Book Reviews

Grand Syntheses in the Making

The Evolution of Life Histories. STEPHEN C. STEARNS. Oxford University Press, New York, 1992. xii, 249 pp., illus. Paper, $29.95.

Beginning in the mid-1920s the fields of genetics, systematics, anatomy, paleontology, ethology, and ecology coalesced around a paradigm of evolution driven primarily by the process of natural selection as originally proposed by Darwin. That unification was mostly completed by the mid-1950s and is now known as the Modern Synthesis. Not all were happy with the results of that synthesis, however. The opposition, which began to swell about 1970, complained about a rigidity in evolutionary theories that saw the natural world as well adapted. The claim was made that the constraints and accidents of history (phylogeny) were being ignored. Although these criticisms had merit, it is fair to say that at the time of the Modern Synthesis the body of evidence demonstrated the centrality of natural selection in shaping evolution. Most of the extreme claims about adaptiveness were due to a misunderstanding of evolutionary theory, often by ecologists; the principal architects of the synthesis always recognized the potential importance of other processes in evolution.

The rising opposition to the synthesis led to a protracted, and sometimes vociferous, debate over the importance of phylogeny. That debate has now mostly ended with the recognition of a need to incorporate developmental processes into evolutionary models. The incorporation is now beginning, and *The Evolution of Life Histories* by Stephen C. Stearns stands as a signpost to the resolution of the debate.

Just when the Modern Synthesis was coming to fruition, another event occurred that is having a profound effect on our understanding of evolution, the publication of the Watson-Crick model of DNA. The advances of the subsequent two decades have fueled an explosion in technology that has brought DNA sequencing and other molecular techniques to the humblest of labs. The result is that, beginning in the mid-1970s, a second major synthesis started within biology, organizing the fields of biochemistry, genetics, molecular biology, cell biology, and developmental biology around a central paradigm of gene expression (what has sometimes been termed the central dogma of molecular biology). We are now in the midst of this Molecular Synthesis, and I feel safe in predicting that its broad outlines will be in place within the next 15 years.

We are moreover on the threshold of the Final Synthesis in biology that will unite the paradigms of evolution (information transmittal) and gene expression (information utilization). I predict that this synthesis will begin some time within the next decade, with development seen as the linking process. The impetus for this synthesis will come from evolutionary biology in an attempt to bring more realism into evolutionary models. This book points toward that synthesis.

The book justifiably focuses on the evolution of life-history traits. Such traits include the number and size of offspring, the timing of maturity, the timing of reproductive episodes, and the processes of aging and death. These traits are often referred to as fitness components because they determine the overall fitness of an individual. Stearns discusses several commonly used definitions of fitness, including the total number of offspring produced in one's lifetime (R_0), the rate of population growth (r), and the time to population extinction. Life-history traits are components of all of them. Because these traits are the most direct determinants of fitness, natural selection on all other traits must funnel through them. Evolution of morphology, physiology, and behavior will occur to the extent that they affect life histories. Thus our understanding of the evolution of life histories is pivotal to our understanding of the process of natural selection.

In *The Evolution of Life Histories* Stearns assembles a view of evolution that includes traditional components of quantitative genetics and demographics and newer concerns over the effects of phylogeny and historical constraint. Each of these issues is reviewed in the first half of the book. One of the strengths of the book is Stearns's non-dogmatic approach to them. Where more than one view of an issue is current, as with the definition of fitness or constraint, all sides are presented. Often Stearns concludes, and I heartily agree, that all viewpoints have merit, their appropriateness depending on the question being posed or the approach being taken. These alternative approaches are all given due consideration. In the second half of the book, Stearns takes the framework that he has erected in the first half and applies it to three central issues of life history—tradeoffs between age and size at maturity, between number and size of offspring, and between longevity and fecundity.

Although this book extends its approach to evolutionary problems by including nonadaptive effects, it still lies clearly within the adaptationist framework. As envisaged by Stearns, current phylogenetic constraints are the result of past adaptations that have become progressively irreversible as they are more deeply embedded within a developmental pathway. Though these ideas are not new, they are clearly laid out here within a structure of analysis that allows for the identification of such constraints.

Stearns focuses almost exclusively on optimality models of life-history evolution, the type he has been instrumental in developing over the past decade. Such models predict the evolutionary equilibrium state while usually ignoring dynamic processes. Even within this framework complications such as frequency-dependence and density-dependence are mostly ignored, although Stearns points out that the latter lack is due to an absence of model development. Not considered are other important classes of models including ESS (evolutionary stable strategy) models, metapopulation models (those that account for spatial structure and migration), and genetic models. The lack of spatially structured genetic models is particularly noteworthy because they are important for our understanding of the evolution of phenotypic plasticity, a topic central to many of Stearns's arguments. I recognize that the concentration on optimality models is due to the need to limit the scope of the book and to these models' being particularly well developed. The successful predictions of optimality models that are amply demonstrated in the book indicate the fruitfulness of this approach. However, uninformed readers may not catch the message that different types of models may make very different predictions. When predictions of a model are not met, an alternative to tinkering with the model and refining the predictions is to abandon the model altogether and examine the problem from a different perspective. Stearns's strong advocacy of an optimality framework may discourage readers from examining other types of models.

Most examples in this book come from the kingdom Animalia, especially vertebrates and arthropods, although examples from other types of organisms are distributed throughout the text. This inclination reflects partly a bias in available data and partly Stearns's own areas of expertise. Stearns expresses regret at not dealing with modular organisms, those such as grasses or corals, which grow by producing new units that are potentially autonomous. The evolution of life-history traits such as aging and trade-offs between growth and fecundity are very different for a possibly immortal organism. For example, models of age vs. size at maturity all assume that the rate of growth decreases with age, whereas a modular organism is likely to have a constant growth rate or even one that increases with age. It is unclear how such a growth pattern would affect, say, age at maturity. Clearly, much needs to be done to extend our understanding of life-history evolution to other types of body plans.

This book is designed to be used as a textbook in an upper-level undergraduate or graduate class. In keeping with this intent, each chapter begins with an overview and ends with a summary and series of questions and projects designed to stimulate discussion. The potential audience for the book is wider, however. It could be profitably read by anyone working on evolutionary questions. For someone wishing to gain insight into some of the central questions facing evolutionary biologists today, the book provides a useful starting point. In that regard, the writing is a curious mix of a very simple (almost simplistic) overview and detailed analysis. The first half skims very quickly over vast areas of biology. Anyone familiar with a particular topic will find that the treatment does not truly do it justice, and those unfamiliar with a topic might have to struggle to follow the nuances of the arguments. Obviously Stearns was faced with the constraint of having to provide sufficient breadth of coverage without having the book balloon out of control. To compensate for the lack of depth he provides an extensive and current list of the literature, both references cited and recommended readings, at the end of each chapter. Thus this book can provide a gateway and a guide to these issues even if it is not sufficient unto itself. Stearns clearly states in the preface that the book was written assuming a background in "calculus, statistics, computer programming, ecology, evolution, and genetics." As a textbook it might be supplemented with additional material on those topics.

This book will undoubtably stimulate many research programs in coming years, some of which will become important components of the Final Synthesis of biology. It lays out major questions facing evolutionary biology today and indicates the types of information needed to address them. One of the most beneficial actions an adviser

Vignettes: Eugene Wigner

Depreciating fame but finding the outlines of lives in such works as *American Men and Women of Science* "too narrowly objective," Eugene Wigner, born in Hungary in 1902 and recipient of the 1963 Nobel prize in physics, has produced a volume of *Recollections* (as told to Andrew Szanton; Plenum Press). Below are some excerpts from that work.

Before I attended the colloquia of the German Physical Society [in 1921], I had thought that the greatest physics was mainly experimental. . . But I noticed that the great physicists at the Thursday colloquia were mostly theoretical. They spoke of quantum theory often and with great respect. . . .Their attitude opened my eyes. Already I knew that I lacked the patience to ever be a great experimentalist. . . . To a young man of my temperament theoretical work was far more promising.

The first year that I truly contributed to physics was 1929. Quantum mechanics had been evolving quite well without my help. So I wondered: what could I do? . . . I realized how much I loved group theory. . . .Group theory had been used by physicists years before I came along. But something kept occurring to me: that group theory had rarely been rigorously applied to quantum mechanics. . . . I began working more seriously now, with the earnest willpower of an untested young man. Properly engaged in something potentially important, I found myself more patient than I would have thought.

One morning in . . . 1930, I received a startling cable from the United States: "Princeton University offers you a one-term lectureship." . . . I learned that Jancsi von Neumann had received a similar cable. . . . It was clearly Jancsi that Princeton really wanted. They had offered him about 1000 dollars a year more than me. . . To be a stranger in a foreign country is a trying experience. . . . Perhaps Jancsi would not have accepted a lone offer. So Princeton also invited Eugene Wigner.

The Hungarian scientists working on the Manhattan Project—principally Szilard, Teller, von Neumann, and Wigner—were thought to be queer by the Americans. They often called us the "Martians." The label was unreasonable. We Hungarians had no more contact with Mars than they did.

Szilard had an excessive regard for his own talents. . . . And yet. . . Szilard was incapable of complacency. He did not always see his own deficiencies, but he saw brilliantly many of the deficiencies of the world. And he worked very hard to correct them, often at some sacrifice to himself. . . . I have been thinking about Szilard since 1925, and I am afraid that I still do not fully understand him. But I think Szilard was leftist for at least two distinct reasons: First, he truly felt that communisim or some similar political system would bring mankind happiness. Second, he felt that the leftist postion would triumph eventually and win him a high political post. . . . It was sometimes hard being Szilard's friend. But it was always deeply interesting.

Between 1920 and 1940, I had largely immersed myself in physics. Between 1940 and 1945, I had learned something about the technology and administration of modern warfare. Now, for the first time, I could study politics closely. I was dismayed. There seemed to be slogans and brutality on the Russian side; slogans and nonsense for the Americans. . . . I wanted the American people to think seriously about Soviet aggression in Europe and how best to stop it.

By 1968, civil defense was no longer a popular subject. I kept trying to arouse my colleagues . . . . But when I made my case, most of them said, "Oh, Eugene. Not again. . . ." My work for civil defense was not popular among the scientists I knew.

Old men have a weakness for generality and a desire to see structures whole. That is why old scientists so often become philosophers. I had seen it happen to Einstein and Polanyi. By 1973, Heisenberg was largely a philosopher, and I was becoming one too. . . . My chief interest in the last 20 years has been to somehow extend theoretical physics into the realm of consciousness.

could take for a new graduate student in evolutionary biology would be to put Stearns's book in her or his hands and say, "Read this."

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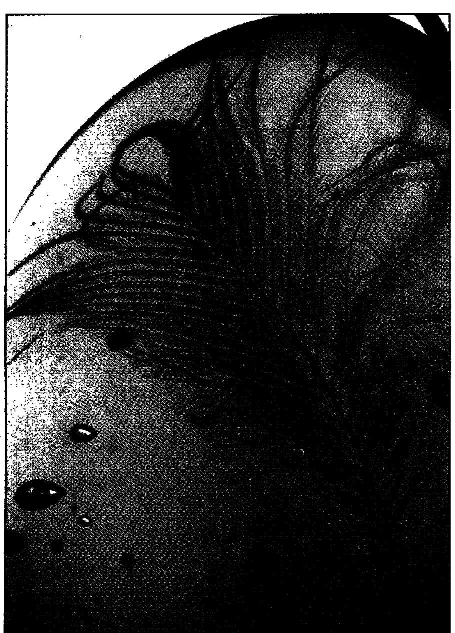
Windows in Time

Life in Amber. GEORGE O. POINAR, JR. Stanford University Press, Stanford, CA, 1992. xvi, 350 pp., illus., + plates. $55.

Dinosaurs capture the popular imagination, but the romance of amber is rapidly gaining ground. Amber is fossilized tree resin, hardened and rendered inert over millions of years of polymerization. Hundreds of deposits of various botanical origins occur around the world, varying in age from the Carboniferous to the Recent. Insects and other small organisms became mired in the sticky ancient resin before it hardened, as did some wafting plant debris. The result: fossils in exquisite three-dimensional detail, sometimes with ultrastructural cellular detail seen in living tissues. The recent publication of DNA sequences from two groups of insects in 25- to 30-million-year-old amber shows that it may provide the most consistent preservation of fossilized DNA. Organisms aren't the only "fossils" in amber: paleoclimatologists debate just how ancient the air in amber bubbles really is.



"A feather in Dominican amber." [From *Life in Amber*; Smithsonian Institution collection]

The paleobiology of such a unique kind of fossil is thus rich and diverse, and *Life in Amber* attempts a synthesis.

The bulk of the book is devoted to brief family-by-family treatments of fungal, plant, and animal inclusions, such as the myriad insects in the Tertiary ambers, particularly those from the Dominican Republic and Mexico. The whole book, in fact, is very similar in scope and format to Sven Larsson's 1978 book *Baltic Amber: A Palaeobiological Study* (Scandinavian Science Press, Klampenborg, Denmark). Larsson was able to draw upon a century of European research on Baltic amber; research on the New World ambers, by contrast, is in its adolescence. Production of a book like this owes a great deal to several individuals in particular. One is Jean Langenheim, whose classic 1969 *Science* article on the botanical origins (as determined with the aid of infrared spectroscopy), localities, and ages of the world amber deposits will always be an invaluable reference. The other is Dieter Schlee, curator of amber at the Staatliches Museum für Naturkunde in Stuttgart. Schlee has globe-trotted in pursuit of breathtaking specimens of fossiliferous and other ambers from around the world. It is a pity that no photographs of fossils from that wondrous collection or other major ones are used to grace the pages, which mostly show just specimens from Poinar's personal collection.

Another unique aspect of "amberization" is the examples of parasites and inquilines preserved with their hosts. A chapter is lavished upon this favorite subject of Poinar's, who is himself a parasitologist. Several specimens in various collections show my favorite such example: a phoretic pseudoscorpion with one claw latched onto the hind end of a wood-boring beetle, hitching a fateful ride.

Arthropods (by far the most numerous and diverse inclusions in ambers) are the first great radiation of terrestrial animals; they originated in the Devonian, and some modern orders appeared in the Permian. The faunas in Tertiary ambers are essentially modern in terms of genera and families, so they reveal little about higher relationships. Yet, evolutionarily, there are some surprises. Between 1940 and 1970 Kjell Ander and Willi Hennig (the renowned insect systematist) found that numerous insect fossils in Baltic amber have their closest living relatives at the southern end of the earth. Within the Dominican amber there are also some startling extinctions, many as yet unpublished. Little is said about this in the concluding section, where in fact Poinar goes awry on biogeography. He confuses the presence of a group in Dominican amber as evidence of Caribbean island vicariance. The age of such a fossil merely establishes a possibility that a certain tectonic scenario influenced modern distributions.

"A mushroom, *Coprinites dominicana* Poinar & Singer, in Dominican amber." [From *Life in Amber*; Poinar collection]

The book is more review than synthesis, and, errors of interpretation and omission aside, it will appeal to any paleontologist and insect biologist. It is to be hoped that it will inspire further American interest in amber paleobiology, which has traditionally been the provence of Europeans.

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Environmental Philosophies

Toward Unity Among Environmentalists. BRYAN G. NORTON. Oxford University Press, New York, 1991. xvi, 287 pp. $29.95.

After Earth Day. Continuing the Conservation Effort. MAX OELSCHLAGER, Ed. University of North Texas Press, Denton, 1992 (distributor, Texas A&M University Press, College Station). xxi, 241 pp. $24.50; paper, $15.95. Philosophy and Ecology.

The environmental movement, so some have observed, is a notably pragmatic affair. While those whose main task is one of dealing with ideas have often found environmental matters to be grist for their mill, they have remained apart from the main scene of action and often appear to be somewhat irrelevant to it. There are few journals of environmental theory, in sharp contrast, for example, to the many publications on economic theory that socialists were long known for. Instead, the environmentalist journals are journals of action, working out the details of concrete policies and exhorting their followers not so much to think rightly as to act rightly.

Amid this context, the main theory has