

Evolution *of the* Insects

DAVID GRIMALDI
MICHAEL S. ENGEL



CAMBRIDGE

CONTENTS

Preface	page xi
Commonly Used Abbreviations	xv
1. Diversity and Evolution	1
Introduction	1
SPECIES: THEIR NATURE AND NUMBER	6
<i>Drosophila</i>	7
<i>Apis</i>	9
How Many Species of Insects?	11
RECONSTRUCTING EVOLUTIONARY HISTORY	15
Systematics and Evolution	15
Taxonomy, Nomenclature, and Classification	33
Paleontology	36
2. Fossil Insects	42
INSECT FOSSILIZATION	42
Types of Preservation	43
DATING AND AGES	62
MAJOR FOSSIL INSECT DEPOSITS	65
Paleozoic	65
Mesozoic	70
Cenozoic	84
3. Arthropods and the Origin of Insects	93
ONYCHOPHORA: THE VELVET WORMS	94
TARDIGRADA: THE WATER BEARS	96
ARTHROPODA: THE JOINTED ANIMALS	97
Marellomorpha: The Lace Crabs	98
Arachnomorpha: Trilobites, Arachnids, and Relatives	98
Crustaceomorpha	107
Mandibulata	107
The Invasion of Land	109
HEXAPODA: THE SIX-LEGGED ARTHROPODS	111
Entognatha: Protura, Collembola, and Diplura	111

4. The Insects	119
MORPHOLOGY OF INSECTS	119
General Structure	119
The Head	121
The Thorax	125
The Abdomen	131
DEFINING FEATURES OF THE INSECTS	137
RELATIONSHIPS AMONG THE INSECT ORDERS	137
A Brief History of Work	137
A Roadmap to the Phylogeny of Insects	144
5. Earliest Insects	148
ARCHAEOGNATHA: THE BRISTLETAILS	148
DICONDYLIA	150
ZYGENTOMA: THE SILVERFISH	150
RHYNIOGNATHA	152
6. Insects Take to the Skies	155
PTERYGOTA, WINGS, AND FLIGHT	155
Insect Wings	156
EPHEMEROPTERA: THE MAYFLIES	160
METAPTERYGOTA	166
PALAEODICTYOPTERIDA: EXTINCT BEAKED INSECTS	168
Palaeodictyoptera	170
Dicliptera	170
Megasecoptera	171
Diaphanopteroidea	172
Paleozoic Herbivory	173
ODONATOPTERA: DRAGONFLIES AND EARLY RELATIVES	173
Geroptera	174
Holodonata: Protodonata and Odonata	174
Protodonata: The Griffenflies	175
Order Odonata: The Dragonflies and Damselflies	178
7. Polyneoptera	188
NEOPTERA	188
WHAT ARE POLYNEOPTERA?	189
Plecopterida	192
Orthopterida	193
PLECOPTERA: THE STONEFLIES	194
EMBIODEA: THE WEBSPINNERS	196
ZORAPTERA: THE ZORAPTERANS	199
ORTHOPTERA: THE CRICKETS, KATYDIDS, GRASSHOPPERS, WETAS, AND KIN	202
Ensifera	208
Caelifera	210
PHASMATODEA: THE STICK AND LEAF INSECTS	211
TITANOPTERA: THE TITANIC CRAWLERS	215
CALONEURODEA: THE CALONEURODEANS	217
DERMAPTERA: THE EARWIGS	217
GRYLLOBLATTODEA: THE ICE CRAWLERS	222
MANTOPHASMATODEA: THE AFRICAN ROCK CRAWLERS	224

CONTENTS

DICTYOPTERA	227
Dictyopteran Relationships	228
Blattaria: The Roaches	230
Citizen Roach: Isoptera (Termites)	238
The Predatory Roachoids: Mantodea (Mantises)	252
Ages of the Dictyoptera	260
8. The Paraneopteran Orders	261
PSOCOPTERA: THE BARK LICE	261
PHTHIRAPTERA: THE TRUE LICE	272
Fossils and Ages	275
FRINGE WINGS: THYSANOPTERA (THRIPS)	280
Feeding Habits	283
Social Behavior	283
Diversity and Relationships	284
Fossils and Origins	285
THE SUCKING INSECTS: HEMIPTERA	287
Sternorrhyncha: Aphids, Whiteflies, Plant Lice, and Scale Insects	289
Auchenorrhyncha: The Cicadas, Plant Hoppers, and Tree Hoppers	303
Coleorrhyncha	312
Heteroptera: The "True Bugs"	314
9. The Holometabola	331
PROBLEMATIC FOSSIL ORDERS	331
Miomoptera	331
Glosselytrodea	332
THE ORIGINS OF COMPLETE METAMORPHOSIS	333
ON WINGS OF LACE: NEUROPTERIDA	335
Raphidioptera: The Snakeflies	337
Megaloptera: The Alderflies and Dobsonflies	340
Neuroptera: The Lacewings, Antlions, and Relatives	341
10. Coleoptera and Strepsiptera	357
EARLY FOSSILS AND OVERVIEW OF PAST DIVERSITY	360
ARCHOSTEMATA	363
ADEPHAGA	366
MYXOPHAGA	370
POLYPHAGA	371
STREPSIPTERA: THE ENIGMATIC ORDER	399
Diversity	402
Relationships to Other Orders	402
Fossils	403
11. Hymenoptera: Ants, Bees, and Other Wasps	407
THE EUHYMENOPTERA AND PARASITISM	413
ACULEATA	429
The Ants	440
The Bees (Anthophila)	454
EVOLUTION OF INSECT SOCIALITY	464

12. Panorpida: Antliophora and Amphiesmenoptera	468
PANORPIDA	468
ANTLIOPHORA: THE SCORPIONFLIES, TRUE FLIES, AND FLEAS	468
MECOPTERIDA: MECOPTERANS AND SIPHONAPTERA	470
Early History	470
Recent Diversity and Relationships	474
The Fleas	480
Evolution of Ectoparasites and Blood Feeders of Vertebrates	489
DIPTERA: THE TRUE FLIES	491
The Brachycera	514
The Cyclorhapha	531
13. Amphiesmenoptera: The Caddisflies and Lepidoptera	548
TRICHOPTERA: THE CADDISFLIES	548
LEPIDOPTERA: THE MOTHS AND BUTTERFLIES	555
Mesozoic Fossils	556
Basal Groups	560
Ditrysia	573
The "Higher" Ditrysians: Macrolepidoptera	581
Butterflies and Their Relatives (Rhopalocera)	590
Mimicry	602
14. Insects Become Modern: The Cretaceous and Tertiary Periods	607
THE CRETACEOUS	607
Flowering of the World: The Angiosperm Radiations	607
Plant Sex and Insects: Insect Pollination	613
Radiations of Phytophagous Insects	622
Austral Arthropods: Remnants of Gondwana?	625
Insects, Mass Extinctions, and the K/T Boundary	635
THE TERTIARY	637
Mammalian Radiations	638
Pleistocene Dispersal and Species Lifespans	642
Island Faunas	642
15. Epilogue	646
WHY SO MANY INSECT SPECIES?	646
Age	646
Design	646
Capacity for High Speciation Rates	647
Low Rates of Natural Extinction	647
THE FUTURE	647
Glossary	651
References	662
Index	733