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# BOOK REVIEWS

## MORPHOLOGICAL EVOLUTION[1]

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Widespread acceptance of the neo-Darwinian theory of evolution throughout much of the middle part of this century reflects this theory's ability to provide rational, scientific explanations for the origin and diversity of life on Earth. Indeed, most of the recent challenges to the Modern Synthesis concern whether it is sufficient to explain and account for all significant features of evolutionary change. The origin and establishment of morphological novelty is one topic that has resisted attempts to bring it under the umbrella of traditional evolutionary dogma. It is this topic which is addressed in *Mechanisms of Morphological Evolution.*

The book is intended to serve two functions: first, to provide an overview of fundamental principles of evolutionary theory, genetics, ecology, and development that are relevant to analysis of long-term morphological evolution; second, to provide a vehicle to promote the author's model for the evolution of novel features and the higher taxa that they frequently define. The target audience comprises advanced undergraduates, evolutionists, and developmental biologists. The book's dual role is reflected in its organization into two parts.

The first eight chapters (part one) review traditional topics in population genetics and evolution, including speciation, intraspecific and interspecific variation, quantitative genetics, artificial selection, and morphometrics. Chapter 8 closes this section with a discussion of "long-term evolution at the species level." Considering the scope of these topics, the chapters are short; specialists in each area likely will learn nothing new in their respective disciplines. Nevertheless, Wallace Arthur succeeds in his aim of identifying fundamental principles in these fields, aided in no small part by numerous case studies which are included as a means of illustrating theory. One highlight for me was the balanced evaluation of the gradualist-punctuationalist controversy. For example, Arthur accepts certain aspects of the theory of punctuated equilibrium, such as its emphasis on speciation in peripheral isolates. Yet, he considers other aspects, in particular the concentration of bouts of morphological change at speciation, to be unwarranted at this time, given the extensive intraspecific geographic variation in morphology that has been documented in many natural populations and the limited data available concerning the heritability of phenotypic variation generally. He also challenges the frequent tendency to equate large-scale morphological change with large-scale, yet unspecified, genetic change, as opposed to polygenic change involving numerous mutations of small effect.

These topics, however, are in effect only preliminary bouts leading up to the main event: specifying the mechanisms that underlie the origin and establishment of truly novel phenotypes—many of which define morphological discontinuities with respect to previously existing forms—and the higher taxa they frequently characterize. This has always been a thorny problem for Darwinian evolution by natural selection, and one that is only partly mollified by adaptationist constructs such as preadaptation and key characters (sensu Mayr, 1963). Central to Arthur's argument is his belief that the modern synthesis "is correct as far as it goes, [that it] needs to be extended, not replaced" (p. xii). What is missing "is a developmental component connecting genotype and phenotype" (p. xi), a component he provides in the form of morphological saltations derived from "natural selection acting on single genes of major developmental effect" (p. xii).

Arthur's thesis is delineated in the remaining seven chapters (part 2), which include topics such as cell differentiation and morphogenesis, developmental genetics, major genes and the origin of higher taxa, evolutionary rates, and morphological complexity. But in contrast to the style followed in earlier chapters, where theory was neatly combined with relevant, real-life examples, I found the reviews presented in these chapters, as well as the main argument stringing them together, much less convincing.

For instance, we are introduced to the concept of "D-genes"—genes that affect development in such a way that novel morphologies or, indeed, entirely new body plans arise literally in a single step. Considering how much this asks of any developmental system, one would expect an extensive treatment of developmental genetics and models of pattern formation to bolster this case. Yet, discussion of these topics is surprisingly brief. Pattern formation is discussed only in terms of diffusible morphogens, with yet another illustration of the "French-flag model" (one wonders at how popular this model of pattern formation would be if the French had chosen stars instead of stripes). There is no mention of epigenetic tissue interactions, nor of changes in their timing or the timing of developmental events generally (i.e., heterochrony) which lately have been promoted as important in the evolution of morphological diversity. Evidence of D-genes is limited mainly

[1] *Mechanisms of Morphological Evolution.* W. Arthur. Wiley, Chichester, New York, Brisbane, Toronto, Singapore, 1984. xv + 275 pp. $36.00.

to the genetics of shell coiling in some gastropods, in which the direction of coiling is determined by a single Mendelian locus with two alleles, and homeotic mutants in *Drosophila.* And while one cannot deny the importance of these systems to an understanding of developmental mechanics, it is not immediately obvious why they represent the same mechanism by which novel phenotypes arise.

Arthur's downplaying of developmental mechanics stems from his belief that the developmental origin of "saltational variants" is well established and not, therefore, a problem; the real problem, he offers, "occurs at the level of the population rather than at that of the individual" (p. 179). This should come as a surprise to many evolutionary biologists. For instance, Futuyma (1979 p. 438) states: "The real problems posed by evolution . . . lie not so much in the potency of natural selection as in the mechanisms by which the variations on which it acts arise . . . . The problem of how new variations arise falls not within the province of mathematical genetical theory, but within that of molecular genetics and developmental biology." The problem, as Arthur sees it, stems from the fact that his saltational variants are not perfect (this would be asking too much of the developmental system); they must be sustained through a maladaptive phase lasting several generations until numerous minor mutations bring the novel structure, or body plan, to a new adaptive peak. Thus, we are introduced to the concept of "n-selection"—a regime in which an organism's survival seemingly is based solely on whether or not it can breed successfully. As this regime entails independence from biotic factors such as competition, the mutation involving a D-gene is therefore also assumed to provide "ecological and reproductive isolation from the wild-type progenitor" (p. 188) in addition to morphological novelty. Saltation indeed.

The main strength of *Mechanisms of Morphological Evolution* is its primary focus on a problem that typically is relegated to a subsidiary role in general treatments of evolutionary biology: how do morphological differences at the level of order, class, or even phylum arise and become established? Arthur does a good job of pointing out aspects of this problem that lack convincing explanations derived from the Modern Synthesis. He also usefully calls attention to the necessity of incorporating population-level phenomena in what traditionally has been considered from a narrow morphological perspective. As an alternative, however, he offers a saltational model that is, at least with respect to certain aspects of genetics, development, and ecology, less realistic than almost any scenario provided by the synthetic view. The answer to this problem must lie between these two extremes, but determination of exactly where the answer is still seems far off.

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# THE NEOLITHIC TRANSITION AND THE GENETICS OF POPULATIONS IN EUROPE: A REVIEW[1]

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One of the more engrossing pastimes that has occupied human geneticists over the last 40 years has been the attempt to make some evolutionary sense out of the patterns of genetic variation that typify the species *Homo sapiens.* The first lesson we have learned from this sort of work is that it is seldom possible to infer the details of evolutionary history from the genetic data alone; there are simply too many factors that have impinged on genetic variation in species to permit unambiguous inference as to causation and timing. The second lesson we have learned is that the more information we have from extraneous (non-genetic) sources, the better job of evolutionary reconstruction we can do. What this means in practice is that we use the genetic data not so much to infer human history as to confirm it. In *The Neolithic Transition and the Genetics of Populations in Europe,* an archaeologist (A. J. Ammerman) and a population geneticist (L. L. Cavalli-Sforza) use the available evidence from genetic marker frequencies to support their claim that early agriculture spread from southwest Asia across Europe, effecting the neolithic transition in the process.

The book begins with a brief description of the origins of agriculture in southwest Asia. A distinction is drawn between the initial development of domestic plant and animal species from wild progenitors and the incor-

[1] *The Neolithic Transition and the Genetics of Populations in Europe.* A. J. Ammerman and L. L. Cavalli-Sforza. Princeton Univ. Press, Princeton, NJ, 1984. xv + 176 pp. $25.00.