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ANNOUNCEMENTS

ON THE SCIENTIFIC LEGACY OF STEPHEN JAY GOULD

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The death of Stephen Jay Gould in May 2002 brought to a close a remarkable career that made him the most widely known evolutionary biologist of his age. While his fame rests largely on the foundation of his columns in *Natural History* magazine and his public appearances, he made substantial contributions to evolutionary biology. His outstanding intellectual contribution was the demonstration that more than natural selection and genetic drift within populations is required to explain evolution.

At the time of the centennial celebration of Darwin's most famous book (Darwin 1859), a time for serious self-congratulation, only one contributor raised major objections to the prevalent and celebrated evolutionary synthesis. E. C. Olson argued that the vaunted explanations were incomplete (Olson 1960). I much remember these days, for I was a graduate student eager to become an evolutionary biologist. When I read Ernst Mayr's book on animal species formation (Mayr 1963), I had a sinking feeling that everything had been done.

Gould also came to intellectual maturity in the 1960s, but as a paleontologist. Paleontologists had numerous examples of dissenters from orthodoxy in addition to Dr. Olson (e.g., O. H. Schindewolf). Steve worked on fossil and recent snails, which preserve their ontogeny in their shells, and so quite naturally became thoroughly immersed in questions of growth and form. The New Synthesis, as many have noted, largely ignored development, but many of us knew that it was key to our understanding of the evolution of morphologies. This became the focus of Steve's first great book, *Ontogeny and Phylogeny* (Gould 1977). This was not only a work of historiography, but also a successful attempt to demonstrate how ontogeny and phylogeny could be studied in a modern age. This book had a profound impact. I wrote a review for *Paleobiology* and distributed a draft to some colleagues and students who convinced me to organize a graduate seminar around the book. George Oster joined me and we attracted a talented group of students. Out of that seminar came a determination to formalize some of the concepts that Steve had presented, especially his ''clock-face model.'' When we asked Steve if he would like to join us in formalizing his model, he enthusiastically agreed, adding some important examples, and the publication of our paper (Alberch et al. 1979) spurred additional attention to the ontogeny/phylogeny issue. From this and related activity emerged a long series of workshops, discussions, and publications on development and evolution, a topic of intense current interest.

During the 1970s Steve worked steadily to develop what I consider to be his most important legacy—a hierarchical theory of evolution. Natural selection was an insufficient explanation for the rich panoply of life on earth and its incredible history. Steve saw evolution as taking place on different tiers, or levels of organization, requiring different kinds of explanations. Bolstering his argument was his work, often with talented collaborators, on topics now widely familiar to evolutionary biologists—punctuated equilibrium, spandrels, constraints on direction of evolution, contingency, selection at the level of species, the role of mass extinctions, and, of course, production of form. He was not working in a vacuum, and many deserve credit for these developments, but he was, I believe, the most articulate and compelling of all, and he reached the greatest audience. He wrote so much on so many topics that I doubt any biologist could have agreed with him on everything, and there are some who disagreed with most of his writings aimed at the professional audience. For example, although I liked much of what he did, I could never accept his view of species and of species selection. Steve rarely paid much attention to phylogenetics. If he had, I think he would have given more attention to lineages and the more general, and to me more acceptable, idea of clade selection. This is a kind of selection that can occur at many levels, including that of species, and I believe that his notion of emergent fitness applies better to clades than to species. But however we might disagree, I think we should all credit Steve with making it respectable to pursue evolutionary questions at many levels of organization and from many explanatory perspectives. He was proud of his paleontological focus and an ardent supporter of the discipline, which he did so much to enliven, but he was much more than a paleontologist.

My memory of Steve is indelibly tied to the celebration of diversity—diversity of approaches, of explanations, of organisms, and of people. He was a central figure in evolutionary biology for 30 years and made a permanent imprint on the field. Without doubt he inspired people in many walks of life to become interested in evolution, but his scientific legacy is far more profound—he changed the way many of us think about evolution and conduct our own research.

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