

Macroevolution

Topic N

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INTRODUCTION

Macroevolution can be defined simply as evolution above the species level. Its subject matter includes the origins and fates of such major novelties as seeds, tetrapod limbs, and insect wings, the waxing and waning of multispecies lineages over long time scales, and the impact of continental drift and other physical processes on the evolutionary process. With its unique time perspective, paleontology has a central role to play in this area: the fossil record provides a direct, empirical window onto large-scale evolutionary patterns and, thus, is invaluable both as a document of macroevolutionary phenomena, and as a natural laboratory for the framing and testing of macroevolutionary hypotheses. This is a vibrant field (if underpopulated relative to the wealth of material and questions within its domain), with a steady stream of papers, books, and symposia and an increasing interaction with a broad range of disciplines from astrophysics to developmental biology. The result has been a number of insights into the processes that have shaped the major evolutionary patterns of present-day and ancient organisms.

ORIGINS

One striking macroevolutionary pattern that has emerged from the fossil record is that major groups and evolutionary novelties have not originated randomly in time and space. The Cambrian explosion at the beginning of the Paleozoic Era resulted in the first appearance of virtually all of the major body plans seen in present-day oceans, along with a number of extinct, enigmatic groups, a remarkable evolutionary burst reflected in the sudden appearance in the fossil record of all but one of the living marine phyla and many of the marine classes. Equally intriguing is the realization that both morphological divergence and the production of higher taxa are less prolific after this Early Paleozoic pulse, although similar evolutionary pulses have also been documented in vascular plants with the invasion of land and in terrestrial insects soon thereafter. One major question has been the relative importance of development (e.g.

changes in canalization) and ecology (e.g. ecospace availability) in promoting and then damping these evolutionary explosions.

In marine and terrestrial systems alike, secondary bursts of evolutionary novelty appear to be concentrated in the wake of mass extinctions, when taxonomic and morphologic divergence is again accentuated (although not so dramatically as in the Early Paleozoic). The timing of these originations lends support to a macroevolutionary hypothesis of incumbency – that early occupants of a resource or habitat can dominate until extinction or other perturbation clears the way for other groups. Still unclear is whether such mechanisms can explain spatial patterns in the origin of novelties, such as the preferential onshore origination of higher taxa in Paleozoic and post-Paleozoic marine invertebrates (and some possible analogs in Paleozoic and post-Paleozoic terrestrial plants) and the preferential tropical origins of many marine invertebrate orders and some terrestrial plant groups.

The mechanisms underlying the origins of novelties remain poorly understood. Interactions with two biological fields have been especially valuable in exploring this macroevolutionary problem and are sure to accelerate in the future. Phylogenetic analysis, including molecular techniques, can provide a genealogical context for the production of novel features, providing essential data on the morphology, ecology and other aspects of probable ancestors or less-derived outgroups; in exchange, paleontology provides data on the age, distribution, and characters of extinct taxa that can significantly change the interpretation of character-state polarities and the sequence of evolutionary transitions. Developmental biology can provide insights at several levels. Developmental patterns at the organismic level, for example, can help to explain how relatively small changes in the timing of development, or heterochrony, can have dramatic morphological results. At the molecular level, knowledge of the operation and phylogenetic distribution of regulatory-gene systems can elucidate how those genetic control systems, some of them extremely ancient, were altered or commandeered to generate novel morphologies. Selected references include Bengtson, 1994; Benton, 1987, 1996; DiMichele & Aronson, 1992; Donoghue *et al.*, 1989; Erwin *et al.*, 1987, 1997; Foote, 1996; Jablonski, 1993; Jablonski & Bottjer, 1990a,b,c; Knoll *et al.*, 1984; Lipps and Signor, 1992; McKinney & McNamara, 1991; McNamara, 1995; Padian *et al.*, 1994; Smith, 1994; and Wagner, 1995a.

DYNAMICS

Much macroevolutionary research was triggered by the realization that many species appeared to be almost static morphologically after their first appearance in the fossil

record rather than evolving continuously. This led to the hypothesis of punctuated equilibrium, which holds that most evolutionary change accrues at the branchpoints of species' histories rather than over the duration of established species. The fossil record does indeed exhibit many examples of stasis but contains not only instances of punctuated equilibria but also punctuated anagenesis (evolutionary histories consisting of stasis and rapid change without branching), gradual anagenesis (constant, directional evolution without branching) and even the gradualistic splitting of lineages that characterized evolution in classical textbooks. Still unclear is whether these different evolutionary tempos and modes are distributed unevenly among taxa, habitats, regions, or ecological categories. Such questions of frequency can be addressed only when rigorous protocols are developed for the study of speciation in the fossil record. Such a protocol has not been formalized, but minimum requirements include multivariate statistical treatment, careful analysis of evolutionary relationships, and – least frequently achieved to date – geographic control on within-species variation.

These observations have prompted an approach to some macroevolutionary patterns, such as trends in the morphology or species-richness within lineages that allowed the operation of evolutionary processes simultaneously at several hierarchical levels. Thus, directional changes or shifts in the number of species contained within subclades of larger groups might be attributed to sorting among units at several different levels, from the familiar one of bodies within populations to species or higher taxa within clades. Factors that accelerate speciation rates within one segment of a clade, for example, might shape the long-term development of that clade as a whole. Differences in speciation or extinction rates have long been recognized among and within higher taxa (e.g. lycopsid *v.* pteridosperm plants, ammonites *v.* bivalves, passerine birds *v.* shorebirds), and may involve not only traits intrinsic to particular organisms, but to physical and biotic context (e.g., Ordovician bivalves *v.* Eocene bivalves). Much more work is needed on the biotic factors that might confer these rate differentials. Furthermore, separating species selection in the strict sense from the waxing or waning of groups, as a byproduct of processes at the individual level, has proven to be difficult in most instances. More generally, empirical research and quantitative theory have lagged far behind the qualitative theoretical arguments in this area.

As in the origin of novelties, phylogenetic information can be extremely valuable in analyzing macroevolutionary dynamics: many macroevolutionary hypotheses can be stated in terms of predictions about phylogeny, for example, on the repeated association of specific characters with changes in evolutionary rate or the topology of

an evolutionary tree or regarding the variation in branch lengths in different regions of an evolutionary tree. Phylogenetic methods that take into account both the strengths and weaknesses of paleontological data are being developed and debated; this interaction with systematic biology will continue to be important, not only for paleobiological research but as a basis for testing hypotheses about molecular evolution, including constancy or variation in rates among groups and through time (which can be assessed directly for groups with accurate phylogenies and a rich fossil record).

As noted above, the relative roles of physical and biotic factors in shaping macroevolutionary patterns also remain hotly debated and surely vary among taxa, times, and places. On the biotic side, rate differentials among higher taxa imply a role for such inherent biological factors as genetic population structure or intrinsic growth rates; the Mesozoic marine revolution and other apparent escalations in predation intensity and in the defenses of potential prey suggest that diffuse interactions among many disparate taxa can have long-term consequences; and the effects of incumbency discussed above argue for at least a preemptive mode of competitive interaction over macroevolutionary timescales. On the physical side, changes in climate, geography, and perhaps atmospheric or ocean chemistry have proven to have overriding effects in some cases, and many of the biotic replacements once thought to reflect competitive interactions now appear to have been mediated by mass extinction (e.g., the replacement of dinosaurs by mammals at the end of the Mesozoic Era). Still problematic is the issue of spatial and temporal scale. The theoretical expectations from ecological theories of competition and predator-prey interactions are difficult to extrapolate meaningfully to macroevolutionary scales, so that new expectations tuned to the dynamics of clades over millions of years need to be developed.

The role of extinction, particularly mass extinction events, has been a major area of research. Whether extinction peaks merely accelerate processes set in motion during times of less intense turnover or play a more special role in the evolutionary process is an area of active research, and the role of extinction events may vary with their magnitude and timing. Some have argued that mass extinctions appear to break the dominance of incumbent groups and open opportunities for diversification and evolutionary novelties, which may help to explain how such events can have such dramatic evolutionary effects despite accounting for only a small proportion of the total extinction that has occurred over the past half-billion years. More work is needed on selectivity during mass extinctions, particularly comparative approaches among extinction events of different intensities. Such studies can also be important for understanding and quite possibly in predicting extinction and recovery patterns in the

present-day biota as human-caused environmental perturbations increase in extent and severity.

The history of multicellular life has been characterized by stable, if weakly bounded, ecological-evolutionary associations at several scales, from communities and community types to the three evolutionary faunas of Phanerozoic oceans. The marine evolutionary faunas have intriguing parallels on land, in the four evolutionary floras among vascular plants and the three evolutionary faunas among tetrapod vertebrates. In each instance, the major faunas and floras appear to have their own characteristic dominant taxa, levels of diversity (increasing in stepwise fashion), and, at least in the marine faunas, characteristic rates of origination and extinction for those dominant taxa (decreasing in turn among the evolutionary faunas – which may help to explain the coincident long-term evolutionary behaviors of their constituent taxa). Still uncertain is exactly what maintains the apparent environmental separation among marine faunas for much of the Phanerozoic, whether similar environmental (or latitudinal) separation occurs in the terrestrial equivalents, and the extent of mixing and dilution among the faunas or floras over their histories. The problem of biotic interaction and ecological scale emerges again when considering the characteristic diversity levels: why should marine diversity at the family level, for example, hold steady for most of the Paleozoic despite extensive turnover (one possible implication is the attainment of a global equilibrium, reset or perhaps never even reached in post-Paleozoic times), and to what extent are the successive higher characteristic diversity levels attributable to physical versus biological controls? The diversity dynamics can be modeled mathematically, but research continues on exactly how to scale the concepts of population interaction up to large-scale patterns in the fossil record. Few deny that permanent and profound changes in ecological structure have occurred in the history of life, as in the Cambrian explosion, the origin of the post-Carboniferous landscape, or the Mesozoic Marine Revolution mentioned above, but the roles such events might have played in resetting the large-scale diversity dynamics of global or regional ecosystems are still being explored.

Selected references include Clyde & Fisher, 1997; Erwin & Anstey, 1995; Gould & Eldredge, 1993; Grantham, 1995; Hitchin & Benton, 1997; Jablonski, 1986, 1995; Jablonski & Sepkoski, 1996; McShea, 1994; Michaux, 1989; Norrell & Novacek, 1992; Patzkowsky, 1995; Sepkoski, 1992, 1996, in press; Valentine, 1990; Vermeij, 1987, 1994; Wagner, 1996.

METHODOLOGIES

Macroevolutionary study has benefited from a steady infusion of quantitative methods from many other fields, from bootstrapping and time-series statistics to the scaling up of survivorship and rarefaction analysis, as well as the generation of novel approaches to morphometrics, phylogenetics and sampling theory. These quantitative tools will greatly expand the scope and depth of macroevolutionary questions addressed in the fossil record, as will the growing array of computerized databases – which as noted above should begin to incorporate a broader spectrum of information, such as localities and environments (see report on databases in paleontology, Topic S).

Mathematical models have also been used to good effect. The most extensively explored methods to date have been models of taxonomic diversification, in which the dynamics of clades or entire faunas are modeled with simple equations to explore the effects of variations in extinction, origination, and the strengths of interaction among and within groups. New work on morphological diversification and its relative concordance or discordance with taxonomic patterns shows much promise. Models of individual body forms, such as Raup's classic work on molluscan shells, have enjoyed less attention lately, but the ability to generate a theoretical morphospace based on a few generative parameters, and then to explore the occupation of that morphospace by living and fossil organisms, remains a macroevolutionary avenue with great potential. In all of these modeling approaches, the aim has not been simply to reduce complex macroevolutionary patterns to a few simple explanatory equations but to improve understanding of how specific changes in each variable in turn would shape macroevolutionary phenomena, and to develop a baseline of expectations for random behaviors against which the patterns of the fossil record can be compared (such as long-term trends in morphology or taxonomic diversity).

The ultimate source of virtually all these data are the rocks and sediments of the fossil record, and the quantitative assessment of potential biases represents an important, expanding area for macroevolution. Taphonomic studies, from actualistic assessment of the fidelity of local assemblages to the quantification of the megabiases of available outcrop area and stratigraphic gap analysis, have begun to provide taxon-, environment- and time-specific assessments of the nature of paleontological data – and for the most part, the news is good on the reliability of paleontological data. Methods for placing statistical confidence limits on such variables as stratigraphic ranges, taxon durations, diversity levels, and extinction intensities are all being developed or refined, although the multitude of sampling situations presented by the stratigraphic record requires much further work before general methods are fully avail-

able. Even now, these approaches allow the investigator to steer a more rigorous course between the defeatist view, that the fossil record is too incomplete and biased to yield robust conclusions, and the literalist one, that the fossil record should be taken strictly at face value whatever its theoretical shortcomings or biases.

Selected references include Benton & Hitchin, 1996; Donovan & Paul, in press; Foote, 1996a,b; Gilinsky & Signor, 1991; Kidwell & Flessa, 1995; Marshall, 1997; Wagner, 1995b.

PROSPECTS AND NEEDS

Macroevolution is an interdisciplinary field, and so one important goal is to strengthen interchange with other branches of paleontology – systematics, biostratigraphy and paleoecology, for example can be crucial to developing rigorous data sets for macroevolutionary study. Interactions with other areas of geology, such as stratigraphy and biogeochemistry are also important, providing a temporal framework and invaluable information on the environmental context – and perhaps even the forcing factors – of macroevolutionary patterns. At the same time, biotic patterns provide an independent data set, distinct from that of geochemistry and other physical proxies, on environmental and climatic change through time. The geological implications of the directional biotic changes mentioned above are still being explored and may have direct application in resource exploration. For example, 90 percent of Oman's petroleum is Precambrian in age and thus is derived from rocks representing radically different ecosystems from those in younger seas. Understanding spatial organization and patterns of evolutionary change in such ancient biotic systems should contribute to more efficient exploration for natural resources.

Electronic databases will play an important role in macroevolutionary studies, but targets should expand beyond the synoptic taxonomic databases that have dominated the field, to include morphological, ecological, phylogenetic and biogeographic information; collecting and standardizing such data will be a major challenge in many instances. The *Treatise on Invertebrate Paleontology* has represented an extraordinarily fertile, international effort at synthesizing the taxonomic, stratigraphic and geographic knowledge of important constituents of the fossil record, and an electronic version of this resource would be a major contribution to the discipline. (Among the most extensive electronic databases presently available are The Fossil Record 2, which may be seen electronically at <http://palaeo.gly.bris.ac.uk/frwhole/fr2.html>, and The Plant Fossil Record Database at <http://ibs.uel.ac.uk/ibs/palaeo/pfr2/prf/htm>.)

Interchange with the biological sciences is probably at an all-time high; this has been beneficial in both directions and should be encouraged. Phylogenetics and developmental biology have already been mentioned as rewarding avenues of interaction. The potential for interaction with ecology is great, but much care is needed to consider the strengths and limitations of the fossil record in terms of temporal and spatial scale. Ecologists and microevolutionists are beginning to appreciate the importance of events over larger time scales than the decades to centuries that are their usual bounds, and a new effort is needed from both neontological and paleontological sides to get beyond a simple extrapolation of ecological phenomena into macroevolutionary time scales.

Macroevolutionary data have more direct implications for present-day environmental issues. The fossil record provides a rich array of natural experiments that can be used to understand and, perhaps, to predict how biological systems behave when, for example, large numbers of taxa are lost regionally or worldwide; regions undergo pulses of biotic interchange; environmental parameters fluctuate significantly, as in global warming or changes in ocean circulation; and recoveries unfold following deep losses in biodiversity. Macroevolution has much to offer conservation biology methodologically, for example, regarding techniques for estimating diversity patterns from incomplete data.

Besides an ongoing, healthy exchange with cognate fields in geology and biology, more integration is needed within macroevolution itself. Taxonomic and phylogenetic approaches and morphological approaches need to be more fully linked, although this is beginning. Each approach has its strengths and may be better suited to a particular set of macroevolutionary problems, but neither is closer to the evolutionary process, because understanding evolutionary process at any hierarchical level requires knowledge of genealogy and the sorting dynamics, on the one hand, and of the phenotypes that interact with the physical and biotic environment on the other. Cross-comparisons among different approaches to reconstructing evolutionary history, for example, morphology- or molecule-based phylogenies *v.* stratigraphic distributions, will be also continue to grow in importance and should help to produce a more rigorous approach to historical analysis in which methods are fitted to the strengths and weaknesses of the system under study. As might be expected in a young science (at least in its present incarnation), empirical analyses have tended to lag behind theory. With a few exceptions, relatively few detailed studies are available for any given problem; this is at least partly a function of the labor-intensive nature of macroevolutionary research, which necessarily must encompass significant periods of time,

numerous taxa, and many characters. As hypotheses are framed in more specific and rigorous terms and as methods become increasingly available for assessing and even factoring out sampling and other biases, this imbalance should be remedied, and a rich balance of data and theory will continue to inform research on large-scale patterns of evolution.

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