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BOOK REVIEW

GRIMALDI D. & ENGEL M. 2005: EVOLUTION OF THE INSECTS. Cambridge University Press, New York and Cambridge, xv + 755 pp., 41 tables, 862 figs, glossary, index. ISBN 0-521-82149-5 Cloth. Price USD 75.00.

Browse the stacks of any major university library and you will be astonished by the number of books and journals devoted to the structure, function, genetics, development, life history, behavior and systematics of insects, to their roles in terrestrial and freshwater ecosystems and to their importance in agriculture, forestry, medicine and biology. However, if you know that some 926,400 extant species have been described worldwide (of an estimated total of 5 million and compared to 43,000 chordate and 248,400 vascular plant species); that their ancestors invaded land over 400 million years ago and evolved powered flight at least 100 million years before the first pterosaurs; and that probably 85% of flowering plant species are insect pollinated with perhaps 400,000 insect species feeding on them; then this mountain of information is not so surprising — with the possible exception of bacteria (though only 4800 spp. are indicated in Fig. 1.3), insects are the most successful organisms in earth history.

This single, splendid volume by two paleoentomologists, David Grimaldi, Curator of Invertebrate Zoology at New York's American Museum of Natural History and Michael Engel, Associate Professor of Ecology and Evolutionary Biology at the University of Kansas, explains, illustrates and synthesizes insect diversity and its history in such depth and with such originality, beauty, clarity, and style that it should induce even the most reluctant biologist to read it no matter his or her persuasion or whether amateur or professional.

The authors capture our interest immediately with some superlatives about the central roles insects play in terrestrial ecosystems and a concise, up-to-date summary of what species are, how to recognize their limits in spite of their variation and how to reconstruct their evolutionary history using cladistic methods and knowledge of their structure, nucleotide sequences, and fossils. A short history of systematics and evolution follows with portraits of Linnaeus, Fabricius, Latreille, Cuvier, Lyell, Darwin, Wallace, Hennig, Usinger and Sokal, representative title pages from some of their works and a brief summary of the rules of zoological nomenclature.

Next, Grimaldi and Engel review the various ways that arthropods have fossilised, explain how such fossils are dated and provide an illustrated tour of the principal Paleozoic, Mesozoic and Cenozoic insect fossil-bearing deposits of the world together with colored graphics showing probable continental position and climate during the Upper Carboniferous, Middle Permian, Lower Jurassic and Upper Cretaceous — all times of major insect diversification. They then summarize the known fossil history of extant and extinct panarthropods (including onychophorans and tardigrades but not pentastomids which molecules and larval structure now tell us are highly derived crustaceans parasitic in the lungs and nasal passages of reptiles) and arthropods, and the invasion of land by stem group arachnids, myriapods, crustaceans and hexapods. They classify the extinct and extant higher arthropod taxa in Table 3.2, debate competing ideas on their phylogenetic relationships, and conclude that hexapods are the sister group of the myriapods, not of (or originating within) the Crustacea as recent molecular phylogenetic analysis and comparative neurogenesis (Harzsch, 2003) would suggest. The authors also mention the panhexapods: strange, recently discovered, marine arthropods from the Lower Devonian of Germany having mostly hexapod characteristics but a long, multisegmented abdomen bearing short, paired, segmented appendages, and review the characteristics, fossil history, way of life and relationships of non-insectan entognath hexapods, the Protura, Collembola and Diplura (fossil proturans have yet to be found).

A short but authoritative introduction to insect structure in Chapter 4 is illustrated with large, clear, fully labeled, colored photographs of the tagmata and appendages of an unnamed grasshopper and katydid and beautifully rendered drawings of primary and secondary segmentation, wing venation and axillary sclerites [they acknowledge but don't use the intricate system of Jarmila Kukalová-Peck based on her knowledge of Paleozoic fossil wing bases but, instead, adapt a version from Wootton (1979)], the spectacular male genitalia of four drosophilids (*Cladochaeta* spp.), and the evolution of the ovipositor in females. The principal ovipositor components, wing base sclerites and wing veins are differently colored and some of these colors are used later to illustrate structural evolution of homologous structures in highly derived representatives of some lineages [e.g. the apocritan ovipositor and aculeate sting in Fig. 11.32; see also their elegant, colored depictions of paraneopteran (Fig. 8.2), antliophoran (Fig. 12.24), and lepidopteran (Fig. 13.19) mouthparts and of the exit systems of female lepidopterans (Fig. 13.30)]. The authors then provide a short history of insect systematics, morphology and paleontology illustrated with photographs of some of the "giants" (Handlirsch, Tillyard, Martynov, Crampton, Hinton, Snodgrass, Wigglesworth, Carpenter, Rohdendorf, Hennig and Kristensen) and reproductions of early, order level phylogenies inferred by Haeckel (1866), Martynov (1938) and Hennig (1953); the latter two remarkably modern (Figs 4.16, 4.22). They classify the currently recognized living and extinct insect orders in Table 4.1 and depict their evolutionary relationships in color in Fig. 4.24 with reference to the geological time scale (as are the other 43 cladograms in the book) and to important events in earth, plant and animal history (the authors' knowledge of other organisms is remarkable considering they are both entomologists).

Most of the book (pp. 119–606) reviews and synthesizes, at the family level, our current understanding of evolution, diversity, way of life, phylogeny and fossil history of living and extinct members of the ectognath Apterygota, Paleoptera, Polyneoptera, Paraneoptera, Neuropterida, Coleoptera and Strepsiptera, Hymenoptera, Panorpida, and Amphiesmenoptera, with a chapter on each. These accounts are accompanied by hundreds of original, spectacularly beautiful, superbly reproduced, and attractively arranged colored photographs or paintings of living and fossil representatives (both juvenile and adult) of each lineage that are, in some instances, printed full page or attractively organised into plates; exquisite drawings of living and reconstructions of fossil (particularly in amber) insects by Grimaldi, and dozens of stereoscan micrographs illustrating adult representatives of some orders and characters of use in recognizing them. One or more cladograms in each chapter summarize the evolutionary relationships of living and fossil taxa and, in four [Figs 7.88 (termite families), 8.31 (neococcoids), 10.3 (superfamilies of Coleoptera), and 13.13 (families and superfamilies of Lepidoptera)] their relative diversity. Careful examination of these reveal the difficulty paleoentomologists face in relating fossils of species in extinct stem groups from the Upper Paleozoic to Middle Mesozoic to members of extant lineages because they lack one or more of the derived characters defining membership in such lineges and have other characters no longer present [e.g., the Mid-Cretaceous amber fossil of a pseudo-polycentropodid scorpionfly with long, mosquito-like mouth-parts, long legs, fly-like forewings and with the hindwings reduced to stubs (Fig. 12.3)]. Numbers on the branches of some cladograms specify the estimated time of origin of each derived character defining membership in descendant lineages and circled numbers, the age of the deposits in which significant fossils of that taxon were found (both are listed and defined in tables printed adjacent to the figures). Finally, in a few cladograms, the branches are differently colored to indicate whether its members were/are terrestrial, aquatic or semi-aquatic as adults and/or juveniles; (Figs 9.4, 12.25), solitary, eusocial or klepto-parasitic (Fig. 11.82), or to show what they fed/feed on and when use of these sources arose (Figs 7.3, 8.1, 12.25, 12.61, 13.13).

Each account also provides estimates of known species diversity in extant families or superfamilies and crisp, original, and often lengthy essays on diverse topics ranging from the origin and function of wings and of paleopterous and neopterous flight; to the evolution, distribution and subsocial behavior of relict wood cockroaches of the genus *Cryptocercus*; the co-evolution and speciation of lice and their hosts (Figs 8.13, 8.14) and their origins within the Psocoptera; the controversial evolutionary relationships and peculiar life histories of strepsipterans; and the origin of fleas within Mecoptera.

The angiosperm radiation of the Mid-Cretaceous (Fig. 14.9) and associated diversification of pollination syndromes and phytophagous insects; the break up of Gondwana (Fig. 14.27), vicariance biogeography and the origin of austral distributions; the end Cretaceous extinctions; and the origin and radiation of bats and their earwig, bug and fly ectoparasites (Fig. 14.43) and of island faunas are wonderfully synthesized in their final chapter on insect diversification in the Cretaceous and Tertiary. Grimaldi and Engel end the book with a short Epilogue suggesting possible reasons insects are so successful, examples of soon-to-be or recently extinct insects, and remarks on the certain dismal future of our flora and fauna (and ourselves) if we don't begin to control our numbers and to reduce our impact on the planet.

Not surprisingly, the authors have little to say, except in passing, about insect physiology, biochemistry, cytology, genetics or development despite the recent discovery of the "molecular toolkit" controlling development in *Drosophila melanogaster* ("that stupid little saprophyte" — W.M. Wheeler) and other animals nor about the burgeoning impact of evolutionary developmental biology or *Evo-Devo* on our understanding of the origin of animal body plans (Carroll, 2005; neither are mentioned in the index). Of course, many authoritative volumes address these topics and Heming (2003) critically surveyed insect reproduction and development within an evolutionary framework in a manner complementary to this book and provided additional, functional reasons for diversification in some lineages.

I found few typos or errors in fact in the book in spite of its astounding breadth and depth. A few noticed:

1) Column titles of the geological time scale in Fig. 2.41 do not agree with those of most geology and paleontology texts (e.g., Valentine, 2004: 522–523).

2) Female zygopteran, aeshnid and petalurid odonates have well-developed ovipositors in spite of what is said in the caption to Fig. 6.28.

3) Phloem is positioned adjacent to the xylem but closer to the *surface* of the stem than to its core (p. 289).

4) There are three <u>not</u> two pairs of imaginal histoblasts in the epidermis of each abdominal segment of larval *Drosophila*.

5) According to Hinton (1963), the pupa evolved from the last, <u>not</u> from an intermediate juvenile instar of an exopterygote ancestor (p. 333).

6) Some similarities listed between the so-called "pronymph" ("prolarva") of exopterygotes and the holometabolous "larva" cited from Truman and Riddiford's (1999) seminal essay on the evolution of complete metamorphosis (p. 334) are misinterpreted: e.g., the pronymphal (second embryonic) cuticle is generally deposited <u>before</u> the first instar cuticle <u>not</u> at the same time even in many endopterygotes; first instar cuticles bear functional sensilla while, with few exceptions, pronymphal cuticles are either smooth or bear microtrichia and various sclerotized hatching devices (Konopová & Zrzavý, 2005); and the central nervous systems of pronymphs and first instar larvae are both well developed, functional and disproportionately large in relation to body size, <u>not</u> reduced (Heming, 2003).

7) The last larval instar not the pupa forms a silken cocoon in some species (Table 12.1; p. 470).

8) In stratiomyids, as in cyclorrhaphans, the puparium does <u>not</u> form within the third instar cuticle but rather develops from it (p. 516).

9) In the Glossary: "Apolysis" is the separation of the old cuticle from the epidermis <u>not</u> from the new cuticle (p. 651). Juvenile hormone does <u>not</u> prevent molting but, instead, is a "status quo" hormone ensuring that the cuticle deposited during a molt is larval/nymphal not pupal or adult (p. 655). It is the propupa <u>not</u> the prepupa that is the first quiescent instar in Thysanoptera and some sternorrhynchans (the propupa in aberrant exopterygotes is a discrete instar separated by molts from adjacent instars while the prepupa of endopterygotes is the pharate pupa) (p. 658).

10) Throughout the text, the authors often assign characters to formal higher taxa names when these are borne only by individual members of such taxa. Genera, families and orders are systematists' conceptions of holophyletic lineages and often differ between one specialist and another. In such instances, characters should be assigned to higher taxa names written in the vernacular [e.g., dermapterans (not Dermaptera) bear terminal forceps].

11) The authors essentially ignore three decades of detailed re-interpretation of body structure and appendages in Paleozoic and Recent arthropods by J. Kukalová-Peck. What were their reasons for doing so?

12) The brief figure captions sometimes do not do justice to the figures.

The volume is strongly bound between yellow-brown covers and has a dust jacket bearing a beautifully composed color photo of a 120 myo fossil grasshopper of the extinct family Eicanidae that also serves as the frontispiece for the book. Significantly, each chapter title is doubly printed: once in bold in smaller type and once, beneath, in larger type in light gray. These eerily reflect the derivation of our modern fauna from the extinct — a tiny detail illustrating the care that went into the book's design. At 2.92 kg and 3,652 references, the book is anything but a coffee-table book even though it looks like one. With the possible exception of Naumann's (1991) multiauthored two volumes on the insects of Australia, this is the single, most authoritative, up-to-date and beautiful book treating all insects and the most wonderfully written (the seamlessness with which one topic melts into another literally "sucks one in"). Although two other excellent volumes treat hexapod fossils comprehensively (Carpenter, 1992; Rasnitsyn & Quicke, 2002), neither pretends to survey the Recent fauna. Reading this book will enable every entomologist to painlessly discover his or her roots.

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