

# Evolution and the fossil record: patterns, rates, and processes

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Received April 4, 1986

GINGERICH, P. D. 1987. Evolution and the fossil record: patterns, rates, and processes. *Can. J. Zool.* **65**: 1053–1060.

Mammals have an unusually good Cenozoic fossil record providing evidence of their evolutionary diversification. We view this record in hindsight, which biases our perception in many ways. Overall worldwide diversity appears to increase exponentially through time, while intensive sampling in local areas indicates that modern levels of diversity were achieved early in the Cenozoic. The evident significance of Pleistocene extinctions depends critically on how extinction rates are quantified. Our taxonomic hierarchy probably reflects the number of major faunal turnovers a group has survived rather than declining intensity of successive turnovers. Morphological innovation and taxonomic diversification appear following intervals of climatic cooling, suggesting that major features of evolution are extrinsically controlled. Favorable stratigraphic settings yield detailed records of gradual anagenesis and cladogenesis in mammals, with intermediates present as evidence of transition. The apparent dichotomy between high evolutionary rates measured by neontologists over short intervals of time and low evolutionary rates measured by paleontologists over long intervals of time disappears when rates are measured on intermediate scales of time. Microevolution and macroevolution are manifestations of common underlying processes expressed on different time scales.

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Les données remarquablement nombreuses sur les mammifères fossiles du Cénozoïque fournissent des preuves de leur diversification évolutive. En examinant ces données avec du recul, il faut admettre qu'elles faussent notre perception de bien des façons. La diversité des mammifères envisagée à l'échelle mondiale semble avoir augmenté de façon exponentielle au cours des âges, alors que des échantillonnages intenses en des localités précises indiquent que les degrés de diversité modernes ont été atteints au début du Cénozoïque. Les conclusions sur l'importance des extinctions au Pléistocène dépendent directement de la façon de quantifier les taux d'extinction. Notre hiérarchie taxonomique reflète probablement le nombre de remplacements faunistiques majeurs qu'a eu à subir un groupe plutôt que l'importance décroissante des remplacements successifs. Les phénomènes d'innovation morphologique et de diversification taxonomique apparaissent à la suite de refroidissements climatiques, ce qui permet de croire que l'évolution est surtout contrôlée par des facteurs externes. Des relevés stratigraphiques favorables ont mis en lumière l'anagénèse et la cladogénèse graduelles des mammifères et les intermédiaires servent d'indicateurs des situations de transition. La dichotomie apparente entre les taux rapides d'évolution mesurés par les néontologistes au cours d'intervalles courts et les taux évolutifs lents mesurés par les paléontologistes sur de longues périodes de temps disparaît lorsque ces taux sont mesurés sur des périodes de temps de longueur intermédiaire. La microévolution et la macroévolution sont les manifestations de processus sous-jacents communs exprimées sur des échelles de temps différentes.

[Traduit par la revue]

## Introduction

The oldest tension in human perception is that between the world as we see it and the world as we think it should be. The former is the basis of science, the latter of politics and religion. Yet neither can be separated clearly from the other. This tension indicates, on one hand, that there is more to life than meets the eye and, on the other hand, that the mind is wonderfully creative, often even deceptive. A tension of perception exists within science too, where the world as we see it is expressed in our observations, our data, and the world as we think it should be is encompassed in theories and hypotheses. Theory, in a way, is the politics and religion of science.

It is often stated, downplaying the role of induction in science, that innocent unbiased observation is a myth: useful observations are always necessarily theory bound. Why then do we not recognize and require the converse, that theories be based on observations? The world of our scientific perception is but one of many worlds we might imagine. We do not have time, energy, nor funds to investigate all possible worlds: if creative induction yields many hypotheses, then emphasis in normal science is rightly placed on deduction, hypothesis testing, with rapid rejection of hypotheses lacking evidence or theories running counter to empirical observation.

Empirical observations combine to form *patterns*; patterns are what we have to work with. Evolution is the science of organic change, change over time, and the principal analytical approach in studying change requires quantification in terms of *rate*. Indeed all attempts to relate change on the scale of our lifetimes to change on the vast scale of our geological past require

comparison in terms of rate. The goal is to understand the history of life in terms of *processes* familiar today. When familiar processes fail, and only when they fail, new processes are required to explain patterns observed in the history of life.

Here I shall attempt to balance theory and observation in discussing recent developments in our understanding of evolution and the fossil record. I shall begin by outlining the evolutionary radiation of mammals as a whole. Next I shall illustrate patterns of evolution at the species level, including documented transitions between successive species. Finally I want to consider problems inherent in comparing evolutionary rates, showing how distributions of microevolutionary and macroevolutionary rates, long thought to be discrete and nonoverlapping, decoupled, grade continuously together when measured on intermediate time scales. Judging from this evidence, microevolution and macroevolution are manifestations, expressed on different time scales, of common underlying processes.

## Cenozoic radiation of mammals

Paleontologists view the world a little differently than colleagues studying living plants and animals. Our charts and graphs reflect this in incorporating time as the principal axis and independent variable. The Cenozoic radiation of mammals is illustrated graphically in Fig. 1, based on Romer's (1966) compilation of generic ranges. Regrettably, this is the only comprehensive listing of generic ranges available at present. Many new genera of mammals have been described in the past 20 years, and the time scale too is now much better known. I

