PREFACE TO THE FIFTH EDITION

In the preface to the previous (fourth) edition of this textbook, we predicted several changes to the discipline of the study of insects – entomology. For many, we were correct, for good and bad. Most changes are associated with human activities, including warming of the planet but also including global trade, such that we have written a new chapter entitled "Insects in a changing world". Insects clearly respond to changes in climate, and this is of immediate concern for the spread of insect-borne diseases affecting our crops, our domestic animals and us. However, at least of equal significance are the insect range expansions associated with trade, as depicted on the cover of this book. Increased global commerce ("free trade") brings with it many accidental passenger insects that impact agriculture and the natural environment, but we did not foresee how many of these would damage our timber industries and landscape trees. Biosecurity, involving increased surveillance at our ports, airports and land borders, is a growing industry requiring personnel trained in entomology. Without such vigilance, we will have pests "without borders" in a homogeneous agricultural world.

We foresaw that increasingly sophisticated molecular genetic techniques would transform many areas of entomology. These studies have particularly informed our ideas of evolutionary relationships at all levels. Our understanding of the relationships among orders has been strengthened in the past five years, and there is much less uncertainty. For example, we are now confident that the hexapods, to which the insects belong, evolved from within the Crustacea, thus forming a group Pancrustacea. Closer to tips of insect phylogenetic trees, the true diversity at species level is being revealed with molecular techniques, including the use of "DNA barcoding". Modelling techniques of increasing sophistication allow exploration of the rate of molecular evolution, which in conjunction with critically examined fossil insects, provide increasingly reliable estimates of the tempo of insect evolution over the past 400 million years.

The relative ease and ever-lower costs of genomics have seen an "explosion" in "whole genomes" across a diversity of species, allowing comparative studies and also to understand the genetic cascades and controllers that shape the physiology and morphology of insects. We are selective in presenting these studies – they are so numerous and yet remain exploratory and not definitive across the whole of the hexapods.

Chapter texts are updated and supplemented with many new boxes and illustrations. In the opening chapter we report some of the dynamism given to the field by "non-mainstream" insect lovers, from recording schemes and citizen scientists to the managers of insect houses. Inevitably, we have to document the effects of insects spreading and damaging plants of interest to us, namely ornamental and environmental trees, including palms, and most worryingly, high-quality Arabica coffee.

This fifth edition was written in Australia, where we are grateful for academic status in the Division of Evolution, Ecology and Genetics of the Research School of Biology at the Australian National University (ANU), Canberra. We retain emeritus status at the Department of Entomology and Nematology at the University of California, Davis, which provides us with remote access to the wonderful online resources of the University of California library system. We thank both institutions for their support.

We are grateful to the following colleagues worldwide (listed alphabetically) for providing information, literature or ideas on many aspects of insect biology and phylogeny: Richard Cornette, Jeff Garnas, Penny

Greenslade, Mark Hoddle, Matt Krosch, Laurence Mound, Karen Meusemann, Mike Picker, Kathy Su, You-Ning Su, Gary Taylor, Alice Wells, Shaun Winterton and Andreas Zwick. The following people kindly gave permission to use one or more of their photographs in the reinstated and expanded colour plates: Denis Anderson, Nicholas Carlile, David Carter, Meredith Cosgrove, Mike Crisp, Janice Edgerly-Rooks, Mark Hoddle, Takumasa Kondo, Mike Lewis, Mamoru Matsuki, Rolf Oberprieler, Rod Peakall, David Rentz, Don Sands, Greg Sherley, Robert Sites, Richard Vane-Wright, Phil Ward, Alex Wild, Alan Yen and Paul Zborowski.

As with every edition of this textbook since 1996, were are so pleased that Karina McInnes (http://www.spilt-ink.com) revived 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. As always, we are grateful to the staff at Wiley-Blackwell, especially Ward Cooper and Kelvin Matthews for their continued support and excellent service, and Audrie Tan who was our production editor in Singapore. We were fortunate to have freelance editor Katrina Rainey to copy edit, as she did our 3rd edition.

PREFACE TO THE FOURTH EDITION

In the five 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 three-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 polydnaviruses; 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.