



---

The Quality of the Fossil Record: Implications for Evolutionary Analyses

Author(s): Susan M. Kidwell and Steven M. Holland

Source: *Annual Review of Ecology and Systematics*, Vol. 33 (2002), pp. 561-588

Published by: [Annual Reviews](#)

Stable URL: <http://www.jstor.org/stable/3069273>

Accessed: 03-01-2016 18:04 UTC

---

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



*Annual Reviews* is collaborating with JSTOR to digitize, preserve and extend access to *Annual Review of Ecology and Systematics*.

<http://www.jstor.org>

# THE QUALITY OF THE FOSSIL RECORD: Implications for Evolutionary Analyses

---

Susan M. Kidwell

*Department of Geophysical Sciences, University of Chicago, 5734 South Ellis Avenue,  
Chicago, Illinois 60637; email: skidwell@uchicago.edu*

Steven M. Holland

*Department of Geology, University of Georgia, Athens, Georgia 30602-2501;  
email: stratum@gly.uga.edu*

**Key Words** paleobiology, taphonomy, stratigraphy, speciation, extinction, phylogeny

■ **Abstract** Advances in taphonomy and stratigraphy over the past two decades have dramatically improved our understanding of the causes, effects, and remedies of incompleteness in the fossil record for the study of evolution. Taphonomic research has focused on quantifying probabilities of preservation across taxonomic groups, the temporal and spatial resolution of fossil deposits, and secular changes in preservation over the course of the Phanerozoic. Stratigraphic research has elucidated systematic trends in the formation of sedimentary gaps and permanent stratigraphic records, the quantitative consequences of environmental change and variable rock accumulation rates over short and long timescales, and has benefited from greatly improved methods of correlation and absolute age determination. We provide examples of how these advances are transforming paleontologic investigations of the tempo and mode of morphologic change, phylogenetic analysis, and the environmental and temporal analysis of macroevolutionary patterns.

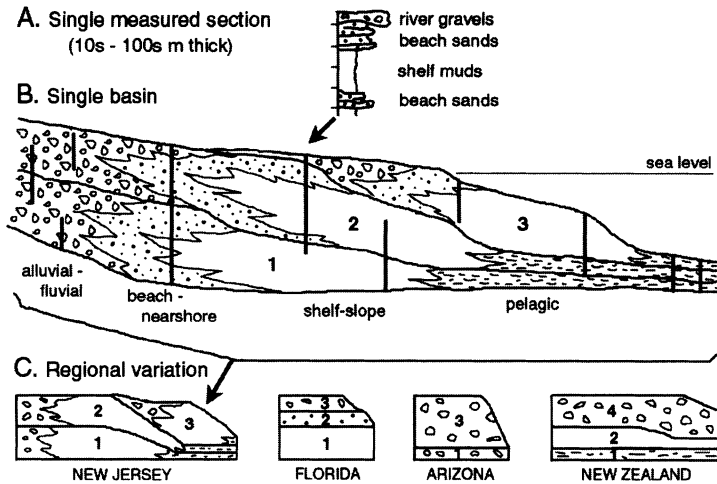
## INTRODUCTION

Ever since Darwin first raised concerns about the completeness of the fossil record as an evolutionary archive, paleontologists have devoted considerable attention to the causes, recognition, and mitigation of gaps in the record (Paul 1982, Donovan & Paul 1998, McKinney 1991, Kidwell & Flessa 1996, Behrensmeyer et al. 2000, Holland 2000). This work has elaborated the many ways in which the record can be an imperfect document of history, including gaps in paleontologic time series from failures in fossil or rock preservation, and distortion of biological trends owing to variable environments and rates of sedimentary accumulation. However imperfect it may be, this record is a unique window into life on earth and provides, at the very least, data on the minimum

possible ages of morphologies and taxa, on taxonomic richness and morphological variety through time, and on the environmental and geographic distribution of life through time. The immense value of such information for evolutionary analysis drives the exploration of the pitfalls of fossil preservation and the development of protocols to maximize the quality and quantity of data retrieved from the record.

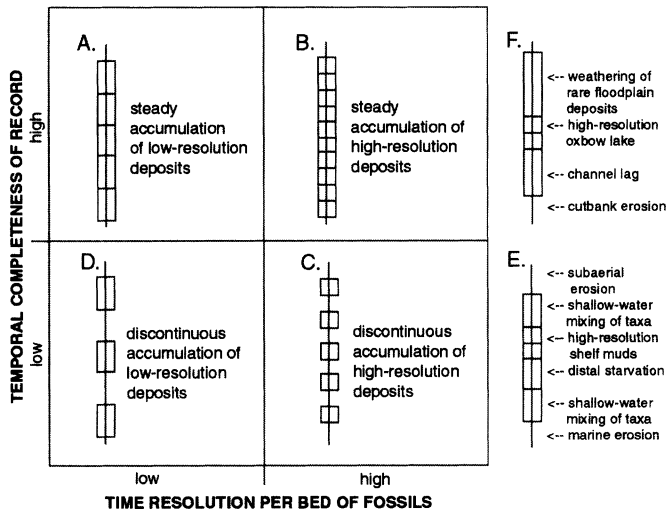
Here we summarize what paleontologists and geologists have learned over the past 20 years about the nature of the stratigraphic record as an archive of biological information, highlight some of the successful strategies that have been developed to deal with incompleteness, and recommend directions for future research (for a comparable treatment of ecological questions, see Kidwell & Flessa 1996). Owing to the breadth of evolutionary questions, paleontologists are concerned with the quality of the record at many scales, from that of populations sampled at a single geological instant, to species-level traits such as geographic extent, evolutionary duration, and interpopulation variation, to clade- and higher-level dynamics that require time series spanning even greater stratigraphic intervals and accurate determination of the relative geologic ages of widely spaced deposits (Figure 1). The natural processes that structure the available record in time and space—the selective postmortem preservation of organic remains (taphonomy) and the selective archiving of the sedimentary deposits that entomb those remains (stratigraphy)—are the subject of this review. These factors are examined at the scale of individual beds (single samples of the finest temporal resolution), stratigraphic sections (time series captured at a single point on earth) (Figure 1A), and geographic regions whose natural boundaries are usually determined by climate and tectonics (Figure 1B,C). Because of our expertise, we emphasize benthic macroinvertebrates whose biomineralized skeletons, together with those of biomineralizing microfossils (foraminiferans, radiolarians, ostracodes, etc.), dominate the marine fossil record. However, many of these issues and solutions devised for them also apply to the fossil record of vertebrates, plants, and soft-bodied organisms.

In general, research into the nature of the fossil record has brought a long-needed shift away from a search for total completeness, which is never achieved, even in neontological sampling. Instead, paleontologists now test for the adequacy of a particular segment of the fossil record, that is, whether data at hand are sufficient to address a specific evolutionary question (Paul 1982). Research has also broadened from a concern with gaps in evolutionary time series—the concept of completeness in Darwin's sense (and see Sadler 1981)—to include additional aspects of data quality (Behrensmeyer et al. 2000, Kowalewski & Bambach 2002). Resolution refers to the level of detail that can be recovered from the fossil record, such as organelle-versus cell-versus tissue-level preservation of anatomy, high versus low degrees of time-averaging (mixing) of successive generations of a species into a single bed, or high versus low resolution on the original spatial distribution of a taxon. Bias refers to the distortion of the underlying biological signal by selective



**Figure 1** Paleontologists are concerned with the quality of the record at many scales. (A) Within a single measured section, that is, the succession of beds visible at a single locale that usually spans only part of a species' full evolutionary duration. The primary concerns are the extent of mixing of generations (time-averaging) within each sedimentary bed that is a few millimeters to a few tens of centimeters thick, the magnitude of time represented by each of the planes that separates beds (stratigraphic gaps) and the potential to mistake a morphological trend that is linked to local environmental change (geographic shifting of a cline) as true evolutionary change. Environments differ in the steadiness of sediment accumulation (frequency of gaps) and in the rate of sedimentation (both affecting time-averaging), and they also differ in their favorableness to the preservation of organic remains. (B) More complete time series are constructed by combining data from many local sections of varying completeness and quality. The *solid lines* running across this cross section separate three temporally distinct depositional units ("sequences"), each comprising a lateral array of depositional environments that have migrated over time first toward and then away from the continent. Each lithologically distinct body within a sequence may be formalized as a stratigraphic formation. Sequence boundaries are recognized by strong offsets in environment and signify larger gaps than those between beds within a sequence. Each of these major gaps diminishes in magnitude seaward. Paleontologic information on the tempo and mode of species evolution and on lineages usually requires compiling data from multiple sequences within a region because species have average durations of ~5 million years (my), and depositional sequences each typically represent ~1–3 my. (C) Paleontologic data from many regional composite time series must be correlated to build global perspectives on biotic change. Regions differ in the completeness of their record and in their dominant environments, owing to differences in their plate-tectonic and climatic histories.

preservation, sediment accumulation, and paleontological collection, including, for example, modification of the relative abundances of morphs because fragile forms have been lost, underestimation of the relative species-richness of clades because of differential preservation potentials of their body plans or of their preferred habitats, or skewing of temporal trends because successive samples could not be collected from comparable habitats or taphonomic conditions. Thus, a collection of fossils from a single bed might contain a high-resolution but highly biased sample of the original morphologic and species composition of the original fauna, and a data set generated by sampling through a series of beds might comprise a fairly complete time series composed of individual high-resolution assemblages but nonetheless might be biased by changes in habitat among successive beds (Figure 2).



**Figure 2** The quality of the fossil record is scale dependent. Fossils extracted from a single bed may constitute a virtual biological census and have a high degree of time resolution (*short blocks in cartoons*) or be time-averaged to some degree, providing a lower time-resolution sample (*long blocks*). The historical time series provided by these segments may be complete, containing fossils from each elapsed increment of time of a particular scale, or may contain significant gaps. End-member combinations of per-bed time resolution and section completeness are illustrated by timelines (A–D) (see text). Real patterns are generally more heterogenous, especially in shallow-marine macrobenthic records (E) (timeline to complement Figure 1A) and continental vertebrate records (F), owing to lateral shifts in environments over time. Compositing paleontologic data from multiple sections and sedimentary basins attempts to compensate for this variability within single sections.

## GEOLOGIC CONTROLS ON THE QUALITY OF THE FOSSIL RECORD

Time-series data vary in completeness, temporal resolution, and compositional bias as a function of depositional environment and geologic history and as a function of the taxonomic group being targeted. These stratigraphic and taphonomic factors are key to acquiring high-quality paleontologic time series at any scale, that is, in acquiring data that are of comparable quality (isotaphonomic samples; see Behrensmeier & Hook 1992).

### Taphonomy: The Fossilization of Biological Remains

Much taphonomic research has been concerned with the rates and variability of postmortem processes, and the challenge now is to move from a phenomenology of the modification and accumulation of organic remains to quantitative models of bias in paleobiological data (for reviews see Behrensmeier et al. 2000, Briggs & Crowther 2001). Four themes of this research are essential components of any quantitative model of preservation and are directly relevant to evolutionary analysis using the fossil record.

**PROBABILITY OF PRESERVATION** Taxa do not have equal probabilities of preservation, with the most obvious demonstration being the poor fossil record of most organisms that lack mineralized skeletons. Preservation of entirely soft-bodied organisms requires unusual environmental conditions that are geologically rare, such as anoxia or catastrophic burial with rapid mineral replacement by specialist microbial communities (Briggs & Crowther 2001). When it occurs, such preservation provides valuable windows into the anatomy and habitats of these groups and can be important simply by virtue of being the earliest record of taxa and morphologic characters. However, stratigraphic horizons with comparable preservation are generally so widely spaced or environment specific that evolutionary time series for these groups are highly incomplete. Similarly, DNA is rarely, if ever, preserved in rocks older than 100,000 years (Bada et al. 1999, Cooper & Poinar 2000), despite a number of early claims.

In contrast, biomineralizing taxa are comparatively well represented and are consequently the focus of most evolutionary analyses by marine paleontologists. For example, ~50% of scleractinian coral, ~75% of echinoid, and ~90% of shelled mollusk species found alive today are represented by dead skeletal material in locally accumulating sediments (reviewed by Kidwell & Flessa 1996). Postdepositional processes can reduce the percentage of taxa preserved; for example, only ~80% of modern shelled mollusk species in the Californian province are preserved in the local Pleistocene record (Valentine 1989). However, at higher taxonomic levels and larger geographic scales, recovery is improved. For example, 100% of Californian molluscan genera have a local fossil record (Valentine 1989),

and from a single intertidal zone, Schopf (1978) found that 75% of lightly mineralized and 100% of well-mineralized genera have a known fossil record somewhere in the world.

Within major biomineralizing groups, taxa lost in the fossilization process are often predictable from body size (small-bodied forms are most susceptible to loss), tissue microstructure (hardparts constructed of aragonite, rather than calcite, or of high organic content, rather than low organic content), population size, and other factors intrinsic to each taxon (Kidwell & Flessa 1996). These basic patterns determine the taxa that are best suited for testing a given evolutionary question. Alternatively, if the study is targeted to a particular taxonomic group, then these same guidelines can be used to identify a "taphonomic control taxon" to determine when absences of the target are biologically, rather than taphonomically, determined (Jablonski et al. 1997). Cyclostome bryozoans, for example, have been used as control taxa for the early evolution of cheilostome bryozoans. The control taxon has similar ecological requirements to the target and a preservation potential that is comparable or less. Thus, if the control taxon is present in a deposit, then the target taxon would be expected to have been preserved and collected if it actually co-occurred in that unit.

**TIME RESOLUTION WITHIN SINGLE BEDS** Because sediment accumulation at the scale of beds is highly episodic in most environments (timed with storms and floods, for example, rather than occurring steadily), net rates of stratigraphic accumulation are commonly slow relative to the life span of individual organisms. Consequently, the skeletal remains of multiple generations typically become mixed within a single bed. This time-averaging of local but noncontemporaneous remains is pervasive in the fossil record: It explains why fossilized individuals are rarely found in their original life orientations, but instead are rotated and disarticulated (Walker & Bambach 1971). When conditions of slow net sediment accumulation are so prolonged that they encompass a period of environmental change, then remains from more than one habitat can become mixed into a single bed, leading to faunal or environmental condensation (Fürsich 1978, Kidwell & Bosence 1991). Thus, a sample from a time-averaged fossil assemblage is not expected to be comparable to a modern biological census; instead, it is a selective summation of individuals that were alive at some point during an extended period of time.

The absolute duration of time-averaging in fossil assemblages can be inferred from Recent sediments in which the organic remains of several different groups have been dated using radiocarbon decay and amino-acid racemization. These studies indicate that in many nearshore marine environments, presently accumulating sediments include mollusk and foraminiferan shells up to several hundreds or a few thousands of years old (Flessa & Kowalewski 1994, Meldahl et al. 1997, Martin et al. 1996, Kidwell & Best 2001). Shell ages range up to 20,000 or 30,000 years in the thin shelly sands that cover continental shelves and record the entire postglacial rise in sea level (Flessa & Kowalewski 1994, Flessa 1998, Anderson et al. 1997).



Areas of more rapid sediment accumulation, such as lagoons, bays, deltas, and lakes, permit less time averaging per bed and approach decadal time resolution for mollusks and pollen over significant periods of time (e.g., Brewster-Wingard et al. 2001, Webb 1993). To achieve a finer, e.g., annual or seasonal level of time resolution within time series, the paleontologist must focus on those cases where deposition was either continuous, such as deep-sea sediments composed of planktonic debris, or frequent, such as varved lake sediments (e.g., Bell et al. 1987), but permanent in either case. Due to episodic sedimentation, high-resolution assemblages also occur scattered within intervals dominated by lower resolution assemblages.

Paleontologists are thus able to generate time series with annual or decadal time resolution in only a few settings, but even in relatively strongly time-averaged records (hundreds or thousands of years per sampled bed), the level of temporal resolution is often many orders of magnitude finer than the average duration of species and high-resolution samples will be present (Jablonski 2000). Moreover, decadal and centennial time averaging is not necessarily disadvantageous to biological analysis because time averaging can smooth the noise of seasonal and annual fluctuations in populations (Peterson 1977). One encouraging result from recent research is the growing evidence that although time-averaged assemblages contain old specimens, they are numerically dominated by taphonomically young shells, that is, by individuals that died during the final phases of time averaging (Meldahl et al. 1997, Olszewski 1999, Kidwell 2002). Such samples should thus have an effective time resolution that is much finer than the full duration of time averaging.

**SPATIAL RESOLUTION** Because population patches—even those of sessile colonies—commonly migrate or shift over time, time averaging generally also entails a certain amount of spatial averaging (Behrensmeyer & Chapman 1993, Miller & Cummins 1990). Spatial mixing from postmortem transport, in which species are preserved in sediments outside their life habitat, does not appear to be a significant bias for many taxonomic groups, including marine macrobenthos, benthic foraminifera, and land mammals not living near major rivers (Behrensmeyer & Dechant Boaz 1980, Kidwell & Flessa 1996, Anderson et al. 1997). Where out-of-habitat transport is significant, it is increasingly well understood (Jackson & Cheetham 1994, Davis 2000) and can even be advantageous from the perspective of gathering spatially coarse occurrence data, such as confirming the regional presence of a taxon. Postmortem transport of a taxon to areas outside its original biogeographic range appears to be negligible in all but a very few predictable groups, such as shelled cephalopods, which occasionally drift for vast distances. Species assemblages atypical of modern conditions are thus more likely to arise from individualistic behaviors of species during life (e.g., Webb 1993, Graham 1993) or from time averaging of individuals from provinces whose boundaries have shifted over time (e.g., Roy et al. 1996).

**SECULAR CHANGES IN PRESERVATION** The quality of the fossil record as a biological archive has almost certainly changed over the course of earth's history for many



reasons (Allison & Briggs 1993a, Kidwell & Brenchley 1994, Kowalewski 1996, Taylor & Allison 1999, Behrensmeier et al. 2000, Behrensmeier 1999). For example, plate tectonics has shifted many continents—particularly North America and Europe, whose fossils dominate the described fossil record—from tropical to non-tropical positions over the Phanerozoic (past ~550 million years). Over the same time, Earth has undergone multiple cycles of greenhouse and icehouse conditions as well as possible changes in seawater chemistry that affect the postmortem solubility of calcium carbonate and other key biominerals. In addition, the acquisition via natural selection of different biominerals, skeletal microstructures, environmental preferences, and life habits by clades affects their preservation potential, as does the evolutionary appearance and expansion of organisms that modify or destroy the remains of other taxa (e.g., shell and bone-crushing predators, scavengers, and burrowing and boring organisms).

Thus arguably, one cannot assume that “typical” samples of the fossil record from one geologic age are taphonomically comparable to those from another, nor can one assume that a major clade has a constant preservation potential over its entire evolutionary duration. However, such bias will impinge mainly on attempts to compare patterns over very large stretches of geologic time (e.g., Paleozoic versus post-Paleozoic).

## Stratal Architecture: The Accumulation of Fossil-Bearing Strata

The past two decades have seen an intense effort by stratigraphers to characterize and understand the architecture of the sedimentary record, including both (a) the origins of individual beds and sets of beds, each representing time intervals of minutes to tens of thousands of years, and (b) their organization into larger packages of strata, with the largest representing a few million, tens of millions, or hundreds of millions of years (third-, second-, and first-order depositional sequences, respectively) (Figure 1B). Much of this stratigraphic work is directly relevant to the quality of evolutionary data, in that stratal architecture determines the duration, timing, and geographic extent of gaps in the sedimentary record as well as the shifting over time of habitats suitable for life or for fossil preservation (Brett 1995, Holland 1995). Six themes of this research are particularly relevant to understanding the quality of the fossil record for evolutionary analysis.

**NATURE AND DISTRIBUTION OF SEDIMENTARY GAPS** Gaps in the stratigraphic record are produced by local episodes of non-deposition, which can be caused by the failure of sediment supply, the bypassing of sediment to other areas, or the net erosion of previously deposited sediment. These gaps are signified by the planar to irregular surfaces that separate one bed from the next, as observed in outcrops. The durations recorded by these individual bedding planes and discontinuity surfaces can be estimated in various ways, and range from a few minutes (e.g., the pause between one avalanche of sediment down a migrating dune face to the next)

up to hundreds of millions of years (e.g., the erosion surface created by tectonic uplift of a formerly largely submerged continental block; Sadler 1981, McKinney 1986, Anders et al. 1987). During these episodes, organisms may continue to produce skeletal and other organic remains (aquatic organisms if the area remains submerged, terrestrial organisms if it is exposed as land). However, these remains are especially prone to destruction through breakage, abrasion, boring, and dissolution because permanent burial is delayed, and erosional exhumation itself can also be a process of selective hardpart destruction. Thus, depending on their duration and the environment in which they form, individual gaps in the sedimentary record can be signified by discontinuity surfaces overlain by no skeletal hardparts, by an abundance of time-averaged hardparts, or by a thin lag of highly damaged hardparts, which will be preferentially biased toward the most physically robust, chemically resistant, ecologically abundant, and stratigraphically youngest forms (Kidwell 1991, 1993; Brett 1995; Rogers & Kidwell 2000). The time resolution and inherent bias of individual fossil assemblages in a stratigraphic section therefore depends on the context of their occurrence: Those that are physically associated with discontinuity surfaces must be approached with caution and are generally best suited for coarse-scale analyses (e.g., presence of a taxon within a geologic period and region).

Some environments are more prone to producing sedimentary gaps than others. Land is primarily an area of erosion and weathering, lakes and shallow-marine environments are primarily sites of sediment accumulation, and the deep-sea is starved of most sediment input other than the deposition of airborne dust, suspended clay, and pelagic organisms. Continental records thus commonly contain many discontinuity surfaces of long duration, so paleontologists commonly target the particular regions (e.g., areas undergoing sustained tectonic subsidence, such as foreland basins) and environments (e.g., lacustrine deltas, alluvial plains, wetlands) that favor more continuous sediment accumulation and postmortem conditions favorable to fossil preservation (Figure 2*D,F*). Lakes provide exceptionally continuous high time-resolution archives within the generally poor continental record (Figure 2*A* or *B*) but tend to be spatially limited and geologically short lived, persisting for a few thousand or tens of thousands of years at most (the Eocene Green River lake system of Wyoming is one of the most famous exceptions). Deposition is also relatively continuous but localized and short lived in estuaries and bays (Figure 2*A* or *C*). Shallow marine shelf and slope (hemipelagic) settings accumulate the bulk of land-derived sediment and in the tropics can be areas of major biogenic carbonate accumulation including reefs. These environments are both widespread and relatively long lived geologically, but deposition is highly variable and episodic on timescales ranging from seasons to millions of years (cycles of sea-level rise and fall), thus generating local sections of heterogeneous quality (Figure 2*A,B,E*). In many instances, this variability is still rapid, indeed, cyclic, relative to the duration of species, and thus has fewer consequences for some evolutionary analyses than for others. Finally, deep-sea records receive slight but highly continuous sediment input. Thus, they typically have few large gaps but can suffer from considerable time averaging and condensation of skeletal input because net stratigraphic

accumulation is so slow (Figure 2A or C). In abyssal depths, calcareous hardparts are also subject to dissolution. Workers consequently focus on oceanic zones of relatively high productivity, where the rain of microplankton and other detritus was most intensive, and concentrate on the most dissolution-resistant taxa where possible. Unfortunately, because these deep-sea environments are prone to burial, deformation, and destruction by plate tectonic processes, nearly everything we know about marine life in the past (especially before the past ~150 million years) is from the shallowest water environments ( $\leq \sim 200$  m).

Within those constraints, however, the international Ocean Drilling Project (ODP; formerly Deep Sea Drilling Project, DSDP) has provided a wealth of richly fossiliferous sedimentary cores for evolutionary analysis at many scales (Jackson & Cheetham 1999, Chapman 2000, MacLeod et al. 2000, Norris 1991, Kucera & Malmgren 1998).

Thus, in any given local section, the number and type of gaps depend heavily on how environments shifted across the area during the time interval under study (Figure 1B). The longer the geologic interval is under study, the greater the potential for temporal variation in environments, which changes the quality of the record that is available to be sampled locally (Figure 1; 2E & F). This is a difficulty for local studies: The paleontologist must broaden the study area in order to be able to track a single habitat over time, and thus studies of long evolutionary time typically are regional in scope. Increasing the length of time encompassed by a study also increases the number of major gaps one can expect to encounter. In general, temporally prolonged gaps such as created by significant relative falls in sea level from ice-sheet formation or tectonic uplift affect larger geographic areas than do short gaps. Large gaps are thus more difficult to overcome by compositing data from multiple sections than are small gaps, such as those created by migrating tidal channels, and so interpretations of paleontologic patterns must generally take the fact of these larger breaks into account.

**RELATIONSHIP BETWEEN THICKNESS AND TIME** The amount of time represented by a given bed varies widely: Ten centimeters of sediment can reflect nearly instantaneous deposition during a storm or flood, several decades of accumulation in a lake or bay, or several thousand years in an offshore habitat. Moreover, a local section can include any number and magnitude of erosional and nondepositional breaks. Consequently, stratigraphic or rock accumulation rates (thickness per unit time) range over 11 orders of magnitude and vary as a function of depositional setting (Sadler 1981). In lakes and the deep sea where sediments accumulate steadily, the relative spacing of fossils through a stratigraphic record can frequently be treated as a simple time series in which rock thickness can be a good proxy for elapsed geologic time between paleontologic events (but see MacLeod 1991 and MacLeod & Keller 1991 for exceptions). This is not feasible, however, in riverine and shallow marine settings where sediment accumulation is much less steady on scales often of thousands to tens of millions of years; apparent rates of evolution will be highly distorted if one takes rock thickness as a proxy for geologic time (Holland & Patzkowsky 1999).

Sadler (1981) proposed a practical method of evaluating the stratigraphic completeness of individual sections, based on the ratio of the rock accumulation rate of the target stratigraphic section over a span of time to the average accumulation rate expected for that sedimentary environment in such a period of time. Thus, if the stratigraphic record needs to be relatively free of gaps of a given length for a particular evolutionary study to be conducted, one can calculate the percent completeness of various candidate local sections at that requisite scale before paleontological sampling is begun.

**CHANGES IN ENVIRONMENTAL CONDITIONS** Due to sea-level changes, climatic changes, and the latitudinal shifts of continents, depositional environments shift laterally over time, causing local stratigraphic sections to preserve a series of different depositional environments. In addition to influencing the completeness and accumulation rate of the rock record, such environmental shifts also exert an ecological and taphonomic influence on the occurrence of taxa in local sections, for example, delaying the first occurrence of a taxon after its actual time of evolutionary origination (because populations cannot immigrate until the appropriate environment exists locally), or causing the last local occurrence of a taxon to pre-date the actual time of extinction (local ecological extirpation usually precedes ultimate evolutionary extinction). In cases where environmental changes are minimal or where taxa are not strongly controlled by environment, numerical modeling indicates that this difference in age, known as range offset, is likely to be on the order of tens to hundreds of thousands of years on average (Holland & Patzkowsky 2002), an estimate in agreement with that seen in Neogene planktonic microfossils (Spencer-Cervato et al. 1994). Given average species durations of 4 million years, such values of range offset would represent on the order of 1% to 10% of the species duration. In contrast, values of range offset in shallow marine shelf are typically on the order of 1–2 million years in shallow marine shelf settings, where environments migrate strongly in response to third-order sea-level fluctuations (Holland & Patzkowsky 2002) (Figure 1). In such circumstances, different amounts of range offset for taxa that overlap in time can cause their relative times of apparent origination (or extinction) in a local section to be reversed. Latitudinal shifts of continents and longer-term sea-level changes could likewise cause local values of range offset of higher taxa to be in the tens of millions of years, so that, for example, the presence of tropical corals in a region will change according to its latitudinal position and sedimentary environment.

Although only recently quantified, this problem of environmental control on species occurrences within their evolutionary range is long recognized by paleontologists. The main method of reducing the artifacts in timing is also long recognized, namely, compositing data from stratigraphic sections over a broad geographic range so that key environments can be collected for each increment of geologic time. In practice, correcting for such environmental control has not been done as routinely as it should be. Furthermore, it is simply not possible in some instances: Geologic processes may have selectively removed the record of particular environments from throughout the known geographic range of the target

taxa, making the removal of such bias in fossil ranges difficult unless areas with very different tectonic and depositional histories are compared (Smith et al. 2001). This is a particular problem for endemic taxa because rises and falls in sea level are likely to affect a relatively small area synchronously, leaving few local environmental refuges for taxa to occupy—and be preserved in—during some intervals of time. Environmental homogeneity of the record and endemism of the biota are thus factors in determining whether a given fossil record is likely to be adequate for testing a particular evolutionary question.

**FORMATION OF A PERMANENT ROCK RECORD** The net accumulation of sediments into a permanent stratigraphic record requires subsidence of Earth's crust, such that deposition exceeds erosion over evolutionarily meaningful intervals of time. The subsidence that generates sedimentary basins is localized both spatially and temporally by plate tectonics. The typical durations of subsidence episodes range from a few millions to a few tens of millions of years in relatively short-lived basins (e.g., rift systems of East Africa and the Gulf of California, small intermontane basins of the Rocky Mountains, basins along strike-slip faults such as the San Andreas) to several hundred million years in more slowly subsiding regions (e.g., continental margins of Atlantic-type ocean basins). As a result, individual biogeographic provinces vary in the completeness or even existence of their stratigraphic records (e.g., Foote et al. 1999) or may undergo windows of preservation and non-preservation, depending on their history of subsidence. Thus, comparative analyses of the diversity dynamics and biogeographic histories of co-occurring clades, all subject to similar natural sampling regimes, will often be more robust than comparisons among widely separated regions or among quite different time intervals. Furthermore, sedimentary basins must survive tectonic destruction during subduction and continental collision. For example, deep-sea environments have a minimal geologic record prior to the Jurassic because oceanic lithosphere undergoes subduction, resulting in the destruction of most accumulated sedimentary record.

**RESOLUTION IN CORRELATION** The resolution of stratigraphic correlation, that is, of establishing the age equivalency of rocks in different areas, can be very high (<1 year in exceptional cases) over short distances, but generally decreases as geographic distance increases. The refinement of geophysical methods of correlation using the remnant magnetism of rocks, which record ancient reversals in earth's magnetic poles, has greatly improved the correlation of continental fossil records within some regions and of Cenozoic age rocks in general. However, it is difficult to establish a global chronology of biological events at the same fine resolution that can be achieved locally and regionally, and this difficulty becomes more acute deeper into the geological past. In Paleozoic and Mesozoic rocks, for example, global correlation generally cannot be achieved with higher resolution than a geologic stage, which has an average duration of ~6 million years. There is thus a trade-off between temporal resolution and spatial coverage in species-level and other evolutionary analyses (Jablonski 2000). Fortunately, recently developed

geochemical correlation methods based on stratigraphic variation in oxygen, carbon, and strontium stable isotopes, as well as methods that tune pelagic lithologic cycles to Milankovitch astronomical cycles, are overcoming the usual tradeoff between temporal resolution and geographic distance and are finding widespread application, especially in the marine record of the last 60–80 million years (Hinnov 2000). For some intervals, these methods allow resolution in global correlation to approach tens to hundreds of thousands of years (Berggren et al. 1995). In addition, major improvements in the precision of radiometric dating are permitting higher resolution correlation throughout the fossil record, as well as better information on the absolute ages of events (Bowring et al. 1993, Bowring & Erwin 1998).

Thus both regional- and global-scale time series for lineages and clades can now be constructed with greater precision and confidence in the relative timing of events and in the rates of evolutionary processes. Advances in radiometric dating have also improved the calculation of evolutionary rates and, combined with a suite of new correlation methods, permit the fine structure of mass-extinction events and major taxonomic radiations to be resolved with much greater confidence (Bowring & Erwin 1998).

**SECULAR CHANGES IN THE STRATIGRAPHIC RECORD** Some of the largest-scale patterns in evolutionary paleobiology, such as Phanerozoic trends in biodiversity, are vulnerable to broad changes in the nature of the stratigraphic record, wrought by physical evolution of the earth. These potential biasing factors include some of the same factors that are thought to cause large-scale trends in the quality of fossil preservation (see section above), and are the subject of intense current research (e.g., Peters & Foote 2001, Powell & Kowalewski 2002, Alroy et al. 2000, Smith 2001). All workers presently express considerable uncertainty about the actual magnitude of artifactual effects, and most of the same issues were hotly debated during the earliest modern work on the subject (e.g., Sepkoski et al. 1981). A new generation of analyses is now possible because of improved geological information, new approaches to modeling, and increasingly powerful database options.

Three factors appear to have greatest potential to bias diversity trends at this scale.

1. The shift of North American and European continents from exclusively tropical latitudes in the Paleozoic to largely temperate latitudes in the Mesozoic and Cenozoic (e.g., Allison & Briggs 1993b). Because most global trends are extrapolated from information drawn primarily from these two regions, some workers have estimated that global post-Paleozoic diversity might be underestimated by two- to fivefold at the genus and species levels given the strong diversity gradients documented for most major groups in modern and earlier times (Allison & Briggs 1993b, Jackson & Johnson 2001).
2. The Pull of the Recent (Raup 1979) inflates late Cenozoic taxonomic richness relative to earlier geologic intervals owing to our knowledge of living biota,



which extends the known stratigraphic ranges of fossil taxa up to the Recent from isolated fossil occurrences. Because no part of the history of a group in the deeper past is ever as well sampled as the modern fauna, the stratigraphic ranges of relatively young taxonomic groups are lengthened artificially by their present-day occurrences. The magnitude of the Pull of the Recent has historically been difficult to quantify (but see Foote 2001, 2002; Jablonski et al. 2002). Pull of the Recent would be expected to be most severe for taxa with poor preservation potential, rare taxa, stenotopic taxa, and taxa confined to poorly sampled geographic provinces; a concerted effort on compiling published and new data on Late Cenozoic occurrences will allow the actual magnitude of this effect to be tested rigorously. Similar effects to the Pull of the Recent occur to a lesser degree elsewhere in the stratigraphic record where the biota of one time interval is much better known than adjacent time intervals.

3. Fluctuations in the volume and environmental composition of the marine rock record that are available to sample track closely two ~300 million year cycles of sea-level rise and fall: Shallow-marine deposition was at a minimum in the late Proterozoic to earliest Cambrian Periods, peaked in the Ordovician, and returned to low levels in the Permian; the second cycle peaked in the Cretaceous and has since undergone a net decline (for some new metrics of available rock record, see Peters & Foote 2001). This first-order sea-level history resembles that of Phanerozoic marine biodiversity at the family level (Sepkoski 1984) except that diversity continues to rise from the Cretaceous to present-day, and new analyses find a close correspondence in stage-by-stage genus diversity (Sepkoski 1997) and available rock (Peters & Foote 2001, Smith 2001), again except for a final rise to present-day levels. The long-standing (Sepkoski et al. 1981) controversy concerns the biological reality of the “excess” diversity in the late Cenozoic. The Paleobiology Database project (<http://paleodb.org>) began as an effort to develop genus-level diversity data that were standardized to sampling intensity. Data are still insufficient to be conclusive (Alroy et al. 2000, Jackson & Johnson 2001), but the design of the database will ultimately allow a standardized sampling of Phanerozoic diversity, including tests of the effects of extrapolation from particular regions or latitudinal spread.

## STUDYING EVOLUTION IN AN INCOMPLETE FOSSIL RECORD

Taphonomy and stratal architecture can undoubtedly distort evolutionary patterns in the fossil record and can even create apparent evolutionary patterns. However, in many cases it is possible to compensate and correct for the imperfections of local sections by tailoring sampling strategies and analytical techniques and by using taxonomic groups suited to the particular question at hand.



## Tempo and Mode of Morphologic Change in Species and Lineages

Morphometric data are collected from the fossil record for a variety of evolutionary studies, ranging from the separation of ecophenotypic variation from evolutionary morphologic change between and during speciation events, to the tracking of clade trajectories through a multivariate morphospace (Foote 1997). A sample of morphologies collected from a single bed of fossils can usually be assumed to be time-averaged to some extent and thus will not be equivalent to a census of a living population, but the consequences for morphometric data are not yet clear. In theory, we expect that time averaging will tend to increase variance and even shift the mode relative to a live census owing to the mixing of populations, but under some circumstances, it might decrease variance by the selective destruction of fragile morphs (Kidwell 1986). In contrast, most empirical tests find neither effect (Bell et al. 1987; Cohen 1989; Bush et al. 1999, 2002; Hunt 2001). One possible explanation is that these particular test taxa are morphologically stable from census to census over the temporal and spatial scales captured by time averaging. Alternatively, time-averaged assemblages might be overwhelmingly dominated numerically by specimens added during the most recent interval of time and thus be closer in temporal resolution to a biological sample than previously thought (Kidwell 2002). Of course, for large-scale morphometric studies focused on the average form of a species rather than on intraspecific population-level variation, the effects of time averaging are unimportant or, at least, will generally be nullified by comparing among similarly time-averaged fossil collections, (for criteria to estimate time averaging, see Behrensmeyer & Hook 1992, Kidwell & Flessa 1996).

Local stratigraphic series of intraspecific morphologies reflect changes over time, but this can be interpreted in direct evolutionary terms only if the record is uncomplicated by environmental change over the same interval. In some settings, most notably the shallow marine records that contain the largest numbers of macrobenthic fossils, up-section changes in morphology reveal more about species' responses to environmental change than their evolutionary histories (Bayer & McGhee 1985; Cisne et al. 1980, 1982; Daley 1999; Ludvigsen et al. 1986; McGhee et al. 1991). Similar ambiguity can arise in nonmarine records, even when data from multiple sections have been composited if, for example, all sections are from a single basin and thus share a single climatic or other environmental history. Many reported cases of gradualism in the fossil record (e.g., Sheldon 1987) are compromised by up-section environmental change, which can be subtle for some environments.

Up-section variation in sedimentation rate can also distort the record of evolutionary patterns within single sections. In particular, intervals of low net sedimentation rates (condensed beds), or gaps formed by erosion or complete nondeposition of sediment, tend to increase the perceived rate of morphologic change (MacLeod 1991) and can generate apparent jumps in morphology. Again, the answer is to acquire good sedimentologic and taphonomic information on the context of fossil

occurrences in local sections (in order to identify sharp changes or events that might be preservational noise), and then composite data from multiple sections, particularly sections with different histories of sedimentation and environmental change (in order to build a time series with the most useful segments of record). Using multiple sections from more than a single basin can permit geographic variation to be isolated successfully from true evolutionary change (Jackson & Cheetham 1994, Lieberman et al. 1995). It is also possible to play one lineage against another: For example, if one shows saltation in the same section where another is evolving gradually at a constant rate, it is difficult to argue that the saltation is an artifact of a gap (e.g., Fortey 1985).

In contrast to gradual and abrupt up-section changes in morphology, morphologic stasis is not produced by any known stratigraphic or taphonomic process and must represent a true evolutionary pattern. In fact, the presence of stasis in numerous lineages over long intervals of geologic time (Jackson & Cheetham 1999) is all the more remarkable given the pervasiveness of time averaging, changes in sedimentation rates, the presence of stratigraphic gaps, and the ubiquity of changing sedimentary environments in the fossil record, all of which would be expected to be reflected by changes in morphology.

## Phylogenetic Analysis

The fossil record is the only direct evidence of the history of life on Earth. As such, fossils have played a variety of roles in phylogenetic analysis. One underlying debate is the extent to which the relative timing of first and last fossil occurrences in the stratigraphic record should be used, given long-standing concerns about the quality of occurrence data, new molecular lines of evidence for determining ancestor-descendant relationships, and widespread adaptation of cladistic methods, which were originally devised to rank relationships on biological evidence alone. At one extreme, investigators have argued that occurrence data are too flawed to play any but a secondary role in phylogenetic reconstruction. At the other extreme, researchers have argued that the fossil record is adequate to play a role equal to morphologic or molecular data (e.g., stratophenetics of Gingerich 1979, stratocladistics of Fisher 1994).

Given the highly variable quality of local and regional records (Figure 1), the feasibility of using fossil occurrence data depends on the taxonomic group and geologic setting of the analysis. For example, where fossil occurrences are based on relatively complete and environmentally homogeneous sections, the succession of closely related taxa probably can be inferred with confidence from the stratigraphic record. This does not eliminate the need to have strong spatial coverage or the need to employ statistical analysis to find the most robust occurrence patterns (e.g., Dowsett 1988). On probabilistic grounds, it has been argued that ancestor-descendant pairs are sufficiently common in the fossil record that phylogenetic methods must be modified to account for their presence or such methods will otherwise produce erroneous results (Foote 1996).

A variety of phylogenetic approaches have been developed to address the history of life as captured by the fossil record. Stratigraphic data can be used to choose among otherwise equivalent phylogenetic trees, such that the tree with the lowest "stratigraphic debt" or implied missing fossil record is the preferred tree. Similarly, stratigraphic debt and morphologic data can be minimized simultaneously, as in the method of stratocladistics (Fisher 1994). Fossils may also be used as tests of phylogenetic estimation through consistency metrics, which compare branching order with appearance in the fossil record, and gap metrics, which quantify the length of nonpreservational gaps implied by a phylogeny (Wagner & Sidor 2000). The stratigraphic consistency index (SCI), perhaps the best known of these metrics, is simply the proportion of phylogenetic nodes that is consistent with the fossil record (Huelsenbeck 1994). Conversely, some have used phylogenies to estimate the incompleteness of the fossil record. Statistical models that assume an incomplete fossil record have been used to test the plausibility of hypothesized ancestor-descendant relationships (Marshall 1995). Many of these models start with the working assumption that stratigraphic gaps follow a Dirichlet or similar distribution; however, the demonstration that gaps commonly do not follow such distributions requires a refinement of these methods. A promising lead is the realization that gaps occur in stratigraphically predictable positions, such that advances in stratigraphic modeling will lead to improved paleontological models of fossil distributions (e.g., Holland 1995, Marshall 1997).

Some recent phylogenetic analyses based on molecular clocks have questioned the veracity of the fossil record in reflecting evolutionary pathways (Heckman et al. 2001, Kumar & Hedges 1998, Murphy et al. 2001, Wray et al. 1996). All of these studies have postulated divergence times between clades that are far in excess of those observed in the fossil record. Few tests of the quality of the fossil record relative to the specific claims of these studies have been made, but in at least one case, investigators have concluded that the quality of the global fossil record would have to be at least an order of magnitude worse in the disputed time interval than in later times for divergence times to be significantly older than the fossil record indicates (Foote et al. 1999). The discrepancy between the fossil record and molecular phylogenies may indicate that older crown group taxa in the fossil record have been unrecognized as such, that older members of crown groups have anomalously low preservation rates, that the early histories of crown groups are hidden in areas with no known fossil record, or that rates of molecular evolution are heterogeneous across groups or vary through a group's history (Foote et al. 1999). All of these are possible solutions to this conflict.

## Environmental Analysis of Macroevolutionary Patterns

At the largest temporal and taxonomic scales, evolutionary patterns have been analyzed most commonly at the global scale, in part owing to the compendia of genus- and family-level stratigraphic ranges by Sepkoski (1984, 1993, 1997). However, it is becoming increasingly clear that novel patterns can be detected when global

data are decomposed into regional or habitat-specific time series. Analyses at these finer scales are vulnerable to artifacts generated by taphonomic and stratigraphic biases, so care must be taken either to seek patterns that are opposed to the predicted effects of the biases or to control for such biases, such as by using taphonomic control taxa to verify taxon absences. For example, post-Paleozoic sampling is more complete in northern temperate regions than in other regions (e.g., Allison & Briggs 1993b), but by controlling for sampling intensity using an inventory of species records across latitude, Jablonski (1993) found that a disproportionate number of marine invertebrate orders first appeared in the tropics. Other evolutionary patterns that appear to be robust to spatial or environmental biases include (a) onshore origination and subsequent offshore expansion of marine invertebrate orders (Sepkoski & Miller 1985, Jablonski & Bottjer 1991, Jablonski et al. 1997) and intercontinental variation, (b) the Ordovician marine radiation (Miller 1997, 1998), (c) late Permian plant extinctions (Rees 2002), and (d) molluscan recovery from the end-Cretaceous mass extinction (Jablonski 1998).

Great caution must be used when extrapolating from such environmental and regional differences to global-scale patterns. For example, Rees (2002) found that earlier global compilations of land-plant diversity were heavily biased toward data from a single paleo-continent, leading to interpretations of worldwide catastrophic die-off of vegetation at the Permian-Triassic boundary when the timing and taxonomic focus of extinction actually varied strongly among regions. In the marine realm, workers are well aware of, but rarely adjust for, a strong collection bias toward North America and Europe, which lay primarily in tropical latitudes in the Paleozoic but were extratropical in the post-Paleozoic. It is possible to compensate for these biases in several ways, including seeking more standardized sampling effort, but also by testing for effects that are disproportionate to known differences in sampling or that are contrary to expected taphonomic and stratigraphic biases.

## Temporal Analysis of Macroevolutionary Patterns

One of the most extensive applications of the fossil record to evolutionary biology concerns patterns of origination and extinction at regional and global scales. Given the broad geographic coverage of these studies, they have necessarily adopted coarse, stage-level temporal resolution (i.e., average ~6 million-year-long time bins) because of the difficulty of high-resolution stratigraphic correlation over long distances. A tacit assumption of these studies is that short-term taphonomic and stratigraphic complications (e.g., within single sections or sets of sections) are eliminated or at least minimized by sampling over broad expanses of time and space. For example, stratigraphic variation in time averaging is not thought to affect Phanerozoic trends in biodiversity. The extent to which such first-order assumptions are true is now being tested in a series of ongoing research projects.

One particular focus of these macroevolutionary studies is the tendency for taxonomic originations and extinctions to occur in brief time intervals. Such clustering

may record real evolutionary dynamics, that is, times when life went through genuine bottlenecks or pulses of elevated extinction and diversification. But it is clear that such episodes demand taphonomic and stratigraphic evaluation because similar patterns can be generated by gaps in the record, which truncate the stratigraphic ranges of taxa that actually became extinct or first appeared in the unrecorded interval of time. Last and first appearances are thus artificially concentrated along major discontinuity surfaces. Rapid up-section changes in environment can produce a similar effect. For example, a rapid switch from species-rich-water marine environments to the species-poor deep-water marine environments at the Cenomanian-Turonian stage boundary in Europe has led to overestimating the actual magnitude of mass extinction in this region (Smith et al. 2001). Many other mass extinction events, such as the repeated regional trilobite extinctions within the Cambrian Period known as biomeres, the end-Ordovician extinction, and the end-Permian extinction were accompanied by rapid changes in sedimentary environment and preserved rock volume that have almost certainly exaggerated to varying degrees the taxonomic breadth and coordinated timing of these extinctions (Osleger & Read 1993, Palmer 1965, Saltzman 1999, Peters & Foote 2001, Smith 2001). However, numerical optimization techniques that simultaneously estimate origination, extinction, and preservation rates (Foote 2003) indicate that most of the "Big Five" mass extinctions in the Phanerozoic marine metazoan record (Raup & Sepkoski 1982) still show elevated extinction above background levels and elevated origination during subsequent recovery periods, even after correcting for changes in fossil preservation rates. Taphonomic and stratigraphic evaluation are thus leading to more conservative yet more confident estimates of evolutionary rates. Moreover, the persistence of such pulses in extinction and origination, even after correcting for unevenness in the fossil record, suggests that the relative changes in sea level that drive major changes in the quality of the fossil record may to some degree drive changes in origination and extinction rate. For example, the sea-level changes that produce stratigraphic gaps and surfaces of abrupt environmental change may also alter the area or nature of habitable shallow marine shelves, climatic changes, and shifts in ocean circulation, all of which may increase speciation and extinction rates (Copper 2001, Wignall & Hallam 1992).

In empirical studies, deconvolving the effects of discontinuous sedimentation and changing environmental conditions from true evolutionary dynamics requires (a) paying close attention to the bed-level and environmental context of sampled horizons and of up-section changes in these qualities so that one can test for homogeneity in data quality and (b) compositing data from a sufficient geographic area to escape any shared similarities among sections in the timing of gaps and in the nature of environmental change. Some workers have used the stereotypic patterns of gaps and environmental change produced by sea-level cycles (Figure 1) to design sampling strategies that can isolate such artifacts from evolutionarily important extinction and biotic invasion events (Patzkowski & Holland 1997, 1999).

As an example of the difficulty of distinguishing stratigraphic artifact from paleobiological events, a pattern named coordinated stasis has been described from

mid-Paleozoic strata of North America based on the persistence over several million years of marine macrobenthic faunas of relatively static ecological structure, taxonomic composition, and fossil morphologies (Brett & Baird 1995). These long blocks of stability are separated by short periods (10,000 to 100,000 years) of ecological restructuring with pulsed origination, extinction, migration, and morphologic change. In the original and subsequent reported examples, the pattern of coordinated stasis has not withstood scrutiny: Turnover is commonly timed with discontinuity surfaces and surfaces of rapid environmental change so that the turnover event may have been much more protracted than a face-value reading of the stratigraphic record would suggest (Baumiller 1996, Goldman et al. 1999, Holland 1996). One study that accounted for taphonomic and stratigraphic effects recognized a much more limited degree of faunal stability (Jackson et al. 1996), and another found no evidence of faunal stability (Patzkowsky & Holland 1997). The "turnover pulse hypothesis" interprets mammalian faunal change in the Cenozoic of Africa in a similar manner (Vrba 1985); subsequent taphonomic and stratigraphic analyses with broader spatial scope have suggested that this too is an artifact of discontinuous stratigraphic accumulation in the original study area (Behrensmeyer et al. 1997).

Although stratigraphic processes are capable of generating artifactual peaks in origination and extinction, limited sampling or the rarity of fossils can have the opposite effect on fossil occurrence data, causing a genuine pulse in origination or extinction to appear as a more gradual pattern in what has been called the Signor-Lipps Effect (Signor & Lipps 1982). When the actual probabilities of finding fossils at any given horizon are taken into account, some apparently gradual extinction records at the Cretaceous-Tertiary boundary are consistent with an extinction pulse that has been degraded by the Signor-Lipps Effect (Marshall & Ward 1996, Sheehan et al. 1991). Rarefaction and related sampling-standardization methods can also be used to correct for the distorting effects of variable sampling size (Miller & Foote 1996, Alroy et al. 2001). Confidence limits on the timing of origination and extinction have been an important recent advance in evaluating the quality of the fossil record (Strauss & Sadler 1989; Marshall 1990, 1997). Early confidence-limit methods made the simplifying assumptions that gaps are randomly distributed and that fossil preservation rates are constant through time, but more recent approaches have replaced these assumptions with more realistic ones, namely, that gaps are nonrandomly distributed and that fossil preservation rates vary through time (Marshall 1997, Holland 2001).

At the broader scale of reconstructing origination and extinction rates over geologic time, statistical methods that evaluate the probability of recovering fossils have allowed paleontologists to evaluate the robustness of observed paleobiological patterns. For example, capture-mark-recapture methods borrowed from field ecology have been used to simultaneously calculate extinction, origination, and preservation probabilities among taxa during the Ordovician radiation (Connolly & Miller 2001). Similarly, numerical optimization techniques have been used to remove the distorting effects of variable preservation probabilities on the record of



Phanerozoic origination and extinction rates (Foote 2001, 2003). These methods explore possible combinations of probabilities of preservation, origination, and extinction through time until a maximal fit to the fossil record is found. Although computationally expensive, they represent the first attempt to address quantitatively the effects of variable preservation on the fossil record of biodiversity and turnover rates.

## CONCLUSIONS

The fossil record is highly variable in quality from place to place as well as over time at a single location. This variation—in the preservation potential of major groups, in the gappiness of the sedimentary record, in environments represented, and in the temporal and spatial mixing of fossils—is systematic and thus has potential to bias paleontological data. However, the variation is quantifiable and is increasingly well understood. Thus progress will continue in the development and application of sampling protocols and statistical methods that compensate for these effects.

In devising strategies, it is important to realize that (a) no single bias applies to all scales of evolutionary analysis or to all taxonomic groups and (b) no scale or type of evolutionary analysis or taxonomic group is completely free of taphonomic and stratigraphic bias. Thus, there is no single “simple fix”: The specific problems faced by the paleontologist depend on the desired temporal and spatial scale of study and the taxonomic group at hand. Recovery of high-resolution evolutionary time series is inherently difficult for certain groups and environments (e.g., nonmineralized groups preserved only in lagerstätten, riverine versus lake environments, and shallow-versus deep-marine habitats). Arguably, the easiest strategies are to shift the target of the high-resolution analysis to conducive clades and settings or to change the focus of the analysis to better match the quality of targeted material: Many taphonomic artifacts at the finest scale, for example, the mixing of morphs from multiple generations or habitats into a single bed by time averaging, are less relevant when working at coarser spatial, temporal, and taxonomic scales. Other taphonomic and stratigraphic effects remain relevant at coarser scales, e.g., the lower preservation potential of taxa with smaller, more gracile, or less fully mineralized skeletons, and some stratigraphic biases come more fully to the foreground in coarser analyses, e.g., when encountering large geographically widespread gaps in the sedimentary record, changes in the proportions of environments available to sample, and declining confidence in the age-correlations necessary for accurate binning of data into composite time series. Some of the worst taphonomic and stratigraphic biases that arise in local sections can be compensated for by compositing data from multiple sections over biologically relevant regions, but in the future, our collection of even coarse-scale data needs to be far more sophisticated: We need to demonstrate, rather than assume, that environmental and taphonomic variation and local incompleteness have been compensated for by coarse binning, and



this requires that fossil occurrences be scored according to their context in the record, rather than entered free of any encumbering information as to environment or quality of source.

Electronic databasing now permits the requisite level of taphonomic and stratigraphic bookkeeping on data quality that was not practical in the past. Basic taphonomic research in modern environments and in the stratigraphic record needs to continue its focus on ranking and quantifying taxa in terms of their preservation potential, both to better parameterize paleobiologic models and to inform empirical analysis. Comparisons of patterns among taxa or environments with different preservation potential may be another underexploited approach to separating taphonomic bias from biological signal in situations where simpler null hypotheses are not adequate. Thus, over the past twenty years, paleontologists have become much better positioned to deal rigorously with their long-standing concerns about the quality of the fossil record. That record is and will remain incomplete, but ongoing advances in taphonomy and stratigraphy—and of course continued work to increase the known record, especially in regions undersampled so far—will ensure that it continues to be a valuable source of insight into the evolution of life on Earth.

## ACKNOWLEDGMENTS

We are grateful to D. Jablonski, M. Foote, and A.I. Miller for helpful reviews. We thank M. Foote for suggesting the title for the latter half of the paper.

**The *Annual Review of Ecology and Systematics* is online at  
<http://ecolsys.annualreviews.org>**

## LITERATURE CITED

- Allison PA, Briggs DEG, eds. 1991. *Taphonomy: Releasing the Data Locked in the Fossil Record*. New York: Plenum
- Allison PA, Briggs DEG. 1993a. Exceptional fossil record: distribution of soft-tissue preservation through the Phanerozoic. *Geology* 21:527–30
- Allison PA, Briggs DEG. 1993b. Paleolatitudinal sampling bias, Phanerozoic species diversity, and the end-Permian extinction. *Geology* 21:65–68
- Alroy J, Marshall CR, Bambach RK, Bezusko K, Foote M, et al. 2001. Effects of sampling standardization on estimates of Phanerozoic marine diversification. *Proc. Natl. Acad. Sci. USA* 98:6261–66
- Anders MH, Krueger SW, Sadler PM. 1987. A new look at sedimentation rates and the completeness of the stratigraphic record. *J. Geol.* 95:1–14
- Anderson LC, Sen Gupta BK, McBride RA, Byrnes MR. 1997. Reduced seasonality of Holocene climate and pervasive mixing of Holocene marine section: northeastern Gulf of Mexico shelf. *Geology* 25:127–30
- Bada JL, Wang XS, Hamilton H. 1999. Preservation of key biomolecules in the fossil record: current knowledge and future challenges. *Philos. Trans. R. Soc. London Ser. B* 354:77–87
- Baumiller TK. 1996. Exploring the pattern of coordinated stasis: simulations and extinction scenarios. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 127:135–46

- Bayer U, McGhee GR. 1985. Evolution in marginal epicontinental basins: the role of phylogenetic and ecologic factors (Ammonite replacements in the German Lower and Middle Jurassic). In *Sedimentary and Evolutionary Cycles*, ed. U Bayer, A Seilacher, pp. 164–220. New York: Springer-Verlag
- Behrensmeyer AK. 1999. Bonebeds through geologic time. *J. Vertebr. Paleontol.* 19 (Suppl. to 3):31–32A
- Behrensmeyer AK, Chapman RE. 1993. Models and simulations of time-averaging in terrestrial vertebrate accumulations. See Kidwell & Behrensmeyer 1993, pp. 125–49
- Behrensmeyer AK, Dechant Boaz DE. 1980. The recent bones of Amboseli Park, Kenya, in relation to East African paleoecology. In *Fossils in the Making*, ed. AK Behrensmeyer, AP Hill, pp. 72–92. Chicago, IL: Univ. Chicago Press
- Behrensmeyer AK, Hook RW. 1992. Paleoenvironmental contexts and taphonomic modes in the terrestrial fossil record. In *Terrestrial Ecosystems Through Time*, ed. AK Behrensmeyer, JD Damuth, WA DiMichele, R Potts, H-D Sues, SL Wing, pp. 15–136. Chicago, IL: Univ. Chicago Press
- Behrensmeyer AK, Kidwell SM, Gastaldo RA. 2000. Taphonomy and paleobiology. See Erwin & Wing 2000, pp. 103–47
- Behrensmeyer AK, Todd NE, Potts R, McBrinn GE. 1997. Late Pliocene faunal turnover in the Turkana Basin, Kenya and Ethiopia. *Science* 278:1589–94
- Bell MA, Sadagursky MS, Baumgartner JV. 1987. Utility of lacustrine deposits for the study of variation within fossil samples. *Palaaios* 2:455–66
- Berggren WA, Kent DV, Swisher III CC, Aubry MP. 1995. A revised Cenozoic geochronology and chronostratigraphy. In *Geochronology, Time Scales and Global Stratigraphic Correlation*, ed. WA Berggren, DV Kent, MP Aubry, J Hardenbol, pp. 129–212. Tulsa, OK: SEPM Spec. Publ. No. 54
- Bowring SA, Erwin DH. 1998. A new look at evolutionary rates in deep time: uniting paleontology and high-precision geochronology. *Geol. Soc. Am. Today* 8:1–8
- Bowring SA, Grotzinger JP, Isachsen CE, Knoll AH, Pelechaty SM, Kolosov P. 1993. Calibrating rates of early Cambrian evolution. *Science* 261:1293–98
- Brett CE. 1995. Sequence stratigraphy, biostratigraphy, and taphonomy in shallow marine environments. *Palaaios* 10:597–616
- Brett CE, Baird GC. 1995. Coordinated stasis and evolutionary ecology of Silurian to Middle Devonian faunas in the Appalachian Basin. See Erwin & Anstey 1995, pp. 285–315
- Brewster-Wingard GL, Stone JR, Holmes CW. 2001. Molluscan faunal distribution in Florida Bay, past and present: an integration of down-core and modern data. *Bull. Am. Paleontol.* 361:199–231
- Briggs DEG, Crowther PR, eds. 2001. *Paleobiology II*. Oxford: Blackwell Sci. 583 pp.
- Bush AM, Powell MG, Arnold WS, Bert TM, Daley GM. 2002. Time-averaging, evolution, and morphologic variation. *Paleobiology* 28:9–250
- Chapman MR. 2000. The response of planktonic foraminifera to the Late Pliocene intensification of Northern Hemisphere glaciation. See Culver & Rawson, pp. 79–96
- Cisne JL, Chandlee GO, Rabe BD, Cohen JA. 1982. Clinal variation, episodic evolution, and possible parapatric speciation: the trilobite *Flexicalymene senaria* along an Ordovician depth gradient. *Lethaia* 15:325–41
- Cisne JL, Molenock J, Rabe BD. 1980. Evolution in a cline: the trilobite *Triarthrus* along an Ordovician depth gradient. *Lethaia* 13:47–59
- Cohen AS. 1989. The taphonomy of gastropod shell accumulations in large lakes: an example from Lake Tanganyika, Africa. *Paleobiology* 15:26–45
- Connolly SR, Miller AI. 2001. Joint estimation of sampling and turnover rates from fossil databases: capture-mark-recapture methods revisited. *Paleobiology* 27:751–67
- Cooper A, Poinar HN. 2000. Ancient DNA: do it right or not at all. *Science* 289:1139

- Copper P. 2001. Reefs during the multiple crises towards the Ordovician-Silurian boundary: Anticosti Island, eastern Canada, and world-wide. *Can. J. Earth Sci.* 38:153–71
- Culver SJ, Rawson PF. 2000. *Biotic Response to Global Change, the Last 145 Million Years*. 501 pages. Cambridge, UK: Cambridge Univ. Press
- Daley GM. 1999. Environmentally controlled variation in shell size of *Ambonychia* Hall (Mollusca: Bivalvia) in the type Cincinnati (Upper Ordovician). *Palaios* 14:520–29
- Davis MB. 2000. Palynology after Y2K—understanding the source area of pollen in sediments. *Annu. Rev. Ecol. Syst.* 28:1–18
- Donovan SK, Paul CRC. 1998. *The Adequacy of the Fossil Record*. Chichester: Wiley & Sons. 312 pp.
- Dowsett HJ. 1988. Diachrony of late Neogene microfossils in the southwest Pacific Ocean: application off the graphic correlation technique. *Paleoceanography* 3:209–22
- Erwin DH, Anstey RL, eds. 1995. *New Approaches to Speciation in the Fossil Record*. New York: Columbia Univ. Press
- Erwin DH, Wing SL, eds. 2000. *Deep Time: Paleobiology's Perspective*. Lawrence, KS: Paleontol. Soc.
- Fisher DC. 1994. Stratocladistics: morphological and temporal patterns and their relation to phylogenetic process. In *Interpreting the Hierarchy of Nature*, ed. L Grande, O Rieppel, pp. 133–71. San Diego, CA: Academic
- Flessa KW. 1998. Well-traveled cockles: shell transport during the Holocene transgression of the southern North Sea. *Geology* 26:187–90
- Flessa KW, Kowalewski M. 1994. Shell survival and time-averaging in nearshore and shelf environments: estimates from the radiocarbon literature. *Lethaia* 27:153–65
- Foote M. 1996. On the probability of ancestors in the fossil record. *Paleobiology* 22:141–51
- Foote M. 1997. The evolution of morphological diversity. *Annu. Rev. Ecol. Syst.* 28:129–52
- Foote M. 2001. Inferring temporal patterns of preservation, origination, and extinction from taxonomic survivorship analysis. *Paleobiology* 27:602–30
- Foote M. 2003. Origination and extinction through the Phanerozoic: a new approach. *J. Geol.* 111: In press
- Foote M, Hunter JP, Janis CM, Sepkoski JJ Jr. 1999. Evolutionary and preservational constraints on origins of biologic groups: divergence times of eutherian mammals. *Science* 283:1310–14
- Fortey RA. 1985. Gradualism and punctuated equilibria as competing and complementary series. *Spec. Pap. Palaeontol.* 33:17–28
- Fürsich FT. 1978. The influence of faunal condensation and mixing on the preservation of fossil benthic communities. *Lethaia* 11:243–50
- Gingerich PD. 1979. The stratophenetic approach to phylogeny reconstruction in vertebrate paleontology. In *Phylogenetic Analysis and Paleontology*, ed. J Cracraft, N Eldredge, pp. 41–77. New York: Columbia Univ. Press
- Goldman D, Mitchell CE, Joy MP. 1999. The stratigraphic distribution of graptolites in the classic upper Middle Ordovician Utica Shale of New York State: an evolutionary succession or a response to relative sea-level change? *Paleobiology* 25:273–94
- Graham RW. 1993. Processes of time-averaging in the terrestrial vertebrate record. See Kidwell & Behrensmeyer 1993, pp. 102–24
- Heckman DS, Geiser DM, Eidell BR, Stauffer RL, Kardos NL, Hedges SB. 2001. Molecular evidence for the early colonization of land by fungi and plants. *Science* 293:1129–33
- Hinnov LA. 2000. New perspectives on orbitally forced stratigraphy. *Annu. Rev. Earth Planet. Sci.* 28:419–75
- Holland SM. 1995. The stratigraphic distribution of fossils. *Paleobiology* 21:92–109
- Holland SM. 1996. Recognizing artifactually generated coordinated stasis: implications of numerical models and strategies for field tests. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 127:147–56
- Holland SM. 2000. The quality of the fossil

- record—a sequence stratigraphic perspective. See Erwin & Wing 2000, pp. 148–68
- Holland SM. 2001. Confidence limits on fossil ranges that account for sequence architecture. *Geol. Soc. Am. Abstr. Program* 33:A31
- Holland SM, Patzkowsky ME. 1999. Models for simulating the fossil record. *Geology* 27:491–94
- Holland SM, Patzkowsky ME. 2002. Stratigraphic variation in the timing of first and last occurrences. *Palaios* 17:134–46
- Huelsenbeck JP. 1994. Comparing the stratigraphic record to estimates of phylogeny. *Paleobiology* 20:470–83
- Hunt G. 2001. Time averaging and morphometric data: Do fossil samples accurately reflect population-level variability? *Paleobios* 21: 69
- Jablonski D. 1993. The tropics as a source of evolutionary novelty: the post-Palaeozoic fossil record of marine invertebrates. *Nature* 364:142–44
- Jablonski D. 1998. Geographic variation in the molluscan recovery from the end-Cretaceous extinction. *Science* 279:1327–30
- Jablonski D. 2000. Micro- and macroevolution: scale and hierarchy in evolutionary biology and paleobiology. See Erwin & Wing 2000, p. 15–52
- Jablonski D, Bottjer DJ. 1991. Environmental patterns in the origins of higher taxa: the post-Paleozoic fossil record. *Science* 252:1831–33
- Jablonski D, Lidgard S, Taylor PD. 1997. Comparative ecology of bryozoan radiations: origin of novelties in cyclostomes and cheilostomes. *Palaios* 12:505–23
- Jablonski D, Roy K, Valentine JW, Price RM, Anderson PS. 2002. Pull of the Recent? What pull of the Recent? An analysis of the marine Bivalvia. *Abstr. Progr. Geol. Soc. Amer.* 34(7): In press
- Jackson JBC, Cheetham AH. 1994. Phylogeny reconstruction and the tempo of speciation in cheilostome Bryozoa. *Paleobiology* 20:407–23
- Jackson JBC, Budd AF, Pandolfi JM. 1996. The shifting balance of natural communities? In *Evolutionary Paleobiology*, ed. D Jablonski, DH Erwin, JH Lipps, pp. 89–122. Chicago, IL: Univ. Chicago Press
- Jackson JBC, Cheetham AH. 1999. Tempo and mode of speciation in the sea. *Trends Ecol. Evol.* 14:72–77
- Kidwell SM. 1986. Models for fossil concentrations: Paleobiologic implications. *Paleobiology* 12:6–24
- Kidwell SM. 1991. The stratigraphy of shell concentrations. See Allison & Briggs 1991, pp. 211–90
- Kidwell SM. 1993. Taphonomic expressions of sedimentary hiatus: field observations on bioclastic concentrations and sequence anatomy in low, moderate and high subsidence settings. *Geol. Rundsch.* 82:189–202
- Kidwell SM. 2002. Time-averaged molluscan death assemblages: palimpsests of richness, snapshots of abundance. *Geology* 30:803–6
- Kidwell SM, Behrensmeier AK, eds. 1993. *Taphonomic Approaches to Time Resolution in Fossil Assemblages*. Knoxville, TN: Paleontol. Soc. Short Courses Paleontol
- Kidwell SM, Best MMR. 2001. Tropical time-averaging: disparate scales and taphonomic clocks in bivalve assemblages from modern subtidal siliciclastic and carbonate facies. *North Am. Paleontol. Conv.* 2001, Program Abstr. *PaleoBios* 21:79
- Kidwell S, Bosence DWJ. 1991. Taphonomy and time-averaging of marine shelly faunas. See Allison & Briggs 1991, pp. 115–209
- Kidwell SM, Brenchley PJ. 1994. Patterns in bioclastic accumulation through the Phanerozoic: changes in input or in destruction? *Geology* 22:1139–43
- Kidwell SM, Flessa KW. 1996. The quality of the fossil record: populations, species, and communities. *Annu. Rev. Earth. Planet. Sci.* 24:433–64
- Kowalewski M. 1996. Taphonomy of a living fossil: the lingulide brachiopod *Glottidia palmeri* Dall from Baja California, Mexico. *Palaios* 11:244–65
- Kowalewski M, Bambach RK. 2002. The limits of paleontological resolution. In *High*

- Resolution Approaches in Paleontology*, ed. PJ Harries, DH Geary. New York: Kluwer/Plenum. In press
- Kucera M, Malmgren BA. 1998. Differences between evolution of mean form and evolution of new morphotypes; an example from Late Cretaceous planktonic Foraminifera. *Paleobiology* 24:49–63
- Kumar S, Hedges SB. 1998. A molecular timescale for vertebrate evolution. *Nature* 392:17–20
- Lieberman BS, Brett CE, Eldredge N. 1995. A study of stasis and change in two species lineages from the Middle Devonian of New York state. *Paleobiology* 21:15–27
- Ludvigsen R, Westrop SR, Pratt BR, Tuffnell PA, Young GA. 1986. Dual biostratigraphy: zones and biofacies. *Geosci. Can.* 13:139–54
- MacLeod N. 1991. Punctuated anagenesis and the importance of stratigraphy to paleobiology. *Paleobiology* 17:167–88
- MacLeod N, Keller G. 1991. Hiatus distributions and mass extinctions at the Cretaceous/Tertiary boundary. *Geology* 19:497–501
- MacLeod N, Ortiz N, Fefferman N, Clyde W, Schultze C, MacLean J. 2000. Phenotypic response of foraminifera to episodes of global environmental change. See Culver & Rawson 2000, pp. 51–78
- Marshall CR. 1990. Confidence intervals on stratigraphic ranges. *Paleobiology* 16:1–10
- Marshall CR. 1995. Stratigraphy, the true order of species originations and extinctions, and testing ancestor-descendant hypotheses among Caribbean Neogene bryozoans. See Erwin & Anstey 1995, pp. 208–35
- Marshall CR. 1997. Confidence intervals on stratigraphic ranges with nonrandom distributions of fossil horizons. *Paleobiology* 23:165–73
- Marshall CR, Ward PD. 1996. Sudden and gradual molluscan extinctions in the latest Cretaceous of Western European Tethys. *Science* 274:1360–63
- Martin RE, Wehmiller JF, Harris MS, Liddell WD. 1996. Comparative taphonomy of foraminifera and bivalves in Holocene shallow-water carbonate and siliciclastic regimes: taphonomic grades and temporal resolution. *Paleobiology* 22:80–90
- McGhee GR Jr, Bayer U, Seilacher A. 1991. Biological and evolutionary responses to transgressive-regressive cycles. In *Cycles and Events in Stratigraphy*, ed. W Ricken, A Seilacher, pp. 696–708. Berlin: Springer-Verlag
- McKinney ML. 1986. How biostratigraphic gaps form. *J. Geol.* 94:875–84
- McKinney ML. 1991. Completeness of the fossil record: an overview. In *The Processes of Fossilization*, ed. SK Donovan, pp. 66–83. New York: Columbia Univ. Press
- Meldahl KH, Flessa KW, Cutler AH. 1997. Time-averaging and postmortem skeletal survival in benthic fossil assemblages: quantitative comparisons among Holocene environments. *Paleobiology* 23:209–29
- Miller AI. 1997. Dissecting global diversity patterns: examples from the Ordovician Radiation. *Annu. Rev. Ecol. Syst.* 28:85–104
- Miller AI. 1998. Biotic transitions in global marine diversity. *Science* 281:1157–60
- Miller AI, Cummins H. 1990. A numerical model for the formation of fossil assemblages: estimating the amount of post-mortem transport along environmental gradient. *Palaios* 5:303–16
- Miller AI, Foote M. 1996. Calibrating the Ordovician radiation of marine life: implications for Phanerozoic diversity trends. *Paleobiology* 22:304–9
- Murphy WJ, Eizirik E, O'Brien SJ, Madsen O, Scally M, et al. 2001. Resolution of the early placental mammal radiation using Bayesian phylogenetics. *Science* 294:2348–51
- Norris RD. 1991. Biased extinction and evolutionary trends. *Paleobiology* 17:388–99
- Olszewski TD. 1999. Taking advantage of time-averaging. *Paleobiology* 25:226–38
- Osleger D, Read JF. 1993. Comparative analysis of methods used to define eustatic variations in outcrop: late Cambrian interbasinal sequence development. *Am. J. Sci.* 293:157–216
- Palmer AR. 1965. Biome—a new kind of biostratigraphic unit. *J. Paleontol.* 39:149–53

- Patzkowsky ME, Holland SM. 1997. Patterns of turnover in Middle and Upper Ordovician brachiopods of the eastern United States: a test of coordinated stasis. *Paleobiology* 23: 420–43
- Patzkowsky ME, Holland SM. 1999. Biofacies replacement in a sequence stratigraphic framework: Middle and Upper Ordovician of the Nashville Dome, Tennessee, USA. *Palaio* 14:301–23
- Paul CRC. 1982. The adequacy of the fossil record. In *Problems of Phylogenetic Reconstruction*, ed. KA Joysey, AE Friday, pp. 75–117. New York: Academic
- Peters SE, Foote M. 2001. Biodiversity in the Phanerozoic: a reinterpretation. *Paleobiology* 27:583–601
- Peterson CH. 1977. The paleoecological significance of undetected short-term temporal variability. *J. Paleontol.* 51:976–81
- Powell MG, Kowalewski M. 2002. Increase in evenness and sampled alpha diversity through the Phanerozoic: comparison of early Paleozoic and Cenozoic marine fossil assemblages. *Geology* 30:331–34
- Raup DM. 1979. Biases in the fossil record of species and genera. *Bull. Carnegie Mus. Nat. Hist.* 13:85–91
- Raup DM, Sepkoski JJ Jr. 1982. Mass extinctions in the marine fossil record. *Science* 215: 1501–2
- Rees PM. 2002. Land-plant diversity and the end-Permian mass extinction. *Geology* 30: 827–30
- Rogers RR, Kidwell SM. 2000. Associations of vertebrate skeletal concentrations and discontinuity surfaces in continental and shallow marine records: a test in the Cretaceous of Montana. *J. Geol.* 108:131–54
- Roy K, Valentine JW, Jablonski D, Kidwell S. 1996. Scales of climatic variability and time averaging in Pleistocene biotas: implications for ecology and evolution. *Trends Ecol. Evol.* 11:458–63
- Sadler PM. 1981. Sediment accumulation rates and the completeness of stratigraphic sections. *J. Geol.* 89:569–84
- Saltzman MR. 1999. Upper Cambrian carbonate platform evolution, *Elvinia* and *Taeniocephalus* Zones (Pteroccephaliid-Ptychaspid biomere boundary), northwestern Wyoming. *J. Sediment. Res.* 69:926–38
- Schopf TJM. 1978. Fossilization potential of an intertidal fauna: Friday Harbor, Washington. *Paleobiology* 4:261–70
- Sepkoski JJ Jr. 1984. A kinetic-model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. *Paleobiology* 10:246–67
- Sepkoski JJ Jr. 1993. Ten years in the library: new data confirm paleontological patterns. *Paleobiology* 19:43–51
- Sepkoski JJ Jr. 1997. Biodiversity: past, present, and future. *J. Paleontol.* 71:533–39
- Sepkoski JJ Jr, Bambach RK, Raup DM, Valentine JW. 1981. Phanerozoic marine diversity and the fossil record. *Nature* 293:435–37
- Sepkoski JJ Jr, Miller AI. 1985. Evolutionary faunas and the distribution of Paleozoic benthic communities in space and time. In *Phanerozoic Diversity Patterns*, ed JW Valentine, pp. 153–90. Princeton, NJ: Princeton Univ. Press
- Sheehan PM, Fastovsky DE, Hoffman RG, Berghaus CB, Gabriel DL. 1991. Sudden extinction of the dinosaurs: latest Cretaceous, Upper Great Plains, U.S.A. *Science* 254:835–39
- Sheldon PR. 1987. Parallel gradualistic evolution of Ordovician trilobites. *Nature* 330: 561–63
- Signor PW, Lipps JH. 1982. Sampling bias, gradual extinction patterns, and catastrophes in the fossil record. *Geol. Soc. Am. Spec. Pap.* 190:291–96
- Smith AB. 2001. Large-scale heterogeneity of the fossil record: implications for Phanerozoic biodiversity studies. *Philos. Trans. R. Soc. London Ser. B* 356:351–67
- Smith AB, Gale AS, Monks NEA. 2001. Sea-level change and rock record bias in the Cretaceous: a problem for extinction and biodiversity studies. *Paleobiology* 27:241–53



- Spencer-Cervato C, Thierstein HR, Lazarus DB, Beckmann JP. 1994. How synchronous are Neogene marine plankton events? *Paleoceanography* 9:739–63
- Strauss D, Sadler PM. 1989. Classical confidence intervals and the Bayesian probability estimates for the ends of local taxon ranges. *Math. Geol.* 21:411–27
- Taylor PD, Allison P. 1999. Bryozoan carbonates through time and space. *Geology* 26:459–62
- Valentine JW. 1989. How good was the fossil record? Clues from the Californian Pleistocene. *Paleobiology* 15:83–94
- Vrba E. 1985. Environment and evolution: alternative causes of the temporal distribution of evolutionary events. *S. Afr. J. Sci.* 81:229–36
- Wagner PJ, Sidor CA. 2000. Age rank/clade rank metrics—sampling, taxonomy, and the meaning of “stratigraphic consistency.” *Syst. Biol.* 49:463–79
- Walker KR, Bambach RK. 1971. The significance of fossil assemblages from fine-grained sediments: time-averaged communities. *Geol. Soc. Am. Abstr. Programs* 3:783–84
- Webb T III. 1993. Constructing the past from late Quaternary pollen data: temporal resolution and a zoom lens space-time perspective. See Kidwell & Behrensmeyer 1993, pp. 79–101
- Wignall PB, Hallam A. 1992. Anoxia as a cause of the Permian/Triassic extinction: facies evidence from northern Italy and the western United States. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 93:21–46
- Wray GA, Levinton JS, Shapiro LH. 1996. Molecular evidence for deep Precambrian divergences among metazoan phyla. *Science* 274:568–73