

# THE QUALITY OF THE FOSSIL RECORD: Populations, Species, and Communities

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## ABSTRACT

Paleontologists have always been concerned about the documentary quality of the fossil record, and this has also become an important issue for biologists, who increasingly look to accumulations of bones, shells, and plant material as possible ways to extend the time-frame of observation on species and community behaviors. Quantitative data on the postmortem behavior of organic remains in modern environments are providing new insights into death and fossil assemblages as sources of biological information. Important findings include: 1. With the exception of a few circumstances, usually recognizable by independent criteria, transport out of the original life habitat affects few individuals. 2. Most species with preservable hardparts are in fact represented in the local death assemblage, commonly in correct rank importance. Molluscs are the most durable of modern aquatic groups studied so far, and they show highest fidelity to the original community. 3. Time-averaging of remains from successive generations and communities often prevents the detection of short-term (seasons, years) variability but provides an excellent record of the *natural range* of community composition and structure over longer periods. Thus, although a complex array of processes and circumstances influences preservation, death assemblages of resistant skeletal elements are for many major

groups good to excellent records of community composition, morphological variation, and environmental and geographic distribution of species, and such assemblages can record temporal dynamics at ecologically and evolutionarily meaningful scales.

## INTRODUCTION

Every paleontologist can tell horror stories of long-distance transport of biological remains, of bones worn or comminuted beyond recognition, and of fossils found mixed with Recent shells along modern beaches. Every paleontologist also can recite some of the glories of the fossil record—for example, feathered *Archaeopteryx* from the Jurassic Solnhofen Limestone, the bizarre soft-bodied taxa of the late Neoproterozoic Ediacara Formation and Middle Cambrian Burgess Shale, exquisite plants from Carboniferous coal, and the spectacular assortment of bats, insects, frogs, and horses with undigested stomach contents in the Eocene Messel oil shale (2, 139). There is an unexceptional middle ground, however, comprising the vast majority of fossil and modern death assemblages, where the biological signal is expected to be damped and biased to some intermediate degree. One of the challenges of taphonomic research is to evaluate postmortem modification in these ordinary assemblages and derive practical guidelines for their use as sources of biological information. As Paul (91) has stressed, what matters is not that the fossil record is incomplete—all science is based on incomplete knowledge—but whether data incorporated in the fossil record are adequate to test particular hypotheses. Here we review the quality of the record with respect to reconstructing biological phenomena at the scale of populations, species, and communities, and we argue that even ordinary data in the fossil record are adequate to address many important biological questions.

There is a growing body of comparative and quantitative data on taphonomic (postmortem) phenomena and their consequences. Much of this work has focused on processes operating in modern environments as keys to understanding the past; this work has had two aims. One has been to use the quality of fossil preservation as evidence of (paleo)environmental conditions, such as wave/current energy, porewater chemistry, climate, directions of sediment transport, and duration of sedimentary hiatuses (3, 41, 77).

The second aim, and the focus here, is the effect of taphonomic processes on the biological signal. What is the quality of the record as an archive of ancient biotic interactions, species distributions, morphological variability in time and space, and community structure and dynamics? This, the original impetus of the field (44; Darwin devoted a chapter of the *Origin* to this), is critical in placing empirical constraints on interpretations of the fossil record. Research approaches include deductive analyses of fossil assemblages, in

which preservational quality of individual specimens and sedimentary context are used to infer likely postmortem modification, and live:dead studies in modern environments, whereby the taxonomic or age-class composition of a death assemblage (shells, bones, leaf litter) is compared with that of the local living community. These empirical approaches have been complemented by probabilistic models and computer simulations aimed at testing both taphonomic and ecological (supply-side) controls on the nature of the record (11, 37, 38, 85, 86; several other papers in 71).

To the uninitiated, the major sources of postmortem bias are assumed to be out-of-habitat transport of carcasses, pollen, leaves, and shells, selective destruction of species and age-classes at the accumulation site, and especially the loss of soft, nonmineralized tissues. An equally important limit on interpretation, however, is time-averaging, that is, mixing of noncontemporaneous material so that specimens from successive generations or ecologically unrelated communities occur within a single sedimentary stratum (56, 57, 128). The interval between death and the time when remains are buried beyond the reach of everyday erosional exhumation and bioturbation determines, along with environmental conditions, the extent to which processes of selective destruction can act upon the raw input from mortality and shedding. The most complete records (in which soft tissues are preserved) of ancient communities are created almost exclusively by permanent, catastrophic burial upon death. In such instances, time-averaging is zero. Even environments prone to episodes of catastrophic burial, however, are characterized by intervening periods of slow or no appreciable net accumulation of sediment. Multiple cohorts of remains may accumulate in surficial sediments during these times, so that the final death assemblage is the product of time-integrated input and its progressive, generally selective, destruction (Figure 1). This is one of the most important adjustments for a biologist to make in dealing with the fossil record or even with modern death assemblages: Sediment accumulation rates are generally much slower than biological generation rates, and so most death assemblages composed of mineralized hardparts are time-averaged to some degree. Resolution in these instances is more analogous to a dataset built by pooling successive years of census data. Whether time-averaging is perceived as an insurmountable problem or a happy advantage, smoothing the noise of short-term variability (92), depends on the question being asked.

In this paper, we discuss the quality of the fossil record with respect to such attributes as spatial resolution, fidelity of species composition, and temporal resolution. For each of these topics, we address 1) the major processes that can modify the original biological signal, 2) estimates on the magnitudes and net effects of these processes, including the methods used to make such estimates, and 3) criteria for recognizing or anticipating bias in assemblages of unknown nature. We conclude with the implications of taphonomic bias for

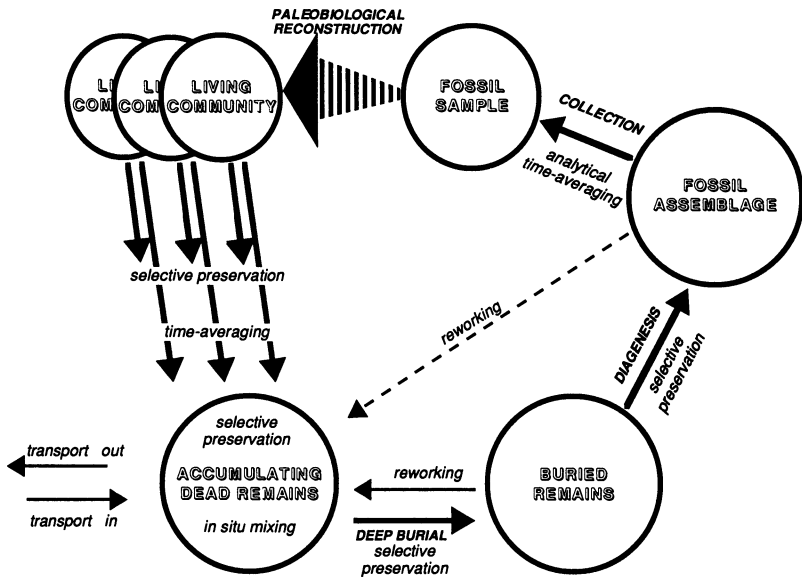


Figure 1 Taphonomic processes and circumstances that, during the fossilization of organic remains, have potential to modify the original biological signal at different postmortem phases.

current issues in (paleo)biology, such as the ability to detect events of speciation, extinction, and ecological perturbation. As invertebrate paleontologists, we stress marine systems, where most of the work has been done. We conclude with implications of these quantitative estimates for current issues in ecology, evolution, and paleobiology.

## THE LOSS OF SOFT TISSUES

The most dramatic contrast in fossil preservation is between organisms having mineralized or highly refractory tissues (composed of calcium carbonate, calcium phosphate, silica, sporopollenin, or lignin; that is, “preservable taxa”) and those that largely or entirely lack such materials (“soft-bodied taxa”).

Soft-bodied taxa can be preserved under unusual conditions, such as rapid sedimentation that catastrophically buries part or all of a community and isolates the remains from scavengers and other taphonomic agents (20, 141). Individual organisms can be preserved with soft tissues intact in a number of small-scale circumstances, including sealing by amber, tar, and encrusting organisms; “pickling” in salt and humic acids; freezing; and mineralization

under anoxic conditions (3, 139). Paleoecological, evolutionary, and biogeographic analysis of soft-bodied groups relies on the rare “preservational windows” created by such special circumstances. For some purposes, widely spaced windows (Fossil-Lagerstätten) are sufficient to track major morphological or ecological trends (21).

Under more ordinary environmental conditions such as relatively slow sediment accumulation on oxygenated seafloors and lakebeds, and on land surfaces characterized by moist and/or warm conditions, soft-bodied taxa have very low preservation potential (2, 3). These taphonomically unfavorable conditions commonly persist into the sediment for some depth because of sediment stirring by burrowing organisms, freeze-thaw cycles, and wave and tide reworking. Burial thus does not ensure preservation until it removes the remains to some threshold depth in the sedimentary column. The potential for destruction does not cease with permanent burial—there are still the perils of rock diagenesis (that is, compaction and chemical changes), tectonism, and erosion—but the many modifications that occur in the initial postmortem stages are certainly most tractable for study (Figure 1).

The destruction of soft-bodied organisms can represent a substantial loss in biological information. Most “reconstructions” of aquatic food webs and energy flows by paleoecologists thus differ fundamentally from those based on living communities both in intent and reality, and such reconstructions are useful only for broad comparisons among similarly preserved assemblages (105). Paleontologists consequently devote most effort to segments of communities with highest potential for preservation—the durable hardparts of molluscs, echinoderms, corals, arthropods, bryozoans, and vertebrates in marine communities, and vertebrates and woody or heavily cuticled plants and pollen in terrestrial systems. These “preservable taxa” are the primary focus of this review.

## SPATIAL RESOLUTION OF HARDPARTS

Except for instances of catastrophic burial, most fossil remains consist of disarticulated elements separated some distance from other parts of the same skeleton or body. Such dispersed elements can only rarely be reassembled into their individual organisms. This difficulty also precludes determining the precise spatial distribution of individuals within their habitats. However, studies in modern environments have repeatedly demonstrated that most postmortem movement of organic remains is within the range of the original life habitat for the source population, or at least within the time-averaged range of the species. Significant, out-of-habitat transport appears limited to a few settings recognizable by independent geological criteria, and to particular sets of organisms.

## *Marine Systems*

In level-bottom marine habitats, cluster analysis reveals strong agreement in live and dead molluscs, with most (80–95%) dead individuals belonging to species documented alive in the same habitat (Tables II–IV in 70; also see 99, 104). The same pattern is exhibited by crabs (93), echinoids (e.g. 89% fragment weight—89; 63), and freshwater molluscs (79–82% fidelity, based on 22, 36, 133). Exotic species thus generally account for few individuals in the death assemblage, even when they constitute a large part of the total species list. Most exotics are derived from immediately adjacent habitats (and see data on crinoids in 84, and data on benthic Foraminifera in 81). Small thin shells, especially of noncementing epifauna and shallow-burrowing infauna, are most likely to be moved from their life habitat (Table IX in 70). These exotics can often be recognized by their incongruence with the embedding sediment or with dominant associated species (e.g. species found in sand whose functional morphology or living relatives indicate ecologic preference for rocky shores).

It was originally assumed that damage to carcasses and individual hardparts could be used to rank transport distances. More recent work indicates, however, that fresh carcasses are highly durable even to energetic tumbling (1, 3) and that most long-distance transport is by relatively nondestructive means (e.g. floating, rafting, bulk movement; Table IX in Ref. 70). Most damage to hardparts results instead from processes operating within the original life habitat. In instances when already damaged hardparts are moved into another habitat, their taphonomic condition may well distinguish them from hardparts in the recipient assemblage, thereby allowing exotics to be identified, but this damage is not a function of distance traveled (e.g. 87).

Among macroinvertebrates, the record for long-distance transport must be held by nektonic cephalopods, with modern representatives showing  $10^2$  to  $10^3$  km of “necro-planktonic drift” outside their known oceanic ranges (101). Individuals may bear evidence of prolonged drift from epizoon overgrowths, such as has been recognized among extinct ammonoids and nautiloids (17, 106). Therefore, the entire group should be treated with caution if the objective is the determination of the original habitat (see also 102 on similar problems with fish and marine mammals). Diving birds can transport the shells of deep-water benthos to cliff-top middens (which may be composed of 100% exotic individuals; e.g. 76), creating bathymetrically anomalous assemblages; here the physical context of the assemblage should be the cause for suspicion. Along with offshore winds, birds can also be important agents of moving intertidal and terrestrial species into fully aquatic settings, but these exotics tend not to be numerically dominant in the recipient assemblage (22, 30, 36, 133; and see hermit crabs, 129). The most impressive out-of-habitat transport

of benthic invertebrates is associated with steep depositional slopes or with settings having episodically very high pulse-type energy, where large numbers of shells can be transported via bulk flow of the seafloor (Table IX in 70). Sedimentary structures associated with the assemblage and its larger geological context are the most valuable clues that an assemblage might be strongly biased by or consist entirely of exotic material.

### *Terrestrial Systems*

Live:dead comparisons for terrestrial vertebrates also indicate high fidelity of death assemblages to source communities at a habitat scale, despite opportunities for transport by predators, scavengers, and streams. Mammalian bone assemblages in eastern Africa have been studied in greatest detail because of the availability of data on the abundance and mortality rates of living megafauna in national parks. In the Amboseli Basin (11), Serengeti plains (16), and eastern (107) and central (122) Zaire, the relative bone frequencies of major species reflect their original habitat preferences, especially for the habitats in which mortality is concentrated (e.g. waterholes, ecotones between forest and grassland). Bones were not sampled from river channels in any of these studies, but field experiments on implanted bones (10; AK Behrensmeyer, personal communication) indicate relatively little downstream transport: The primary taphonomic effect of river channels seems to be in mixing material of different ages in the channel lag by erosional reworking of overbank deposits (Figure 2). Downstream floating of bloated carcasses may be the primary, although still rare, means of transport by water (rivers, coasts, open sea). Transport by scavengers and predators apparently does not exceed the natural range of movements of the prey when alive, especially for large-bodied prey (13, 77). Raptors also tend to sample relatively small areas ( $\sim$  few  $\text{km}^2$ ), but their concentrations may nonetheless include remains from several prey habitats, and so taphonomic evidence for this mode of concentration (distinctive fragmentation, size distribution, and selective partial digestion of skeletal elements) is an important clue to possible bias in the assemblage (4, 13). Sedimentary context (e.g. within a channel or in overbank deposits; Table 2.8 in Ref. 13) is also important in anticipating spatial resolution in fossil assemblages.

The spatial fidelity of plant death and fossil assemblages is more variable. At the high end, litter rain onto the forest floor is closely linked to source trees. In dense forests, leaves, seeds, fruits, and flowers generally do not fall further from the trunk than the height of the tree ( $\sim 20^\circ$  cone projected down from the treetop; 43, 50). Thus there is great potential for detailed reconstructions of spatial heterogeneity using terrestrial litter or its fossilized equivalent (26). Wind transport is a minor source of bias for comparatively heavy macrofloral



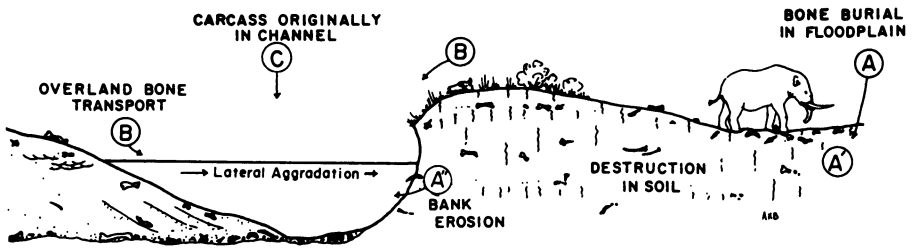


Figure 2 Model for postmortem input of bones to the sedimentary record of a river channel-floodplain system, showing potential for time-averaging, selective destruction, and reworking. (From Behrensmeier 1982).

elements (43, 66), but water transport can be significant for species living along the water's edge (25, 62, 97, 113). Fortunately, variation in postmortem transport is fairly systematic. For example, riparian and coastal species are most prone to transport because they are most likely to fall directly into water; evergreen leaves float and resist decay longer than deciduous leaves (see review in 113); leaf assemblages from large, relatively low-energy rivers contain more long-distance exotics than do those from small, high-energy streams (e.g. 90% of species are exotic—58; 113); and lakes that are broader than the height of surrounding vegetation capture more wind-transported exotics than do lakes of small surface area (113). Attention to the sedimentary/environmental context of the assemblage is thus essential in anticipating the probable spatial resolution and in identifying those species most likely to be exotic. Unfortunately, the quiet forest-floor leaf assemblages that contain fewest exotics also have low preservation potential due to oxidation, root-bioturbation, and rapid decomposition by fungi and invertebrates during the initial seasons or years of exposure, depending on moisture and soil acidity (18a, 26, 62, 103). This does not diminish the usefulness of modern death assemblages for botanists, but it does diminish the likelihood of their being preserved in the older fossil record. Leaf assemblages that accumulate on the floors of deep (and thus more permanently anoxic) lakes and on lake-head deltas and stream point-bars of rapid sedimentation have the highest likelihood of preservation (103, 113). The larger the lake, the greater the inclusion of exotic material. This coarser spatial resolution may be an advantage for reconstructing regional vegetation in some situations (e.g. 123).

The spatial resolution of pollen assemblages varies depending upon the natural "trap" (lake, peat bog, moss polster, soil) (48, 49, 120) and on how the palynologist measures compositional changes. Accumulation-rate data from assemblages in lakes < 100 ha reveal only the broadest, regional-scale



differences in pollen production (e.g. between tundra and forest) because of the effect of pollen resuspension and mixing within lakes (65), whereas pollen percentage data from the same assemblages typically allow the resolution of 10-km scale variation in forest composition (65, 134). In all studies of lake and peatland traps, the size of the trap and its distance from vegetation are the strongest factors in spatial resolution, as this determines the relative influence of wind-blown as opposed to gravity- and water-transported pollen (65, 120). Vegetational variation at the scale of hundreds of meters can commonly be resolved using small traps (15, 65). In contrast, pollen assemblages from alluvial fans, streams, and marine settings tend to have spatial resolutions at the scale of the drainage basin at best, since they are prone to selective water-transport, recycling of extant pollen from temporary reservoirs, and reworking of material from older rocks in the drainage basin (48, 125). Insect faunas have relatively similar postmortem dispersal behaviors (34, 46).

### *Common Patterns*

Possibly the most important lesson on spatial resolution from these studies is that postmortem transport generally does not homogenize death assemblages across entire landscapes. In most settings, exotic species are not numerically dominant, and thus habitat-scale patchiness in species composition is commonly resolvable, even in time-averaged assemblages. Apparent discrepancies in the distribution of living organisms and dead remains are due primarily to habitat-shifting over time (and thus shifting in areas of input of various species) and not to the signal being smeared by postmortem transport of remains (and see numerical models 12, 85, 86). Settings in which exotics are significant should generally be identifiable by independent sedimentologic evidence. Moreover, the exotic species themselves tend to be smaller and less massive than indigenous remains, ecologically discordant with indigenous material or with the host sediment, characterized by different degrees of postmortem damage, or all of the above.

## FIDELITY OF SPECIES COMPOSITION

Selective preservation, which operates even among “preservable” mineralized taxa, has been the focus of most taphonomic research. Anatomical attributes such as size, shape, density, mineralogy, and ultrastructure can influence the physical and chemical behavior of hardparts and also determine their attractiveness to bioeroders (raspers, borers) and other organisms that influence the fates of dead hardparts (3, 41, 77). These attributes vary among taxa, among

age- or size-classes within species, and among skeletal elements of a single carcass. Staff et al (115), for example, documented postmortem “half-lives” of only ~2 months for 1 mm shells but immeasurably long half-lives for 10 mm adult specimens of the same molluscan species in Texas lagoons. Environments also differ in the likelihood of hardpart preservation: Bones, for example, appear to be destroyed more quickly in tropical rainforests than on dry savannas, and they last longest under temperate and subarctic conditions (5, 9, 67, 121; RW Graham, personal communication). The “law of numbers” also applies: taxa that are rare in life and/or have slow generation times (and thus produce few dead per unit time) have a lower likelihood of being fossilized in sufficient abundance to be discovered. Finally, the circumstances of death influence postmortem preservation: Catastrophic burial generally favors hardpart preservation, for example, whereas shell-crushing and prey-swallowing predators do not.

The net effects of these processes on the composition of the final assemblage is difficult to predict: Quantitative rate data are not available for all groups in all environments; we still have little insight on the constancy of rates over the decades to thousands of years that typify time-averaging; and we do not understand how the various processes reinforce or cancel out one another. Consequently, paleontologists have relied primarily upon empirical live:dead studies, whereby the composition of a modern death assemblage or Pleistocene fossil assemblage is compared with the local living community.

### *Molluscan Assemblages*

Most live:dead studies have been conducted for shelled molluscs. At first reading of this literature, fidelity appears to vary widely, but metaanalysis suggests that much of the variance arises from differences in the quality of live data (especially single census versus replicates over time), in sampling density per habitat, and in differences in fidelity metrics (70; SM Kidwell, in preparation). When these artefacts are removed, live:dead agreement is high for many measures of community structure, despite the fact that post-mortem processes probably destroy a huge proportion of the total shells produced.

For example, for 16 studies in temperate and subtropical latitudes, 90% of species living in intertidal settings are also recorded dead there; relevant numbers in other habitats are 98% in coastal subtidal settings and 75% in marine bights and on the continental shelf (Tables II-V in 70). In streams and lakes the value is 95% (22, 36, 133). Values are lower when live communities are compared with local Pleistocene fossil assemblages (e.g. 61% of molluscs living along San

Nicolas Island, California, are present in uplifted Pleistocene marine terraces; 99), but, as is also seen among modern death assemblages (70), values rise as the geographic scale becomes coarser (e.g. 77% of species found alive today within the Californian Province are also present in Pleistocene assemblages somewhere within that Province; 126). Molluscan species that fail to be recorded in death assemblages tend to be small and thin-shelled, numerically rare, composed of organic-rich microstructures (e.g. nacre, prismatic calcite), or all of the above (70, 126; SM Kidwell, in preparation). This selectivity is consistent with the results of short-term experimental studies on shell durability. Palmqvist (90) also found slight systematic differences in preservation potential of trophic groups among marine molluscs: 93% of primary consumers (filter-feeders, browsers, detritivores) leave dead remains versus 87% of predators, scavengers, and parasites. If live communities are compared with local Pleistocene assemblages, the numbers are 81% and 72% respectively (90).

Molluscan death assemblages typically have diversities (numbers of species) twice that of shelled molluscs sampled alive in the same habitat at any single time. Consequently, low estimates of fidelity result when calculated as the percentage of dead species also found alive (54% in intertidal habitats, 33% in coastal subtidal habitats, and 45% on the open shelf; Tables II-V in 70). Similar values are found in freshwater habitats (55%; 22, 36, 133). In most instances, however, low estimates of live:dead fidelity arise from an inadequately sampled live community rather than from taphonomic processes such as selective destruction and import of exotic species: When the death assemblage is compared to a species list compiled from replicate censusing of the live community over time, thereby improving the sampling of ephemeral and otherwise sparse species, agreement rises significantly to ~75%, demonstrating the importance of time-averaging in building dead diversity (70; similar pattern in crabs—93). Several lines of evidence (rarefaction of replicate live samples; maximum longevity of individuals in community; long-term ecological and hydrographic data) suggest that several years of replicate sampling are required to build an adequate species list for live communities in intertidal settings, several decades in coastal subtidal settings, and close to a century on the continental shelf, presumably because these are the time scales over which natural cycles in species recruitment and “rare events” attain a steady state condition (temperate-latitude data only; numbers are probably higher in the tropics) (70). By implication, these are minimum estimates for the duration of time-averaging for these death assemblages. The remaining 25% of the dead species list could be interpreted as the sum of additional ecological noise (e.g. as yet unsampled live species; species that have become extinct locally because of environmental change over the period recorded by the death assemblage) and true taphonomic bias (i.e. species that do not live and have never lived in

the area, but which have been transported in from exotic habitats or exhumed from significantly older strata).

Intuitively, one expects poor agreement between live communities and death assemblages in terms of species' relative abundances, due to differences in population turnover rates (input) and preservation potential (destruction): The death assemblage should be biased numerically toward species that are short-lived and/or taphonomically robust. However, molluscan death assemblages consistently show strong fidelity to relative abundances in the live community. For example, in 12 out of 14 marine habitats in which data were based on at least five sample stations (but only a single census), rank orders are not significantly different between live and dead when the full species lists are compared (SM Kidwell, in preparation). Even higher live:dead agreements are attained if abundance is measured in terms of shell "biomass" (e.g. two habitats studied by 114). Numerical relative abundance relationships are also well preserved in freshwater molluscan assemblages (22, 36, 133), in many instances with precise agreement in rank order (total numbers of species and specimens here, however, are much smaller than in marine assemblages). Taphonomists have noted this agreement in individual datasets from the earliest live:dead studies (28, 131, 132), but paleontologists have been reluctant to accept it as a general pattern because it is counter-intuitive to the alarmingly high rates of postmortem destruction reported from some environments (e.g. the 60-day half-lives for bivalves mentioned above; 115).

There are at least two possible explanations for good agreement in molluscan relative abundance. The first is that species relative abundances in death assemblages are dominated by the most recent cohorts of dead shells added from the living community, rather than all cohorts being integrated over the entire period of time-averaging, a hypothesis consistent with dead-only species tending to be numerically rare. The second possible explanation is that although species vary in their rates of dead-shell production due to differences in population dynamics (opportunistic boom-and-bust behavior versus slow-growing and larger-bodied stress-tolerant and equilibrium species), destruction may vary in such a way as to take a proportionately higher toll on species having the highest dead-shell production rates, so that the net death assemblage more nearly resembles standing relative abundances. Such a systematic pattern of selective destruction would not be unreasonable, given that short-lived species tend to be smaller (75) and that juveniles are underrepresented in most assemblages (35). Distinguishing between these and other possible explanations requires more fieldwork, especially on shell carbonate budgets, because it is clear that much (most?) biogenic carbonate is recycled through dissolution (e.g. 130). However, the high correlation between molluscan death assemblage composition and community composition is useful even if the underlying causes are not yet known.

### *Other Benthos*

Lower levels of live:dead fidelity are found for marine organisms with more fragile tests, as one might predict. In back- and peri-reef habitats along the Egyptian shore of the Red Sea, for example, only 76% of regular and irregular echinoid species found alive ( $n = 17$ ) left recognizable fragments in the local death assemblage; 74% of species in the death assemblage ( $n = 19$ ) were also documented alive (89). Species found both dead and alive comprised 89% of total fragment weight, and so, as for the molluscs, species suspected of being exotic are not dominant in the death assemblage. The only live:dead study of scleractinian corals indicates that death assemblages have lower diversities than does the source living community, suggesting that the aragonitic skeletons of at least some growth forms are more prone to destruction than echinoderm and mollusc skeletons (J. Pandolfi, personal communication–90a). The only live:dead study of crabs that we know (93) indicates that half the species found alive in a single census were present dead; the most abundant species in the death assemblage was not found alive but does occupy the area during other seasons of the year. Fidelities are thus strongly group dependent.

### *Land Animals*

Live:dead data on vertebrate assemblage fidelity are limited to mammals on African savannas. In Amboseli basin, Kenya, bones surveyed for six major habitats were compared with six years of data on live species richness, relative abundances, and population turnover rates (12). Of the 47 species of wild mammals with body weights  $\geq 1$  kg, 72% were found in the bone assemblage, but as in molluscan assemblages, this varied with trophic group and body size. From 95 to 100% of large herbivores and carnivores ( $>15$  kg body weight) were present, compared with only 60% and 21% of small herbivores and carnivores, respectively. Rank ordering of species in the bone assemblage showed strong agreement with that expected from turnover rates and standing abundances. Bias related to body size was still evident, however. Among ungulates, the largest herbivores ( $>200$  kg) had higher than expected numbers in the bone assemblage (e.g. elephants and rhinos 2–10 times higher, although still rare), and small herbivores ( $<100$  kg) were less abundant than expected. Bone assemblages were dominated by seasonal migrants, especially those of the dry season when mortality is highest. A study of four riverside habitats of eastern Zaire found a similar underrepresentation of small-bodied species in the bone assemblage (107, and see 111 for similar size bias among freshwater fishes). Rapid burial of small bones by trampling and by blowing sand are possible explanations for bias against small species, as are preferential fragmentation by trampling, more rapid rates of weathering, and more complete destruction by carnivores and scavengers (12, 107). In both mammalian stud-

ies, however, death assemblage diversity is not enriched relative to the living community the way it typically is among molluscs; the implication is that bones have significantly lower preservation potential in nonmarine records than do molluscs in shallow marine deposits.

A similar bias against small species is found in comparing the living mammal community with Pleistocene and older fossil assemblages (39, 142). Although small mammals may be preserved in correct rank order relative to one another, they are typically underrepresented relative to large-bodied species; this discrepancy is exacerbated when fossil assemblages are surface collected rather than bulk sampled (142).

Little taphonomic work has been published for insects. There is, however, a preservational bias against less sclerotized taxa and, based on a comparison between Quaternary packrat midden assemblages and modern pitfall traps in the same rockshelters, herbivores are underrepresented in the fossil faunas and scavengers are overrepresented (46).

### *Land Plants*

The extent to which leaf litter records species diversity varies greatly with climatic regime, which produces differences in forest heterogeneity (24, 26). For example, a single sample of 350–450 naturally shed leaves captures ~80% or more of forest species in the surrounding hectare in temperate settings, but much less in tropical settings. Litter production is also closely correlated with plant relative abundance as measured by trunk basal area, at least for temperate forests (27, 43).

Pollen assemblages can provide high-fidelity records with respect to species presence/absence when averaged over a very large area (see discussion under spatial resolution), but the fidelity of relative abundance data varies greatly depending upon what part of the total pollen spectrum is examined. Assemblages from Quaternary lakes are dominated by wind-pollinated plants because their pollen is produced in larger quantities, is released more easily from reproductive organs, and is more aerodynamic; this dominance pertains even in wet tropical settings where the forest canopy is dominated by insect-pollinated trees (65). For this wind-pollinated part of the community, pollen assemblages are faithful recorders of plant relative abundances in the source area (measured as total number of trees or trunk basal area in the forest, or using the abundance of co-occurring macrofloral remains; 65, 66) within the effective pollen source area, especially when the forest is relatively homogeneous. By contrast, animal-pollinated plants are almost always grossly underrepresented because their larger, heavier pollen falls much nearer the source tree and in smaller amounts per tree. Spatial resolution is thus higher than for wind-pollinated taxa, but relative abundance in an assemblage is generally a poor proxy



of the importance of these animal-pollinated plants in the surrounding vegetation (65).

## TEMPORAL RESOLUTION

Time-averaging refers to the pooling of successive populations and communities into a single assemblage of remains, presumably because the rate of sediment accumulation and burial is slow relative to population turnover (128) (Figure 2). When sediment accumulation rates are low, noncontemporaneous remains can accumulate on the same surface. In addition, remains of one age can be mixed with those of earlier or later deposits by physical and biotic processes. Physical processes include decimeter-scale erosion and redeposition by storms and tides, and meter-scale erosion by stream cutbanks, all of which rework remains into younger deposits. Burrowing organisms displace skeletal remains over tens of centimeters, with occasional instances of meter-scale bioturbation. Mixing within the sedimentary column may alone produce a time-averaged fossil assemblage, but most time-averaged deposits are the result of a combination of both near-contemporaneous mixing and low sediment accumulation rates, which place sequential deposits in relatively close vertical succession.

Hypothetically, time-averaging can produce a fossil assemblage that differs significantly from an instantaneous census of the live community in several distinctive ways:

*Summing of input.* Preserved diversity may sum the biota from both normal conditions and short-term, chance recruitment events. Normally rare species that produce an abundance of skeletal remains during brief pulses may thus come, in the death assemblage, to outnumber the normally dominant species. Age or size-class distributions may also be modified in this way.

*Cumulative destruction.* Cohorts of organic remains deposited early in the period of time-averaging will experience a longer interval of mixing and postmortem destruction than will younger cohorts, and thus the earlier cohorts should suffer greater modification, loss, and repositioning within the sediment. Moreover, within any given cohort, less durable elements will be modified or lost before more durable ones. In the final assemblage, the most durable portions of the youngest cohorts thus might contribute the strongest biological signal.

*Environmental change.* The effects of time-averaging can be even more insidious in that local environmental conditions may change over the period of time-averaging, so that a single fossil assemblage telescopes the record of different conditions into a single deposit. Successive cohorts thus may be from different communities and subject to different styles of taphonomic modifica-



tion. The longer the period of time-averaging, the more likely environmental change becomes.

Temporal mixing may also occur when fossils of significantly greater age are eroded from nearby deposits and deposited in an accumulation of recently dead remains. The disparity in ages can be great. For example, Miocene (~15 million year old) shark teeth and mollusc shells are currently eroding from the cliffs of Chesapeake Bay, where they mix with the shells of living molluscs. In the fossil record, such extreme age-mixing is recognized by the geological context (erosion surfaces, adjacent unmixed fossils) and the co-occurrence of species that are normally separated by large stratigraphic intervals. Fortunately, this magnitude of fossil mixing is rare. In a compilation of more than 3000 fossil mammal assemblages, only 10 contained species mixed from deposits more than one million years older than the principal fauna (J. Alroy, personal communication).

### *Determining the Duration of Time-Averaging in Modern Death Assemblages*

The scale of time-averaging is the difference between the time of death of the oldest individual in the assemblage and the time of death of the youngest. This is not necessarily equal to the duration represented by the bed of enclosing sediments. Single volcanic ash falls and submarine turbidity flows, for example, occur over only a few hours or days, but nonetheless might entomb the remains of earlier generations as well as animals or plants killed during the sedimentary event. On the other hand, the duration represented by the fossil assemblage could be much less than that of the enclosing bed. Where rates of hardpart destruction are high, for example, fossils may represent only the youngest cohorts contributed to the sedimentary unit.

The age of the oldest shell (or bone) in a currently forming death assemblage is a simple measure of the time represented by the accumulation; in fossil or subfossil deposits, two or more dates are necessary to establish both the older and younger age-limits for the assemblage. The most obvious way to determine the duration of time-averaging is to date fossils directly, an approach that has been very useful in deposits younger than 40,000 years in which the radiocarbon method can be applied to shell carbonate, vertebrate bone, and plant material (52).

Amino acid racemization geochronology is another technique that can provide estimates of the age of bone and shells; it is based on the progressive postmortem increase in the ratio of D-alloisoleucine and L-isoleucine (A/I) (7, 136). Significant variation in A/I within an assemblage can indicate time-averaging (59). Although less precise than radiocarbon dating and subject to a variety of local effects (7, 88), the technique is less expensive and has a greater time range (up to 1.5 million years in mid-latitudes) (137).

Finally, historical records can also provide some absolute-age estimates of time-averaging. Bones of the American bison—locally extinct for more than 100 years—can be found among modern bones in the channel of the East Fork River, Wyoming (10), and shells of the American oyster *Crassostrea virginica* are still found on British beaches despite its apparent failure to become naturalized following commercial introductions that lasted until 1939 (18). The presence of such remains provides a minimum estimate for the duration of time-averaging in surficial sediments.

Enough evidence has now accumulated to estimate the duration of time-averaging for many of the depositional environments represented in the fossil record (71). Some evidence is from direct-dated fossils, while extrapolations from sedimentation rates, the likely persistence of hardparts, and resampling studies provide other estimates.

At the shortest time scales of days to seasons are the rare instances in which fragile tissues and behavioral ephemera are preserved in spectacular detail: the tracks of a passing herd, the digested remains of a meal preserved in dung and owl pellets, and individuals and in some instances entire communities trapped by tree sap, floods, or thick ash falls. Although some already-dead material can be swept up along with living organisms, these event-deposits nonetheless offer the finest temporal resolution available within the time-averaging spectrum.

Remains that accumulated over only a few seasons or decades are also rare. Notable examples are pollen, insect, and some fish assemblages from delicately laminated deposits in some lakes (14, 47, 135) and some marine predator middens (octopus, crab).

Vertebrate assemblages from terrestrial soils and land surfaces and plant material from unlaminated lake sediments and peats probably have temporal resolutions of decades to thousands of years (59, 61, 96). Vertebrate predator middens probably also mostly lie within this time span, as illustrated by boreal and temperate wolf dens (61) and accumulations in caves (19, 118).

Direct age data indicate that assemblages from many habitats are time-averaged over a hundred to several thousand years. These includes molluscan and benthic foraminiferal assemblages from nearshore marine settings (53, 80), and molluscan assemblages from large lakes (33). The record of benthic and planktonic microfossils in deep-sea sediments is also commonly resolvable to this scale (23, 42). Pleistocene and Holocene plant material in arid environments is sometimes preserved in packrat middens. These are rich sources of information on past changes in vegetation (15), but the typical time-span recorded by a midden sample is approximately 2000 years (KW Flessa, DM Smith, unpublished). Most vertebrate assemblages hosted by river channels also reflect accumulation over this time scale (10). Data from deltas, aggrading clastic shelves, carbonate platforms, and reefs are too sparse for confidence,

but the high net sedimentation rates in these environments suggest that many of their fossil assemblages probably also fall within the hundreds-to-thousands-of-years range (this excludes assemblages concentrated during marine reworking of these deposits).

The longest durations of time-averaging commonly encountered are on the order of thousands to tens of thousands of years. These characterize marine and terrestrial settings with very low net rates of sediment accumulation. However, with the exception of modern sediment-starved and sediment-bypassed temperate shelves (53), relatively few directly dated assemblages constrain our estimates. The erosion and redeposition of major river deposits as the channel migrates across a floodplain suggest extensive time-averaging (10; Figure 2), and large caves are famous for their low sediment input and temporal persistence. Cave deposits can commonly be subdivided to produce higher resolution samples, but the presence on some modern cave floors of bones and dung from late Pleistocene vertebrates (e.g. 83) indicates significant time-averaging. Death assemblages from modern reefs have not been surveyed systematically. We expect that reef deposits are extensively time-averaged because their highly porous and invaginated structure permits colonization at many levels within the framework, especially during periods when construction is primarily outward rather than upward.

### *Recognizing Scales of Time-Averaging in Fossil Assemblages*

Funds, facilities, and historical records are not always available for direct determination of time-averaging, and even though they may preserve organic carbon, most deposits are well beyond the range of radiocarbon and amino-acid methods. In such instances, indirect approaches must be used. These methods can also be used to rank the relative temporal resolution of modern death assemblages. Corroboration by direct-dating in Quaternary records increases our confidence in the use of indirect methods for the older fossil record (57, 70, 71).

**ARGUMENT BY ANALOGY** Paleontologists commonly use analogous Recent deposits to guide interpretations of fossil assemblages. If the sedimentary deposit that contains the fossils is known in modern settings to be characterized by low time-averaging, then the fossil assemblage is inferred to have comparable temporal resolution. There are limitations, of course, to a strict uniformitarian approach. Some ancient depositional environments—for example, the vast shallow inland seas of the Mesozoic and Paleozoic—have few analogs in the modern world. Also, organisms producing hardparts have evolved substantially through geologic time, so that the durable aragonitic shells of Recent molluscs, for example, may not provide good taphonomic analogs for the thin calcitic brachiopod shells that characterize many Paleozoic assemblages. Kid-

well & Brenchley (72) have argued that the greater durability of post-Paleozoic skeletonized fauna has in fact resulted in greater time-averaging in younger shallow marine deposits. Hardpart destroyers and modifiers have also evolved, introducing additional opportunities for rates of destruction to change.

**STATE OF HARDPART PRESERVATION** Many indirect approaches to estimating time-averaging have focused on the condition of the fossils themselves, since a specimen's condition should only worsen with increasing exposure to taphonomic processes after death. However, attempts to calibrate such a "taphonomic clock" (69) in absolute years have yielded mixed results. Behrensmeyer (9) documented the progressive disarticulation and weathering of vertebrate skeletons on African savannas and found that the transformation from pristine to highly degraded elements occurred within ~15 years. Owing to differences in ultraviolet radiation and colonization by boring organisms, the disintegration of bones appears to be slower in temperate and subarctic conditions and faster in rainforests (5, 67, 121; RN Graham, personal communication). Among marine molluscs, shell color and luster are progressively altered in older shells, but other modifications such as abrasive rounding, fragmentation, and encrustation show little correlation with the specimen's age-since-death over the 10,000 years investigated so far (54, 74, 94, 138). These varying results may be explained by the frequent but unpredictable episodes of burial and exhumation that most hardparts experience, especially in shallow marine settings. Temporary burial clearly slows or stops the taphonomic clock for many kinds of shell damage, especially those that proceed most rapidly at the sediment-water interface. Outside of anoxic lake sediments, pollen undergoes an analogous series of decompositional stages caused by oxidation and corrosive porewaters (36a, 64), and the tests of Foraminifera and other microfossils reveal they are subject to partial dissolution by porewaters, bioeroders, and ingestion by predators (73, 124). Clearly, the resolving power of the taphonomic clock will vary with different kinds of damage and also among depositional environments.

Although the taphonomic condition of molluscs is a poor timekeeper over  $10^2$ – $10^4$  years, it does allow discrimination of shells that have been reworked into Recent assemblages from 100,000-year-old deposits (52, 55, 138). Reworked fossils may also be distinguished by the presence of exotic sediment filling shell interiors, and such fossils are commonly composed of highly resistant material (56). The presence of reworked fossils in a deposit is an indication of extensive time-averaging, and when the disparity in age or in original environment is substantial, such potentially misleading fossils may be easily recognized and thereby eliminated from subsequent paleobiological analysis.

**STRATIGRAPHIC CONTEXT** Insights into temporal resolution can also be drawn from surrounding rocks; this may be one of the strongest lines of evidence for the older stratigraphic record (69). Reworked fossils, for example, are commonly associated with erosional surfaces, and the low net sedimentation rates that permit prolonged time-averaging are indicated by diagnostic minerals, submarine crusts, and deep and well-developed soils. Fossil assemblages from beds containing evidence of extensive biological reworking are also likely to be time-averaged to some degree.

### *Relative Degrees of Time-Averaging*

A direct quantitative determination of time-averaging is not always possible, and, in such instances, relative classification schemes are useful. The following scheme (70) divides the spectrum of time-averaging into four categories based on phenomena that can be recognized from the ecological and geological context of individual assemblages. These relative degrees can be quantified by analogy with the time scales at which these phenomena operate in the modern world.

**ECOLOGICAL SNAPSHOTS** These reflect zero or minimal time-averaging. They are recognized by taphonomic features such as a high proportion of articulated specimens and/or soft-tissue preservation, and by ecological and sedimentological features indicating sudden death (escape structures, anoxic minerals). While selective mortality or preservation may not result in the participation of all species or age classes in the original community, snapshot assemblages approximate the samples an ecologist might take during a collecting trip. Such records are rare but provide an extraordinarily detailed, high-resolution picture of the life of the past. Quantitatively, snapshot assemblages are inferred to provide temporal resolution of minutes to years.

**WITHIN-HABITAT TIME-AVERAGED ASSEMBLAGES** These are assemblages time-averaged from a single, temporally persistent community over a period of relative environmental stability. Many generations are mixed within the assemblage, including both transient and ecologically persistent species. Samples of pollen from lake laminae, bone assemblages within overbank deposits, and many shallow-marine shell accumulations fall within this category. Quantitatively, these assemblages probably mostly reflect accumulation over years to thousands of years.

**ENVIRONMENTALLY CONDENSED ASSEMBLAGES** These are assemblages time-averaged over periods of significant environmental change (climate, substrate, water depth), and so species with environmental tolerances that did not overlap may be preserved together. Evidence for environmental change typically

comes from the associated sediments but may be corroborated by the mixture of species that are ecologically incompatible and yet show no evidence of lateral transport. As an example, shells of intertidal and shallow subtidal molluscs found in surficial seafloor sediments at 50 m depth in the North Sea today are relicts of communities indigenous to that site 8000 to 9000 years ago when the sea level was lower (29, 45). Vast areas of modern continental shelves are characterized by shelly sands produced by environmental condensation over the most recent, postglacial rise in sea level. Bone accumulations in caves are also good examples of environmental condensation through changes in terrestrial climate. Quantitatively, these assemblages form over time spans of centuries to tens of thousands of years.

**BIOSTRATIGRAPHICALLY CONDENSED ASSEMBLAGES** These assemblages incorporate species with evolutionary ranges that do not overlap, indicating time-averaging over very long periods during which one or more local species become extinct or make their first appearance in the stratigraphic record. The period of accumulation, in many instances, spans major environmental changes as well as evolutionary time. Although noteworthy because of the potential to confound evolutionary patterns, examples are very rare. Quantitatively, this is time-averaging on an evolutionary time scale, reflecting accumulation and mixing at a site over hundreds of thousands to millions of years.

## IMPLICATIONS: PUTTING THE DEAD TO WORK

### *Using Death Assemblages for Rapid Assessment of Modern Community Composition*

The rain of dead hardparts and their accumulations in surficial sediments are, for many groups, good proxies for species' presence and relative abundances in the source community; paleontologists have established the spatial resolution of such samples and correction factors for biases.

Relative abundances of pollen in lake sediments, for example, reflect the distance-weighted "pollen source strengths" of wind-pollinated trees within a  $10^1$ – $10^2$ -km radius; these strengths are, in turn, closely correlated with the standard diversity measure of trunk basal area (65). Pollen and insect assemblages from packrat middens have higher spatial resolution but less relative abundance fidelity, and thus they are appropriate for a different set of questions (or provide answers with a different level of confidence). Leaf litter rain is an excellent means of approximating forest diversity and basal trunk area from 0.1–1.0 hectare areas, depending upon forest heterogeneity (linked to latitude); litter on the forest floor can be gathered and used as a substitute for "rain" because destruction on the ground is so rapid (24, 26). Bone assemblages also



appear to have high fidelity to source community composition at the habitat scale (12, 122), but data as yet are limited to semiarid tropical African areas. Molluscan death assemblages, based on data largely limited to clastic settings in north temperate latitudes, show similar high fidelity at the habitat scale despite more prolonged time-averaging (70; SM Kidwell, in preparation).

### *Death Assemblages as Baselines of Modern Community Change*

One way to assess the environmental impact of human activities is to compare the compositions of local biota before and after the event/change. In many instances, however, historical records on community composition do not extend far enough back in time, are based on anecdotal information, or must be extrapolated from other sites. Moreover, preimpact communities are often known only from a single census, rather than from time series that would reveal the full range of natural variation in the community. In such instances, the composition of the local death assemblage can serve as an excellent proxy for pooled, ecological data, especially if attention is focused on relatively durable groups (36, 40, 93, 95, 100). In some instances, time-resolution even within time-averaged assemblages is sufficient to reconstruct a fine-scale (decadal) history of biotic response, for example, pollen records of forest disease and land clearance by humans (65, 135) and diatom records of recent lake acidification (30a).

The widespread outbreak in the past 30 years by the coral predator *Acanthaster planci* (crown-of-thorns sea star) on Australia's Great Barrier Reef provides a revealing example of the strengths and weaknesses of death assemblage data in marine settings (140). Although it does identify *Acanthaster* as a long-standing member of the reef community, the sedimentary record has little promise for resolving questions such as whether past outbreaks have been identical in intensity, duration, or frequency over time-scales of concern to reef-management, because of mixing by bioturbation and uncertainties associated with radiocarbon dates (which can resolve ages hundreds of years apart, but not decades).

### *The Long-Term Stability of Communities*

The high-resolution fossil records of pollen and insects preserved in undisturbed lake sediments have provided strong evidence for the individualistic behavior of species over the past 18,000 years: Community associations appear to have been transient in the face of climatic change (47, 112). The taphonomic reliability of these patterns lends credence to similar patterns reported for terrestrial vertebrates (60) and marine invertebrates (127), the individual assemblages of which are subject to more prolonged time-averaging. In such settings, mixing of noncontemporaneous faunas has been an alternative inter-



pretation for ecologically anomalous associations of species. By focusing on those depositional settings and taxa that are not prone to time-averaging, the long-term cohesion of biotic communities can be tested with paleontological data.

### *The Significance of Morphological Variation*

Morphology is the basis for recognizing fossil species, and morphological change is the evidence for evolution in the fossil record. Morphological variation may have taphonomic as well as biological causes, however, including the selective destruction of morphs, the production of "new" deformed morphs during post-burial compaction, and the mixing of multiple generations or populations through time-averaging (14, 68). These taphonomic components of variation complicate comparisons between fossil and living populations and comparisons among fossil samples. For example, because variation in a single population of hardparts is likely to be less than among the hardparts derived from many populations, an increase in variation between two successive fossil assemblages could simply reflect an increase in time-averaging. In addition, clinal variation in space or time can be pooled through range shifts during the period of time-averaging, obscuring microevolutionary trends (14). Samples for analysis of microevolutionary change in fossil populations should thus come from taphonomically comparable assemblages.

On the other hand, long-term evolutionary stasis can be assessed by spacing samples so widely that time-averaging is unlikely to produce artificial overlap between successive samples. This strategy has been effective in a growing number of analyses (e.g. late Cenozoic bryozoans and bivalves; 31, 116). However, any significant degree of time-averaging will complicate the interpretation of rapid evolutionary changes in morphology, whether in branching or phyletic mode. These effects can blur such changes into apparent gradualism or, if time is unrecorded by the rocks, sharpen them into apparent instantaneousness.

An additional source of uncertainty arises in some studies from "analytical time-averaging," that is, the pooling of specimens from overly thick stratigraphic intervals or the deliberate pooling of samples from different localities for which precise age-equivalence is not clear (13). This may artificially inflate levels of morphological variation as effectively as true, taphonomic time-averaging (109). For a complete discussion of the effects of "observational" as well as preservational completeness on evolutionary patterns, see McKinney (82).

### *Geographic and Environmental Distributions*

Taphonomic research strongly suggests that the presence of a fossil at a given site is unlikely to mislead in terms of its original broad geographic distribution.

For example, lateral transport is rarely sufficient to shift fossils outside their original biogeographic province. For many taxa, including most benthic invertebrates, the presence of fossils in particular environments is also unlikely to be misleading, as burial is usually within the life habitat. This means that, with a few general caveats (e.g. be wary of data from environmentally condensed assemblages and of reliance on rare species, which are most likely to be exotic), the reconstruction of biogeographic and environmental histories for various taxonomic groups is justified.

### *Are Extinctions Sudden or Gradual?*

There is increasing appreciation for the importance of taphonomic processes in shaping the fossil record of extinction. For example, many individuals with potential for fossilization can nonetheless be destroyed, with the result that the geographic and stratigraphic (evolutionary) ranges of species will tend to be less than those of the original living populations. Moreover, individuals that evade destruction can still be mixed with fossils of slightly different age; downward piping into older sediments will make a species appear to have arisen earlier than it really did, and reworking into younger sediments will delay its apparent extinction (37). The net result of these antagonistic trends is uncertainty in the actual timing of local and global origination, immigration, and extinction. Probabilistic models have been proposed to quantify error bars for species' ranges, using the actual patchiness of a fossil species' occurrence as a guide (78, 119).

These issues rise to the fore in debates over the nature and timing of mass extinctions, those geologically brief times in earth history when large and taxonomically diverse arrays of organisms disappeared from the record (51). For example, a strict literalist's reading of the fossil record suggests that the demise of many species preceded the Cretaceous-Tertiary boundary (32) and that a few dinosaurs even survived past it (98). When the effects of taphonomy and sampling are taken into account, however, the fossil record is more compatible with sudden extinction (108, 110). Post-Cretaceous dinosaur remains, which are restricted to river-channel deposits, are almost certainly reworked from older strata (6).

The timing of extinction is also important in the debate over the role of humans in animal extinctions during the late Pleistocene and Holocene. The hypothesis of Pleistocene overkill is that the demise of many North American mammals coincided with the arrival of humans on the continent (79). If the arrival of humans on Pacific islands several thousand years ago coincided with the extinction of many of the resident birds (117), human activity can again be implicated in many local extinctions. Establishing the relative and absolute temporal resolution of fossil assemblages is thus critical to establishing cause and effect relationships in extinction.

## CONCLUSIONS

In a recent review of pollen taphonomy, ST Jackson (65) concluded:

The relationship between pollen assemblages and their source vegetation is complex but comprehensible. The complexity derives from the numerous physical and biological processes intervening between the vegetation and the pollen assemblages. The comprehensibility derives from the fact that the effects of the processes can be predicted from theory and are supported by empirical correspondences. Distortions and biases, once understood, can be corrected for qualitatively or quantitatively.

Comparable statements can now be made for other major groups in the fossil record, most notably the comparatively well-studied macroflora, mammals, and benthic molluscs. We still have much to learn about environmental (including latitudinal) variation in fidelity and its underlying causes, and we need more work on developing criteria to recognize various degrees of time-averaging in the older fossil record. Moreover, work has barely begun on the question of long-term evolutionary changes in the production of preservable remains and the taphonomic processes that affect them. Studies of modern death assemblages have nonetheless established the basic dimensions of the problem, and they are giving us essential quantitative insights into rates of postmortem modification and possible correction factors for the Cenozoic at least. Also, despite clear limits on what can be inferred from hardpart assemblages due to the pervasiveness of time-averaging and selective destruction, these are still hugely informative records of past life: At biologically meaningful spatial and temporal scales, the fossil record is a robust archive of ecological and evolutionary information. Paleocologists and evolutionary paleobiologists have become able to put rigorous confidence limits on their data and to gauge a system's suitability for answering a given question. As biologists increasingly appreciate the importance of processes operating on broad temporal and spatial scales, the fossil record will become an essential means of extending the time-frame of observation on population and community behaviors.

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