Genetic engineering was created from investigations on three rather obscure phenomena seemingly far removed from any practical human health concerns: phage carrying bacterial genes, λ ends that stuck together, and restriction of foreign DNA by certain bacterial hosts. The technology that resulted from these investigations has revolutionized many aspects of our life.

Presented with Hatch's very personal perspective on the history of our discipline, I was not tempted to search for particular topics of interest. Rather, I read the book from beginning to end, often stopping to smile and think. And Hatch (or Carol?) provides yet another special favor: some 75 scientists are depicted here as an artist imagines they looked at about the age of 20. With this sort of reverse Dorian Gray maneuver, *Operators and Promoters* reveals molecular biology as an ever-youthful enterprise.

BOOKS: EVOLUTION

Explaining Exuberant Diversification

Axel Meyer

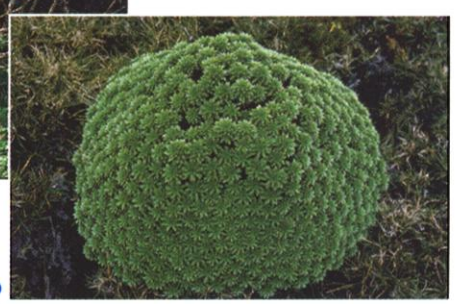
Diversity catches our attention. Biologists have long sought explanations for the remarkable diverse groups that characterize some of the major theaters of evolution. Groups such as the *Geospiza* finches of the Galapagos Islands and the species flocks of hundreds of endemic species of cichlid fishes in the great rift lakes of East Africa. have become celebrations of the creative power of evolution. They are among the most notable examples of a phenomenon termed "adaptive radiation," which also encompasses marsupials in Australia; *Anolis* lizards in the Caribbean; and honeycreepers, drosophilid flies, and silverswords in Hawaii.

The Ecology of Adaptive Radiation
by Dolph Schluter

Oxford University Press, New York, 2000. 296 pp. Price $85, £49.50. ISBN 0-19-850523-X. Paper, $34.95, £24.95. ISBN 0-19-850522-1.

Dolph Schluter, a professor at the University of British Columbia, has made some of the most important contributions to our understanding of evolutionary radiations. Early in his career, he worked on Darwin's finches in the Galapagos. More recently, he has studied the postglacial evolution of populations of three-spine sticklebacks in coastal lakes of the Pacific Northwest. In *The Ecology of Adaptive Radiation* (a recent title in the Oxford Series in Ecology and Evolution), he sets out to identify the mechanisms that cause adaptive radiation.

Schluter defines adaptive radiation, like George G. Simpson did almost five decades before him (*1*), as "the evolution of ecological and phenotypic diversity within a rapidly multiplying lineage." Starting from a single ancestral species, the radiation gives rise to a large number of phenotypically divergent species, each with traits that allow it to efficiently use some particular resources of their shared environment. The evolution of morphological and functional differences among the species lets them exploit different ecological resources, permitting the coexistence of several closely related species in the same habitat. Adaptation and speciation have long been major themes in evolutionary biology, with the groundwork in theory and empirical data dating from the beginnings of research in the field, more than 150 years ago. Both themes are combined in adaptive radiation, which includes adaptive phenotypic divergence and above-average rates of speciation.



Plants do it too. The Hawaiian silversword alliance exploits a wide range of habitat types, including cold arid alpine settings, hot exposed cinder cones, wet bogs, and dimly lit forest understories. The 28 living species are exceedingly closely related but vary greatly in their morphology and physiology, as these four examples suggest (top to bottom: *Dubautia knudsenii, D. waialealae*; on the opposite page, top to bottom: *Wilkesia hobdyi, Argyroxiphium sandwicense*). (An excellent overview of this adaptive radiation is available at www.botany.hawaii.edu/faculty/carr/silversword.htm.)

The "modern synthesis" in evolutionary biology has included a range of traditional explanations for the origin of adaptive radiations. The principal focus of these models is on divergent natural selection, under which species come to occupy different ecological niches and thereby avoid direct competition. Other models stress the colonization of a new habitat, usually an island or a lake, with few competitors and hence many new ecological opportunities (i.e., a wide resource spectrum with many adaptive peaks). The extinction of a previously domineering group offers another means of opening up ecological opportunities and facilitating diversification. Lastly, adaptive radiations may be initiated when a group acquires a "key innovation," enhancing its ecological opportunities by enabling it to exploit a different set of resources.

Some of these circumstances are rather fortuitous and unpredictable. Explanations for particular radiations often involve a combination of several factors: intrinsic, nonecological ones (such as genetic drift), as well as extrinsic biotic and abiotic conditions. And some of the explanatory hypotheses are more retrospective ad hoc interpretations than a priori predictions. As such, they don't easily lend themselves to much beyond the description of potential factors, and they rarely permit the rigorous ecological testing of theoretical results. Random drift, divergent natural selection, and sexual selection are all processes that could lead to divergence among closely related species. The difficult task is to gauge the relative importance of these various processes in shaping diversity. In many empirical studies, evidence for divergent natural selection is weak or absent, the importance of resource competition remains unclear, ecological opportunity is not sufficiently quantified, and the presumed importance of key novelties is not rigorously tested in a comparative phylogenetic context.

The Ecology of Adaptive Radiation presents an impressively thorough evaluation of the empirical evidence that has accumulated since Simpson's synthesis for the relative importance of these four major factors. In particular, Schluter focuses on what he calls the ecological theory, which highlights the significant role of divergent natural selection that leads to differential use of resources and ultimately reproductive isolation. He evaluates the evidence

CREDITS: (TOP) GERALD CARR, BOTANY DEPARTMENT, UNIVERSITY OF HAWAII; (BOTTOM) ARTHUR C. MEDEIROS

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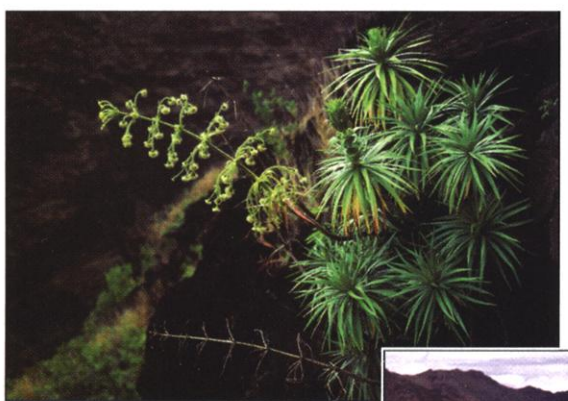
favoring the conclusions that natural selection really is divergent and that populations and species are sufficiently separated on a fitness landscape. In addition, he considers the empirical support for different types of ecological speciation.

Claims that sexually selected changes in mate recognition traits could be a major factor in speciation have recently received considerable attention (*2*, *3*). Schluter discusses the relevance of sexual selection during ecological speciation and phenotypic divergence. He also covers the continuing debates over whether adaptive radiation can occur when the diverging species are geographically separated and, the conflicting alternative, whether some sort of segregation (by range or habitat) is required if



CREDIT: GERALD CARR, BOTANY DEPARTMENT, UNIVERSITY OF HAWAII

the species are to diverge. So far, the most compelling evidence for sympatric speciation—which may still involve fine-scale spatial separation of the diverging populations—comes from recent studies on cichlid fish that inhabit lakes within volcanic craters in Cameroon (*4*) and Nicaragua (*5*). Schluter's own work on Canadian sticklebacks may also provide evidence for "parallel speciation" in sympatry, but debates continue over exactly which geographic scenario applies (*6*, *7*). Nonetheless, such parallel speciation, in which independent populations experience similar selection environments and separately evolve reproductive isolation, provides strong evidence for the implicated mechanisms of adaptive radiation.

Interestingly, these cases from Cameroon, Nicaragua, and Canada may each involve more than one mechanism of selection; sexual selection through assortative mating can be coupled with a trophic polymorphism or ecological processes such as differential use of resources. Schluter is no fan of these ideas involving sexual selection and sympatry. He firmly believes that ecological forces and divergent selection drive speciation, even in parallel settings. To support his position, he discusses some of the growing evidence for an ecological basis for postmating isolation (*3*). However, the genetic mechanisms involved are often unclear, hybridization between different morphological forms is frequently still possible, and selection against intermediate morphologies and hybrids is sometimes weak or undocumented (*2*, *3*).

Schluter gives little attention to the evolution of adaptive radiations of higher taxonomic groups or evolutionary radiations, as these species-rich lineages are also called. He is more interested in the microevolutionary processes. Thus, he devotes much of the book to a treatment of adaptive radiation at lower taxonomic levels, such as populations and, particularly, species (the fundamental unit of ecology, systematics, and conservation). His focus relies on the justifiable assumption that the empirical investigation of the mechanisms and ecological circumstances leading to phenotypic differentiation and speciation is best performed at these lower levels.

The comparative study of biological taxa has been greatly enhanced by new methods that offer researchers the opportunity to test precise hypotheses on the phylogenetic framework obtained from molecular data (*6*). Such data also help estimate the timing and sequence of speciation events, allowing further quantification and statistical testing of the patterns of adaptive radition. With continuing advances in genomics, researchers may soon be able to identify the genes and the molecular evolutionary processes that underlie key innovations, morphological variation within populations and between species, and reproductive isolation. Genomics, therefore, is one of the most tantalizing approaches for future research on the topics discussed in this book.

Schluter succinctly and clearly details the progress that has been made toward a theory of adaptive radiation during the last five decades. He also offers readers an abundant supply of fresh concepts and methods that will facilitate further progress. *The Ecology of Adaptive Radiation* is an absolute "must read" for all graduate students in the fields of ecology and evolution and for anyone interested in evolutionary diversity. It will become a classic.

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BROWSINGS

Frogs, Flies, and Dandelions. The Making of Species. *Menno Schilthuizen*. Oxford University Press, Oxford, 2001. 353 pp. $25, £17.95. ISBN 0-19-850393-8.

Anyone who wonders about the origin of species will enjoy and learn from Schilthuizen's detail-filled survey of efforts to answer this central question of evolutionary biology. The author discusses the nature of species; explores the roles of geographical isolation, genetic drift, and sexual selection in the creation of biodiversity; and shows how new species may appear gradually or instantaneously. He provides lucid verbal explanations of theoretical approaches and presents the fascinating details from numerous empirical studies. Although written for the nonspecialist, his comprehensive and up-to-date account also offers researchers working on speciation an idea of forthcoming developments in their field.

The Coldest March. Scott's Fatal Antarctic Expedition. *Susan Solomon*. Yale University Press, New York, 2001. 407 pp. $29.95, £19.95. ISBN 0-300-08967-8.

Seeking to rescue Scott from his critics, Solomon argues that he was an honest, talented leader who was doomed by very unusual circumstances rather than error. Her comprehensive case weaves together details drawn from historical diaries and letters with more recent meteorological data. During their return from the South Pole in March 1912, Scott and four companions encountered exceptionally harsh conditions that she believes they could not have predicted: temperatures near –40°C, more than 10°C below normal values for the time of year. Solomon also offers a new interpretation of the polar party's final days, 11 miles shy of a vital depot of food and fuel. She concludes they could not have been trapped by a 10-day blizzard and suggests that the deaths of Scott's last two companions may have been "a matter of choice rather than chance."