VIEWPOINT

The Future of the Fossil Record

David Jablonski

The fossil record provides a powerful basis for analyzing the controlling factors and impact of biological evolution over a wide range of temporal and spatial scales and in the context of an evolving Earth. An increasingly interdisciplinary paleontology has begun to formulate the next generation of questions, drawing on a wealth of new data, and on methodological advances ranging from high-resolution geochronology to simulation of morphological evolution. Key issues related to evolutionary biology include the biotic and physical factors that govern biodiversity dynamics, the developmental and ecological basis for the nonrandom introduction of evolutionary innovations in time and space, rules of biotic response to environmental perturbations, and the dynamic feedbacks between life and the Earth's surface processes. The sensitivity of evolutionary processes to rates, magnitudes, and spatial scales of change in the physical and biotic environment will be important in all these areas.

It is hard to resist the fossil record as a source of spectacular evolutionary triumphs, grotesqueries, and catastrophes. But of course it can be much more than that—a laboratory of evolutionary experiments, sometimes richly replicated, as in regional extinction pulses, and sometimes confoundingly unique, as in the Cambrian explosion of metazoan life 530 million years ago. The next wave of research will build on an array of empirical and methodological advances that, judging by the outcome of several recent workshops on new directions for the coming decades (*1*), will foster a paleontology that is more interdisciplinary than ever.

Paleontology has recently accelerated on several fronts. Combined with advances in allied fields in the earth and life sciences, from high-resolution geochronology to molecular developmental biology, paleontology is beginning to take a renewed approach to a wide array of new and old scientific issues. A battery of new ways to generate and test hypotheses by using the ever-growing breadth, volume, and quality of empirical data is being abetted by the development of synoptic global and regional databases (Fig. 1) and by the influx of techniques for simulation and mathematical modeling. Analyses with methods derived from probability theory, for example, can now directly confront sampling biases once considered crippling (*2*). Among the opportunities opened by these developments, four key, interrelated research questions have emerged at paleontology's intersection with evolutionary biology (*1*).

1) What are the rules that govern biodiversity dynamics, and do they apply at all temporal and spatial scales? The overall trend of plant and animal biodiversity—whether measured in terms of taxa, range of body forms, or modes of life—has been one of net increase through geologic time. However, this general trend has been anything but smooth. Diversification has occurred episodically, has been interrupted by extinction events, and has had (in the oceans anyway) at least one prolonged episode of little net change.

The complex trajectory of taxonomic diversity through time has proven robust to continued sampling (*3*) (Fig. 1) and, as shown by simulations, to very different phylogenetic approaches to grouping species into higher taxa (*4*). But diversity time series become increasingly jagged and disparate at lower taxonomic levels and on regional scales, both because sampling is less complete and because lower-diversity lineages really are almost inevitably more volatile. Just how do diversity dynamics at these finer scales sum to produce the global, family-level pattern? At least some biotic shifts that appear to be protracted when analyzed globally, such as the massive Ordovician diversity increase in the sea and the Mesozoic modernization of marine predators and of prey defenses, are more abrupt but occur at slightly different times when examined regionally (*5*). When diversity dynamics are dissected into constituent clades (that is, monophyletic evolutionary lineages—for example, crabs or their scallop prey), how well can clade-specific turnover rates be predicted by biotic factors such as body size and feeding habits (*6*), and how often do clade dynamics interact to damp or enhance those rates (*7*)? When are "taxon-free" dynamics, based strictly on the acquisition and persistence of morphological traits or the occupation and emptying of regions within morphometrically defined multivariate spaces ("morphospaces"), most concordant or most out of phase with taxonomic trends (*8*)? Paleontologists, now taking advantage of advances in phylogenetic methods, have just begun to explore these questions. The answers will give us a much fuller view of the interplay between the two great themes of evolutionary biology: diversity and adaptation.

2) Why are major evolutionary innovations unevenly distributed in time and space? One of the most striking patterns to emerge from the fossil record is that biological innovations—the breakthroughs that open new ecological opportunities and evolutionary pathways—do not arise randomly. Regardless of exactly when the major lineages actually split, the Cambrian explosion represents a uniquely rich and temporally discrete episode of morphological invention for the metazoan phyla (*9*). Smaller pulses follow mass extinctions, not least being the exuberant Cenozoic radiation of mammals, after 100 million years of fairly monotonous morphologies in the shadow of the dinosaurs.

Understanding both the onset and the termination of such bursts is a major challenge. Critical tests for the trigger or damper of the Cambrian explosion have been difficult. Potential mechanisms are plentiful and fall roughly into an extrinsic set of ecological or physical triggers and brakes (*10*) and an intrinsic set of thresholds in the increasing complexity and later stabilization of developmental systems. However, without a time machine to perform reciprocal transplant experiments between Cambrian and modern seas, the rival hypotheses so far have resisted falsification; clearly, broadly multidisciplinary work is essential to crack this problem.

The origin of evolutionary novelty, like biodiversity dynamics, appears to have a strong spatial component. For post-Paleozoic marine invertebrates, and for at least some plant and vertebrate groups, major novelties first occur mainly in disturbed habitats—for example, onshore marine settings—and in the tropics. Where phylogenetic relationships are known in detail (and more work here would be especially valuable), these first appearances tend to be primitive species basal to their groups. Yet lower level novelties, such as those defining species and genera, are evidently freer to originate according to the environmental and latitudinal gradients of their individual clades. Here is where Van Valen's maxim that "evolution is the control of development by ecology" (*11*) comes into full play. What is it about certain environments or regions that elicits, or conversely dampens, major evolutionary novelty? Do these factors change through time, and could there be unsuspected patterns in the types of novelties that conform to or break the spatial rules—for

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example, novelties generated in particular ways, such as through changes in developmental timing?

The long-simmering partnership of paleontology and developmental biology is heating up nicely. Rapidly expanding knowledge of the molecular mechanisms underlying the development of complex forms, and the remarkable conservation of developmental pathways among groups, can be combined with the fossil record to provide a multilevel portrait of the sequence of events leading to the origin and elaboration of complex features such as arthropod limbs or the tetrapod skull (*12*).

Such interactions with developmental biology are potentially important on finer evolutionary scales as well. For example, the growing ability to dissect regulatory pathways and their embryogenic expression in extant species should permit a new assessment of the role of developmental buffering mechanisms in the species-level stasis that has proven to be so pervasive in the fossil record (*13*). This pervasiveness in turn demands critical tests of two major alternatives to explain how long-term evolutionary trends arise in a hierarchical system of taxa where the lowest ranks tend to be static: sorting among those taxa by differential origination and extinction (*14*) and biased production of new forms.

3) How does the biosphere respond to environmental perturbations at global and regional scales? Life has been buffeted by asteroid impacts, rapid climate changes, shifts in oceanic and atmospheric chemistry, continent-scale biotic interchanges, and a host of other perturbations. The fossil record provides the basis for a comparative calibration of biotic responses to different types and magnitudes of disturbance. For example, the ability of systems to return to their initial states does not appear to scale exactly with the size of the perturbation: some mass extinctions have more profound effects than others (*15*).

At all scales, diversity dynamics, in the broad sense defined above, are almost certainly shaped by the interplay of physical and biological processes. A major focus will be to test the relative roles of driving mechanisms, using the next generation of models that treat dynamics in terms of underlying components such as speciation and extinction rates across a range of spatial and temporal scales. Such dynamical models can be tested against potential environmental drivers, from sea level to temperature to productivity, by using time series that are increasingly refined as a result of improved geochemical techniques. For example, some of the scenarios for the great end-Permian mass extinction are ruled out by the sheer rapidity of isotopic excursions in the latest Permian (*16*).

The initial state of the system must be a crucial variable for understanding responses to perturbation, but this has been little explored. To take one possibility, do biotic systems respond differently during global greenhouse versus ice-age intervals (for example, because greenhouse sea levels are higher and thus damp temperature variation) or according to the recency of similar perturbations (for example, do taxa or ecosystems fatigue or harden with repeated stresses)? General, predictive rules for the nonlinear response of biological systems to perturbation will be of more than academic interest given the stresses being imposed on today's biosphere by human activities.

One clear message from the fossil record is that, as in American politics, incumbency confers a significant advantage at almost every scale. Perturbations that break such incumbencies play an important role, for good or ill, in removing dominants and opening opportunities for other groups. Although such transitions are usually ascribed to global events, as in the evolutionary exploits of the mammals after the dinosaurs' demise, some evidence suggests that local or regional perturbations may facilitate major biotic changes as manifest at a given locale (*5*). The geographic structure detected in the Ordovician diversification (*5*) and the post-Cretaceous marine rebound (*17*) also attests that the interregional variation of responses to large-scale perturbation will be an important area for evolutionary paleontology.

4) How have biological systems influenced the physical and chemical nature of the Earth's surface and vice versa? In the long and complex path from the anoxic, exclusively microbial Archean sea to the highly heterogeneous modern system, the major biological, sedimentary, and geochemical transitions are roughly coincident in time. Combining the biological record (bodies, behavioral traces, and molecules), with increasingly high-resolution geochemical methods, researchers are beginning to focus on time intervals when significant changes occurred in biological materials and biogeochemical cycling, on how steady states are maintained, and on the roles of biological innovations in perturbing and stabilizing those cycles. Biotic changes probably altered the nature of the fossil record itself, not only through increases in the robustness of skeletal materials and the activities of predators, but also biogeochemically because of burrowers that acidify pore waters by sediment irrigation (*18*). Such secular and broadly fluctuating changes need to be quantified and factored into the next generation of large-scale paleontological analyses.

Some innovations, such as the origin of photosynthesis, land plants, and mineralized skeletons in marine microplankton, undoubtedly drove changes in the physical environment. The Proterozoic origin of complete guts in multicellular animals, for example, may have accelerated carbon deposition to the sea floor by packaging wastes in fecal pellets, which significantly altered nutrient fluxes and ultimately enhanced the buildup of oxygen in the atmosphere and the ocean (*19*). But does the relatively mild geochemical response to most Phanerozoic events, such as the massive carbonate deposition that gave the Cretaceous Period its name, relative to high-amplitude geochemical variations seen in the Proterozoic, reflect an increased ability of organisms to modulate the inorganic world? Comparative studies and modeling should help to answer this question.

Physical perturbations, from tectonics to orbital parameters, clearly impinge on the biota. The challenge, then, is to determine how biological factors damp or amplify external forcing. For example, changes in the density and composition of the terrestrial flora must have changed albedo, rainfall, and chemical weathering over geologic time. As geochemical linkages become better understood, sur-

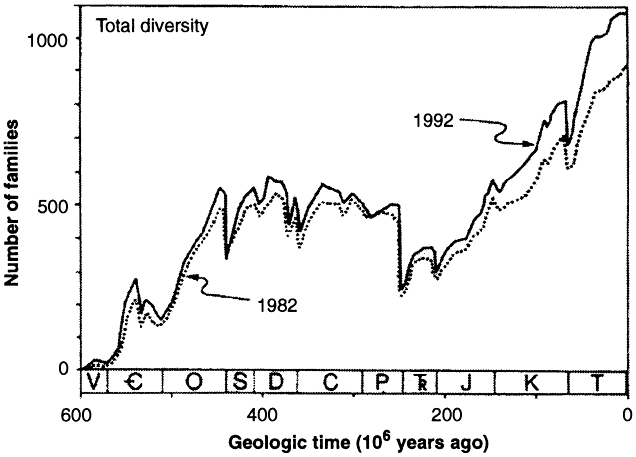

Fig. 1. The fossil record of marine diversity has been robust over the past decade. Our picture of the global history of marine animal diversity did not change significantly after 10 years of additional compilation and synthesis, which substantiated major features such as the Cambrian Explosion, the Big Five mass extinctions, the Paleozoic diversity plateau, and the post-Paleozoic rise to diversity levels well above those of the Paleozoic (*3*). V, Vendian; Ꞓ, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Ʀ, Triassic; J, Jurassic; K, Cretaceous; T, Tertiary.

prising feedbacks are likely to emerge. For example, long-term oscillations in ocean chemistry (for example, the Mg/Ca ratio), driven by changes in spreading rates at midocean ridges, may have favored or undermined skeletal construction of different reef-building organisms through the Phanerozoic (*20*).

Paleontology sits squarely at the interface between the earth and life sciences. The most powerful contributions will emerge from analysis of evolutionary dynamics at different scales and hierarchical levels over deep time and of the diverse ways life has driven, and been driven by, changes in the Earth's atmosphere, oceans, and lithosphere.

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VIEWPOINT

The Evolution of Species Interactions

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Interactions between species are as evolutionarily malleable as the species themselves and have played a central role in the diversification and organization of life. This malleability creates complex geographic mosaics in interspecific interactions that can evolve rapidly over decades, blurring the distinction between evolutionary time and ecological time and making the study of coevolution crucial for human health and welfare.

The history of evolution and biodiversity is fundamentally a history of the evolution of species interactions. Species in pure isolation simply do not make sense. Most living organisms have evolved in ways that absolutely require them to use a combination of their own genetic machinery and that of one or more other species if they are to survive and reproduce. Indeed, most described species take this to an extreme, living symbiotically on other species as parasites, commensals, or mutualists. In turn, most organisms must devote a large share of their resources to defense. Even now, among human populations one-third of deaths are caused by infectious disease. The more we learn about the diversity of life and the structure of genomes, the more it appears that much of the evolution of biodiversity is about the manipulation of other species—to gain resources and, in turn, to avoid being manipulated.

Many of the major events in the diversification of life can be traced back to the appearance of novel species interactions (*1, 2*). The consequences of these events are so pervasive—and, in some cases, the genomes of the species so completely anastomosed—that it is easy to forget how central they have been to life on Earth: mitochondria and the origin of the eukaryotic cell; chloroplasts and the origin of plants; dinoflagellates and the origin of coral reefs; lichens, mycorrhizae, and rhizobia and the process of terrestrial plant succession; gut symbionts and animal digestion. Other interactions between free-living species are equally pervasive. A majority of plants would quickly become extinct without their animal pollinators (*3*). Even in a gene-centered view of evolution, it is the armies of gene packages we call species that wage the genetic wars and create the genetic alliances.

The Coevolutionary Framework

Despite the central importance of species interactions to the diversification of life, we still know little about how the genomes of separate species become intermeshed. The organizing framework for attacking the problem is the theory of coevolution, the process by which species undergo reciprocal evolutionary change through natural selection. Not all interactions are highly coevolved, but the potential for coevolution to drive rapid and far-reaching change is always there. Unlike adaptation to the physical environment, adaptation to another species can produce reciprocal evolutionary responses that either thwart these adaptive changes or, in mutualistic interactions, magnify their effects. We now have convincing examples of coevolution forging obligate mutualisms among free-living species such as yuccas and yucca moths (*4*); creating divergence in traits among competing fish, lizards, mammals, and other taxa [for example, (*5*)]; producing locally matched chemical defenses in plants and counterdefenses in insects (*6*); and maintaining genetic diversity among populations of interacting parasites and hosts (*7, 8*). It is this interactive and iterative process that makes coevolution such a potentially powerful evolutionary process in shaping biodiversity. It may be the most important process organizing the diversity of life.

Nevertheless, understanding precisely how coevolution molds the evolution of species interactions remains one of the most difficult challenges in evolutionary biology, because most species interact with multiple species. It is evident that species can coevolve with more than one other species. Legumes have simultaneously evolved sophisticated coevolutionary relationships with their rhizobia and with their pollinators. Many parasites evolve adaptations to multiple hosts by partitioning their interactions into different life history stages. But specific hypotheses on multispecific coevolution are only now developing, including that of coevolutionary alternation, whereby parasites may alternate among a group of host species over thousands of years, constantly evolving to prefer the host species with the currently lowest level of defense (*9*).

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