EVOLUTION OF THE INSECTS

Insects are the most diverse group of organisms to appear in the 3-billion-year history of life on Earth, and the most ecologically dominant animals on land. This book chronicles, for the first time, the complete evolutionary history of insects: their living diversity, relationships, and 400 million years of fossils. Whereas other volumes have focused on either living species *or* fossils, this is the first comprehensive synthesis of *all* aspects of insect evolution. Current estimates of phylogeny are used to interpret the 400-million-year fossil record of insects, their extinctions, and radiations. Introductory sections include the living species, diversity of insects, methods of reconstructing evolutionary relationships, basic insect structure, and the diverse modes of insect fossilization and major fossil deposits. Major sections cover the relationships and evolution of each order of hexapod. The book also chronicles major episodes in the evolutionary history of insects: their modest beginnings in the Devonian, the origin of wings hundreds of millions of years before pterosaurs and birds, the impact that mass extinctions and the explosive radiation of angiosperms had on insects, and how insects evolved the most complex societies in nature.

Evolution of the Insects is beautifully illustrated with more than 900 photo- and electron micrographs, drawings, diagrams, and field photographs, many in full color and virtually all original. The book will appeal to anyone engaged with insect diversity: professional entomologists and students, insect and fossil collectors, and naturalists.

David Grimaldi has traveled in 40 countries on 6 continents collecting and studying recent species of insects and conducting fossil excavations. He is the author of *Amber: Window to the Past* and is Curator of Invertebrate Zoology at New York's American Museum of Natural History, as well as an adjunct professor at Cornell University, Columbia University, and the City University of New York.

Michael S. Engel has visited numerous countries for entomological and paleontological studies, focusing most of his field work in Central Asia, Asia Minor, and the Western Hemisphere. In addition to his positions as Associate Professor in the Department of Ecology and Evolutionary Biology and Associate Curator in the Division of Entomology of the Natural History Museum at the University of Kansas, he is a Research Associate of the American Museum of Natural History and a Fellow of the Linnean Society of London.

David Grimaldi and Michael S. Engel have collectively published more than 250 scientific articles and monographs on the relationships and fossil record of insects, including 10 articles in the journals *Science, Nature,* and *Proceedings of the National Academy of Sciences.*

Evolution of the Insects

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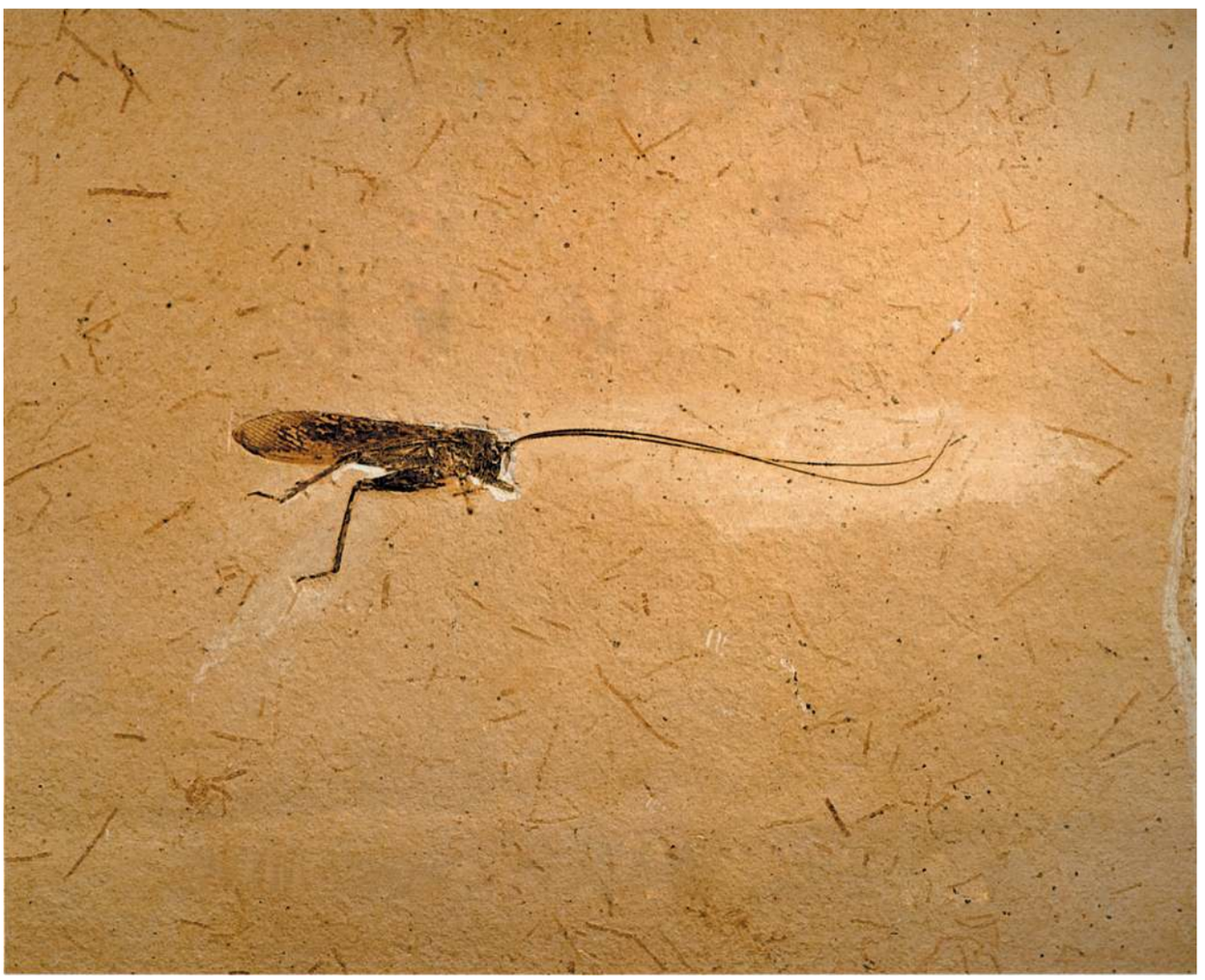

An orthopteran of the extinct family Elcanidae in 120 MYO limestone from Brazil's Santana Formation. AMNH; length of elcanid (including antennae) 98 mm(3.8 in.).

For the entomophiles,

winged and larval

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PREFACE

Writing a book on a subject as vast as the evolution of the most diverse lineage of organisms had one simple justification for us: it was needed. Having taught Insect Diversity and Insect Systematics at the City University of New York, Columbia University, Cornell University, and the University of Kansas, we became acutely aware of a gaping hole in entomology. No volume integrates the unprecedented diversity of living and extinct insects, particularly within the evolutionary framework of phylogeny. Some excellent texts, popular books, and field guides cover insect identification, structure, and living diversity, as well as physiology, behavior, and general biology, of which *The Insects of Australia* (Naumann, 1991a) is perhaps the best example. For our lectures to students we thus found ourselves pulling an extremely scattered literature together. Instead of trudging through the insect families – interesting as they are – we found that students were fascinated by an approach of folding Recent insect diversity into one large context of phylogeny, biogeography, ecology, and the fossil record. The big picture engaged them. After four years of intensive literature research and writing, study and imaging of important museum specimens, and thousands of figures, we like to think we've succeeded in our goal.

Our approach to the volume was tempered by our own experience and interests with fossil insects. Entomologists typically ignore fossils, and since we too work on speciose groups of living insects, we have always been intrigued by the dismissiveness of most entomologists. Why ignore such illuminating parts of evolutionary history? We hope that this book will reveal to our colleagues the significance, and even esthetics, of insect fossils. There are several comprehensive treatments of the insect fossil record, particularly the hexapod section of the *Treatise on Invertebrate Paleontology* (Carpenter, 1992) and the more recent *History of Insects* by Rasnitsyn and Quicke (2002). But these volumes are devoted entirely to fossil insects, so something more inclusive, and accessible, was needed.

Compiling a book like this is humbling, not only because of the scope of the subject, but also because discoveries and new work reported every month in paleontology and insect systematics continually revise the field. As this book was nearing completion, for example, two large projects were launched. One of these is the U.S. National Science Foundation's *Tree of Life* project, which seeks to examine the phylogeny of major groups of organisms using all existing data and vast new morphological and DNA data. The other is the Dresden conference on insect phylogeny, which met for the first time in 2003 (e.g., Klass, 2003), and which is intended to meet every few years. Like the insects themselves, our understanding is thus evolving. As more genes become sequenced for hundreds more species of insects, for example, phylogenetic hypotheses will be revised, or at least discussed. But, thirty years ago a book like this would have been very different and much slimmer. Our knowledge of insect relationships has advanced tremendously over this period of time, and dozens of spectacular fossil deposits of insects have been discovered. Tomorrow's discoveries will reinforce, revise, and entirely redefine our present knowledge, but one needs to start somewhere. The optimal moment is always elusive. We hope that thirty years from now – indeed, twenty – much of what we present here will not fall far from the mark. Should we be so fortunate, new editions of this volume will attempt to keep abreast of developments.

Working at the American Museum of Natural History has also given us a keen appreciation for appealing to the nascent naturalist and scientist, not only to the landed professional. We were very deliberate in developing a volume that would be visually engaging to insect and fossil collectors, general naturalists, botanists, and other biologists, as well as to student and professional entomologists. Although we tried to avoid the thick jargon of entomology and systematics, it was not entirely avoidable (some of the jargon is useful), and we hope our colleagues will understand this was done deliberately to make the subject more digestible. The nearly 1,000 images were also included to make the book more engaging. Should the images and captions whet the reader's appetite, a healthy meal of text is also available.

A volume like this would not have been possible without the assistance of authoritative colleagues around the world,

who kindly reviewed large chunks of text. These authorities include: chapter 1: Lee Herman, Valerie Schawaroch, and Craig Gibbs; chapter 2: Derek Briggs (fossilization) and Vladimir Blagoderov (deposits); chapter 4: Ismael A. Hinojose-Dìaz; chapter 5: Michael Ohl; chapter 7: Daniel J. Bennett, George W. Byers, and Kumar and Valerie Krishna (termites); chapter 8: Niels P. Kristensen, Lance Durden (Phthiraptera), Bruce Heming (Thysanoptera), Penny Gullan (Sternorrhyncha), and Nils Møller Andersen (Heteroptera); chapter 9: Michael Ohl; chapter 10: Lee Herman, Caroline Chaboo, Jim Liebherr, Marc Branham, and Jeyaraney Kathirithamby; chapter 11: Ricardo Ayala and Charles D. Michener; chapter 12: George Byers (Mecoptera), Robert Lewis (Siphonaptera), and Dalton Amorim and Vladimir Blagoderov (Diptera); chapter 13: Niels Kristensen (entire), David Wagner and Eric Quinter (Lepidoptera), and Phil DeVries (butterflies); chapter 14: Dalton S. Amorim, Amy Berkov, Peter Cranston (entire), and William L. Crepet (angiosperms). Charles D. Michener and Molly G. Rightmyer generously reviewed various sections. We take all responsibility for the final version of the book since, in a few cases, we felt compelled to disagree with reviewers.

Numerous colleagues and institutions loaned images: Alex Rasnitsyn; Bryn Mawr College; Carl Rettenmeyer; Carlos Brandão; Caroline Chaboo; Carsten Brauckmann; Deutsche Entomologische Institut; Thomas D. Seeley; Dieter Waloszek; Enrique Peñalver; Helmut Sturm; Holger H. Dathe; Horst and Ulrike Aspöck; Jim Davis; Librarians of the American Museum of Natural History, particularly Mary DeJong; Liz Brozius; Michael Dolan; Nick Fraser; Bibliothèque Centrale of the Museum National d'Histoire Naturelle; Ray Swanson; *Science News*; Scott Elias; University of Massachusetts, Amherst; Wilfried Wichard; and Xavier Martínez-Delclòs. In this regard, we are particulary grateful for being able to use the portraits of important entomologists provided by George W. Byers and the many beautiful images of living insects and of entomologists provided by our colleagues Phil DeVries, Janice Edgerly-Rooks, Valerie Giles, Steve Marshall, Cristina Sandoval, Ray Swanson, and Alex Wild.

We are also grateful to the many individuals who assisted us in our museum travels to examine important specimens, particularly Peter Jell (Queensland Museum), Robert Jones (Australian Museum), Phil Perkins (Harvard University), Alexandr P. Rasnitsyn (Paleontological Institute, Moscow), Andrew J. Ross (Natural History Museum, London), and Tim White (Yale University). Many people provided loans and gifts of specimens: Dalton Amorim, David Wagner, Jeff Cumming, Jens von Holt, Jeyaraney Kathirithamby, Keith Luzzi, Ken Christiansen, Klaus-Dieter Klass, Lance Durden, Mike Picker, Penny Gullan, Robert Lewis, Roy Larimer, Susan Hendrickson, and the late Jake Brodzinsky. We are extremely grateful for the hard work and generosity of the New Jersey amber collectors, particularly Keith Luzzi, Paul Nascimbene and the late Steve Swolensky. Roy Larimer and Keith Luzzi have been extremely generous with their time and resources in the field, and they are two of the finest field workers we know.

Particularly generous were Dr. Herbert Axelrod and Dott. Ettore Morone. Dr. Axelrod donated the collection of Santana Formation fossils to the American Museum of Natural History (AMNH), and provided generous funding over the years in support of research on this collection. The senior author often visited Ettore for the study of his magnificent collection of Dominican amber, and he was as accommodating and gracious a host as one could ever have. Images of beautiful specimens from these two collections grace the volume throughout.

Our work over the years has been funded by various sources: the National Geographic Society; Sigma Xi, the Scientific Research Society; the U.S. National Science Foundation; Kansas Technology Enterprise Corporation-Kansas NSF EPSCoR (KAN29503); the late Henry G. Walter, former trustee of the AMNH; Henry and Meryl Silverstein; and donations in memory of Steve Swolensky.

Last, and hardly least, Mr. Robert G. Goelet, Chairman Emeritus and Trustee of the American Museum of Natural History, has been steadfast in his generosity toward the wonderful collection of amber fossils at the AMNH, for funding fieldwork, and for funding Michael S. Engel as a research scientist at the AMNH for two enjoyable years. Mr. Goelet also generously donated funds to help defray the cost of publication for this book to make it more available, indeed, possible. We hope this volume is a pleasant reminder of your former teacher, the late Professor Frank Carpenter.

Production of this book would not have been possible without the skilled assistance of four AMNH staff. Paul Nascimbene (Collections Specialist) has been a dedicated and diligent preparator of thousands of amber and rock fossil specimens; and Simone Sheridan (Curatorial Assistant) meticulously attended to databases, references, and specimen preparation. Tam Nguyen (Senior Scientific Assistant) and Steve Thurston (Graphic Artist) produced most of the images. Tam did all the SEMs and many of the photomicrographs. Steve rendered cladograms and other diagrams, and both he and Tam composed many of the plates. The thousands of images for the book would have been impossible without the use of fine optics, lighting, and digital photography available from Infinity, Inc., and MicrOptics, Inc., all made possible by the expertise of Roy Larimer. Words fail to express the complete extent of our gratitude to these people.

The gestation of this book took longer than we expected, so we deeply appreciate the patience of our students and colleagues while we cloistered ourselves. The patience and support of the editors at Cambridge University Press, Kirk Jensen, Shari Chappell, and Pauline Ireland, are also appreciated. We

are especially grateful to Ward Cooper, former Acquisitions Editor at Cambridge, for his initial interest in this work, his enthusiasm for the project, and his calming influence. Camilla Knapp was a Production Editor *par exellence*, who should never have to endure a work of this size and complexity again. This volume could not have come to fruition without her skill and experience.

Everyone is a product of their past, and to a large extent this volume reflects several influential teachers of ours, whose tutelage and support we will always fondly remember: Thomas Eisner, Charles Henry, John Jaenike, James Liebherr, Charles Michener, Quentin Wheeler, and the late George C. Eickwort and William L. Brown, Jr. Lastly, without the stalwart patience and support of our families and loved ones, we could not possibly have waded through this work: Karen, Rebecca, Emily, Nicholas, and Dominick; Jeffrey, Elisabeth, Donna, and A. Gayle. They quietly endured our absences and steadily encouraged us. They understand.

COMMONLY USED ABBREVIATIONS

MY	million years
MYA	million years ago
MYO	million years old
BP	base pairs (of DNA)
DNA	deoxyribonucleic acid
RNA	ribonucleic acid
YA	years ago

Time Periods

T	Tertiary
K	Cretaceous
J	Jurassic
Tr	Triassic
P	Permian
C	Carboniferous