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THE TRANSFORMATION OF PALEONTOLOGY AND ITS IMPORTANCE FOR EVOLUTIONARY BIOLOGY

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In 1984 English geneticist John Maynard Smith summarized the state of affairs of paleontology and whether it had achieved sufficient epistemological status that it could be seated at the proverbial "high table" of evolutionary biology. The stimulus for this assessment was a series of Tanner lectures provided by Stephen J. Gould at Cambridge University that extended into current evolutionary theory the relevance of punctuated equilibrium and a hierarchical context for evolutionary levels of selection. Maynard Smith's initial worry was, beginning with George G. Simpson's contribution to the modern synthesis in 1944, that the paleontologist did not "... propose novel mechanisms of his own." From Maynard Smith's account of the lectures and ensuing panel discussion, it is clear that considerable ferment was afoot. At the end, Maynard Smith pronounced the lectures "entertaining and stimulating" and welcomed long-missing paleontologists to the "high table" of evolutionary biology.

Twenty-five years later, David Sepkoski and Michael Ruse have edited a stimulating and eminently readable, historical account of the revolution in paleontology and the emergence of the field that became known as paleobiology. From 1970 to 1985, a major conceptual transition began in paleontology that has diversified into almost every subfield of evolutionary and ecological and biology that can be informed by the fossil record. This transformation is discussed from various vantage points by the scientists that participated in the transformation as well as historians and philosophers of science who have delved into this most intriguing and consequential period of paleontology. As Sepkoski puts it in the introductory chapter to the volume, "... it is widely acknowledged that something important happened to paleontology in the last few decades, and the chapters that make up this volume will tell versions of that story from a variety of perspectives."

The following 26 chapters are organized into three principal themes. Part 1, "Major Innovations in Paleontology," presents nine accounts from various perspectives of the debates in paleontology at the beginning of the transformation, beginning with Sepkoski's chapter that is a historical introduction to what follows. Sepkoski documents the early twentieth-century subordination of paleobiology to geology and its widespread perception as a utilitarian discipline whose singular purpose was to provide time and environmental context to economic stratigraphy, certainly in North America. In Europe, with the work of Austrian Othenio Abel (1912), the case was made for the incorporation of biology into paleontology, ostensibly to test Darwin's ideas in the *Origin*, but also to suggest that the independent phenomenology of the fossil record may provide new theoretical insights into evolutionary patterns not available to biology. This torch was acquired by Simpson, who was influenced by Abel's ideas, untranslated into English, and incorporated them into the Modern Synthesis, with colleagues such as Ernst Mayr and Theodosius Dobzhansky principally during the 1940's (Simpson 1944). Simpson and psychologist Anne Roe also pioneered new approaches with publication of *Quantitative Zoology* in 1939 that included techniques from standard statistical demography and population genetics to understand diversity patterns in the fossil record, important during the revitalization of the 1970s and 1980s. However, the "biologicization" of paleontology sparked a backlash, in which the well-noted J. Marvin Weller urged paleontologists to follow their "geological roots" and used the emerging term, paleobiologist, as a derisive epithet. This response was countered by Norman Newell during the 1950s and 1960s, an intellectual successor to Simpson, who asked the kinds of questions that a biologist would ask of the fossil record, and addressed these issues by promoting quantitative analyses of invertebrate data. Given this historical backdrop, it is no surprise that the formative period from 1970 to 1985 was both primed and ripe for a major revamping of the field. The journal, *Paleobiology*, founded in 1975, provided a forum for exploring new quantitative and theoretical ways of assessing the history of life. Notable contributions were the hypothesis of punctuated equilibrium, a hierarchical view of units of selection, the role of extinction in the history of life, and other macroevolutionary issues addressed at greater length in this section.

The next six chapters of Part I present assessments of the development of research programs in paleobiology, and evaluations of whether they made it to the "high table." Michael Benton examines the completeness of the fossil record and controversies that contrast the fossil record with molecular data for establishing the dates of clade origins. Benton notes that the fossil record documents two facts: the abundance of the rock record (and its inverse, missing time), and the literal rendering of life's history. He concludes that a combination of exceptional fossil deposits that preserve soft-bodied organisms and molecular trees suggests that understanding of the major features of the history of life is quite good. Richard Fortey profiles the role that Paleozoic continental distributions and their latitudinal positions had in understanding Paleozoic marine diversity. Episodes of continental dispersion versus amalgamation and their paleolatitudinal positions had major effects on Paleozoic marine diversity. Aldridge and Briggs present the twists and turns of identifying the enigmatic "conodont animal," which eluded decipherment for over a century, although their apparatuses of tooth-like structures were locally abundant as fossils. A serendipitous discovery in a museum, acquisition of a search image for detecting certain soft-bodied fossils in Paleozoic deposits, and knowledge of vertebrate tooth histology, now provides a more resolved sense of early chordate relationships and their ecologic context. J. William Schopf, fleshes out a historical account of the search for the most ancient records of life, delving into the personalities of several highly influential researchers that investigated the environments, ecology, biochemical evolution, and phyletic relationships of Precambrian microorganismic lineages and microbiotas. Beginning during the 1960s, several key developments, including correct assessment of the biological nature of ancient microfossils and use of minerals to predict the presence of life, presented an intriguing portrait of very ancient life under nonactualistic conditions. John Horner examines the history of understanding dinosaur biology, providing an eclectic mix of particulars: physiology, feeding biomechanics, nesting and migration behavior, phylogeny, and recent research elucidating the structure of dinosaur tissues. Horner entered the "conversion period" in which dinosaurs were viewed with new methodologies, quantitative analytical techniques, and conceptual modes. Tim White analyzes issues that have caused angst among anthropologists. Early controversy centered on relative timing of the African ape and human split, based on molecular versus fossil data, which initially gave irreconcilable timings and punchy commentary. This was followed years later by debates of the impact of cladistic methods on hominid phylogeny, and then the role that punctuated equilibrium had on understanding the mode and pace of species origins and durations. White adjudges that this stürm und drang has been destructive for anthropology; he sees integration of paleoanthropology into paleobiology and evolutionary biology as an optimistic development that will revive the field.

The last two chapters discuss two live issues that have confronted paleobiology. Patricia Princehouse analyzes the reception among evolutionary biologists of punctuated equilibrium and the particular mechanism responsible for speciation in the fossil record. Punctuated equilibrium was demonstrated in many instances, but speciation mechanisms in the fossil record—such as species sorting, species selection or other processes—were most contentious. Princehouse ends her chapter by saying that a scientific field such as paleobiology is "a system of objective relations involving a competitive struggle between positions already won" (Sapp 1983), the most relevant quote of the book. She ends optimistically that paleobiology "had the nomothetic goods to compete at and even remap the top levels of the biological sciences." A different take on whether paleobiology had the nomothetic goods is discussed by Francisco Ayala, who reviews issues pertaining to molecular evolution and paleobiology, expressed in the broader debate of molecules versus fossils. Ayala discusses the effect of time inhomogeneity in the molecular clock by evaluating wildly disparate divergence times that have appeared lately, including times of origin of *Drosophila* species groups, mammalian orders, major fungal lineages, and metazoan phyla. Ayala concludes that the molecular clock is robust if rate variability can be established and tailored to relevant questions. A distinct expectation is closer convergence of molecular and fossil dates for times of clade origin.

In Part II, "The Historical and Conceptual Significance of Recent Paleontology," Derek Turner begins by asking the question of whether paleobiology's research program encompasses experimental manipulation. Refreshingly, Turner describes that the experimental approach in paleobiology is philosophically and methodologically no different than that of biology. In other words, the subjects of interest need not be alive—which is often the case in biology anyway, the difference being whether the recent dead or the long-departed dead are studied. Two techniques are cited as constituting the experimental approach in paleobiology: compilations of large datasets, and manipulating computer models that delve into a past process or pattern. (Question: why are these two aspects of paleobiology the ones criticized most by many biologists?) Todd Grantham presents a history and state of the art of taxic paleobiology, presenting a timely summary of the arguments between biologists and paleobiologists regarding use of taxic data retrieved from the fossil record. Exploration of patterns and inferred processes from taxic data has been an effective method in understanding the fossil record, evidenced by perusal of *Paleobiology*, and has been essential to seeing how life responded to processes such as sudden extinction and prolonged global change, or why certain taxa survive and others do not during crisis intervals. Grantham concludes, even though there has been minimal collaboration with biologists, taxic paleobiologists have demonstrated the robustness of their approach, protestations of orthodox cladists notwithstanding, and have fruitful relationships with macroevolutionists and conservation biologists. David Fastovsky presents a fascinating review of the relationship between dinosaurs and the scholarly and public communities, focusing on the ambient social and political milieu of understanding the iconic *Tyrannosaurus rex*. He indicates that study of dinosaurs cannot be divorced from our collective cultural inheritance, and fortunately, the basic biology and ecological context of dinosaurs now are now positioned as testable hypotheses. Susan Turner and David Oldroyd provide a narrative describing the travails of Reginald Sprigg in Australia and the delay in accepting the true evolutionary significance of Ediacaran fossils. This unorthodox assemblage of early, multicellular marine organisms, unlike any biota that exists today, eventually became recognized for their crucial evolutionary importance, resulting in eventual establishment of the global stratotype for this interval of time in the Flinders Range. A contribution from Manfred Laubichler and Karl Niklas provides brief biographical sketches of three researchers, Otto Jaekel, Walter Zimmermann, and Otto Schindewolf, and place their work and influence in the German morphological tradition of paleontology. Laubichler and Niklas attribute much of the current thought in evo–devo, phylogeny and macroevolution to the earlier academic tradition of classical German morphology.

Next, Sepkoski adds to what previously has been said about punctuated equilibrium, and provides insight into the differing philosophical preconceptions between Tom Schopf and Steve Gould in the reception of the hypothesis. Schopf believed that evolution proceeded as a continuous and dynamic steady-state whereas Gould viewed the process as interrupted by occasional bouts of "radical" species-level change. In Huss' contribution, importance is attached to the role of models in establishing a nomothetically based paleobiology, namely the MBL computer model developed in a 1972 in a meeting at the Marine Biological Laboratory at Woods Hole, Massachusetts, organized by Schopf with four of the other early pioneers of quantitative paleobiology—Gould, Dave Raup, Dan Simberloff, and Jack Sepkoski. The MBL group sought to understand the literal shape of evolution if selection was taken out of the process, by allowing hypothetical modeled clades to undergo a probabilistic process of branching, persistence, and termination. Their results, expressed as spindle diagrams, visually mimicked shapes of real clades from the fossil record, the dynamics of which were explored in subsequent papers. Huss concludes that models such as simulation added a new tool to paleobiology, presenting null hypotheses to test empirical data from a fossil record that may be fraught with errors in data collection, analyses, or interpretation. In a very different bent, Cain assesses the "ritual patricide" of Simpson by Gould's perceived concern that the "old guard" was threatening to derail new developments, particularly punctuated equilibrium. Lastly, Arnold Miller develops the intellectual background to the seminal consensus paper (Sepkoski et al. 1981), which provided support for establishment of a distinctive diversity pattern in the Phanerozoic fossil record based on five independent evolutionary and ecological measures. Publication spurred considerable discussion, including whether the conclusions could be correct given the influence of rock-record on organismic diversity. Miller concludes that this article was a major lynchpin for the macroevolutionary agenda of the past 25 years.

By now, I think you get the flavor of this volume. Part III, "Reflections on Recent Paleobiology," deals with expansions and elaborations on disparate topics broached in Parts I and II. I would not belabor in detail these chapters, other than mention how the transformation was implemented at personal, broader sociological and subdisciplinary levels. Jim Valentine reflects on examples of how paleobiology necessarily is more integrative than biological research. Richard Bambach employs ecological studies of fossil communities as a way of establishing the independent ontology of paleobiological evidence. Based on her experiences as a student, Rebecca German contrasts leadership and educational styles of three "schools" and personalities involved in the palebiologic renaissance—The University of Chicago (Tom Schopf), University of Rochester (Dave Raup), and Harvard University (Steve Gould). Tony Hallam recounts that punctuated equilibrium was sometimes received unfavorably and lineage patterns in the fossil record were interpreted more parsimoniously as shifts in developmental timing. This contrarian perspective is reechoed by Arthur Boucot, who provides a view of community evolution in which species evolve as a consequence of their associational links. An interview by David Sepkoski with David Raup recounts the important role of his career in the development of quantitative paleobiology.

It is the penultimate chapter, by David Jablonski, where paleobiology's major ongoing and future contributions, previewed in the earlier chapters, is presented to the evolutionary biological community. They are:

(1) Providing more highly resolved spatiotemporal data that approach biological scales of study.
(2) Using the richness of fossil morphological data for understanding the evolution of specific developmental novelties, critical evolutionary transitions, and infilling or evacuation of morphospace.
(3) Establishing the role that the physical environment and intrinsic biological processes have in triggering and driving evolutionary processes.
(4) Exploring in greater detail evolutionary processes occurring at the infraspecies, species, and superspecies levels, such as allocating traits to particular parts of the hierarchy.
(5) Understanding the specific role of selectivity, intensity and feedback on processes such as extinction, diversification, and novel ecological associations.
(6) Decomposing global temporal patterns of the fossil record into subpatterns occurring at local and regional scales, particularly for clades and habitats.

It is these overarching and currently implemented deep-time opportunities that can reciprocally invigorate evolutionary biology and paleobiology, particularly as "the blending of fields across scales . . . can yield enormous scientific benefits."

In the last chapter, Michael Ruse addresses whether paleobiology is now seated at the "high table," returning to the initial rhetorical question of this volume. The majority of the chapters overwhelmingly have the self-congratulatory answer of "yes," although a few seem neutral. From my reading, it is clear that not all parts of paleontology contributed equally. Of the four standard subfields of paleobiology, invertebrate paleontology contributed most and vertebrate paleontology to a lesser extent, albeit in different areas; virtually nothing was mentioned of micropaleontology and paleobotany. It also seems that there is inordinate emphasis on punctuated equilibrium as the defining feature of the emergence of paleobiology. (In my count, punctuated equilibrium is significantly mentioned in a third of the book's 27 chapters.) Punctuated equilibrium certainly provided significant thrust for launching the field, resulting from publication in Schopf's *Models in Paleobiology* (1972). But looking back, there were other gems in that volume that also defined the field, such as Raup's models on morphology. By the late 1980s, punctuated equilibrium was a spent force, the argumentation reduced to one of occurrence frequencies of the two modes, rather than tests of mechanisms. Paleobiology moved on to other macroevolutionary issues, such as how particular clades emerge from selective filters to form the fabric of the history of life, and issues spotlighted above by Jablonski's six items.

Returning to the concluding essay, Ruse links the expansion of paleobiology to the extent in which it retains a Darwinian explanatory core on one hand and yet proposes hypotheses that are "anti-Darwinian" (I would substitute "nondarwinian") on the other. Importantly, Ruse concludes that the incorporation of a newfound epistemological infrastructure of theories, hypotheses, analytic methodologies and crucially, values, allowed paleobiology to achieve new paradigmatic status. This is a robust assessment, but I think Ruse equivocates. He ends with a more appropriate question: Is what happened in paleobiology during the last 40 years revolutionary? To that, he answers "yes," a view supported in the book, as its authors map out an intellectual landscape increasingly shared between paleobiology and evolutionary biology.

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