

Fourth Edition

THE INSECTS

AN OUTLINE OF ENTOMOLOGY

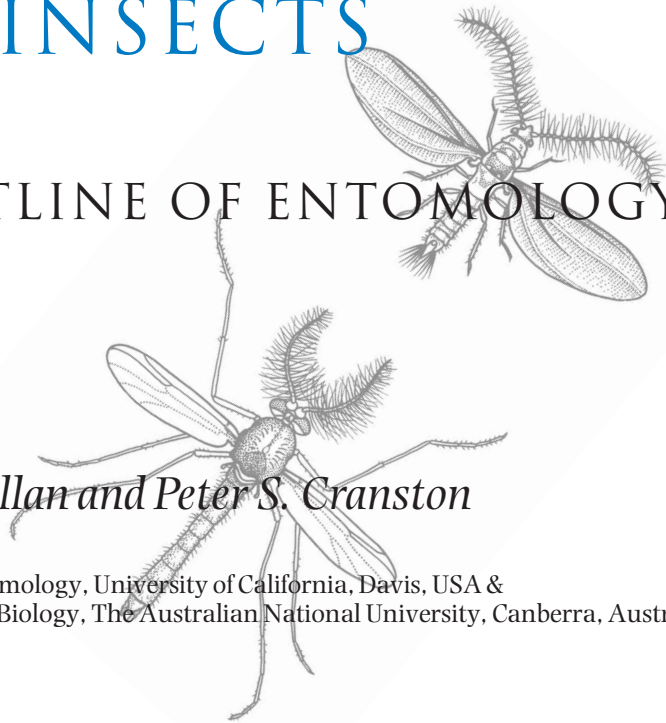
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With illustrations by
Karina H. McInnes

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THE INSECTS

An Outline of Entomology

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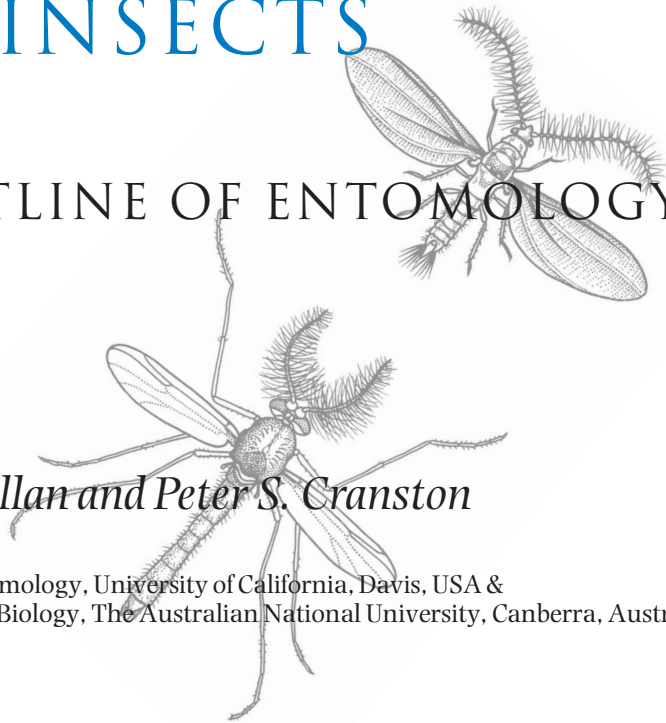
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PREFACE TO THE FOURTH EDITION

In the 5 years since the previous (third) edition of this textbook, the discipline of entomology has seen some major changes in emphasis. The opening up of global commerce (free trade) has brought with it many accidental passengers, including both potential and actual pestilential insects of our crops and ornamental plants, and our health. Efforts to prevent further incursions include increased surveillance, in what has become known as biosecurity, at our ports, airports, and land borders. Entomologists increasingly are employed in quarantine and biosecurity, where they predict threats, and are expected to use diagnostics to recognize pests and distinguish those that are new arrivals. The inevitable newly arrived and established pests must be surveyed and control measures planned. In this edition we discuss several of these “emergent” threats from insects and the diseases that some can carry.

Molecular techniques of ever-increasing sophistication are now commonplace in many aspects of entomological study, ranging from genomic studies seeking to understand the basis of behaviors, to molecular diagnostics and the use of sequences to untangle the phylogeny of this most diverse group of organisms. Although this book is not the place to detail this fast-evolving field, we present the results of many molecular studies, particularly in relation to our attempts to reconcile different ideas on evolutionary relationships, where much uncertainty remains despite a growing volume of nucleotide sequence data from a cadre of informative markers. In addition, ever more insects have their complete mitochondrial genomes sequenced, and the whole nuclear genome is available for an increasing diversity of insects, providing much scope for in-depth comparative studies. Important insights have already come from the ability to “silence” particular genes to observe the outcome, for example in aspects of development and communication. Inevitably, new molecular information will change some

views on insect relationships, physiology, and behavior, even in the short time between completion of this new revision and its publication. Thus we present only well established views.

In this edition of the textbook, we have updated and relocated the boxes concerning each major grouping (the traditional orders) from the chapter in which their generalized ecology placed them, to the end of the book, where they can be located more easily. We have used the best current estimates of relationships and implement a new ordinal classification for several groups. Strong evidence suggests that (a) termites (“Isoptera”) are actually cockroaches (Blattodea), (b) the parasitic lice (“Phthiraptera”) arose from within the free-living bark and book lice (“Psocoptera”) forming order Psocodea, and (c) the fleas (“Siphonaptera”) perhaps arose within Mecoptera. We discuss (and illustrate with trees) the evolutionary and classificatory significance and applications of these and other findings.

The updated chapter texts are supplemented with an additional 18 new boxes, including on the topical subjects of the *African honey bee* and *Colony collapse disorder* (of bees) in the sphere of apiary, *beewolf microbial defense*, and the use of *bed nets* and resurgence of *bed bugs*, *Dengue fever*, and *West Nile virus* in relation to human health. New boxes are provided on *how entomologists recognize species*, on important *aquatic insects* and *energy fluxes*, and on *evolutionary relationships of flamingo lice*. Some case studies in emergent plant pests are presented, including the *Emerald ash borer* that is destroying North American landscape trees, and other insects (*light brown apple moth*, *citrus psyllid* and *fruit flies*) that threaten US crops. We relate the astonishing success story in classical biological control of the *glassy-winged sharpshooter in the Pacific* that provides hope for rejuvenation of this method of pest control.

Much of this fourth edition was written in Australia. We acknowledge the generosity and companionship

of everyone in Botany and Zoology within the School of Biology at the Australian National University (ANU), Canberra, where we spent 10 weeks as ANU Visiting Fellows in early 2009. We also appreciate the hospitality of Frances FitzGibbon, with whom we stayed for the period that we were based at ANU. Thank you Frances for the use of your spare bedroom with the view of the Australian bush with its many birds and the occasional group of kangaroos. Our home Department of Entomology and the academic administration at UC Davis approved our 3-month sabbatical leave to allow us quality time to revise this book. We are grateful to the staff in our home department for logistic support during the time we worked on the book and especially Kathy Garvey for assistance with an illustration. We are grateful to the following colleagues worldwide (listed alphabetically) for providing information and ideas on many aspects of insect biology and phylogeny: Eldon Ball, Stephen Cameron, Jason Cryan, Mark Hoddle,

Kevin Johnson, Bob Kimsey, Karl Kjer, Klaus-Dieter Klass, Ed Lewis, Jim Marden, Jenny Mordue, Geoff Morse, Laurence Mound, Eric Mussen, Laurence Packer, Brad Sinclair, Vince Smith, and Shaun Winterton. However, any errors of interpretation or fact are our responsibility alone. We thank our students Haley Bastien, Sarah Han, Nick Herold, and Scott McCluen for their assistance in compiling the index.

Most importantly, we were so pleased that Karina McInnes was able to recall her entomological pen-and-ink skills to provide us with a series of wonderful illustrations to capture the essence of so many insects, both friends and foes of the human world, going about their daily business.

We are grateful to the staff at Wiley-Blackwell, especially Ward Cooper, Rosie Hayden, and Delia Sandford for their continued support and excellent service. We were fortunate to have Nik Prowse edit the text of this edition.

PREFACE TO THE THIRD EDITION

Since writing the earlier editions of this textbook, we have relocated from Canberra, Australia, to Davis, California, where we teach many aspects of entomology to a new cohort of undergraduate and graduate students. We have come to appreciate some differences which may be evident in this edition. We have retained the regional balance of case studies for an international audience. With globalization has come unwanted, perhaps unforeseen, consequences, including the potential worldwide dissemination of pest insects and plants. A modern entomologist must be aware of the global status of pest control efforts. These range from insect pests of specific origin, such as many vectors of disease of humans, animals, and plants, to noxious plants, for which insect natural enemies need to be sought. The quarantine entomologist must know, or have access to, global databases of pests of commerce. Successful strategies in insect conservation, an issue we cover for the first time in this edition, are found worldwide, although often they are biased towards Lepidoptera. Furthermore, all conservationists need to recognize the threats to natural ecosystems posed by introduced insects such as crazy, big-headed, and fire ants. Likewise, systematists studying the evolutionary relationships of insects cannot restrict their studies to a regional subset, but also need a global view.

Perhaps the most publicized entomological event since the previous edition of our text was the “discovery” of a new order of insects – named as Mantophasmatodea – based on specimens from 45-million-year-old amber and from museums, and then found living in Namibia (south-west Africa), and now known to be quite widespread in southern Africa. This finding of the first new order of insects described for many decades exemplifies several aspects of modern entomological research. First, existing collections from which mantophasmatid specimens initially were discovered remain important research resources; second, fossil specimens have

significance in evolutionary studies; third, detailed comparative anatomical studies retain a fundamental importance in establishing relationships, even at ordinal level; fourth, molecular phylogenetics usually can provide unambiguous resolution where there is doubt about relationships based on traditional evidence.

The use of molecular data in entomology, notably (but not only) in systematic studies, has grown apace since our last edition. The genome provides a wealth of characters to complement and extend those obtained from traditional sources such as anatomy. Although analysis is not as unproblematic as was initially suggested, clearly we have developed an ever-improving understanding of the internal relationships of the insects as well as their relationships to other invertebrates. For this reason we have introduced a new chapter (Chapter 7) describing methods and results of studies of insect phylogeny, and portraying our current understanding of relationships. Chapter 8, also new, concerns our ideas on insect evolution and biogeography. The use of robust phylogenies to infer past evolutionary events, such as origins of flight, sociality, parasitic and plant-feeding modes of life, and biogeographic history, is one of the most exciting areas in comparative biology.

Another growth area, providing ever more challenging ideas, is the field of molecular evolutionary development in which broad-scale resemblances (and unexpected differences) in genetic control of developmental processes are being uncovered. Notable studies provide evidence for identity of control for development of gills, wings, and other appendages across phyla. However, details of this field are beyond the scope of this textbook.

We retain the popular idea of presenting some tangential information in boxes, and have introduced seven new boxes: Box 1.1 Collected to extinction?; Box 1.2 Tramp ants and biodiversity; Box 1.3 Sustainable use of mopane worms; Box 4.3 Reception of

communication molecules; Box 5.5 Egg-tending fathers – the giant water bugs; Box 7.1 Relationships of the Hexapoda to other Arthropoda; Box 14.2 Backpack bugs – dressed to kill?, plus a taxonomic box (Box 13.3) concerning the Mantophasmatodea (heel walkers).

We have incorporated some other boxes into the text, and lost some. The latter include what appeared to be a very neat example of natural selection in action, the peppered moth *Biston betularia*, whose melanic *carbonaria* form purportedly gained advantage in a sooty industrial landscape through its better crypsis from bird predation. This interpretation has been challenged lately, and we have reinterpreted it in Box 14.1 within an assessment of birds as predators of insects.

Our recent travels have taken us to countries in which insects form an important part of the human diet. In southern Africa we have seen and eaten mopane, and have introduced a box to this text concerning the sustainable utilization of this resource. Although we have tried several of the insect food items that we mention in the opening chapter, and encourage others to do so, we make no claims for tastefulness. We also have visited New Caledonia, where introduced ants are threatening the native fauna. Our concern for the consequences of such worldwide ant invasives, that are particularly serious on islands, is reflected in Box 1.2.

Once again we have benefited from the willingness of colleagues to provide us with up-to-date information and to review our attempts at synthesizing their research. We are grateful to Mike Picker for helping us

with Mantophasmatodea and to Lynn Riddiford for assisting with the complex new ideas concerning the evolution of holometabolous development. Matthew Terry and Mike Whiting showed us their unpublished phylogeny of the Polyneoptera, from which we derived part of Fig. 7.2. Bryan Danforth, Doug Emlen, Conrad Labandeira, Walter Leal, Brett Melbourne, Vince Smith, and Phil Ward enlightened us or checked our interpretations of their research speciality, and Chris Reid, as always, helped us with matters coleopterological and linguistic. We were fortunate that our updating of this textbook coincided with the issue of a compendious resource for all entomologists: *Encyclopedia of Insects*, edited by Vince Resh and Ring Cardé for Academic Press. The wide range of contributors assisted our task immensely: we cite their work under one header in the “Further reading” following the appropriate chapters in this book.

We thank all those who have allowed their publications, photographs, and drawings to be used as sources for Karina McInnes’ continuing artistic endeavors. Tom Zavortink kindly pointed out several errors in the second edition. Inevitably, some errors of fact and interpretation remain, and we would be grateful to have them pointed out to us.

This edition would not have been possible without the excellent work of Katrina Rainey, who was responsible for editing the text, and the staff at Blackwell Publishing, especially Sarah Shannon, Cee Pike, and Rosie Hayden.

PREFACE TO THE SECOND EDITION

Since writing the first edition of this textbook, we have been pleasantly surprised to find that what we consider interesting in entomology has found a resonance amongst both teachers and students from a variety of countries. When invited to write a second edition we consulted our colleagues for a wish list, and have tried to meet the variety of suggestions made. Foremost we have retained the chapter sequence and internal arrangement of the book to assist those that follow its structure in their lecturing. However, we have added a new final (16th) chapter covering methods in entomology, particularly preparing and conserving a collection. Chapter 1 has been radically reorganized to emphasize the significance of insects, their immense diversity and their patterns of distribution. By popular request, the summary table of diagnostic features of the insect orders has been moved from Chapter 1 to the end pages, for easier reference. We have expanded insect physiology sections with new sections on tolerance of environmental extremes, thermoregulation, control of development and changes to our ideas on vision. Discussion of insect behaviour has been enhanced with more information on insect–plant interactions, migration, diapause, hearing and predator avoidance, “puddling” and sodium gifts. In the ecological area, we have considered functional feeding groups in aquatic insects, and enlarged the section concerning insect–plant interactions. Throughout the text we have incorporated new interpretations and ideas, corrected some errors and added extra terms to the glossary.

The illustrations by Karina McInnes that proved so popular with reviewers of the first edition have been retained and supplemented, especially with some novel chapter vignettes and additional figures for the taxonomic and collection sections. In addition, 41 colour photographs of colourful and cryptic insects going about their lives have been chosen to enhance the text.

The well-received boxes that cover self-contained themes tangential to the flow of the text are retained. With the assistance of our new publishers, we have more clearly delimited the boxes from the text. New boxes in this edition cover two resurging pests (the phylloxera aphid and *Bemisia* whitefly), the origins of the aquatic lifestyle, parasitoid host-detection by hearing, the molecular basis of development, chemically protected eggs, and the genitalia-inflating phalloblaster.

We have resisted some invitations to elaborate on the many physiological and genetic studies using insects – we accept a reductionist view of the world appeals to some, but we believe that it is the integrated whole insect that interacts with its environment and is subject to natural selection. Breakthroughs in entomological understanding will come from comparisons made within an evolutionary framework, not from the technique-driven insertion of genes into insect and/or host.

We acknowledge all those who assisted us with many aspects of the first edition (see Preface for first edition following) and it is with some regret that we admit that such a breadth of expertise is no longer available for consultation in one of our erstwhile research institutions. This is compensated for by the following friends and colleagues who reviewed new sections, provided us with advice, and corrected some of our errors. Entomology is a science in which collaboration remains the norm – long may it continue. We are constantly surprised at the rapidity of freely given advice, even to electronic demands: we hope we haven’t abused the rapidity of communication. Thanks to, in alphabetical order: Denis Anderson – varroa mites; Andy Austin – wasps and polydnviruses; Jeff Bale – cold tolerance; Eldon Ball – segment development; Paul Cooper – physiological updates; Paul De Barro – *Bemisia*; Hugh Dingle – migration; Penny Greenslade – collembola facts; Conrad Labandeira – fossil insects; Lisa Nagy – molecular basis for limb development; Rolf Oberprieler

– edible insects; Chris Reid – reviewing Chapter 1 and coleopteran factoids; Murray Upton – reviewing collecting methods; Lars-Ove Wikars – mycangia information and illustration; Jochen Zeil – vision. Dave Rentz supplied many excellent colour photographs, which we supplemented with some photos by Denis Anderson, Janice Edgerly-Rooks, Tom Eisner, Peter Menzel, Rod Peakall, Dick Vane-Wright, Peter Ward, Phil Ward and the late Tony Watson. Lyn Cook and Ben Gunn provided help with computer graphics. Many people assisted by supplying current names or identifications for particular insects, including from photographs. Special thanks to John Brackenbury, whose photograph of a soldier beetle in preparation for flight (from Brackenbury, 1990) provided the inspiration for the cover centerpiece.

When we needed a break from our respective offices in order to read and write, two Dons, Edward and Bradshaw, provided us with some laboratory space in the Department of Zoology, University of Western Australia, which proved to be rather too close to surf, wineries and wildflower sites – thank you anyway.

It is appropriate to thank Ward Cooper of the late Chapman & Hall for all that he did to make the first edition the success that it was. Finally, and surely not least, we must acknowledge that there would not have been a second edition without the helping hand put out by Blackwell Science, notably Ian Sherman and David Frost, following one of the periodic spasms in scientific publishing when authors (and editors) realize their minor significance in the “commercial” world.

PREFACE AND ACKNOWLEDGMENTS FOR FIRST EDITION

Insects are extremely successful animals and they affect many aspects of our lives, despite their small size. All kinds of natural and modified, terrestrial and aquatic, ecosystems support communities of insects that present a bewildering variety of life-styles, forms and functions. Entomology covers not only the classification, evolutionary relationships and natural history of insects, but also how they interact with each other and the environment. The effects of insects on us, our crops and domestic stock, and how insect activities (both deleterious and beneficial) might be modified or controlled, are amongst the concerns of entomologists.

The recent high profile of biodiversity as a scientific issue is leading to increasing interest in insects because of their astonishingly high diversity. Some calculations suggest that the species richness of insects is so great that, to a near approximation, all organisms can be considered to be insects. Students of biodiversity need to be versed in entomology.

We, the authors, are systematic entomologists teaching and researching insect identification, distribution, evolution and ecology. Our study insects belong to two groups – scale insects and midges – and we make no apologies for using these, our favourite organisms, to illustrate some points in this book.

This book is not an identification guide, but addresses entomological issues of a more general nature. We commence with the significance of insects, their internal and external structure, and how they sense their environment, followed by their modes of reproduction and development. Succeeding chapters are based on major themes in insect biology, namely the ecology of ground-dwelling, aquatic and plant-feeding insects, and the behaviours of sociality, predation and

parasitism, and defence. Finally, aspects of medical and veterinary entomology and the management of insect pests are considered.

Those to whom this book is addressed, namely students contemplating entomology as a career, or studying insects as a subsidiary to specialized disciplines such as agricultural science, forestry, medicine or veterinary science, ought to know something about insect systematics – this is the framework for scientific observations. However, we depart from the traditional order-by-order systematic arrangement seen in many entomological textbooks. The systematics of each insect order are presented in a separate section following the ecological-behavioural chapter appropriate to the predominant biology of the order. We have attempted to keep a phylogenetic perspective throughout, and one complete chapter is devoted to insect phylogeny, including examination of the evolution of several key features.

We believe that a picture is worth a thousand words. All illustrations were drawn by Karina Hansen McInnes, who holds an Honours degree in Zoology from the Australian National University, Canberra. We are delighted with her artwork and are grateful for her hours of effort, attention to detail and skill in depicting the essence of the many subjects that are figured in the following pages. Thank you Karina.

This book would still be on the computer without the efforts of John Trueman, who job-shared with Penny in second semester 1992. John delivered invertebrate zoology lectures and ran lab classes while Penny revelled in valuable writing time, free from undergraduate teaching. Aimorn Stewart also assisted Penny by keeping her research activities alive during book

preparation and by helping with labelling of figures. Eva Bugledich acted as a library courier and brewed hundreds of cups of coffee.

The following people generously reviewed one or more chapters for us: Andy Austin, Tom Bellas, Keith Binnington, Ian Clark, Geoff Clarke, Paul Cooper, Kendi Davies, Don Edward, Penny Greenslade, Terry Hillman, Dave McCorquodale, Rod Mahon, Dick Norris, Chris Reid, Steve Shattuck, John Trueman and Phil Weinstein. We also enjoyed many discussions on hymenopteran phylogeny and biology with Andy. Tom sorted out our chemistry and Keith gave expert advice on insect cuticle. Paul's broad knowledge of insect physiology was absolutely invaluable. Penny put us straight with springtail facts. Chris' entomological knowledge, especially on beetles, was a constant source of information. Steve patiently answered our endless questions on ants. Numerous other people read and commented on sections of chapters or provided advice or helpful discussion on particular entomological topics. These people included John Balderson, Mary Carver, Lyn Cook, Jane Elek, Adrian Gibbs, Ken Hill, John Lawrence, Chris Lyal, Patrice Morrow, Dave Rentz, Eric Rumbo, Vivienne Turner, John Vranjic and Tony Watson. Mike Crisp assisted with checking on current host-plant names. Sandra McDougall inspired part of Chapter 15. Thank you everyone for your many comments which

we have endeavoured to incorporate as far as possible, for your criticisms which we hope we have answered, and for your encouragement.

We benefited from discussions concerning published and unpublished views on insect phylogeny (and fossils), particularly with Jim Carpenter, Mary Carver, Niels Kristensen, Jarmila Kukalová-Peck and John Trueman. Our views are summarized in the phylogenies shown in this book and do not necessarily reflect a consensus of our discussants' views (this was unattainable).

Our writing was assisted by Commonwealth Scientific and Industrial Research Organization (CSIRO) providing somewhere for both of us to work during the many weekdays, nights and weekends during which this book was prepared. In particular, Penny managed to escape from the distractions of her university position by working in CSIRO. Eventually, however, everyone discovered her whereabouts. The Division of Entomology of the CSIRO provided generous support: Carl Davies gave us driving lessons on the machine that produced reductions of the figures, and Sandy Smith advised us on labelling. The Division of Botany and Zoology of the Australian National University also provided assistance in aspects of the book production: Aimorn Stewart prepared the SEMs from which Fig. 4.7 was drawn, and Judy Robson typed the labels for some of the figures.

Chapter 1

THE IMPORTANCE, DIVERSITY, AND CONSERVATION OF INSECTS



Charles Darwin inspecting beetles collected during the voyage of the *Beagle*. (After various sources, especially Huxley & Kettlewell 1965 and Futuyma 1986.)

Curiosity alone concerning the identities and lifestyles of the fellow inhabitants of our planet justifies the study of insects. Some of us have used insects as totems and symbols in spiritual life, and we portray them in art and music. If we consider economic factors, the effects of insects are enormous. Few human societies lack honey, provided by bees (or specialized ants). Insects pollinate our crops. Many insects share our houses, agriculture, and food stores. Others live on us, on our domestic pets or our livestock, and yet more visit to feed on us where they may transmit disease. Clearly, we should understand these pervasive animals.

Although there are millions of kinds of insects, we do not know exactly (or even approximately) how many. This ignorance of how many organisms we share our planet with is remarkable considering that astronomers have listed, mapped, and uniquely identified a comparable diversity of galactic objects. Some estimates, which we discuss in detail below, imply that the species richness of insects is so great that, to a near approximation, all organisms can be considered to be insects. Although dominant on land and in fresh water, few insects are found beyond the tidal limit of oceans.

In this opening chapter, we outline the significance of insects and discuss their diversity and classification and their roles in our economic and wider lives. First, we outline the field of entomology and the role of entomologists, and then introduce the ecological functions of insects. Next, we explore insect diversity, and then discuss how we name and classify this immense diversity. Sections follow in which we consider some cultural and economic aspects of insects, their aesthetic and tourism appeal, their importance as foods for humans and animals, and how and why they may be reared. We conclude with a review of the conservation of insects, with examples, including text boxes on the conservation of the large blue butterfly in England, the effects of tramp ants on biodiversity, and the issue of sustainable human use of mopane “worms”: the caterpillars of African emperor moths.

1.1 WHAT IS ENTOMOLOGY?

Entomology is the study of insects. Entomologists, the people who study insects, observe, collect, rear, and experiment with insects. Research undertaken by entomologists covers the total range of biological disciplines, including evolution, ecology, behavior, anatomy, physiology, biochemistry, and genetics. The unifying

feature is that the study organisms are insects. Biologists work with insects for many reasons: ease of culturing in a laboratory, rapid population turnover, and availability of many individuals are important factors. The minimal ethical concerns regarding responsible experimental use of insects, as compared with vertebrates, are a significant consideration.

Modern entomological study commenced in the early 18th century when a combination of the rediscovery of the classical literature, the spread of rationalism, and the availability of ground-glass optics made the study of insects acceptable for the thoughtful privately wealthy. Although people working with insects hold professional positions, many aspects of the study of insects remain suitable for the hobbyist. Charles Darwin’s initial enthusiasm in natural history was as a collector of beetles (as shown in the vignette for this chapter). All his life he continued to study insect evolution and communicate with amateur entomologists throughout the world. Much of our present understanding of worldwide insect diversity derives from studies of non-professionals. Many such contributions come from collectors of attractive insects such as butterflies and beetles, but others with patience and ingenuity continue the tradition of Jean Henri Fabre in observing close-up activities of insects. We can discover much of scientific interest at little expense concerning the natural history of even “well-known” insects. The variety of size, structure, and color in insects (see www.wiley.com/go/gullan/insects) is striking, whether depicted in drawing, photography, or film.

A popular misperception is that professional entomologists emphasize killing or at least controlling insects, but in fact entomology includes many positive aspects of insects because their benefits to the environment outweigh their harm.

1.2 THE IMPORTANCE OF INSECTS

We should study insects for many reasons. Their ecologies are incredibly variable. Insects may dominate food chains and food webs in both volume and numbers. Feeding specializations of different insect groups include ingestion of detritus, rotting materials, living and dead wood, and fungus (Chapter 9), aquatic filter feeding and grazing (Chapter 10), herbivory (= phytophagy), including sap feeding (Chapter 11), and predation and parasitism (Chapter 13). Insects may live in water, on land, or in soil, during part or all of their lives. Their

lifestyles may be solitary, gregarious, subsocial, or highly social (Chapter 12). They may be conspicuous, mimics of other objects, or concealed (Chapter 14), and may be active by day or by night. Insect life cycles (Chapter 6) allow survival under a wide range of conditions, such as extremes of heat and cold, wet and dry, and unpredictable climates.

Insects are essential to the following ecosystem functions:

- nutrient recycling, via leaf-litter and wood degradation, dispersal of fungi, disposal of carrion and dung, and soil turnover;
- plant propagation, including pollination and seed dispersal;
- maintenance of plant community composition and structure, via phytophagy, including seed feeding;
- food for insectivorous vertebrates, such as many birds, mammals, reptiles, and fish;
- maintenance of animal community structure, through transmission of diseases of large animals, and predation and parasitism of smaller ones.

Each insect species is part of a greater assemblage and its loss affects the complexities and abundance of other organisms. Some insects are considered **keystone species** because loss of their critical ecological functions could collapse the wider ecosystem. For example, termites convert cellulose in tropical soils (section 9.1), suggesting that they are keystones in tropical soil structuring. In aquatic ecosystems, a comparable service is provided by the guild of mostly larval insects that breaks down and releases the nutrients from wood and leaves derived from the surrounding terrestrial environment.

Insects are associated intimately with our survival, in that certain insects damage our health and that of our domestic animals (Chapter 15) and others adversely affect our agriculture and horticulture (Chapter 16). Certain insects greatly benefit human society, either by providing us with food directly or by contributing to our food or materials that we use. For example, honey bees provide us with honey but are also valuable agricultural pollinators worth an estimated US\$15 billion annually in the USA. Estimates of the value of non-honey-bee pollination in the USA could be as much as \$5–6 billion per year. The total economic value of pollination services for the 100 crops used directly for human food globally has been estimated to be in excess of \$200 billion annually (based on 2005 production and consumption data). Furthermore, valuable services, such as those provided by predatory beetles and bugs or

parasitic wasps that control pests, often go unrecognized, especially by city-dwellers, and yet such ecosystem services are worth billions of dollars annually.

Insects contain a vast array of chemical compounds, some of which can be collected, extracted, or synthesized for our use. Chitin, a component of insect cuticle, and its derivatives act as anticoagulants, enhance wound and burn healing, reduce serum cholesterol, serve as non-allergenic drug carriers, provide strong biodegradable plastics, and enhance removal of pollutants from waste water, to mention just a few developing applications. Silk from the cocoons of silkworm moths, *Bombyx mori*, and related species has been used for fabric for centuries, and two endemic South African species may be increasing in local value. The red dye cochineal is obtained commercially from scale insects of *Dactylopius coccus* cultured on *Opuntia* cacti. Another scale insect, the lac insect *Kerria lacca*, is a source of a commercial varnish called shellac. Given this range of insect-produced chemicals, and accepting our ignorance of most insects, there is a high likelihood of finding novel chemicals.

Insects provide more than economic or environmental benefits; characteristics of certain insects make them useful models for understanding general biological processes. For instance, the short generation time, high fecundity, and ease of laboratory rearing and manipulation of the vinegar or common fruit fly, *Drosophila melanogaster*, have made it a model research organism. Studies of *D. melanogaster* have provided the foundations for our understanding of genetics and cytology, and these flies continue to provide the experimental materials for advances in molecular biology, embryology, and development. Outside the laboratories of geneticists, studies of social insects, notably hymenoptera such as ants and bees, have allowed us to understand the evolution and maintenance of social behaviors such as altruism (section 12.4.1). The field of sociobiology owes its existence to entomologists' studies of social insects. Several theoretical ideas in ecology have derived from the study of insects. For example, our ability to manipulate the food supply (grains) and number of individuals of flour beetles (*Tribolium* spp.) in culture, combined with their short life history (compared to mammals, for example), gave insights into mechanisms regulating populations. Some early holistic concepts in ecology, for example ecosystem and niche, came from scientists studying freshwater systems where insects dominate. Alfred Wallace (depicted in the vignette of Chapter 17), the independent and

contemporaneous discoverer with Charles Darwin of the theory of evolution by natural selection, based his ideas on observations of tropical insects. Hypotheses concerning the many forms of mimicry and sexual selection have been derived from observations of insect behavior, which continue to be investigated by entomologists.

Lastly, the sheer numbers of insects means that their impact upon the environment, and hence our lives, is highly significant. Insects are the major component of macroscopic biodiversity and, for this reason alone, we should try to understand them better.

1.3 INSECT BIODIVERSITY

1.3.1 The described taxonomic richness of insects

Probably slightly over 1 million species of insects have been described; that is, have been recorded in a taxonomic publication as “new” (to science), accompanied by description and often with illustrations or some other means of recognizing the particular insect species (section 1.4). Since some insect species have been described as new more than once, due to failure to recognize variation or through ignorance of previous studies, the actual number of described species is uncertain.

The described species of insects are distributed unevenly amongst the higher taxonomic groupings called orders (section 1.4). Five “major” orders stand out for their high species richness, the beetles (Coleoptera), flies (Diptera), wasps, ants, and bees (Hymenoptera), butterflies and moths (Lepidoptera), and the true bugs (Hemiptera). J.B.S. Haldane’s jest – that “God” (evolution) shows an inordinate “fondness” for beetles – appears to be confirmed since they comprise almost 40% of described insects (more than 350,000 species). The Hymenoptera have more than 115,000 described species, with the Diptera and Lepidoptera having at least 150,000 described species each, and Hemiptera almost 100,000. Of the remaining orders of living insects, none exceed the approximately 20,000 described species of the Orthoptera (grasshoppers, locusts, crickets, and katydids). Most of the “minor” orders have from some hundreds of to a few thousand described species. Although an order may be described as minor, this does not mean that it is insignificant: the familiar earwig belongs to an order (Dermaptera) with fewer

than 2000 described species and the ubiquitous cockroaches belong to an order (Blattodea, including termites) with only about 6600 species. Nonetheless, there are only twice as many species described in Aves (birds) as in the “small” order Blattodea.

1.3.2 The estimated taxonomic richness of insects

Surprisingly, the figures given above, which represent the cumulative effort by many insect taxonomists from all parts of the world over some 250 years, appear to represent something less than the true species richness of the insects. Just how far short is the subject of continuing speculation. Given the very high numbers and the patchy distributions of many insects in time and space, it is impossible in our timescales to inventory (count and document) all species, even for a small area. Extrapolations are required to estimate total species richness, which range from some 3 million to as many as 80 million species. These various calculations either extrapolate ratios for richness in one taxonomic group (or area) to another unrelated group (or area), or use a hierarchical scaling ratio, extrapolated from a subgroup (or subordinate area) to a more inclusive group (or wider area).

Generally, ratios derived from temperate/tropical species numbers for well-known groups such as vertebrates provide rather conservatively low estimates if used to extrapolate from temperate insect taxa to essentially unknown tropical insect faunas. The most controversial estimation, based on hierarchical scaling and providing the highest estimated total species numbers, was an extrapolation from samples from a single tree species to global rainforest insect species richness. Sampling used insecticidal fog to assess the little-known fauna of the upper layers (the canopy) of Neotropical rainforest. Much of this estimated increase in species richness was derived from arboreal beetles (Coleoptera), but several other canopy-dwelling groups were much more numerous than believed previously. Key factors in calculating tropical diversity included identification of the number of beetle species found, estimation of the proportion of novel (previously unseen) groups, allocation to feeding groups, estimation of the degree of host-specificity to the surveyed tree species, and the ratio of beetles to other arthropods. Certain assumptions have been tested and found to be suspect: notably, host-plant specificity of herbivorous insects, at

least in some tropical forest, seems very much less than estimated early in this debate.

Estimates of global insect diversity calculated from experts' assessments of the proportion of undescribed versus described species amongst their study insects tend to be comparatively low. Belief in lower numbers of species comes from our general inability to confirm the prediction, which is a logical consequence of the high species-richness estimates, that insect samples ought to contain very high proportions of previously unrecognized and/or undescribed ("novel") taxa. Obviously any expectation of an even spread of novel species is unrealistic, since some groups and regions of the world are poorly known compared to others. However, amongst the minor (less species-rich) orders there is little or no scope for dramatically increased, unrecognized species richness. Very high levels of novelty, if they exist, realistically could only be amongst the Coleoptera, drab-colored Lepidoptera, phytophagous Diptera, and parasitic Hymenoptera.

Some (but not all) recent re-analyses tend towards lower estimates derived from taxonomists' calculations and extrapolations from regional sampling rather than those derived from ecological scaling: a figure of between 4 and 6 million species of insects appears realistic.

1.3.3 The location of insect species richness

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

Despite the lack of necessary local species inventories to prove it, tropical species richness appears to be much higher than that of temperate areas. For example, a single tree surveyed in Peru produced 26 genera and 43 species of ants: a tally that equals the total ant

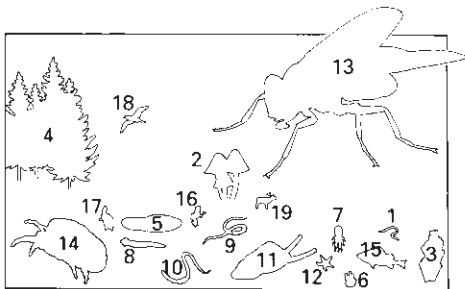
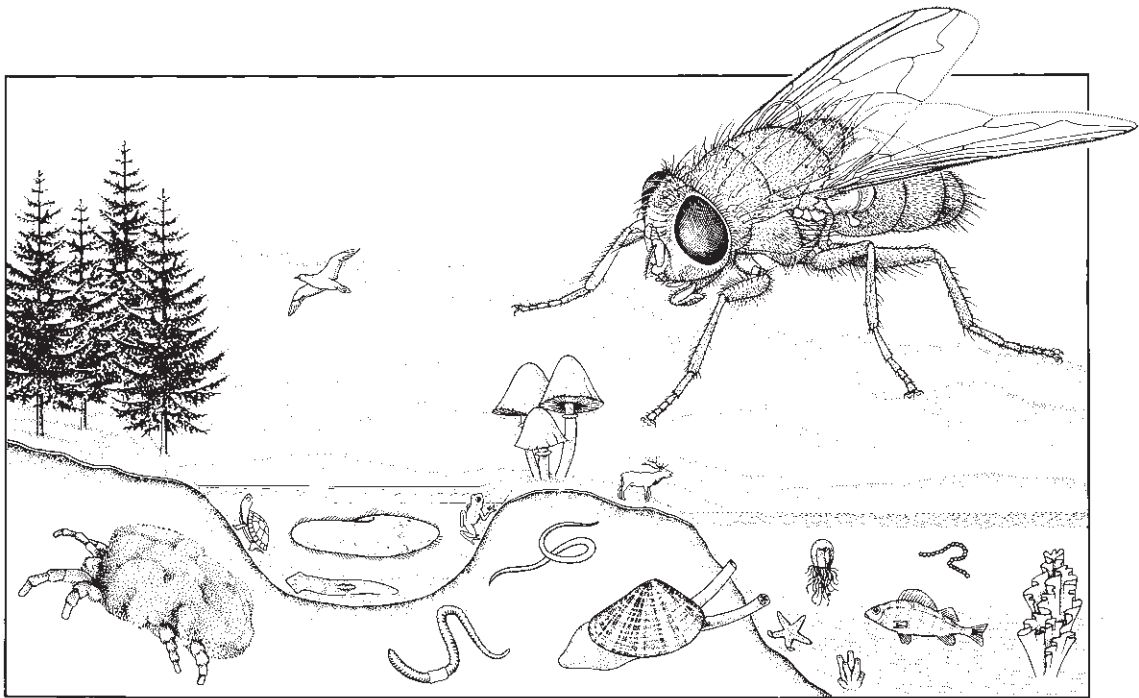
diversity from all habitats in Britain. Our inability to be certain about finer details of geographical patterns stems in part from the inverse relationship between the distribution of entomologists interested in biodiversity issues (the temperate northern hemisphere) and the centers of richness of the insects themselves (the tropics and southern hemisphere).

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

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

1.3.4 Some reasons for insect species richness

Whatever the global estimate is, insects surely are remarkably speciose. This high species richness has been attributed to several factors. The small size of insects, a limitation imposed by their method of gas exchange via tracheae, is an important determinant. Many more niches exist in any given environment for small organisms than for large organisms. Thus, a single acacia tree, that provides one meal to a giraffe, may support the complete life cycle of dozens of insect species; a lycaenid butterfly larva chews the leaves, a bug sucks the stem sap, a longicorn beetle bores into the wood, a midge galls the flower buds, a bruchid beetle destroys the seeds, a mealybug sucks the root



- | | |
|----------------------------------|--|
| 1 Prokaryotes | 5 Protozoa |
| 2 Fungi | 6 Porifera (sponges) |
| 3 Algae | 7 Cnidaria (jellyfish, corals, etc.) |
| 4 Plantae (multicellular plants) | 8 Platyhelminthes (flatworms) |
| | 9 Nematoda (roundworms) |
| | 10 Annelida (earthworms, leeches, etc.) |
| | 11 Mollusca (snails, bivalves, octopus, etc.) |
| | 12 Echinodermata (starfish, sea urchins, etc.) |
| | 13 Insecta |
| | 14 Non-insect Arthropoda |
| | 15 Pisces (fish) |
| | 16 Amphibia (frogs, salamanders, etc.) |
| | 17 Reptilia (snakes, lizards, turtles) |
| | 18 Aves (birds) |
| | 19 Mammalia (mammals) |

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

sap, and several wasp species parasitize each host-specific phytophage. An adjacent acacia of a different species feeds the same giraffe but may have a very different suite of phytophagous insects. The environment can be said to be more fine-grained from an insect perspective compared to that of a mammal or bird.

Small size alone is insufficient to allow exploitation of this environmental heterogeneity, since organisms must be capable of recognizing and responding to environmental differences. Insects have highly organized sensory and neuro-motor systems more comparable to those of vertebrate animals than other invertebrates.

However, insects differ from vertebrates both in size and in how they respond to environmental change. Generally, vertebrate animals are longer lived than insects and individuals can adapt to change by some degree of learning. Insects, on the other hand, normally respond to, or cope with, altered conditions (e.g. the application of insecticides to their host plant) by genetic change between generations (e.g. leading to insecticide-resistant insects). High genetic heterogeneity or elasticity within insect species allows persistence in the face of environmental change. Persistence exposes species to processes that promote speciation, predominantly involving phases of range expansion and/or subsequent fragmentation. Stochastic processes (genetic drift) and/or selection pressures provide the genetic alterations that may become fixed in spatially or temporally isolated populations.

Insects possess characteristics that expose them to other potential diversifying influences that enhance their species richness. Interactions between certain groups of insects and other organisms, such as plants in the case of herbivorous insects, or hosts for parasitic insects, may promote the genetic diversification of eater and eaten (section 8.6). These interactions are often called coevolutionary and are discussed in more detail in Chapters 11 and 13. The reciprocal nature of such interactions may speed up evolutionary change in one or both partners or sets of partners, perhaps even leading to major radiations in certain groups. Such a scenario involves increasing specialization of insects, at least on plant hosts. Evidence from phylogenetic studies suggests that this has happened, but also that generalists may arise from within a specialist radiation, perhaps after some plant chemical barrier has been overcome. Waves of specialization followed by breakthrough and radiation must have been a major factor in promoting the high species richness of phytophagous insects.

Another explanation for the high species numbers of insects is the role of sexual selection in the diversification of many insects. The propensity of insects to become isolated in small populations (because of the fine scale of their activities) in combination with sexual selection (sections 5.3 and 8.6) may lead to rapid alteration in intra-specific communication. When (or if) the isolated population rejoins the larger parental population, altered sexual signaling deters hybridization and the identity of each population (incipient species) is maintained in sympatry. This mechanism is seen to be much more rapid than genetic drift or other forms

of selection, and need involve little if any differentiation in terms of ecology or non-sexual morphology and behavior.

Comparisons amongst and between insects and their close relatives suggest some reasons for insect diversity. We can ask what are the shared characteristics of the most speciose insect orders, the Coleoptera, Hymenoptera, Diptera, and Lepidoptera? Which features of insects do other arthropods, such as arachnids (spiders, mites, scorpions, and their allies) lack? No simple explanation emerges from such comparisons; probably design features, flexible life-cycle patterns, and feeding habits play a part (some of these factors are explored in Chapter 8). In contrast to the most speciose insect groups, arachnids lack winged flight, complete transformation of body form during development (metamorphosis) and dependence on specific food organisms, and generally are not phytophagous. Exceptionally, mites, the most diverse and abundant of arachnids, have many very specific associations with other living organisms, including plants.

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

Barriers to large size include the inability of the tracheal system to diffuse gases across extended distances from active muscles to and from the external environment (Box 3.2). Further elaborations of the tracheal system would jeopardize water balance in a

large insect. Most large insects are narrow and have not greatly extended the maximum distance between the external oxygen source and the muscular site of gaseous exchange, compared with smaller insects. A possible explanation for the gigantism of some Palaeozoic insects is considered in section 8.2.1.

In summary, many insect radiations probably depended upon (a) the small size of individuals, combined with (b) short generation time, (c) sensory and neuro-motor sophistication, (d) evolutionary interactions with plants and other organisms, (e) metamorphosis, and (f) mobile winged adults. The substantial time since the origin of each major insect group has allowed many opportunities for lineage diversification (Chapter 8). Present-day species diversity results from either higher rates of speciation (for which there is limited evidence) and/or lower rates of species extinction (higher persistence) than other organisms. The high species richness seen in some (but not all) groups in the tropics may result from the combination of higher rates of species formation with high accumulation in equable climates.

1.4 NAMING AND CLASSIFICATION OF INSECTS

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

anywhere, whatever the local name (and there are many) for this disease-transmitting mosquito. Ideally, all taxa should have such a Latinized binomen, but in practice some alternatives may be used prior to naming formally (section 17.3.2).

In scientific publications, the species name often is followed by the name of the original describer of the species and perhaps the year in which the name first was published legally. In this textbook, we do not follow this practice but, in discussion of particular insects, we give the order and family names to which the species belongs. In publications, after the first citation of the combination of genus and species names in the text, it is common practice in subsequent citations to abbreviate the genus to the initial letter only (e.g. *A. aegypti*). However, where this might be ambiguous, such as for the two mosquito genera *Aedes* and *Anopheles*, the initial two letters *Ae.* and *An.* are used, as in Chapter 15.

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

Depending on the classification system used, some 25 to 30 orders of Insecta may be recognized. Differences arise principally because there are no fixed rules for deciding the taxonomic ranks referred to above; only general agreement that groups should be monophyletic, comprising all the descendants of a common ancestor (section 7.1.1). Orders have been recognized rather arbitrarily in the past two centuries, and the most that can be said is that presently constituted orders contain similar insects differentiated from other insect groups. Over time, a relatively stable classification system has developed but differences of opinion

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

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

remain as to the boundaries around groups, with “splitters” recognizing a greater number of groups and “lumpers” favoring broader categories. For example, some North American taxonomists group (“lump”) the alderflies, dobsonflies, snakeflies, and lacewings into one order, the Neuroptera, whereas others, including ourselves, “split” the group and recognize three separate (but clearly closely related) orders, Megaloptera, Raphidioptera, and a more narrowly defined Neuroptera (Fig. 7.2). The order Hemiptera sometimes was divided into two orders, Homoptera and Heteroptera, but the homopteran grouping is invalid (non-monophyletic) and we advocate a different classification for these bugs shown in Fig. 7.6 and discussed in section 7.4.2 and Taxobox 20 at the end of the book. New data and methods of analysis are further causes of instability in the recognition of insect orders. As we show in Chapter 7, two groups (termites and parasitic lice) previously treated as orders, belong within each of two other orders and thus the ordinal count is reduced by two.

In this book we recognize 28 orders for which relationships are considered in section 7.4, and the physical characteristics and biologies of their constituent taxa are described in taxoboxes in the section at the end of the book. A summary of the diagnostic features of all 28 orders and a few subgroups, plus cross references to fuller identificatory and ecological information, appear in tabular form in the reference guide to orders in the Appendix (placed after the Index).

1.5 INSECTS IN POPULAR CULTURE AND COMMERCE

People have been attracted to the beauty or mystique of certain insects throughout time. We know the importance of scarab beetles to the Egyptians as religious items, but earlier shamanistic cultures elsewhere in the Old World made ornaments that represent scarabs and other beetles, including buprestids (jewel beetles). In Old Egypt the scarab, which shapes dung into balls, is identified as a potter; similar insect symbolism extends also further east. Egyptians, and subsequently the Greeks, made ornamental scarabs from many materials including lapis lazuli, basalt, limestone, turquoise, ivory, resins, and even valuable gold and silver. Such adulation may have been the pinnacle that an insect lacking economic importance ever gained in popular and religious culture, although many human societies recognized insects in their ceremonial lives. The ancient Chinese regarded cicadas as symbolizing rebirth or immortality. In Mesopotamian literature the *Poem of Gilgamesh* alludes to odonates (dragonflies/damselflies) as signifying the impossibility of immortality. In martial arts the swaying and sudden lunges of a praying mantis are evoked in Chinese praying mantis kungfu. The praying mantis carries much cultural symbolism, including creation and patience in zen-like waiting for the San (“bushmen”) of the Kalahari. Honey ants (*yarumpa*) and witchety grubs (*udnirringitta*) figure amongst the personal or clan totems of Aboriginal Australians of the Arrernte language groups. Although important as food in the arid central Australian environment (see section 1.6.1), these insects were not to be eaten by clan members belonging to that particular totem.

Totemic and food insects are represented in many Aboriginal artworks in which they are associated with cultural ceremonies and depiction of important locations. Insects have had a place in many societies for their symbolism, such as ants and bees representing hard workers throughout the Middle Ages of Europe, where they even entered heraldry. Crickets, grasshoppers, cicadas, and scarab and lucanid beetles have long been valued as caged pets in Japan. Ancient Mexicans observed butterflies in detail, and lepidopterans were well represented in mythology, including in poem and song. Amber has a long history as jewellery, and the inclusion of insects can enhance the value of the piece.

Most urbanized humans have lost much of this contact with insects, excepting those that share our domicile, such as the cockroaches, tramp ants, and hearth crickets that generally arouse antipathy. Nonetheless, specialized exhibits of insects – notably in butterfly farms and insect zoos – are very popular, with millions of people per year visiting such attractions throughout the world. Also, insects are still very much part of Japanese culture, especially but not only for children; there are insect video games, numerous suppliers of entomological equipment, thousands of personal insect collections, and beetle breeding and rearing is so popular that it can be called beetlemania. In other countries, natural occurrences of certain insects attract ecotourism, including aggregations of overwintering monarch butterflies in coastal central California and Mexico, the famous glowworm caves of Waitomo, New Zealand, and Costa Rican locations such as Selva Verde representing tropical insect biodiversity.

Although insect ecotourism may be in its infancy, other economic benefits are associated with interest in insects. This is especially so amongst children in Japan, where native rhinoceros beetles (Scarabaeidae, *Allomyrina dichotoma*) sell for \$3–7 each, and longer-lived common stag beetles for some \$10, and may be purchased from automatic vending machines. Adults collect too with a passion: a 7.5 cm example of the largest Japanese stag beetles (Lucanidae, *Dorcus curvidens*, called *o-kuwagata*) may sell for between 40,000 and 150,000 yen (\$300 and \$1250), depending on whether captive reared or taken from the wild. Largest specimens, even if reared, have fetched several million yen (>\$10,000) at the height of the craze. Such enthusiasm by Japanese collectors can lead to a valuable market for insects from outside Japan. According to official statistics, in 2002 some 680,000 beetles, including over 300,000 each of rhinoceros and stag beetles, were imported, predominantly originating from southern and Southeast Asia. Enthusiasm for valuable specimens extends outside Coleoptera: Japanese and German tourists are reported to buy rare butterflies in Vietnam for \$1000–2000, which is a huge sum of money for the generally poor local people.

Entomological revenue can enter local communities and assist in natural habitat conservation when tropical species are reared for living butterfly exhibits in the affluent world. An estimated 4000 species of butterflies have been reared in the tropics and exhibited live in butterfly houses in North America, Europe, Malaysia, and Australia. Farming butterflies for export

provides economic benefits in Papua New Guinea and Kenya, and sales from Costa Rica are estimated to be in excess of \$1 million per year. Eggs or wild-caught larvae are reared on appropriate host plants, grown until pupation, and then freighted by air to the increasingly popular live butterfly exhibits of North America and Europe. Papilionidae, including the well-known swallowtails, graphiums, and birdwings, are most popular, but research into breeding requirements now allows an expanded range of potential exhibits to be located, reared, and shipped. In East Africa, the National Museums of Kenya in collaboration with many biodiversity programs supported local people of the Arabuko-Sukoke forest-edge in the Kipepeo Project to export harvested butterflies for live overseas exhibition. Commenced in 1993, and self-sustaining since 1999, the project has provided an enhanced income for these otherwise impoverished people, and has supported further nature-based projects including honey production.

In Asia, particularly in Malaysia, there is interest in rearing, exhibiting, and trading in mantises (Mantodea), including orchid mantises (*Hymenopus* species; see sections 13.1.1 and 14.1) and stick-insects (Phasmatodea). Hissing cockroaches from Madagascar and burrowing cockroaches from tropical Australia are reared readily in captivity and can be kept as domestic pets as well as being displayed in insect zoos in which handling the exhibits is encouraged.

Questions remain concerning whether wild insect collection, either for personal interest or commercial trade and display, is sustainable. Much butterfly, dragonfly, stick-insect, and beetle trade relies more on collections from the wild than rearing programs, although this is changing as regulations increase and research into rearing techniques continues. In the Kenyan Kipepeo Project, although specimens of preferred lepidopteran species originate from the wild as eggs or early larvae, walk-through visual assessment of adult butterflies in flight suggested that the relative abundance rankings of species was unaffected regardless of many years of selective harvest for export. Furthermore, local appreciation has increased for intact forest as a valuable resource rather than viewing it as “wasted” land to clear for subsistence agriculture. In Japan, although expertise in captive rearing has increased and thus undermined the very high prices paid for certain wild-caught beetles, wild harvesting continues over an ever-increasing region. The possibility of over-collection for trade is

discussed in section 1.8, together with other conservation issues.

1.6 INSECTS AS FOOD

1.6.1 Insects as human food: entomophagy

In this section we review the increasingly popular study of insects as human food. Probably 1000 or more species of insects in more than 370 genera and 90 families are or have been used for food somewhere in the world, especially in central and southern Africa, Asia, Australia, and Latin America. Food insects generally feed on either living or dead plant matter, and chemically protected species are avoided. Termites, crickets, grasshoppers, locusts, beetles, ants, bee brood, and moth larvae are frequently consumed insects. Although insects are high in protein, energy, and various vitamins and minerals, and can form 5–10% of the annual animal protein consumed by certain indigenous peoples, Western society essentially overlooks entomological cuisine.

Typical “Western” repugnance of entomophagy is cultural rather than scientific or rational. After all, other invertebrates such as certain crustaceans and mollusks are favored culinary items. Objections to eating insects cannot be justified on the grounds of taste or food value. Many have a nutty flavor and studies

report favorably on the nutritional content of insects, although their amino acid composition needs to be balanced with suitable plant protein. Nutritional values obtained from analyses conducted on samples of four species of insects cooked according to traditional methods in central Angola, Africa are shown in Table 1.2. The insects concerned are: reproductive individuals of a termite, *Macrotermes subhyalinus* (Blattodea: Termitidae), which are de-winged and fried in palm oil; the large caterpillars of two species of moth, *Imbrasia ertli* and *Usta terpsichore* (Lepidoptera: Saturniidae), which are de-gutted and either cooked in water, roasted, or sun-dried; and the larvae of the palm weevil, *Rhynchophorus phoenicis* (Coleoptera: Curculionidae), which are slit open and then fried whole in oil.

Mature larvae of *Rhynchophorus* species have been appreciated by people in tropical areas of Africa, Asia, and the Neotropics for centuries. These fat, legless grubs (Fig. 1.2), often called palmworms, provide one of the richest sources of animal fat, with substantial amounts of riboflavin, thiamine, zinc, and iron (Table 1.2). Primitive cultivation systems, involving the cutting down of palm trees to provide suitable food for the weevils, are known from Brazil, Colombia, Paraguay, and Venezuela. In plantations, however, palmworms are regarded as pests because of the damage they can inflict on coconut and oil palm trees.

In central Africa, the people of southern Zaire (presently Democratic Republic of Congo) eat caterpillars

Table 1.2 Proximate, mineral, and vitamin analyses of four edible Angolan insects (percentages of daily human dietary requirements/100 g of insects consumed). (After Santos Oliveira et al. 1976, as adapted by DeFoliart 1989.)

Nutrient	Requirement per capita (reference person)	<i>Macrotermes subhyalinus</i> (Termitidae)	<i>Imbrasia ertli</i> (Saturniidae)	<i>Usta terpsichore</i> (Saturniidae)	<i>Rhynchophorus phoenicis</i> (Curculionidae)
Energy	2850 kcal	21.5%	13.2%	13.0%	19.7%
Protein	37 g	38.4	26.3	76.3	18.1
Calcium	1 g	4.0	5.0	35.5	18.6
Phosphorus	1 g	43.8	54.6	69.5	31.4
Magnesium	400 mg	104.2	57.8	13.5	7.5
Iron	18 mg	41.7	10.6	197.2	72.8
Copper	2 mg	680.0	70.0	120.0	70.0
Zinc	15 mg	–	–	153.3	158.0
Thiamine	1.5 mg	8.7	–	244.7	201.3
Riboflavin	1.7 mg	67.4	–	112.2	131.7
Niacin	20 mg	47.7	–	26.0	38.9

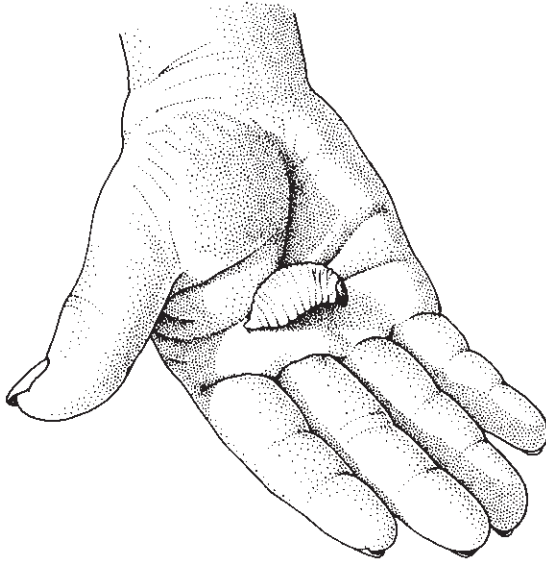


Fig. 1.2 A mature larva of the palm weevil, *Rhynchophorus phoenicis* (Coleoptera: Curculionidae), a traditional food item in central Angola, Africa. (Larva after Santos Oliveira et al. 1976.)

belonging to 20–30 species. The calorific value of these caterpillars is high, with their protein content ranging from 45 to 80%, and they are a rich source of iron. For instance, caterpillars are the most important source of animal protein in some areas of the Northern Province of Zambia. The edible caterpillars of species of *Imbrasia* (Saturniidae), an emperor moth, locally called mumpa, provide a valuable market. The caterpillars contain 60–70% protein on a dry-matter basis and offset malnutrition caused by protein deficiency. Mumpa are fried fresh or boiled and sun-dried prior to storage. Further south in Africa, *Imbrasia belina* moth caterpillars, called mopane, mopanie, mophane, or phane, are utilized widely. Caterpillars usually are de-gutted, boiled, sometimes salted, and dried. After processing they contain about 50% protein and 15% fat – approximately twice the values for cooked beef. Concerns that harvest of mopane may be unsustainable and over-exploited are discussed under conservation in Box 1.3, below.

In the Philippines, June beetles (melolonthine scarabs), weaver ants (*Oecophylla smaragdina*), mole crickets, and locusts are eaten in some regions. Locusts form an important dietary supplement during outbreaks, which

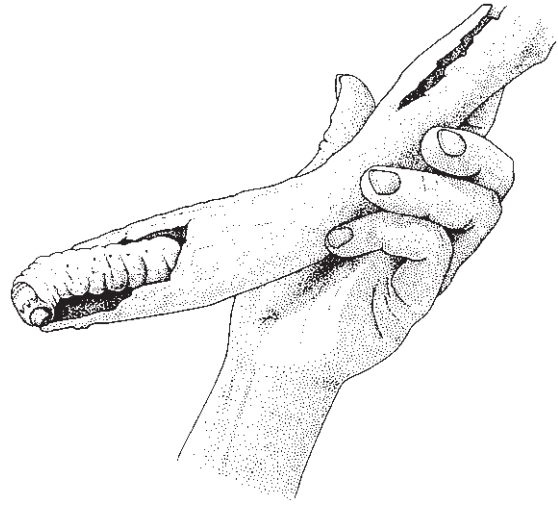


Fig. 1.3 A delicacy of the Australian Aborigines: a witchety (or witjuti) grub, a caterpillar of a wood moth (Lepidoptera: Cossidae) that feeds on the roots and stems of witjuti bushes (certain *Acacia* species). (After Cherikoff & Isaacs 1989.)

apparently have become less common since the widespread use of insecticides. Various species of grasshoppers and locusts were eaten commonly by native tribes in western North America prior to the arrival of Europeans. The number and identity of species used have been poorly documented, but species of *Melanoplus* were consumed. Harvesting involved driving grasshoppers into a pit in the ground by fire or advancing people, or herding them into a bed of coals. Today people in Central America, especially Mexico, harvest, sell, cook, and consume grasshoppers.

Australian Aborigines use (or once used) a wide range of insect foods, especially moth larvae. The caterpillars of wood or ghost moths (Cossidae and Hepialidae) (Fig. 1.3) are called witchety grubs from an Aboriginal word “witjuti” for the *Acacia* species (wattles) on the roots and stems of which the grubs feed. Witchety grubs, which are regarded as a delicacy, contain 7–9% protein, 14–38% fat, and 7–16% sugars as well as being good sources of iron and calcium. Adults of the bogong moth, *Agrotis infusa* (Noctuidae), formed another important Aboriginal food, once collected in their millions from aestivating sites in narrow caves and crevices on mountain summits in south-eastern Australia. Moths cooked in hot ashes provided a rich source of dietary fat.