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stochastic, whereas development was orderly, decidedly nonrandom. Norton Zinder, a geneticist famous for his discovery of bacterial transduction, recalls, "She really didn't want to speak about transposition. She was talking about regulation and development. And that's what she was pissed off at [us about], and nobody would take that seriously. *Everybody* took seriously the transposition."

So, unlike Mendel, who was eventually recognized for his most important discoveries, McClintock was lauded only for her discovery of transposition, not for the contribution that she thought was really important. Although unhappy about this, McClintock exhibited a zest for living and for science till near the end of her days. Her life has served as a role model for women in science and as an example of the success that can come from unconventional thought and an independent approach. By stripping away the myth and revealing the very human scientist, Comfort has given us a more accessible role model as we begin to celebrate the centennial year of her birth.

BOOKS: MOLECULAR BIOLOGY

A Highly Personal Perspective

Mark Ptashne

Diagnosed with colon cancer in 1986, Harrison (Hatch) Echols, a molecular biologist at Berkeley, devoted parts of each of his last six years to writing a narrative history and textbook of his field. His unfinished project has now

been edited and completed by his wife, Carol Gross, also a professor at Berkeley. The result is an absorbing and lucid survey of molecular biology and how, in many cases, it got to where it now is.

Operators and Promoters has a subplot: it is also a kind of self-portrait of Hatch. The picture emerges in bits scattered throughout the text in the form of opinions about science, scientists, and the so-

ciology of science. He disapproves of the War on Cancer, declared some 30 years ago, saying it was "about as useful as declaring a 'War on Earthquakes.'" He resurrects his proposal, which was seriously debated at a 1970 Cold Spring Harbor meeting on phage lambda, that individuals eschew independent publication and instead gather by discipline once a year to decide what is worth telling the outside world. And so on. These and other thorny matters are not argued in detail; they tell us more about Hatch than about the issues.

Perhaps I can add to this portrait. Hatch presented himself as the archetypal Californian: tie-dyed shirt, hair in a ponytail, hesitant of speech—in short, way laidback. At a Gordon Conference, I fell for this ruse and found myself on a tennis court with him. Hatch's demeanor didn't

change much, but the balls came over the net with lethal speed and precision. It was something like being a civilian taking a stroll through Jurassic Park. I took up golf.

As with Hatch himself, there's more to *Operators and Promoters* than first meets the eye. Hatch has chosen to recount the development of molecular biology by emphasizing, to a surprising degree, who did what. This approach has

Operators

and Promoters

The Story of

Molecular Biology

and Its Creators

by Harrison Echols

Edited by Carol A. Gross

University of California

Press, Berkeley, 2001.

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0-520-21331-9.

its dangers, but in this case it is used to fine effect. Rather than reading that such and such was done, we read that so and so (often a graduate student or postdoctoral fellow) did such and such. The active voice helps make the text flow.

Hatch also enlivens his account by telling slightly offbeat stories. For example, in describing the development of the

Jacob-Monod view of the world, he describes how Mel Cohn and Annamari Torriani isolated a mutant bacterium that was unable to grow on lactose but perfectly inducible for β galactosidase when challenged with an inducer other than lactose. That led Cohn to postulate, correctly, the existence of a lactose permease (his strain being mutant in that permease). It seems a small point, but Monod's response is revealing: "If

we have to think about silly things like permeability, this field is hopeless—let's forget this mutant."

Hatch had interesting opinions about what is and is not important. My favorite is directed toward those—surely not you, gentle reader—who got a headache whenever someone started explaining the Holliday model for "the molecular basis of genetic recombination." We read an explanation of the model (accompanied, as are discussions throughout the book, by simple black-and-white drawings) and then the bracing words: "The Holliday model is one of the great ideas of modern biology."

Hatch draws attention to intellectual threads, and he searches for what made experiments possible, for what the critical insights were. Lest we forget, what Watson and Crick really learned from Pauling were the "Pauling Principles": figure out how the building blocks of the macromolecule can fit together, and the total structure may emerge. DNA replication seemed a complicated mess, too much so



Hatch Echols

to ever reproduce in a test tube, until Kornberg guessed that most of that complexity was required to synthesize the building blocks, the triphosphates. Use presynthesized triphosphates, he thought, and it's a different story. The development of recombinant DNA technology might have been stuck had it not been for Mandel's discovery that calcium treatment of bacteria allowed efficient uptake of DNA. And the

Brenner, Jacob, Meselson experiment that demonstrated the existence of mRNA failed until, at the last minute, Brenner surmised that they had to raise the magnesium concentration to protect the ribosomes floating in high-density cesium chloride.

There is a special emphasis on the pervasive influence of the study of phage lambda, to which Hatch made important contributions. How genes are regulated; how DNA molecules recombine at specific, widely separated sites, as during excision of the phage chromosome from the host chromososome upon induction; how that excision can produce a phage carrying a host gene, explained by the celebrated insight (nicely described here) of Allan Campbell; how certain enzymes direct socalled general recombination and others the process of repair of DNA damage; how the phenomenon of host restriction, which led to the discovery of host-restriction endonucleases, works; and how the initiation of DNA replication is controlled. All these and more, as studied with lambda, had an enormous impact on the subsequent developments, according to Hatch. And who would argue with that proposition? He illustrates the point, after expressing his enthusiasm for the development of recombinant DNA technology and its commercialization, with this paean to the virtues of basic science:

IV debated at a 1970 Cold Spring Harbor The author is at the Memorial Sloan Kettering Cancer Center, 1275 York Avenue, Box 595, New York, NY 10021, USA. E-mail: M-Ptashne@mskmail.mskcc.org

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 everyouthful 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

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. 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.

Dolph Schluter, a professor at the University of British Columbia, has made some of the most important contributions to our understanding of evolutionary radi-

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ations. 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 ecologi-

cal 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.

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.



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 quanti-



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.)

fied, 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

Some of these circumstances are rather

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