RATES OF EVOLUTION

How fast is evolution, and why does it matter? Rates of evolution and whether evolution is gradual or punctuated are actively debated topics among biologists and paleontologists. This book compiles and compares examples of evolution from laboratory, field, and fossil studies, analyzing them to extract their underlying rates. It concludes that while change is slow when averaged over many generations, change is rapid on the generation-to-generation time scale of the evolutionary process. Chapters cover the history of evolutionary studies, from Lamarck and Darwin in the nineteenth century to the present day. An overview of the statistics of variation, dynamics of random walks, processes of natural selection and random drift, and effects of scale and time averaging are also provided, along with methods for the analysis of evolutionary time series. Containing case studies and worked examples, this book is ideal for advanced students and researchers in paleontology, biology, and anthropology.

PHILIP D. GINGERICH is Professor Emeritus of Earth and Environmental Sciences, Ecology and Evolutionary Biology, and Anthropology at the University of Michigan, as well as Curator Emeritus of Vertebrate Paleontology. His honors include the Henry Russel Award, Distinguished Faculty Achievement Award, and Collegiate Professorship at the University of Michigan; the Charles Schuchert Award from the Paleontological Society; the André Dumont Medal from the Belgian Geological Society; and the Romer-Simpson Medal from the Society of Vertebrate Paleontology. He is a fellow of the American Academy of Arts and Sciences and the American Philosophical Society, and was previously president of the Paleontological Society.

Philip Gingerich, renowned among paleontologists for his research on the evolution of mammals, has been a leading authority on rates of evolution for more than three decades. His analyses of evolution on different time scales have been critical to understanding this important, sometimes controversial, subject. *Rates of Evolution: A Quantitative Synthesis* will provide insights and statistical approaches that will interest a broad range of researchers and students working in evolutionary biology and paleontology.

– *Professor Douglas Futuyma,* Stony Brook University

This book is a deeply thought-out, scholarly and lucid account of how to connect measurements of contemporary evolution with evolution as revealed in the fossil record. Rigorous and quantitative throughout, it will be a stimulating primer for professional evolutionary biologists. There is no other book like it.

– *Professor Peter Grant,* Princeton University

Using evidence from many fields of biology, paleontology, and beyond, Gingerich's *Rates of Evolution* is a comprehensive synthesis of a pillar of the evolutionary paradigm. This book is a sophisticated analysis of quantitative empirical data integrated with evolutionary theory. It is destined to be an authoritative reference and much-cited classic in evolutionary biology.

– *Professor Bruce MacFadden,*
Florida Museum of Natural History, University of Florida

RATES OF EVOLUTION

A Quantitative Synthesis

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**In memory of my father, Orie Jacob Gingerich (1919–1982),
who encouraged my interest in numbers and
introduced me to statistics**

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Preface

I was educated in the light of evolution's Modern Synthesis. My professor when I first became interested in paleontology and evolution was Glenn L. Jepsen, who hosted the 1947 Princeton Conference on Genetics, Paleontology, and Evolution. Jepsen, Ernst Mayr, and George Gaylord Simpson co-edited the resulting volume on *Genetics, Paleontology, and Evolution* (Jepsen et al., 1949). I was fortunate to meet architects of the Modern Synthesis early in my education. Starting field work as an undergraduate helped me see the evidence and logic of Darwin's "slow and gradual modification" of species "through descent and natural selection" (Darwin, 1859, p. 312).

My doctoral dissertation was a study of population variation in the common European and North American Paleocene mammal *Plesiadapis*, with application of the classic stratigraphic principles of superposition, faunal succession, and correlation to understand its evolution through time. Large samples of *Plesiadapis* were available in the Princeton University collection, resulting from 40 years of field work that Jepsen started when he himself was a student.

I was well into my dissertation research in 1972 when fellow Yale graduate student Peter Dodson and I visited the American Museum of Natural History. At the end of the day we met Niles Eldredge. Peter knew Niles and they talked about Niles' forthcoming theory of "punctuated equilibria" developed with Harvard professor Stephen Jay Gould. On the trip back to New Haven I questioned Peter about punctuated equilibria, and was surprised at what I learned. Peter explained that according to punctuated equilibria, new species do not evolve where their ancestors are found, and they do not arise from any perceptible transformation of those ancestors. The history of life is rather one of "homeostatic equilibria" perturbed, "punctuated," rarely by random events of speciation. When published, punctuated equilibria was promoted as an alternative to phyletic gradualism. I was a graduate student with a substantial investment in an empirical dissertation documenting lineages changing through time in the fossil record.

With new expectations inspired by the theory of punctuated equilibria, I set aside my dissertation research and went to work in the Peabody Museum basement measuring *Hyopsodus* molar teeth. *Hyopsodus* is the most common fossil mammal in the North American early Eocene, and it is known from thousands specimens in the Yale collection, recovered from many levels in a thick sequence of strata exposed in the Bighorn Basin of Wyoming. *Hyopsodus* molars do not grow: They erupt at a definitive size related to the body size of the full-grown animal. If punctuated equilibria were true, I expected to find that the size of *Hyopsodus* molars in a species would remain relatively stationary from stratum to stratum through time. The only change should come when new species appeared, and these too should then remain stationary for the remainder of their existence. What I found, however, was a pattern of molar size changing and branching through time as the species themselves changed, branched in a gradual pattern reminiscent of the diagram in Charles Darwin's *Origin of Species*. The *Hyopsodus* study was published as a research article in *Nature* in 1974.

Gould and Eldredge responded in various ways. They first speculated that the overall increase in tooth size and body size in *Hyopsodus*, *Haplomylus*, and *Pelycodus* in the study interval might mean that early Eocene climate cooled through time, causing larger-bodied, northern populations to move south into Wyoming (Gould and Eldredge, 1977, pp. 130–131). Then they proposed that guidelines be redrawn to feature segments of stasis, averaging change when necessary to achieve this. Parallel change was regarded as stasis (p. 131). Gould and Eldredge's most interesting observation was documented in a table of rates (in percent change per million years), where they wrote, echoing J. B. S. Haldane (1949):

> We must consider the characteristic rates of supposed gradualistic events. When this is done, one cardinal fact emerges: they are too slow to account for most important evolutionary phenomena, particularly for adaptive radiations and the origin of new morphological designs… How can we view a steady progression yielding a 10% increase in a million years as anything but a meaningless abstraction?
>
> *(Gould and Eldredge 1977, p. 133)*

How indeed? Knowing of Haldane's study of rates, and realizing that punctuated equilibria had no explicit scale, my interest in evolution turned to rates and scales. This book, long in gestation, is the result.

This brings me to a short, provocative, important study on the west coast of Britain by Lewis Fry Richardson (1961) and Benoit Mandelbrot (1967). In this, Richardson and Mandelbrot showed, counterintuitively, that the coast has no fixed length. Its length is variable and depends on the length of the ruler, the scale, used to measure it. Richardson used log-log plots of total length versus measurement scale to quantify the dependence, and found a slope of −0.25. Mandelbrot

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interpreted this as a "fractional dimension" of 1.25. The coastline of Britain is thus more complicated, "rougher," than a one-dimensional Euclidean line, but it is less complicated, smoother, than the line one might draw to fill a two-dimensional area on a Euclidean plane (something we all did as children with crayons in a coloring book).

I fear that no reader will understand this book on rates of evolution without first understanding Richardson's and Mandelbrot's analysis of length, scale, and the coast of Britain. Maybe I am wrong. Maybe for some it will prove easier to understand what is presented here, and this will then help in understanding Richardson and Mandelbrot. To be provocative I will say in advance that there are very few smooth one-dimensional lines anywhere in nature, and *no* one-dimensional evolutionary lineages. Even stasis is not smooth.

Illustration and modeling go hand in hand. Every model has an underlying geometry that can be illustrated, and the best way to affirm that a model works is to illustrate it. This is especially important for models that involve dynamic simulation. The best way to confirm that a simulation works is to make it draw itself. Underlying geometry and model affirmation are two reasons for many of the illustrations presented here.

Finally, I will end with an impression. When I was an undergraduate I majored in geology and paleontology but took many courses in biology. There was an understanding at the time that paleontologists such as George Gaylord Simpson, Glenn Jepsen, and many others, were authorities on the history of life. There was an understanding too that biologists such as Theodosius Dobzhansky, Ernst Mayr, and many others, were authorities on the process of evolution. In the heyday of the Modern Synthesis there were conferences like the Princeton Conference on Genetics, Paleontology, and Evolution where paleontologists and biologists met to learn from each other.

Now science is a bigger enterprise, there is more specialization, and there is seemingly less communication between paleontologists and biologists. As a consequence, paleontologists understand less about the process of evolution from a biological point of view, and biologists understand less about the history of life from a paleontological point of view. Paleontologists seem happy to invent processes of evolution to fit the histories of life that they study, and biologists seem happy to invent histories of life to fit the processes they study. Neither benefits from the constraint of the other. It would be better to communicate more widely. Here, returning to my youth, I attempt to bridge paleontology and biology. Hopefully readers benefit from the reciprocal illumination.

Acknowledgments

First and foremost, my anthropologist–statistician wife of many years, B. Holly Smith, aided and encouraged completion of this study. Long-time colleagues in paleontology and evolutionary biology at the University of Michigan, especially Daniel C. Fisher and Philip Myers, listened as my ideas developed and raised important questions along the way. PhD student William C. Clyde, now at the University of New Hampshire, understood what I was doing and worked to improve it. Former postdoctoral scholar P. David Polly, now at Indiana University, helped and encouraged completion. I thank all five. I owe a debt too to the successive cohorts of students who forced me to think critically about rates in the courses and seminars I taught on fossil mammals and evolution.

Sources of rate information are cited in the text, but some colleagues contributed unpublished information as well. Jennifer Babin-Fenske, Coordinator of EarthCare, City of Greater Sudbury, provided information on whirligig beetles. Michael A. Bell, Stony Brook University, provided measurements and other information on three-spine sticklebacks. Mary Bomberger Brown at the University of Nebraska provided information on cliff swallows. Sandra Carlson at the University of California, Davis, provided information about generation times in brachiopods. Nicholas M. Caruso, Virginia Tech University, provided measurements and information on generation times in plethodontid salamanders. Alan Cheetham, United States National Museum, provided ages and Mahalanobis D values for *Metrarabdotos* species samples. The late Douglas Falconer, University of Edinburgh, provided measurements of the mice in his selection experiments. Theodore Garland helped with branch lengths and other information needed in Chapter 13. Ann E. McKellar, Environment Canada, provided a copy of her data compilation on body weight variability in mammals. Philip Myers, University of Michigan, helped with understanding Galápagos rats. Kathleen M. Scott, Rutgers University, provided a copy of her large set of ungulate postcranial measurements. Trisha Spanbauer, University of Nebraska, provided measurements of *Cyclostephanos*

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