

Macroevolution: Dynamics of Diversity

The fossil record typically exhibits very dynamic patterns of innovation, diversification and extinction. In contrast, molecular phylogenies suggest smoother patterns of evolutionary change. Several new studies reconcile this difference and reveal more about the mechanisms behind macroevolutionary change.

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Do the evolutionary mechanisms available to manipulation, such as laboratory or field studies of adaptation and population genetics, reveal the full scope of evolutionary processes, or are there processes that operate over longer timescales and that are responsible for the diversity of life, both today and in the fossil record? This question encompasses the tension between microevolutionists and macroevolutionists (originally mainly paleontologists, but recently including evolutionary developmental biologists and others). Historically, a strictly microevolutionary approach developed in the 1930s as a response to orthogenesis — the idea that life has an innate drive to evolve in particular directions, independent of their adaptive value — and other anti-Darwinian evolutionary views [1]. Over the past decades, much paleontological work has focused on documenting the patterns of macroevolution, with less attention given to the underlying mechanisms. With the advent of evolutionary developmental biology (evo-devo), approaches to macroevolution have come to include the sources of variation. Several recent papers [2–4] now shed new light on macroevolutionary processes by modeling the structure of phylogenetic patterns, analyzing the distribution of changes in body size through time and uncovering the changing developmental mechanisms.

Phylogenetic Inference of Diversity

The discrepancy between plots of the diversity of taxa through time as inferred from molecular phylogenies and those based on counts documented by the fossil record has long been troubling, largely because molecular phylogenies appear to underestimate the frequency of extinction. In their recent study,

Morlon and colleagues [3] modify earlier birth–death models [5,6] and develop an analytical model for molecular data that encompasses variation in rates of the origin and extinction of species, changes in diversity and undersampling of phylogenetic diversity. Existing models assume that rates of species origin are constant through time, or across a phylogeny. However, the authors [3] have added important modifications to their model, allowing both origin and extinction rates, which combine to control the overall rate of diversification, to change each time two lineages diverge. In contrast to earlier models, this model identifies episodes of past loss of diversity.

The authors applied this model to the evolution of cetaceans (whales, dolphins and porpoises). The fossil record of cetaceans shows a global increase in diversity from about 30 million years ago to a peak in the mid-Miocene (about 10 million years ago) followed by a rapid decline to the 98 cetacean species living today. There is a well-established molecular phylogeny for 87 of the 89 extant species. Thus, they serve as an excellent test case for this model: can the model accurately recover the fossil history of the group, using only the phylogenetic data of living cetaceans?

Most of the diversity of living cetaceans is clustered among four families, each of which has many younger species than the older 10 families. With models that allow for different patterns of rate variation in different clades, the model's results matched those from the fossil record quite well. Moreover, the analysis allowed the authors to examine the changes in origin and extinction rates over time. Only three families, the Delphinidae (dolphins), Phocoenidae (porpoises) and Ziphiidae (beaked whales) show constant speciation rates

and expanding diversity. Each of the other families are either at equilibrium diversity or show a negative net diversification rate. Provided further work can validate and extend these models, they could be applied to clades with a sparse, or entirely absent, fossil record, unveiling previously hidden macroevolutionary patterns and providing new insights into evolutionary dynamics.

Punctuations Are Not Passé

While the inclusion of rate heterogeneity was critical to the success of the model produced by Morlon *et al.* [3], the pattern of variability of rates of morphological evolution was recently explored by Uyeda and colleagues [2]. They analyzed the evolution of vertebrate body size on timescales ranging from the recent to the deep fossil record. Their analysis supports a model of rare bursts of extensive evolutionary change in a sea of shorter-term fluctuations. The resulting 'blunderbuss pattern' of morphologic divergence over time shows a bounded pattern of morphological change over timescales of up to 1 million years (the flare of the blunderbuss), as previously reported [7], as well as increasing divergence between samples over longer timescales (the long tail of the gun barrel). Thus, this large-scale analysis yields both dynamic stasis over the shorter timescales (<1 million years), but phenotypic divergence only accumulates over longer timescales.

The authors tested the body size measurements against four stochastic models: bounded evolution, which matches the short-term fluctuations in the data but does not accommodate increasing divergence over time; and three unbounded models, each of which generates increasing phenotypic divergence with time: Brownian motion, which generates linear increases in phenotypic divergence; a single large burst of morphological change at a random time; and a final model involving multiple bursts of phenotypic change. The multiple-burst model best captured the pattern of divergence, but leaves a critical question unresolved: Why is the extent of morphological evolution constrained over shorter time-periods, but accumulates through bursts of phenotypic change on longer

timescales? This inhomogeneity of rate is consistent with the results of the Morlon *et al.* [3] paper, but requires a mechanistic explanation. The authors propose that the bounded divergences represent morphological evolution within adaptive zones with little long-term accumulation of change. This is essentially Futuyma's solution to the punctuated equilibrium controversy [8]. Futuyma [8] suggested that the population structure of many species constantly generated new populations, which diverge morphologically to some degree from the average phenotype of the species. Only occasionally did the morphology of a species diverge sufficiently from this evolutionary churn to be recognized as a new species or genus. The bursts of evolutionary change over longer timescales remain to be explained but could reflect episodic changes in the optimal adaptive phenotype as the environment changes, as the authors suggest, the construction of new ecological environments, or the longer waiting time for significant developmental innovations.

Evolution of Development

The analyses of Uyenda and colleagues [2] are likely to sample very different sources of morphological change. Developmental gene regulatory networks are hierarchically structured, with different characteristic rates of change at different levels of the hierarchy [9]. A recent analysis by Lowe *et al.* [4] of genome-wide sets of putative regulatory regions has identified long-term changes in developmental mechanisms in vertebrate macroevolution. This indicates three distinct episodes of regulatory innovation, each involving different components of the genome

[4]. Lowe and colleagues [4] systematically dissected the regulatory basis for these differing patterns of change in 40 vertebrates species, focusing on conserved *cis*-regulatory elements (specifically conserved non-exonic elements) which have been shown to act as developmental regulators. The species examined range from fish to more recently diverged placental mammals, providing good coverage of the history of vertebrate evolution. The authors were able to infer when on the branching tree different conserved non-exonic elements came under evolutionary constraint, and established the functional class of each associated gene.

The results showed consistent patterns across each of the animals studied: early vertebrate evolution was dominated by regulatory changes in transcription factors and their allied developmental genes. A second phase in regulatory innovation encompassed changes in extracellular receptor-binding sequences and a decline in changes in transcription factors and developmental genes occurred along both the fish and tetrapod lineages. The placental mammal lineages exhibit a third phase of innovation in posttranslational protein modification, while changes in transcription factors, developmental genes, and receptor genes declined to background levels. It will be of great interest to establish whether similar patterns occur among other lineages of bilaterian animals.

These robust dissections of phylogenetic pattern, evolutionary rate, and developmental mode reveal complex and dynamic patterns of evolutionary change on timescales inaccessible to evolutionary studies of living species. In each of these papers

[2–4] the results document a greater range of evolutionary processes, including great differences in origin and extinction rates in different clades through time, bursts of phenotypic change interrupting intervals of greater phenotypic quiescence, and a structuring of the developmental sources of evolutionary change. The generality of these results will become more apparent as the new techniques and approaches of these papers are extended beyond vertebrates to the rich fossil records of various invertebrate clades.

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DOI: 10.1016/j.cub.2011.11.007