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Book Review

Handbuch der Zoologie. Band/Volume IV. Arthropoda: Insecta. Teilband/Part 35. Lepidoptera, Moths and Butterflies. Volume 1: *Evolution, Systematics, and Biogeography*. Ed. Niels P. Kristensen. Berlin, Walter de Gruyter. 1999. x + 491 pp. Price DM398.

This is a lovely and extraordinarily detailed book for anyone who wants to know about lepidopteran systematics. But it's a funny old world. Intensive agriculture and commercial development are known to be causing one of the biggest mass extinctions this planet has seen. Meanwhile in the universities, the decline of botany, zoology, and entomology courses, especially those dealing with systematics, means that there may soon be hardly any experts who can tell us what we are losing. Systematists today are perhaps renowned more for quarrels over theory rather than for taxonomic work on actual organisms. And yet the current crop of systematists have more encyclopaedic knowledge than ever before, and enough buyers apparently exist to guarantee a market for lavish and meticulously detailed monographs, like this one, on an enormous variety of plant and animal groups. The rather complicated title of this volume of the venerable *Handbuch der Zoologie* attests to the exponential expansion of knowledge; originally, one assumes that the whole Insecta was to have fitted into a single volume, Volume IV. Instead, this is the first volume of two of the 35th part (many of which have presumably been volumes in their own right) of the second edition of the Insecta volume. This is a first-rate product of perhaps never-to-be-repeated systematics excellence existing at the end of this century.

Evolution, Systematics and Biogeography means in practice one chapter of historical introduction, 18 chapters of systematics, one on the evolution of larval food preferences, and one on biogeography. This does make the current *Handbuch*, or at least this volume, more specialized and rather less a general reference work for evolutionary biologists than one might think from the title. Originally, there were to have been three volumes on Lepidoptera. The second volume, on morphology and physiology, is "in an advanced state of preparation". The third, on behaviour and ecology, was abandoned, rightly, in my view, on the grounds that these subjects would not have been very useful with Lepidoptera providing the only examples. Presumably the same might also be true of Lepidoptera genetic evolution, apart from phylogeny, since both are hardly mentioned, except in the chapter on evolution of host usage.

Over 10% of the world's described species are butterflies and moths (the estimate was by a hymenopterist, and so the fraction could well be more; and there may be over 300 000 species undescribed according to Kristensen). This excellent summary of the systematics of the group is therefore to be welcomed. The specialization displayed by this volume is an inevitable consequence of the growth of knowledge about the group, and personally I am extremely grateful for a convenient summary in one place of the topics on my study organisms about which I am least knowledgeable. In any case, it is clear that restricting the scope of the work to systematics and related fields has assisted its completion; the only other complete treatment of a 'megadiverse group' in the new *Handbuch* was Willi Hennig's volume on Diptera that came out in 1973.

The short historical introduction by Kristensen is valuable and interesting, although closer to a list of book names than a narrative. In the phylogeny and palaeontology chapter, by Kristensen and Andrzej Skalski, the grand task of laying out the phylogeny of the superfamilies

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is taken on. According to Kristensen's earlier analysis, updated here, the Lepidoptera are monophyletic, while their base consists of a highly pectinate series of clades with the Trichoptera (caddis flies) as a sister group. Curiously, there is no discussion of which caddis flies, if any, are sisters to Lepidoptera. It is astonishing to find in the section on fossils that there are only about 600–700 known specimens of fossil Lepidoptera, compared with 120 000–500 000 species in the extant Lepidoptera. Vertebrate biologists can only dream about that kind of incompleteness of the fossil record.

A howling furore exists in the systematic literature over how to assign names to higher taxa. Most classifications are now to some extent explicitly phylogenetic, but wanting your classification to reflect genealogy doesn't tell you how to go about it, to paraphrase Darwin. Some systematists argue that retention of the Linnean hierarchy and a usable nomenclature requires recognition of paraphyletic groups as named taxa. Another group advocates abolishing taxon names altogether, and simply numbering the nodes of clades instead. David Carter and Niels Kristensen here adopt a more intermediate phylogenetic stance. They point out that the names of monophyletic families, in addition to those of genera and species, have taken on an important role of their own in modern systematics. They therefore allow nomenclature based on families to creep upwards towards monophyletic superfamilies ('-oidea'), but do not allow many formal taxon categories to creep down from the order level. Instead, certain well-known clades are given informal traditional names such as 'Heteroneura', 'Ditrysia' and 'Macrolepidoptera', while names like 'Heterocera' (moths) and 'Micro-lepidoptera' are excluded on grounds of paraphyly. The system works well, but it must be remembered that, in such a diverse group, basal superfamilies like the Micropterigoidea and the Agathiphagoidea are in fact at an enormously greater rank than derived and highly diverse groups like the Geometroidea and Noctuoidea. Another potential criticism of the system is that 27 out of 46 superfamilies (mainly basal ones) are 'redundant', that is they each have only a single family. However this debate is resolved, I hope that glorious names like Agathiphagidae and Heterobathmioidea are retained in some form.

With the hors d'oeuvres over, the meat courses of this book consist of 16 chapter treatments of individual taxonomic groups. While these are arranged systematically and largely systematic in content, the biology of each family is briefly and usefully reviewed. The treatments are of an extremely high standard, and carried out for the most part by acknowledged experts on the groups. Because I note that I am already over my word limit, I will not treat each one individually, while I recognize that the main value of the book is in these chapters. I will, however, note with relief that insect systematics is no longer just a province of pipe-smoking, tweed-jacketed men, three women make major contributions: Patricia Gentili, Marianne Horak, and Maria Alma Solis.

Finally as a dessert, we have the two chapters on more evolutionary topics. The chapter by Jerry Powell, Charlie Mitter and Brian Farrell on larval food plant use in Lepidoptera was extremely interesting and treated in a very up-to-date way. The major conclusion is that the association of lepidopteran taxonomic groups with particular host plant families is far from random, although there has been a great deal of host switching. Coevolution has occurred, but it is mostly of the 'diffuse' rather than 'parallel speciation' mode. The chapter on biogeography by Jeremy Holloway and Ebbe Schmidt Nielsen was less satisfying, at least to me, but this may be because I work on biogeography myself to some extent. It seemed to have been updated to about 1996, but the updating was far from complete. The authors classify theories of biogeography into 'Q-mode' (relationships of areas) and 'R-mode' (relationships of single taxonomic groups between areas) on the one hand, and dispersalist, vicariance and panbiogeographic theories on the other. I feel that obvious models of speciation and range evolution fall between the standards provided by these theories. For example, a 'dispersal' event may lead to 'vicariance' by range displacement. One of many concrete examples is the invasion by the American grey squirrel in Britain, leading to peripherally isolated populations of the indigenous red squirrel being formed as a result of competition by the grey in the central part of the range; this example is human-caused, but

it is obvious that similar processes happen all the time in biogeography. The possibility of 'shifting balance', a subspecies-level version of the same type of process, may add gene flow between the competing clades, as well as replacement, to the confusing biogeographic picture. The allopatric 'Pleistocene refugium theory' for tropical Africa and America is treated here rather uncritically: this theory in my view lacks much attempt to explain how adaptive and evolutionary change affects range changes, quite apart from a lack of evidence. However, even though I don't like the angle taken, I find the review very useful because of its broad coverage and many references.

Overall, this is an excellent book, a must for those who need state of the art Lepidoptera systematics works on their bookshelves. And if you don't need it, your library certainly does!

James Mallet