

**Rates of evolution in Plio-Pleistocene
mammals: six case studies**

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Rates of evolution in Plio-Pleistocene mammals: six case studies

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Evolution, in general, means change over time: The end is different from the beginning. Change is not inevitable, but it seems to be common. And some change can almost always be observed, given enough time. When do we see change? How much time does it take? To study evolution we have to measure change and time, and to understand evolution we have to know how the two are related.

Evolution in biology is often described as a process, but it is really a collection of processes – including the processes of mutation, dispersion, drift, and selection – that together produce whatever change we see. These processes may each be complicated individually, and their interactions produce additional complexity. Evolution is widely acknowledged as a fundamental concept in biology, and yet we have a surprisingly anecdotal and casual knowledge of how evolutionary change takes place. One way to improve this understanding is to quantify change over time in terms of rate. Evolutionary rates are quantitative expressions relating change to time.

Evolution takes place on many scales of time. Field and laboratory experiments can be designed to study change on short time scales, and fossils provide the most direct and best information about evolution on long time scales. The principal problem with the fossil record is that the time scales involved, typically millions of years, are so long that they are difficult to relate to the time scales of our lifetimes (and those of other organisms). Biologists as a group have a surprisingly poor understanding of evolution on a geological scale of time, and paleontologists as a group have a surprisingly poor understanding of evolution on a biological scale of time. One reason for this is that we have almost no

record of changes on intermediate scales of time, scales of hundreds or thousands of years, that would permit evolution on a laboratory scale of time to be related to evolution on a geological scale.

Fortunately biologists can sometimes study evolution on a scale of hundreds or thousands of years by taking advantage of accidents and events that have affected organisms, (e.g., chance colonization events) and have been documented in human history. And in favorable circumstances, paleontologists, too, can resolve time on scales of hundreds or thousands of years. It is generally true that time is easier to resolve the less far back we are in geological time, and the Pleistocene, spanning much of the past 2 million years, is important in this regard. The six Plio-Pleistocene studies discussed here illustrate a paleontological approach to understanding evolution on a wide range of time scales.

Quantification of evolutionary rates

Quantification of evolutionary rates is still in its infancy, and the history of ideas on this can be summarized rather easily. Time is uniquely important in paleontology, and it comes as no surprise that paleontologists figure prominently in the quantification of evolutionary rates. George Gaylord Simpson provided the first substantial treatment of rates in his book *Tempo and Mode in Evolution* (1944). At that time the geological time scale was poorly calibrated numerically, and Simpson was unwilling to trust estimates of the durations of epochs. He published a table of various measures of tooth size in horses and showed graphically that if the length of the ectoloph evolved at a constant rate, then the height of the paracone did not (Simpson, 1944, Figure 2). Simpson also provided a graph of these two characteristics plotted against geological time, showing that in all likelihood neither had evolved at a constant rate (Simpson, 1944, Figure 4). He noted that the slopes of lines in his graphs were proportional to rates of evolution, but did not attempt to quantify these. Simpson's most noteworthy contribution to quantification was recognition from the beginning that proportional change, not absolute change, is the quantity of interest, and consequently that a proportional (logarithmic) scale is the appropriate measurement scale for morphology.

J. B. S. Haldane (1949) quantified evolutionary rates in terms of proportional change and proposed the *darwin*, defined as change by a factor of e per million years (where e is the base of natural logarithms), as a convenient rate unit. Haldane calculated rates of evolution in horses

