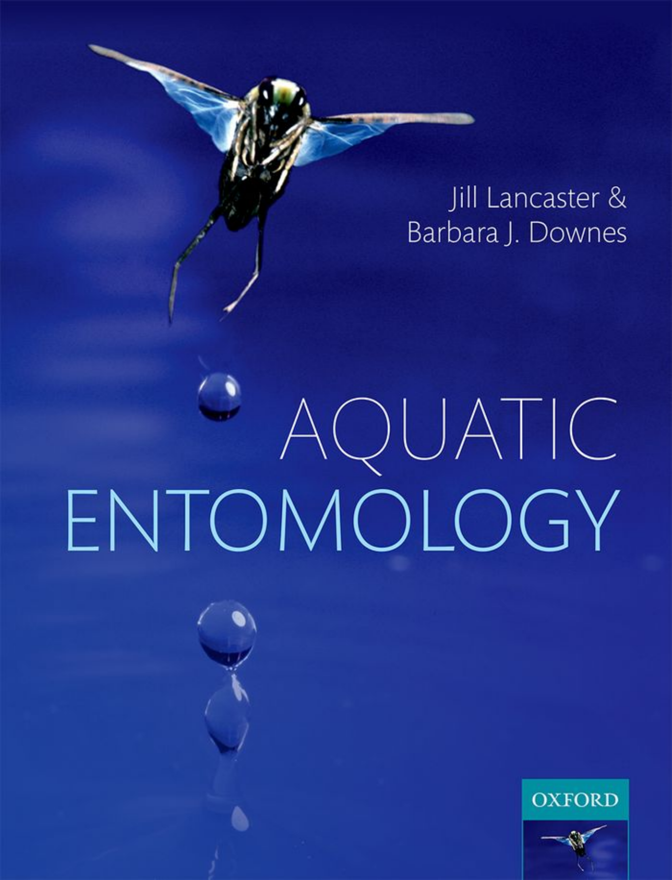

Jill Lancaster &
Barbara J. Downes

AQUATIC ENTOMOLOGY

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Jill Lancaster and Barbara J. Downes

The University of Melbourne, Australia

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Preface

After many years using freshwater ecosystems and aquatic insects as model systems to test ecological ideas, we have learnt—repeatedly—that understanding the basic biology of these fantastic animals is often pivotal to successful and insightful outcomes. Aquatic insect species are a minority of the total insect diversity, but they are no less fascinating and have long been the focus of attention for researchers, collectors, and amateurs alike. The persistent presence of aquatic insects in the Earth's fauna for over 300 million years, their numerical dominance in contemporary freshwaters (and some saline ones), and the diversity of roles they play in aquatic ecosystems speak for the importance of this group. In an academic context, aquatic insects have served as model systems for the development of understanding into many aspects of insect behaviour, biomechanics, developmental biology, ecology, epidemiology, evolution, physiology, etc., so there are many aficionados of this group.

While aquatic insects figure in diverse fields of basic research, they also feature strongly in applied research aimed at understanding and quantifying human impacts on freshwater environments. As a result of the latter, aquatic insects are widely used in monitoring programs or assessment tools that aim to detect human impacts or assess the condition of water bodies. In our opinion, a surprisingly high proportion of research on aquatic insects, both basic and applied, and commensurate, freshwater monitoring programmes and assessment tools reflect little direct knowledge of the structure and function of insects. We find this both understandable and worrying. It is understandable for two main reasons. First, there are numerous, often excellent texts on entomology (general entomology and its various sub-disciplines) and also on freshwater ecology, but aquatic insects often get short shrift from both. Surprisingly few texts focus strongly on aquatic entomology or bring together a broad range of information on the biology of aquatic insects, how they function in water (which is markedly different from air), and how they mange to cross the aquatic–terrestrial boundary twice during their complex life cycle. There is a wealth of information on aquatic insects, but it is scattered across the scientific literature and has not, before now, been gathered together; hence it has not been easy to access. Second, some, perhaps many, of the new cohorts of freshwater researchers or those entering management agencies receive little formal training in zoology (many have followed degree programmes in engineering, hydrology, environmental science, or physical geography), and teaching entomology is largely out of fashion in tertiary-level education, with a few notable exceptions (mainly in the USA). Hence, these new generations have typically not been exposed to entomology in all its wonderful facets.

Nevertheless, the lack of entomological knowledge among many freshwater researchers and prospective managers is worrying, because, without a sound understanding of the organism, there is always a risk of misguided programmes of research and monitoring, erroneous interpretations of ecological data, and missed insights or opportunities to push the scientific frontiers. It is also worrying because the parlous status of freshwaters around the world means that the managers and researchers charged with their well-being will be best able to protect these systems only if they are well acquainted with the basic biology of aquatic insects.

Thus, our aim was to fill that conspicuous gap in the literature and produce a book that will inform, support, and strengthen the work of a diverse body of researchers and managers of freshwater systems. This book is not about the ecology of aquatic insects, but instead focuses on the basic biology of aquatic insects that underpins so much that is important to ecological research and water resources management. Nevertheless, much of this material will also be of interest to entomologists more widely and very many others. The scope of the material is very broad and draws upon research in a huge range of disciplines, but only touches the surface of some very extensive research areas. It is not intended to replace any general entomology texts, but may be a valuable companion to other texts on entomology, freshwater ecology, biomechanics, ecohydrology, water resources management, etc., depending on readers' interests. As such, this book will be a useful reference text for tertiary subjects in the aforementioned disciplinary areas, at both later-year undergraduate and postgraduate levels. It should also be a very useful text for those researching freshwater ecosystems, including research higher-degree students. Nevertheless, we have tried to include explanations of the basic terminology of entomology throughout in a way that will be accessible to anyone with a strong interest in insects, including non-academics.

This book would not have come into existence if not for the support of others. Jill is deeply indebted to the Leverhulme Trust (UK) for a Leverhulme Trust Research Fellowship which provided relief from teaching during the initial planning and writing stages. Without that support, this project would not have even started. At Oxford University Press, Ian Sherman was courageous enough to take on this project and patient as we slipped ever further behind schedule; Helen Eaton and Lucy Nash provided gentle prodding, encouragement, and technical information about the publishing world. We thank the Australian Society for Limnology for generously funding the index. Many other colleagues helped in diverse ways, including reading and commenting on chapters, suggesting references, providing original images, or supplying specimens and photographs that became figures. We are grateful to them all for their comments, insights, and generosity: Amanda Arnold, Gerald Baker, Leon Barmuta, Andrew Brooks, John Bush, Gerry Closs, Peter Cranston, Petra Ditsche-Kuru, David Dudgeon, David Hu, P.S. (Sam) Lake, Richard Marchant, Barbara Peckarsky, Stephen Rice, Belinda Robson, Andrew Sheldon, Ian Stocks, and Handoko Wahjudi. Any errors are our own.

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Melbourne
March 2013

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PART 1

Introduction to Aquatic Insects

The first part of this book introduces the aquatic insects, some basic aspects of their biology, morphology, and evolutionary history, and discusses where these insects may be found in nature. All of this information may be considered a basic starting point to any entomological investigation. The first step in learning any discipline is to become familiar with its jargon, and entomology has numerous unique terms. Many of these words are used to describe body parts and a basic familiarity with these words is essential to comprehend later chapters. Additionally, the names of orders and some of the common families are also essential. Not only are these words used repeatedly throughout the book, familiarity with the types of insects found in different orders is necessary to appreciate some of the more detailed aspects of their biology.

We start in Chapter 1 with key characteristics that are common to all insects, starting with the main types of life cycles. Different life cycles entail different developmental stages, and which life cycle predominates varies among orders. We follow this with a description of the basic body plan and parts of insects and then, having armed the reader with some terminology and this basic information, we describe the main features of insects in the fully and partially aquatic orders. Readers with a good grasp of entomology and its associated terminology may confidently skip Chapter 1, but may still find useful material in Chapter 2. Chapter 2 briefly explores the evolutionary history of insects and tackles questions such as, when did insects become aquatic? And what kinds of aquatic insects appeared first? The places and times in which animals evolved are important information for many types of research, but particularly investigations into the distributional ranges of species (i.e. biogeography). This is because the explanations for where some species, genera, or families are found (around the world or regionally) lie in events that happened in the past. If a taxon evolved before major episodes of continental drift or under a different climatic regime compared to now, then these historical effects can be reflected strongly in its modern distribution. If we are unaware of such historical events, there is a risk of assuming, incorrectly, that distributions are caused by proximate (i.e. modern) environmental gradients. There is another important aspect to understanding what drives distribution patterns. Aquatic insects may be found in an enormous array of different environments from rain puddles to lakes and ponds, rivers and streams, estuaries and beaches, and even the open ocean. Each of these types of environments offers diverse living places, but these entail quite specific adaptations for successful habitation. Thus, knowing the global or regional range of species is merely the starting point to understanding where they may be found. Accordingly, Chapter 2 describes some of the extraordinary range of aquatic environments and some of their characteristic insect denizens.

While appearing esoteric, issues of these sorts are critically important to investigations into the impacts of human beings and other applied research questions. Currently, there is much interest in developing models that will predict whether distributional ranges will expand or shrink under climate change, with excessive water extraction from rivers, and so forth. Without a good grasp of how history has shaped modern day distributions and how insects are distributed within habitats, often over relatively small spatial scales, such models are likely to produce misleading predictions. This is why the basic information presented in Chapters 1 and 2 is a critically important starting point.

CHAPTER 1

Insect body structure and the aquatic insect orders

1.1 Introduction

From a systematic perspective, the class Insecta lies within the phylum Arthropoda, which is a very large group of invertebrates that all have an exoskeleton and jointed limbs. The name is derived literally from the ancient Greek words *arthro*, meaning 'joints', and *pod*, meaning 'foot'. The name Insecta is derived from the Latin *insectum*, meaning 'cut into sections', but *insectum* is probably a rendering of the ancient Greek *entomos*, which also means 'cut into sections'. Along with the insects, the arthropods include spiders, mites, crustaceans (e.g. crabs, lobsters, shrimp, etc.), centipedes, millipedes, and many others, but only the insects have six legs as adults. Nevertheless, statistically speaking, most animals are insects, i.e. more than half the animals alive at any one time are insects. In addition to being numerous, insects are extremely diverse with very many extant species. Approximately 1.5 million species of insect have been described and current estimates suggest that there may be as many as 4 million species in total. While aquatic insects make up a minority of the total, the number described is still in the order of 10^5–10^6 species, but, as will become clear, many insects are semi-aquatic to varying degrees so precise estimates of exact numbers are difficult.

Importantly, the aquatic insects do not form a distinct taxonomic group within the class Insecta. Some orders contain only species that are aquatic in some life stage (e.g. mayflies, stoneflies, dragonflies), but other orders contain both aquatic and terrestrial species (e.g. beetles, bugs). Insects evolved on land and multiple orders secondarily invaded aquatic environments (Section 2.4) and, therefore, aquatic insects are essentially terrestrial insects that have found a way to live underwater. Consequently, aquatic insects are enormously variable in morphology, development, physiology, and ecology. Accordingly, most generalizations we can make about their diets, habitats, behaviour, and so forth are weak at the coarse taxonomic level of order. While a good starting point for the novice, almost all such generalizations have many exceptions. As will become clear in later chapters, the diversity of ways in which insects have evolved an aquatic existence at some point in their life cycles is truly enormous.

Nonetheless, morphology and life cycles have features that are common to all insects. All insects follow the same basic body plan and some understanding of the basic body structure is essential to any treatise on aquatic insects. Entomology is rife with subject-specific terminology to describe different body parts and, although this can be frustrating, this vocabulary is necessary. This chapter provides a brief description of the types of life cycles of insects (Section 1.2) and then explains the external morphology of insects (Section 1.3), followed by descriptions of the insect orders that contain species that are wholly or partially aquatic (Section 1.4). The form and function of many body parts will be discussed in detail in subsequent chapters. Additionally, much more detailed descriptions and beautiful illustrations of the various taxa are available in general entomology texts and texts devoted to particular orders or identification guides. Readers wishing for more information are advised to consult such sources, while readers familiar with this material may wish to skip ahead to Chapter 2.

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1.2 Insect life cycle

There are three main patterns of development within the insects: ametaboly, hemimetaboly, and holometaboly; the latter two are also referred to as incomplete and complete metamorphosis, respectively. During their postembryonic growth (i.e. once hatched from the egg), insects pass through a series of juvenile instars (stages of growth) until they become adults. Each instar is terminated by a moult. Ametabolous insects are wingless (the Apterygota) and comprise some of the oldest insects. Uniquely, they moult as adults, but none are aquatic and will not be discussed further. In the hemimetabolous insects (the Exopterygota), juvenile instars resemble one another and the later instars broadly resemble the adult, except that adults have wings and genitalia. The life cycle of most hemimetabolous insects has three stages (egg, juvenile, and adult), whereas most holometabolous insects (the Endopterygota) have four stages (egg, juvenile, pupa, adult). Juveniles and adults of holometabolous insects are very different from one another in morphology and habit. They undergo striking changes (complete metamorphosis), spread over two moults, in the formation of the adult. The final juvenile instar, the pupa, has become specialized to facilitate these changes. Other than the pupa, this book will refer to all juvenile stages as 'larvae'; other authors refer to only the juveniles of the holometabolous insects as larvae and use the term 'nymph' to refer to juveniles of the Hemimetabola. Arguments can be made to support both schemes and some researchers hold strong views on the subject, but we will use the simplest scheme. For virtually all aquatic insects, the transition from juvenile to adult involves a transition from aquatic to terrestrial habits, i.e. they have complex life cycles. Where both juveniles and adults are aquatic (e.g. some Coleoptera and Hemiptera), adults typically retain the terrestrial habit of breathing air rather than obtaining oxygen dissolved in water.

1.3 Insect body plan

Insects have segmented bodies, like other members of the Arthropoda, and have an exoskeleton made of cuticle. The outer layer of cuticle is hardened (tanned) to various degrees and forms the exocuticle. These hardened regions (sclerites) may be fused to form apparently solid structures, such as the head capsule, or may be separated by joints or flexible regions where the exocuticle layer is missing and the cuticle remains membranous. In the majority of insects, and especially the adults, the cuticle is heavily sclerotized and forms a series of dorsal and ventral plates along the body: the terga and sterna. In many larvae, however, virtually the entire cuticle is thin and flexible, although clearly segmented. The segments of the insect body are differentiated into three main parts: the head, thorax, and abdomen. Segmentation is clear in the thorax and abdomen, but has virtually disappeared in the head.

1.3.1 Head

At the anterior end of the body, the head is typically a heavily sclerotized capsule, bearing mouthparts and some major sense organs (Figure 1.1). Thus, the head and associated organs are central to the insect's ability to acquire food resources and to collect information about the environment, which subsequently may influence myriad behaviours. The head capsule is formed from several plates or sclerites (e.g. gena, frons, clypeus) that meet at suture lines. Both adults and larvae have distinct head capsules, although in some larval Diptera the head capsule may be incomplete or reduced (e.g. Tabanidae) or withdrawn into the thoracic segments (e.g. some Tipulidae).

The most noticeable sense organs are usually a pair of compound eyes, comprising hundreds to thousands of individual facets or ommatidia, and a pair of antennae. Between the compound eyes, there may be up to three ocelli (Figure 1.1), each on a separate sclerite. Ocelli are often referred to as simple eyes, but their sensory function can be far from simple (Taylor and Krapp 2008). Larvae of the holometabolous orders lack compound eyes and ocelli, but have eyes called stemmata. These are often called 'lateral ocelli', but stemmata are morphologically and functionally different from true ocelli (Gilbert 1994). The antennae are highly variable among taxa and life stages (Schneider 1964) but they are typically segmented, with two differentiated basal segments (the scape and pedicel) and a distal, often whip-like flagellum composed of many similarly shaped elements. The scape is set in a membranous

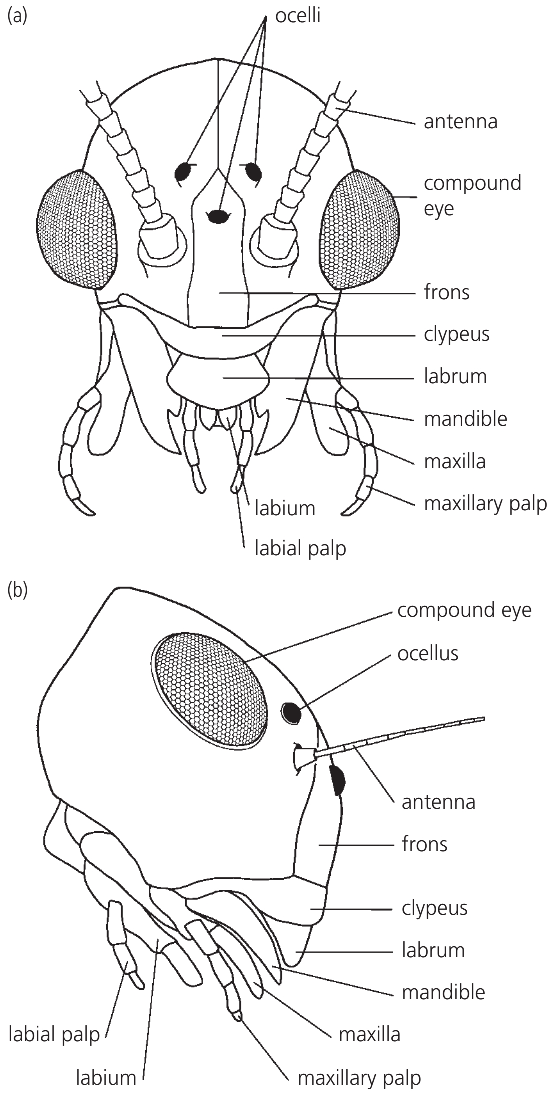

Figure 1.1 Structure of the head. Hypothetical insects viewed from (a) the front, and (b) the side.

socket and, in the majority of insects, movement of the whole antenna is effected by muscles inserted on the scape and attached to the head capsule.

The mouthparts and their various structures function, collectively, to acquire food, to reduce large food items into smaller bite-sized pieces (in some groups), and to move food into the mouth, which is the start of the alimentary canal. In the plesiomorphic condition (also called the primitive or ancestral form), the head is oriented so that the mouthparts lie ventrally and

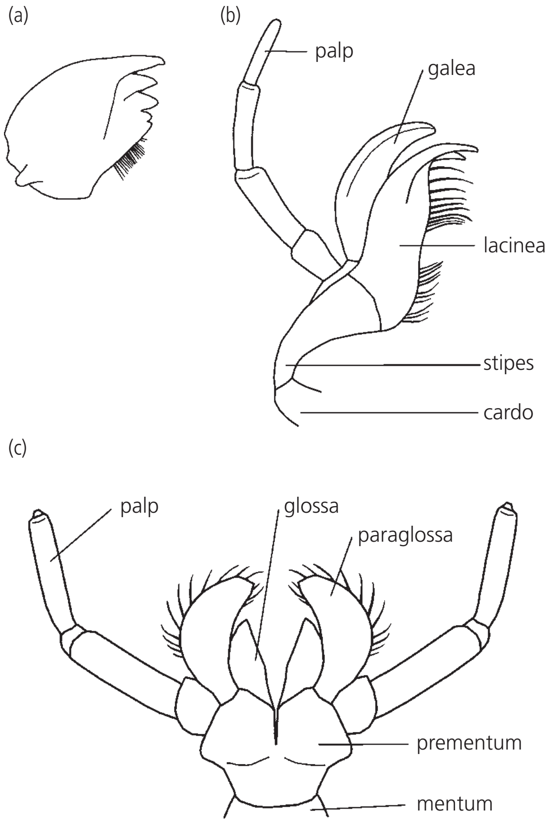

Figure 1.2 Structure of the mouthparts, as illustrated by a larval stonefly, *Cosmioperla* (Eustheniidae). (a) Mandible, (b) maxilla, and (c) labium.

the mouthparts are for chewing. Typical chewing mouthparts, with only minor modifications, occur in many larval Ephemeroptera and Trichoptera, and the adult Odonata. The primary mouthparts consist of a labrum, a pair of mandibles, a pair of maxillae, and a labium, with the mouth situated at the base of the labium. In a typical chewing insect, the labrum (Figure 1.1) is a broadly flattened plate with a membranous ventral (inner) surface, which bears chemosensilla. The mandibles (Figure 1.2) are heavily sclerotized and vary in shape according to the insect's diet: in herbivorous forms there are cutting edges and grinding surfaces; in carnivorous forms the mandible may possess sharply pointed 'teeth' for seizing prey, cutting, and tearing. The maxillae each bear a segmented maxillary palp attached to the main stipe (Figure 1.2), although this palp may be reduced or lost in some species. The labium bears a pair of segmented labial palps (Figure 1.2), arranged laterally to a pair of glossae and paraglossae. The glossae and paraglossae may be fused together to form a single ligula, as in many larval Chironomidae. There are, or course, many variations on this general scheme and the mouthparts of some groups have become highly modified and specialized for particular feeding habits (Chapter 13).

1.3.2 Thorax

The thorax is the centre for insect locomotion. In the adult, each of the three thoracic segments (pro-, meso-, and metathorax) typically bears a pair of legs, and the meso- and metathorax each have a pair of wings. All larvae lack wings, although developing wings may be visible in the wing buds of hemimetabolous orders, and many larvae have a distinct three-segmented thorax with three pairs of true legs. In some holometabolous groups, especially the Diptera, larvae lack a distinct thorax and true legs, although prolegs may be present (e.g. larval Simuliidae and Chironomidae). In cross-section, the thorax of adults is essentially a box frame made of terga, sterna, and, in some, sclerites that lie between the terga and sterna (Figure 1.3). The wings are attached to the wing processes and each leg is inserted in a coxal cavity. The thoracic sclerites have internal cuticular ridges that are attachment points for flight and walking muscles. The box-like frame of these segments is not completely rigid as wing movement is, in part, brought about by flexure of the terga, which is itself caused by muscle contraction and relaxation (Section 9.2). The thoracic segments of larvae that have true legs are analogous to the adult thorax, but much simpler and less box-like given the absence of wings.

The true legs are typically for walking, crawling, and running, but may be specialized for other functions, such as swimming or grasping prey. Each leg consists of six segments: the coxa, trochanter, femur, tibia, tarsus, and pretarsus (Figure 1.4). A narrow, annulated, and flexible membrane (the corium) lies between adjacent segments and facilitates articulation. Except for the trochanter, which is fused to the femur, articulation usually occurs between all the segments. The femur is generally the largest leg segment. The tarsus is usually subdivided into between

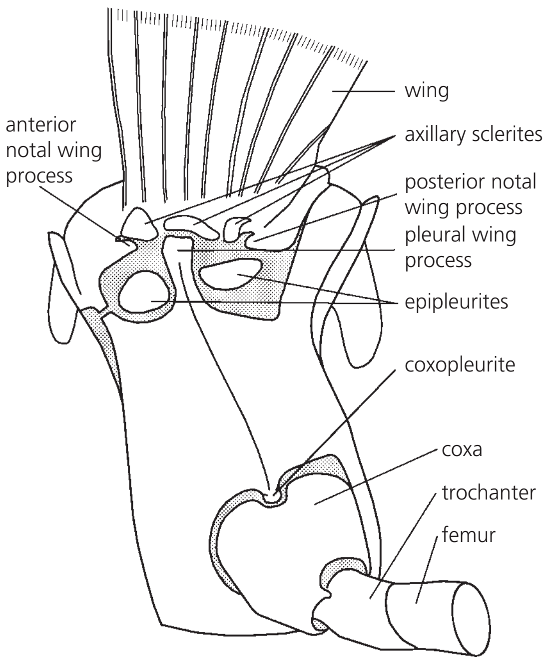

Figure 1.3 Structure of a thoracic wing-bearing segment of a hypothetical adult (lateral view). The pleural wing process acts as a fulcrum for wing movement. The anterior and posterior notal wing processes give support to small axillary sclerites on the wing base. The epipleurites are small plates for insertion of muscles attached to the wing sclerites, leg segments, and other parts of the thorax. The coxopleurite is an articulation point between the thorax and coxa.

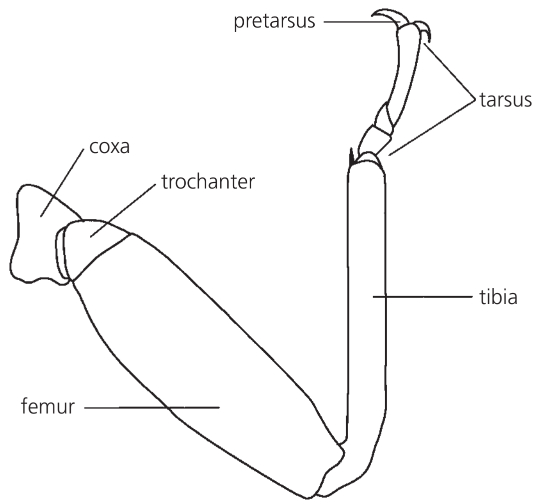

Figure 1.4 Structure of a typical walking leg, as illustrated by the third leg of a larval stonefly, *Eusthenia venosa* (Eustheniidae).

two and five tarsomeres; the pretarsus usually takes the form of a paired tarsal claw in adults and a single or paired claw in larvae. Between the tarsal claws of adult insects may be a medial lobe (arolium) which, along with other foot pads (empodium and pulvilli), play various roles in allowing insects to adhere to surfaces (Figure 1.5); this is how flies walk on the ceiling (Beutel and Gorb 2001; Gorb 2008). The thoracic prolegs (sometimes called parapods) found in some larvae (e.g. many Diptera) are not true legs; they are unsegmented, fleshy, and often bear claws or hooks.

The majority of adult, winged insects have one or two pairs of functional wings. Reduced wings or the complete absence of wings (Section 9.6) is a secondary condition. The wing is a flattened evagination of the body wall and is composed of integument. The dorsal and ventral integument layers become closely apposed and form the wing membrane. Channels through the wings, the veins, are strengthened by the surrounding cuticle and may contain nerves and trachea (tubes through which gas exchange occurs). The spaces between veins are called cells. The arrangement of veins varies markedly among the insect orders and is an important taxonomic feature (Figure 1.6). The typical wing condition may be modified in many different ways (Wootton 1992), but generally these fall into two broad categories: those that lead to improved flight (directly or indirectly), and those in which the wing takes on an entirely unrelated function. Aerodynamically, a two-winged condition is usually more efficient than four wings and wing-coupling mechanisms that link together the fore and hind wing have evolved in several insect orders (e.g. Trichoptera, Lepidoptera). The two-winged condition has been achieved in other orders through the loss, functionally, of the forewings (Coleoptera) or the hind wings (e.g. Diptera, some Ephemeroptera). In these insects, the wings are no longer used directly in flight, but are still present and may be modified for other functions. For example, the heavily sclerotized forewings (elytra) of Coleoptera are mainly protective in function; the modified hind wings (halteres) of Diptera are highly specialized inertial sensing systems that function according to the same principle as a vibratory gyroscope and are used in flight stabilization (Taylor and Krapp 2008) (see Chapter 9 for further discussion of flight).

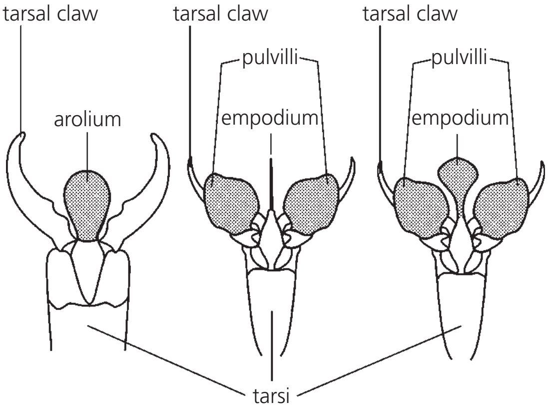

Figure 1.5 Some examples of the insect 'foot' (ventral views). Stippling indicates areas that are used for attachment.

Source: From Beutel and Gorb (2001). Reproduced with permission from John Wiley & Sons.

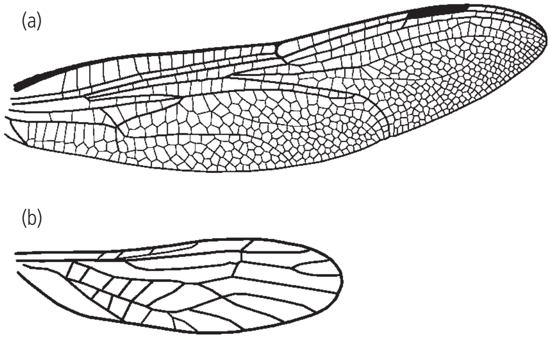

Figure 1.6 Forewings of (a) a dragonfly, *Hemianax papuensis* (Aeshnidae), that has many small cells, and (b) a stonefly, *Isoperla grammatica* (Perlodidae) that has a comparatively simple wing with few large cells. Note: images are not to scale.

1.3.3 Abdomen

The segments of the abdomen generally have a rather simple structure; they are usually distinct from one another and most lack appendages, at least in the adult stage. The plesiomorphic number of abdominal segments appears to be 12, but most insects have 10 or 11 segments, several of which may be reduced (mainly at the posterior end). Perhaps the chief differences between adults and larvae in the structure of the abdomen relates to the reproductive structures. Indeed, it is generally impossible to sex larvae as they lack reproductive structures.

The external genitalia of adult insects are extremely diverse in morphology and, because of their specific form, external genitalia are widely used for taxonomic purposes. The genital opening (gonopore) is generally on or at the posterior edge of the eighth or ninth sternum in the female, and the ninth sternum in the male. The genital segments (eighth and ninth) are modified in various ways to ensure that only males and females of the same species are able to connect during sperm transfer (i.e. reproductive isolation) and for oviposition. In many orders, the terga and sterna of the genital segments remain distinct plates, and appendages on the genital segments are modified in various ways (Figure 1.7). Females of most orders have an ovipositor for egg laying; exceptions include the Ephemeroptera, most Plecoptera and Trichoptera, which release eggs directly from the gonopore. There are two kinds of ovipositor: a true or appendicular ovipositor formed from the appendages of abdominal segments 8 and 9, and a substitutional ovipositor comprising the posterior abdominal segments, which are telescoped or retracted within the more anterior segments of the abdomen (Figures 11.1, 11.2). When extended, the segments of a substitutional ovipositor form a long, narrow tube that facilitates egg-laying in inaccessible places, and sometimes the abdomen tip is sclerotized for piercing tissues (e.g. plants).

A range of other abdominal appendages can be found in both the larvae and adults of many aquatic insects. Paired cerci, appendages of the eleventh segment, are typically elongate, multi-segmented structures that often function as sense organs. A median terminal filament, which arises from the last abdominal segment, may also be present and have a tail-like appearance. External abdominal gills, often segmentally arranged along the abdomen, are conspicuous in the aquatic larvae of many orders, and remnant gills may be visible on some adults

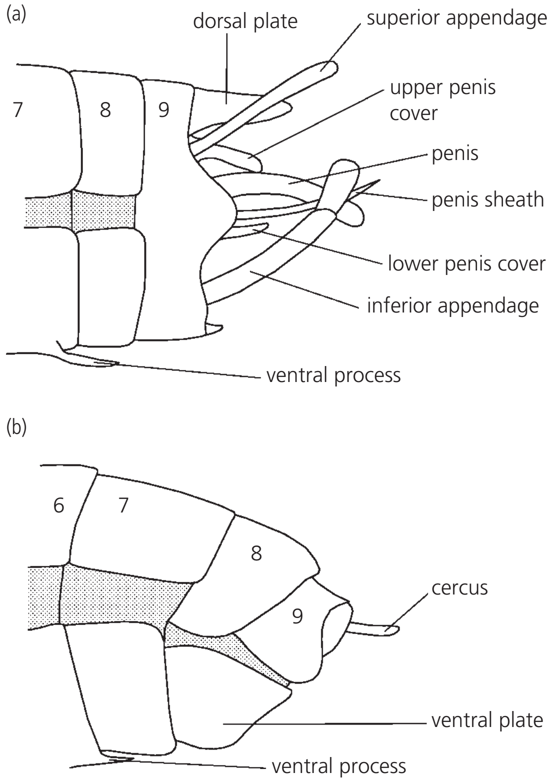

Figure 1.7 Lateral views of the abdomen and external genitalia of a hypothetical (a) male and (b) female caddisfly. Abdominal segments are numbered. The female lacks a true ovipositor.

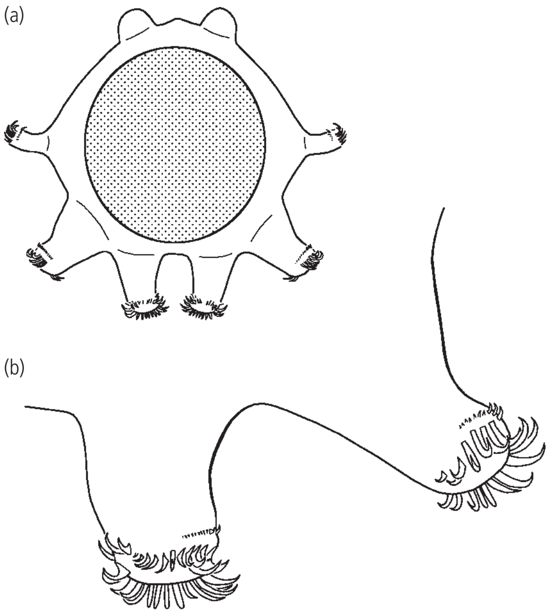

Figure 1.8 An example of abdominal prolegs. (a) Cross-section through the third abdominal segment of a tabanid larva, *Tabanus kingii*, which lives under stones in swiftly flowing streams and has a pair of ventral prolegs, plus sub-ventral and dorsal swellings analogous to prolegs. (b) An enlarged view of one ventral and one sub-ventral proleg with crotchets.

Source: Adapted from Hinton (1955). Reproduced with permission from John Wiley & Sons.

(e.g. some Plecoptera). The last abdominal segment may also bear papillae, spiracles, lobes, and hairs that function in gas exchange. Prolegs are also present on the abdominal segments of the larvae of holometabolous taxa (e.g. Lepidoptera and some Diptera such as Chironomidae, Tabanidae, Empididae), and their structure varies among taxa (Figure 1.8). They are leg-like, fleshy outgrowths of the body wall, not true legs, and they lack sclerotized segments. Used for locomotion, prolegs are usually in pairs, on the ventral surface of the abdomen, and have various crotchets, hooks, or friction pads on the tip to grasp the substrate. Unusually, a few taxa also have extra prolegs arranged dorsally or laterally, as in Figure 1.8.

1.4 Aquatic insect orders

The aquatic insects are usually split into the fully and the partially aquatic orders. Virtually all taxa within the fully aquatic orders have juvenile stages that are aquatic and adult stages that are terrestrial (Ephemeroptera, Odonata, Plecoptera, Trichoptera, Megaloptera). In the other orders, those species that are aquatic often have aquatic juveniles and some also have aquatic adults, yet the adults of many other species are largely terrestrial (Hemiptera, Lepidoptera, Diptera, Neuroptera, Coleoptera). Inevitably, there are exceptions to this scheme and some orders (e.g. Orthoptera, Hymenoptera, Mecoptera) have only a very few species that are aquatic and we will call these rarely aquatic orders. The names of most of these orders end with the suffix '-ptera', which is derived from the ancient Greek word *pteron*, meaning 'wing'.

The text that now follows is a brief introduction to the aquatic orders, with a description of the distinctive external morphology of adults and larvae, and some comments about their biology. This is not intended to be an identification guide, an exhaustive review of the literature, or a summary of everything known about the order. The reader is referred to specialist texts for each group and to alternative identification guides that often include biological information organized in a taxonomic manner.

1.4.1 Ephemeroptera—mayflies

The Ephemeroptera are hemimetabolous insects and their name is derived from the ancient Greek word *ephemeros*, meaning 'lasting for a day', and refers to the brief life of the adult. Some adults may live as long as a few days, but many live for only a few hours and adult life can be as short as 37 minutes (Taylor and Kennedy 2006). Over 3000 species of mayfly from 42 families and over 40 genera have been identified and are extant (Barber-James et al. 2008).

The adults (also called imagos) have antennae that are small (aristate) and the compound eyes are usually sexually dimorphic, with males having larger eyes than females. Adults have vestigial mouthparts and do not feed. Although they still have a gut, it serves no alimentary function (Section 14.3). The prothorax is small, the meso- and metathorax are fused and large. Two pairs of wings are present, the hind pair is always greatly reduced in size and is absent in some species. At rest, the wings are usually held vertically above the body. Wings are usually transparent, the forewings are triangular and the wing surface has a regular series of corrugations, with longitudinal veins lying on either a ridge or a furrow. Recently, brachypterous (short-winged) and flightless mayflies have been identified in the Madagascan genus *Cheirogenesia* (Ruffieux et al. 1998). For most species, much of the adult life is spent on the wing and the legs are sometimes reduced. The forelegs of most mayflies are sexually dimorphic; those of the male have very long tibiae and tarsi and are used to clasp the female during mating. At the posterior end of the adult abdomen are two or three caudal filaments: two cerci plus, in some species, a vestigial or well-developed median terminal filament. Males tend to have longer caudal filaments than females. Uniquely, male mayflies have two penes, females have two gonopores and no ovipositor.

Unique among insects, the mayflies have two, winged stages. The first stage, the subimago, emerges from the final larval stage and usually moults to the second imago stage within 24 hours. The subimago is usually duller in colour than the imago, as is most evident in the wings, which appear dull or translucent in the subimago compared to the clear wings of the imago. The subimago usually has a fringe of hairs on the posterior margin that is absent in the imago. Although subimagos are winged and superficially resemble adults much more than larvae, they are generally sexually immature. The transition from subimago to imago often involves reduction or loss of larval features (e.g. mouthparts) and maturation or expansion of adult features, such as the genitalia and male forelegs (Edmunds Jr and McCafferty 1988; Harker 1999). See Section 12.4 for further discussion.

The body forms of mayfly larvae are diverse, although similarities are apparent for species that occur in particular habitats, e.g. running versus still water, versus burrowing habits. The compound eyes, ocelli, and short antennae are similar to the adults. Mouthparts are well developed and generally of a biting form. As in the adult, the meso- and metathorax are fused, and the dorsal surface is heavily sclerotized. The legs of most species terminate in a single tarsal claw, but in *Camelobaetidius* spp. (Baetidae) the tip of the tarsal claw is divided into 17–24 denticles, which give the claw a rake-like appearance (Salles et al. 2003 (2005)). The abdomen terminates with a pair of long cerci and usually a long median caudal filament, giving the appearance of three tails. Along the abdomen are between four and seven pairs of tracheal gills. Gill shape varies with larval habit: typically, lamellate or plate-like gills in open water species, plumose in burrowing species. Gills are important for gas exchange, although gas exchange can occur over diverse body surfaces (Chapter 3).

The adults of many mayflies are renowned for aggregating in huge mating swarms, often near water. This behaviour may be advantageous in ensuring that mates are found, especially given that adults are short-lived, or that wound-be predators are satiated before a significant proportion of the population is lost (Sweeney and Vannote 1982). A few species display obligate or facultative parthenogenesis, and the potential for parthenogenetic reproduction may be present in many mayfly species (Funk et al. 2010). The aquatic larval stage is the dominant life-history stage, with larval stages generally in the order of weeks to months, but development times may be as long as three years. Larvae moult many times (ranges of 10 to 50 moults have been reported, Ruffieux et al. 1996), the number of moults varies between species and may vary within species depending on environmental factors. The range of larval habitats is extremely wide, in running and standing waters, and varies among species. Most larvae are herbivorous or detritivorous, although a few are carnivorous (Müller-Liebenau 1978; Gattolliat and Sartori 2000).

1.4.2 Odonata—dragonflies and damselflies

The name Odonata is derived from the ancient Greek word *odous*, meaning 'tooth', and refers to the serrated mandibles. They are hemimetabolous insects with terrestrial adults and aquatic larvae; both adults and larvae are carnivorous. Approximately 5680 extant species of Odonata from 32 families have been identified (Kalkman et al. 2008). The extant Odonata are divided into two suborders: the heavy-set Anisoptera or dragonflies and the more slender Zygoptera or damselflies. The odonates are generally considered to be tropical species and, although many species do occur at high latitudes and altitudes, the highest species richness occurs at low latitudes.

Adult Odonata are remarkable for their colours on the body and the wings, arising from reflections in thin layers of cuticle and from pigment in the cells. Males are often more brightly coloured than females. The head is freely articulated with the thorax and much of the head is occupied by well-developed compound eyes; together, these characteristics facilitate incredible visual capability in many directions. The antennae are short (aristate) and, apparently, carry few sense organs. The biting and chewing mouthparts are powerful, as is often characteristic of carnivorous taxa. The prothorax is small, whereas the meso- and metathorax are large and fused together into a pterothorax. The legs are ventral (the legs of many adult insects project laterally; Section 8.2), weak, and generally unsuitable for walking, but are armed with various spines and hairs that serve to grasp prey. The Odonata are high-performance fliers (Marden 2008), with extensive flight muscles in the pterothorax (50–60 per cent of total body mass in some males, Marden 2008). Fore- and hind wings are identical in damselflies; hind wings are somewhat broader than the forewings in dragonflies. A prominent pterostigma (a pigmented patch) is often present near the tip of each wing. Other wing features such as the nodus (Section 9.4.1) are also characteristic of odonates. Perhaps the most remarkable characteristics of odonates are the suite of modified copulatory structures they possess (especially in males) and their complex reproductive behaviours (Section 10.6.1).

The heads of odonate larvae broadly resemble those of the adults and have prominent compound eyes. Their mouthparts are unique and prey are captured using a 'mask', which is an elongated labium with a pair of hinged, hook-like labial palps, and various setae, spines, and teeth for skewering prey (Chapter 13). At rest, the mask is folded and held between the legs, but it can be extended very rapidly. In contrast to the adults, the larval thoracic segments are roughly equal in size, the legs are well-developed and project laterally. The abdomen is tipped with five abdominal appendages (including two small cerci) that are small in Anisoptera, but three (the epiproct and two paraprocts) are enlarged to form caudal lamellae in Zygoptera. These caudal lamellae serve a range of functions including gas exchange, sensory reception, and may act as tail fins during swimming (Section 8.3.2). In contrast, the Anisoptera have rectal gills and water is continually pumped in and out of the rectum (Komnick 1982).

Adult odonates typically hunt in flight. Dragonflies tend to catch prey that are also on the wing, whereas damselflies tend to catch prey that are resting. After emergence, immature or 'teneral' adults typically spend some time away from water until they become sexually mature. During this maturation period, which lasts from a few days to weeks, some Odonata migrate or travel over long distances (Chapter 9). Odonates may spend a long time attached to one another during reproduction and are often very conspicuous flying around in pairs (Chapter 10). Larvae are facultative predators and will feed on almost all appropriately sized prey (i.e. larvae are typically gape-limited). Larvae adopt primarily an ambush foraging strategy, remaining immobile until prey come within range of the mask, and prey are detected using vision and tactile stimuli (Rebora et al. 2004). Many forms burrow in the substrate or hide among detritus; others escape detection by predators through camouflage. There are normally 10–15 instars, but the duration of larval development is highly variable and can range from one or two months to several years.

1.4.3 Plecoptera—stoneflies

The Plecoptera are hemimetabolous and their name is derived from the ancient Greek words, *plektos*, meaning 'braided', and *pteron*, and refers to the prominent venation of the wings. Approximately 3500 species of Plecoptera from 16 families have been identified worldwide and are extant (Fochetti and Tierno de Figueroa 2008). The stoneflies are often considered to be cold-water species, with few species occurring at low latitudes, but there are many tropical species nevertheless, especially in the family Perlidae.

The adult stonefly body is generally dorso-ventrally flattened. The head is large and bears a pair of elongate antennae, well-developed compound eyes, and three ocelli. Mouthparts are generally for biting, but are weak, and the mandibles are vestigial in a few families. The thorax has three distinct segments and the prothorax is large. Usually present are two pairs of membranous wings, folded flat over the abdomen when at rest. Brachypterous (shortened wings) and apterous (wingless) species also occur, with shortened wings in both sexes or only in the males, and some normally fully winged species tend to become short-winged at high altitudes and latitudes (Section 9.6.1). Gills that are found in larval stages may persist in adult stages, but tend to shrivel and may leave scars. The genitalia of both sexes are diverse in form and unlike those of most other insects. The males of some northern-hemisphere families have a small lobe at the front of the subgenital plate that is used to drum during courtship (Section 10.5).

Stonefly larvae closely resemble the adults, except for the absence of wings and, in most species, the presence of several pairs of gills. The head is large, dorso-ventrally flattened, with large, laterally placed compound eyes and ocelli are often present also. The mouthparts are generally robust. Legs are always well-developed and the three-segmented tarsus ends in two claws. Developing wing-pads on the meso- and metathorax may differ noticeably between the sexes in species with brachypterous males. In the plesiomorphic condition, there are five or six pairs of abdominal gills, but in many groups these are reduced in number and secondary respiratory structures may appear anteriorly (on the submentum, neck, thorax, coxae) or may encircle the anus. The abdomen terminates in a pair of long, multi-segmented cerci that have sensory functions.

Most stoneflies have aquatic larvae and terrestrial adults, although adults of a few species are not fully terrestrial and some larvae may have terrestrial habits. For example, *Capnia lacustra* (Capniidae) is a wingless stonefly whose adults and larvae are both found at depth in Lake Tahoe, USA (Jewett 1963). Similarly, two species of *Baikaloperla* (Capniidae), endemic to Lake Baikal, Siberia, are also apterous and the adults appear to be entirely aquatic. In contrast, the larvae of a few species of Gripopterygidae in Patagonia and New Zealand have larvae that live terrestrially on cold, wet mountains far from water (Illies 1963). Indeed, there seems to be a tendency among larvae of New Zealand Gripopterygidae to leave the water (Winterbourn 1966; McLellan 1977), and several Australasian Notonemouridae also live terrestrially on wet surfaces (Hynes and Hynes 1975).

Adult stoneflies are typically weak fliers (or flightless) and this influences many aspects of their ecology as adults. Many stoneflies skim across water surfaces, often using fairly rudimentary wings and wing motions, or by using their wings as sails (Marden and Kramer 1994, 1995; Marden et al. 2000) (Section 8.5.2). At high latitudes and altitudes, adult emergence may begin when there is still snow on the ground and adults are commonly seen walking across the snow—the so-called winter stoneflies. Their dark bodies preferentially absorb solar radiation against the white snow, and this allows them to survive and be active on a cold surface (Section 4.2). Adult longevity varies among species and may last from a few days to a couple of weeks. Larval stoneflies occur in a wide range of running and standing waters, typically where temperatures are cool and dissolved oxygen concentrations are high. Development is slow, often taking more than a year, and there are many instars, with diapause common in larvae and eggs. Often the life history is timed so that larvae are not exposed to warm conditions, and diapausing eggs or larvae may be buried in the sediment during warm seasons.

1.4.4 Trichoptera—caddisflies

The name Trichoptera is derived from the ancient Greek words *tricho*, meaning 'hair', and *pteron*, and refers to the many hairs that are usually present on the wings. The Trichoptera are holometabolous, typically with terrestrial adults, aquatic larvae and pupae, and primarily aquatic eggs. Over 12,600 extant species of Trichoptera from 46 families have been identified (de Moor and Ivanov 2008), making it the most species-rich of the fully aquatic orders. Trichoptera are closely related to the order Lepidoptera (butterflies and moths) and the two groups are similar in many respects. A notable difference is that the wings of adult caddisflies are covered in hairs, whereas the wings of butterflies and moths are covered in scales.

Adult caddisflies are moth-like in appearance and often drab in colour. The antennae are long and the compound eyes usually small (but are very large in some males). The mouth parts are reduced, but the hypopharynx is well-developed and in some groups it is modified for sucking up liquids. The prothorax is small, but the meso- and metathorax are well developed. The legs are long, with spurs, setae, bristles, or spines (particularly on the tibia); the tarsi have five segments with ventral spines on each segment. Almost all adults have two pairs of membranous wings covered in hairs, although flight ability varies among taxa. Wing venation resembles some ancient Lepidoptera and, similar to moths, at rest the wings are often held like a peaked roof over the abdomen. Abdominal segment 5 may have a pair of slender filaments or raised ovoid processes that may be connected to pheromonal glands.

Larval caddisflies are perhaps best known for their ability to build cases, although many do not. Cases are built with silk and often incorporate objects from the surrounding environment (e.g. sand, twigs, pieces of leaves). All caddis are capable of producing silk and some larvae that do not build cases construct a non-portable silken web. Proteinaceous silk is produced in a pair of elongate salivary glands, which occupy much of the body cavity (Glasgow 1936; Engster 1976b). The silk is emitted as a double-stranded, single filament (Engster 1976a) from a single spinneret at the tip of the labium. The head is well sclerotized, bears a pair of very short antennae, two lateral clusters of stemmata, and the mouthparts are generally chewing. The thorax is variably sclerotized and the legs are well developed, with unsegmented tarsi and a single tarsal claw. The forelegs are often fairly short and used for holding food and for constructing cases or nets, rather than for walking. The first abdominal segment of some case-bearing families has three prominent, retractile papillae. These papillae may help the larva to maintain position in the centre of the case and allow water to flow efficiently over the abdominal surface and gills (Chapter 3). On the last abdominal segment only are two prolegs, which each have a single curved claw. The prolegs may be large, mobile, and used to anchor the larva to the substrate or net; or may be small and immobile, and function primarily to grip the case. Many species have gills, which are usually simple filamentous structures on the abdomen and occasionally on the thorax.

Adult caddis generally do not eat, but most are capable of sucking up nectar and liquids, and some may live for several weeks. Species that inhabit ephemeral systems typically emerge as adults as the water disappears, and adults of these species may be relatively long-lived. Adults of some species swarm prior to mating and, unusual among aquatic insects, many communicate via pheromones (Chapter 10). Larval development typically involves five instars and may be rapid; diapause usually occurs in the final larval or adult instar, and more rarely in the egg stage. The majority of species have aquatic larvae; only a few are semi-aquatic and they live in moist terrestrial places (e.g. the limnephilids, *Limnephilus centralis* and *Enoicyla pusilla,* of northern Europe). The larvae of most species are benthic and live on the bottom of water bodies or attached to submerged plants, etc., but some can swim with their cases (e.g. *Triaenodes*, Leptoceridae). Larval caddisflies are extremely diverse in their feeding habits and diet, and some are parasitic on other caddisflies (Wells 2005). Larvae of the family Hydropsychidae are notable for being able to produce sound underwater, a rare accomplishment among immature insects (Chapter 7).

1.4.5 Megaloptera—alderflies, dobsonflies, and fishflies

The Megaloptera is a relatively small order with only two families (Sialidae, Corydalidae) and 328 extant species have been identified (Cover and Resh 2008). The name is derived from the ancient Greek words *megas*, meaning 'big' or 'great', and *pteron*, and refers to the large, winged adult. The Sialidae are commonly known as alderflies, the Corydalidae as dobsonflies or fishflies. The Megaloptera are holometabolous with aquatic larvae, but the adults, eggs, and pupae are terrestrial.

As the prefix 'mega-' implies, adult Megaloptera are generally large-bodied insects. The Corydalidae are generally bigger than the Sialidae and wingspans of 16 cm have been recorded. At rest, the wings are held like a peaked roof over the abdomen. The head has well-developed compound eyes and long, slender antennae. Mouthparts are adapted for chewing, and the mandibles are particularly long in some male corydalids and sometimes called tusks, although their function is unknown. The legs are generally short, and the tarsi have five segments and end in two claws. The abdomen lacks cerci.

Larval corydalids, often called hellgrammites, are among the largest of the larval Megaloptera (some reach 8 cm in length). The megalopteran head is well sclerotized, with chewing mouthparts and large mandibles. The prothorax is heavily sclerotized, but the meso- and metathorax less so. The legs terminate in two claws of unequal size. The abdomen bears seven or eight pairs of abdominal filaments, or gills. Larval fishflies have a pair of dorsal respiratory tubes on abdominal segment 8 that can be used for air breathing. The abdomen of sialids ends in a single, long filament, whereas the corydalids have a pair of anal prolegs.

The adult megalopterans are poor fliers, relatively short-lived (approximately one week) and most do not feed, or feed on nectar and other sugar solutions. Larvae are ambush predators and consume a wide range of aquatic invertebrates. Most species pass through 10–12 larval instars and development in large species may take up to five years, although smaller species can complete development in one. Prior to pupation, larvae leave the water and most burrow into soil or moss, or under stones where pupation occurs (Mangan 1994).

1.4.6 Hemiptera—true bugs

The Hemiptera are primarily terrestrial taxa in which members of three infraorders may be considered to be aquatic or semi-aquatic (these are sometimes referred to as the aquatic Heteroptera). The Nepomorpha (back swimmers, water boatmen, water scorpions) have at least one life stage that is truly aquatic; the Gerromorpha (water skaters, water measurers) are semi-aquatic and live on the water surface. The Leptopodomorpha (shorebugs) also have a water dependency and are sometimes classified as semi-aquatic (Polhemus and Polhemus 2008), but this group will not be discussed here. The extant aquatic and semi-aquatic species of Hemiptera fall into 19 families and there are approximately 4430 species in 301 genera (Polhemus and Polhemus 2008). The Hemiptera are hemimetabolous insects and the order name is derived from the ancient Greek words *hemi*, meaning 'half', and *pteron*, and refers to the nature of the wings, in which the forewing (the hemielytra) is usually sclerotized basally and only the distal portion is membranous.

Body size among species of adult aquatic Hemiptera is very variable, ranging from < 1 mm in *Micronecta* (Corixidae) to > 11 cm in *Lethocerus* (Belostomatidae). In the adults, the compound eyes are usually well developed and the antennae typically have four or five segments. The heads of some species (e.g. Hydrometridae) are very elongate, with small eyes some distance away from the pronotum. All members of the Hemiptera have suctorial mouthparts and essentially a liquid diet: the mandibles and maxillae form two pairs of piercing stylets that are contained within a flexible, segmented labium. The pronotum is large, and the meso- and metanotum are generally small, with some exceptions (e.g. the Hydrometridae and Gerridae have an elongated mesothorax). Usually two pairs of wings are present, although brachyptery and aptery are common. The forewings are partially sclerotized whereas the hind wings are membranous and, at rest, are folded beneath the forewings. The structure of legs is remarkably diverse within the aquatic Heteroptera, and these include modifications for swimming, catching prey, and rowing over the water surface. Most species have five larval instars.

Most aquatic Heteroptera are carnivorous, although some, such as the Corixidae, appear to be at least partially scavengers or detritivores. Prey are subdued by injection of a venom consisting of toxins and proteolytic enzymes, and then digested fluids are sucked up the stylets. Sound production is widespread in adult aquatic Heteroptera: among the surface-dwellers, gerrids communicate by surface waves and veliids stridulate, and underwater sound production via stridulation has been documented in virtually all families of Nepomorpha (Section 7.3).

In the aquatic Nepomorpha, small instars breathe dissolved oxygen, as do all stages of the Micronectinae and Aphelocheiridae. Adults and most older instars come to the surface to pick up an air bubble that also functions as a physical gill (Section 3.4). In some species the air bubble may be held under the wings (e.g. adult water boatmen, Corixidae) or attached to hairs (e.g. backswimmers, Notonectidae). Although the Nepomorpha are fully aquatic, their ability to breath air (primarily the adults) allows them to persist out of water for relatively long periods of time, for example, when in flight, or when some belostomatids crawl out of streams to avoid imminent flash floods (Lytle 1999; Lytle and White 2007).

The semi-aquatic Gerromorpha spend most of their life on the water surface, but some adults may leave the water during dispersal or for over-wintering. Many species, and particularly juveniles, live in marginal aquatic habitats such as wet soils, floating plants, and mosses at the water's edge. Walking on water depends on a species' ability to manipulate and control the air-water interface, and there are various biological and physical means by which this can be achieved (Section 8.5). Because the Gerromorpha live primarily on the water surface, they do not face many of the osmotic stresses associated with living within water and some occur on extremely saline water, such as the well-known marine and wingless species of *Halobates* (Gerridae) that occur on the open ocean (Cheng 1985; Andersen and Cheng 2004).

1.4.7 Lepidoptera—aquatic moths

The Lepidoptera is a large and primarily terrestrial order and only a fraction of the 10^5 described species have aquatic larvae. Over 730 extant species of aquatic Lepidoptera have been identified. The vast majority are in the family Crambidae (formerly the family Pyralidae) (Mey and Speidel 2008) and a few are scattered across other families such as Arctiidae and Cosmopterigidae (Rubinoff 2008). The name is derived from the ancient Greek words *lepidos*, meaning 'scales', and *pteron*, and refers to the scales on the wings. The Lepidoptera are holometabolous, and the aquatic species generally have aquatic larvae, eggs, and pupae, but terrestrial adults.

A major portion of the adult lepidopteran head capsule is covered by compound eyes. The antennae are variable in form, but often long and slender in aquatic species. In most species, the mouthparts (primarily the maxillae) are modified as a suctorial proboscis, which is coiled beneath the thorax when not in use. The anterior region of the foregut is modified as a pharyngeal sucking pump, to draw fluids up the proboscis. The mesothorax is the largest of the pterothoracic segments and bears large tegulae (scale-like lobes overlapping the base of the forewing), a characteristic feature of the order. Both pairs of wings are generally large and covered with scales (modified hairs).

The larva (caterpillar) has a heavily sclerotized head that typically bears a ring of stemmata, short antennae, and strong, biting mouthparts for feeding on aquatic plants. The prementum (the labium) carries a spinneret, which receives the ducts of the silk glands (modified salivary glands). Most species have three pairs of true legs on the thorax and five pairs of abdominal prolegs on segments 3 to 6 and on segment 10. Prolegs usually bear curved hooks (crochets) arranged in species-specific patterns. The only way to identify a caterpillar as truly aquatic is by the presence of filamentous gills (often branched) or the presence of a case or retreat, often made from leaf fragments or other vegetable matter. Caddisfly-like cases made of mineral substrates glued together with silk also occur in aquatic moths, such the amphibious larvae of the Hawaiian genus *Hyposmocoma* (Cosmopterigidae) (Rubinoff 2008; Rubinoff and Schmitz 2010).

Adults often form aggregations on the undersides of boulders or hanging rocks. Some adults can be found far from water, suggesting a propensity to disperse. A few brachypterous species are aquatic as adults, such as *Acentria ephemerella* (Crambidae). In common with many terrestrial Lepidoptera, most pond-dwelling species lay eggs on a larval food plant on, under, or close to the water. In contrast, stream-dwelling species typically lay eggs on submerged rock surfaces and the larvae eat lichens, algae, and mosses at or below the water surface. Many larvae of the Crambidae have been used in biological control programmes to suppress growth of aquatic weeds (Chapter 13). There are generally five to seven larval instars.

1.4.8 Diptera—true flies

The name Diptera comes from the ancient Greek word *dipteros*, meaning 'two-winged', and refers to the fact that flies have only one pair of membranous wings. As mentioned earlier, the second pair have been modified to form halteres, which are important organs for flight stabilization (Taylor and Krapp 2008). The Diptera are holometabolous and, among the aquatic species, it is almost exclusively the larvae and pupae that are aquatic in habit. The aquatic Diptera are species-rich with extant species described from 24 families. The most species-rich families, with more than 2000 species each, are the Chironomidae (Ferrington Jr 2008a), Tipulidae (de Jong et al. 2008), Simuliidae (Currie and Adler 2008), Culicidae (Rueda 2008), Psychodidae, and Ceratopogonidae (Wagner et al. 2008). Traditionally, there were two suborders of Diptera, the Nematocera (e.g. blackflies, midges, mosquitoes) and the Brachycera (e.g. horseflies, hoverflies, danceflies), and most aquatic species are in the families of Nematocera. However, the Nematocera is paraphyletic and the Brachycera is sister to only part of the Nematocera, so these are not 'good' suborders and the systematic relationships within the Diptera are still under some debate. Nevertheless, the dipteran families grouped within each of these two categories share some morphological characteristics and, for convenience, these names will be used in the discussion to follow. Because of their diverse morphology and the polyphyletic nature of aquatic Diptera, it is difficult to generalize about their morphology or biology, and the following discussion is necessarily brief.

Adult Diptera are generally soft-bodied with relatively large and mobile heads. The compound eyes are well developed, and the antennae are variable in structure (longer in the Nematocera than the Brachycera). Mouthparts are generally adapted for sucking. In some, the mandibles and maxillae are modified into a piercing proboscis, whereas in others the labium dominates the proboscis. The pro- and metathoracic segments are narrow and fused with the much larger mesothorax, which bears the single pair of membranous wings. Legs typically have tarsi with five segments.

Larvae of the aquatic Diptera are usually elongate and cylindrical, the body segments are usually distinct and the cuticle only weakly sclerotized. The head typically is a distinct sclerotized capsule (eucephalic) in the larvae of the Nematocera (e.g. Chironomidae, Simuliidae, Culicidae), but usually incomplete and retractile (hemicephalic or acephalic) in the Brachycera (e.g. Tabanidae, Empididae). In parallel, antennae and mouthparts are well developed in the Nematocera, whereas variable degrees of reduction and modification occur in the Brachycera. Mouthparts show great diversity of form, in accordance with the diverse feeding habits. Unusually, in some groups the antennae are modified as feeding apparatuses, including the filter-feeding cephalic fans of some larval Simuliidae and the prehensile antennae for capturing prey in larval Chaoboridae (Section 13.3). The eyes of larvae are usually simple (one to three stemmata), but apparently compound eyes are present in some Culicidae and Chaoboridae. The three thoracic segments are fused in some larval Diptera (e.g. Simuliidae, Culicidae, Chaoboridae). All dipteran larvae lack jointed thoracic legs, but prolegs may be present on the thorax and/or the abdomen.

With the exception of a few that do not feed, adult Diptera feed entirely on fluids. Most feed on nectar or the fluids from decaying organic matter, sap, faeces, etc., but a few groups (e.g. Tabanidae, Culicidae, Ceratopogonidae) are adapted for feeding on body fluids (usually blood) of other animals. The majority of body-fluid feeders have a fine proboscis to pierce the skin and penetrate directly into the fluid, and the blood-sucking habit is usually confined to the females. Taxa without piercing mouthparts can usually eject digestive fluids onto solid food that is 'dissolved' before being eaten. Most adults have a muscular cibarium for sucking fluids and, for the blood-sucking species, a large pharyngeal pump is also present.

1.4.9 Neuroptera—lacewings and spongillaflies

The name Neuroptera is derived from the ancient Greek words *neuron*, meaning 'sinew' or 'tendon', and *pteron*, and refers to the pronounced veins on the wings. Of the 17 families of Neuroptera, only two (Osmylidae and Sisyridae) have aquatic larvae, and 73 aquatic species have been described (Cover and Resh 2008). The larvae of the Sisyridae (spongillaflies) are wholly aquatic, whereas the Osmylidae (lacewings) have only semi-aquatic larvae. The Neuroptera are holometabolous, with aquatic larvae, but terrestrial adults, eggs, and pupae. The Neuroptera are often described alongside the Megaloptera, with which they have evolutionary and morphological affinities.

The adult aquatic Neuroptera range in size from the small Sisyridae (5–6 mm wing length), to the larger Osmylidae (11–14 mm wing length). The head has well-developed compound eyes, long slender antennae, and generally three ocelli in the Osmylidae, but none in the Sisyridae. Mouthparts are for chewing; the mandibles are well developed and asymmetrical. The thoracic segments are well developed and bear two pairs of membranous wings, although adults are generally weak fliers. At rest, the wings are held like a peaked roof over the abdomen like many other insects.

The larval head is well sclerotized, with relatively long antennae. Of the mouthparts, the mandibles and maxillae form two tubes or suctorial jaws, which project forward in front of the head. In the Sisyridae, these mouthparts are extremely long and thin. The legs terminate in two claws of unequal size and the tarsi are generally one-segmented. Ventral, abdominal gills are present in the Sisyridae, but absent in the Osmylidae.

There are only three larval instars in the aquatic Neuroptera, perhaps the smallest number of instars for any aquatic insect. Larvae of the Sisyridae are usually found associated with freshwater sponges (typically those of the family Spongillidae) that they feed upon with piercing mouthparts. As with the Megaloptera, eggs are laid in batches on vegetation or branches overhanging the water; when neonates hatch, they drop into the water. Neonate spongillaflies drift until contact is made with a sponge and they may remain associated with that same sponge for the entire larval life. Just before pupation, larvae leave the water (sometimes travelling up to 20 m away), climb onto mosses, plants, or other objects, and spin a silk cocoon. Larval Osmylidae are largely semi-aquatic and live primarily in moss on the edge of streams, but will enter the water and feed on aquatic prey. They are carnivorous. Prey are pierced with the suctorial jaws, a salivary secretion paralyzes the prey, and then body fluids are sucked out.

1.4.10 Coleoptera—beetles

The beetles are perhaps the most species-rich of any insect order. Approximately 30 of the 170 families have aquatic or semi-aquatic representatives, but most are classified into one of six families (Dytiscidae, Hydraenidae, Hydrophilidae, Elmidae, Scirtidae, Gyrinidae) and into two of four suborders (Adephaga, Polyphaga). Approximately 18,000 extant and aquatic or semi-aquatic species of beetle have been described (Jäch and Balke 2008). The name Coleoptera is derived from the ancient Greek words *koleos*, meaning 'sheath', and *pteron*, and refers to the sheath-like nature of the hardened forewings (elytra). The Coleoptera are holometabolous, but the degree to which various life stages have aquatic habits varies among and within families. The truly aquatic beetles all have aquatic larvae and most have aquatic adults—exceptions include the Scirtidae where adults are terrestrial. Because of their diversity and the polyphyletic nature of aquatic beetles, it is difficult to generalize about their morphology or biology, and the following discussion is necessarily brief.

Adult beetles are heavily sclerotized. Compound eyes are usually present and large, and divided into upper and lower pairs in Gyrinidae (Section 6.4). The typically eleven-segmented antennae vary in form. Mouthparts are typically of the chewing type. The prothorax is the largest of the thoracic segments and, in many species, can be moved independently of the other thoracic segments. The meso- and metathorax are fused in a pterothorax, which is often invisible from above, or visible only as a small, typically triangular-shaped scutellum. Forewings are modified as hard elytra that may be smooth, pitted, striated, or variously textured. Elytra meet in the midline but are rarely fused and, except in a few taxa that lack hind wings (e.g. some Elmidae), the hind wings are membranous and typically folded beneath the elytra when not in use. In flight, the elytra are held horizontally, at right angles to the long axis of the body. Legs, especially the hind legs, are often modified for swimming, i.e. widened and often fringed with hairs. Tarsi are normally five-segmented and terminate in paired claws, although one segment may be reduced. In the Meruidae, a recently discovered family of aquatic beetle living in cascades over bedrock outcrops, the tarsal claws are pectinate (bear many teeth) and this gives rise to their common name of 'comb-clawed cascade beetles' (Spangler and Steiner Jr 2005).

The shapes of beetle larvae are highly varied, although in all species the head is well developed and sclerotized. The antennae generally have three or four segments, although some are longer (e.g. larval

Scirtidae), and six or fewer stemmata on each side of the head form the eyes. Three thoracic segments are readily distinguished and thoracic legs are usually present, although legs may be reduced (e.g. some Curculionidae). Abdominal prolegs are normally absent and some beetle larvae have filamentous abdominal gills. The tip of the abdomen may be modified or bear various structures for gas exchange, such as sclerotized respiratory horns.

The habits of aquatic beetles are as diverse as the group: most are benthic in habit; adult Gyrinidae swim at the water's surface; adults of other species can 'walk' upside down on the underside of the surface film (e.g. some Hydraenidae and Hydrophilidae; Section 8.6.2); many are adept at swimming and diving (e.g. Dytiscidae); and some live exclusively on aquatic plants. Very few species have aquatic pupae; larvae usually leave the water to pupate or construct a submerged air-filled cocoon. Exceptions include the water-pennies (Psephenidae) where pupae respire by means of spiracular gills. In adults, respiration underwater is primarily via an air bubble trapped under the elytra or attached to the ventral surface (Section 3.4). Larvae never carry external air reservoirs: some have tracheal gills and are independent of atmospheric air (e.g. Elmidae), others access air at the water's surface (e.g. many Dytiscidae), or by tapping into the air spaces in the stems of aquatic plants (e.g. Noteridae).

Feeding habits are very varied among species and often between life stages of the same species, although the majority are probably carnivores and/or scavengers. Some groups are algivorous (larval Elmidae); others are strictly phytophagous (Chrysomelidae, Curculionidae) and have been used in biological control programmes for nuisance aquatic plants. A very few species are parasitic, such as the beaver beetle *Platypsyllus castoris* (Leiondidae), where wingless and virtually eye-less adults and larvae are ectoparasites of Palaearctic and Nearctic species of beaver (*Castor fiber* and *C. canadensis*) (Peck 2006; Whitaker Jr 2006).

1.4.11 Rarely aquatic insects

Of the Orthoptera (grasshoppers and crickets), approximately 188 species are considered to be water-dependent to some degree, but only approximately 80 species would be considered aquatic (Amédégnato and Devriese 2008). The name Orthoptera comes from the ancient Greek *orthos*, meaning 'straight' or 'perpendicular', and *pteron,* and may refer to the straight wings. These are hemimetabolous insects and both larvae and adults of aquatic species occur in water. Adults generally have two pairs of wings and the forewings (tegmina) are thickened and somewhat sclerotized, although they are generally weak fliers and brachypterous and apterous forms also occur. Females typically have a well-developed, appendicular ovipositor, and males have concealed copulatory structures. Compound eyes are well developed and mouthparts are of the chewing type. The hind legs of almost all species are enlarged for jumping. In many aquatic species, the hind femora are enlarged, the tibiae are variously flattened, and equipped with spines, spurs, and sometimes fringes of hairs, that aid swimming. Like their terrestrial counterparts, aquatic Orthoptera are typically herbivorous and feed on aquatic macrophytes. Most members of the order lay eggs in soil or in burrows, but aquatic species often oviposit on or within aquatic plants, often just below the water surface. They are air breathers and dense patches of hair, typically on the abdomen and forewing, may facilitate carrying air bubbles underwater.

The Hymenoptera is a very large order of holometabolous insects, which includes the familiar bees, wasps, and ants. In total, 150 species from 11 families in the suborder Apocrita have been described and recognized as aquatic and all are parasitoids (Bennett 2008). The name Hymenoptera is derived from the ancient Greek words *hymenos*, meaning 'membrane', and *pteron*, and refers to the membranous wings. The aquatic wasps have terrestrial adults and larvae that are parasitic upon other aquatic organisms, often insects (this excludes wasps that are parasitic only on the terrestrial stages of aquatic insects). Most aquatic Hymenoptera are endoparasitoids of larvae that occur in tissues of aquatic plants, although some are ectoparasitic (e.g. *Agriotypus* spp., Ichneumonidae) and oviposit on larvae, prepupae, or pupae (Chapter 11). Adults have two pairs of membranous wings that are coupled by hamuli and have simple venation. The plesiomorphic condition is herbivory, but mouthparts of some groups have been modified for predation. As parasitoids, females generally have a long, needle-like ovipositor. Many aquatic wasps have characteristics that are uncommon in other wasps and that appear to be adaptive to life underwater: short, dense hairs on the body and wings that allow the wasp to be hydrophobic and to maintain a plastron of air around the body; and elongated, strongly curved claws that can grip the substrate and prevent the female floating to the surface or being swept in currents when searching for hosts (Bennett 2008). The larvae are generally maggot-like and their morphology is typical of internal parasites.

Mecoptera (scorpion flies) is a relatively small order of holometabolous insects. Only nine species are aquatic, all of which are in the family Nannochoristidae and all occur in the southern hemisphere (Australia, New Zealand, South America) (Ferrington Jr 2008b). The name Mecoptera is derived from the ancient Greek words *mekos*, meaning 'long', and *pteron*, and refers to the relatively long wings. The aquatic species have terrestrial adults, which only occur close to water, and aquatic larvae. The head of adult Mecoptera is typically elongate, with the clypeus and labrum prolonged ventrally into a broad rostrum with biting mouthparts. In the Nannochoristidae, however, the rostrum is narrow and needle-like. Compound eyes are well developed, the legs are long and thin, and there are usually two pairs of identical membranous wings. The abdomen has short cerci. Males have very prominent genitalia, often swollen and turned upwards, which give them a scorpion-like appearance. Larvae of most Mecoptera are caterpillar-like, but the aquatic larvae are active predators, with dorso-ventrally flattened bodies and thoracic legs, but no prolegs. The stemmata of some last-instar larvae (*Nannochorista*, Nannochoristidae) form quasi-compound eyes composed of ten or more stemmata (Melzer et al. 1994), although the stemmata are simple in larval *Microchorista* (Nannochoristidae). Normally, the thorax has only the pronotum sclerotized and the apex of the abdomen is modified into a suction disc, but in the Nannochoristidae, the abdomen ends in a pair of anal hooks. Rather little is known about the ecology of the aquatic Mecoptera.