

Tropical Lepidoptera, 3(2): 155-156

BOOK REVIEW

THE DEVELOPMENT AND EVOLUTION OF BUTTERFLY WING PATTERNS,

by H. Frederik Nijhout.

1991. Smithsonian Institution Press, Washington and London. 297 pp., 8 color pls., 159 b & w illustr., hardcover (18.5 x 26.0 cm), softcover (17.5 x 24.4 cm). ISBN 0-87474-921-2 (cloth), ISBN 0-87474-917-4 (pbk). Price: \$45.00 (cloth), \$20.00 (pbk).

Most lepidopterists who collect and study butterflies became intrigued originally by their subjects because of the spectacular and intricate color patterns on the wings of these wonderful insects. We marvel at the preciseness of mimicry in wing patterns, the differences between the sexes in many species, and the insights provided into patterns of evolution and of taxonomic relationships. Now in this new book, the foremost worker on the development of butterfly wing patterns, H. Frederik Nijhout, Professor of Zoology at Duke University, has painted in brilliant verbal pictures and accompanying illustrations a superb analysis of the development and evolution of butterfly wing patterns.

Dr. Nijhout has organized his fascinating book into eight chapters. In the Preface, the author acknowledges his intellectual debt to B. N. Schwanwitsch and F. Süffert, who in the 1920's, first saw that the wide diversity of butterfly wing patterns might be achieved by permutation and recombination of a relatively small number of basic units. In fact, they and other early workers on wing patterns discovered that nearly all the color patterns of butterflies and moths can be described as permutations of a single general theme, the "nymphalid ground plan." While Nijhout confesses that he has rejected this ground plan hypothesis at times in the past decade as a working model, and has attempted to approach the relationships among pattern elements and patterns in fresh and different ways, he found that he always returned to this nymphalid ground plan as representing an accurate summary of the homologies in butterfly color patterns. After this interesting Preface, he acknowledges the help of many current lepidopterists, before commencing the eight chapters that form the basis of the book.

Chapter 1, entitled "The Material Basis of Wing Color Patterns," covers the general development and morphology of the wings as well as their component scales. The balance of the chapter is devoted to discussing the sources of color in butterfly wings, including the production of structural colors and the variety of pigments (melanins, ommochromes, pterins, and flavonoids) in pigmental colors. The final part of the chapter is devoted to a short discussion of the problems of pattern formation in a cellular monolayer.

The second chapter deals with pattern elements and homologies. Building on the elements of the nymphalid ground plan, Nijhout looks at symmetry patterns in pattern evolution, including ripple patterns, dependent patterns, dislocation of pattern elements, ocelli, and other themes and variations on this common nymphalid ground-plan pattern.

Most tropical lepidopterists will find Chapter 3, "The Analysis of Wing Patterns," to be one of the most interesting in the book. Using many tropical examples, such as *Stichophthalma* (Morphi-

nae: Amathusiini), *Pierella* (Satyrinae), *Kallima* (Nymphalinae), *Iphiclides* (Papilionidae), *Heliconius* (Heliconiinae), and *Idea* (Danainae), the author looks at most of the sub-groups of butterflies from the viewpoint of finding common elements. The author makes a very important statement here that ought to be noted by lepidopterists everywhere and taken to heart: "Homologies of wing veins, leg segments, and body parts are universally used in the classification and systematics of butterflies, just as homologies among wing pattern elements are universally ignored" (p. 84). He aptly suggests that wing patterns "provide a potentially rich source of taxonomic and phylogenetic information" and that "all these characters are two-dimensional and observable without dissection." The use of morphometric analysis, therefore, ought to provide many useful insights into the evolution and taxonomy of butterflies.

While Chapter 3 and the preceding chapter dealt with pattern structure and diversity from the perspective of a nymphalid ground plan, Chapter 4 ("Exploring Pattern Morphospace") analyzes the morphology of the patterns in a single wing cell and explores the nature of the diversity of these patterns. Again, the author chooses a variety of taxa that possess useful pattern elements for analysis, and here he looks in particular at taxa that possess wing cell patterns which are clearly serially repeated. Of course, these involve a range of patterns but actually serial repetitions constitute the majority of pattern types among the butterflies. Examples include such characters as arc-shaped pattern elements, wishbone-shaped elements, and border ocelli.

The next three chapters deal with the developmental processes that give rise to the color pattern. Chapter 5, "Experimental Studies on Color Pattern Formation," describes different surgical methods that have been used to study the determination of pattern formation in the developing adult. Specific types of injuries are inflicted in perturbation experiments to build a map of how the response varies in time and space in the normal development of the pattern. Such operations on the wing of the pupal stage may involve small cauteries done early in the pupal stage at various places on the wing surface, killing the cells that serve as sources for the organizing or inducing signals in development. Many of these experiments have been done on moths rather than butterflies -- hence, moth examples are given at length -- but the development of ocelli and other elements in the American buckeye butterfly, *Precis coenia* (Nymphalinae), is discussed in detail, and similar pattern associations among other species of *Precis* worldwide are analyzed.

Chapter 6, "Genetics, Mimicry, and Polyphenisms," provides some of the most interesting material of all to the reader as it analyzes a wide range of studies of the genetics of color patterns.

While many workers have studied the modes of inheritance of various spots and patches of color on the wings of an assortment of species, as Nijhout points out, "There has never been an attempt to interpret the identity and homologies of these parts of the pattern." Without a study of the homology of these elements, it is difficult or impossible to have a basis "for critically judging how color patterns and mimicry systems evolve." Thus Nijhout looks at a variety of genetic studies in butterflies from this viewpoint, including melanisms in pierids and other butterflies, and Batesian mimicry in the females of *Papilio dardanus*, *Papilio memnon*, *Papilio polytes*, and *Hypolimnas bolina*. A very interesting discussion of super genes and regulatory gene loci includes a careful look at the wing pattern genes, pattern loci, and other features of the known information we have on the genetics of pattern formation in neotropical *Heliconius*. The end of this chapter includes a review of seasonal polyphenisms in the species of butterflies that have seasonally distinct phenotypes or morphs (usually associated with the wet and dry season in the tropics, and with the spring and summer climates in temperate zones). In the species that have been studied intensively, these morphological differences are strictly controlled by the photoperiod or temperature regime under which the species is reared. This discussion is extremely fascinating to read, and it covers a wide variety of examples from the tropics as well as the temperate zone.

Chapter 7, "Models and Mechanisms," attempts to deduce the basic developmental and physiological processes that underlie the origin and diversity of form in color pattern development in the Lepidoptera. Nijhout lays out explicitly the expectations of a model for color pattern formation and then proceeds to lay out a detailed two-gradient model. Some problems not solved by this model are discussed at length, including special cases.

The last chapter, Chapter 8 ("Evolution of a Process"), looks at the problem of morphological evolution in color pattern, concentrating on patterns as adaptations initially and then looking at the evolution of pattern in terms of mechanisms. Both gradualistic change and saltational change may occur within the system that produces these phenotypic effects. The author concludes with various suggestions as to how we can study pattern evolution or other examples of morphological evolution. Overall, the body of work summarized in this book can be fairly said to represent the most direct, comprehensive, and integrated exploration of development in morphological evolution in any group of organisms.

Several interesting appendices are worthy of special note in this review. The first appendix summarizes eight different phylogenetic schemes used by various authors in studying the butterflies in general and some of the special groups. The second appendix deals with the "Higher Classification of the Nymphalidae," and is authored by Donald J. Harvey of the Smithsonian Institution as a separate contribution. The third appendix deals with genera surveyed for two figures in Chapter Two, showing diversity of border ocelli in the Nymphalidae and diversity of parafocal elements in the same family. A comprehensive bibliography and excellent detailed index bring the book to a close.

The Smithsonian Institution Press is to be congratulated on publishing this outstanding analysis of the development and evolution of butterfly wing patterns. The genius of Nijhout's

approach, in both his papers and this superb book-length compendium of knowledge, is his clear demonstration that the enormous diversity of natural lepidopteran patterns rises principally from quantitative variations in a relatively small set of generating factors or rules involving the size, shape, position, and color of wing pattern elements. As a result of his studies and those of other workers, the Lepidoptera have become the group of organisms that best illustrates how genes control the developmental processes that lead to pattern formation and adult morphology in organisms. Lepidopterists with any interest at all in systematics, evolution, mimicry, and associated phenomena dealing with color pattern analyses will want to purchase this book for their personal libraries, and will be fascinated by the many new insights that Nijhout provides into these important subjects.

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