Variations on a theme?

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The Development and Evolution of Butterfly Wing Patterns. By H. Frederik Nijhout. *Smithsonian Institution Press: 1991. Pp. 297. $45 (hbk), $20 (pbk).*

HOW does one-dimensional DNA guide three-dimensional development? Colour patterns, which develop in only two dimensions, are simplified systems that could provide insights into this riddle. So it is perhaps surprising that virtually no biologists study manipulable pattern systems such as butterfly wings.

Nijhout has been the exception since 1978 when he outlined a general hypothesis of how butterfly wing patterns are formed. He proposed that many colour patterns could be generated by a series of related, or 'homologous' foci on the midlines of wing cells. These might act as sources and sinks of diffusible substances that regulate pigment production in the scale cells. Nijhout amplifies the hypothesis in this book by showing that the elements of a "nymphalid ground-plan", similar to the pattern of *Argynnis* or *Speyeria* (fritillaries), can act as foci for both simple patterns (such as those of *Heliconius*) and complex ones (such as those of the undersides of *Charaxes*). Nijhout is well known for his elegant experiments on *Precis* eyespot patterns, which, with morphological analyses of normal butterflies, aberrations and pattern genetics, form the support for his hypothesis.

After reading the book I am even more convinced that the evolution of butterfly wing patterns has few constraints. Nonhomologous pattern elements align within and between wing surfaces to produce perfect leaf mimicry in *Kallima*; patterns may be complex for camouflage, or simple for mimicry or sexual signalling, with often both present on the same butterfly, each on a different wing surface; and when one colour pattern will not do, polymorphisms or seasonally variable patterns evolve. Because anything can happen, it is difficult to find testable homologies for all patterns, yet this is precisely what Nijhout attempts.

Well, not quite. Nijhout points out that "ripple patterns" — rhythmic repeats such as those on *Urania* moths — are never exactly the same on left and right wings. By contrast, most other patterns are symmetrical, and are assumed to be generated by interactions between the nymphalid ground-plan and wing veins. No other hypotheses are discussed in the book. For example, the possibility that *Heliconius* evolved their unusually simplified mimetic patterns by a non-ground-plan innovation is not considered by Nijhout, whereas in 1978 he thought that "colour fields" such as those in *Heliconius* demanded a separate explanation. Nor is Atuhiro Sibatani's alternative hypothesis for eyespot development mentioned, although the relevant paper (1980) is cited by Nijhout in a section on homeotic patterns.

Even if the ground-plan is accepted, Nijhout seems to deduce homologies in the book by guesswork. For *Charaxes* and some papilionids, Nijhout guesses that the alignment of a pair of underside bands with a single upperside band indicates homology: the upperside band must then be a composite of the two underside elements. But this explanation ignores selection acting on the pattern's function on a partially translucent wing. The unmentioned alternative hypothesis is that the upperside band is homologous with only one or none of the aligned underside elements, just as alignments of nonhomologous elements are expressed within and between adjacent wing surfaces in *Kallima*. For *Heliconius*, Nijhout assumes that black, red and brown fields are "pattern" components of the ground-plan, whereas yellow and white are "background". As he points out, this might neatly explain the extraordinary genetic interaction elucidated by J. R. G. Turner in the forewing band of *H. melpomene*. But some *Heliconius* genes (in *H. erato* the *Y* gene; in *H. melpomene* the *D* and *Yb* genes) can replace red patches with yellow by 'overprinting'. Genes shaping overprinted patches affect both colours equally, and a colour switch here seems more likely than a mechanism obeying Nijhout's rules.


Heliconius charitonia (zebra butterflies). The farthest butterfly is marked as part of a capture–release study. From *Sarapiqui Chronicle: A Naturalist in Costa Rica* by Allen M. Young. Smithsonian Institution Press, $40 (hbk), $16.95 (pbk).

Nijhout ends with an evolutionary message. Pattern homologies suggest that mimicry and other colour patterns may evolve by macromutations at homologous genetic pattern elements. Sound familiar? Although not referenced, Richard Goldschmidt is famous for proposing the same idea in 1945 on the basis of a similar nymphalid ground-plan. Nijhout is even more radical, suggesting that in the müllerian mimics *H. erato* and *H. melpomene*, even the genes that control the colour patterns may be homologous. I am cited erroneously as agreeing with this genetic homology between *Heliconius* mimics; in my paper I actually discuss homologies between races 'within' rather than 'between' species. The forewing bands of *H. erato* and *H. melpomene* seem to me to have about as little in common genetically as might possibly be imagined for such nearly identical colour patterns. Any similarities that do exist between other genes may be due to simple inheritance of simple mimetic patterns in both species, requiring similar gene action. Crosses between related *Heliconius* species cause a breakdown in pattern, suggesting that clarity of intraspecific pattern inheritance is due to modifying loci rather than to the major loci alone. Even if one of these genes were homologous between species, evolution in *Heliconius* is so rapid that one would not expect to find homologies just by looking at the pattern — molecular and linkage studies are also necessary. My own not-so-radical conclusion for *Heliconius* is that selection, rather then macromutation at homologous genes, has been primarily important for the evolution of mimicry.

Nevertheless, the book is both valuable and interesting. It is the first to collate a wide array of information about the biochemistry, development, morphology and genetics of lepidopteran patterns (there is no material on the molecular biology of development, because the relevant studies remain to be done). Some of the homology hypotheses in this book could be tested using cladistics: the inclusion of Don Harvey's radical reclassification of the Nymphalidae is an added bonus in this respect. Without the unifying hypothesis of variations around a ground-plan, perhaps the book would never have been written, and that would have been a great loss. Read this book, but keep alternative ideas in mind. ☐

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