

field in Patagonia earlier in this century; he wears a gaucho outfit, including *bombachas*, *alpargatas*, and *faja*." Only a paleontologist who had himself intensively explored all aspects of South American mammal history could have written so rich and compelling a biography of his fellow explorers.

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Evolution in Slow Motion

Living Fossils. NILES ELDREDGE and STEVEN M. STANLEY, Eds. Springer-Verlag, New York, 1984. xii, 291 pp., illus. \$45. Casebooks in Earth Sciences.

This volume, one of a series of casebooks in earth science, is more biological than geological, with an emphasis on "living." The editors' introduction is followed by 32 case histories, written by 31 authors, and two brief terminal essays by the editors. The goal is to provide enough case histories to enable an interested individual to decide if there is anything to the supposed phenomenon of arrested evolution.

What is a living fossil? To me the term relates to relicts, phylogenetically isolated groups with few living representatives, which closely resemble groups known only as fossils. When I checked Webster's unabridged dictionary I discovered that I was close to the apparently accepted definition. The unexpected (to me) criterion of the editors is that a living species must bear great anatomical similarity (bordering on identity) to a fossil species that occurs very early in the history of the lineage. One expects to find case histories of such forms as horseshoe crabs, coelacanths, *Peripatus*, *Nautilus* (all present), *Sphenodon*, and *Lingula* (both absent). But this book abounds in potential living fossils, from elephant shrews to odd corals, and the criteria for choice of subjects admit even such surprises as tree squirrels (*Sciurus*). Regrettably all plants are excluded. Of course, most of the authors devote considerable attention to the question of whether their particular organism is a living fossil.

A major theme is the issue of whether bradytely (very sluggish evolution) requires special explanation or is just the extreme tail of a normal distribution of evolutionary rates. A second theme is the relation of speciation to morphological change. Since speciation in the fossil record is morphological change, many

arguments, especially by the editors, are confounded by the failure to separate these concepts properly.

Though many of the chapters are fairly straightforward and factual, a few stand out as contributions to evolutionary theory. Elisabeth Vrba's thoughtful contrast of the impala (the living fossil) and its sister group (blesbok-hartebeest-wildebeest group) is a good example. She places organisms in environments and takes into account factors (such as selection pressures) shunned by those with more taxic approaches, yet considers species-level implications (her "effect hypothesis") without giving species emergent properties. Peter Ward presents an exceptionally interesting analysis of *Nautilus* and argues that living nautiloids might be a rapidly speciating group constrained in its morphology by the need for effective swimming and maintenance of a buoyancy control system. The resulting morphological stasis masks evolutionary dynamism. Many living groups may have narrow bounds on the range of morphological divergence permitted, determined by organismal-level features, and they evolve as "living fossils" even though they may be speciose (as in the case of various urodele genera).

There are other good chapters (for example, Daniel Fisher's on horseshoe crabs), but most deal with cold facts outside a broad biological framework. Some make too much out of too little. Still, the book as a whole is a success—a rich source of information, references, and, occasionally, stimulation.

At the crux of the question of why we have living fossils is the debate concerning taxic and adaptive approaches in macroevolutionary theory. My impression is that in the data chapters only Vrba and Ward really address the issue and that only Ward grapples with the species question. We still are far from knowing whether slow evolution, even approximating stasis, results from slow rates of speciation (either because morphological change is concentrated in speciation events or because it is an incidental effect of speciation), from organismal-level systems of developmental and functional constraints that transcend speciation events, or from some combination of these and other factors.

T. J. M. Schopf, whose untimely death we mourn, questioned the entire notion of living fossils and thought that we focus too much attention on the persistence of traits that interest us. He had a point. Morphological evolution is very important for some groups and occurs rapidly. Other organisms live in worlds

dominated by sensory modalities, for example, odors or other chemical cues, that do not require morphological change for persistence. The fossil record preserves morphologies. Morphology alerts us to the existence of evolution and demands explanation for its diversity. But our explanations must be based on realistic species concepts and assessment of the biological context in which evolution takes place.

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Environmental Physiology

Biochemical Adaptation. PETER W. HOCHACHKA and GEORGE N. SOMERO. Princeton University Press, Princeton, N.J., 1984. xx, 538 pp., illus. \$60; paper, \$19.50.

Hochachka and Somero's *Strategies of Biochemical Adaptation*, published in 1973, was an effort to bridge the interests of biochemists, physiologists, evolutionists, ecologists, and population biologists. The book was an overwhelming success. It was particularly useful for students confused by the more encyclopedic approach of many comparative physiology textbooks.

Biochemical Adaptation is a dramatic updating and expansion of the 1973 work. The authors have augmented its virtues, corrected many of its weaknesses, and pointed toward research horizons that were previously unapproachable. The central concern of the book is to elaborate the basic adaptive mechanisms employed by organisms living in diverse environments and to identify common biochemical strategies of adaptation. The authors have not attempted to cover every type of environment or mode of adaptation. Rather, they have focused on specific research topics or environmental parameters with respect to which some general statements can be made, conclusions drawn, or questions posed.

The book relies heavily on research from a limited repertoire of organisms, with particular emphasis on fish, mammals, and a few invertebrates. The selectivity of species and research topics does not diminish the value of the book. The examples are appropriate and accomplish the goals delineated in the preface. The authors' contagious enthusiasm and the clarity of their writing make this book an excellent teaching tool. For courses with an evolutionary emphasis,

however, instructors may wish to provide supplemental readings that represent a broader variety of trophic levels and taxonomic categories and to distinguish more clearly than the authors do between physiological and evolutionary adaptation.

Biochemical Adaptation is very well organized. It begins with an overview of the basic mechanisms and strategies of cellular and biochemical adaptation. After laying the metabolic groundwork, the book traverses such diverse topics as enzyme adaptation, anoxia, hypoxia, diving adaptation, anhydrobiosis, hibernation, water-solute problems, oxygen transport, and pressure effects. Several special topics are addressed that the authors think deserve particular attention in light of the extent of recent research or the potential for future research. Though all 12 chapters are well written and illustrated, those on exercise adaptation, limiting oxygen availability, mammalian developmental adaptations, temperature adaptation, and adaptation to the deep sea are particularly interesting.

The chapter on temperature adaptation presents a particularly thought-provoking treatment of protein adaptations, including thermally induced adjustments of enzyme catalytic efficiencies, differential interspecific compensation of the partitioning of free-energy terms (ΔG^\ddagger , ΔH^\ddagger , and ΔS^\ddagger), interspecies conservation of Michaelis-Menten constants, temperature adaptations of allelic isozymes, and thermal effects on both enzyme concentrations and protein subunit assembly. The authors introduce "compensation plots" (ΔH^\ddagger versus ΔS^\ddagger) for homologous enzymes from a series of evolutionarily divergent species. Since these plots are empirically found to be linear for a variety of enzyme reactions and $\Delta G^\ddagger = \Delta H^\ddagger - T\Delta S^\ddagger$, it follows that ΔG^\ddagger for a given enzyme reaction must be relatively invariant, whereas the partitioning of energy between ΔH^\ddagger and ΔS^\ddagger varies tremendously among species. The possible evolutionary significance of this and related phenomena is of course fascinating. The apparent evolutionary constraints on ΔG^\ddagger may appear to be contrary to the authors' assertion that "the critical energy change is always ΔG^\ddagger ." However, since free energy of activation is exponentially related to catalytic rate, even very small differences in ΔG^\ddagger could have profound effects on rate constants.

The last chapter of the book, which deals with the role of pressure, should capture the imagination of even the most jaded reader. Students may be conceptually prepared to consider the influences of temperature on enzyme catalysis, pro-

tein conformation, and polymerization, but the effects of pressure on these processes may be somewhat foreign to even the most sophisticated. The authors do an admirable job in introducing the subject, calling upon appropriate literature to illustrate the phenomena. This chapter finishes with some of the adaptations of diverse organisms living near the deep-ocean hydrothermal vents, which were discovered only a few years ago. It leaves the reader with the expectation that the most exciting research and discoveries on vent organisms are yet to come.

The general conclusion to which one is led by the book is that organisms possess elegant biochemical adaptations that allow them to flourish in a myriad of diverse environments. Though these often include unique and even bizarre modes of adaptation, they are but "variations on a fundamental theme." Understanding the detailed mechanisms of such adaptations and the rationale for the various adaptive strategies will help unlock the secrets of speciation, habitat partitioning, and the driving forces of evolution.

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Plants and Herbivores

Herbivory. The Dynamics of Animal-Plant Interactions. MICHAEL J. CRAWLEY. University of California Press, Berkeley, 1983. \$45. Studies in Ecology, vol. 10.

One goal of ecology is to decipher the principles that determine the distribution and abundance of organisms in nature and how those features change over time. The major impediment to realizing this goal is the fact that the distribution and abundance of a particular species are influenced by the other species with which it interacts. Since most species interact with many others, specifying how the web of interactions influences the population dynamics of a given species becomes an exceedingly complex task.

The volume by Crawley exemplifies one approach to that task and illustrates admirably both the complexity inherent in interspecific interactions and a general methodology one may adopt for understanding it. The author begins by pointing out that much is known about how herbivory can influence plant growth rates, mortality, reproductive output,

and competitive ability and about how plant density and physiological state can influence herbivore growth, mortality, and reproduction. The key word here is "can." Crawley's exhaustive review of these effects in the second and third chapters quickly convinces one that there is no universal effect of herbivores on plants or vice versa. In some plant species, massive defoliation reduces seed set, in others it does not. In some it increases mortality, in others it does not. The feeding rates of some insect species increase in response to changes in foliage quality, those of others decrease, and those of still others are not affected. The populations of some herbivores (for example snowshoe hares and *Cactoblastis* moths) seem to be limited in size by availability of food, whereas those of others (for example the *Opuntia*-feeding cochineal *Dactylopius opuntiae* and the spruce budworm) seem to be regulated by predators and parasites. This variety of interactive effects should surprise no one in the field, but nowhere is it so carefully and thoroughly documented as here.

Crawley's survey could lead one to conclude that there are no general principles governing plant-herbivore population dynamics and that a quantitative description of the population dynamics of any plant-herbivore system requires a unique model tailored to the unique attributes of that system. Indeed, such an approach is common among agricultural entomologists, who must predict very precisely the population sizes of pest species in order to predict levels of crop damage and optimal times for application of pesticides. However, Crawley's method of modeling plant-herbivore population dynamics illustrates that an alternative approach not only is possible but may in fact reveal principles not apparent from other approaches.

Crawley uses what may be termed the "modular" approach to modeling plant-herbivore dynamics, which should be familiar to ecologists as that adopted by M. P. Hassell and his colleagues for modeling predator-prey dynamics. The rate of change of each species is represented as the difference between birth and death rates, which in turn can be represented by a variety of different submodels or "modules." For example, one may use for plant birth rate a submodel that assumes that fecundity is independent of density, one that assumes that it is density-dependent in a fashion described by the traditional logistic equation, or one that includes parameters that represent effects of impaired plant growth due to defoliation. Similarly, for