Time Scale and Evolution

Causes of Evolution. A Paleontological Perspective. ROBERT M. ROSS and WARREN D. ALLMON, Eds. University of Chicago Press, Chicago, IL, 1991. xiv, 479 pp., illus. $65; paper, $24.95.

In 1985, Stephen Jay Gould presented an agenda for paleobiology based upon three discontinuous "tiers" of time at which distinct evolutionary processes operate. The first tier encompasses the ecological moment, the time scale of Darwinian natural selection. Gould designated as the "paradox of the first tier" our failure to find progress in life's history as expected from Darwin's theory. He postulated that this paradox would be resolved by studying processes acting in opposition to natural selection at two larger time scales: a second tier, encompassing species selection operative in "normal geological time" (trends during millions of years), and a third tier encompassing periodic mass extinctions. Whereas first-tier processes are accessible to study by both neontologists and paleontologists, second- and third-tier processes are almost exclusively the domain of paleontology. *Causes of Evolution* documents recent paleontological progress in resolving these interacting causal processes of evolution.

Fifteen contributions address the roles of abiotic versus biotic and internal versus external causes of macroevolutionary trends. Abiotic and biotic denote physical and biological conditions, respectively (Allmon and Ross, chapter 1). Intrinsic factors are qualities of individual organisms, populations, or species, whereas extrinsic factors originate outside the biological system. Gould (foreword) notes that extrinsic and biotic causes dominate traditional Darwinian explanations of evolution. Environmental selection generates evolutionary trends from randomly produced organismal variation, with biotic competition serving as the major selective factor underlying progressive evolution.

The macroevolutionary predictions of the first-tier process of Darwinian natural selection remain controversial. From this perspective, Geerat Vermeij has predicted that species will show progressive adaptive improvement through time in response to increased hazards of their biotic environments, a phenomenon that he calls "escalation." Coevolution between predators and their prey constitutes the model system for escalation. Marine bivalves, for example, are expected to demonstrate progressive strengthening of their shells as their gastropod predators evolve more effective ways to penetrate them. Kitchell in her contribution to this volume discredits the hypothesis of escalation and its prediction of progressive evolutionary trends, arguing that escalation fails adequately to incorporate the reciprocity of predator-prey interactions. The escalation model treats the predator as an extrinsic environmental factor that determines the selection acting on the prey species, and vice versa. Kitchell argues that because a prey species may utilize diverse strategies to respond to predation, the fitness values of its traits depend on the interaction of both intrinsic and extrinsic factors and are highly variable even when predation is constant. When she reevaluates the expected outcome of predator-prey coevolution mathematically by modeling the interactive intrinsic and extrinsic causal factors, she finds that stasis and the reversal of trends replace unidirectional escalation. She maintains that these predictions of the modeling effort are upheld by the fossil record.

Jackson and McKinney study escalation empirically using bryozoans, corals, and coralline algae observed throughout the Phanerozoic. Macroevolutionary trends are attributed to escalation in the defenses employed against routine biotic and abiotic hazards. The trends are evident, however, only at the interspecific level, and they cover time scales of 80 to 500 million years. The second-tier process of species selection is therefore invoked to explain them. It is unclear whether Jackson and McKinney invoke species selection in the strict sense, requiring that species-level emergent properties underlie differential speciation and extinction rates among lineages, or whether the observed trends result from effect sorting, in which organismal-level properties mediate differential speciation and extinction rates. Nonetheless, their conclusion, coupled with Kitchell's results, inverts Gould's paradox of the first tier; progressive adaptation may be caused by second-tier rather than first-tier processes.

Stanley investigates second-tier processes further by documenting a positive correlation between rates of speciation and rates of extinction in the animal world. Species selection is expected to favor the alternative combination of high speciation rates with low extinction rates. Speciation and extinction are simultaneously promoted, however, by increased behavioral complexity and habitat fragmentation, and inhibited by increases in ecological breadth, size, and stability of populations. Cronin and Ikeya distinguish the biotic and abiotic factors influencing speciation rates by comparing the speciation rates of different cenozoic ostracode crustaceans with the opportunities for speciation provided by climatic and tectonic events. Biotic traits affecting the geography, temperature tolerance, and population structure of species are found to be particularly important for mediating the influence of abiotic factors on speciation.

Stanley uses the term "catastrophic species selection" to denote third-tier processes of mass extinction that select for certain biological traits. Several marine taxa that normally experience relatively low rates of extinction are seen to be victimized preferentially by mass-extinction events. Valentine notes that such events may disrupt the tendency for clades that have low background extinction rates to become domi-

	EXTRINSIC FACTORS	INTRINSIC FACTORS	TOTAL
BIOTIC FACTORS	80 (38%)	37 (18%)	117 (55%)
ABIOTIC FACTORS	80 (38%)	14 (7%)	104 (45%)
TOTAL	160 (76%)	50 (24%)	211

"Frequency of sorts of evolutionary factors considered in the journal *Paleobiology* in the years 1975–87. In each cell, the top number is the frequency out of 146 papers classified, the bottom number the percentage of the total number of factors considered (211). (Some papers considered more than one factor.) Papers that did not extensively discuss forces influencing evolutionary patterns were not classified." [From the opening chapter of *Causes of Evolution*]

nant in the fossil record. Other trends established over shorter time scales appear not to be reversed by periodic mass extinction. Jablonski and Bottjer find that catastrophic perturbations appear not to influence environmental patterns in the origination of morphological novelties and corresponding taxa of marine invertebrates. Orders originate preferentially in shallow, onshore environments, whereas no such bias is observed for the origins of lower taxonomic units. The trends studied by Jackson and McKinney likewise transcend mass extinction events.

This book should serve as a model and stimulus for further studies of the interacting evolutionary processes that emerge at the different tiers of evolutionary time. It guides us to look for syntheses of abiotic, biotic, internal, and external causes acting at multiple hierarchical levels of biological complexity. Gould's three tiers alone may not be adequate, however, to identify all causal discontinuities in evolutionary time. Milankovitch climatic cycles have been identified elsewhere (by K. D. Bennett) as a separate tier of evolutionary time (a periodicity of approximately 20,000 to 100,000 years) falling between Gould's first and second tiers. Studies of marine invertebrates (Cronin and Ikeya) and terrestrial mammals (Heaton) of the Quaternary provide evidence for causal processes originating at this level. On a more microevolutionary scale, discrimination of the opposing causal processes of organismal versus interdemic selection would require further subdivision of Gould's first tier.

These papers demonstrate the exciting and unique role of paleontology in identifying the causal processes of evolution. All neontologists who have ignored recent developments in paleobiology should read this book to see what they have been missing. Even this explicitly paleontological account includes some important neontological contributions, emphasizing the complementarity of these perspectives. Dorit shows how the combination of comparative morphological and molecular phylogenetic data can be used to test hypotheses of intrinsic and extrinsic causes of evolution on a fine evolutionary time scale. Bleiweiss shows the importance of ecological studies for avoiding bias in the interpretation of fossil diversity. I hope that the major impact of this book will be to forge a synthesis of paleontological and neontological approaches which together will illuminate the dynamic causes of macroevolution.

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A Sociopolitical Shift

The Mississippian Emergence. BRUCE D. SMITH, Ed. Smithsonian Institution Press, Washington, DC, 1990. xviii, 280 pp., illus. $39.95.

Hierarchically organized Native American societies called Mississippian chiefdoms developed about a millennium ago in the eastern part of what is now the United States. Until recently, the immediate cultural antecedents of these ranked social systems were shrouded in mystery. Archeological work in several regions has at last begun to bridge the seemingly great chasm once thought to separate the acephalous tribes of the Late Woodland period from Mississippian period chiefdoms. *The Mississippian Emergence* is an ambitious synthesis of archeological information on this profound cultural transition.

The volume includes—ranked here in order of emphasis—compendia of basic observations on archeological remains, descriptions of the principal transformations in cultural systems, and models identifying the most fundamental determinants of cultural change. The studies focus on, but are not restricted to, the period A.D. 750 to 1150.

Single sites are the subject of four chapters. Two of these describe Mississippi River valley sites in Arkansas, Powell Canal (John House) and Zebree (Phyllis Morse and Dan F. Morse), and one covers the Range site in Illinois (John E. Kelly). Martha A. Rolingson describes a long-term research project at the Toltec mound center in central Arkansas. She also provides a valuable overview of previous excavations in the structurally complex mounds of major Mississippi River valley sites.

Two regional summaries focus on segments of the Mississippi River valley: the American Bottom in Illinois (Kelly) and the area between the Ohio and Arkansas rivers (Morse and Morse). Similar reviews cover eastern Tennessee (Gerald F. Schroedl, C. Clifford Boyd, and R. P. Stephen Davis), west-central Alabama (Paul D. Welch), and the Fort Walton area in the adjoining parts of Florida, Alabama, and Georgia (John F. Scarry). Presumed cultural boundaries within these regions are defined on the basis of site distributions and ceramic styles.

In the final chapter James A. Brown, Richard A. Kerber, and Howard D. Winters consider the role of trade in the late prehistoric Midwest and Southeast, particularly the use of prestige goods by elite groups to buttress superordinate social positions and to further their political objectives. An examination of utilitarian Mill Creek chert hoes, building on Winters's earlier work, shows how studies of artifact distribution can contribute to the identification of prehistoric exchange networks.

This volume is particularly valuable as a guide through the morass of culture-specific detail, new and old cultural classification schemes, and debates over dating that dominate the archeological literature. New data from recent excavations are combined with already published information, much of it available only in technical reports with limited distribution. Emphasis is placed on defining regional cultural trajectories and the nature of accommodations to local biotic and social landscapes. The wide distribution of small quantities of nonlocal objects and evidence for warfare underscore the need for a closer examination of intergroup cooperation and antagonism.

As regional chronologies are becoming increasingly fine-grained, the timing of some critical transformations in evolving sociopolitical systems can be identified with assurance, whereas others remain as obscure as ever. It is apparent, however, that many significant cultural changes occurred rapidly—over periods spanning generations, not centuries. Taken together, these studies again show that there is no support for the often cited, but long outdated, idea that peripatetic people carrying a distinctive cultural baggage spread the Mississippian way of life. More limited population movement, however, took place in response to challenges posed by varied ecological and social settings.

Readers will not find lengthy discussions of current debates about cultural evolution here. When discussing particular regional trajectories, the authors repeatedly stress relationships among new subsistence strategies, especially a reliance on maize; population growth; and more complex forms of social organization. Other factors receive less attention, although Kelly discusses technological innovations in pottery and Brown *et al.* argue for the pivotal role of exchange in the origin of chiefdoms.

Suggestions regarding causal relationships, when made, are tailored to individual cultural sequences, although population growth and pressure are common themes. To simplify greatly, new subsistence and food-processing strategies fostered population increase (Kelly and Schroedl *et al.*) or resource acquisition practices were modified to feed more people (Welch and Scarry). In both scenarios, larger populations required more elaborated forms of sociopolitical organization. Members of the superordinate social stratum exercised some variable mix of political authority and managerial control over economic activities, and their exalted positions were legitimized in part by religious beliefs. Other chiefdoms subsequently