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Preface

H.M.S. Endeavour, captained by James Cook, visited the east coast of Australia from April to August 1770. Amongst the far-reaching accomplishments from that visit, Joseph Banks and Daniel Solander initiated study of the animals and plants of this island continent. Banks, and his assistants, collected the first suite of insects to be taken back to Europe for study – from several localities from Botany Bay northward. Some insects clearly impressed Banks – he reported the towering mounds of termites he saw at Cooktown as reminding him of ‘the Druidic monuments I have seen in England’. Almost 240 new species from this collection were described formally in 1775 by J.C. Fabricius, a leading disciple of Linnaeus and one of the most influential entomologists of the era. His later ‘Philosophia Entomologica’, published in 1778, is regarded by many people as the first real entomology textbook and Fabricius was perhaps the first entomologist to appreciate the massive variety of insects. In the ‘Philosophia’ he noted that the number of species ‘is almost infinite’ and that ‘if they are not brought in order, entomology will always be in chaos’. Before the Endeavour voyage, Fabricius had met Banks and Solander in London in 1767–1768 and, no doubt, urged them to bring back insects from the voyage.

Several of those first-collected Australian insects are common species that are easily recognisable today – the common brown butterfly (*Heteronympha merope*), the yellow-winged grasshopper (*Gastrimargus musicus*), and the green mantis (*Orthodera ministralis*) are examples. Another was a widely-distributed bull ant, *Myrmecia gulosa*, collected first at Botany Bay, and it is tempting to speculate that Banks might even have been the first European to suffer the pain of their attack! We know that members of his party were stung by the green tree ant (*Oecophylla smaragdina*) further north – for, in the Endeavour Journal, Banks recorded ‘their stings were by some esteemed not much less painfull than those of a bee’. These insects and many others, named under Linnaeus’ then radical binomial system, were allocated to genera described from other parts of the world and with which European workers were familiar: most have since then proved to be far more distinctive and transferred to more recently-described genera, many of them restricted to Australia and, sometimes, also its neighbours. For example, the very first Australian insect (and, indeed, animal) to be named was a scarab beetle that Fabricius called

'*Scarabaeus barbarossa*', but is now referred to the genus *Haploscapanes*, which contains only a handful of named species, all from the Australian region. Numerous similar revisions have helped to emphasise the unusual nature of Australia's insects – and, indeed, they are no less characteristic and endemic than the better-publicised mammals and birds. As further exploration occurred, the richness and complexity of insects became gradually clearer, with few species from Australia even remotely familiar to their describers in the northern hemisphere. It seems that no insects were collected on Cook's second voyage, but the visit to Adventure Bay, Tasmania in January 1777 (on the third voyage, with H.M.S. Resolution) yielded more, with ten species described by Fabricius in 1787. Cook recorded that the insects seen there were 'in considerable variety'.

Insects are the most diverse of all animal groups, and characterising and understanding the Australian insect fauna is 'a work in progress'. From the First Fleet onward, changes began to occur, with arrivals of alien animals and plants either accidentally or being introduced for settler commodities and agriculture. The insect fauna was no longer pristine, with progressive arrivals from overseas of insects (including fleas and lice as parasites of domestic stock and companion animals), some having substantial impacts on human welfare as consumers of crops and stored products. Those early arrivals were not documented, of course, but many later introductions have been – honeybees, for example, were brought to Australia in 1822 as amongst the first of suites of insects deliberately imported, for a variety of purposes but without consideration of any future impacts in the Australian environment.

In parallel, however, visiting and resident naturalists had greater opportunity to collect and study Australia's native fauna, and are still doing so. More than 200 years later, we still have only vague ideas about the diversity of many groups of our insects, with various 'scientific guesstimates' based on collection contents and expert opinions. Many species have not been studied or, even, collected and it is common for any visiting specialist working on a particular family of beetles, flies, wasps or other large group to discover large proportions of hitherto undescribed species to augment the total. Many surprises remain. Our largest known stick insects, giants of the order with one given the appropriate species name '*gargantua*', have been described only in the last few years – the female of this particular giant, with body length exceeding 30 cm (and spanning more than twice this with legs extended) is known only from a small area of tropical rainforest in northern Queensland, and is one of the world's largest insects. But at the other extreme, many minute insects are amongst the 'black holes' of our formal knowledge. Enormously diverse, of serious interest to only a few specialists (most of them based far from Australia), they remain undercollected and difficult to appraise. Some tiny wasps, that pass their early life within a single egg of a small barklouse or leafhopper, are only about one fifth of a millimetre long: considerably smaller than a large single-celled *Amoeba* but with all the structural complexity of much larger insects miniaturised into this speck of life. This variety of size was familiar to early entomologists, but is still surprising to many other people, and the practical difficulties of studying the richness of insect life renders estimates of their diversity somewhat intangible.

We simply do not know how many native insect species occur in Australia. Recent suggestions of more than 200,000 different species assure them an easy top place for diversity amongst the entire fauna; and the figure is debated – it cannot be refuted, and may even be an underestimate. Methods of collecting and studying insects have advanced from Banks' day, but the principles of needs for capture, preservation, curation, and expert examination and diagnosis are constant. Fabricius initiated the taxonomic foundation on which we must still build, with the realisation that even now perhaps only a quarter or fewer of our native insects have been given formal names. Early descriptions of species are brief, commonly only one or two lines of Latin and addressing a very limited range of characters. They contrast with the lengthy diagnoses now the norm for differentiating similar or allied forms. Fabricius' contention (in Mantissa Insectorum 1787) that 'Too many words are the real trouble of entomology', was founded in an era when recognising entities regarded as species was altogether a simpler exercise than it is now. For example detailed measurements and good illustrations, involving morphological details often necessarily based in delicate dissections and microscopical examination, are now almost mandatory in describing insect species and differentiating related forms. Differences based on structural features are increasingly being augmented by molecular data and statistical analyses to clarify relationships.

This book is about this 'considerable variety': what it comprises, how and where insects live, their peculiarities and roles in Australian environments, and their interactions with humanity. It is an introduction to the natural history of insects in Australia, and some of the remarkable features of the fauna that render insects the richest and most successful animals with which we, sometimes uneasily, share the planet. I hope to introduce the study of insects, entomology, through their evolution and adaptations to the variety of Australia's terrestrial and freshwater environments they so capably dominate. This is not a formal textbook, but covers much of the ground that an elementary entomology text may include, in a framework intended to help people lacking formal biological training or knowledge of insects to begin to understand the major general features and causes of insect variety, and emphasising the importance of Australia's insects, how they 'work', and the needs for conserving their diversity and sustaining their participation in ecological processes and systems. The sequence commences with several general introductory chapters on insect structure, evolution, biology and ecology, helping to illustrate the richness, variety and peculiarities of the Australian fauna. Later chapters summarise the main entomological features of some of Australia's key environments, and the final chapters address aspects of interactions between people and insects and the importance of increasing efforts for documentation and conservation. I have tried to avoid much of the technical 'jargon' that readers can find so offputting and an impediment to understanding, and the sequence of general themes are each treated from basic principles; an Appendix summarises main features of the different insect orders. Each chapter contains suggestions for further reading but, except in a few cases in which I have referred directly to specific papers, close referencing is not given, as likely to disrupt the book. I hope that biologists who recognise allusions to their work without direct citation will forgive this approach. Many of the references cited are classics, and for many I have indicated their relevance: all are available readily. With similar intent, I have not attempted to provide a full illustrated synopsis of Australia's insects; more comprehensively illustrated books are cited in Chap. 1, for example. My purpose has been, rather, to provide a limited range of illustrations of some representatives of major insect groups that help to 'tell a story', to consolidate points in the text, and that indicate particular features or habits that aid understanding of insect variety. Deliberately, many are of common or widespread species that can be discovered easily, some in home gardens, and so that can become familiar with relatively little effort. Much of the book's content draws on basic information and principles, and so transfers easily to the insects of any other part of the world.

The book is, I hope, based in good science and is intended to be accessible to non-entomologists as a means of introducing insects to a wide non-specialist readership and, in particular, of demonstrating the bases of the immense – indeed 'considerable' – ecological, functional and taxonomic variety that renders the Australian insect fauna so intriguing, and also so important to sustain. Two major strands of modern conservation are education (linked with informed understanding and advocacy) and scientific knowledge. Insects have long suffered from both image problems and that non-entomologists, including the great majority of ecologists and managers charged with conserving Australia's unique biota and ecosystems, do not appreciate their taxonomic and biological subtleties and complexity that influence the scale of attention needed to sustain them. The book indicates some of the ambiguities and complexities of documenting insect diversity in Australia and discovering how insects have exploited this vast geographical arena – and so contributes to defining the steps needed to assure the wellbeing of this unique biological heritage.

Acknowledgments The contents of this book are derived from many sources, only a few of which are cited specifically. New information on Australia's insects is published in a range of relevant journals, such as Australian Journal of Entomology, Australian Entomologist, Australian Journal of Zoology, Austral Ecology, and Invertebrate Systematics, all of which focus on research in the region, and many syntheses of relevant topics can be found in the Annual Review of Entomology and elsewhere. Selection of examples to include or omit for limitations of space has been a complex and idiosyncratic exercise, and informed readers may justifiably consider some suboptimal and would opt for a different array from which to discuss general themes and principles. Photographs supplied by colleagues are acknowledged individually in the legends, and it is a pleasure to reiterate my thanks to these friends who responded so generously to my requests for this use.

I appreciate comments from reviewers of the original proposal, and the continuing support of Zuzana Bernhart at Springer, together with the friendly cooperation and advice during production from Elisabete Machado. Production has been facilitated immensely by the careful help of Ms. Juno Martina George.

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Contents

Chapter 1
The Basic Insect Pattern: Theme and Variations

Introduction: Insects and Their Close Relatives

Even defining 'an insect' can be difficult! But any understanding of their massive variety must start from a clear picture of the basic structural template that forms the foundation for any such definition and later diversification. That progressive differentiation has taken place through adaptive modification of almost any structure present, and defining that body plan is vital in distinguishing true insects from other animals. Examining some of the evolutionarily older kinds of insects helps us to characterise that pattern, as well as to suggest some of the reasons why insects as a group appear so successful and have persisted largely unchanged in their fundamental design for so long.

Insects are arthropods, members of that vast phylum of invertebrate animals that share a hard external skeleton and have jointed limbs, ancestrally a pair for each body segment. Within the arthropods, they are accompanied by spiders, mites, crabs and other crustaceans, myriapods such as centipedes and millipedes, and a host of others, each of which has a reasonably consistent body plan that enables us to recognise them. So, also, with insects. Characteristically, insects have six legs and their body is divided into three major regions, the anterior head, central thorax and posterior abdomen. Sometimes these regions are clearly separated – as in a 'waist' (although, paradoxically, in wasps and their relatives, that waist is actually after the first bit of the abdomen!) between thorax and abdomen; hence the name 'insect' (cut into), in marked contrast to the body of many other arthropods. This much is straightforward, but the integrity of defining insects in this way is disrupted by the existence of several other groups of small arthropods that share this pattern and so join them in the Hexapoda, the six-legged arthropods. These, the springtails (Collembola), proturans (Protura), and diplurans (Diplura) have historically all been placed in the class Insecta, but each is now considered an entire independent class equivalent to the whole of the true insects. The reasoning for this is complicated, and rests on the form of the mouthparts. The three small groups are collectively called 'Entognatha' (or entognathous hexapods) to emphasise that their mouthparts

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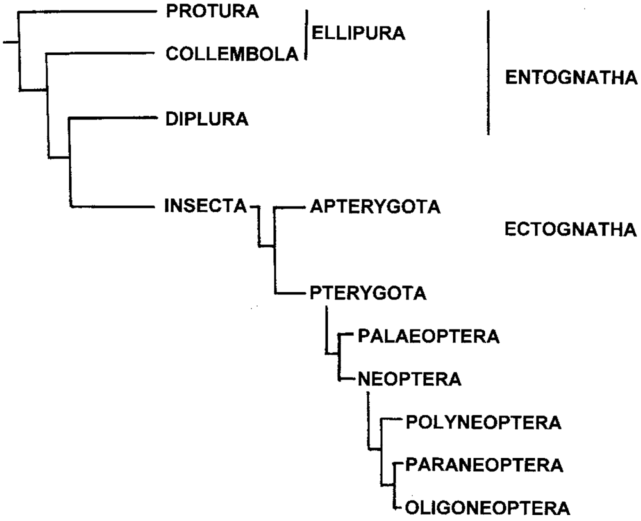

Fig. 1.1 Broad groupings of insects and other hexapod classes. The three classes of Entognatha were all earlier considered to be insects, but all 'true insects' are ectognathous, with the winged forms (Pterygota) comprising several major lineages (see text)

are enclosed in extended folds from the front of the head, in contrast to the exposed mouthparts of the true insects, which are thereby 'Ectognatha'. However, even Entognatha is probably not a single lineage, and Diplura are probably nearer to the basal insect line of evolution than the other two, again assessed on the articulation of the mouthparts. Even within the unambiguous Insecta, the most ancestral forms include one small order, bristletails (Archaeognatha), with jaw (mandible) articulation different from all others. These broad groupings are summarised in Fig. 1.1, and at least enable us to define 'insects' in discrete taxonomic terms that are universally accepted.

However, simple observation of many insects reveals many departures from the above basic pattern used so far to define them. Many butterflies have only four legs; some adult insects have even lost all their legs (as in female Strepsiptera, living inside their hosts) and the traditional body divisions may be difficult to discern; when we include highly modified immature stages (larvae), of which more later, the appearance is often very different. A typical 'maggot', the larva of many true flies (members of one of the largest orders of insects, Diptera, see Chap. 3) is basically a tapered cylinder, without any head, the modified mouthparts enclosed in the anterior end, no obvious differentiation between any body regions, and no legs. Such radical departures emphasise the extent of modifications that insects may undergo to exploit different environments and ways of life, and also make it very difficult for field biologists to associate early stages of many insects with the corresponding adults. Nevertheless, the basic pattern forming the foundation for these is at least reasonably consistent, and the basis also for classification of insects into their major groups, orders. Insect systematics and recognition is based largely on external structural features, with relationships inferred from patterns of change and transition that occur. Nowadays, this information can be augmented, and in some cases questioned, from results of molecular analyses, but each of the approximately 30 orders of insects alive today can be recognised, and diagnosed formally, on a particular combination of structural features common to all its members and differentiating the order from all others (Appendix, p. 223). Simplistically, recognition of a dragonfly, beetle, moth, grasshopper, or many others is generally straightforward, even though assessing the relationships between the orders may not always be so. Even experienced entomologists can be misled by the bizarre appearance of some forms. Just as the first specimens of the platypus sent back to England caused naturalists to speculate that they had been manufactured, or birds of paradise were presumed to lack feet, some Australian insects have at first seemed not to fit any conventional ideas. The initial formal description of the orthopteran known as the 'Cooloola monster' (*Cooloola propator*, from Queensland) was introduced by the following comment: 'After some amusement at the technical excellence of the apparently manufactured monster, it was determined that it was a genuine complete cricket-like insect'. Occasional other oddities have proved difficult to allocate even to order, but discovery of entirely new orders is unlikely to occur very often, although specialists continue to debate whether some of the long-recognised orders should retain their current boundaries or divisions. The most recently erected insect order, the southern African Mantophasmatodea (heelwalkers, rock crawlers, with features of both praying mantids and stick insects), was named following discovery of living insects in 2002. However, since then it has been relegated to a suborder and combined with another small non-Australian group within the existing order Notoptera. But, in short, the basic body plan of insects is both definable and has become differentiated to produce the largest suites of animals ever to grace Earth.

The Insect Body Plan

The structural plan of true insects is exemplified well by a rather 'basic' insect such as an adult of the field cricket (*Teleogryllus commodus*) or the Australian plague locust (*Chortoicetes terminifera*), both members of the order Orthoptera and notable for their intrusions into pasture and cropping systems. This 'basic body' (Fig. 1.2) comprises three very different-looking regions. The head is a solid capsule, with the antennae (chemosensory structures), three pairs of mouthparts, and large compound eyes the major features. Small 'simple eyes' (ocelli) are also present. The thorax is also a solid box, with three pairs of legs and in most crickets and other insects, two pairs of wings (p. 14). The abdomen is elongate, more delicate in appearance and with posterior elaboration used in mating by both sexes and egg-laying by females. All of the appendages noted are derived from the serial appendages of the basic arthropod, so also help to indicate the number of segments in the theoretically complete insect body. The pattern is clearest for the thorax, where the three segments

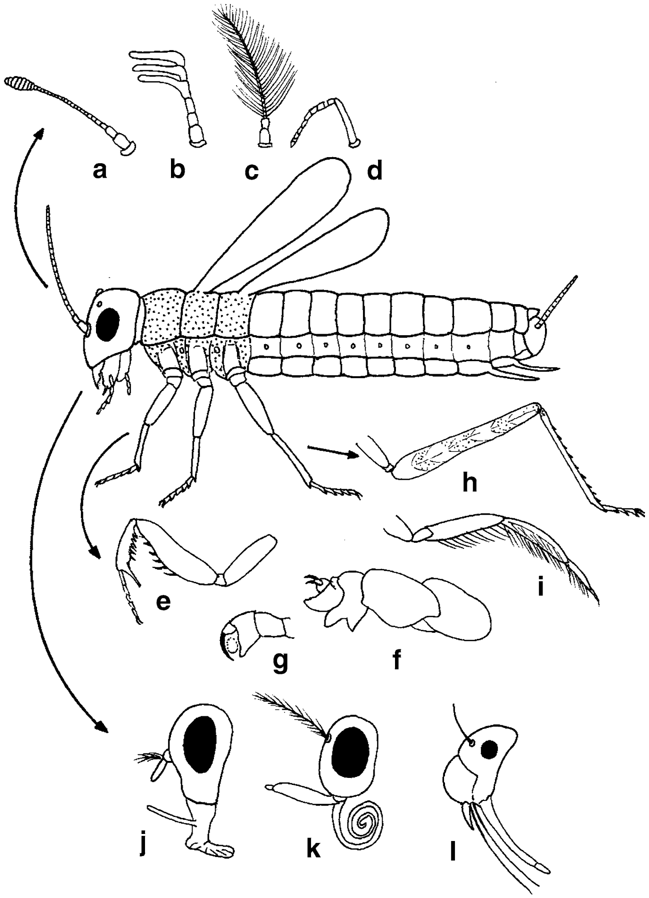

Fig. 1.2 Generalised adult body pattern of an insect, indicating the three main regions; head (with large compound eyes, antennae and mouthparts), thorax (dotted, with legs on all three segments and two pairs of wings), and abdomen: insets show some variations on the form of antennae (**a**–**d**), legs (**e**–**i**) and mouthparts (**j**–**l**) to indicate some of the extensive modifications that enable insects to adopt different ways of life. Main diagram shown with slender 'filiform' antennae: others are (**a**) clubbed, or 'clavate', as in butterflies; (**b**) flanged or 'flabellate', as in some beetles; (**c**) feathery, 'plumose' as in some moths; (**d**) elbowed, 'geniculate', as in ants. Legs: (**e**) fore leg of mantid, adapted for grasping prey (cf Fig. 6.3); (**f**) fore leg of mole cricket, broadened for digging; (**g**) parasitic louse, for firm gripping of host hair or feather; (**h**) enlarged hind leg of grasshopper, for jumping; (**i**) hind leg of water beetle, flattened and with fringe of long hairs, as paddle for swimming. Heads; main diagram with chewing mouthparts, as in a grasshopper: (**j**) fly, with mouthparts composed of labium, expanded as 'sponge' for semiliquid diets; (**k**) butterfly or moth, a long coiled proboscis adapted for sucking nectar from flowers; (**l**) plant bug, with long slender stylets for piercing vegetation and ingesting plant sap

each retain the pair of appendages, as legs and contributing also to construction of wings on the second and third segments. The six segments of the head are fused together, and appendages modified to form antennae (segment 2), and the mouthparts (segments 4–6), and the abdomen appendages are lost other than for those constituting genitalic structures on segments 8 and 9 of the 11 total. Remnants of the limbs are present on the more anterior segments in some very primitive wingless insects, giving us clues to the derivation of the more posterior structures in crickets and others.

The insect body as a whole thus comprises 20 segments arranged into three ‘blocks’ (tagmata) adapted primarily for rather different roles: the head for sensory perception of new environments as the insect encounters them, and for feeding, the thorax for locomotion, and the abdomen for reproduction. Because solid muscle attachments are needed for mouthparts, legs and wings to operate effectively, the head and thorax are indeed usually very solid structures. Conversely, the abdomen is flexible, with a lateral membrane rather than solid ‘wall’. It can be distended for storing food, food reserves, or eggs, and also allows versatility in mating – some insects adopt postures that could be envied by compilor(s) of the Kama Sutra, but which usually involve juxtaposition of the abdominal tip of the two sexes – and depositing eggs in many hidden habitats such as under bark, in the ground, or in other insects or even other animals. In some insects, the abdomen also has two posterior ‘cerci’, filamentous sensory organs, broadly analogous to ‘posterior antennae’ and which tend to be reduced or lost in the most advanced insects.

Any or every appendage and other structure can be changed massively from this basic form, and it is useful to look at some of these divergences here, as a prelude to seeing how they operate in different kinds of insects with differing ways of life, and keeping in mind that the variations have both functional roles, and value in diagnosing and recognising different kinds of insects. Several representative variations of antennae and mouthpart form are shown in Fig. 1.2, each condition diagnostic for some insect group(s), and collectively helping to emphasise the strong linkages between structure and function, the last reflecting ‘way of life’. Again, the cricket provides basis for comparison.

The cricket’s antennae are long (although not as long as in many other similar Orthoptera, in which they can reach several times the body length) and slender. They are technically ‘filiform’ or threadlike, and are made up of numerous small jointed lengths, commonly (but not embryologically) termed ‘segments’ but more properly ‘antennomeres.’ Many other insects have much shorter antennae, and the basic appearance can be much different, with branches, flanges (Fig. 1.2b), numerous lateral projections, or apical thickenings so that they can seem feathery (plumose: Fig. 1.2c) or clubbed (clavate: Fig. 1.2a). The effect of these ornamentations is to increase the surface area available for chemical receptors. In some moths, the form of the antennae differs markedly between the sexes within the same species: those of males are strongly feathery, and of corresponding females, slender. Such differences indicate rather dissimilar needs. In this case, for example, females of many moths, such as codling moth (*Cydia pomonella*) and Oriental fruit moth (*Grapholita molesta*), both pests of orchard crops, do not fly but attract mates by emitting a highly specific pheromone scent. The males detect the scent through their antennae and respond by flying upwind along the increasing concentration gradient to encounter a potential mate. This behaviour, by which males of some species may be attracted from up to several kilometres away, has been used in aspects of pest management for these species, by attracting males to artificial pheromones on crops and so keeping them from mating, thereby reducing the next generation of the pest. Of less economic importance, collectors may use a female moth to attract males as specimens. Not all moths ‘work’ in this way, but this example illustrates well how the appearance and structure of an insect appendage allows us to interpret or infer some important aspect of its biology.

Likewise for mouthparts. Diversification of feeding habits is a major component of insect evolution and their spread of ecological roles and interactions, and is reflected in modification of any or all of the mouthparts. In the cricket, again regarded as a ‘basic’ representation, these comprise a pair of strong jaws (mandibles, on segment 4) that dismember food – in this case, predominantly vegetation; behind these are the paired maxillae (on head segment 5), very different in appearance from the tough mandibles and including a sensory structure (maxillary palp) and ‘accessory jaws’; and the third pair on segment 6 are structurally similar maxillae with reduced palps but fused in the midline to constitute a single structure, the labium. This arrangement is found in many different insects with chewing habits, whether herbivores or carnivores, but this structure is clearly not well-adapted to ingest liquid diets, such as plant sap or blood. The functional need is then for some structure with a role equivalent to that of a drinking straw or hypodermic syringe that can probe or penetrate the plant or animal surface and imbibe the liquid. This is accomplished independently, and by rather different modifications in several widely disparate groups of insects. In some it involves transformation of the cricket-like mandibles and maxillae into slender piercing ‘stylets’, each forming part of the circumference of a tube (proboscis) through which liquid is passed. The whole of this delicate structure in sucking bugs (Hemiptera, Fig. 1.2l) and some Diptera (such as mosquitoes) is supported by a broadened protective labium. The functionally similar structure of Lepidoptera is formed from maxillae alone, and can be coiled under the head when not in use (Fig. 1.2k), so not impeding manouverability: because of their need to take nectar from flowers, some Lepidoptera have a proboscis several cm or more long – the record is perhaps of a hawk moth from Madagascar, in which this structure extends about 30 cm, enabling it to gain nectar from orchids with very deep flowers and act as a pollinator for these! Other mouthpart variations occur. In bushflies and other advanced Diptera, the major structure is from the labium alone, flattened and expanded at the apex which is adpressed to surfaces of dung, carrion, plants or other foodstuffs to sponge up semiliquid materials (Fig. 1.2j). As with many other structures, mouthpart form can be taxonomically diagnostic as well as functionally informative.

Moving to the thorax appendages, any or all the parts of the typical insect leg (Fig. 1.2e–i) can also be changed – whereas we naturally think of walking or running as their primary function, other roles are common. In our cricket/locust examples, the hind legs are conspicuously elongated and strengthened for jumping; many aquatic insects have legs broadened and/or fringed with long hairs to increase their surface area for ‘rowing’ on or under water; mole crickets have unusually strong and broad front legs for digging into soil; and the spined and grasping front legs of mantids are used to capture other insects (and on occasion other animals, even small birds) as prey – in an adaptation paralleled by some predatory bugs, lacewings and flies in which the forelegs have assumed similar form. Insect courtship may involve elaborate displays including ‘leg-waving’, and legs are also involved in the sound production (stridulation) and reception in many Orthoptera.

Wings are discussed more fully later, as a key feature of insects, but the basic principle of multiple modifications from a single basic form is common to all the structures we have noted, with numerous cases of parallels – as in the grasping forelegs of some predatory insects, above. Adoption of a similar habit or way of life by groups of insects that are only distantly related can commonly lead to a problem of capability being solved by the same basic adaptation evolving independently. But, however unusual or bizarre any insect may appear, it has a fundamental structure derived from a pattern similar to that of the cricket with which we started this section.

The abdomen is more uniform, largely reflecting that the serial appendages so prone to modification are restricted to the posterior end. However the most ancestral groups of true insects, the silverfish (Zygentoma) and bristletails (Archaeognatha) show us how these reproductive structures may be derived from the same basic limb form. In these very primitive lineages the underside of some (even, most) of the abdominal segments have paired narrow ‘styles’ projecting rearwards from the posterior margin. These represent part of the base (coxa) of the leg, and have disappeared from the more anterior abdominal segments in advanced insects. The coxae of normal thoracic legs of some of these insects also bear a style, clearly indicating he homology described above.

Inside Insects

The internal structure of insects, also, follows a rather basic and consistent pattern to accommodate the needs for digestion, respiration, reproduction, movement and the variety of other metabolic and developmental processes and responses to the local environment. This pattern, summarised in Fig. 1.3, shows the characteristic relative positions of the major anatomical systems. Thus (1) the alimentary system (dotted in Fig. 1.3a) is the most conspicuous as a continuous tubular ‘gut’ from the anterior mouth to the posterior anus, along the whole length of the body; (2) the circulatory system is predominantly dorsal to this, with a mid-dorsal vessel (sometimes called the aorta anteriorly and the ‘heart’, posteriorly, but a single tube) along the midline; (3) the central nervous system, in contrast, is ventral with anterior concentration of nervous tissue as a brain, encircling the gut in the head; (4) the respiratory system, as a series of tubular tracheae, extends throughout the body, with air admitted from the exterior through a series of paired lateral openings, spiracles; and (5) the reproductive system is predominantly posterior, with reproductive openings for mating and oviposition situated below the anus.

All these systems are within a body cavity, the haemocoel, and can be displayed easily in dissection of a freshly killed cockroach or grasshopper. The body cavity contains haemolymph, in which all the above structures are bathed. Haemolymph is

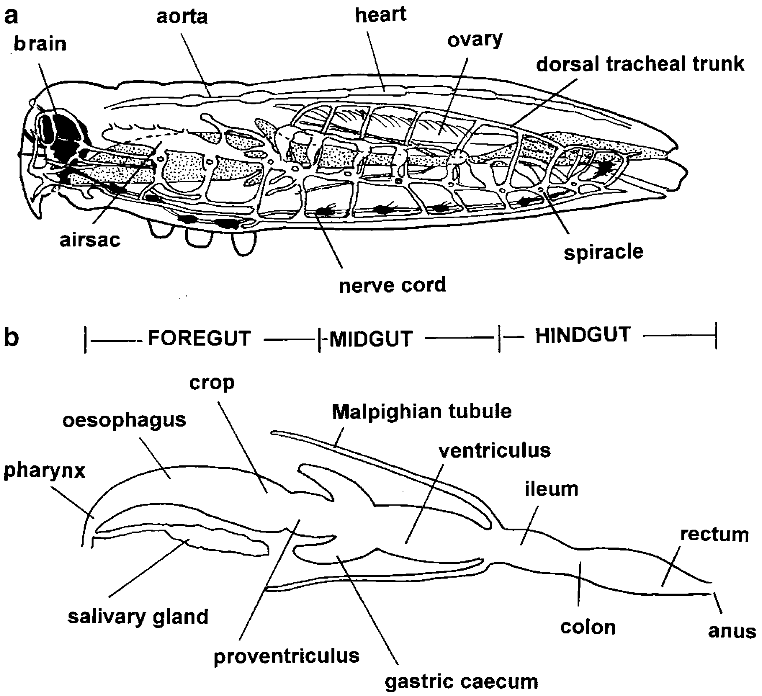

Fig. 1.3 (**a**) General internal anatomy of an insect, to show organisation of various organ systems. (**b**) Digestive tract, indicating different regions

the blood of insects but, unlike vertebrate blood, has only a minor role in respiration and is involved more in nutrient and waste metabolite transport and in some immune interactions. Haemolymph can provide defence against disease, parasites, or physical injury, such as by forming clots that can seal wounds through the cuticle, or cellular reactions that encapsulate disease-causing organisms (including eggs of parasitoid wasps, p. 85) and isolate them. Waste products are filtered from the haemolymph by special structures, the Malpighian tubules, and discharged into the gut and, thence, to the exterior. The haemocoel also contains material loosely termed the ‘fat body’, a more-or-less evident layer of fat around the gut or lining the body cavity and which has complex metabolic roles in storage and reorganisation of nutrients and regulating their supply to the insect. Both the haemocoel and the gut of insects contain microorganisms of various kinds. Some are clearly needed by the insects, and are mutualistic. Wood-feeding termites depend on single-celled protistans to break down cellulose into digestible components, for example, but the true roles of many of these characteristic symbionts are still unclear.

Each of the major anatomical systems can undergo modifications for particular ways of life, but they are used only to a very limited extent in classifying insects – not least because the hard external structures are much more accessible for study, and remain available and unchanged in long-dead specimens in collections.

However, some understanding of the variety of internal structure helps in interpreting the variety of life styles that insects may exhibit.

Thus, the alimentary canal is divisible into several distinct regions, differing in appearance and primary function The relative development of these may reflect the diet of the insects, predominantly whether it is solid or liquid, or plant or animal material, so that the gut may be generalised, or specialised to deal with particular food materials. Insects such as grasshoppers and caterpillars that ingest solid vegetable food tend to have simple, short, muscular guts, strong enough to resist abrasion from plant or animal fragments and wide enough for those particles to pass easily. In contrast, many liquid-feeders have long, more convoluted narrow intestines that allow greater surface contact with the liquid, and protection from abrasion is not an issue. Many sap-sucking bugs and other liquid-feeders have to take in large volumes of food, because the nutrients they need are very dilute in excess water; some bugs have a special ‘filter chamber’ to eliminate excess water and concentrate the food for digestion. Whatever the diet, the gut may also need to store food at times, because many insects can feed only intermittently.

The basic pattern of the gut divisions is shown in Fig. 1.3b. Food enters through the mouth, near which the salivary glands open. The saliva is sometimes used to commence digestion of food outside the body, and may be injected by liquid-feeding insects for this purpose and to aid ingestion. The gut itself is conventionally divided into three main regions, the anterior foregut, central mid-gut and posterior hind gut. The fore gut comprises the oesophagus, through which food passes to the crop (in which food may be stored) and insects taking solid food have a proventriculus (or gizzard, often muscular and with internal hardened spines or ridges by which food particles are broken down). The mid-gut is the major region for digestion, with the surface area for the enzymes produced in this region to interact with food sometimes increased markedly by pouches or gastric caeca from the central ventriculus. In many insects it is lined by a peritrophic membrane separating the food from the gut wall and increasing circulation of enzymes and which is shed at intervals together with any post-digestion food residue. Thus, the diet of dragonfly larvae can best be studied by allowing wild-caught larvae to eject their faecal pellets surrounded by peritrophic membrane, and which encapsulate the remains of their arthropod prey from their recent meals. Dissection of these pellets provides many characteristic fragments (such as hard parts of arthropod mouthparts or legs, that cannot be digested) that can be identified, often quite precisely.

The Malpighian tubules, carrying metabolic wastes as noted above, open to the intestine at the junction between mid-gut and hind gut, and their number and form can also characterise particular insect groups. Major functions of the hind gut are absorption of useful materials from faeces and urine before these are egested, and the three successive regions, commonly differentiated as ileum, colon and rectum, differ in relative extent across taxa. In some insects, such as larvae of antlions and other lacewings (Neuroptera), the hind gut is blocked, so no faecal material can be passed until the insect matures.

A liquid-filled body cavity also provides an internal ‘hydrostatic skeleton’ that enables soft-bodied insects such as maggots and similar larvae to crawl, through waves of muscular contraction being transmitted along the body. Insects with a hard exoskeleton move mainly through direct action of muscles attached to this. Insects have only striated muscles, and those associated with the wings and powering flight or other strenuous movement are particularly well developed. Circulation of haemolymph occurs through passing it along the dorsal vessel, with segmental openings with valves to help ensure a one-way flow toward the anterior. The ventral nerve cord consists of a series of segmental concentrations of nervous tissue ('ganglia') linked by paired longitudinal connective nerves. Their basic pattern is of a pair of ganglia for each body segment, but considerable modifications have occurred through these becoming fused or concentrated to varying extents. Most consistently, all the head ganglia are joined to form the brain (dorsal) and suboesophageal ganglion (ventral) around the fore gut, and the numerous other patterns range from all thoracic and abdominal ganglia being distinct to, at the other extreme, all forming a single mass within the thorax. However, nerves radiate from the ventral cord to all muscles and sensory structures to govern the insect's responses and behaviour. In addition to the conspicuous sense organs, such as eyes and antennae noted earlier, the variety of less obvious structures reflect the needs to respond to both internal and external changes, and to a great variety of environmental cues. Numerous specialised hairs, bristles and related structures on the body surface are linked with individual nerve fibres and are highly adapted receptors for mechanical, positional, chemical, audial or temperature or humidity cues – so that sounds produced by other insects, (whether mates or antagonists), and chemicals such as pheromones, and changes in the external environment can all be detected effectively and appropriate responses be made. The repertoire of sensory structures and responses for any insect may include many individualistic components that facilitate precise responses.

Insects obtain oxygen and eliminate waste carbon dioxide through a system of ramifying internal tubes, tracheae and smaller tracheoles, with external openings (spiracles) through which air is taken from or eliminated to the outside environment. One pair of spiracles opening laterally from each thoracic and abdominal segment is the primitive pattern, but Recent insects never have more than two thoracic and eight abdominal spiracles, and many have far fewer. Dragonfly larvae ('mudeyes') and some others have no spiracles at all – in larval dragonflies, gaseous exchange takes place across the wall of the rectum, into which water is pumped, and mayfly larvae obtain oxygen by diffusion across the lateral abdominal gills. Likewise larvae of some internal parasitoids (p. 86) also lack spiracles and have finely ramifying tracheoles over much of the body surface to enable gas exchange across the body wall. Many insects with spiracles can close them, reducing water loss in more arid environments.

Reproductive structures also follow a rather basic pattern, as a foundation for innumerable variations in size, shape, complexity and development in both sexes, in relation to functions and reproductive behaviour. These functions are complex. A female insect of a bisexual species needs to mate, store and transmit sperm, produce varying numbers of eggs (from few to many, all together or over an extended period and perhaps store these over many weeks or months) as well as lay them, perhaps in precisely selected locales. Some taxa are viviparous, so that larvae are the first stage to be released to the outside world, and many insects are parthenogenetic. Males need to produce and store sperm and transmit it to the female. They may also have adaptations to enhance their chances of success in competition for mates: males of some butterflies (such as the big greasy, *Cressida cressida*, a swallowtail from Queensland) actually plaster the female reproductive opening with a secretion that hardens to form a 'chastity belt' (technically, a 'sphragis') to prevent subsequent matings with other males. And some male dragonflies use spines on their reproductive appendages to 'rake out' sperm from any previous matings before depositing their own. Much of the intricate behaviour of insects relates to increasing chances of reproductive success and larger numbers of progeny, and their often complex behavioural strategies link strongly with structural adaptations in the reproductive system.

As in other animals, hormones in insects play pervasive roles in moulting, development and many aspects of reproduction and metabolic regulation. They are produced from various internal organs and transported by the haemolymph. Three major groups of hormones are usually distinguished as central to reproductive and growth functions, and these are termed the ecdyosteroids, the juvenile hormones and the neurohormones (or, more commonly, neuropeptides). The first are concerned with moulting as a critical process in insect growth and maturation; the second are involved with control of metamorphosis and reproductive development; and neuropeptides influence almost all other aspects of metabolism as well as reproduction and the regulation of juvenile hormone production. They are integral drivers of 'how insects work'.

Entire texts have been written on almost every aspect of insect structure and physiology, and numerous articles in scientific journals and reviews continually present new information and interpretation of their functions and evolution. Part of the story of insect variety is linking structure and function, and appraising how all aspects of insect morphology and metabolism enable the insect to cope with (and capitalise on) its environment, to fit it to develop, disperse, find and use the resources it needs throughout its life, and to regulate its behaviour and lifestyle to persist and cope with changes in that environment in both space and time. The idiosyncrasies of any insect species or group reflect these needs. With a few exceptions of apparent or relative environmental uniformity (such as the flour or grain storage environments of some stored products beetles) insects live in environments that are patchy and variable, and within these they may encounter a range of conditions of humidity and temperature, of food supply, and of other species that may facilitate or oppose their own wellbeing. But, even within a warehouse or sack of flour, conditions change – in aeration, nutritional quality and in the number of individual insects present as populations increase with little initial opposition, so that density of insects may lead to crowding and competition for food and space, and change the interactions between individuals (and species) as more frequent and less easily avoided encounters occur between them. Such situations can induce changes in hormone balance that, in turn, induce behavioural or other changes. Parallels are numerous in more open environments, but there may be a greater variety of 'escapes' possible. However, increased density is associated with, for example, changes in some normally solitary grasshoppers to induce them to enter a gregarious phase, as ‘locusts’, in which changed behaviour reflects modifications in both hormonal balance and sensory responses. Sensory capability to select food, oviposition sites, mates and other necessities, and how and when to disperse are all critical components in an insect’s life. Not all such decisions may be positive, particularly in interactions with plants or other animals, from which a wide array of outcomes may be possible, as we see later. Interactions between individuals and different species are mediated largely by sensory mechanisms.

Further Reading

The first three references below are to entomology texts of varying complexity, and provide more formal information on insect structure and biology. The next two are amongst several well-illustrated guides to insect recognition and biology in Australia. The last is a major, indispensable, source of information on published knowledge on Australian insects

CSIRO (1991) The insects of Australia. Melbourne University Press, Melbourne (The most comprehensive, two-volume, text on Australian insects)

Gullan PJ, Cranston PS (2010) The insects. An outline of entomology, 4th edn. Wiley/Blackwell, Oxford (Latest edition of a very successful general entomology text)

(Note that various chapters of either of the above are valuable ‘further reading’ to most chapters of the current book)

New TR (1996) Name that insect. A guide to the insects of southeastern Australia. Oxford University Press, Melbourne (An introduction to the regional fauna)

Brunet B (2010) Australian insects: a natural history. French’s Forest, New Holland

Zborowski P, Storey R (2010) A field guide to insects in Australia. French’s Forest, New Holland

Daniels G (2004) Bibliography of Australian entomology, 1687–2000 (2 volumes). Privately published, Mt Ommaney

Chapter 2
Fossils and Major Insect Adaptations

Introduction: The Process of Insect Evolution

This structural diversity of insects, and the biological variety it reflects, did not develop all at once. Insects as we would recognise them from modern forms have been around for at least 300 million years, as amongst the first major diversifications of arthropods on land. Over this vast period, we can detect several changes and transitions in structure that appear now to have been 'pivotal events' in leading to their success and fostering their recent abundance. However, the fossil record from which we infer those changes remains cryptic in places: assembling unambiguous evidence from ancient insect fossils is not always easy, and it is not surprising that uncertainties persist – or that the opinions of various specialists may differ widely over how particular fossils may be interpreted! In this chapter, some background to the information on insect evolution derived from the fossil record is outlined, together with its relevance to study of the insects around us today.

The conventional belief is that insects evolved during the Devonian period, about 360 million years ago in the middle of the Palaeozoic era. Until recently, the few relevant fossils available from that early time, or even earlier, are Archaeognatha (from about 380 to 390 million years ago) and the non-insect Collembola. They have no trace of wings. The oldest of these early fossils, from Scotland, are almost 400 million years old and the collembolan *Rhyniella praecursor* was long believed to be the world's oldest hexapod. The 'true insects' appeared first in the Devonian of North America. Very recently, however, a fossil from the Scotland deposits (*Rhyniognatha hirsti*) has been reappraised and is now considered a 'real' insect, leading to the implication that insects actually originated in the Silurian period and that wings may have evolved considerably earlier than is commonly supposed. The challenge to find supporting fossil evidence for this remains.

Modern Archaeognatha are still wingless, and exemplify the insects termed 'Apterygota' (non wing-bearing) as the ancestral condition from which other insects arose. They and silverfish are the modern representatives of this truly ancient lineage.

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