Book Reviews

Mechanisms of Speciation

Geographic Variation, Speciation, and Clines. JOHN A. ENDLER. Princeton University Press, Princeton, N.J., 1977. x, 248 pp., illus. Cloth, $16; paper, $6.95. Monographs in Population Biology, 10.

One of the major unresolved controversies in the field of evolutionary biology concerns the universality of the model of geographic speciation championed by Ernst Mayr. According to this model the geographic variation of a species is unimportant in speciation even when local adaptation results in a mosaic of markedly different subspecies separated by steep clines (geographic gradients in allele frequencies). Mayr argued that significant geographic differentiation is prevented by gene flow between the populations and by the fact that conspecific individuals have common homeostatic mechanisms based on genetic coadaptation. These forces are ostensibly so strong that the genetic differentiation and reorganization commonly associated with speciation cannot occur unless some populations become geographically isolated for a period of time. Consequently, this model of geographic (or more properly allopatric) speciation called for the development of generally untestable historical hypotheses to account for the original fragmentation of the species range and for the subsequent reunion of the derivative populations. The outcome of this secondary contact would be determined by whether reproductive isolating mechanisms evolved during the period of isolation or immediately following reunion. If antihybridization mechanisms failed to evolve, then the speciation process would be reversed and the hybrid zone, with its morphologically variable populations, would broaden and disappear as the daughter populations fused.

This model of population differentiation and speciation has dominated the field for 35 years despite serious challenges in the pages of *Science* (Throckmorton and Hubby, 1963; Ehrlich and Raven, 1969; Endler, 1973) by workers who argued that the internal cohesive forces of a species were not as strong as Mayr supposed. Further casting doubt on the allopatric model, studies of hybrid zones around the world presented three types of problems that could not readily be dealt with by it. First, many zones of increased variability (presumed to be secondary in origin) are much older and more stable than expected. Second, there is far less evidence for the reinforcement of premating reproductive isolating mechanisms than one would predict if geographic speciation were the norm. Finally, the distinction between zones of primary intergradation and secondary contact (traditionally a clear guide to the systematic status of the interacting populations) cannot be made in some cases.

Recognizing these problems, M. J. D. White, B. C. Clarke, J. Murray, and others have suggested alternative modes of geographic speciation. Their models of stasipatric and parapatric speciation received relatively little application, however, outside the particular groups for which they were developed. Now Endler has provided a model for geographic differentiation and parapatric speciation that has much greater generality. This important contribution should stimulate some much-needed rethinking about the geographic aspects of evolution and the origin of species.

Following brief introductory chapters on modes of speciation and gene flow, the monograph begins in earnest in chapter 3, in which Endler considers the genodynamics of clines. He investigates the causes of regional differentiation and, in particular, the causes of sharp differentiation in the absence of barriers to gene flow and spatially abrupt changes in the environment. Using single-gene models, he shows how steep or step clines may evolve even when the alleles involved are responding to selective gradients weaker than those that can easily be measured in nature. Such differentiation may occur even when gene flow is high, provided the gene-flow distance is small relative to the length of the selective gradient. Endler discusses the factors that tend to displace step clines spatially from their positions of selective neutrality and the conditions under which step clines will be stable in time and space. Most important, he shows that the distinction between primary and secondary intergradation cannot be made on the basis of the conventional observations of a given natural cline. The presence of relatively more variable populations in some hybrid zones does not prove that they are the result of secondary contact; it is a consequence of the expected binomial sampling variance and will occur in all areas of intermediate gene frequency.

In chapter 4 Endler uses oligogenic models to show how modifier genes can alter a major gene cline. Extending B. C. Clarke's work on coadapted clines he argues that we should recognize two types of modifiers. Some, which have a positive or neutral effect on various allelic combinations of the major gene, will tend to spread throughout the range of the species. Others, which have a negative effect on some genotypes (for example heterozygotes of the major gene), will spread only in some parts of the species range. The latter type of modifiers can cause a steepening of the major gene cline and result in differential coadaptation on either side of the step. Endler reports experiments with *Drosophila melanogaster* in which he found that the initial stages of differential coadaptation could evolve along a smooth cline even in the face of 40-percent gene flow between adjacent demes.

Then, using O'Donald's mathematical model, Endler shows how the presence of coadaptive modifiers in a cline could lead to the evolution of assortative mating if the modifiers resulted in a net deficiency of major-gene heterozygote fitness. This process can result in the formation of stable hybrid zones and even parapatric speciation. Endler concludes that almost all published examples that are used to justify the allopatric speciation model can be used also to justify the parapatric speciation model. For example, he discusses this reviewer's work on two species of frogs (*Pseudophryne*) contiguously distributed in southern Australia. The frogs are very similar in morphology, behavior, and ecology, and the hybrid zone between them is characterized by increased variability, reduced viability, and increased developmental problems. The frogs were postulated by Littlejohn to have separated and diverged during the Pleistocene and to have come together more recently to form their present distribution. Endler argues that the zone may be the result of parapatric differentiation. The few differences between these taxa could be explained on the basis of a few color-controlling genes and the hybrid-zone effect explained on the basis of a few coadaptive modifiers together with clinal selection patterns between the differing habitats of the frogs.

In the final chapter Endler discusses the problems of distinguishing between primary and secondary intergradation: the problems of interpreting step clines and hybrid zones. He examined studies on over 60 such phenomena for estimates of cline width, gene-flow distance, selection gradients, and age of interaction. Only a few of the studies contain enough data to permit rough tests of the hypotheses developed, but the agreement between quantitative theory and nature is surprisingly good. Endler shows that it will be impossible to distinguish between primary and secondary intergradation because they result in the same types of geographic phenomena and may evolve from gradient clines in the same order of magnitude of time. He concludes with a discussion of hybrid zones involving birds, reptiles, and insects in tropical South America. He notes that because the time courses to extremely steep clines are short enough to have evolved since the last glaciation it is not necessary to postulate Pleistocene forest refugia to explain existing hybrid zones. In marked contrast to prevailing practice, he argues that they might be explained in terms of contemporary selective gradients and dispersal patterns.

Given that this volume will (and should) be widely cited it is unfortunate that it was not better written. Endler makes extensive use of jargon: step clines become "more and more linear" and may even move "off of the species' range." There are more than 60 errors of a grammatical or typographical kind, including such gems as "more complete," "more continuously," and the inexcusable "data is." Poor sentence construction results in numerous annoying ambiguities. A large portion of the volume is devoted to mathematical modeling, and more care might have been taken with the choice of symbols: some have different uses on adjacent pages, and one even has two different meanings in the same table. Some help is provided in the form of a short glossary, but definitions of 11 algebraic symbols are omitted (including K, which has four different uses). Also found in the glossary are some terms whose meanings are unique to this volume and whose definitions are left out of the text. I shall not comment on the mathematical models themselves beyond noting that they are generally sound (four errors were detected) and that there have been some important contributions made to the theory of clines by Karlin, Nagylaki, and others in the three years since this book was completed. There is an extensive bibliography (758 references) on geographic variation and clines. The wealth of citations is, however, a little deceptive, as many of the "classic" cases reported during the 1940's and 1950's have proved invalid. For example, the Californian salamander, *Ensatina eschscholtzi*, is not a good example of a ring species, as the overlapping populations hybridize, and the continued presentation of all Moore's experimental crosses of "*Rana pipiens*" as cases of intraspecific hybridization is unacceptable.

How appropriate are oligogenic models in simulating the processes of speciation? Although Endler never asks this question, many readers will. Twelve years of biochemical genetics suggests that these models may be appropriate; electrophoresis, even when we allow for cryptic variation within electromorphs, provides no evidence for extensive reorganization of gene pools during speciation. There is every indication that changes at a few loci are sufficient for speciation and that geographic variation rather than genetic revolution may be the critical prerequisite.

How well does existing population genetics theory allow us to interpret nature? Unfortunately, as Lewontin has noted, it is neither empirically nor dynamically equal to the task. Furthermore, it is an equilibrium theory and consequently the role of history is constantly denied. One of Endler's main contributions is to confront theory with history and show how the two might interact. The encounter underscores the fact that theory far outpaces verification in this area of science. We will be unable to assess the relative importance of the various modes of speciation until we develop a methodology for distinguishing between their products in nature. While Endler's requirements for the interpretation of a natural cline (measurement of gene flow and all components of fitness, and a knowledge of the history of the interaction) are simply unrealistic, much can be done to improve the present situation. The measures of gene flow and natural selection, for example, need refining in both empirical and theoretical studies. The extent to which gene flow varies with direction, population density, and position within the species range has yet to be established. Endler's efforts point to the need for more critical studies of carefully chosen situations in nature. Until these are done and the various hypotheses are tested, it is likely that clines and hybrid zones will remain taxonomists' nightmares and evolutionists' delights.

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Achievements and Prospects

International Cell Biology, 1976–1977. Papers from a congress, Boston, Sept. 1976. B. R. BRINKLEY and KEITH R. PORTER, Eds. Rockefeller University Press, New York, 1977. xvi, 694 pp., illus. $30.

Cell biology, as George Palade reminds us in the introduction to this volume, is a science reborn. Out of general physiology and by way of ultrastructure, it arose from an intelligent selection of problems appropriate to the time and to the emerging technologies of investigation. The exceptional advance of cell biology has been due in no small part to general adherence by those who work in the field to a generative program: the integration of ultrastructure and chemistry with the physiological function of cells and their organelles. This volume places on display several outcomes of the program—obviously enough, the more successful outcomes were selected for emphasis—but it does more than that. Already evident in the contents is an emerging new program, one that is to deal with regulation, operating not only within organelles and at a level indistinguishable from the structures and molecules themselves, but also at a distance: from the genome in cells and from the assemblage as a whole, or from the integrative systems, in tissues, organs, and organisms.

It is in no way a slur on the discipline to note that some of its unique preoccupations of one or two decades ago, for example, mitochondria, ribosomes, and chloroplasts, have been taken over by other, and sometimes more self-contained, scientific enterprises, such as biochemistry. These take-overs are a measure of success. By the same token, a measure of the power and maturity of cell biology as it is now practiced is the pervasive concern with regulatory mechanisms. Many of the contributions of this volume give evidence of that maturity and of the centrality of cell biological concepts and techniques to genetics, biochemistry, and developmental biology as they are now practiced.