BOOK REVIEWS

Evolutionary Transitions

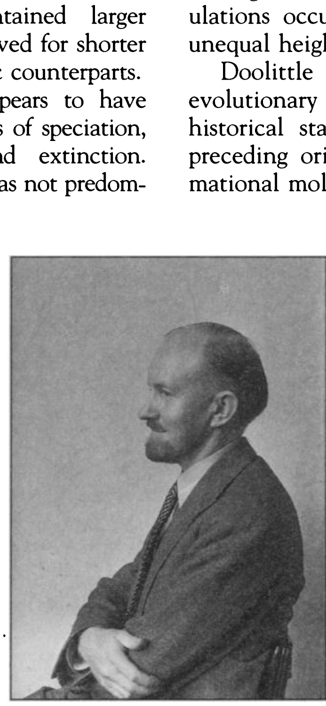
Tempo and Mode in Evolution. Genetics and Paleontology 50 Years after Simpson. WALTER M. FITCH and FRANCISCO J. AYALA, Eds. National Academy Press, Washington, DC, 1995. x, 325 pp., illus. $49.95. From a colloquium, Irvine, CA, Jan. 1994.

In 1944, George Gaylord Simpson anticipated that readers of his new book, *Tempo and Mode in Evolution*, would find its attempted synthesis of paleontology and genetics "particularly surprising and possibly hazardous." Simpson's words describe what his own reaction might be at seeing the progression of this synthesis 50 years later, the subject of this volume. The surprise would be phenomenal new discoveries in both paleontology and genetics. Paleontologists have extended the known fossil record well into the Precambrian (Proterozoic eon), revealing enormous contrasts between the dominant evolutionary tempos and modes of the Proterozoic and subsequent Phanerozoic eons, and have established a far more significant role than Simpson envisioned for extinction in Phanerozoic evolution. The emergence of molecular evidence bearing on evolution and the use of bacterial chemostats as experimental systems for studying evolutionary tempo and mode are equally unanticipated genetic developments. The hazard is a tendency of this synthesis to downgrade Simpson's own field of paleontology by giving primacy to genetics.

Simpson highlighted tempo and mode because these are topics through which paleontology makes a unique contribution to evolutionary theory. Tempo encompasses evolutionary rates measured on a geological time scale, and mode constitutes the genetical and morphological means by which evolving lineages differentiate. Simpson identified three fundamental modes: speciation, the splitting of a population into separately evolving lineages; phyletic evolution, directional change evolving within species; and quantum evolution, rapid shift of a population between distinct adaptive zones through an unstable inadaptive phase. Traditional Darwinism emphasizes gradual change achieved through the phyletic mode. Gould presents here a macroevolutionary reconstruction of Darwinism that gives Simpson's other modes and extinction increased significance, thereby restoring a central role for paleontology in evolutionary theory.

Recent paleontological studies document episodically increasing rates of speciation and extinction through time. Schopf describes Proterozoic life dominated by extremely slowly evolving prokaryotes, especially cyanobacteria. Established lineages exhibited large populations, ecological versatility, and long-term stasis. Extinction was rare, becoming a significant factor only late in the Precambrian, primarily among ecologically specialized eukaryotes. Likewise, Knoll's studies of single-celled eukaryotes show that Cambrian assemblages contained larger numbers of species that survived for shorter periods than their Proterozoic counterparts.

Phanerozoic evolution appears to have been dominated by high rates of speciation, ecological specialization, and extinction. Raup argues that extinction was not predominantly selective as Darwin envisioned it. Extinction of widespread species is rare except during episodes of mass extinction, when the killing event is beyond the experience of the species and outside the reach of natural selection. A series of mass extinctions produced major restructurings of the biosphere in which dominant groups were eliminated and formerly minor ones expanded and diversified.



George Gaylord Simpson, 1938. [Neg. no. 290411, photo by C. H. Coles; courtesy Department Library Services, American Museum of Natural History]

The fossil record of the Hominidae has improved more than 100-fold since 1944. McHenry interprets this record as supporting punctuated equilibrium; major evolutionary trends result not from gradual phyletic change but from changes concentrated in discrete events of speciation. Morphological evolution was mosaic, with many apparent trends representing accumulation of rapid shifts between successive species that overlapped in geological time.

Paleontologists increasingly invoke properties of genetic systems to explain discontinuous evolutionary patterns. Knoll attributes a late Precambrian acceleration of protistan evolution to genetic innovations including exon shuffling and sexual life cycles. Valentine attributes the explosive appearance of body plans in Cambrian bilaterians to regulatory genetic changes and associated developmental repatternings made possible by homeobox genes. The Cambrian explosion occurred largely or entirely within organisms having a single *Hox/HOM* cluster, but major increases in organismal complexity later in the Phanerozoic apparently involved duplications of this cluster.

Lenski and Travisano link genetic and paleontological phenomena using bacterial chemostats. Experimental lines demonstrate rapid change followed by stasis, replicating macroevolutionary dynamics. The crucial role of chance (historical accidents) in adaptive evolution is demonstrated by observing that replicate lines diversify in fitness even with controlled environments and very large populations. Sustained divergence among lines in mean fitness supports a Wrightian model in which replicate populations occupy different fitness peaks of unequal height in an adaptive landscape.

Doolittle and Brown divide molecular evolutionary tempo and mode into three historical stages: a pre-Darwinian period preceding origins of self-replicating informational molecules; a progressive Darwinian period between stage 1 and the first modern cells; and a postprogressive Darwinian period featuring evolutionary specialization but no general tendency for later forms to outperform earlier ones. Maizels and Weiner present a fascinating hypothesis for the second stage in which transfer RNAs evolved initially for replicational functions and later were co-opted for protein synthesis. Additional papers examine molecular evolution in the third phase, including studies of the molecular clock, properties of genetic systems, and molecular estimation of population genetic parameters.

This volume provides a dramatic illustration of how profoundly evolutionary practice and theory have advanced in the last 50 years, and of how important Simpson's themes of tempo and mode remain to the evolutionary synthesis of paleontology and genetics.

Allan Larson
Department of Biology,
Washington University,
St. Louis, MO 63130–4899, USA