A View of Evolution

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A View of Evolution

Phylogenetic Patterns and the Evolutionary Process. Method and Theory in Comparative Biology. NILES ELDREDGE and JOEL CRACRAFT. Columbia University Press, New York, 1980. x, 350 pp., illus. $27.50.

The great evolutionary synthesis of the 1930's and 1940's was the work of many biologists approaching evolutionary questions from the viewpoints of genetics (Dobzhansky, for example), systematics (Mayr), or paleontology (Simpson) or through a variety of disciplines (Huxley). The result was three decades of relative agreement among evolutionary biologists. A successful welding of genetics with natural history in the broad sense had been accomplished, and a general understanding of evolutionary processes had been attained. Discoveries at the level of populations were projected in such a way as to explain nearly all important evolutionary phenomena—change within populations through time, multiplication of species, origin of evolutionary novelties, adaptive radiations, differential rates of origination and extinction of taxa, and the establishment of new ways of life. There always have been dissenters, however, and they slowly have gained strength. Challenges to prevailing orthodoxy now appear at ever increasing rates and have given new vitality to the venerable field of what the authors of this book like to call "comparative biology." Whatever one calls it, that area of science concerned with evolutionary processes and phylogenetic patterns is now in a state of excitement and flux. The vast majority of workers still would be termed "syntheticists," or, if dissenters, at least "transformationalists" (those who emphasize the adaptive change of intrinsic properties of organisms, such as morphology, as the central evolutionary question).

Eldredge and Cracraft represent the point of view of one group of dissenters. They do not want to be misunderstood, and so they repeat, again and again and again, that no smooth extrapolation of microevolutionary (within-population) processes leads to explanation of macroevolutionary (among-species) phenomena. Definitions are important in understanding the authors, and none more so than that of "macroevolution." This troublesome word means the origin of evolutionary novelty to some workers and certainly carries with it some notion of adaptation in the minds of most evolutionists. Since Eldredge and Cracraft have as one goal no less than a new theory of macroevolution, it is essential that it be kept in mind that to them macroevolution is no more than "change in species composition within a monophyletic group in space and time, best thought of, perhaps, as a process of differential species origination and survival within monophyletic taxa" (pp. 15–16). Indeed, they do not deal with many matters that historically have been treated as parts of macroevolutionary theory, such as the origins of evolutionary novelties. A strong argument is made that only historical analysis can elucidate patterns of evolution.

Throughout the book an appeal is made for the analysis of evolution from a hierarchic viewpoint. Emphasis is placed on levels of phenomenology so that, for example, microevolution, speciation, and macroevolution are considered as separate, not necessarily connected, phenomena. To the authors, the origin of evolutionary novelties is a population-level phenomenon. The importance of such novelties ("apomorphies") is that they can be used to analyze the genealogical history of groups, which, they argue, can be approached scientifically only through the methods of a group of workers generally termed "cladists." In fact, this is mainly a book about cladistics, its philosophical underpinnings, its theoretical significance, and its pragmatic implications. Early on, phenetics and evolutionary systematics are swept aside with a few derogatory comments. Throughout the book there is a constant and annoying attack on those termed "syntheticists" such as Dobzhansky, Simpson, Mayr, and Bock. Cladistics is asserted over and over to be the true scientific way. While in many respects the presentation of cladistic principles is useful, it is incomplete, rather biased, and poorly organized. Readers are regularly referred to later chapters for further explanation. Such embarrassing pragmatic problems as what constitutes a character for analysis and how robust are cladograms are quickly passed over or ignored. In other words, this is something of a tract, rather than a manual.

Species and speciation receive much attention. A case is made that species are the units of evolution, in the sense that any evolutionary novelty survives and has significance only when it becomes a species character. Though the authors acknowledge some pragmatic difficulties in applying strict cladistic methodology to species problems, they nonetheless make species the centerpoint for some of the most important arguments in the book.

In order for the ideas in this book to have any relevance, species must be real, bounded units in space and time. Species cannot be gradually transformed into new species through time; they are seen as discrete entities in nature that have origins, histories, and extinctions. In short, the authors' theory demands that species be discrete, and should one species be shown to transform gradually into another in time, without splitting, then despite large amounts of time and great morphological change the authors would continue to consider the lineage to be a single species. One might argue that this is an empirical question and look to the fossil record, but Eldredge and Cracraft argue that one cannot study speciation from fossil records.

Those who work on species-level problems are aware of cryptic species and realize that not all speciation events result in significant morphological change. Eldredge and Cracraft recognize this fact, and they are not so naïve as to insist that speciation results in morphologically distinct species. Rather, they believe that speciation produces discrete, bounded units that offer the only opportunity for a kind of stepwise morphological divergence. It is curious that the authors give so little credence to the possibility that morphological divergence through time within species that came to have geographically separated populations, coupled with simple extinction of intervening populations, could lead eventually to species that are distinct in space but continuous in time (that is, species that have never "speciated"). Explicit recognition is given to the possibility of speciation by geographic subdivision, and it is even noted that some workers believe that this may be the dominant mode of speciation in some groups of vertebrates. Yet so intent are the authors on separating themselves from the "syntheticists" that they write (p. 270), "Only a view that species are transitory, arbitrarily defined segments of an evolutionary continuum permits the notion that within-population phe-

nomena may be extrapolated directly to higher levels. Recognition of the existence of species as discrete entities in effect contradicts the vision of change in gene content and frequency—whether or not affected by natural selection—as a continuous process from the population on up through the phylum." It appears that the entire thesis of this book rests on species concepts.

If one can accept that species are the discrete units of space and time that this book demands, one can learn a lot about the ways in which differential origination and extinction of species lead to phylogenetic patterns. There are many pages of useful analysis, although a serious flaw of the entire book is the apparent fervor of the authors and their need to repeat the central ideas over and over. The book could have been half as long.

Readers will search in vain for any meaningful discussion of the origin of adaptations. Nor will they find many references to molecular data or methods of analysis. Such authors as A. C. Wilson, Romero-Herrera and co-workers, Goodman, and Zuckerkandl are ignored. Even modern accounts of speciation theory by White and Endler are ignored, and this is most curious because this topic plays such a dominant role in the book. Thus much of the excitement of modern comparative biology is viewed as not relevant to this misleadingly titled book.

Is there anything new in this book? For those who have not followed the arguments in *Systematic Zoology* during the past decade and who have not read Steven Stanley's book (*Macroevolution*, Freeman, 1979), the answer certainly will be "yes," and I urge you to read this book to bring yourselves up to date concerning one important view. For me, a series of familiar arguments are here brought together in one place, in a rather novel and entertaining presentation. But there is little that is new. The most important lesson for me was the realization that a concept of discrete species is critical to cladistics theory. The authors essentially argue that macroevolution can be reduced to a problem of cladistics. Though I am in firm agreement with them that we must struggle to untangle the history of taxa before we speculate about evolutionary patterns, I am equally firm in my belief that there is much more method and theory of evolutionary processes and phylogenetic patterns than one could learn from this book.

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Implications of Parasitism

Evolutionary Biology of Parasites. PETER W. PRICE. Princeton University Press, Princeton, N.J., 1980. xii, 240 pp., illus. Cloth, $17.50; paper, $6.95. Monographs in Population Biology, 15.

The author of this monograph has two goals. The explicit goal is to develop generalizations of significance for evolution and ecology from a comparative study of parasites. The implicit goal is to convert the reader to his own enthusiasm for parasites. The two goals combine unhappily.

Price seeks proselytes among those who say that parasites are essentially predators, among those who glorify mammals and birds as testaments to evolutionary progress, and among those who argue that parasitism is an evolutionary dead end. It is important to him "to establish that no group of organisms on this earth can surpass the parasites in their potential for continued adaptive radiation."

Enthusiasm can be the source of useful inspiration, but here it distorts suggestions and conclusions that have merit. Early in the book Price presents arguments that the majority of insects are parasites—70 percent of British insects, for example. Since three-quarters of all species are insects and nematodes, mites, protozoans, and bacteria are parasites as well, the significance of predators, of nonparasitic herbivores and carnivores, and of saprophages becomes, to him, trivial. This view is a consequence of a definition that includes as a parasite any species in which the individual obtains all of its nourishment from an individual of another species. Hence most of the insect defoliators of plants become parasites, not herbivores. The resulting diversity of life forms is so great that Price's "generalizations" are dominated by exceptions. He is forced to define a generalization by a kind of majority vote: If a conclusion applies to more than 50 percent of the species, then it becomes a generalization. But also Price's desire to convince the reader of the great abundance and diversity of parasites leads him to conclude that examples could be found to defend any thesis. What, then, are the rules for disproof? What are the precisely defined conditions within which a principle is appropriate?

The irony is that Price's basic conclusions are derived from examples drawn from a narrower spectrum. That spectrum is characterized by small animals that search for discrete patches from which an individual obtains its nourishment for a significant part of its life. Even then, subcategories exist that generate apparent exceptions. Those subcategories include insect parasitoids of other insects as well as internal parasites of vertebrates, such as helminth parasites. For those organisms search processes are different, as are conditions within the hosts. As a consequence, both adaptive and competitive pressures are different. If Price had made even a modest effort to define strategic classes of parasites, his conclusions would have been much more focused and significant.

But if the reader can place the missionary zeal in perspective and can erect a classification of his or her own, then the book offers suggestions that are important and a rich set of examples that are useful for testing alternative ideas.

Those animals that search for patchy, transient resources are faced with difficulties that Price argues must lead to low probabilities of colonization and high probabilities of extinction. The result is systems dominated by instability. Hence the extensive body of literature that emphasizes a fixed point equilibrium and damped oscillations around the equilibrium hardly seems appropriate. It represents an essentially static view in which the underlying structure cannot evolve. Price labels such conditions as equilibrium ones and everything else as nonequilibrium. Even the developers of equilibrium models view those models only as instructive metaphors of a tiny part of reality, stepping-stones to a richer set of metaphors that have a closer relation to reality. Hence Price sets up a situation where anything of interest in nature must fall into his second, "nonequilibrium" category. There are different causes and kinds of stability and instability behavior within that category that generate different classes of variability, however, and it is these kinds of variability that underlie the evolution of structures. But at least Price joins that growing number of natural and social scientists who see instabilities as a center of interest. And his emphasis on within- and between-patch dynamics contributes examples for useful understanding.

The remainder of the book concentrates on questions of adaptation and community structure. Price notes the prevalence of parthenogenesis among parasites and argues that genetic variation among them is likely to be richer than proponents of sexual reproduction would believe. That is a condition that would bolster his argument that parasites are highly adaptive, capable of rapidly tracking changes in host and environment. It speaks against his more con-