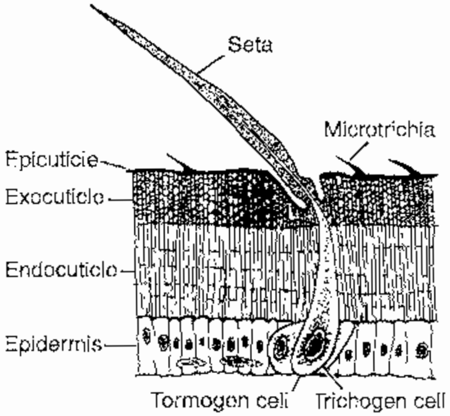

Fig. 1.3 Diagrammatic section through the arthropod integument.

tightly cross-linked with quinones, providing extra strength from the additional cross-linkages formed with the cuticular proteins. The sclerotised cuticle is hard and dark in colour.

The cuticle is often penetrated by fine pore canals which allow the passage of secretions from the epidermis to the surface. The cuticle has many outgrowths in the form of scales, spines, hairs and bristles. These outgrowths fall into two categories: those which are simply fine foldings of the outer layer of the cuticle (**microtrichiae**) and those which are articulated, such as setae (**macrotrichiae**). Microtrichiae can be very fine and give the arthropod distinctive, often irridescent, colour patterns. The articulated setae are attached to the cuticle by a thin membrane in a pit knows as the alveolus. Setae are hollow outgrowths of the epicuticle and exocuticle, secreted by a **trichogen cell** (Fig. 1.3). The socket is secreted by a **tormogen cell**.

Movement is made possible by the division of the cuticle into separate plates, called **sclerites**. Primitively these plates are confined to segments and the cuticle of each segment is divided into four primary plates: a **dorsal tergum**, two **lateral pleura** and a **ventral sternum** (Fig. 1.4). However, this pattern has frequently disappeared either because of fusion or subdivision of the segments.

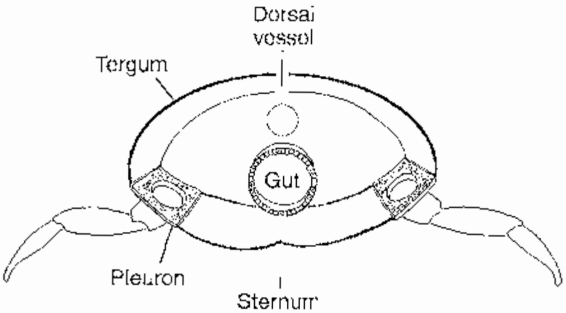

Fig. 1.4 Cross-section through the exoskeleton of a generalised arthropod, showing the tergum, pleuron and sternum of a single segment.

Plates are connected by flexible intersegmental or articular membranes, where the cuticle is not sclerotised and is flexible. These joints allow the body to move. In most arthropods the intersegmental membrane is folded beneath the segment in front (Fig. 1.5). The muscles attach on the inside of the exoskeleton, the opposite of the vertebrate body plan. Muscles are often attached to rod-like invaginations of the cuticle called **apodemes** (Fig. 1.5). The soft, flexible, unsclerotised cuticle present at the joints of the adult arthropod exoskeleton also occurs in the integument of larval arthropods.

Colour is very important in many groups of arthropds, providing warning colouration, sexual recognition signals or camouflage, for example. The colours of most arthropods are produced by the deposition of yellow, orange and red carotenoid or brown melanin pigments within the cuticle. However, iridescent greens and purples may result from structural features of the cuticle itself, such as microtrichia, which selectively scatter or reflect light of specific wavelengths.

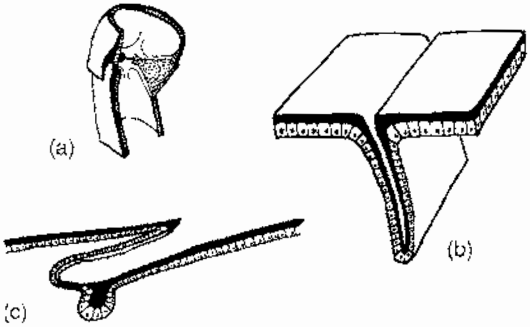

Fig. 1.5 (a) Articulation of a generalised arthorpod leg joint. (b) A multicellular apodeme. (c) Intersegmental articulation, showing the intersegmental membrane folded beneath the segmental exoskeleton (after Snodgrass, 1935).

1.6.3 Jointed legs

The name arthropod is derived from the ancient greek *arthron*, meaning joint, and *pous*, meaning foot. Primitively each arthropod segment bears a pair of leg-like appendages. However, the number of appendages has frequently been modified through loss or structural differentiation. In insects there are always three pairs of legs. In mites and ticks there are three pairs of legs in the larval life-cycle stage and four pairs in the nymphal and adult stages. The cuticular skeleton of the legs is divided into tube-like segments connected to one another by articular membranes, creating joints at each junction (Fig. 1.5). The legs are usually six-segmented.

1.6.4 Spiracles and gas exchange

The process of getting oxygen to the tissues has been solved in many different ways by the various groups of arthropods. For some of the smallest arthropods we will meet in this text, the exoskeleton is thin and lacks a waxy epicuticle. For these animals oxygen and carbon dioxide simply diffuse directly across the cuticle. However, this method of gas exchange is only functional over very short distances and for very small animals. In most of the terrestrial groups of arthropod ectoparasite to be considered in this book, the protective cuticle is punctured by a number of openings. In the insects these openings are called **spiracles**; in the mites and ticks they are called **stigmata**. Spiracles or stigmata may be set in a sclerotised cuticular plate called a **peritreme**. Insects, at most, have two pairs of thoracic and eight pairs of abdominal spiracles. This number is frequently reduced. Mites and ticks may have anything from none up to four pairs of stigmata, when present, usually located on the anterior half of the body.

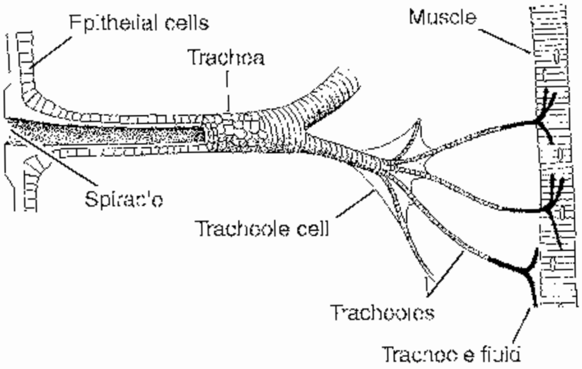

Fig. 1.6 A spiracle, trachea and tacheoles (after Snodgrass, 1935).

Typically spiracles or stigmata open into a chamber or atrium with a mechanism for opening or closing, called a valve. The openings lead to cuticle-lined air-conducting tubes called **tracheae**, formed by invagination of the epidermis during development. The tracheae form longitudinal and transverse tracheal trunks that interconnect among the segments. The tracheae branch repeatedly as they extend to all parts of the body (Fig. 1.6). In some, particularly fast flying insects, part of the tracheal system is expanded to form air sacs. The branches of the tracheae end within the cells of muscles and other tissues in extremely fine **tracheoles** which are the principal sites of gas exchange. The ends of the tracheoles contain fluid and are usually less than 1 µm in diameter. Tracheoles are particularly numerous in tissues with high oxygen requirements.

Other types of arthropod, not considered here, show completely different adaptations for gas exchange; the terrestrial scorpions and spiders for example have book lungs, while the aquatic crustaceans have gills.

Ventilation

Oxygen enters through the respiratory openings and passes down the trachea, usually by diffusion along a concentration gradient. Carbon dioxide and (in terrestrial insects) water vapour move in the opposite direction. Water loss is a major problem for most terrestrial arthropods and for them gas exchange is often a compromise between getting enough oxygen into the body while making sure that they do not desiccate. Hence in periods of inactivity the respiratory openings are often kept closed, only opening periodically.

Diffusion is only effective over small distances. Hence, in large and active insects active pumping movements of the thorax and/or abdomen may be used to help to ventilate the outer parts of the tracheal system. Rhythmic thoracic movements or compression/telescoping of the abdomen help to expel air from the outer trachea or the air sacs. Co-ordinated opening and closing of the spiracles usually accompanies ventilation movements and serves to effect a unidirectional flow of air. Anterior spiracles open during inspiration and posterior ones during expiration.

1.6.5 The arthropod circulatory system

The arthropod circulatory system is relatively simple, consisting of a series of central cavities or sinuses, called a **haemocoel**, separated by muscular septa. The haemocoel contains blood, called **haemolymph**. In contrast to vertebrates, the haemolymph is not involved in gas exchange. The volume of the haemolymph may be substantial: 20 40% of body weight. Haemolymph is a watery fluid composed of an aqueous solution of inorganic ions, lipids, sugars, amino acids, proteins, organic acids and other compounds and cells. It is often clear and colourless but in some species may be pigmented green, blue (or rarely red). All chemical exchanges between organs are mediated by the haemolymph: hormones are transported, nutrients are distributed from the gut, wastes are removed from the excretory organs. However, haemolymph does not come into contact directly with the cells because the internal organs and the epidermis are covered by a basement membrane.

In most mites the circulatory system consists only of a network of sinuses. Circulation probably results from contraction of body muscles. Insects, on the other hand have a functional equivalent of the heart, the **dorsal vessel** (Fig. 1.7). This vessel varies in position and length in different arthropod groups, but in all of them the dorsal vessel consists essentially of a wide tube with one or more chambers, running along the length of the body and perforated by pairs of lateral openings called **ostia**. The ostia only permit a one-way flow of haemolymph into the dorsal vessel. The dorsal vessel lies in a compartment of the haemocoel called the **pericardial sinus**.

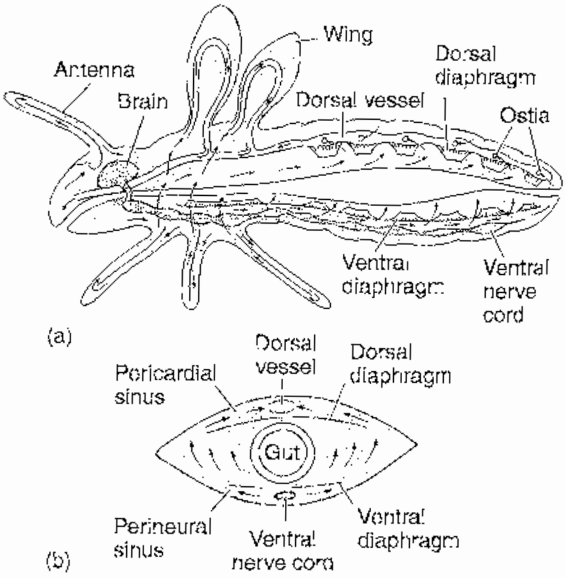

Fig. 1.7 Generalised arthropod circulatory system. (a) Longitudinal section through the body. (b) Transverse section through the abdomen (reproduced from Gullan & Cranston, 1994, after Wigglesworth, 1972).

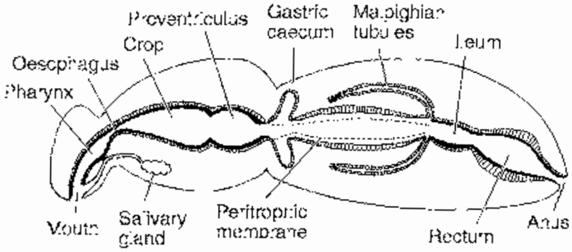

Fig. 1.8 Generalised digestive tract of an arthropod, showing the fore-, mid- and hindgut. The cuticular linings of the foregut and hindgut are indicated by thick lines.

The dorsal vessel pumps haemolymph forward towards the head and eventually into sinuses of the haemocoel in the head. Haemolymph then percolates back through the haemocoel to the pericardial sinus, until it is again picked up by the dorsal vessel. The pericardial sinus is separated from the main compartment of the haemocoel by a septum known as the dorsal diaphragm (composed of musles and connective tissue). The dorsal diaphragm supports the dorsal vesssel and is punctured by a series of segmental openings. There is also a ventral diaphragm, associated with the ventral nerve cord. Circulation is aided by peristaltic contractions of the ventral diaphragm, which direct the haemolymph backwards and laterally. Haemolymph is generally circulated to appendages unidirectionally by various tubes, septa, valves and pumps. Muscular pumps are called accessory pulsatile organs and occur at the base of the antennae and legs.

1.6.6 The arthropod nervous system

Arthropods have a complex nervous system associated with the well-developed sense organs, such as eyes and antennae, and behaviour that is often highly elaborate.

The central nervous system consists of a dorsal brain in the head which is connected by a pair of nerves which run around the foregut to a series of ventral nerve cord ganglia (Fig. 1.7). In the embryo each segment gives rise to a pair of ganglia which then fuse to form a single ganglion, and this pattern can still be seen in primitive arthropods. The ganglia are connected between segments by pairs of connective nerves. In more advanced arthropods ganglia may be fused. In blowflies, for example, there is only a single thoracic ganglion and no abdominal ganglia, and in the mites and ticks there is only a single cephalothoracic ganglion.

1.6.7 Digestion and absorption

The gut of an arthropod is essentially a simple tube that runs from mouth to anus (Fig. 1.8). Nutrients are absorbed across the gut wall

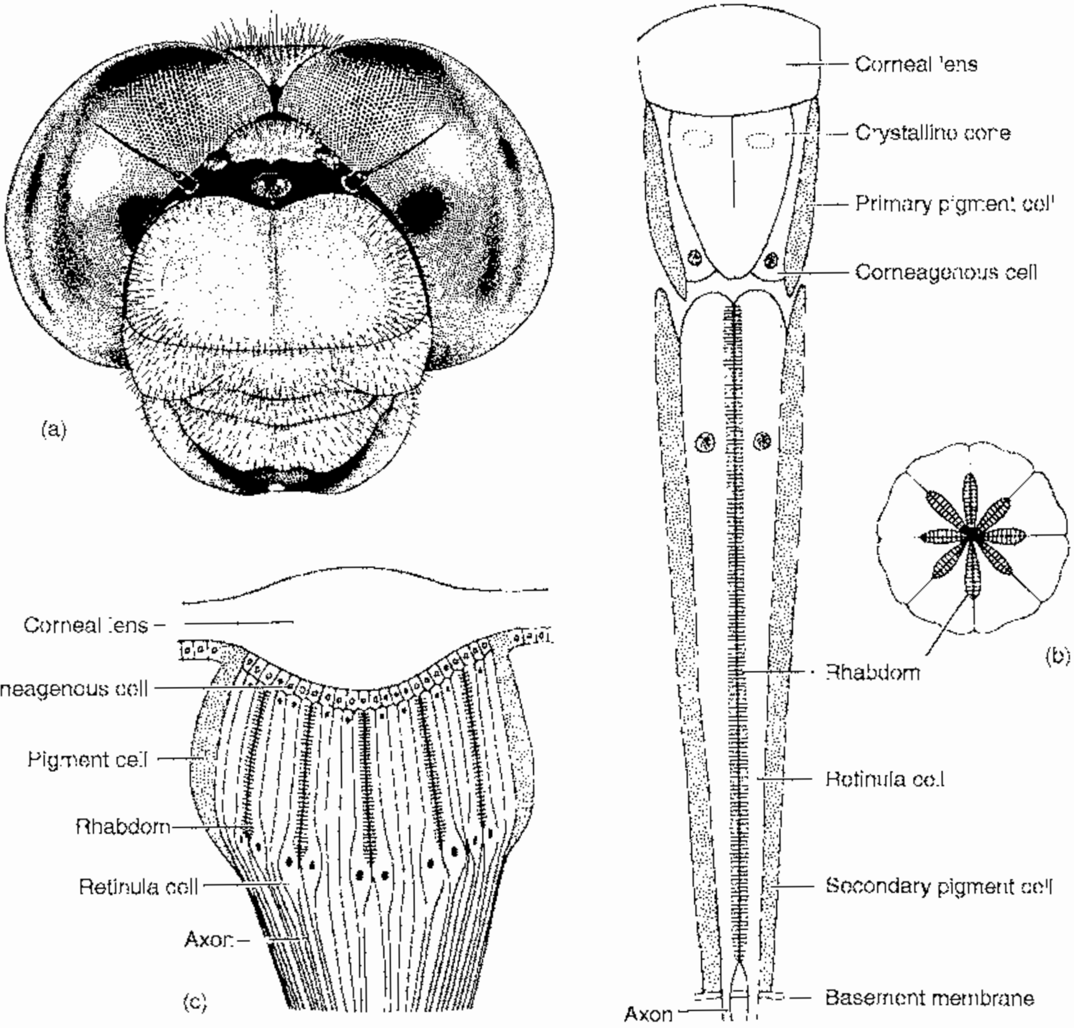

Fig. 1.9 (a) Head of a dragon fly, showing two large compound eyes and, between them, three ocelli. (b) Longitudinal section through an ommatidium with an enlargement of a transverse section. (c) Longitudinal section through an ocellus (from Gullan & Cranston, 1994).

directly into the haemolymph. The precise shape of the gut varies between arthropods, various outpockets or large digestive glands being present, depending on the precise nature of their diet.

In insects, the gut is divided into three sections: the foregut, midgut and hindgut (Fig. 1.8). The foregut and hindgut consist of invaginations of the exoskeleton at the mouth and anus, respectively; therefore they are lined with cuticle. In fluid-feeding arthropods there are prominent dilator muscles which attach to the walls of the pharynx, to form a pump. The foregut is concerned primarily with the ingestion and storage of food, the latter usually taking place in the **crop**. Between the foregut and the midgut is a valve called the **proventriculus**. In some arthropods, the proventriculus may be armed with teeth and functions in the crushing and grinding of food. The midgut is the principal site of digestion and absorption. It has a cellular lining which secretes digestive enzymes. Absorption takes place largely in the anterior of the midgut, in large outpockets called gastric caecae. The hindgut terminates in an expanded region, the rectum, which functions in the absorption of water and the formation of faeces. Nitrogenous wastes are eliminated from the haemocoel by long, thin projections called the **Malpighian tubules**, which open into the gut at the junction of the mid- and the hindgut. In mites and ticks the gut follows a broadly similar plan, but may be simplified, often with only one pair of Malpighian tubules.

1.6.8 Arthropod sense organs

The sensory receptors of arthropods are usually associated with modifications of the chitinous exoskeleton. One common type of receptor is connected with hairs, bristles and setae. The bristle may be designed so that it acts as a mechanoreceptor, movement triggering the receptor at its base. Alternatively, the bristle may carry chemoreceptors. Other common modifications for receptors are slits or pits in the exoskeleton. These may house chemoreceptors or the opening may be covered by a membrane with a nerve ending attached to its underside, to detect vibrations. Such receptors may be scattered over the body or concentrated on appendages such as the legs or antennae.

Most arthropods have eyes, but these can vary greatly in complexity. Some contain only a few photoreceptors. For example, in the **stemmata** of larval holometabolous insects and the **ocelli** of larval and adult hemimetabolous insects, a corneal lens overlies from 1 to 1000 sensory cells (Fig. 1.9). These simple eyes do not form images but are very sensitive at low light intensities and to changes in light intensity. Other types of arthropod eye, known as compound eyes, are large and complex with thousands of retinal cells (Fig. 1.9).

The **compound eyes** of insects and many crustaceans are composed of many long, cylindrical units. Each unit, called an **ommatidium** is covered at its outer end by a translucent cornea, called a **facet**, derived from the cuticle. The facet, which is often hexagonal, functions as a lens. Internal to the cornea, the ommatidium contains a long, cylindrical element called the crystalline cone which functions as a second lens. Behind this, elongated **retinula** nerve cells, usually eight in number, are packed together in a tail, translucent cylinder. Each retinula cell is wedge-shaped and the inner part of each, known as a **rhabdomere**, is folded to form microtubules running perpendicular to the axis of the ommatidium. The junction of these microtubules running down the centre of the retinula cells is known collectively as the **rhabdom**. The retinula cells contain black or brown photosensitive molecules of a protein–retinene complex called rhodopsin.

The retinula nerve cells are also surrounded by a ring of light-absorbing pigment cells which screen the light entering each ommatidium from its neighbour.

The rhabdomeres of an ommatidium function as a single photoreceptor unit and transmit a signal that represents a single point of light. Individual ommatidia cannot form a detailed image and only overall light intensity is registered. Each ommatidium points in a slightly different direction. The image formed by a compound eye, therefore, represents a series of apposed points of light of different intensities, termed an apposition image. The detail available depends on the number of ommatidia present. There is no mechanism for accommodation and the principal function of a compound eye is in detecting movement as an image passes from one ommatidium to the next. This is assisted in many arthropods by the fact that the total corneal surface is highly convex, resulting in a wide visual field. In addition, many arthropods have colour vision, mediated by variations in the visual pigment in the retinula cells.

However, an apposition image does not work well at low light intensity. Therefore, in arthropods adapted for living in conditions of low light intensity, the screening pigment is retracted so that light can pass from one ommatidium to the next, forming a superposition image. While this image is less sharp, this maximises light gathering, making it more likely that a rhabdom will be stimulated than if it was dependent only on light entering its own facet. In addition, a mirror-like layer at the back of the eye, known as the tapetum, serves to reflect light a second time through the rhabdom.

1.6.9 Arthropod reproduction

In arthropods the sexes are separate and mating is usually required for the production of fertile eggs. However, in some species males may be absent and females reproduce by **parthenogenesis**, producing identical genetic copies of themselves. Most arthropods lay eggs. However, some species, such as the flesh flies, are ovoviviparous and retain their eggs internally until they hatch. They then larviposit live first-stage maggots. Other species, such as the sheep ked or tsetse fly, are viviparous, retaining the larvae and nourishing them until they are fully developed.

The female reproductive system is composed of a pair of **ovaries** (Fig. 1.10). Each ovary is divided into egg tubes, or **ovarioles**. The ovarioles join the lateral oviduct which in turn meets a median oviduct. This often ends in an **ovipositor**. A portion of the median oviduct may be expanded to receive the **aedeagus** during copulation.

The male reproductive system is usually composed of a pair of testes, each subdivided into a set of sperm tubes or follicles in which the formation of sperm takes place (Fig. 1.10). The follicles join the **vas deferens**, which is often expanded into the **seminal vesicle** which stores the sperm. The vas deferens join a common ejaculatory duct which ends in the external genitalia, with an intromittent organ, the penis, or aedeagus. Accessory glands produce secretions which may form a packet, called a **spermatophore**, which encloses the sperm and protects it during insemination.

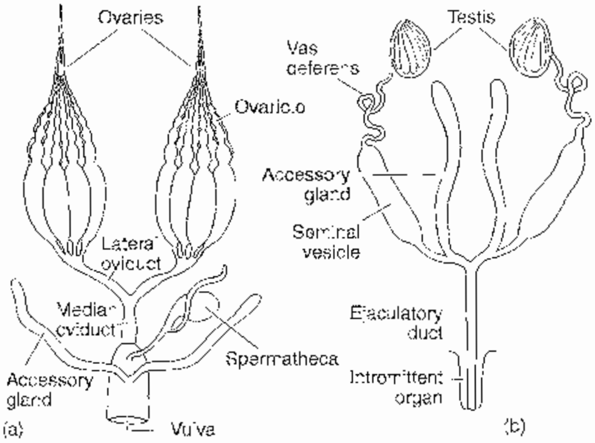

Fig. 1.10 Generalised (a) female and (b) male reproductive systems (from Gullan & Cranston, 1994, after Snodgrass, 1935).

Sperm may be delivered directly to the female during copulation or, as in some species of mite, the spermatophore is deposited on the ground and the female is induced to walk over and pick up the spermatophore with her genital opening. Sperm are usually stored by the female in simple seminal receptacles or more complex organs called spermathecae. As an ovulated egg passes down the median oviduct it is fertilised by sperm released from the spermathecae. Accessory glands join the median or lateral oviducts and in many species produce secretions that coat and protect the eggs.

1.6.10 Arthropod size

The patterns of arthropod anatomy and physiology are intimately related to their size. The largest terrestrial insects and spiders weigh no more than about 100 g and the smallest are less than 0.25 mm in length. Only marine forms have managed to attain relatively large sizes; the Japanese spider crab, *Macrocheira*, may have a leg-span of over 3.5 m. The respiratory and circulatory systems described above, for example, are both efficient for arthropods but would not work for larger animals. The exoskeleton can provide remarkable rigidity but, because mass increases by the cube while surface area increases by the square, an exoskeleton for a mammal-sized arthropod would be too heavy to allow it to move. Small size also gives arthropods the appearance of great strength because the power of a muscle is proportional to the area of its cross-section, while the mass it moves is proportional to volume. Hence, small animals have muscles with a low cross-sectional area-to-volume ratio, relative to larger animals. Thus, a cat flea can jump about 30 cm, which would correspond to a jump of about 300 m for a human.

1.7 PATTERNS OF ARTHROPOD DEVELOPMENT

1.7.1 Moulting

An external skeleton results in problems for a growing animal, since it essentially encases it in a frame of fixed size. The solution evolved by arthropods is the periodic shedding of the exoskeleton, called **moulting** or, more properly, **ecdysis**.

Before the old skeleton is shed the epidermis detaches itself from the old cuticle (**apolysis**) and secretes a new epicuticle. The new epicuticle is soft and wrinkled at this stage. Enzymes (chitinases and proteinases) are then produced which pass through the new epicuticle and begin to erode the old endocuticle; the exocuticle is not affected. Muscle attachments and nerve connections are unaffected and the animal can continue to behave normally. Following digestion of the endocuticle new undifferentiated tissue, known as procuticle, is also produced. Exocuticle is absent along specific paths known as moulting lines. The old skeleton splits along these predetermined lines and the animal pulls out of the old encasement.

The soft, whitish exoskeleton of the newly moulted animal is stretched, often by the ingestion of air or water. Once expanded, quinones cross-link cuticular proteins of the new procuticle, particularly in its outer layers, forming exocuticle. This cross linking results in hardening and darkening of the cuticle. Endocuticle continues to be deposited, on a daily cycle, for some time after moulting, producing daily growth lines that can be used to estimate age in some species of insect. The internal tissues of the animal may then be expanded to fill the new frame.

The stages between moults are known as stages, or **stadia**, and the form of the stadium as the **instar**. This terminology is confusing and is often confused in the scientific literature. But, in its simplest form, moults that give rise to new characters produce new instars. Hence, for example, a fly larva moults twice, but the larva remains morphologically very similar; these are therefore correctly termed the first, second and third stages of the larval instar.

The duration of each stadium becomes longer as the animal becomes progressively older. In many insects the growth which is achieved at each moult is predictable and dependent on the size of the previous stadium or instar. For example, according to Dyer's law, when the number of the stadium is plotted against the logarithm of some measurement on the insect's exoskeleton, a straight line is obtained.

1.7.2 Simple and complex life-cycles

In arthropods, growth and maturation from egg to adult may be accomplished via a number of different developmental paths. In most, the juvenile stadia broadly resemble the adult, except that the genitalia and, where appropriate, wings are not developed. The juveniles, usually called **nymphs**, are similar to the adults in appearance, feeding habits and habitat. The animal makes a new cuticle and sheds the old one at intervals throughout development, typically four or five times, increasing in size before the emergence of the adult. This is often described as a simple life-cycle with incomplete or partial metamorphosis, known as hemimetabolous metamorphosis (Fig. 1.11). In general, the same cells or tissues that make larval structures go on to make the same structures in the adults after the final moult.

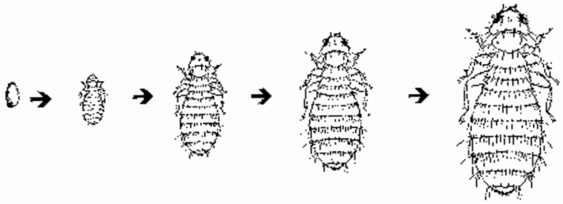

Fig. 1.11 Life-cycle of the louse, *Menopon gallinae*, displaying hemimetabolous metamorphosis and passing through three nymphal stages prior to emergence as a reproductive adult (modified from Herms & James, 1961).

In other arthropods, however, particularly some higher insects, there has been a trend towards increasing functional and structural divergence in juvenile and adult stages (Fig. 1.12). The juvenile instar, which may be referred to as a **larva**, **maggot**, grub or caterpillar, has become concerned primarily with feeding and growth and may bear no physical resemblance to the adult. In contrast, the adult, or **imago**, has become the specialised reproductive and dispersal instar. In the juvenile stages the cuticle is usually soft and pliable and is not differentiated into hardened plates. These stages depend on a hydrostatic skeleton, provided by fluid pressure in the haemocoel, for support and movement. To reach the adult form, the larva must undergo complete metamorphosis, during which the entire body is reorganised and reconstructed. The transformation between the juvenile and the adult is made possible by the incorporation of a pupal stage, which acts as a bridge between juvenile and adult. The juvenile feeds, moults and grows until it has reached its final juvenile stadium. In many species of fly (Chapter 4), the cuticle of the final larval stage contracts and tans to form a protective shell, the **puparium**. In other insects, such as the fleas (Chapter 6), the larva may spin a protective cocoon of silk produced by the salivary glands, prior to a final moult within the cocoon. The **pupa** lies within the puparium or cocoon. The pupa does not feed and is generally (but not always) immobile. However, it is metabolically very active as old larval tissues and organs are lost or remoulded and replaced by adult organs. During the process of pupation, tissues undergo histolysis and are reassembled in the adult form. The pupa is probably a highly modified final juvenile stage, which has become specialised for the breakdown of larval structures and reconstruction of adult features.

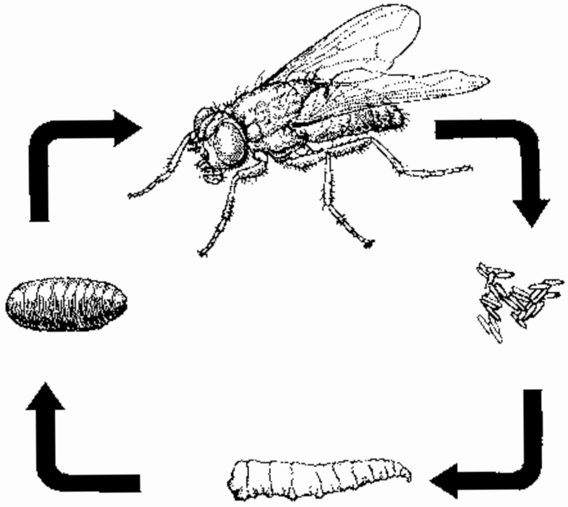

Fig. 1.12 Life-cycle of a fly (Diptera) displaying a holometabolous life-cycle, with the egg giving rise to maggot-like larva, pupa and finally reproductive adult (from Gullan & Cranston, 1994).

When pupal development is complete, the cocoon or puparial case contains a fully developed, **pharate** adult. The adult bursts out of the cocoon using body spines and a projection on the head or, in the case of the higher (cyclorrhaphous) flies, from the puparium using an inflatable membranous sac on its head, called a **ptilinum**. Once free of the cocoon or puparium the newly emerged **teneral** adult begins to stretch its still soft cuticle, prior to hardening and darkening. This pattern of development is described as a complex life-cycle with holometabolous metamorphosis.

1.8 THE CLASSIFICATION OF DIVERSITY

To make sense of the diversity of animal species, they are classified into biological units. These units are usually based on similarities in morphological characters, but may increasingly be based on isoenzyme electrophoresis and DNA analysis. The structure of the classification aims to describe biologically meaningful groups, usually attempting to represent evolutionary pathways. There are six basic categories into which organisms are classified:

- Phylum
- Class
- Order
- Family
- Genus
- Species

The species is the basic operational biological unit, from which all other levels of classification ascend. A species is generally considered to be a group of interbreeding natural populations that are reproductively isolated from other such groups. Hence, even if able or induced to interbreed, matings between species usually result in infertility or reduced fertility of the hybrid offspring. Groups of species are assembled into the next rank of classification, the genus.

All animals and plants are named according to a binomial system, devised by the Swedish naturalist Carl Linnaeus in the eighteenth century. The first word of an organism's name is the generic name and is identical for all members of each genus. The second word is the specific name, unique to each species. Once the generic name has been given in full in a text, it may be shortened to its initial letter. Many specific names describe some characteristic feature of the species, for example the name of the tsetse fly, *Glossina pallidipes*, means the *Glossina* with pale feet.

Even within a species not all populations are exactly the same and often there may be considerable variation associated with geographical, environmental, seasonal and genetic factors. Within a species, geographically isolated populations may be classified as subspecies, with each subspecies showing slight morphological differences but still being capable of interbreeding normally where populations overlap.

At the other end of the spectrum, the complexities of animal taxonomy have brought about the need to introduce numerous intermediate ranks in the classification, such as the subgenus, subfamily, suborder and also, for particularly complicated groups, a range of other terms such as species complex, tribe and super family. There is no fixed limit to the number of categories that can be used. It is important to remember, however, that these groups are artificial creations of the taxonomist who is attempting to give order to the confusing diversity of arthropod forms. There is, therefore, no single 'correct' classification and, indeed, arthropod systematics is often the subject of heated debate!

It is helpful to note that the names of superfamilies usually end in '-oidea', families in '-idae' and subfamilies in '-inae'.

1.9 THE ORIGINS OF ARTHROPODS

As described previously in this chapter, the phylum Arthropoda can be well defined by the presence of seven features:

- Segmented bodies
- Exoskeleton
- Jointed limbs
- Tagmatisation
- Dorsal blood vessel
- Haemocoel
- Ventral nerve cord

However, within the phylum there is considerable variation in morphology and the evolutionary origins of the different groups are far from clear.

There is general agreement that the arthropods probably evolved from some primitive **polychaete** stock or an ancestor common to both. Polychaetes are a class of metameric annelid worms, with a pair of paddle-like appendages on each segment. However, there has been considerable debate about whether the arthropods arose from a single common ancestor (monophyletic origin) or arose from a number of more or less related ancestors (polyphyletic origin).

The initial monophyletic view was based on analysis of morphological similarities and suggested that all arthropods arose from a basic trilobite or pre-trilobite stem (Fig 1.13). The trilobites were believed to be the most primitive of all known arthropods. Once abundant in the oceans 500 million years ago, they are now extinct. Trilobites had oval, flattened bodies, usually about 3–10 cm in length, with a thickened dorsal cuticle and ventral appendages. The majority of trilobites appear to have been bottom dwellers and crawled over mud and sand using their walking legs. It was proposed that, from the primitive trilobites, one line may have led to a subphylum known as the Mandibulata, containing the crustaceans (for example crabs, shrimps and barnacles), myriapods (millipedes and centipedes) and insects (for example flies, locusts and ants). A second line may have led to a subphylum known as the Chelicerata, containing an aquatic group, the merestomes (for example horseshoe crabs) and a terrestrial group, the arachnids (for example spiders, scorpions, mites and ticks).

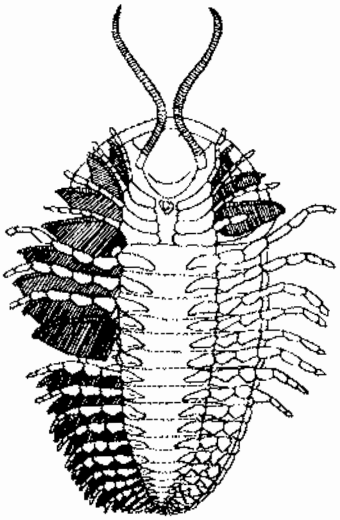

Fig. 1.13 A trilobite (ventral view) (reproduced from Fox & Fox, 1964).

However, while there was general agreement that the chelicerates constitute a natural group, as do the insects and the myriapods, the crustaceans did not appear to fit easily within the insect–myriapod assemblage. There was growing acceptance that insect–myriapod mandibles are structurally different to crustacean mandibles and that the superficial similarities reflect convergent evolution, that is these features have arisen independently in each group, rather than reflecting any close phylogenetic ancestry.

The monophylectic view, therefore, was largely replaced by a polyphylectic scheme, due largely to the work of Manton. This suggested that, given the diversity of the arthropod groups, they must have arisen as a number of independent branches from the basic polychaete stock. From marine polychaete ancestors, several groups may have invaded land independently, giving rise to ancestral forms from which the myriapod–insect assemblage arose. Independently marine, perhaps bottom-dwelling, groups may have given rise to the crustaceans, the trilobites and chelicerates.

However, more recently the use of DNA analysis and cladistic techniques have given renewed support for a monophyletic origin of arthropods from annelid worms. Nevertheless, there is still considerable debate about the precise relationships of the various arthropod groups within the phylum. For example, analysis of ribosomal DNA places the Myriapoda closer to the Chelicerata than the Insects (Hexapoda) and Crustacea. In contrast, studies of mitochondrial DNA support the view, outlined above, that the Crustacea, Myriapoda and Insecta may be considered together in one subphylum Mandibulata, with the Chelicerata as a second subphylum; which is the relationship between the various groups presented here (Fig. 1.14).

1.10 LIVING ARTHROPOD GROUPS

Only two classes, the Arachnida and the Insecta, contain species of major veterinary importance (Fig. 1.15).

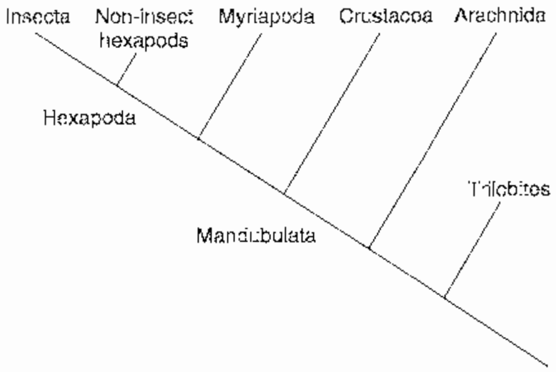

Fig. 1.14 Relationships of the major classes of arthropod.

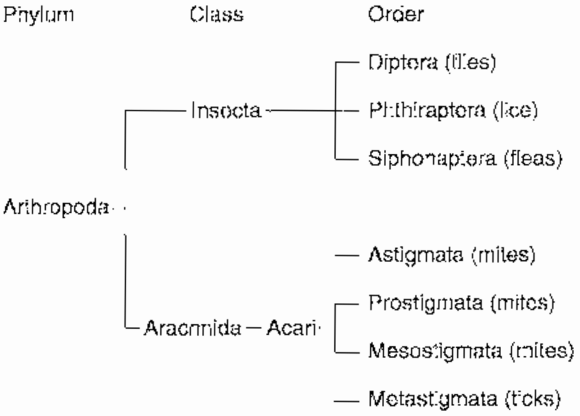

Fig. 1.15 The arthropod orders of verinary importance.

1.10.1 Arachnids

Members of the class Arachnida are a highly diverse group of largely carnivorous, terrestrial, chelicerate arthropods. They are characterised by having the body divided into two parts, the cephalothorax and the **abdomen**. The unsegmented cephalothorax is usually covered dorsally by a solid carapace. In primitive forms the abdomen is divided into two; however, in most forms this segmentation has been lost.

On the cephalothorax the first pair of appendages, which are positioned in front of the mouth and which are used in feeding, are called **chelicerae**. The name Chelicerata comes from the ancient Greek *chele*, meaning claw, and *keras*, meaning horn. The mouthparts do not have true jaws. The second pair of appendages appear behind the mouth and are called pedipalps. Their precise structure and function varies from order to order. The arachnids do not possess antennae or wings and they only have simple eyes.

In the class Arachnida there is only one group of major veterinary importance, the sub-class **Acari** (sometimes also called Acarina), containing the mites and ticks. Other major sub-classes or orders of arachnid include the scorpions (Scorpiones), spiders (Araneae) and pseudoscorpions (Pseudoscorpiones) (Fig. 1.16).

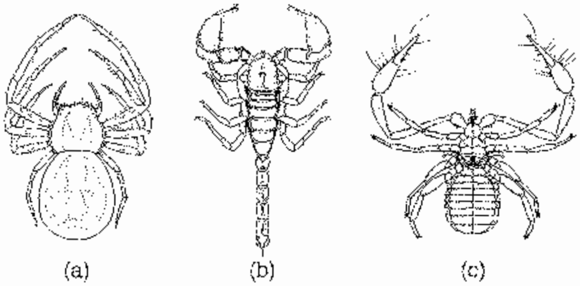

Fig. 1.16 Common orders of the class Arachnida. (a) A spider (*Xysticus cristatus*), (b) a scorpion (*Buthus occitanus*) and (c) a pseudoscorpion (*Chelifer cancroides*) (reproduced from Savory, 1935).

The subclass Acari is an extremely diverse assembly, grouped together more from taxonomic convenience than true phylogenetic homogeneity. They are the most abundant of the arachnids; over 25 000 species have been described to date. They are usually small, averaging about 1 mm in length. However, some ticks may be over 3 cm in length. The cephalothorax and abdomen are broadly fused and abdominal segmentation is inconspicuous or absent, so that the body appears sack-like. The pedipalps are usually short, sensory structures associated with the chelicerae in a discrete structure called a gnathosoma. The body posterior to the gnathosoma is known as the **idiosoma**. There are four basic life-cycle stages: the egg, a six-legged larva, eight-legged nymph and eight-legged adult. However, these may be further divided into pre-larva, larva, protonymph, deutonymph, tritonympha and adult. There may also be more than one moult in each of these instars. In many Acari, pre-larval and larval instars take place within the egg or have been lost. In others, one or more of the nymphal instars may be omittted.

In the adult, the idiosoma is subdivided into the region that carries the legs, the podosoma, and the area behind the last pair of legs, the opisthosoma. The legs are six-segmented and are attached to the podosoma at the coxa, also known as the epimere. This is then followed by the trochanter, femur, genu, tibia and tarsus.

There are three main lineages of extant mites: the Opiloacariformes, the Parasitiformes and the Acariformes. The Opiloacariformes are thought to be the most primitive of the living mites and are not parasitic. The Parasitiformes possess one to four pairs of lateral stigmata posterior to the coxae of the second pairs of legs and the coxae are usually free. The Parasitiformes include the ticks, described as the Ixodida or Metastigmata, and the gamesid mites or Mesostigmata. The Acariformes do not have visible stigmata posterior to the coxae of the second pair of legs and the coxae are often fused to the ventral body wall. The Acariformes includes the mite-like-mites, the Sarcoptiformes and Trombidiformes, often described as the Astigmata and Prostigmata, respectively. The terms Metastigmata, Mesostigmata, Astigmata and Prostigmata relate to the position of the respiratory openings on the body and provide a convenient way of distinguishing the four orders of parasitic importance. Hence, this is the classification system that will be followed here (Fig. 1.15). The mites and ticks and the veterinary problems they cause will be considered in detail in Chapters 2 and 3, respectively.

1.10.2 Insects

The insects are a very large and successful class, constituting about 90% of all known arthropods. Members of the class Insecta can be distinguished from the other arthropods by the presence of only three pairs of legs in adults, and the broad division of the tagmata into three sections: head, thorax and abdomen (Fig. 1.17).

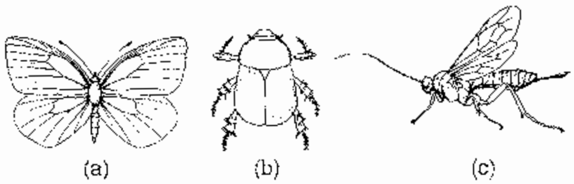

Fig. 1.17 Common orders of the class Insecta: (a) a butterfly (Lepidoptera), (b) a beetle (Coleoptera) and (c) a parasitic wasp (Hymenoptera) (reproduced from Gullan & Cranston, 1994).

The head carries the main sensory organs: the single pair of antennae, a pair of compound eyes and, often, three simple eyes, or ocelli. The mouth is surrounded by mouthparts composed of three pairs of appendages: the mandibles or jaws, followed by a pair of maxillae, then by the labium. These appendages are serially homologous with the legs. However, the mouthparts of different insects show a remarkable variety of specialisation which is related to their various diets, and which will be considered in detail in the appropriate chapters of the text.

The thorax, which forms the middle region of the body, is composed of three fused segments: the prothorax, the mesothorax and the metathorax. On each of these segments there is a single pair of legs. Each leg is composed of six segments. The basal section of the leg articulating with the body is the coxa, which is followed by a short, triangular trochanter. There then follows the femur, the tibia, one to five segments of the tarsus and, finally, the pretarsus composed of a pair of claws. The legs of insects are generally adapted for walking or running but, as we will see, some are modified for specialised functions such as jumping (fleas) or clinging to the hairs of their host's body (lice).

Many groups of insect have two pairs of wings articulating with the mesothorax and metathorax. Some groups of primitive insects have never developed wings while others, such as the fleas and lice, which once had wings, have now lost them completely. Others, such as some of the hippoboscids, which we will meet in Chapter 4, have wings for only a short time as adults, after which they are shed. The wing consists of a network of sclerotised veins which enclose regions of thin, transparent cuticle called cells. The veins act as a framework to brace and stabilise the wing and may carry haemolymph and nerves. The arrangement of the veins tends to be characteristic of various groups of insect species and so is important in identification and taxonomy. Wings are a key reason for the success of the class, allowing insects to migrate, locate distant food sources, escape predators, find mates and colonise new habitats. In several groups of insect, such as grasshoppers, true bugs and beetles, the front wings have been modified to various degrees as protective coverings for the hind wings and abdomen. In the true flies (the Diptera) the hind wings have been reduced to form a pair of club-like halteres, which are used as stabilising organs to assist in flight.

The abdomen is composed of 9 to 11 segments, although the tenth and eleventh segments are usually small and not externally visible and the eleventh segment has been lost in most advanced groups. The genital ducts open ventrally on segment 8 or 9 of the abdomen and these segments often bear external organs that assist in reproduction. The genitalia are composed of structures which probably originated from simple abdominal appendages. In the male, the basic external genitalia consist of one or two pairs of claspers, which grasp the female in copulation, and the penis (aedeagus). However, there is considerable variation in the precise shape of the male genitalia in various groups of insect and these differences may be important in the identification of species. In the female the tip of the abdomen is usually elongated to form an ovipositor.

Within the class Insecta there are generally considered to be 29 orders, of which only three, the flies (Diptera), fleas (Siphonaptera) and lice (Phthiraptera), are of veterinary importance. Adult flies and their veterinary importance will be discussed in Chapter 4 and the problems caused by fly larvae in Chapter 5. Fleas and lice will be considered in Chapters 6 and 7, respectively.

1.10.3 Other living arthropod classes

Crustacea

There are probably more than 26 000 species of Crustacea. Almost all are aquatic and the majority are marine. The class includes such familiar animals as the crabs, lobsters, shrimps, crayfish and woodlice, as well as many thousands of tiny planktonic species that play an essential role in marine food webs (Fig. 1.18).

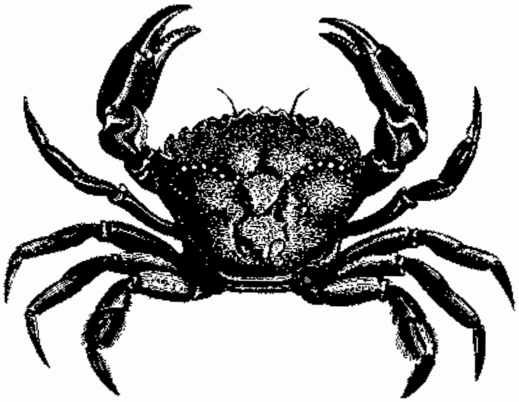

Fig. 1.18 The crustacean, *Carcinus maenas* (from Bell, 1853).

Their bodies are organised into a head and segmented thorax, often combined in a cephalothorax, and posterior abdomen. Anteriorly the head bears five pairs of appendages, the first two of which are the antennae. The third pair of appendages is the mandibles which flank the mouth and behind these are two pairs of feeding appendages. Behind the head, the thorax is often covered by a carapace which arises as a fold of the head and which may overhang the sides of the body.

Primitively, each of the many segments of the throrax and abdomen carries a pair of modified appendages. Crustacean appendages are described as biramous, since typically they are composed of an inner and an outer branch. However, the structure is very variable since the segments have undergone various degrees of fusion and reduction and the thoracic and abdominal appendages are often modified to perform specific specialised functions, such as swimming, crawling, sperm transmission or egg brooding.

The Crustacea are of little or no veterinary importance, with the exception perhaps of copepod crustaceans, known as 'fish lice'. Copepod crustaceans are specialised ectoparasites which attach to the gill filaments or fins and feed by piercing and sucking.

Myriapoda

The Myriapoda contains the familiar millipedes (Diplopoda) and centipedes (Chilopoda) as well as two groups of small, soil-dwelling arthropods the Pauropoda and the Symphyla.

The centipedes and millipedes are relatively long, narrow-bodied and multi-legged. All have a segmented head with a pair of antennae (Fig. 1.18). The remainder of the body is composed of many similar leg-bearing segments. The number of segments and the number of legs increase at each moult throughout life – this is described as anamorphic. There is no metamorphosis (**ametaboly**). Millipedes have two pairs of legs per segment while centipedes have one pair. Millipedes are predominantly herbivorous or saprophagous (feeding on decaying vegetation). In contrast, the centipedes are mainly nocturnal predators, feeding on other arthropods or small vertebrates which they kill using poison injected from the modified first pair of legs, which resemble pincers.

1.11 ARTHROPOD DISTRIBUTIONS

The general distribution of animals is strongly determined by geography and climate. In reflecting geographical divisions, the world is often divided into six zoogeographical regions, each region containing its characteristic animal and plant species (Fig 1.19). Each region is usually isolated by physical boundaries such as deserts, mountains and oceans. Each region contains many species of animal and plant which are **endemic** (native to the region) or which are indigenous (have dispersed or migrated there naturally). Superimposed on these regions, differences in temperature and rainfall caused by differences in latitude, altitude and 'continentality', create further divisions into climatic biomes: tropical, sub-tropical, temperate and polar (Fig. 1.19). The distribution of many species of animal may be strongly limited to specific biomes, either directly by climate or indirectly through the effects of climate on the habitat and resources that the animal requires.

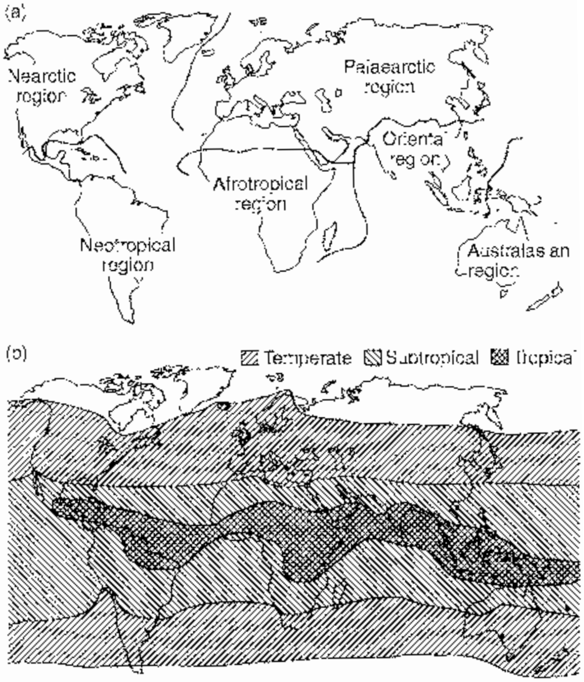

Fig. 1.19 (a) World zoogeographic zones. (b) World climatic biomes.

This book focuses on the ectoparasites of temperate habitats in the **Nearctic** and **Palaearctic** regions, which together form one large realm known as the **Holarctic**. Nevertheless, when dealing with arthropod pests of veterinary importance, it is notable that they have been able to spread worldwide, carried with livestock and humans. In many cases they are also largely protected from the effects of climate by the warm microclimate of their host's body and the houses and other buildings that humans construct. Hence the zoogeographic regions and climatic biomes freqently prove to be an inadequate description of the distribution of ectoparsitic arthropods and, where appropriate, ectoparasites of various regions of the temperate southern hemisphere will also be discussed.

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