

# The big picture

Sean B. Carroll

Macroevolution: “a vague term for the evolution of great phenotypic changes, usually great enough to allocate the changed lineage and its descendants to a distinct genus or higher taxon” — from D. J. Futuyma, *Evolutionary Biology* (Sinauer, Sunderland, 3rd edn, 1998).

Evolutionary change occurs on different scales: ‘microevolution’ is generally equated with events at or below the species level whereas ‘macroevolution’ is change above the species level, including the formation of species. A long-standing issue in evolutionary biology is whether the processes observable in extant populations and species (microevolution) are sufficient to account for the larger-scale changes evident over longer periods of life’s history (macroevolution).

Outsiders to this rich literature may be surprised that there is no consensus on this issue, and that strong viewpoints are held at both ends of the spectrum, with many undecided. Traditionally, evolutionary geneticists have asserted that macroevolution is the product of microevolution writ large, whereas some palaeontologists have advocated the view that processes operating above the level of microevolution also shape evolutionary trends. Is one of these views wrong, or could they both be right?

One obstacle to a more unified, multi-disciplinary view of evolution is the vague meaning of the term macroevolution, and its different connotations in different disciplines. This is not merely a matter of semantics: scientific and broader public issues are at stake. The origins of major innovations and the underlying causes for the radiation of forms during various episodes in life’s history are among the most interesting and challenging questions in biology. We must know whether, as G. G. Simpson asked, macro-

evolution differs fundamentally in kind or only in degree from microevolution. Furthermore, one of the latest political strategies of the creationist faction in the United States is to ‘accept’ microevolution but to bar macroevolution from the classroom on the misguided grounds that aspects of macroevolution are controversial and that therefore its scientific foundation is ‘unproven’.

My argument has three parts. First, that the concept of macroevolution is better clarified when broken down into its two major component parts: phyletic and morphological evolution. Second, these two components are governed by at least partly distinguishable mechanisms. And third, because there is no evidence that the intrinsic genetic and developmental mechanisms underlying morphological evolution differ across any evolutionary scales, the distinction between these scales is really only descriptive, not mechanistic.

## Deconstructing macroevolution

‘Macroevolution’ is a different concept for different kinds of biologists. For a palaeontologist, the fossil record frames a picture of the origins and extinctions of species, that is, phyletic evolution. For a developmental biologist or population geneticist, macroevolution is generally synonymous with morphological evolution, essentially independent of timescale or phylogenetic context. These different conceptual frameworks inspire different research agendas in the search for mechanistic explanations at different levels of biology.

One of the evolutionary phenomena for which the mechanistic discontinuity between macroevolution and microevolution has most often been asserted is the burst of innovation and diversification associated with major radiations of forms — for example, the dramatic phyletic and morphological evolution seen in the explosive Cambrian radiation of animal phyla. Explanations for the Cambrian patterns of phyletic evolution tend to focus on extrinsic environmental and ecological factors as catalysts for the rapid diversification of clades (sets of species each descended from a common ancestral species). There is also currently much interest in identifying the intrinsic genetic and developmental mechanisms for the morphological diversification of taxa in the Cambrian.

The crucial question is whether there is any evidence that distinct macroevolutionary mechanisms affect morphological or phyletic evolution. There are no reports of higher-level genetic mechanisms (genome rearrangements or ‘macromutations’) distinct from microevolutionary genetic mechanisms underlying speciation, the large-scale mor-

## Macroevolution

*“Many geneticists assert that macroevolution is the product of microevolution writ large, but some palaeontologists believe that processes operating at higher levels also shape evolutionary trends.”*

phological diversification of various body plans, or the origin of major innovations. On the contrary, an unexpected degree of genetic similarity exists between morphologically and phylogenetically divergent taxa, suggesting that the distinction between macro- and microevolution in terms of morphological change is descriptive, not mechanistic.

On the other hand, the differential success of some clades has led to the proposal that there are properties of species that make them, as units, subject to selection (for example, occupancy of a certain ecological zone). The controversial idea of species selection differs from the microevolutionary view of natural selection in regarding variations between species, rather than characteristics of individuals within a species, as the basis for evolutionary change. One major difficulty with species selection is the requirement for selection to act, with equal intensity and no differential effect, on all individuals across a species’ geographical range. Should these (some would say unlikely) conditions not be met, species selection breaks down into essentially conventional microevolutionary processes.

## Macro- = Micro- = Evolution

The ‘big picture’ of evolution continues to grow, with diverse disciplines addressing biological mechanisms across many levels of organization (molecules, organisms, populations) and timescales. The subdivision of evolution into two scales no longer reflects our understanding of the unity and diversity of evolutionary mechanisms. However, more important than redefining macroevolution is recognizing that discipline- or scale-bound considerations of only one component of evolution, or of solely extrinsic or intrinsic mechanisms, are inadequate. Long-standing boundaries between evolutionary disciplines are dissolving, to allow richer concepts of evolution to emerge. ■

Sean B. Carroll is at the Howard Hughes Medical Institute and Laboratory of Molecular Biology, University of Wisconsin–Madison, 1525 Linden Drive, Madison, Wisconsin 53706-1596, USA.

## FURTHER READING

Erwin, D. H. *Evolution & Development* 2, 78–84 (2000).  
Leroi, A. M. *Evolution & Development* 2, 67–77 (2000).  
Lerner, L. S. *Nature* 407, 287–290 (2000).

TOM BEAN/CORBIS



Micro or macro? A trilobite fossil.