

Macroevolution is more than repeated rounds of microevolution

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SUMMARY Arguments over macroevolution versus microevolution have waxed and waned through most of the twentieth century. Initially, paleontologists and other evolutionary biologists advanced a variety of non-Darwinian evolutionary processes as explanations for patterns found in the fossil record, emphasizing macroevolution as a source of morphologic novelty. Later, paleontologists, from Simpson to Gould, Stanley, and others, accepted the primacy of natural selection but argued that rapid speciation produced a discontinuity between micro- and macroevolution. This second phase emphasizes the sorting of innovations between species. Other discontinuities appear in the persistence of trends (differential success of species within clades), including species sorting, in the differential success between clades and in the origination and establishment of evolutionary novelties. These

discontinuities impose a hierarchical structure to evolution and discredit any smooth extrapolation from allelic substitution to large-scale evolutionary patterns. Recent developments in comparative developmental biology suggest a need to reconsider the possibility that some macroevolutionary discontinuities may be associated with the origination of evolutionary innovation. The attractiveness of macroevolution reflects the exhaustive documentation of large-scale patterns which reveal a richness to evolution unexplained by microevolution. If the goal of evolutionary biology is to understand the history of life, rather than simply document experimental analysis of evolution, studies from paleontology, phylogenetics, developmental biology, and other fields demand the deeper view provided by macroevolution.

INTRODUCTION

Since all evolutionary change involves intraspecific modification and speciation, in a trivial sense, macroevolution could be reducible to microevolution. The novel associations of morphological characters and developmental processes recognized as phyla did not arise through some processes of “phylization,” but through speciation. At issue is not the efficacy of natural selection (contrary to some misunderstandings, e.g., Dawkins 1996), but whether the larger scale patterns in the history of life simply reflect the accumulation of microevolutionary events over long spans of time, or whether a more inclusive view of evolutionary processes is required. In particular, paleontologists and other macroevolutionists point to a range of phenomena that suggest discontinuities between microevolution and some forms of speciation, and in the interactions within and between clades.

Vermeij’s (1987, 1994) documentation of the morphological changes induced in gastropods since the Jurassic by the action of shell-crushing predators, particularly crabs, could simply be the manifestation of numerous, individual microevolutionary trends. Narrow apertures, spines, and other antipredatory defenses may have become widespread while many once common but susceptible morphologies vanished through natural selection extended through the Mesozoic. The same trend, however, could also have been pro-

duced by differential sorting of species within lineages, or differential sorting between lineages, where lineages with predation-resistant morphologies are more successful, a macroevolutionary process. It is unclear whether a microevolutionary null model should be preferred to a hierarchical one (on any basis but personal preference), and in the absence of sufficient data there is no way to resolve the issue. The distinction is real, however, and is subject to empirical evaluation.

Physicists ignore the actions of individual atoms because the generalities that produce physical laws are exhibited by collections of atoms. Similarly, ecologists have recognized that the analysis and experimental perturbation of local communities, while useful, blinds them to processes exhibited at broader spatial and temporal scales (e.g., Brown 1995; Maurer 1999). These ecological generalities are not apparent at more circumscribed levels of analysis, yet they reveal the significance of processes operating beyond the scope of traditional ecological studies. Patterns of community structure and regional differences in biodiversity, immigration, and local extinction each emerge at the level of macroecology. Unlike statistical physics, however, where laws derive from a statistical summation of individual behavior, the emergent properties of macroecology and macroevolution reflect a hierarchical structure and the importance of different scales of process and analysis.

Paleontologists have proposed a number of patterns and processes that suggest a hierarchical structure to the evolutionary process, with explicit discontinuities between levels (see particularly Gould 1985; Bennett 1997). Such discontinuities may exist at the level of speciation, with the most widely discussed example being punctuated equilibrium, and in the generation of trends, particularly those within clades through differential success of species. The formation of larger-scale patterns of differential success of clades through long spans of time may constitute a further discontinuity. Finally, the empirical distribution of evolutionary novelties through time suggests that the origin of evolutionary innovation may be distinct from much of traditional microevolution. I begin with a brief discussion of macroevolution and then consider each of the discontinuities noted above, and the generation of evolutionary novelties.

WHAT IS MACROEVOLUTION?

The term macroevolution was introduced by Iurii Filipchenko, a Russian geneticist and developmental biologist and mentor of Theodosius Dobzhansky. Filipchenko distinguished between Mendelian inheritance within species and non-Mendelian, cytoplasmic inheritance responsible for the formation of taxa above the species level. In contrast to latter views, speciation was not seen as the crux of the distinction between micro- and macroevolution, since Filipchenko saw speciation as continuous with microevolutionary change (Alexandrov 1994). The discontinuity lay above this level: “. . . the origin of the characters [that differentiate the] higher systematic categories [requires] some other factors than does the origin of the lower taxonomic units” (Filipchenko 1927, p. 91, cited by Burian 1994, p. 134). Filipchenko’s views meshed with the later efforts of such macromutationists as Osborne and Goldschmidt.

Dobzhansky (1937) introduced macroevolution to English-speaking evolutionists but decisively rejected any discontinuity between micro- and macroevolution. Dobzhansky appears to have been agnostic about the potential of macroevolution and in an oft-cited passage wrote: “. . . there is no way toward an understanding of the mechanisms of macroevolution, which require time on a geological scale, other than through a full comprehension of the microevolutionary processes . . . For this reason we are compelled *at the present level of knowledge* reluctantly to put a sign of equality between the mechanisms of macro- and micro-evolution . . .” (Dobzhansky 1937, p. 12; emphasis added). Dobzhansky was rejecting purveyors of saltationist changes and orthogenesis while leaving open the possibility of a more scientific approach to macroevolution (Burian 1994).

Simpson (1944) recognized the seemingly discontinuous origin of major clades as the greatest challenge to the incor-

poration of paleontology into the Modern Synthesis. Rejecting the macromutationist views of Goldschmidt, Schindewolf, and others, Simpson noted: “Macro-evolution involves the rise and divergence of discontinuous groups, and it is still debatable whether it differs in kind or only in degree from micro-evolution. If the two proved to be basically different, the innumerable studies of micro-evolution would become relatively unimportant and would have minor value in the study of evolution as a whole.” (1944, p. 97)

Simpson’s macroevolution emphasized the origin of species and genera, while he coined the term mega-evolution for the origin of higher taxonomic categories. In his view, the discontinuities between larger groups were of far greater evolutionary significance than between species and genera. Simpson also defined quantum evolution as a rapid shift from one adaptive zone to another through genetic drift, differing in both rate and kind from speciation and phyletic evolution. Yet in 1953 he rejected this view, suggesting that quantum evolution is simply a rapid form of phyletic evolution (see Gould 1980, 1994). Simpson’s views remained the major statement on macroevolution for the following two decades, although the subject received relatively little attention during the 1960s.

The concept of punctuated equilibrium led to a renewal of interest in macroevolution with the claim that speciation often imposed a fundamental discontinuity between phyletic evolution and the formation of species. Since Cuvier in the 1820s and Phillips in the 1840s, paleontologists had recognized that species appear suddenly in the fossil record, often show no directional morphologic change during their existence, and then disappear, frequently to be replaced by closely related species. Paleontologists had discounted the evolutionary significance of these observations by invoking the incompleteness of the fossil record, slavishly following the example of Darwin in the *Origin of Species*. But Eldredge and Gould (1972) asserted that the fossil record was not sufficiently incomplete to produce the observed pattern as an artifact (since confirmed by many analyses, e.g., Holland and Patzkowsky 1999; Foote et al. 1999). They argued that speciation occurred rapidly, in events, and that any morphological change between events had little influence on speciation (see Erwin and Anstey 1995, on development of the theory).

SPECIATION

Recent studies of the fossil record have documented a host of speciation patterns, including punctuated anagenesis (stasis and rapid change but without branching), gradualism (gradual morphological divergence), and gradualistic anagenesis (constant directional evolution without branching) as well as cladogenesis (Erwin and Anstey 1995). The anal-

ysis of speciation patterns in the cheilostome bryozoan genera *Metrarabdotos* and *Stylopoma* remains one of the most rigorous, involving quantitative morphometrics and detailed sampling of the fossil record, with the morphometrically defined species confirmed by genetic analysis in many cases (see Jackson and Cheetham 1999). A pattern of punctuation and morphological stasis is overwhelmingly supported. Critically, whether population genetics can account for any of these trends is not at issue. Population genetic models can produce virtually any pattern of morphological evolution and thus provides no clear basis for choosing between opposing models. Perhaps the most telling examples of the disjunction between speciation and intraspecific change comes from the paucity of evolutionary change associated with the climatic upheavals of the Pleistocene glaciations. Yet abundant evidence from marine (Jackson 1995) and insect faunas (Coope 1995) demonstrates that following a turnover associated with abrupt climate changes at the onset of the Pleistocene glaciations, subsequent climatic events and sea level changes caused little subsequent speciation or extinction (Bennett 1997).

The empirical studies required to satisfactorily demonstrate *any* pattern of speciation are time consuming, but in lineages where multiple characters have been studied with sufficient rigor (see Erwin and Anstey 1995) punctuated equilibrium is common (Jackson 1995; Jackson and Cheetham 1999), suggesting the presence of a discontinuity between intraspecific, adaptive evolution and the processes that influence species formation.

TRENDS: DIFFERENTIAL SUCCESS WITHIN LINEAGES AND CLADES

Why do some clades expand and persist more than other clades, and how is this related to speciation? Two processes of origination and persistence of clades have been proposed: species sorting and species selection. Sorting is the differential success of species from whatever cause, and implies neither species selection nor natural selection (Vrba and Gould 1986; see also Grantham 1995). If, as the evidence suggests, speciation is generally punctuated, then macroevolutionary trends must result from differential origination and extinction of species within clades (Stanley 1979). Within-clade differences in speciation and extinction rates have long been recognized in the fossil record (e.g., McNamara 1990; Wagner 1996) and are one form of macroevolutionary sorting.

Species selection, unlike species sorting, requires that species be units of selection, and thus there must be properties of the species, rather than the sum of the properties of individuals, upon which selection can act. Arguments for species selection have focused on the issue of whether species constitute individuals. If speciation occurs as discrete events,

rather than through a lengthy process, this necessarily implies that species have a definite birth, persistence, and death. Furthermore, if species are (usually) discrete from related species, interact with the environment, and reproduce with high fidelity (i.e., during branching give rise to daughter species with similar characteristics to the parent species) they constitute individuals and are thus subject to selection, in a fashion analogous to natural selection (see discussions in Stanley 1979; Eldredge 1989; Grantham 1995; Gould and Lloyd 1999). If species do not have the characteristics described above, they are members of a class, but not individuals (atoms of gold are members of a class, but not individuals). (Phylogenetic systematics likewise views species as having clear births and deaths, but for reasons independent of punctuated equilibrium, but see also Maddison 1997).

As individuals, species are subject to selection if they exhibit variation in properties of the species as a whole, rather than as a collection of individuals, if that variation is heritable, and if the differences lead to differential success. The empirical evidence for species selection is based largely on correlations between species and genus survival and geographic range. Jablonski (1987, 1995) found an association between larval ecology of Late Cretaceous marine molluscs and extinction rates: planktotrophic developers exhibited a statistically significantly lower extinction rate than non-planktotrophs, reflecting greater dispersal ability and broader geographic range. Jablonski (1987) compared closely related species and concluded that geographic range is heritable at the species level: species vary in geographic range, this variation generates differential survival, and the geographic range of descendent species is correlated (heritable, in Jablonski's view) with ancestral species ranges. Similar geographic range data are widespread in the literature, although usually not discussed as examples of species selection (e.g., Brown 1995, although Brown's is less clear-cut than Jablonski's).

The differential success of clades can result in the loss of adaptive phenotypes, even if beneficial (Strathmann 1978). If an adaptive trait is relatively easy to acquire early in the evolution of a clade, but more difficult to acquire thereafter, elimination of that trait may lead to a loss of adaptive diversity. Strathmann documents the loss of larval planktotrophy from a large number of invertebrate classes, limiting the future evolutionary flexibility of these groups.

LARGE-SCALE PATTERNS: DIFFERENTIAL SUCCESS OF CLADES

Darwin, famously, wondered why beetles were so successful. The fossil record provides many examples of the waxing and waning of ecologically related groups; competition, on a geological time-scale, has been invoked as a generator of

these patterns. Paleontological studies have addressed this issue through the empirical stratigraphic distributions of genera or families within higher taxa, generally assumed to be either monophyletic (Foote 1996; Sepkoski and Kendrick 1993).

In their paper, Sepkoski et al. (2000) show that the decline of cyclostome bryozoans relative to cheilostome bryozoans follows a coupled logistic model of clade displacement based on competitive interactions (with the addition of a perturbation corresponding to the end-Cretaceous mass extinction). Cyclostomes have a low rate of extinction as measured from the fossil record, and the model provides a basis for understanding how they could have gradually been replaced by competitively superior cheilostomes. In a fascinating twist, the fossil record preserves a corroborating ecological record of competitive interactions between these encrusting marine organisms through time. Thus both macroevolutionary and microevolutionary patterns are consistent with a critical role for competition.

Sepkoski applied such coupled logistic models to a variety of clades and groups. He defined three great Evolutionary Faunas, encompassing the Cambrian, Paleozoic, and post-Paleozoic (Sepkoski 1981), and suggested that competition fueled the transition between them (Sepkoski 1984, 1996). Yet the differential success of clades is at least partly due to differences in intrinsic rates of extinction and persistence (Valentine 1990), and competition between clades may be unnecessary as a means to explain biotic transitions (Miller 1998). Moreover, global diversity compendia are composites and different biogeographic regions exhibit distinct evolutionary histories, perhaps reflecting regional environmental conditions more than global ecological processes (Miller 1998; Erwin 1998). The translation between ecological competition and longer-term clade dynamics is clouded by such issues as incumbency. The species that first occupies a habitat normally maintains possession until extinction or environmental change removes it, allowing in a competitor. Over time competitively superior clades normally win, but not because they displace the weaker clade, but rather because the weaker clade is removed by an external force (e.g., Rosenzweig and McCord 1991).

The fossil record illustrates that perturbations control the removal of incumbents and allow the success of other groups at a variety of scales. At the largest scale of mass extinctions, survival may follow a different set of rules (Jablonski 1986, 1989, 1995 and see Erwin 1990 on Paleozoic gastropods; Benton 1996 on tetrapod evolution). Jablonski (1986, 1989; Jablonski and Raup 1995) demonstrated that survival of marine genera between mass extinctions is often related to high species richness and geographically widespread species. But this pattern fails during mass extinctions, when survivorship is linked to geographic distribution of the genus, and is independent of the patterns found among species. Thus, species,

whether they originated through microevolution or punctuated equilibrium, may be well adapted to the long intervals between mass extinctions, but fortuitously not possess, or be members of clades that possess, the characters that enhance survivorship during mass extinctions.

Post-extinction rebounds provide an excellent opportunity to determine the relative importance of ecological and developmental factors in morphologic innovation (Erwin et al. 1987). For example, Foote (1999) compared taxonomic diversity and morphological disparity of Phanerozoic crinoids, with particular attention to the basal Paleozoic radiation and the rebound following the great end-Permian mass extinction. His results show rapid increases in morphologic disparity during each event, consistent with exploitation of ecological opportunities. A subsequent decline in morphological diversification matches the fall in taxonomic originations. Yet the post-Paleozoic crinoids occupied a narrower range of architectures, a pattern consistent with an increase in developmental constraint during the Paleozoic. As discussed previously, environmental perturbations also control patterns of clade replacement, community change, and speciation. In each case discontinuities appear between microevolution and macroevolution.

THE ORIGINS OF NOVELTY

Considerations of the origins of novelty bring the history of the concept of macroevolution full circle. Paleontologists have established the hierarchical structure of evolutionary change, with convincing evidence for at least some discontinuities between intraspecific, microevolutionary change, and the larger-scale patterns seen in the fossil record. Biologists, in contrast, have often continued to associate the term macroevolution with the origination of large morphological variation rather than sorting among hierarchical levels. The extraordinary recent work in comparative developmental biology has triggered renewed interest in the origination side of macroevolution.

One of the most striking macroevolutionary patterns is the nonrandom origination of evolutionary novelties in time. Even more than other aspects of evolutionary change, successful innovations require ecological opportunity, developmental possibility, and an appropriate environmental setting, and changes in these factors evidently limit further innovation. Microevolution provides no satisfactory explanation for the extraordinary burst of novelty during the late Neoproterozoic-Cambrian radiation (Valentine et al. 1999; Knoll and Carroll 1999), nor the rapid production of novel plant architectures associated with the origin of land plants during the Devonian (Kendrick and Crane 1997), followed by the origination of most major insect groups (Labandeira and Sepkoski 1993). Each burst was followed by relative quiescence,

as the pace of morphological innovation fell (Erwin et al. 1987; Eble 1999).

Non-random appearance of major groups continues at lower taxonomic levels as well. Eighteen of 25 durably skeletonized post-Paleozoic marine orders first appear in near-shore environments, yet the first appearance of genera and families displays no such environmental bias (Jablonski and Bottjer 1990; but see Jacobs and Lindberg 1998). Whether this represents differential origination in nearshore regions or differential success with originations occurring over a broader spectrum of environments remains unclear.

In the case of the Cambrian radiation, perhaps the paradigmatic macroevolutionary event, the rapid morphological transitions have raised the question of how the developmental aspects differed from evolution during other intervals. Such innovation does not appear to reflect the acquisition of new regulatory pathways, for much of the regulatory machinery is shared between higher metazoans (e.g., Erwin 1999; de Rosa et al. 1999; Valentine et al. 1999; Knoll and Carroll 1999). Repatterning and redeployment of this pre-existing developmental potential within a novel ecological milieu, possibly aided by changes in the physical environment, was largely responsible for this episode, but what sort of developmental changes could have been involved?

Repatterning of regulatory cascades has long appeared to be the most satisfactory explanation. Akam (1998) suggested a revised selector gene model involving an expansion of the number of enhancers to provide the required differential gene expression in different settings within protostomes, and perhaps lower deuterostomes. The extensive whole-genome duplication within basal vertebrates evidently provided them with a different path to morphological complexity (Akam 1998; Valentine personal communication). Whether such changes constitute macroevolution has been the subject of dispute. For example, Purugganan (1998) has argued that such changes are microevolutionary, while Gellon and McGinnis (1998) proposed an explicitly hierarchical model of evolution of Hox elements. Duboule and Wilkins (1998) essentially split the difference, arguing that the recruitment of genes for new functions has progressively altered patterns of morphological change, from gradual to more discontinuous. Such developmental constraints are notoriously easy to invoke, and difficult to demonstrate (Raff 1996), however, and recent work on Cambrian trilobites has overturned the paradigmatic example of developmental entrenchment associated with the Metazoan radiation (Hughes et al. 1999).

More generally, several roles for developmental macroevolution are possible. The recent discovery that mutations or high temperatures within heat shock protein 90 (Hsp90) release previously masked genetic variation suggests a relationship between environmental stress and the exposure of greater variation to selection (Rutherford and Lindquist

1998). Hsp90 evidently normally prevents the phenotypic expression of this variation but when the action of this molecular chaperone is inhibited the variation is expressed and rapidly becomes fixed. As noted by Rutherford and Lindquist and other commentators (Wagner et al. 1999; McLaren 1999), this suggests a system for modulated evolvability.

The difficulty is relatively clear. We have learned enough about developmental evolution to propose a broad spectrum of hypotheses, but lack sufficient knowledge of the processes to evaluate their generality. The available evidence is sufficiently tantalizing to warrant continued study. Perhaps the greatest difficulty is that claims for the macroevolutionary potential of various modes of developmental innovations lack a metric. How different is different? Further, so little is known about the population genetic aspects of developmental changes that many models may appear plausible. The possibility, even the likelihood, that there have been long-term changes in the nature of the process (Erwin 1999; Duboule and Wilkins 1998) further complicates the issue.

CONCLUSION

Is macroevolution more than repeated rounds of microevolution? Macroevolution encompasses a variety of patterns and processes involving species and larger clades. Some of these patterns can plausibly be described as the result of microevolutionary processes extended across the great expanses of time and space provided by the fossil record. Sepkoski's competition-driven models of clade replacement are an example of such processes. But discontinuities have been documented at a variety of scales, from the punctuated nature of much speciation, to patterns of community overturn, the sorting of species within clades by differential speciation and extinction, and finally mass extinctions. These discontinuities impart a hierarchical structure to evolution, a structure which impedes, obstructs, and even neutralizes the effects of microevolution. As is so often the case in evolution, the interesting question is not, is macroevolution distinct from microevolution, but the relative frequency and impact of processes at the various levels of this hierarchy.

Much of this discussion has focused on pattern, rather than process. Yet the greatest opportunities for progress in macroevolution may come from comparative developmental biology (Gilbert et al. 1996). Here the questions range from whether developmental involvement in speciation is distinct from adaptive intraspecific evolutionary change, to the relationship between major morphological shifts and evolution of developmental control genes. The exploding comparative data on developmental evolution promise surprising insights into the basis for macroevolutionary patterns.

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