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Taphonomy and paleobiology

Anna K. Behrensmeyer, Susan M. Kidwell, and Robert A. Gastaldo

Abstract.—Taphonomy plays diverse roles in paleobiology. These include assessing sample quality relevant to ecologic, biogeographic, and evolutionary questions, diagnosing the roles of various taphonomic agents, processes and circumstances in generating the sedimentary and fossil records, and reconstructing the dynamics of organic recycling over time as a part of Earth history. Major advances over the past 15 years have occurred in understanding (1) the controls on preservation, especially the ecology and biogeochemistry of soft-tissue preservation, and the dominance of biological versus physical agents in the destruction of remains from all major taxonomic groups (plants, invertebrates, vertebrates); (2) scales of spatial and temporal resolution, particularly the relatively minor role of out-of-habitat transport contrasted with the major effects of time-averaging; (3) quantitative compositional fidelity; that is, the degree to which different types of assemblages reflect the species composition and abundance of source faunas and floras; and (4) large-scale variations through time in preservational regimes (megabiases), caused by the evolution of new bodyplans and behavioral capabilities, and by broad-scale changes in climate, tectonics, and geochemistry of Earth surface systems. Paleobiological questions regarding major trends in biodiversity, major extinctions and recoveries, timing of cladogenesis and rates of evolution, and the role of environmental forcing in evolution all entail issues appropriate for taphonomic analysis, and a wide range of strategies are being developed to minimize the impact of sample incompleteness and bias. These include taphonomically robust metrics of paleontologic patterns, gap analysis, equalizing samples via rarefaction, inferences about preservation probability, isotaphonomic comparisons, taphonomic control taxa, and modeling of artificial fossil assemblages based on modern analogues. All of this work is yielding a more quantitative assessment of both the positive and negative aspects of paleobiological samples. Comparisons and syntheses of patterns across major groups and over a wider range of temporal and spatial scales present a challenging and exciting agenda for taphonomy in the coming decades.

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What is Taphonomy?

The fossil record is rich in biological and ecological information, but the quality of this information is uneven and incomplete. The same might be said for many types of neobiological information, but in such cases, sampling biases are imposed by scientists and are explicable as part of a research design. With fossils, natural processes have done the sampling and created the biases before research begins. Taphonomy seeks to understand these processes so that data from the fossil record can be evaluated correctly and applied to paleobiological and paleoecological questions.

Efremov (1940: p. 85) first defined taphonomy as “the study of the transition (in all its details) of animal remains from the biosphere into the lithosphere,” naming a field that we

characterize more generally as “the study of processes of preservation and how they affect information in the fossil record” (Behrensmeyer and Kidwell 1985). Since the 1950s, the analysis of postmortem bias in paleobiologic data has been one of the prime motivations of the field, but taphonomy has always been a multi-tasking science (e.g., see historical reviews in Behrensmeyer and Kidwell 1985; Cadée 1991), and this remains true today. States of preservation of biotic remains are not only (1) indicators of how faithfully biological history has been recorded (issues of paleobiologic data fidelity and resolution), but are also (2) testaments to environmental conditions (the aegis of “taphofacies”), and (3) evidence of important aspects of biological evolution (skeletal and biochemical novelties, live/dead

interactions and feedbacks), because organisms not only produce potential fossils but also are highly effective recyclers of plant and animal material. Strictly speaking, the logical limits of taphonomy are defined by its focus on processes and patterns of *fossil preservation*¹, but in practice, taphonomy serves a broader role in stimulating research on all types of biases affecting paleontological information, including those introduced by collecting, publication, and curation methods on the one hand, and stratigraphic incompleteness on the other (see also Lyman 1994; Donovan and Paul 1998; Holland this volume).

Taphonomy today is focused first and foremost on a geobiological understanding of the earth, grounded on the postmortem processes that recycle biological materials and affect our ability—positively and negatively—to reconstruct past environments and biotas. The classic flowchart of taphonomic transformations (Fig. 1) is now underpinned by a much fuller and quantitative understanding of interim states and pathways of fossilization, owing to an explosion of interest in the field since the early 1980s. Some of the most notable advances have been in (1) microbial, biogeochemical, and larger-scale controls on the preservation of different tissue types; (2) processes that concentrate biological remains; (3) the spatio-temporal resolution and ecological fidelity of species assemblages; and (4) the outlines of “megabiases” (large-scale patterns in the quality of the fossil record that affect paleobiologic analysis at provincial to global levels and at timescales usually exceeding ten million years). These advances are highlighted in this review because of their impact on paleobiologic analysis and their promise as research themes in the coming decades. Such advances reflect an increasingly ecumenical approach in terms of scientific methods (field measurements, ma-

nipulative experiments, analyses of synoptic data sets, probabilistic models) and scientific disciplines (tools and expertise from biogeochemistry, geomicrobiology, isotope geochemistry, geochronology, ecology, biomechanics, archeozoology, anthropology, sedimentology, sequence stratigraphy; see recent reviews and syntheses in Wilson 1988a; Allison and Briggs 1991a; Donovan 1991; Gifford-Gonzalez 1991; Lyman 1994; Brett 1995; Briggs 1995; Haglund and Sorg 1997; Claassen 1998; Martin 1999).

Taphonomy still is strongly oriented toward modern analogues as a means of identifying and quantifying processes, but increasingly exploits the stratigraphic record for hypothesis testing. Reliance on the fossil record to “bear its own witness” is an absolute necessity for some facies and taxa, but constitutes a powerful independent method even for environments and groups that are well represented in the Recent world. Regardless of subject, however, most taphonomists remain determinedly empirical in approach, dedicated to assembling baseline information on taphonomic patterns and processes. Such work usually targets individual fossil assemblages or modern analogues for particular groups of organisms (protists to vertebrates) and types of environments (glacial to abyssal plain). This fact-gathering focus is typical of a relatively new field of study, but a theoretical component also is beginning to develop, with proposals for general models for organic preservation (e.g., Lyman 1994; Kowalewski 1997). There have been a number of forays into the realm of taphonomic theory by paleobiologists seeking to distinguish sampling biases from biological patterns. These include attempts to account for preservational biases using assumptions of random preservation and “hollow curve” models for original taxonomic abundance as well as models that test the effects of incomplete fossilization, stratigraphic incompleteness, nonrandom distributions of facies and hiatuses, and blurring of generations by time-averaging on our ability to evaluate phylogenies, rates of evolution, and tempo and mode of speciation (Marshall 1990, 1994; Gilinsky and Bennington 1994; Foote

¹ It often falls to Taphonomy to answer the most basic of paleontological questions, “What is a fossil?” Material definitions concerning degree of mineralization and criteria based on age considerations are problematic for Holocene to sub-Recent organic remains. Hence, we prefer a more flexible definition: “A fossil is any nonliving, biologically generated trace or material that paleontologists study as part of the record of past life.”

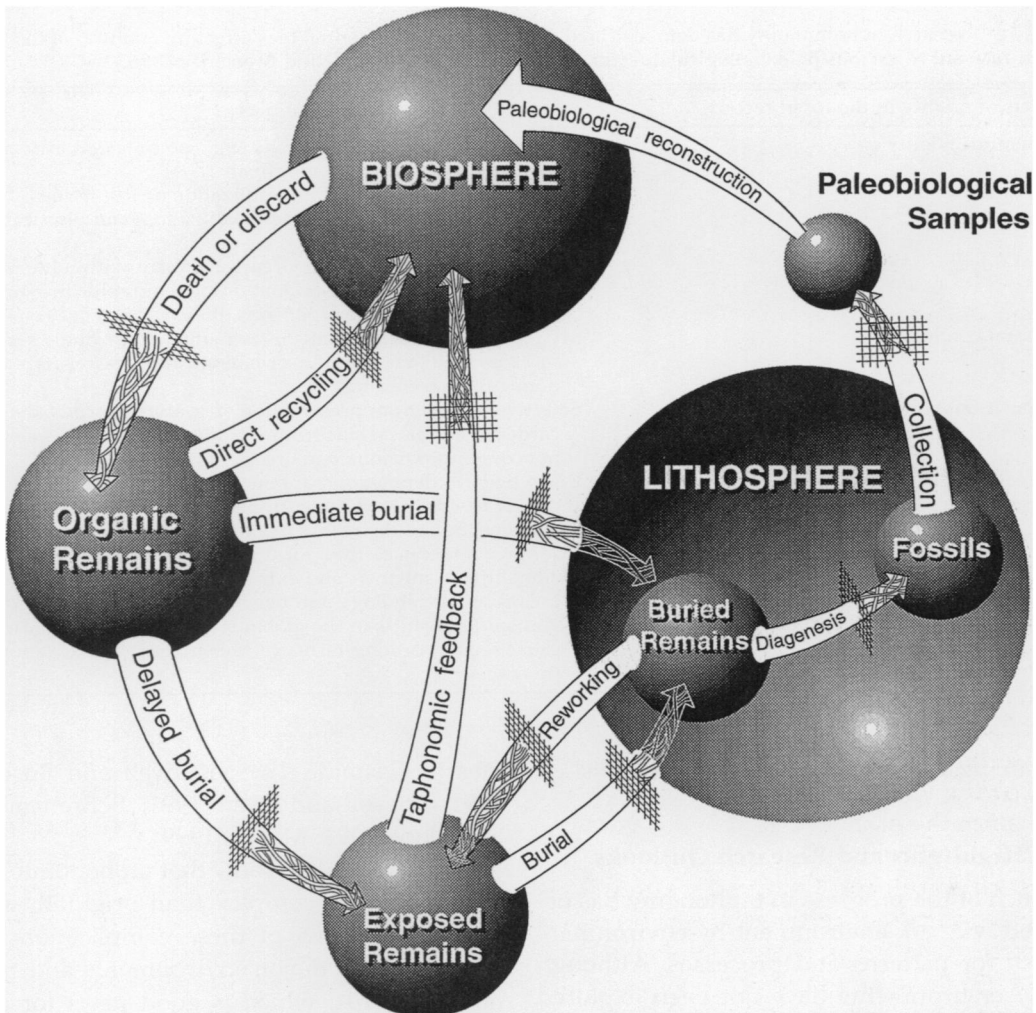


FIGURE 1. The main pathways for organic remains from death to paleobiological inference. Each path is affected by taphonomic processes and circumstances that filter the information as it passes to the next stage. Taphonomy is the study of how biological, chemical, and physical processes operating between each stage preserve or destroy organic remains and affect information in the fossil record (Behrensmeier and Kidwell 1985).

1996; Foote and Raup 1996; Roopnarine 1999; Wagner 2000a; Simões et al. 2000a; and see papers in this volume by Wagner, Holland, Alroy et al., and Jablonski). Arguments about whether the lack of a fossil record is evidence for original absence (e.g., Vrba 1995; Foote et al. 1999; Valentine et al. 1999; Novacek et al. 2000) also draw upon underlying assumptions about how taphonomy works at a more general level.

Here we review highlights of taphonomic research from the past 15 years, since the tenth anniversary issue of *Paleobiology*, and suggest

some promising directions for the future. This review is organized by scales of processes in order to underscore two key points. One is the wide array of different qualities of the fossil record that paleobiologic analysis depends upon and that taphonomic analysis is relevant to; these qualities range from the preservation of DNA molecules to the analytic comparability of samples from disparate regions and geologic periods (Table 1). A second is the multidisciplinary nature of taphonomic analysis at all scales, illustrated by the variety of new techniques and lines of evidence that are

TABLE 1. Research in taphonomy has demonstrated many sources of potential bias affecting qualities of the fossil record relevant to various paleobiological questions. (Adapted from Kidwell and Brenchley 1996.)

Aspects of quality in the fossil record	Sources of bias
Biochemical fidelity	Shifting of original compositions (e.g., isotopic and molecular) by diagenesis and metamorphism
Anatomical fidelity	Destruction or incomplete mineralization of soft tissues; disarticulation, fragmentation, recrystallization, and physical deformation
Spatial fidelity	Transport out of life position, rearrangement within life habitat, transport out of life habitat or biogeographic province (e.g., necroplanktonic organisms, pollen)
Temporal resolution	Mixing of noncontemporaneous remains within single sedimentary units via physical or biological processes (taphonomic time-averaging)
Compositional fidelity	Selective destruction/preservation of species, morphs, discarded body parts; bias from introduction of exotics and noncontemporaneous remains
Completeness of time series	Episodicity in deposition; taphonomic or diagenetic obliteration of fossils in surviving lithofacies (producing gaps and condensation of the record); poor preservation of some environments (deposits thin, localized, or readily eroded)
Consistency in preservation over Geologic time	Major shifts in intrinsic and extrinsic properties of organisms, including morphology and behavior in relation to other organisms—or shifts in the global environment, which can cause secular or long-term cyclic changes in preservation (megabiases)

now being brought to bear on both established and new issues in paleobiology.²

Highlights and Research Outlooks

Much of the progress in taphonomy has occurred via an environment-by-environment search for patterns and processes. Although many environments have not been explored fully, it is clear from available actualistic and stratigraphic studies that depositional context is extremely important in controlling the quality and nature of fossil preservation. Environmental setting determines such important factors as the likelihood of immediate burial, exhumation and reworking, the biogeochemistry of the early diagenetic environment, and the nature of the local community that generates or is capable of recycling tissues (i.e., is mortality typically attritional or catastrophic, are biominerals undersaturated or in surplus?). From such considerations the general taphonomic attributes of most major fossil-preserving facies now can be sketched as a framework for more detailed testing (e.g., ta-

bles in Gastaldo 1988; Kidwell and Bosence 1991; Speyer and Brett 1991; Behrensmeyer and Hook 1992; Martin 1999).

Detailed studies show that taphonomic systems are more complex than originally supposed, but many of these complications are shared across major environments and taxonomic groups, which is good news for data comparability and the potential for unifying theory. Contrary to the impressions given by basic paleoecology texts, some taphonomic features previously thought to be diagnostic of a particular taphonomic process or circumstance are now recognized as having a different dominant cause or resulting from multiple processes (the concept of "equifinality" [Lyman 1994]). A good example is the disarticulation and fragmentation of animal hardparts: a growing body of actualistic evidence indicates that, in both continental and marine settings, such damage is overwhelmingly biogenic (from predation, scavenging, etc.) rather than an index of physical energy (e.g., Haynes 1991; Jodry and Stanford 1992; Behrensmeyer 1993; Cadée 1994; Cate and Evans 1994; Lyman 1994; Oliver and Graham 1994; Best and Kidwell 2000a; for Cambrian exam-

² Taphonomy also provides guidelines concerning how humans can become fossilized. See Mirsky 1998 and Haglund and Sorg 1996 for user-friendly reviews.

ple see Pratt 1998). Moreover, in the absence of recycling metazoans, damage is dependent upon the state of decay of connective tissues rather than the distance of hydraulic transport (e.g., Allison 1986; Kidwell and Baumiller 1990; Greenstein 1991; Ferguson 1995). Similarly, rounding of hardparts is more likely to result from repeated reworking within a high-energy environment than from abrasion during long-distance transport, as demonstrated by comparing indigenous shells from beaches versus exotic shells in turbidites, or bones that have been trampled or chewed versus those transported in rivers (Behrensmeyer 1982, 1990; Potts 1988; Davies et al. 1989; Andrews 1990; Meldahl and Flessa 1990; Kidwell and Bosence 1991; Spicer 1991; Gastaldo 1994; Lyman 1994; Llona et al. 1999; Nebelsick 1999). Paleoanthropologists and archeologists have learned that many taphonomic agents, including humans, can cause similar patterns of bone modification, skeletal-part representation, and faunal composition; these patterns are heavily influenced by which bones and taxa are the most durable and identifiable in the face of destructive processes (Grayson 1989; Gifford-Gonzalez 1991; Lyman 1994).

A second complicating realization, derived primarily from experiments on marine macroinvertebrates, is that many taphonomic processes are inconstant in rate over time. Carcasses of regular echinoids, for example, fracture like live echinoids until microbial decay is sufficiently advanced for connective ligaments to be weaker than the calcite plates, a period of "ambiguous" behavior that lasts a few hours in tropical temperatures but days or weeks in cold water; once this decay threshold is passed, the disintegration of the test proceeds at a much faster rate than in pre-threshold specimens (Kidwell and Baumiller 1990). As a second example, the postmortem "disappearance," probably by dissolution, of aragonitic shells from early postlarval mollusks in Texas lagoons is very rapid initially but slows logarithmically, so that loss is best described as a taphonomic half-life (Cummins et al. 1986a,b). In contrast, the episodic movement of plant debris downstream, the alternating burial/exposure of shells on seafloors and the reworking of bones in channels all provide examples of non-

steady rates of postmortem modification, which are linked to chaotic aspects of the extrinsic environment and over long periods of time could appear to be linear.

Controls on the Preservation of Biological Remains

Most individual organisms never become fossils, but taphonomic research has discovered much about the circumstances that capture rich samples of past life. These samples may be quite different from those of living systems because of postmortem processes, but there is plenty to work with, whether the tissues of interest (1) are composed exclusively of volatile organics (e.g., nucleic acids, amino acids, simple sugars, starch; see Briggs this volume), (2) include refractory organics (lignin, collagen, cellulose, chitin, glycolipids, resins, sporopollenin [see Briggs 1993]), or (3) are mineralized during life (major biominerals are aragonite, calcite, apatite, various forms of silica).

Preservation depends on an array of processes and conditions operating at different scales (Fig. 1). These are

1. *the supply side of the equation*: rate of input, total volume, and composition (durability) of biological remains delivered to the environment;
2. *the nature of the pre-burial environment*: selectivity and intensity of modification by local physical, chemical and biological agents at the sediment-air or sediment-water interface. Modification may be destructive (as in the case of bioerosion, scavenging, and dissolution) or stabilizing (as in the case of bioencrustation and den/burrow formation);
3. *the rate (immediacy) and permanence of burial*, which determines how long tissues are exposed to processes operating on the sediment surface as opposed to those within the sedimentary column; and
4. *diagenetic conditions within the upper part of the sedimentary column* (highly dynamic mixed zone), where organic remains and sediments are still subject to bioturbation, meteoric effects, microbial processes, and possible physical reworking. Postburial modification may stabilize (e.g., mineral coatings, infillings, replacements) or reduce biochemical fidelity

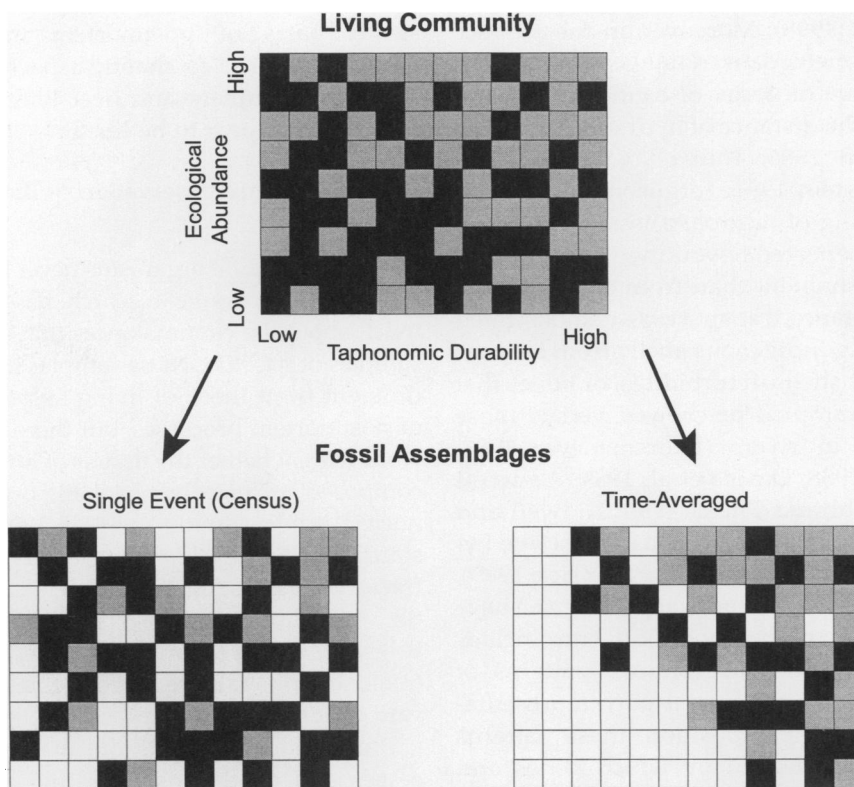


FIGURE 2. Schematic portrayal of information changes in two different types of fossil assemblages compared with a hypothetical living community at one point in time. Each cell is a species characterized by two variables, ecological abundance during life and taphonomic durability of the remains; the living community consists of equal numbers (50:50) of species that are permanent residents (black cells) and transients (gray cells, e.g., highly mobile forms or those on seasonal or longer-term population cycles). White cells in the fossil assemblages indicate species that are not preserved. The single-event assemblage (census) will capture most of the resident and some of the transient species (in this example, 80% and 37% of the cells (species) in the life assemblage, respectively) and is not strongly affected by taphonomic durability. In contrast, the attritional, time-averaged assemblage will be biased toward higher durability and more abundant species, capturing 44% of the resident and 52% of the transient species. A similar graphic model could be applied to all types of organisms or organic parts, with varying results for census versus time-averaged assemblages depending on the range of durability, type of community, environment, and length of time-averaging.

and anatomical detail (hydrolysis, continued maceration, dissolution, recrystallization).

Beyond these near-surface factors, which embed the remains in a consolidated sedimentary matrix, the long-term survival of fossilized material is determined by

5. *the fate of the larger sedimentary body.* The key factors here are strongly linked to tectonic setting, which determines rates of sediment aggradation and compaction, depth of eventual burial (and thus nature of later diagenesis and metamorphism), and structural deformation. The longest-surviving fossil-bearing sequences occur in stable cratonic margins or

interiors and in continental rift margins or aulocogens (failed branches of continental rifts) that have escaped tectonic recycling. Examples include Archaean and Proterozoic earliest life deposits (Grotzinger 1994; Walter et al. 1995) and Devonian through Carboniferous land plants and animals (Kidston and Lang 1920; Rolfe et al. 1994).

Fossil assemblages commonly are parsed according to the way remains initially accumulated in the depositional system, i.e., in terms of major types of supply-side input (Fig. 2). Attritional (time-averaged) assemblages reflect the release of discarded organic prod-

ucts (e.g., pollen, leaves) and input from normal mortality over periods of years to millennia. Single-event (census) assemblages reflect unusual events such as sudden anoxia, severe storms, pathogen outbreaks, droughts, and volcanic eruptions that kill large numbers of individuals at one time (minutes to months). In the former case, it may take considerable time and slow net sediment accumulation to amass a dense concentration of organic remains in a single bed in the absence of some other concentrating process; in the latter, this may happen literally overnight.

Soft-Part Preservation.—The taphonomy and diagenetic biogeochemistry of metazoan soft tissues and biomolecules have been the subject of intense field and laboratory study in the last 15 years (Allison and Briggs 1991b; Henwood 1992a; Briggs 1993; Briggs and Kear 1994a,b; Allison and Pye 1994; Westall et al. 1995; Bartley 1996; Briggs et al. 1997, 1998; Bartels et al. 1998; Davis and Briggs 1998; Duncan et al. 1998; Orr et al. 1998; Briggs this volume). Delicate molecules like DNA are extremely difficult to preserve, as would not surprise anyone who has struggled to extract good material from living organisms, and the oldest confidently identified DNA is less than 100 k.y. old (Bada et al. 1999; Wayne et al. 1999). Although cinematically fabled, amber is not favorable for DNA preservation. Resins are not airtight, and so generally only the most refractory portions of insects are fossilized (Stankiewicz et al. 1998; but see preservation of volatile structures in amber via dehydration [Henwood 1992a,b]).

Laboratory degradation of metazoan carcasses under oxic and anoxic conditions demonstrates the relative reactivities of tissue types, means of retarding decay, and absolute rates of decay. Such data are used not only to (1) rank tissue reactivities, but (2) rank rates of mineral precipitation in fossil specimens, (3) establish criteria for recognizing oxic and anoxic subenvironments (diagenetic minerals precipitate in distinctive Eh-pH fields created by different anaerobic microbial communities), and (4) provide absolute time limits on the contemporaneity of co-occurring fossils (Allison 1988; and see McGree 1984, and for plants Ferguson 1995). Apparently, only phos-

phatization proceeds rapidly enough to preserve undegraded volatile muscle and visceral tissues in three dimensions (including embryos [Xiao and Knoll 1999]), whereas calcite and pyrite are sufficient to preserve structures composed of more slowly decaying chitin, lignin, and collagen (Allison 1988; Allison and Briggs 1991b; Underwood and Bottrell 1994). Instances of successful in vitro precipitation of minerals provide further insights into the dynamics of fossilization of soft tissues: "phosphatization" may consist of (1) fine-grained 0.3- μ apatite that precipitates in the tissues themselves (subcell features preserved), (2) 1- μ apatite that replaces invasive bacteria and creates a fully 3-D pseudomorph of cells or tissues, and (3) comparable replacement but of *noninvasive* bacterial coats, which replicate only the outlines of cells or tissues (Wilby and Briggs 1997; and see Franzen 1985; Martill 1990; Xiao and Knoll 1999; also Taylor 1990 and Evans and Todd 1997 for replication of soft tissues by biological overgrowth).

Laboratory and field studies on animal soft-tissue preservation and konservat-lagerstätten have greatly elaborated and deepened our understanding of the multiple advantages of anaerobic decomposition. Anaerobic decomposition is in fact slower (Kristensen et al. 1995) and far less effective (efficient) in decomposing refractory material than aerobic decomposition, thus prolonging the window for preservation. If it is linked to low oxygen in overlying water, this excludes predators and scavengers and keeps them from destroying tissues before these can be encased by microbial mats (fostering local anoxic conditions) or become buried in sediment below the redox discontinuity level (Seilacher 1984; Seilacher et al. 1985; Wilby et al. 1996; Palaios 1999; and see Janzen 1977 on microbial strategies against metazoan scavenging). Even though anaerobic decomposition proceeds almost as fast as aerobic decomposition on volatile material, only anaerobic microbial processes liberate the appropriate cations and levels of alkalinity to precipitate early diagenetic phosphate, calcite, pyrite, siderite, and other minerals (Allison and Briggs 1991b). In terms of soft-tissue preservation, a little decay of organic matter is thus good (Allison 1988; Chaf-

etz and Buczynski 1992) because, by depleting oxygen, the local chemical environment is driven to anaerobic conditions that favor mineral precipitation in and around the organics, which is essential to their long-term preservation.

A general model for superb soft-part preservation thus has the following requisites: (a) a carcass (microbe, catkin, worm, wombat) in good condition at time of death (death without significant morbidity or other damage to body parts); (b) postmortem isolation of the carcass from scavengers and physical disruption; (c) decomposition retarded until mineralization is accomplished; and (d) avoidance of later reworking (advantages of entombment within tree stump, incised valley fill, karst depressions, structural graben, or aulocogen [e.g., Lyell and Dawson 1853; Dawson 1882; Archer et al. 1991; Cunningham et al. 1993]). Points a–c can be accomplished via catastrophic burial (obrution), for example from ash falls and sediment avalanches on land and from various sedimentary processes in water (Baird et al. 1986; Demko and Gastaldo 1992; Wing et al. 1993; Crowley et al. 1994; Rolfe et al. 1994; Yang and Yang 1994; Downing and Park 1998; Brett et al. 1999; Feldmann et al. 1999; Hughes and Cooper 1999; Labandeira and Smith 1999).

However, contrary to stereotypes, enclosed water bodies having acidic, hypersaline, or anoxic conditions are highly effective environments for preservation *without* unusual sediment burial events, and in fact this is a more common means of konservat-lagerstätte formation (e.g., Seilacher et al. 1985; Whittington and Conway Morris 1985; Martill 1988; Barthel et al. 1990; Briggs and Crowther 1990; Brett and Seilacher 1991; Schaal and Ziegler 1992; Bartley 1996; Bartels et al. 1998). Heat and chemical transformation of volatiles to more refractory forms (e.g., charcoal, kerogen, graphite [Butterfield 1990; Lupia 1995; Vaughan and Nichols 1995]), before or after burial, is one means to lengthen the window of opportunity for mineralization (point c above). Alternative paths are acidity, which is antimicrobial, and pickling (subaqueous dehydration via salt); both can retard decomposition sufficiently for slowly polymerizing silica to replace subcel-

lular to tissue-grade structures with high fidelity (e.g., Knoll 1985; Scott 1990). Anoxia is a highly efficient agent of konservat-lagerstätte formation in aquatic systems when it affects overlying waters (accomplishing points a–c above). This may result from elevated temperature or organic matter overload (e.g., a phytoplankton bloom), and is the cause rather than the effect of metazoan mortality (e.g., Stachowitsch 1984). Although catastrophic death is important (for point a), it turns out that *mass* death is not a prerequisite for superb preservation of multiple individuals in one sedimentary layer, as evidenced by the wide spacing of metazoan specimens within classic konservat-lagerstätten (Seilacher et al. 1985). Even in overall aerobic environments, single carcasses can be highly effective in depleting oxygen from the immediate environment within sediment or under microbial mats, creating their own locally anaerobic conditions favorable to diagenetic mineralization (e.g., Schäfer 1972; Spicer 1980; Martill 1985; Baird et al. 1986; Allison et al. 1991b).

Taphonomic Feedback.—Both soft and hard biological remains can develop positive feedback systems that significantly enhance their own chances for preservation, especially where remains are densely concentrated. For example, skeletal hardparts can alter water flow dynamics, promote trapping and binding of sediment, and increase the erosion resistance of seafloors (Kidwell and Jablonski 1983; Seilacher 1985; Behrensmeier 1990). Also, unusually high inputs of carcasses can overwhelm the capacity of normal recycling processes (e.g., scavengers faced with a surfeit of carcasses; oxygen depletion by dead organic matter in aquatic systems). Concentrations of remains also can create favorable diagenetic conditions, “self-buffering” local porewaters to reduce overall hardpart dissolution or promoting replacement of associated remains (e.g., Kotler et al. 1992; Schubert et al. 1997). Concentrations can have negative effects as well. For example, shell-rasping grazers become a major destructive force only where dead shells reach a critical abundance in tidal channels (Cutler 1989), and drought concentrations of animals around water holes focuses death and skeletal input but also may increase

physical destruction and exhumation via trampling and digging (Haynes 1985, 1988, 1991).

Preservation of Mineralized and other Refractory Tissues.—Most aspects of this subject—the supply side, pre-burial effects, rates of burial, early diagenesis, and permanent incorporation into the stratigraphic record—have received heightened attention in the last 15 years, and we refer the reader to several excellent review volumes for details (Donovan 1991; Allison and Briggs 1991a; Lyman 1994; Martin 1999; Martin et al. 1999a).

A major focus for work on the postmortem sedimentology and biology of hardparts (i.e., biostratinomy) has been paleoenvironmental analysis (taphofacies analysis, sensu Speyer and Brett 1986; Parsons and Brett 1991), and these efforts are proving to have direct as well as indirect value to paleobiology. For benthic systems, for example, analysis of styles of fossil preservation and concentration reveal bed-by-bed and facies-level differences in key ecological factors such as frequency of storm reworking and oxygen levels that would be undetectable from inorganic matrix alone (e.g., Norris 1986; Parsons et al. 1988; Meyer et al. 1989; Brett et al. 1993; Ausich and Sevastopulo 1994). Determinations of the extent to which different marine and continental environments bear distinctive “taphonomic signatures” also provide a means of recognizing exotic, out-of-habitat material in fossil assemblages (e.g., Davies et al. 1989; Miller et al. 1992), or material reworked from older deposits that are ecologically or evolutionarily irrelevant to the host deposits (e.g., Argast et al. 1987; Plummer and Kinyua 1994; Trueman 1999).

Insights from hardpart condition derived from analysis of death and fossil assemblages increasingly are complemented by actualistic experiments on rates and controls on modification. This work provides insights into recycling processes themselves, for example, the huge importance of organisms as agents of skeletal transport and modification in modern systems (described above; thus affecting the limits to back-extrapolation over geologic time) and of factors intrinsic to the hardpart producers themselves (i.e., the roles of body

construction and ecology in determining different hardpart fates in the same environment; “comparative taphonomy” of Brett and Baird 1986, with implications for differential representation of taxa sensu Johnson 1960). For example, in modern shallow marine settings, mollusk shell fragmentation commonly varies independently of water energy or bears direct evidence of being the product of predators and scavengers rather than physical environment itself (Feige and Fürsich 1991; Cadée 1994; Cate and Evans 1994; Best and Kidwell 2000a), and branching colony form among scleractinian corals significantly increases postmortem disintegration relative to massive and encrusting forms (Greenstein and Moffat 1996; Pandolfi and Greenstein 1997a; and for bryozoans see Smith and Nelson 1994).

Most actualistic studies of this type previously focused on variation among taxa within a single major group, or variation among environments for a single taxon, but now include benthic foraminifera (Martin et al. 1999b), gastropods (Walker 1989, 1995; Taylor 1994; Walker and Voight 1994), bivalves (Parsons 1989; Meldahl and Flessa 1990; Parsons and Brett 1991; Cutler and Flessa 1995; Best and Kidwell 2000b), echinoids (Greenstein 1993; Nebelsick 1995), crinoids (Meyer and Meyer 1986; Llewellyn and Messing 1993; Silva de Echols 1993; Baumiller et al. 1995), brachiopods (Daley 1993; Kowalewski 1996a), and various shell-encrusters (Bishop 1989; Walters and Wethey 1991; Lescinsky 1993, 1995; McKinney 1996). In continental settings, intensive work on rates of litter decomposition (Boulton and Boon 1991; Ferguson 1995) and on sources and signatures of macrofloral material in deltas and other organic-rich coastal environments (Gastaldo et al. 1987) provides a valuable basis for comparison with the stratigraphic record. Lab and field investigations have also targeted arthropods (e.g., Wilson 1988b; Henwood 1992a; Martinez-Delclos and Martinell 1993; Labandeira and Smith 1999; Wilf and Labandeira 1999; Smith 2000; Labandeira et al. in press), fish, birds, and other lower vertebrates (Elder and Smith 1984; Smith et al. 1988; Wilson 1988c; Oliver and Graham 1994; Blob 1997; Stewart et al. 1999; Llona et al. 1999), and mammals including hu-

mans (Frison and Todd 1986; Haynes 1988, 1991; Fiorillo 1989; Andrews 1990; Blumenschine 1991; Behrensmeyer 1993; Kerbis Peterhans et al. 1993; Sept 1994; Tappen 1994a; Haglund and Sorg 1997; Cruz-Urbe and Klein 1998; Cutler et al. 1999). Zooarcheologists and paleoanthropologists have contributed important actualistic research linking damage patterns to taphonomic processes in their efforts to distinguish human from non-human bone modification and assemblage formation. Over the past 15 years, zooarcheologists have made important advances in characterizing bone modification patterns for specific taphonomic agents and developing more accurate methods for analyzing skeletal-part ratios (e.g., inclusion of limb shaft fragments, which were formerly omitted from such analyses, has a significant impact on archeological inferences [Bartram and Marean 1999]). This work is featured in some major volumes (Bonnichsen and Sorg 1989; Solomon et al. 1990; Hudson 1993; Lyman 1994; Oliver et al. 1994) as well as individual field and laboratory studies of hyenas (Blumenschine 1986, 1988, 1991; Marean 1992), lions (Dominguez-Rodriguez 1999), predatory birds and small mammals (Andrews 1990; Cruz-Urbe and Klein 1998; Stewart et al. 1999), and other pre- and postdepositional processes (Lyman 1985, 1994; Noe-Nygaard 1987; Marean et al. 1991, 1992; Tappen 1994b).

Actualistic studies of hardpart modification are also determining the security—and pitfalls—of “traditional” paleontologic inferences about spatial resolution and time-averaging of skeletal assemblages (and see next section). Among the questions amenable to experimentation and measurement are, How far are fossilizable materials transported outside the original life habitat? What proportion of material is moved (how great is the dilution factor for indigenous material in the ultimate host deposit)? Over what periods can biological materials survive in various environments, how different are those periods, and to what extent can these periods of potential time-averaging be interpreted from fossil condition? These questions have generated research on possible “taphonomic clocks” of damage accrual (for individual specimens or

assemblages overall), how such clocks vary among groups, and how they behave with elapsed time-since-death (do rates of deterioration decrease, increase, or remain steady for a specimen held under “constant” postmortem conditions)?

Comparisons of death assemblages with local live communities are one powerful means of assessing out-of-habitat transport and time-averaging that has been applied to many marine and continental groups (reviewed by Kidwell and Flessa 1995; and next section). Direct dating of mollusk shells in death assemblages is increasingly used to explore time-averaging and taphonomic clocks in marine systems (e.g., Powell and Davies 1990; Flessa et al. 1993; Flessa and Kowalewski 1994; Martin et al. 1996; Meldahl et al. 1997a; Kowalewski et al. 1998), and the results (1) settled disputes on scales of time-averaging (commonly thousands of years even for intertidal and shallow subtidal assemblages, and tens of thousands on the open shelf, contrary to rapid rates of individual shell destruction that can be measured experimentally); (2) established the highly probabilistic and unsteady rather than monotonic accrual of damage with elapsed time-since-death (owing to erratic exposure to taphonomic agents); and (3) established the probabilistic nature of down-core stratigraphic ordering in shell ages (linked to relative rates of sediment aggradation and physical and bioadvection). A very promising direction of new research involves comparisons of major co-occurring taxa, such as mollusks versus benthic foraminifera (Martin et al. 1996; Anderson et al. 1997) and lingulid brachiopods (Kowalewski 1996a,b), where bioclasts have disparate postmortem durabilities and thus high potential for “disharmonious” scales of time-averaging.

For the paleobiologist collecting in the field, one of the most obvious taphonomic aspects of the record is the concentration of fossils in select beds or horizons and the nonrandom quality of fossil preservation. Work on this topic continues to be primarily stratigraphic rather than actualistic, and such studies consider (1) how concentrations are distributed with respect to gradients in biological input, sediment reworking, and net sediment accu-

mulation; (2) whether such concentrations can be utilized for basin analysis (stratigraphic applications, including error-bars in biostratigraphy [see Holland this volume]); and (3) whether diverse concentration types have implications for the qualities of paleontologic information (e.g., positive versus negative effects of hiatuses in sedimentation, likely scales of time-averaging, and selective preservation). Much of this work is framed in a sequence-stratigraphic context and encompasses a range of continental (Behrensmeyer 1987, 1988; Dodson 1987; Eberth 1990; Behrensmeyer and Hook 1992; Gastaldo et al. 1993a; Rogers 1993; Smith 1993; Badgley and Behrensmeyer 1995; Smith 1995; Wilf et al. 1998; Rogers and Kidwell 2000) and marine settings (Kidwell 1991, 1993; Doyle and Macdonald 1993; Fürsich and Oschmann 1993; Ausich and Sevastopulo 1994; Brett 1995; Rivas et al. 1997; Kondo et al. 1998; Fernández-López 2000; also various papers in Kidwell and Behrensmeyer 1993). This and other research in the stratigraphic record is yielding new evidence for particular modes of accumulation, including predation (Wilson 1988c; Fernández-Jalvo et al. 1998; Andrews 1990), trapping (Richmond and Morris 1996), fluvial reworking (Schmude and Weege 1996; Smith and Kitching 1996), and drought-related or other types of mass death (Sander 1989; Rogers 1990; Fiorillo 1991; see also Eberth et al. 1999). Actualistic studies based on core samples in modern environments (e.g., Gastaldo and Huc 1992), as well as studies that track hardpart reworking under different energy and net-sedimentation conditions, would be valuable additions to continuing stratigraphic efforts.

In terms of future directions, marine studies have continued to focus on midlatitude settings, but attention to fully tropical settings is increasing. This includes both reefs and associated pure carbonate sediments (Miller 1988; Parsons 1989; Miller et al. 1992; Dent 1995; Perry 1996, 1999; Stoner and Ray 1996; Zuschin and Hohenegger 1998) as well as siliciclastic and mixed composition seafloors (Best and Kidwell 2000a), which rival carbonate sediments volumetrically on modern tropical shelves. In addition, many field surveys now include time-lapse experimental arrays

over multiple years (Walker 1988; Callender et al. 1994; Best and Kidwell 1996; Walker et al. 1998; Parsons et al. 1999; Kennish and Lutz 1999) and in situ assessment of porewater geochemistry (Goldstein et al. 1997; Walker et al. 1997; Best et al. 1999). Rather than deducing early diagenetic conditions or taphonomic consequences, these can be measured directly, and the new multiyear rate information provides more explicit links to radiocarbon-calibrated studies of skeletal deterioration.

Finally, the microscopic modification and breakdown of mineralized microstructures before and during shallow burial—that is, “weathering” and early diagenesis—still receive relatively little attention, notwithstanding their huge importance in recycling biological materials. These relatively ordinary and pervasive processes are a counterpart to the extraordinary processes that preserve soft tissues, and deserve the same highly focused level of geologic, geochemical, and geomicrobiological analysis. Although the signatures of such processes may be less obvious than other kinds of damage, and require SEM to fully identify (e.g., Cutler and Flessa 1995), skeletal materials in all environments are subject to attack from some combination of the following: physical oxidation, hydrolysis, and UV light (especially in continental settings); microbor-ing (by algae, fungi, larvae, etc. everywhere); microbial maceration (of microstructural organic matrix, in both aerobic and anaerobic conditions); and dissolution (of mineral phase within hardparts; including back-precipitation and recrystallization of minerals, which may reset isotopic ratios [Budd and Hiatt 1993]). Limited actualistic work to date indicates strong environmental differences in rates and specific pathways, but except in cases of rapid permineralization (e.g., Downing and Park 1998), hardparts generally become less resistant to destruction during reworking and time-averaging. For example, compared with bones in dry, highly seasonal, savannah settings (Behrensmeyer 1978a; Lyman and Fox 1989), those in rainforests appear to weather more slowly but are soft and spongy from the activities of bioeroders such as fungi (Kerbis Peterhans et al. 1993; Tappen 1994b; and see Cadée 1999 for supratidal example). Degrada-

dation in temperate and arctic settings generally is slow (Noe-Nygaard 1987; Andrews and Cook 1989; Sutcliffe 1990), indicating that bones on the surface have a longer opportunity for burial in cold environments. Bone weathering stages based on actualistic studies (e.g., Behrensmeyer 1978a) have been applied to the fossil record (e.g., Potts 1986; Fiorillo 1988; Cook 1995) with some success, although distinguishing primary weathering damage from similar features (e.g., cracking) acquired after burial or during diagenesis can be problematic.

In marine settings, there is growing evidence that microbial processes are at least as important as physico-chemical ones in the "dissolution" of molluscan shell both on the seafloor and during shallow burial, preferentially attacking organic-rich microstructures and proceeding at similar rates in both anaerobic and aerobic settings (Poulicek et al. 1988; Cutler and Flessa 1990; Glover and Kidwell 1993; Clark 1999; for brachiopods see Emig 1990; Daley 1993; Daley and Boyd 1996). Body size clearly has a strong effect on the preservation of macrobenthic shells (as also among continental bone assemblages [e.g., Behrensmeyer and Dechant Boaz 1980]), and there is growing evidence that rate of shell disintegration declines over time during early diagenesis (Cummins et al. 1986b; Glover and Kidwell 1993). Thus the dynamics of "loss budgets" may be complex. For example, in an innovative and highly influential set of field experiments in Texas lagoons, Cummins et al. (1986b) documented taphonomic "half-lives" as short as 60 days for mm-scale postlarval shells, suggesting very high rates of carbonate shell recycling (and see Staff et al. 1985, 1986). However, they subsequently calculated that nearly all shell carbonate produced in those sediments must be preserved to obtain the observed shell content in the long-term record; that is, virtually all of the larger shells that constitute the bulk of the skeletal biomass produced by the live community must survive (Powell et al. 1992). Other actualistic and stratigraphic evidence shows that the molluscan fossil record is time-averaged but relatively high-fidelity (various live/dead studies and paleontologic analyses based on the $> \sim 2$ -mm

size fraction; for review and synthesis see Kidwell and Bosence 1991), and the Texas study supports this by illuminating how biological information can be captured in shelly death assemblages, even under conditions that may seem unfavorable on the basis of short-term loss rates.

Spatial and Temporal Resolution

Postmortem import and export of remains to an accumulation site, and the mixing of multiple generations of organisms and/or communities during time-averaging, determine the spatial and temporal resolving power of a fossil assemblage. Along with the differential destruction of species that occurs during these processes, space- and time-averaging of organic input also affect compositional fidelity of a fossil assemblage (Fig. 2). In this paper, "*fidelity*" refers to how closely (faithfully, accurately, truthfully) the fossil record captures original biological information, be it spatial patterning or the presence/absence and relative abundances of species; and "*resolution*" refers to the acuity or sharpness of that record, i.e., the finest temporal or spatial bin into which the fossil remains can confidently be assigned.

Although much more work is required for a full taxonomic and environmental picture, a taphonomic highlight of the past 15 years has been the tremendous advance in quantifying the magnitudes and selectivities of postmortem transport and time-averaging, both in modern systems and the stratigraphic record, using a diverse array of scientific methods for different groups (Figs. 3, 4). Some key hypotheses of paleontologic reconstruction, for example order-of-magnitude estimates of time-averaging, down-core stratigraphic mixing of cohorts, and how damage accrues over elapsed time, have been tested directly via radiometric and other dating of modern death assemblages (particularly the series of papers on molluscan assemblages of the Gulf of California; citations in preceding section). Both time-averaging and its relationship to "spatial averaging" also have been explored productively via probabilistic modeling (various authors in Kidwell and Behrensmeyer 1993).

The expanding baseline of information on

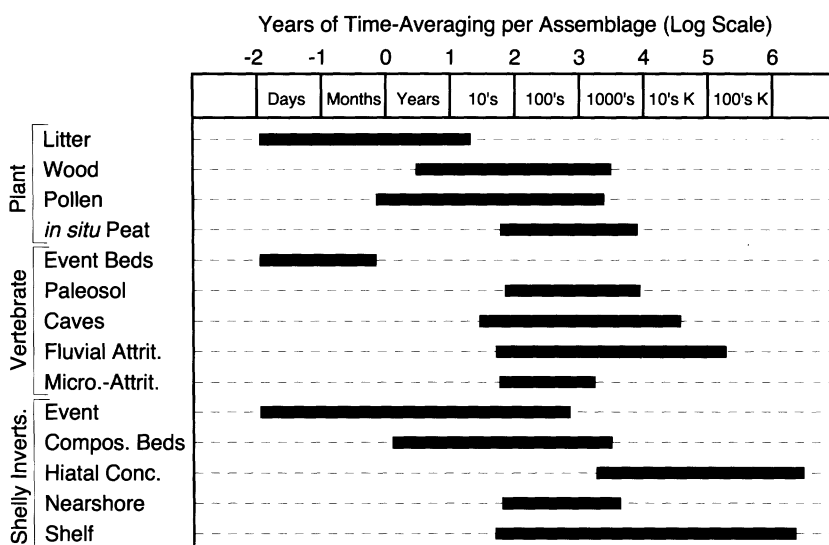


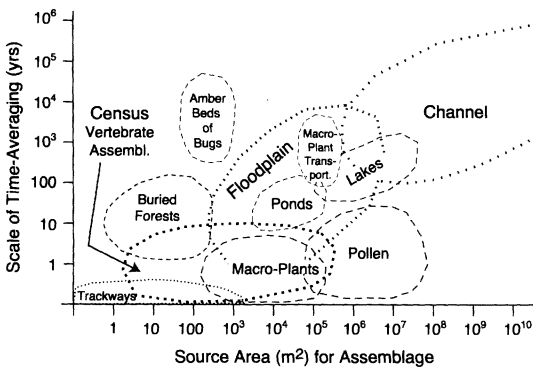
FIGURE 3. Estimated limits on time-averaging of selected types of continental plant tissues and vertebrate and marine invertebrate assemblages. The different categories (tissues versus deposits) reflect the fact that paleobotanists regard tissue type as playing the most important role in time-averaging for plant remains, while paleozoologists regard depositional environment or process as more important. Modified from Kidwell and Behrensmeier 1993.

modern and ancient systems also is fostering conceptual models, such as the reciprocal nature between the durability of remains and their likely temporal and spatial acuity (Kowalewski 1997), and how the attributes of temporal, spatial, and compositional fidelity vary independently. For example, a mass-burial event from which mobile species and adults escaped can produce an assemblage with high time- and space-resolution but low compositional fidelity (e.g., Fig. 5), whereas if the live community is transported en masse during the fatal event (e.g., avalanching, turbidity currents), the temporal resolution and ecological fidelity of the assemblage may be high but spatial fidelity very low. Alternatively, a time-averaged assemblage in which hundreds or thousands of years of input are mixed (relatively low temporal resolution) may nonetheless contain virtually all *preservable* species that lived in the area over that time, and perhaps even in fairly accurate proportions (thus facies-level spatial resolution, and high ecological fidelity of a durable subset of the original community) (Fig. 5).

Spatial Fidelity.—Although the presence of a taxon in a fossil assemblage suggests that it occupied that site, particularly if “rooted” in

life position (the highest possible spatial fidelity and resolution), biological remains can be transported out of their original life habitats, thereby becoming allochthonous and potentially problematic from the standpoint of paleocommunity reconstruction. Allochthonous or “exotic” wind-dispersed spores and pollen can account for high proportions of taxa in some samples, especially in areas with little local vegetation (e.g., middle of large lakes, offshore marine environments, and ice [Farley 1987; Calleja et al. 1993; Traverse 1994]). In contrast, animal-pollinated pollen, leaves, and other macroscopic phytodebris are relatively heavy and their records tend to have quite high spatial fidelity, although depositional context must be considered. For example, on temperate and tropical forest floors, actualistic tests indicate that litter sampled at any one point is derived largely from the surrounding 1000–3000 m² of vegetation (Burnham et al. 1992; and see Gastaldo et al. 1987; Burnham 1989, 1993, 1994; Meldahl et al. 1995; and for pollen see Jackson 1994). Such easily degraded material must be buried quickly to be preserved, but careful sampling of preserved spatial associations of taxa can capture extremely high-resolution macrofloral records

A. Continental Depositional Settings



B. Benthic Marine Depositional Settings

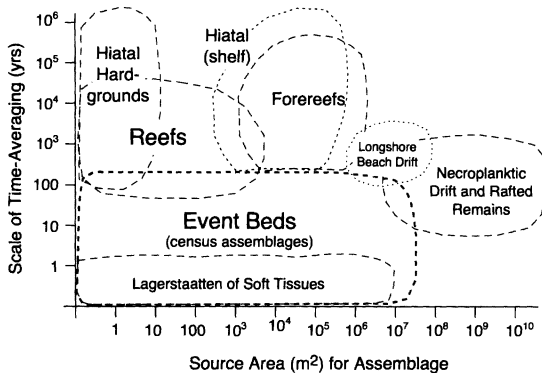


FIGURE 4. Spatial and temporal representation in fossil assemblages for different major groups of organisms, in continental and benthic marine depositional settings. A, Continental settings: dotted lines show areas of the time/space plot occupied by vertebrate remains, dashed lines plant remains; estimate for pollen excludes trees because certain morphotypes can be transported hundreds of miles by water (e.g., Farley 1987) or thousands of miles by wind (e.g., Calleja et al. 1993) prior to settling from the water or air column, respectively. B, Benthic marine settings include shelly macroinvertebrates and exclude nektonic and planktonic contributions to the fossil assemblage, because spatial resolution of these components can depend upon current drift.

sufficient for detailed reconstructions of diversity and community interrelationships (Wing and DiMichele 1995; Gastaldo et al. 1993b, 1996, 1998; Davies-Vollum and Wing 1998). Moss polsters and small-diameter ponds collect pollen (both wind- and animal-pollinated types) from smaller areas of source vegetation than do large ponds (Jackson 1994). Fluvial channels and river deltas typically include—but usually are not dominated by—plant remains from upstream parts of their drainage basin (e.g., Scheihing and Pfefferkorn 1984; and see Collinson 1983; Gastal-

do et al. 1987; Jackson 1989; Traverse 1990; Burnham 1990; Thomasson 1991; Webb 1993).

The skeletal hardparts of vertebrates and benthic invertebrates almost always are preserved out of life position, but actualistic studies indicate that out-of-life-habitat transport generally affects relatively few individuals in a given fossil assemblage (see reviews by Rich 1989; Allen et al. 1990; Behrensmeyer 1991; Kidwell and Bosence 1991; Behrensmeyer and Hook 1992; Kidwell and Flessa 1995; also specific studies by Behrensmeyer and Dechant Boaz 1980; Miller 1988; Miller et al. 1992; Nebelsick 1992; Greenstein 1993; Stoner and Ray 1996; Anderson et al. 1997; Flessa 1998; Cutler et al. 1999). Again, depositional context is crucial in determining spatial fidelity, and in providing warning flags for highly biased assemblages (Fig. 4). For example, in settings dominated by gravity-driven or surge transport of normal sediments, bioclasts may be *entirely* exotic in origin (e.g., in washover fans, tidal channels and their deltas, turbidites, base-of-slope settings). Organisms can be important transporters of biological remains, but there is great variation in the magnitude of this transport: some predators leave debris at the kill site; others concentrate it in a den or midden within the prey's life habitat (e.g., hyenas, crabs, fish, most owls), although in some cases prey remains end up outside of their life habitat (wolf dens, diving seabirds). Finally, the sprinkling onto seafloors of rocky intertidal shells rafted by seaweed (Bosence 1979), vertebrate debris from necroplanktic carcasses ("bloat and float" [Schäfer 1972]), downstream transport of bones (Behrensmeyer 1982; Dechant Boaz 1994; Aslan and Behrensmeyer 1996), and wind-transport of remains on land (Oliver and Graham 1994) can be highly effective modes of transport, but can be taphonomically subtle in terms of recognition and impact on the composition of fossil assemblage.

Natural history observations contribute to our conception of the possible, and net effects of transport on composition have been investigated by lab and field experiments (Behrensmeyer 1982; Frison and Todd 1986; Lask 1993; Prager et al. 1996; Blob 1997; and others previously cited; see also many live/dead com-

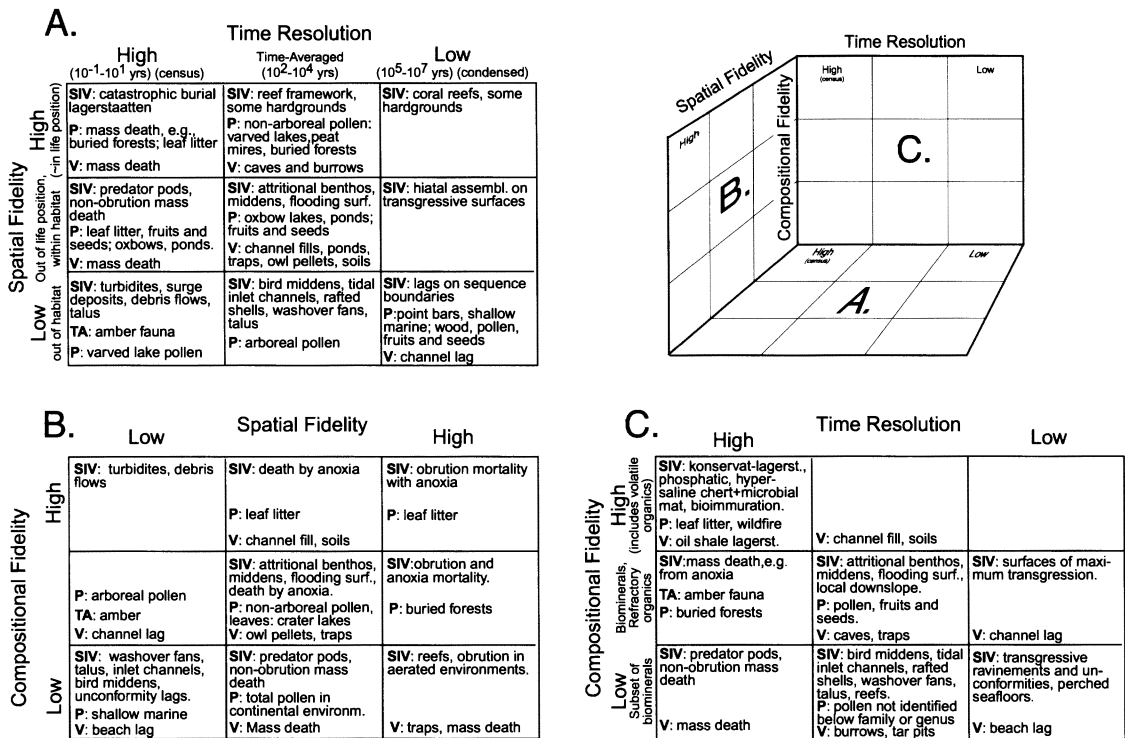


FIGURE 5. Schematic diagram in which each axis represents the summed results of preservational processes affecting time resolution, spatial fidelity, and compositional fidelity relative to the living community, showing that virtually all combinations of these aspects of record quality are possible. Note that we are restricting Compositional Fidelity to the accuracy by which the fossils represent the species present, species abundances, and population structure of the original community. In addition to the major sources of taphonomic bias represented in this diagram, some organic parts, such as pollen, wood, and bovid teeth, have inherent limitations with respect to taxonomic assignment, and these restrict the attainable level of fidelity even when preservation is excellent. SIV = shelly invertebrates, P = plants, V = vertebrates, TA = terrestrial arthropods (mostly insects).

parisons discussed in next section). It is difficult to retrodict or to reconstruct the effects of extinct organisms as agents, but overall, out-of-habitat postmortem transport does not appear to be an overwhelming taphonomic problem in ordinary depositional settings. Biological remains do not become homogenized in composition across broad environmental gradients either in modern or in ancient settings (see review by Kidwell and Flessa 1995).

Time-Averaging.—Because population turnover rates of individual taxa are less (often much less) than net rates of sediment accumulation, the biological remains of successive, noncontemporaneous populations of organisms may be admixed within a single bed, a concept first articulated by Walker and Bambach (1971). Multiple lines of evidence indicate that the degree of time-averaging within any

assemblage, i.e., the period of time represented by the biological components of any fossil assemblage, varies over many orders of magnitude (from virtually zero to millions of years; Fig. 3) and depends upon many factors (see papers in Kidwell and Behrensmeier 1993; Kidwell 1998). These include (1) tissue types, (2) the habitat and specifically the frequency of burial events and exhumation events, and (3) the depth of bioturbation within the sedimentary column relative to net sediment accumulation rates (Fürsich and Aberhan 1990; Kidwell and Bosence 1991; Behrensmeier and Hook 1992; Cutler 1993; Martin 1993; Kowalewski 1997). Robust hardparts can survive multiple reworking events, even within slowly accumulating sedimentary records (stratigraphic condensation), and can also survive exhumation and incorporation into quite different younger sedimentary de-

posits (stratigraphic leakage) (e.g., Cadée 1984; Henderson and Frey 1986). Highly disparate ages of co-occurring fossils generally are linked to settings of erosion (such as modern coastlines of Pleistocene or Tertiary strata [Wehmiller et al. 1995]), or prolonged low net sedimentation (e.g., modern sediment-starved continental shelves, where shells from 20,000 years ago to present co-occur in thin sedimentary veneers from most recent marine transgression [Kidwell and Bosence 1991; Flessa and Kowalewski 1994; Flessa 1998]). Such examples involve tissues that are particularly durable at death (mollusk shells, vertebrate teeth, pollen and spores) or have been made more durable by diagenesis during temporary burial (much vertebrate material associated with marine lags; steinkerns or concretions of delicate shells or refractory skeletons [Fürsich 1978; Kidwell 1991]).

Does time-averaging significantly impact our understanding of paleobiological systems? The answer to this question depends on the scale of time-averaging and the quality of information required to answer the paleobiologic question(s) at hand (Paul 1998). Time-averaged blurring of critical paleobiological events, such as the demise of the dinosaurs (Rigby et al. 1987; Argast et al. 1987), can have an obvious effect on evolutionary reconstructions. But there are many more subtle consequences of time-averaging. Catastrophic burial events such as volcanic ash falls (e.g., Voorhies 1992) can capture instantaneous samples of landscapes and organisms caught in the "wrong place at the wrong time." From a preservational perspective, the trapped invertebrates, vertebrates, and macroflora may provide highly "correct" spatial and proportional representations of the community at that spot and instant in time. However, these catastrophically trapped organisms may be admixed with (or at least deposited within very close stratigraphic proximity to) seeds, palynological components, and bones already present in the soil. Depending upon the type of soil and its maturity (Retallack 1990), these pre-event remains may represent populations that existed in the area prior to the catastrophic event, and/or populations that never lived at the locality (e.g., some wind-transported

pollen). Moreover, mass mortalities of animals rarely capture complete communities because agents of death often are taxon or age-class specific (Greenstein 1989), and organism size and mobility also are important factors (Krantz 1974). In aquatic systems, mass mortalities tend to capture unusual communities or communities in unusual states (e.g., anoxia is more common in small shallow bodies of water than in large open ones; mass death of single-species aggregations may occur following spawning events [Brett and Seilacher 1991]).

Because of the diverse ecological and taphonomic scenarios that are possible, time-averaging can have a number of effects on the species diversity and composition of fossil assemblages. However, for organisms that produce durable materials, the *usual* effect is to inflate diversity compared with what an ecologist would measure ("census") at any single moment (Fürsich and Aberhan 1990). For example, among 81 different data sets comparing live marine mollusks and dead shells from the same sediments, all contain two to ten times more dead species than species censused alive in the same habitat, even when the numbers of live *individuals* outnumber dead individuals (Kidwell in press; same phenomenon for vertebrates, see Behrensmeyer 1993). When additional live-censuses are taken and their species pooled, the known live fauna begins to more closely resemble the richness of the death assemblage. This demonstrates that, in contrast to any single, instantaneous census taken by an ecologist or captured by a catastrophic mortality, time-averaged death assemblages are fundamentally different types of samples of communities, summing biological input over longer periods (Peterson 1977; other examples in Kidwell and Bosence 1991). Other studies of marine and continental biomineralizing groups indicate that the probability of incorporation into a time-averaged death assemblage declines with tissue durability—from ~95% for shelled mollusks to ~75% for echinoids and land mammals and ~50% for marine decapods (Kidwell and Flessa 1995). These general relationships contrast with time-averaged assemblages of low-durability organisms, in which species richness

may be significantly undersampled relative to the actual number of species that occur in the living community (e.g., leaf assemblages [Wing and DiMichele 1995]).

In very specific depositional settings, it is possible to use stratigraphic evidence or biological inference to constrain the absolute time over which biological remains have accumulated. The best circumstances are where there is high temporal resolution based on radiometric dates (e.g., Potts et al. 1999), or a natural cyclicity within the biotic system (e.g., seasonal deciduousness [Gastaldo et al. 1996]) or in sediment deposition (e.g., lacustrine varves [Bell et al. 1987; Wilson 1993; Wilson and Barton 1996; Briggs et al. 1998]). Variability in bone weathering stages has been used as an indicator of time-averaging (e.g., Potts 1986), and geochemical signals acquired early in diagenesis show promise as a way of calibrating relative degrees of time-averaging in vertebrate accumulations (Trueman 1999). Generally, however, paleontologists estimate the absolute and relative durations of time-averaging by a process of elimination (see papers in Kidwell and Behrensmeyer 1993; Kidwell 1998). Assemblages with a high proportion of life-positioned and/or articulated specimens, and especially those incorporating nonmineralized tissues with known rates of decay, can be categorized as snapshot-type census assemblages with minimal time-averaging (but see discussion above) (Fig. 2), whereas the opposite extreme of highly condensed or lag material may be recognized by the highly disparate diagenetic styles or biostratigraphic ages of co-occurring material and (usually) close association with a significant stratigraphic discontinuity surface (Fürsich 1978). Interpretation of material of intermediate-scale time-averaging, which accounts for the vast majority of land vertebrate and shelly invertebrate assemblages, depends on depositional context (Kidwell and Bosence 1991; Behrensmeyer and Hook 1992) and, less confidently, state of fossil preservation (see below). The less durable the material, the shorter the window for time-averaging and accrual of progressive damage. In fact, most assemblages of non-woody plant material and nonmineralized invertebrates have probably under-

gone very little time-averaging. In leaf assemblages it is even possible to infer greater time-averaging than is actually the case. For example, plant debris resting on a volcanic ash may represent canopy leaves shed as an immediate response to ash loading (Burnham and Spicer 1986), but could be mistaken for litter from a longer-term recolonization of the ash-fall deposit.

Paleobiologists have hoped to find a signature of degrees of time-averaging in the state of fossil preservation, but so far this has proved elusive. Although old shells are more consistently in poor condition than young shells (Powell and Davies 1990; Flessa et al. 1993; Meldahl et al. 1997a,b) and shell ages tend to increase down-core (Kershaw et al. 1988; Cutler and Flessa 1990; Flessa et al. 1993), neither the taphonomic grade (e.g., degree of abrasion or encrustation) nor the precise relative stratigraphic positions of skeletal remains in the sedimentary column are infallible criteria for reconstructing the ages of individual elements within molluscan assemblages. Individual shells within the same intertidal assemblage can vary in ^{14}C ages by more than 1000 years, quantifying the scale of time-averaging within a "bed," and the age range increases to $\sim 20,000$ years for assemblages from offshore subtidal areas (Flessa and Kowalewski 1994; Kowalewski et al. 1998). This is a consequence of overall robustness of molluscan shells compared with other shelly macroinvertebrates (Kidwell and Behrensmeyer 1993; Kidwell and Flessa 1995; Kowalewski 1996b) and can result in an "over-complete" record when net sedimentation rates are low—i.e., time represented by fossils is greater than that represented by sediment (Kowalewski 1996b; condensed assemblages of Fürsich 1978; Kidwell and Bosence 1991).

This contrasts with the relatively low durability of weathered bone material, which is less likely than fresh bone to survive to become fossilized in continental environments (Behrensmeyer 1978a). Most transported and/or attritional fossil bone assemblages consist of durable, unweathered elements such as teeth, jaws, and fragmentary limb parts, and the average state of fragmentation or disintegration is a poor index of the duration of

surface exposure or the degree of time-averaging. However, high variability in weathering state, fragmentation, or abrasion in a single assemblage can indicate a complex taphonomic history, which should, on average, correlate with greater time-averaging. The relationship between bone damage variability and time interval of accumulation needs testing via comparative studies in both modern environments and the stratigraphic record. For example, weathering or abrasion features could be examined in concert with new chemical approaches to time-averaging in bone deposits, which suggest that variability in rare-earth elements is correlated with mixed spatial bone sources, hence greater time-averaging (Trueman and Benton 1997; Trueman 1999). The mixed preservational quality of a single type of shell also is taken as the best criterion for time-averaging within marine assemblages (Johnson 1960; Fürsich 1978; Kidwell and Aigner 1985; papers in Kidwell and Behrensmeyer 1993).

Such extrinsic and intrinsic time-averaging factors, along with analytical time-averaging (i.e., postcollection pooling of specimens from different sites or stratigraphic intervals [Behrensmeyer and Hook 1992]), reduce the resolving power of fossil assemblages for many paleobiological questions, especially those concerning species interactions, community composition, and fine-scale patterns of evolution, compared with what is possible in studies of modern biotas or fossil records dominated by census assemblages (i.e., macrofloral and nonmineralizing animals). Given the thousands of years of time-averaging that are apparently common within modern molluscan assemblages, for example, Kowalewski (1996b) has concluded that many paleobiological questions below a millennial timescale cannot be addressed (and see limits on reconstructing environmental change by Roy et al. 1996; Behrensmeyer 1982; Olszewski 1999; and see Martin et al. 1999b). Anderson et al. (1998) believe that it is possible to isolate shorter-term preservational and community trends in time, but the hardpart assemblage must be the product of episodic rather than continuous time-averaging.

Relationship between Space and Time.—Does

time-averaging capture the long-term spatial variability of populations in an area? In other words, does time-averaging equal spatial-averaging? Given an environment characterized by time-averaged death assemblages, would one expect to find within a single-point sample a record of almost all the preservable taxa that ever occupied the environment (McKinney 1991). Time-space equivalence would depend on two conditions. One is that, over the period of time-averaging, the physico-chemical properties of the sample site must vary sufficiently to permit colonization by the entire range of organisms in the community. This condition will generally be met only for sites that are large relative to the size of the organism, for example hundreds of square meters for sessile invertebrates or plants. A second condition is that, following burial, all components of the spatially variable faunas or floras must have an equal chance for preservation. This condition could be met for taxa with similar kinds of organic or biomineralized remains. It is not possible at present to provide an answer to the time-space equivalency question, although the possibility is tantalizing for paleoecologists with good vertical but poor lateral exposures. Multiple spatial samples of time-equivalent fossil assemblages are needed to test this hypothesis; evaluating diversity over the sample area thus provides a way to assess potential spatial completeness. For example, Bennington and Rutherford (1999) used multiple, small samples across the exposure and then calculated cluster confidence intervals to estimate completeness.

Compositional Fidelity of Fossil Assemblages

In the last 15 years, taphonomists have applied a variety of research approaches to evaluating the compositional fidelity of fossil assemblages, i.e., the quantitative faithfulness of the record of morphs, age classes, species richness, species abundances, trophic structure, etc. to the original biological signal (e.g., Fig. 2). Research has included (1) extrapolations from laboratory and field measurements of rates of destruction of tissue types in modern systems; (2) deductive analyses of fossil assemblages, in which the preservational quality

of individual specimens and sedimentary context are used to infer likely postmortem modification of taxonomic composition (informed by point 1); and (3) actualistic live/dead studies, in which the composition of a death assemblage (shells, bones, leaf litter, pollen) is compared with the local living community. These empirical approaches are complemented by probabilistic models and computer simulations aimed at testing both taphonomic and ecological (supply-side) controls on the nature of the record (Cutler and Flessa 1990; Miller and Cummins 1990, 1993; Behrensmeyer and Chapman 1993; Cutler 1993; and see Roopnarine et al. 1999 and Roopnarine 1999 for simulations of taphonomic effects on speciation patterns).

Most live/dead tests of fidelity have focused on single taxonomic groups in a limited suite of environments—as in ecological studies, there are logistical limits to the scope of an investigation. Methodological differences can make comparisons difficult across taxonomic and environmental divides (e.g., single versus multiple pooled censuses of the live community; visual survey versus sieving of upper sedimentary column for dead hardparts; methods of estimating individuals from collections of disarticulated and discarded body parts). However, we are beginning to develop a clear sense of how the construction and life habits of organisms and their postmortem environment combine to determine death assemblage fidelity for several systems (e.g., various papers in Martin et al. 1999a). There also is an increasing number of comparative taphonomic studies across taxonomic and environmental boundaries (e.g., Jackson and Whitehead 1991; Martin et al. 1996; Anderson et al. 1997). Virtually all of these live/dead studies have been concerned with the species compositions of assemblages, rather than with trophic group, age-class and morph composition, or population size (species abundance) (but see Cummins 1986a; Palmqvist 1991, 1993; Behrensmeyer 1993), and with numerical rather than biomass metrics (but see Behrensmeyer and Dechant Boaz 1980; Staff et al. 1985).

One of the clearest contrasts in fossil preservation—and thus in the fidelity of paleon-

tological information—is between organisms having mineralized or highly refractory tissues and those lacking such materials (“soft-bodied taxa”) (Fig. 2). Soft-bodied taxa have negligible preservation potential under ordinary environmental conditions, such as oxygenated seafloors and lake beds, and land surfaces characterized by moist and/or warm conditions (see earlier section), and the destruction of these organisms can represent a substantial loss in biological information. In marine sands and muds, for example, such taxa constitute 30–100% of species (Schopf 1978; Staff et al. 1986; Kidwell and Bosence 1991; Massé 1999; and for hardground example, see Rasmussen and Brett 1985), and in the macroflora a large proportion of the nonwoody (herbaceous) species can be missing from litter samples (Scheihing 1980; Burnham 1989; Burnham et al. 1992). Thus, unless based on konservat-lagerstätten with census-level time resolution, most “reconstructions” of food webs and energy flows by paleoecologists differ fundamentally from those of living communities, and are useful only for comparison with similarly preserved (isotaphonomic) assemblages (Scott 1978; Behrensmeyer and Hook 1992) or simulations based on living communities (e.g., Behrensmeyer and Chapman 1993; Miller and Cummins 1993).

One clear pattern from existing studies is that there is tremendous variance in fidelity even among “preservable” groups, linked to the durability of their hardparts (for review see Kidwell and Flessa 1995). In the marine realm, this is a function of hardpart construction: mollusks and nonagglutinating benthic forams appear to have approximately equal durabilities and high fidelities, in terms of species representation, and are followed in decreasing order by scleractinian corals, echinoids, decapods, and agglutinating foraminifera (and for freshwater mollusks see Briggs et al. 1990; Warren 1991; Cummins 1994). There are few actualistic data for the postmortem durability of brachiopods (but see Daley 1993; Kowalewski 1996a) and bryozoans (but see Smith and Nelson 1994; Hageman et al. 2000), and no live/dead comparisons or direct age-dating for these phyla to our knowledge. Hence information for these and other groups

remains largely based on inferences from the fossil record (e.g., lithology-specific diagenetic selection against small specimens of trilobites [Chatterton and Speyer 1997]).

Research on reef corals is expanding from analysis of damage styles (Scoffin 1992; Pandolfi and Greenstein 1997a) to evaluations of ecological fidelity (Greenstein and Pandolfi 1997; Pandolfi and Greenstein 1997b; Greenstein et al. 1998). Results so far are mixed: deepwater settings yield high live/dead taxonomic agreements like those for mollusks, whereas in shallow water, environmental zonation is preserved but taxonomic congruence is low, with strong underrepresentation of massive growth forms and overrepresentation of (rapidly growing) branching forms among the dead. Reef systems present quite different conditions for live/dead analysis than soft sediments: (1) dead specimens are commonly overgrown and thus more difficult to detect than live (see also this problem for reef-encrusting and -boring bivalves, where dead richness is *lower* than live richness, contrary to unlithified seafloors [Zuschin et al. 2000]); (2) resolution of corallite skeletal anatomy is essential for species-level identification of coral death assemblages, and thus systems with greater time-averaging (and thus potential for taphonomic modification) or higher proportions of fragile forms (e.g., Indo-Pacific versus Caribbean) will yield lower taxonomic fidelities; (3) among colonial organisms, the percentage of an "individual" that is alive or dead must be estimated rather than simply scored live/dead, and decisions must be made about how to count fragments on the seafloor, if at all; and (4) similarly, decisions must be made about whether dead material sieved from sedimentary pockets should be counted and how best to integrate this with live/dead data for in situ corals based on stretched-line scuba transects.

In the continental realm, fidelity among land mammals is strongly affected by body-size distributions within habitats, agent of accumulation, and climate. Natural-history observations and the few existing live/dead studies of bones on open land surfaces suggest that cool temperatures associated with high latitudes and altitudes promote longer

bone survival compared with low latitudes, and within each of these zones, dry land surfaces can be more favorable than moist ones (Behrensmeyer 1978a; Noe-Nygaard 1987; Kerbis Peterhans et al. 1993; Sept 1994; Tappen 1994a,b; Elias et al. 1995; Stewart et al. 1999). Thus, taxonomic fidelity should be greater in cool and/or dry climates where bones have higher preservation potential. For the continental macroplant record, Burnham (1989, 1993) demonstrated differences in systematic representation of taxa within modern forest-floor leaf litters and channel deposits, and also found that different depositional settings within the same regime provide dissimilar fidelities. Within the subtropical fluvial regime, for example, channel and channel margin (for-bank) accumulations of leaves represent 13–47% and 38–48% of the riparian vegetation, respectively. Counterintuitively, autochthonous levee and floodplain settings adjacent to these primarily allochthonous assemblages may provide a fidelity record with as little as 29% of local vegetation represented (range from 29% to 58% depending upon sample site). Because arborescent plants along the river margin act as a barrier to the lateral movement of canopy materials, there is very little mixing among microhabitats. Different climatic regimes are characterized by different levels of fidelity, and using comparative work in subtropical, tropical, and temperate climates, Burnham developed ways to extrapolate and calculate credible values of standing taxonomic richness by applying the appropriate climatic factor (Burnham 1993; see also Gastaldo and Staub 1999).

Tests of the relative fidelity of macrofloral and pollen records underscore the limitations of any single type of paleoecological record and the benefits of a comparative approach (Gastaldo and Ferguson 1998). For example, Gastaldo et al. (1998) incorporated megafloral, carpological (fruits and seeds), palynological, and biogeochemical data to evaluate a late Oligocene abandoned fluvial channel. They demonstrated that leaf fossils recorded deciduous riparian plants; fruits and seeds not only confirmed the presence of riparian elements but increased alpha diversity nearly threefold because these body parts represented under-

story and herbaceous ground-cover plants that were not preserved as wood or leaves; palynological and palynofacies debris confirmed the presence of some, but not all, riparian taxa and added evidence for other local (algae) and regional components; and the biogeochemical data reflected variations in megafloreal contribution to the channel. For other examples see Jackson and Whitehead 1991 and Ferguson 1995.

In addition to the need for quantitative estimates of fidelity in more environments and taxonomic groups, existing actualistic data sets could be examined for taphonomic "rules of thumb" applicable to the fossil record. For example, do fidelity levels improve as data are pooled from increasingly large geographic areas (i.e., within sample, within facies/habitat, within basin, within province) (Kidwell and Bosence 1991; Cutler 1991; Wing and DiMichele 1995; Olszewski and West 1997; Hadly 1999)? Temporally nested studies and simulations could reveal how stable death-assemblage composition is during the first few hundreds of thousands to one million years of burial (i.e., live versus dead in modern environments, uplifted Holocene strata, and/or Pleistocene fossils). The degree of fidelity might be expected to decline because of the cumulative wear and tear of diagenesis, limited outcrop areas for sampling different facies, changes in biogeographic range and community structure, and, eventually, extinction. However, data so far indicate that the agreement between live and dead floras/faunas can remain rather high over periods of a million years or more (e.g., Wolff 1975; Damuth 1982; Valentine 1989; Greenstein and Moffat 1996), so much so that it permits recognition of the uniqueness of recent environmental degradation (Greenstein et al. 1998). For example, Valentine (1989) reports that Pleistocene marine faunas in California include 77% of the living mollusk species from the Californian province, with most "live-only" species being numerically rare and restricted to deeper-water habitats that are not well represented in onshore Pleistocene outcrops. Data from other marine and continental groups could be similarly tested for sensitivity to geographic and temporal scale of anal-

ysis. All of these results underscore the potential value of death assemblages for environmental impact and other studies bearing on conservation biology (Powell et al. 1989; Davies 1993; and see review by Kidwell and Flessa 1995).

Several more fundamental difficulties still challenge our application of these insights to assessing fidelity in the older metazoan fossil record. One is the problem of evolutionary ecology: not only have the durabilities of animal hardparts changed over time (e.g., with changes in mineralogy, microstructure, body size, skeletal robustness), but organisms that interact with skeletal hardparts also have evolved. Such organisms are some of the most important agents of postmortem destruction in modern systems (e.g., shell and bone-crushing predators and scavengers, various bioeroders, sediment-irrigating bioturbators, and, of course, fungi and other microbes, whose roles and histories as biological recyclers may be important but still are difficult to assess [Robinson 1990, 1991]). How reasonable is it—and how far back into the past is it reasonable—to extrapolate present-day estimates of death-assemblage fidelity into the paleoecological past (i.e., taphonomic uniformitarianism)? The Cenozoic and Cretaceous may be within the reach of modern estimates of molluscan and scleractinian fidelity, but what do we do with older records? To move beyond arguments based on taphonomic uniformitarianism, for both Paleozoic and post-Paleozoic material, it is essential to determine whether death assemblages that appear to be highly biased in composition have distinctive damage patterns—i.e., to link taphofacies studies of damage (e.g., dead specimens of Species X are in poor condition, but those of Species Y are in good condition) to information on live/dead agreement. Greenstein (1999) has begun such work on reef corals, and this should be incorporated into other live/dead investigations.

Abundance of species in modern ecosystems is a key variable for characterizing diversity and various measures of dominance, and reconstructing such information from the fossil record is important for investigating the history of biodiversity. Taphonomic processes

have the potential to alter abundances in many significant ways—for example, via differential destruction during time-averaging and because of different population turnover rates of local species—even if the import of exotic species is minor. Many live/dead investigations have generated adequate data to test agreement in rank order and relative abundance, but the numbers of studies are still too few for most groups to provide a credible basis for using abundance data in paleobiological reconstructions. For marine mollusks, meta-analysis indicates high live/dead agreements (Kidwell 1999; and for freshwater mollusks, see Briggs et al. 1990; Warren 1991; Cummins 1994). Quaternary lake deposits also provide a firm basis for assessing reliability in palynological abundance data. For the wind-pollinated part of plant communities, pollen assemblages are faithful recorders of plant relative abundances in the source area, especially when the forest is relatively homogeneous, but animal-pollinated plants are almost always grossly underrepresented because of low pollen yield per tree and because most of this large and heavy pollen falls very near the source tree (see reviews by Jackson 1994 and by Jackson and Overpeck this volume). In contrast, vertebrate paleontologists regard both relative abundances and rank-ordering of species as suspect (i.e., guilty of bias unless proven otherwise) (e.g., Badgley 1982, 1986; Barry et al. 1991; but see Behrensmeyer and Dechant Boaz 1980).

Finally, morphological fidelity of fossil populations is also a taphonomic concern, but has received relatively little work. Preserved morphologic variance might be affected in several ways, for example from time-averaging of multiple generations (broadening variance) and from differential destruction of fragile or small morphs (skewing variance or limiting recognition of true polymorphism) (Kidwell and Aigner 1985). Bell et al. (1987, 1989) provide a powerful empirical example where, because of the occurrence of both mass-mortality (census) and time-averaged assemblages in the same stratigraphic unit, the effects of time-averaging on morphological variance and character association could be evaluated entirely with fossil evidence. Capturing true pic-

tures of morphologic variability in fossil material, and distinguishing between taphonomic, sample-size, and biological controls on this variability, bears on issues of numbers of species and their stability in taxonomy. Thus, these considerations are critical to biostratigraphy, evolutionary analysis, and estimates of species richness (Hughes and Labandeira 1995). Increasing numbers of morphometric studies are based on taphonomically astute sampling, for example restricting samples to single bedding planes or horizons of constant and (hopefully) known time-resolution, and keeping close track of lithologic context to control for or assess ecopheny; but the question of bias in morphologic representation at present is still largely a qualitative assessment.

Megabiases

“Megabiases” refers to bias in relatively large-scale paleobiologic patterns, such as changes in diversity and community structure over tens of millions of years, and variation in the quality of the record between mass and background extinction times or among different climate states, biogeographic provinces, and tectonic settings (Behrensmeyer and Kidwell 1985; and see treatments by Kowalewski and Flessa 1996; Martin 1999). Baseline information accumulated since then has stimulated new thinking on two reciprocal fronts: (1) broad-scale changes in climate, plate tectonics, ocean-atmosphere chemistry, and biological evolution as likely drivers of secular change in taphonomic processes (Fig. 6); and (2) the probable impact of such changes on the quality of paleontologic evidence used to reconstruct and parameterize geological and biological phenomena.

Given that Earth history can be divided into periods with different atmospheric and surface conditions, and given that the history of life also presents intervals with distinct bodyplans and life habits, it seems plausible that the geologic record would be characterized by a series of discernable “taphonomic domains” (Fig. 6). Reflecting secular changes in the nature of life and environments on Earth at a global scale, these domains would constitute the broadest-scale biases in the quality of pa-

leobiological information. Superimposed on them would be province-scale and/or shorter-term secular and cyclical variation in taphonomic processes, and intervals of unique taphonomic conditions, e.g., those associated with regional or global mass extinctions and/or major perturbations in Earth's environmental condition. We refer to all such broad-scale taphonomic patterns and trends—affecting paleontologic analysis at provincial to global levels, over timescales of >10 m.y., or among major taxonomic groups—as megabiases.

Important taphonomic shifts may result from the evolution of organic form and behavior that makes organisms intrinsically more or less likely to fossilize, and from changes in extrinsic biotic and abiotic controls on preservation (Fig. 6). Examples of intrinsic changes include evolution in the composition and structure of mineralized skeletons, body size, mobility/life habit including burrowing behavior and pollination, deployment of life forms into new environments, and (for plants) evolution of deciduous versus perennial growth habits (for references, see discussion below). Examples of extrinsic biotic changes include the increasing depth of bioturbation through the Phanerozoic (Thayer 1983; Retallack 1990; Droser and Bottjer 1993; Buatois et al. 1998; McIlroy and Logan 1999), the evolution of more effective shell and bone crushers/ingestors (Vermeij 1977, 1987; Behrens-meyer and Hook 1992) and other biodegraders such as fungi (Robinson 1990, 1991), and the shift to detritivore and herbivore dominance on land (DiMichele and Hook 1992; Labandeira 1998) (Fig. 6). Extrinsic physical changes include fluctuations in the temperature and geochemistry of Earth's atmosphere and oceans (Berner and Canfield 1989; Maliva et al. 1989; Berner 1991; Martin 1995; Malinky and Heckel 1998; Stanley and Hardie 1998), and tectonic and climatic effects on the original extent and preservation of particular environments through geological time (e.g., the "wetlands bias" in the global plant record, variation in total sedimentary rock volume, the proportion of tropical continents, and lagerstätte-preserving lithographic limestone basins [Tardy et al. 1989; Sepkoski et al. 1991;

Gastaldo 1992; Allison and Briggs 1993a; Oost and de Boer 1994).

Although the potential impact of such large-scale processes has been recognized for some time (Efremov 1940), they remain largely unexplored aside from some aspects of the marine record. Various case studies illustrate the continuing debate over the relative importance of taphonomic versus biologic signals, and of intrinsic versus extrinsic taphonomic effects. For example, in the fossil record of unique events, such as the profound biotic changes at the Precambrian/Cambrian boundary, did multicellular life really "explode" about 550 m.y. ago, or are we simply seeing the opening of a new taphonomic window? This particular change appears to represent a linked shift in metazoan evolution and organic recycling. Given the extensive field work on late Precambrian deposits over the past two decades, it is very unlikely that shelly organisms existed in any abundance prior to the end of the Precambrian. The evolution of biomineralization indeed represents a major taphonomic event in the intrinsic preservation potential of multicellular organisms. On the other hand, debate continues over the role of taphonomic processes in the concomitant disappearance of the globally distributed soft-bodied Ediacaran fauna (Fedonkin 1994; McIlroy and Logan 1999). Researchers have hypothesized that, given the overall aerobic environments of deposition, some Ediacaran organisms had tougher body construction or ways of life that enhanced their intrinsic preservational characteristics, and that the geological disappearance is a signal of actual biological extinction (e.g., Seilacher 1984, 1994), whereas others have inferred a sharp decline at this time in the extrinsic environmental conditions that permitted the development and early cementation of microbial mats (Fedonkin 1994). Capable of preserving soft-bodied organisms as "death masks," this taphonomic mode existed in late Precambrian seas as long as effective grazers and bioturbators ("grave robbers") were absent, but disappeared when such organisms invaded this environmental zone (Gehling 1999). A comparable taphonomic mode persists in Recent hypersaline tidal flats and lagoons where most metazoans are excluded, but in normal marine environments

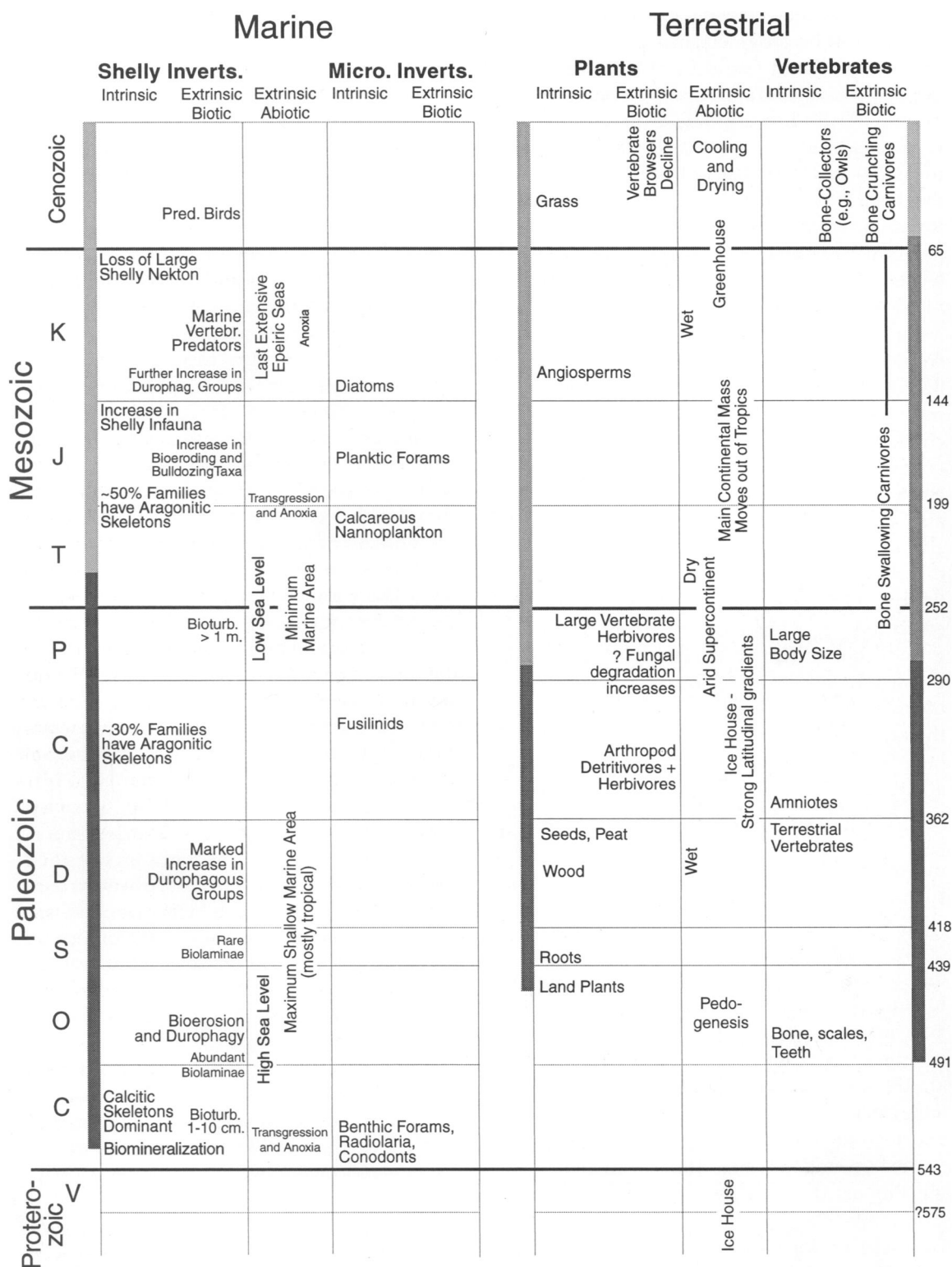


FIGURE 6. Intrinsic and extrinsic changes with the potential for major effects on taphonomic processes and organic preservation over geologic time. This chart provides a preliminary framework for examining hypotheses concerning changing "taphonomic domains" through the fossil record for the marine and continental realms as well as possible

it became extinct as a means of preserving soft-bodied multicellular organisms at the beginning of the Cambrian (for related studies, see Sepkoski et al. 1991; Knoll et al. 1993; Knoll and Sergeev 1995; Kah and Knoll 1996).

Through the Phanerozoic, other proposed megabiases in the marine realm relate to both intrinsic and extrinsic biotic and abiotic factors. At the intrinsic end of the spectrum, styles of echinoid preservation and thus qualities of data appear to have diversified as echinoid constructional morphology diversified (Greenstein 1992); the frequency of lingulid brachiopod preservation has declined, possibly because of decreasing biomineralization during life (Kowalewski and Flessa 1996); and increases in the physical scale, taphonomic complexity and probable time-averaging of shell beds is linked to shelly macrobenthos acquiring biomechanically tougher hardparts and expanding into more energetic environments (Kidwell and Brenchley 1994, 1996; Li and Droser 1997; Simões et al. 2000b; and see Ausich 1997 for intrinsic factors in encrinurites). In addition, aragonitic and calcitic biominerals may confer different degrees of resistance to predation as well as to postmortem destruction (Stanley and Hardie 1998). In contrast, primarily extrinsic factors have been invoked to explain the changing frequency of metazoan konservat-lagerstätten over the Phanerozoic (bioturbation, basin type, clay mineralogy) (Aronson 1992; Allison and Briggs 1993b; Butterfield 1995; Oost and de Boer 1994), and both intrinsic and extrinsic factors appear to have played a role in changing patterns of marine mineralization (both replacement of hardparts and early cementation of sediments) over Precambrian and Phanerozoic time (ocean saturation states, ecology and biomineralogy of target taxa, abundance of other organisms as elemental sources) (Walker and Diehl 1985; Knoll et al. 1993; Grotzinger

1994; Kah and Knoll 1996; Schubert et al. 1997).

The histories of sedimentary basins on timescales of 10^6 – 10^7 years could impart significant trends in the quality of fossil records, within the broader domains described above. Continental depositional systems could exhibit several distinct phases of organic preservation. For example, as a foreland basin changed from underfilled to overfilled, physical and chemical conditions should favor plant preservation in early phases (high water table, low oxidation) and vertebrate preservation in later phases (paleosols with CaCO_3 , concentration of vertebrate remains through fluvial reworking) (e.g., as suggested in Demko et al. 1998; for analogous tectonic and sequence-stratigraphic variation in the quality of marine fossil records, see Kidwell 1991, 1993; Brett 1995). Climate change also should impose major shifts in the quality of the fossil record, with wet cool conditions favoring plant preservation, drier warmer times bone phosphate, and fluctuating CCD levels governing the preservation of deep-sea microfauna (Martin 1999; and for possible storm-bed effects, see Brandt and Elias 1989). This potentially affects the fossil record at a wide range of timescales, from regular fluctuations in preservation caused by orbital cycling, to longer-term shifts in latitudinal gradients that modify the extent of habitable and preservable biotic space, to the drift of continents across major global climate belts. Moreover, processes and circumstances favorable to preservation of one major group often are less favorable for others, resulting in potential temporal disjunctions between the marine and continental record, and the plant and land vertebrate record.

Taphonomic processes and circumstances associated with mass extinction events could constitute a recurring set of phenomena with a different set of biases relative to the intervals

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links between these two realms. The points of inception of potentially important changes in intrinsic and extrinsic variables are indicated on the chart (see text for references). Shading variations on the vertical bars indicate possible taphonomic domains for shelly invertebrates based on depth of bioturbation, for plants based on the development of relatively refractory tissues and evolution within biodegraders such as fungi, and for vertebrates based on body size and changes in bone-processing capabilities of predators and scavengers. Revised dates for period boundaries from D. Erwin (personal communication 2000).

between such events. For instance, after a mass extinction event, a depleted array of consumers could lead to reduced biological recycling, allowing better preservation during the period of biotic recovery (Hunter 1994; Williams 1994; Cutler and Behrensmeier 1996; D'Hondt et al. 1998). It is also possible that climatic or chemical stress prior to a mass extinction could affect taphonomic processes, either directly with increasing frequency of mass deaths or indirectly through the organisms, with poorer preservation indicating increased competition for scarce organic or biomineral resources. The record of mass death events also can be affected by long-term changes in taphonomic processes that control destruction and permanent burial. In many marine and continental settings where bioturbators or physical reworking can mix sediments over 10 to 100+ cm, instantaneous inputs from local mass death may have no net stratigraphic signature because the debris is rapidly homogenized with background attritional input (as in Greenstein 1989; and see Badgley 1982; Mel-dahl 1990; Behrensmeier and Chapman 1993; Cutler and Behrensmeier 1996). Through the Phanerozoic, the stratigraphic frequency of documented mass mortalities thus may be partly controlled by evolutionary changes in bioturbation depth and intensity.

Strategies for Addressing Taphonomic Biases

One of the goals of taphonomy is to establish patterns, and preferably quantitative magnitudes and causes, of bias in the fossil record. Paleontologists are developing new ways to evaluate shortcomings both in the record itself and in our sampling of it, and many researchers now approach these issues rigorously and proactively. Generally speaking, approaches to biases, both real or hypothesized, have ranged from assuming or reasoning that the record itself—or our knowledge of it—is too poor for biological analysis, to assuming or reasoning that the record can be taken at face value. These usually reflect different starting points for analysis—guilty of overwhelming bias until proven otherwise, or innocent until proven biased. Paleontologists who take this latter approach are not neces-

sarily being willfully blasé, but may reason (geologically, statistically) that taphonomic bias is relatively small and thus a second-order effect, or conclude that bias is random relative to the variable under study and thus unlikely to create artificial patterns. In other situations, the strategy is to normalize the data or adjust the metric to compensate for probable or known biases (e.g., rarefaction, comparisons of data trends with unevenness in sampling intensity, which may be a function of rock availability as well as taphonomic processes), use of taphonomic control taxa, Lazarus and other gap analyses (see discussion below; also Sepkoski and Koch 1996; Foote this volume; Holland this volume). A variant of this strategy is analytic time- and space-averaging (Behrensmeier and Hook 1992), whereby paleontologists group (bin) data more coarsely than nature and thereby reduce noise introduced by variation at lower scales; this is axiomatic in many macroevolutionary and global analyses. Another strategy, once the quality of the record has been evaluated, is simply to sidestep biased or incomplete information by rephrasing the hypothesis or shifting the emphasis of the study to suit the quality of the data (see discussion in Paul 1992).

The construction and analysis of paleobiological data sets usually entails many taphonomic assumptions, and several points must be kept in mind in designing strategies. One is the precise meaning of the terms “bias” and “incompleteness.” *Bias* by definition is neither uniform nor random (occurring unpredictably), but instead is a skewing of information in some systematic way. This is a different concern from the *incompleteness* of data, which, as used in paleontology, refers to the extent of knowledge—that is, how fully the available pool of information has been sampled and thus how stable and detailed our picture of that system is thought to be (Paul 1992, 1998). Incomplete information can provide a fair and true (unbiased) sampling of reality, and confidence intervals can be calculated for it (e.g., Sadler 1981; Strauss and Sadler 1989; Marshall 1990, 1994; McKinney 1991; see also various papers in Gilinsky and Signor 1991). Collection curves and other growth-of-information

curves are longstanding examples (see Paul 1992). But if gaps in information preferentially fall, for whatever reason, within particular biota, segments of time, or environments within the scope of the analysis, then incompleteness can be transformed into the more serious problem of bias.

A second point is that bias and incompleteness can both be either *natural* or *analytical* in origin. For example, gaps can result from hiatuses and barren intervals in the stratigraphic record, but gaps also are generated analytically by coarse sampling schemes and by variation in monographic effort. Natural taphonomic bias includes the tendency for small-bodied individuals or species in a group to be underrepresented, and for transgressive records to be thin and/or faunally condensed relative to regressive deposits. Potential sources of analytic bias include relying heavily on North American and European records in the construction of *global* data sets, and interpreting at face value species richness data from samples with disparate scales of time-averaging or positions on growth-of-knowledge curves.

A third point to be clear on, whether devising a strategy or evaluating one used by others, is the reality that is being targeted—the actual history of life, the fossil record of life (a taphonomically filtered subset of information), the known fossil record (an analytic subset influenced by geopolitics), or a data set based on some analytic subset of the known fossil record (published data, unpublished data, and/or new fieldwork). Data that are complete at one scale (e.g., compendia from the published fossil record) may be neither complete nor unbiased at another more inclusive scale (e.g., the actual fossil record). Conversely, data that are incomplete and biased at a fine scale (e.g., major gaps in the local record because of facies controls on the original presence or postmortem preservation of species) might yield adequate information at a broader scale of analysis (e.g., presence of the higher taxon in the region anytime within a coarser time interval).

Finally, some metrics will be less sensitive to *incomplete* data than others—for instance, medians rather than absolute minima and

maxima, ratios (e.g., predator-prey) rather than absolute numbers of taxa, rates and patterns of change rather than specific trajectories, evenness rather than total species richness (e.g., Foote this volume; Alroy et al. this volume). Factoring out *bias*, on the other hand, requires analytic dissection of the data at hand. For example, from an innocent-until-proven-guilty stance, does evolutionary rate, geographic range, or numbers of species per genus actually covary with preservation categories, such that using samples of diverse preservational quality in a single data set would yield a misleading paleobiologic interpretation (e.g., Jablonski 1988; Foote and Raup 1996)? From a guilty-until-proven-innocent stance, do observed spikes of taxonomic first and last appearances in stratigraphic sequences rise above levels expected at those horizons because of stratigraphic truncation and condensation (e.g., Holland 1995, 1996; Holland and Patzkowsky 1999), or because of collector-induced variation in sample size?

By virtue of their size and scope, data sets on broad-scale paleobiological patterns entail a particular set of taphonomic issues. For example, the marine metazoan diversity pattern (Sepkoski 1978, 1993), the continental plant record (Knoll et al. 1984; Kendricks and Crane 1997), and major branching points in vertebrate evolution (Maxwell and Benton 1990; Benton 1998) are interpreted to reflect biological history at a global, stage-sized bin level, and this may be correct at that scale of analysis, although as yet there has been no comprehensive analysis of biases. Some major potential sources of bias, such as those pertaining to variation in outcrop area and volume, the “pull of the Recent” (intensive sampling of extant fauna extends the stratigraphic ranges of poorly sampled fossils), monographic effort per geologic period, and effect of hyper-rich lagerstätten (involving taxa that occur in a single interval), have been addressed, at least coarsely (e.g., for the marine record, see Sepkoski et al. 1981). Moreover, the basic patterns (e.g., trends in numbers of families over time) have remained stable in spite of expanding knowledge of the fossil record (Sepkoski 1993; Benton 1998). Such “growth of knowledge” curves (Paul 1992, 1998) support con-

fidence in the adequacy of information on the *known* fossil record for trends at this scale, and this type of analysis can be applied at many levels in the taxonomic, temporal, and spatial hierarchies (see examples in Donovan and Paul 1998; and for morphospace occupation, see Foote 1997).

Research is now focusing on biodiversity patterns and biases at finer geographic scales, with the effects of environmental (facies) and biogeographic variation on numbers of recorded taxa and range limits (e.g., Raymond and Metz 1995; Vrba 1995; Wing and DiMichele 1995; Alroy 1996; Behrensmeyer et al. 1997), including the effects of nonrandom patterns in facies and hiatuses through stratigraphic sequences (Holland 1995). To what extent, for example, does the acknowledged weighting of published fossil data toward North America and Europe influence the perceived global pattern? Determining whether subregions have distinctly different biodiversity patterns will indicate the extent to which uneven sampling across the globe might bias our perception to date of global trends. When diversity through time within particular geological intervals is examined closely, different patterns do emerge for different regions, and ongoing research is testing the relative roles of intrinsic biologic factors, biological response to regional environmental conditions, and taphonomic issues linked to regional environments (Miller and Foote 1996; Miller 1997; Waisfeld et al. 1999). Databases that track the environmental context and taphonomic character of paleontologic occurrences—that is, that are not done in a lithologic vacuum—are an important next step in evaluating both natural (taphonomic) and anthropogenic (analytic) sampling bias with respect to global biodiversity patterns.

In many kinds of studies, but especially in evolutionary ecology, rarefaction (Sanders 1968; Raup 1975; Miller and Foote 1996) has been widely used as a means to standardize samples (e.g., to compare species richness in samples of disparate size). To infer that differences in rarefied diversity over time or space have biological explanations, however, one must assume that the samples are isotaphonomic, i.e., that information for each bin is de-

rived from an equivalent suite of natural sampling conditions. One strategy is to limit analysis to samples from a specific habitat or suite of habitats or facies (e.g., Bambach 1977); this assures greater taphonomic equivalence, although it also limits the universality of the results. The longer the interval of time, the more important it is to sample within a single taphonomic domain: if natural taphonomic regimes have shifted through time, and thereby altered the proportional preservation of bodyplans, growth stages, or habitats (megabias), then a major assumption behind biological interpretation of rarefied data is potentially violated, notwithstanding the within-habitat design. For example, unconsolidated lower shoreface facies from the Cenozoic record, which include faunally condensed shell gravels, are likely to yield higher species richnesses for both taphonomic and analytic reasons than predominantly lithified units from the Mesozoic (Kidwell and Jablonski 1983; Kidwell and Brenchley 1996), and, owing to bioturbation, neither of these records preserves as high a proportion of discrete storm-bed concentrations as the Paleozoic (Brandt 1986; Sepkoski et al. 1991). Thus, for a variety of reasons, taphonomic biases might be expected to inflate the raw alpha diversity of benthic communities in each erathem to a greater degree than the one before it, making a biological interpretation of diversity increase ambiguous unless sampling is standardized. Cross-time analysis of comparable samples, even if piecemeal—e.g., lithified Mesozoic with lithified Cenozoic, Paleozoic storm-beds with Mesozoic storm-beds—is one obvious next step.

Another approach would be to characterize taphonomic regimes and study their effects on apparent taxonomic diversity using sampling standardization within each regime and in combined samples. At basinal scales, nonrandom geographic and temporal variations in completeness and taphonomy can in fact account for a large part of apparent faunal turnover patterns through time (Brett 1995; Holland 1995; Behrensmeyer et al. 1997), and thus scaled-up versions of similar biases might affect regional to global patterns. Benton (1998), for example, suggests that some marked shifts in Phanerozoic vertebrate diversity through

time are not evidence of evolutionary events but are an artifactual "lagerstätten effect" of pooling data from scattered horizons of superb preservation with information from deposits of more ordinary fossil preservation (this has been rejected as insignificant in the periodicity of marine metazoan extinctions [Sepkoski 1990; and see Foote this volume and Alroy et al. this volume]).

At both large and small scales of investigation, establishing taphonomic equivalence (isotaphonomy) has become an important research goal. The aim is to achieve meaningful biological comparisons across space and time, and in particular to reduce dependency on modern analogues. Isotaphonomy is particularly critical for establishing the credibility of species abundance trends and other diversity measures derived from the fossil record. Criteria for defining isotaphonomic assemblages should include as many lines of evidence as possible without prohibitively limiting sample size: geological setting, general climatic regime, lateral and vertical scale of the fossiliferous unit, paleogeochemistry, body-part representation, and other indicators of taphonomic processes including time-averaging. This approach is relatively new and several strategies are possible. Benton (1998; also Briggs and Clarkson 1990) suggests comparing similar types of lagerstätten at different times as snapshots of "true" diversity, although such deposits commonly record unusual conditions of mortality and environment that limit their fidelity with respect to true or average diversity (see previous sections). Moreover, and as a general caveat, there are huge pitfalls (commonly unacknowledged) to extrapolating regional or global signals from single locales. An alternative starting point is to establish broader equivalence in depositional environments or taphofacies; hence, vertebrate faunas from channel fill versus levee versus floodplain paleosol settings might be compared through time, and all are combined for a representation of the diversity of the fluvial system as a whole. Clyde and Gingerich (1998) take such an approach in examining mammalian community response to environmental change in the late Paleocene using isotaphonomic samples from floodplain

paleosol settings. Many macroplant assemblages are from specific types of wetlands environments (e.g., wet floodplain, proximal channel, abandoned channel, and channel), making them somewhat isotaphonomic by default (ditto the records of soft-bodied animals), but water chemistry, rates of aggradation, and climate can vary in ways that affect that preservation (Gastaldo 1994; Demko et al. 1998; Gastaldo and Staub 1999). "Next-generation" analysis of macroevolutionary trends requires such critical appraisal, both as a means of estimating confidence limits and as a means of testing environmental forcing factors. Although challenging, this is a logical next step toward integrating taphonomic advances into mainstream paleobiology.

An additional challenge in paleobiologic analysis, especially of broad-scale patterns, is the significance of missing taxa, and the use of "taphonomic control taxa" has been proposed as one way to determine when absences are meaningful (Bottjer and Jablonski 1988; Jablonski et al. 1997). These are biologically abundant taxa with hardparts that are comparably or less robust than those of the target taxon, and preferably relatively close taxonomically. The reasoning is that if the control taxon is present, then the target should have also been preserved if it co-occurred in that unit; moreover, the author who reports the control taxon would have been likely to report the target taxon if present. Thus, cyclostomes may serve as control taxa for tracking the environmental and evolutionary expansion of cheilostome bryozoans, isocrinids for millerocrinid crinoids, and other small infaunal veneroids for tellinid bivalves. Likewise, teeth of *Hipparion* have been used as a control for the appearance datum of the similarly sized horse *Equus* in Africa (Behrensmeyer 1978b), and turtles as a control for crocodiles in an analysis of climatic effects in the Cretaceous/Tertiary extinction (Markwick 1998).

Foote et al. (1999) used similar taphonomic reasoning to challenge molecular evidence for an Early Cretaceous origin of modern Eutherian mammal orders, arguing instead that these groups did not arise much before their earliest known geologic record in the latest Cretaceous or Paleocene. The frequent lack of

ancestral taxa in the fossil record often is attributed to evolution in stratigraphically underrepresented peripheral or poorly preserved habitats (e.g., for "uplands" habitats for Cretaceous angiosperms and vertebrates, see Olson 1966 and Retallack and Dilcher 1986; and for Mesozoic plant taxa now recognized in the Upper Carboniferous and Permian, see DiMichele et al. in press). However, Foote et al. (1999) take an important step beyond this by quantifying preservation rates for other Cretaceous mammals and arguing that, unless the taphonomy of the earliest eutherians differed radically from other mammal taxa in the Mesozoic (i.e., body sizes, habitats/facies, life habits) and in such a way that severely reduced the quality of their record, then the probability of missing modern eutherian orders throughout the Cretaceous is very low (barring, they note, a "Garden of Eden" in which all these orders both originated and remained in an undersampled region for tens of millions of years).

This approach touches upon a problem that needs resolution if we are to calibrate taphonomic effects on appearance events—namely, the effect of a taxon's live abundance, spatial distribution, and temporal range on its probability of preservation. Rare, localized, and geologically short-lived species, such as might initiate a major new lineage, could be particularly vulnerable to taphonomic bias (see earlier discussion of Valentine 1989), and the record of continental taxa might suffer disproportionately for both taphonomic (patchy preservation) and biologic (e.g., greater importance of endemism in origination?) reasons. For example, detailed study of Cenozoic vertebrate assemblages indicates that distinct faunal communities can exist in adjacent basins or portions of basins for long periods of time (10^6 – 10^7 yr) (Behrensmeyer 1978b; Bown and Beard 1990). Whether this segregation is taphonomic or ecologic in origin, it indicates how a taphonomic control approach might impart misleading results on vertebrate presence/absence at this temporal and spatial scale, and raises the issue of how such facies control might "scale up" to global patterns over tens to hundreds of millions of years and at higher taxonomic levels (DiMichele and

Aronson 1992). These concerns would apply to other taxa that lack transitional forms in the fossil record; credible evidence that a taxon is absent for evolutionary rather than taphonomic reasons requires a good understanding of both the completeness of sampling and the possible taphonomic bias in the fossil-bearing deposits (and see discussion on bias relevant to bio-events in Sepkoski and Koch 1996).

In contrast to inverse-type models, where one works back from paleontologic patterns ("what bias could generate this pattern?"), quantitative forward modeling of taphonomic processes and effects from the input perspective is in its infancy. Existing studies illustrate the great potential of this strategy for addressing biases and limits to the resolution of the fossil record. This modeling can be conducted at many scales and provides an important means of bridging the gap between actualistic data and stratigraphic patterns at the assemblage level. Behrensmeyer and Chapman (1993), for example, take this approach in using computer simulations to create artificial time-averaged vertebrate assemblages, based on a modern African assemblage and known rates of bone input. They show that hundreds to thousands of years of time-averaging is needed to capture all of the major taxa in potential fossil localities (i.e., time-averaging is good, and even necessary, for producing an accurate portrayal of species presence and rank order) (also see Miller and Cummins 1990, 1993 on marine taxa). Building upon empirical evidence that modern molluscan death assemblages are dominated by the shells of recent cohorts (Meldahl et al. 1997a), Olszewski (1999) models time-averaging and predicts the sample size necessary to ensure retrieval of specimens from each component time segment in the source assemblage, i.e., a complete sample of the entire span of time-averaging. There have also been immense strides in conceptualizing and testing the effects of incomplete preservation and stratigraphic gaps on evolutionary patterns in the broadest sense, including tempo and mode of speciation, and in using estimates of phylogeny to infer the quality of the fossil record. For recent entries to this large literature, see Carroll 1997, Roopnarine et al. 1999, and Wagner

2000a; also chapters by Alroy et al., Foote, Holland, and Wagner in this volume.

Focal Areas for the Future

Taphonomy's continuing challenge is to evaluate the prolific but problematic fossil record for systematic patterns in preservation that may constitute bias in information quality, and to develop accurate ways to measure and use such patterns in paleobiologic analysis. Over the last few decades, paleontologists have become more sanguine about the quality of paleontologic data. There are two aspects to this: (1) an appreciation that all data, paleontologic or otherwise, are incomplete, and that the critical question is whether they are adequate to address the question at hand (Paul 1998); and (2) a realization that taphonomic comparability or noncomparability of samples across time and space must be taken into consideration in deriving biological patterns from paleontological data. This means that, ideally, samples used to examine temporal and spatial trends should be from comparable depositional contexts and preservational states, even if absolute scales of time-averaging or spatial fidelity cannot be specified. Alternatively, when the point is to compare or combine biological factors such as diversity across environments, regions, and geological domains, an opposite approach is required that takes into account and compensates for clearly different qualities of data. Today this is largely done by taphonomic uniformitarianism, i.e., extrapolating modern-day rates and error estimates back in time. A challenge for next-generation research is to assess the very real limits imposed by secular changes in fossilization through the geological record.

There are particular focal areas for taphonomy that are likely to generate important contributions in the next several decades. Comparison across plants, invertebrates and vertebrates is a promising growth area for taphonomy's broader contributions to understanding geobiological processes and to developing a theoretical basis for the field. Enough now is known about each major group to suggest some common denominators, such as the effects of bioturbators and bioeroders, as well as some contrasts in approaches and problems,

including the wide differences in susceptibility to time-averaging of major taxonomic groups. Is it possible to develop a general index of relative "preservation potential," including likely degrees of time-averaging, for different body-plans, life strategies, and ecological settings? Can we establish a basis for recognizing "abnormal preservation," indicating profound shifts in taphonomic regimes, such as post-extinction differences in shelly faunas? It should be possible to take assemblage-level processes and biases, and develop hypotheses about how these operate at a larger scale as a basis for defining "normal" circumstances of preservation for individual taxa and for different types of communities.

To advance these aims, and to summarize our preceding highlights of the discipline, we recommend the following key focal areas for future taphonomic research relevant to paleobiology:

1. Field and lab experiments on the budget of input and permanent burial and on the rates, agents, pathways, and conditions of *recycling* of biological materials, especially the relatively subtle geochemical and geomicrobiological aspects of "weathering" on and just below the depositional interface.

2. Quantification of *time-averaging* for a broader array of taxonomic groups and depositional settings, including the relative contributions of successive cohorts of material. In part, such work can test and amplify the hypothesis that time-averaged assemblages are dominated by the most recent cohorts, as suggested by recent empirical work on marine mollusks. Recognizing scales of time-averaging via damage levels and other tangible clues in surviving fossil material is a key aspect of this research.

3. Actualistic estimates of the *compositional fidelity* (for species richness, abundances, age groups, etc.) of assemblages for a broader array of taxonomic groups and depositional settings, including explicit attention to whether fidelity can be inferred from observed levels of damage (i.e., taphofacies information) and to how fidelity varies as a function of geographic scale of investigation and the geologic aging of an assemblage.

4. Long-term *stratigraphic trends* in the qualities (Table 1) of the fossil record, including use of the Pleistocene or Neogene as a reflection of the Recent in order to investigate taphonomic modification associated with longer periods of time/space averaging, lithification, and other aspects of the “permanent” fossil record.

5. A major initiative in *probabilistic and other quantitative modeling* as a means of testing existing hypotheses and formulating new hypotheses to test in the stratigraphic record and Recent systems.

After several decades of intensive research, taphonomists now visualize the fossil record of taxa with mineralized or highly refractory tissues as dominated by time-averaged assemblages, with widely spaced horizons and intervals bearing higher resolution records of taxa and paleocommunities. This contrasts with groups lacking readily preserved tissues: macroplant and soft-bodied animal records clearly are subject to much less time-averaging per assemblage than is true for pollen, marine shelly faunas, or land vertebrates, and preservation is limited to a narrower range of environmental conditions. The result is a series of geographically and temporally narrow windows of high anatomical and temporal resolution, relatively widely separated in space and time, producing a historical record with many gaps. Hence the fundamental trade-off now recognized in taphonomy: the better the preservation of individual organisms and the finer the temporal resolution of individual samples, the less likely these are to be repeated at close and regular intervals through geological time. The tendency for the taphonomically most robust groups to exhibit the greatest time-averaging (and thus spatial averaging) (reciprocal model of Kowalewski 1997) is a key corollary of this pattern. Taphonomy’s agenda for the future revolves around better understanding the genesis and fidelity of these different types of records (time-averaged and time-specific), how their attributes are affected by local to global-scale tectonic, climatic, and biotic conditions, and how these taphonomic differences affect our assessment and understanding of paleobio-

logic phenomena such as evolutionary rates and diversity through time in marine versus continental organisms.

Recent and future contributions of taphonomy are relevant to an array of *paleobiologic* issues including the following (Jablonski 1999):

1. *Paleocommunity structure and composition, and how this changes through time in response to environmental perturbations, especially climate shifts.* Establishing paleocommunity structure depends heavily on studies in recent ecosystems, but neontologic and paleontologic views of communities differ in their focus on what controls species distribution and behavior (live versus dead), their selective treatment of particular taxonomic groups, and especially their degrees of temporal sampling. More exchange between neo- and paleoecologists, with an emphasis on collecting new types of field data and modeling fossil assemblages using actualistic data, could generate new insights and a stronger foundation for reconstructing paleocommunities. As a basis for this, we need more quantitative information on the potential spatial fidelity, temporal mixing, and compositional fidelity (percent living and preservable species) for a wider array of environments and taxonomic groups. By empirically linking levels of bias (inferred qualities) to damage profiles (observed states of preservation of species) and depositional modes, we also can develop criteria for isotaphonomic equivalence across space and time, both between Recent and ancient biological systems and through comparative work within the stratigraphic record.

2. *The history of biodiversity dynamics at different scales, from individual assemblages to global tallies of diversity (numbers of species, genera, families, etc.).* There is a clear need for better understanding of taphonomic effects on Phanerozoic (and Precambrian) diversity patterns. Large-scale shifts in taphonomic regime (links between organic preservation and the chemical and physical states of the earth as well as faunal/floral evolution) or between recurring taphonomic states (e.g., due to climate) as suggested in Figure 6, may be contributing confounding patterns to the diversity curves. These megabiases will not necessarily be elim-

inated by approaches such as rarefaction, and modeling what happens to diversity measures over stratigraphic shifts in taphofacies could help to clarify the effects of taphonomy on rarefaction “universes.” Controlling taphonomic biases using isotaphonomic approaches may permit us to develop robust Phanerozoic diversity patterns for particular environments, and this should be complemented by greater efforts to develop nonactualistic means of estimating and compensating for bias when isotaphonomy is impossible. And the explosion of understanding of the chemical and physical aspects of fossil preservation (soft and hard parts) provides a framework for assessing the stratigraphic patterning of census assemblages (including konservat-lagerstätten) and judging what we are missing in other parts of the fossil record.

3. *Rates of evolutionary events (originations, radiations, extinctions, and rebounds after extinctions), including major periods of faunal and floral change at the end of the Permian, the K/T boundary, and the Pleistocene.* Establishing rates depends on accurate biostratigraphic records of taxonomic presence, absolute dating of these records, and comparisons that are matched for the durations over which change was measured. An important goal for taphonomy is to develop more rigorous measures of “preservation potential” for different types of organisms and provide alternative tests of biostratigraphic range limits for comparison with those based on abundance patterns and gap analysis. There should be a search for sub-Recent and Plio-Pleistocene analogues in which known extinctions or appearances are recorded in stratigraphic sequences with high temporal resolution to provide comparisons for the more distant geological record. New understanding of processes of preservation and destruction at the molecular to sequence stratigraphic scales could feed into simulations of real versus apparent records of taxonomic ranges. Likewise, increased appreciation of the limits to resolution provided by space- and time-averaging can help to provide reality checks and quantification of error-bars in correlating environmental change with major biotic events in Earth history.

4. *Correspondence of the macroevolutionary his-*

tory of the biotic system to secular and cyclic geochemical and geophysical changes in Earth and its atmosphere. Taphonomy’s continuing role is to characterize sampling biases that affect macroevolutionary reconstructions, but it contributes an additional perspective on macroevolution through its focus on the recycling of organic and inorganic materials. Such processes have undoubtedly responded to and also affected environmental changes on Earth. Thus, improved information on geologic intervals and settings where physical, chemical, and biological recycling has been particularly effective or particularly ineffective in breaking down organic materials is essential. Investigation of the macrotaphonomic history of the biotic system will involve integrating different scales of evidence for plants, invertebrates, and vertebrates, and developing hypotheses about how taphonomic patterns through time relate to Earth’s physical and chemical history.

Beyond the paleobiologic issues discussed in this review, taphonomy has much to contribute to the fields of ecology, biogeochemistry, sedimentary geology and stratigraphy, paleoanthropology, and conservation biology. We look forward to even greater cross-disciplinary collaborations of information and scientific methods to apply to taphonomic data and questions. Facts—the next generation of data acquisition and analysis of individual taxa and assemblages—will continue to be fundamentally important to all aspects of taphonomy in the coming decades. But there also should be much more attention to synthesis, at the local, regional, and global levels. Next-generation research can target data acquisition that feeds into the search for larger patterns and provides tests for interim hypotheses about global-scale changes in taphonomic regimes and megabiases affecting the largest-scale paleobiological interpretations of the history of life.

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