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BOOK REVIEWS

THE DEVELOPMENT AND EVOLUTION OF BUTTERFLY WING PATTERNS, by H. Frederik Nijhout. 1991. Smithsonian Institution Press, Washington and London. xvi + 297 pp., 159 figures, 8 color plates. Hard cover (ISBN-0-87474-921-2), $45.00; soft cover (ISBN-0-87474-917-4), $20.00; 18 × 26 cm.

Because they are diverse and easy to observe, not to mention beautiful, butterfly wing patterns provide an excellent opportunity for pursuing questions about the development and evolutionary history of morphological patterns. Certainly there are few contemporary scientists who have exploited this potential more than H. Frederik Nijhout. His recent book, *The Development and Evolution of Butterfly Wing Patterns*, summarizes his work and ideas, and makes clear his valuable empirical and theoretical contributions. Butterfly wing patterns are the material theme of this book, which offers a unique and thorough compilation of the existing information on this topic that will be useful for a long time. The conceptual theme is homology and it is in this arena that the books does less than it could. I will begin with an overview of the book and then deal with the concept of homology and how it is handled by Nijhout.

The book is attractively constructed and priced and begins with a nice chapter that summarizes butterfly wing structure and explains pattern production mechanisms. The next three chapters (about a third of the book) are devoted to describing a set of proposed homologies for the diverse pattern elements found both within and between species of butterflies. This set is known as the nymphalid ground plan and is an update of schemes initially proposed independently by Schwanwitsch and Süffert in the 1920's. Chapters 5–7 are devoted to presenting empirical and theoretical results on the developmental and genetic mechanisms that control wing pattern in butterflies. The book concludes with a chapter on the extent to which mechanical and developmental constraints might influence the evolution of butterfly wing patterns, followed by three appendices, a bibliography, and an index. While I realize that the intended focus of this book is butterfly wing patterns, this is to the near and unfortunate exclusion of discussion of studies of homology in the color patterns of other insects or vertebrates.

Copiously illustrated, the book has almost 160 figures and all are crisp and clear. However, many are large and detailed showing numerous pattern variants. The most extreme figure (2.21) shows 110 different shapes found in the parafocal elements among the nymphalids. Similarly, the text contains many lengthy and subjective descriptions and interpretations of specific cases, instead of concise, quantitative summaries and analyses of the observed patterns of variation. This does not make for easy reading or for ready assessment of the support for Nijhout's points.

The nymphalid ground plan is best understood as an hypothesized set of homologies for the similar pattern elements found on butterfly wings both within and among species. Now, what does it mean to a biologist to say that two traits with some common features are homologous? This question has been debated in an extensive and still growing literature since the comparative anatomist, Richard Owen, first proposed the term in the mid-1800's. To most modern evolutionary biologists homology suggests that the similarity in traits reflects similarities in the developmental pathways producing the traits as well as a common ancestry. Hence, to say that two pattern elements that are similar are homologous is to say that they arise by similar processes during development and that they both arose from the same ancestral pattern element. An alternative explanation is that the similarity in the pattern elements is a result of convergent evolution of traits with different developmental and evolutionary antecedents.

Despite the central place of homology in this book and the extensive discussion of this term in the literature, Nijhout spends only a single paragraph explicitly dealing with what he means by homology. His preferred definition, put forth by H. V. Roth in 1984, is that homologous traits need only share a developmental pathway. In his view, issues of the common evolutionary history of homologies are secondary and not a necessary part of the definition. I think most phylogeneticists would regard common evolutionary

history as an essential criterion for homology. Even H. V. Roth suggests that the shared developmental pathways of homologous traits are "controlled by genealogically related genes" (p. 13, 1984, *Biological Journal of the Linnean Society* 22:13–29). The stated definition notwithstanding, it is clear throughout the book that the evolutionary past frequently figures prominently in Nijhout's recognition of homologies.

But Nijhout seems at times a little cavalier in his application of his preferred definition. In his discussion of experiments on forewing and hindwing eyespots, he concludes that, "we can be as certain about their homology across butterflies as we can about any system of homologies in the animal kingdom. Yet the processes that give rise to these two types of eyespots appear to be different. . . ." (pp. 113–114). In the discussion that follows, this statement is justified by the citation of an alternative criterion for homology proposed by Van Valen: continuity of developmental information. However, Nijhout does not make clear what general conditions make appropriate the use of this criterion versus some other. Again, I think the book would have benefitted greatly from a full discussion of Nijhout's views on the concept of homology, its definition, and application.

Although Nijhout points out that the ground plan is not to be taken as a putative ancestral coloration for butterflies, the ground plan homologies can be taken as an hypothesis of shared developmental pathways and common ancestry. Such an hypothesis can be tested in two ways. One way is to generate predicted phylogenetic relationships among the species within groups of butterflies. These predictions derived from wing patterns can then be tested for concordance with phylogenies developed from other characters, e.g., wing venation, DNA sequences, etc.

Nijhout makes a cogent and well-taken plea for systematists and phylogeneticists to use and test the ground plan in this way. In Chapters 3 and 4, Nijhout offers a number of phylogenetic relationships within various genera that are predicted by the nymphalid ground plan. However, Nijhout could have improved the case for the ground plan if he had provided some clear tests of the phylogenies proposed by the ground plan. As the presentation stands many questions remain. What other systems of homologies and resulting phylogenies have been proposed or examined? How and why were they rejected? Does the nymphalid ground plan permit one to construct phylogenies that are concordant with those from other data? What taxonomic issues have been or might well be resolved using the homologies hypothesized in the ground plan? Are there other taxa in which study of pattern homologies have helped resolve taxonomic and phylogenetic issues?

Relevant to the issues of taxonomy the book contains an Appendix by Donald J. Harvey entitled "Higher Classification of the Nymphalidae." In it Harvey presents a *newly revised* classification for the nymphalids between the level of family and genus. Its inclusion in this book seems odd on two counts. First, although Harvey acknowledges the input of some very able reviewers, the precise review process through which this classification has gone is unclear. Does the revised classification (published as an appendix) have the same standing as a paper published through regular journal review processes? Second, its precise relevance to the rest of the book is unclear in that it is rarely referenced by Nijhout and does not use the nymphalid ground plan to resolve any taxonomic or phylogenetic issues in the way Nijhout suggests in Chapter 4.

The other way to test a set of homologies such as the nymphalid ground plan is to see if the pattern elements proposed to be homologous in fact share developmental pathways and genetic control mechanisms. Results from manipulation (Chapter 5) and genetic (Chapter 6) experiments and a model for wing pattern development (Chapter 7) are described in detail but not with the explicit purpose of testing the ground plan in this way. Here as elsewhere in the book the ground plan is presented more as a given and not as a tentative and testable hypothesis. Nijhout does conclude that his work and that of others show that a seemingly limitless diversity of patterns can be produced by slight changes in the location and shape of inductive signal sources and sinks, in the thresholds of responding cells, and in the genes controlling pattern.

Two other salient features of the ground plan should be mentioned. First, the plan does not homologize the color of pattern elements, but only their position, shape, and presence. Nijhout points out that two identical pattern elements can look very different if colored in different ways. What potential information about development and evolution

is omitted by not fully incorporating the variable of color into the system of homologies? Nijhout provides no specific answer to this question. Second, the plan is subjective in that there is no effort to quantify the similarities between pattern elements that lead to a hypothesis of homology. In general the lack of quantification in the description of pattern elements and in efforts to test Nijhout's ideas is notable.

The last chapter speculates on the impact of developmental or phylogenetic constraints and selection on the evolution of butterfly coloration. There are two key conclusions. First, many of the features of pattern elements (e.g., the shape of small elements such as parafocal elements) are probably not under direct selection and their evolution will be determined by what sort of pattern production mechanisms are available. This view seems plausible but highly speculative in that it broadly assumes interspecific similarity in the features of the visual system of predators and in the contexts of encounters. Second, the pattern-generating systems are so flexible that the evolutionary paths along which butterfly wing pattern may travel, driven by selection or other processes, are virtually limitless. This is good news for adaptationists whose hypotheses are often criticized for assuming few if any constraints on the trajectories evolution can take.

In summary, this book stands as a clear and current record of Nijhout's ideas and of his view of his and others' work on the evolution and development of butterfly wing patterns. It is unique and of interest as a treatise on phylogenetic and developmental questions about these wing patterns. However, the reader must keep in mind that Nijhout presents only a single hypothesis for the inter- and intraspecific similarities in butterfly wing patterns and that the test of this hypothesis is incomplete. My hope is that researchers in this area will be stimulated by the challenge of generating and testing new sets of homologies as alternatives to the nymphalid ground plan.

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A FIELD GUIDE TO EASTERN BUTTERFLIES, by Paul A. Opler (illustrated by Vichai Malikul, with foreword by Roger Tory Peterson). 1992. Peterson Field Guide Series, No. 4. Houghton Mifflin, Boston. xvii + 396 pp., 541 color paintings, 104 color photographs of living insects, and 348 range maps. Hardcover, 12 × 19 cm, ISBN-0-395-36452-3, $24.95; softcover, 11.5 × 18 cm, ISBN-0-395-63279-X, $16.95.

Was a new eastern field guide necessary? The total of 422 species described by Alexander B. Klots in his original guide in 1951 has expanded to 524 species, through the recognition of many more occasional immigrants and the addition of a few recently described species, minus a few species submerged to subspecies status. With this, and the acquisition of much new biological information, forty years was not too soon for an update.

The browser picks up this new field guide, turns to the color plates to see how the butterflies look, and sees—flowers! Thereafter follow three pages of photos of immature stages: first things first. And now nine pages, 68 superb photographs, of living butterflies doing what we most enjoy seeing them do: nectaring, basking, puddling. Their characteristic postures are clearly evident. Finally, on 35 color plates we see the expected formally sequenced, conventionally spread depictions of the great majority of the 524 species covered in the book, as color paintings ranging from superb (most of them), to barely adequate (only a few: i.e., in the genus *Erynnis*—but *Erynnis* are the *bêtes noires* of most lepidopterists).

By using this sequence, Opler is subtly emphasizing points made in his introductory chapters: the dependence of butterflies on their botanical substrates, and the fact that users of this book who wish to observe and photograph butterflies will greatly outnumber those who make collections of specimens. While acknowledging changing attitudes and