

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.

Anna K. Behrensmeyer. Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, MRC 121, Washington, D.C. 20560. E-mail: Behrensmeyer.Kay@NMNH.SI.edu

Susan M. Kidwell. Department of Geophysical Sciences, University of Chicago, 5734 South Ellis Avenue, Chicago, Illinois 60637. E-mail: skidwell@midway.uchicago.edu

Robert A. Gastaldo. Department of Geology, Colby College, Waterville, Maine 04901-4799. E-mail: ragastal@colby.edu

Accepted: 30 June 2000

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.”

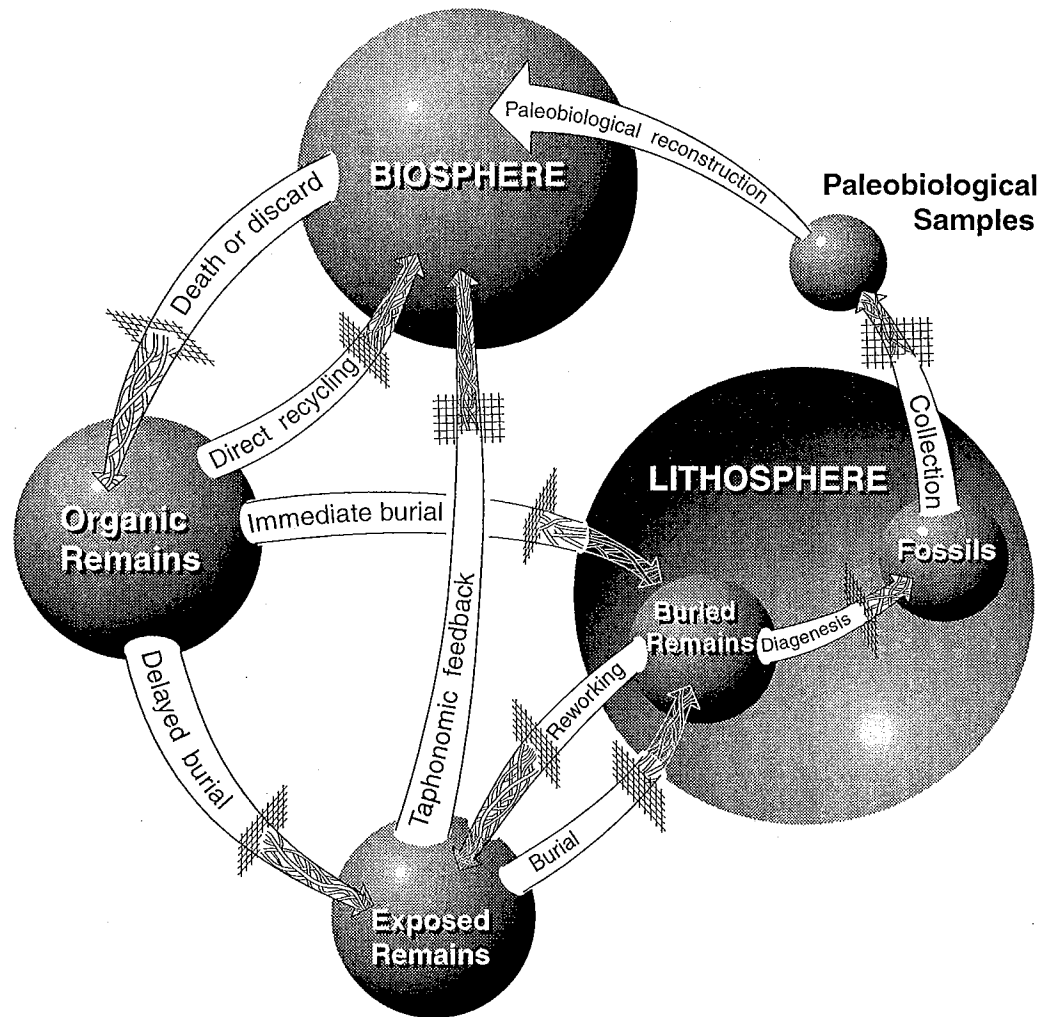


FIGURE 1. The main pathways for organic remains from death to paleobiological inference. Each path is affected by taphonomic processes and circumstances that filter the information as it passes to the next stage. Taphonomy is the study of how biological, chemical, and physical processes operating between 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

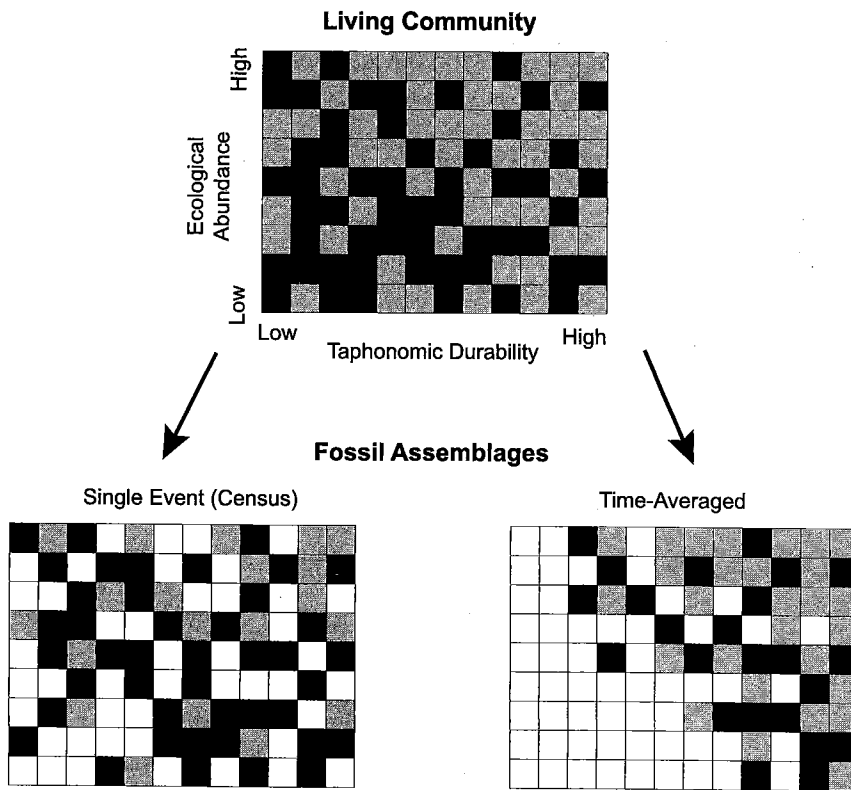


FIGURE 2. Schematic portrayal of information changes in two different types of fossil assemblages compared with a hypothetical living community at one point in time. Each cell is a species characterized by two variables, ecological abundance during life and taphonomic durability of the remains; the living 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 (obtrusion), 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-Uribe 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-Rodrigo 1999), predatory birds and small mammals (Andrews 1990; Cruz-Uribe 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). Degr-

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., Behrensmeier 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., Behrensmeier 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 Behrensmeier 1993).

The expanding baseline of information on

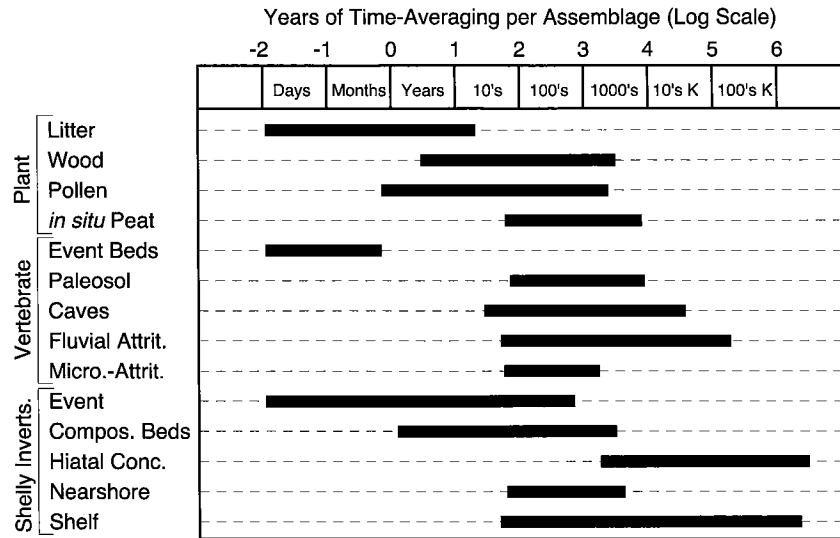


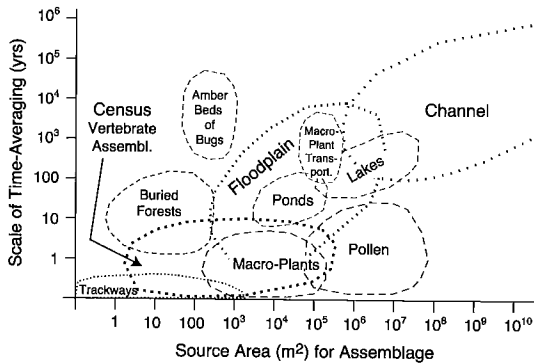
FIGURE 3. Estimated limits on time-averaging of selected types of continental plant tissues and vertebrate and marine invertebrate assemblages. The different categories (tissues versus deposits) reflect the fact that paleobotanists regard tissue type as playing the most important role in time-averaging 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

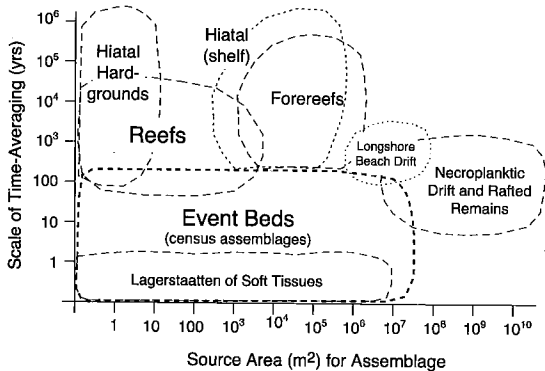


FIGURE 4. Spatial and temporal representation in fossil assemblages for different major groups of organisms, in continental and benthic marine depositional settings. A, Continental settings: dotted lines show areas of the time/space plot occupied by vertebrate remains, dashed lines plant remains; estimate 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; Behrensmeier 1991; Kidwell and Bosence 1991; Behrensmeier and Hook 1992; Kidwell and Flessa 1995; also specific studies by Behrensmeier 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 (Behrensmeier 1982; Dechant Boaz 1994; Aslan and Behrensmeier 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 (Behrensmeier 1982; Frison and Todd 1986; Lask 1993; Prager et al. 1996; Blob 1997; and others previously cited; see also many live/dead com-

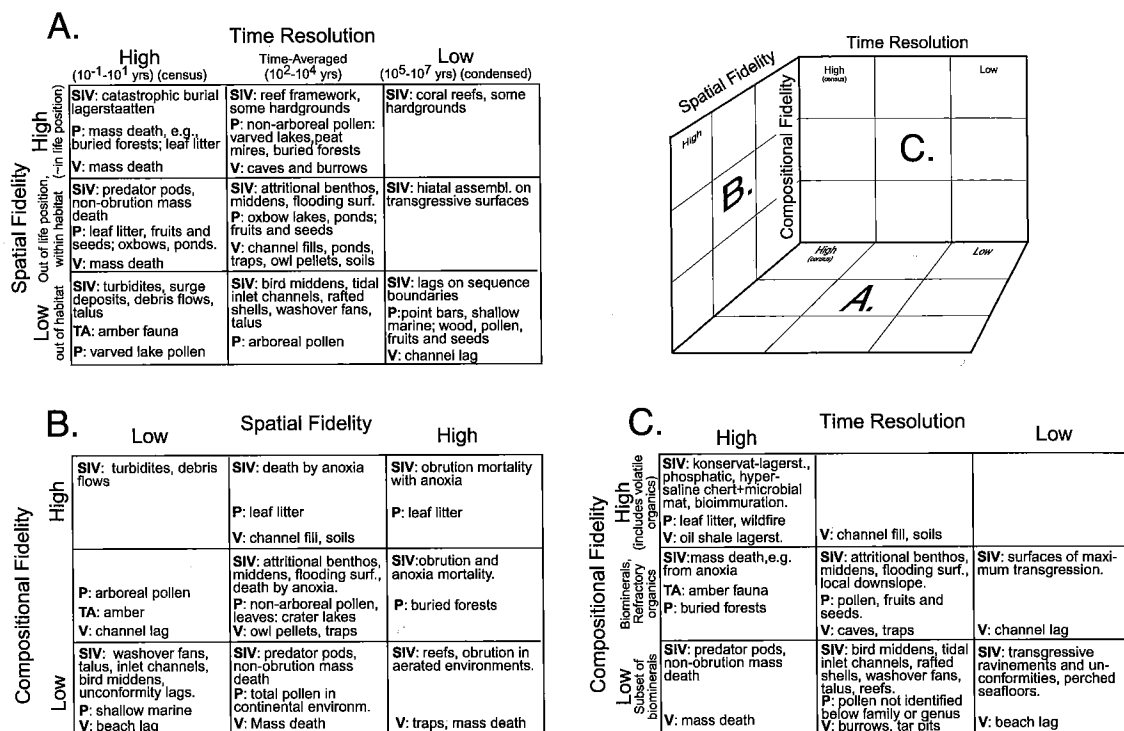


FIGURE 5. Schematic diagram in which each axis represents the summed results of preservational processes affecting time resolution, spatial fidelity, and compositional fidelity relative to the living community, showing that virtually all combinations of these aspects of record quality are possible. Note 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 Behrensmeier 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 "overcomplete" 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 Behrensmeier 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 [Behrensmeier 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; Behrensmeier 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 (Scheiing 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 (forbank) 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 megafloreal, 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 bioorders, 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; Retalack 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 (Bernier and Canfield 1989; Maliva et al. 1989; Bernier 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

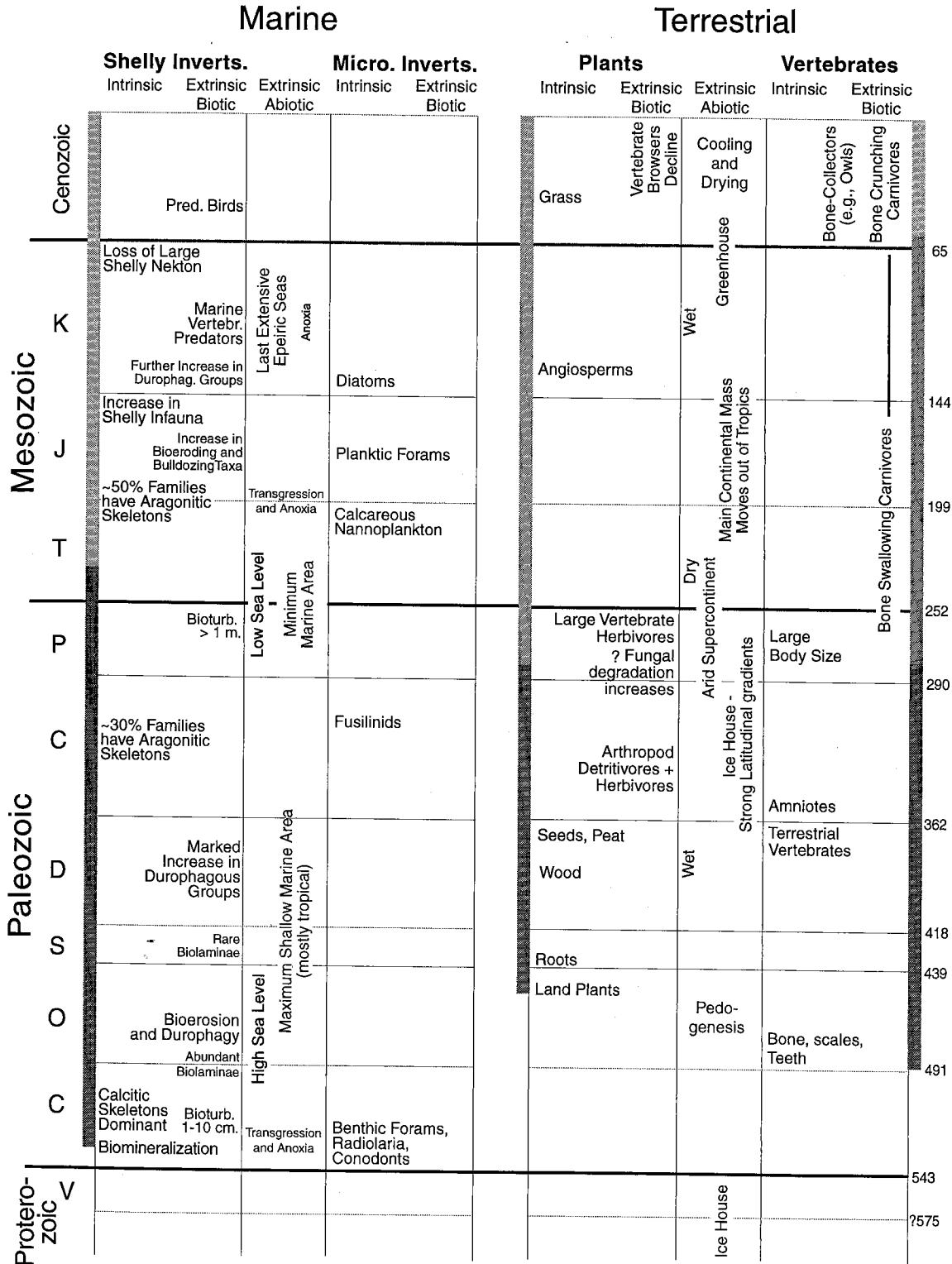


FIGURE 6. Intrinsic and extrinsic changes with the potential for major effects on taphonomic processes and organic preservation over geologic time. This chart provides a preliminary framework for examining hypotheses concerning changing "taphonomic domains" through the fossil record for the marine and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

←

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; Kendrick 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-

confidence 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; Behrensmeier 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; Behrensmeier 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 milleriacrinid 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.

Acknowledgments

We thank the editors of this special issue for their encouragement and suggestions during the writing of this article, and A. I. Miller, R. R. Rogers, and D. Jablonski for helpful reviews.

Literature Cited

- Allen, J. R. L., R. A. Spicer, and A. K. Behrensmeyer. 1990. Transport—hydrodynamics. Pp. 227–235 in Briggs and Crowther 1990.
- Allison, P. A. 1986. Soft-bodied animals in the fossil record: the role of decay in fragmentation during transport. *Geology* 14: 979–981.
- . 1988. Konservat-Lagerstätten: cause and classification. *Paleobiology* 14:331–344.
- Allison, P. A., and D. E. G. Briggs, eds. 1991a. Taphonomy, releasing the data locked in the fossil record. Plenum, New York.
- . 1991b. The taphonomy of soft-bodied animals. Pp. 120–140 in Donovan 1991.
- . 1993a. Paleolatitudinal sampling bias, Phanerozoic species diversity, and the end-Permian extinction. *Geology* 21: 65–68.
- . 1993b. Exceptional fossil record: distribution of soft-tissue preservation through the Phanerozoic. *Geology* 21:527–530.
- Allison, P. A., and K. Pye. 1994. Early diagenetic mineralization and fossil preservation in modern carbonate concretions. *Palaios* 9:561–575.
- Allison, P. A., C. R. Smith, H. Kukert, J. W. Deming, and B. Bennett. 1991. Deep-water taphonomy of vertebrate carcasses: a whale skeleton in the bathyal Santa Catalina Basin. *Paleobiology* 17:78–89.
- Alroy, J. 1996. Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. *Palaeogeography, Palaeoclimatology, Palaeoecology* 127:285–311.
- Alroy, J., P. L. Koch, and J. C. Zachos. 2000. Global climate change and North American mammalian evolution. In D. H. Erwin and S. L. Wing, eds. *Deep time: Paleobiology's perspective*. *Paleobiology* 26(Suppl. to No. 4):259–288.
- Anderson, L. C., B. K. Sen Gupta, R. A. McBride, and M. R. Byrnes. 1997. Reduced seasonality of Holocene climate and pervasive mixing of Holocene marine section: northeastern Gulf of Mexico shelf. *Geology* 25:127–130.
- Anderson, L. C., R. A. McBride, M. J. Taylor, and M. R. Byrnes. 1998. Late Holocene record of community replacement preserved in time-averaged molluscan assemblages, Louisiana chenier plain. *Palaios* 13:488–499.
- Andrews, P. 1990. *Owls, caves, and fossils*. University of Chicago Press, Chicago.
- Andrews, P., and J. Cook. 1989. Natural modifications to bones in a temperate setting. *Man* 20:675–691.
- Archer, M., S. J. Hand, and H. Godthelp. 1991. *Riversleigh: the story of animals in ancient rainforests of inland Australia*. Reed Books, Balgowlah, New South Wales.
- Argast, S., J. O. Farlow, R. M. Gabet, and D. L. Brinkman. 1987. Transport-induced abrasion of fossil reptilian teeth: implications for the existence of Tertiary dinosaurs in the Hell Creek Formation, Montana. *Geology* 15:927–930.
- Aronson, R. B. 1992. Decline of the Burgess Shale fauna: ecologic or taphonomic restriction? *Lethaia* 25:225–229.
- Aslan, A., and A. K. Behrensmeyer. 1996. Taphonomy and time resolution of bone assemblages in a contemporary fluvial system: the East Fork River, Wyoming. *Palaios* 11:411–421.
- Ausich, W. I. 1997. Regional encrinites: a vanished lithofacies. Pp. 509–519 in C. E. Brett and G. C. Baird, eds. *Paleontological events: stratigraphic, ecological and evolutionary implications*. Columbia University Press, New York.
- Ausich, W. I., and G. D. Sevastopulo. 1994. Taphonomy of Lower Carboniferous crinoids from the Hook Head Formation, Ireland. *Lethaia* 27:245–256.
- Bada, J. L., X. S. Wang, and H. Hamilton. 1999. Preservation of key biomolecules in the fossil record: current knowledge and future challenges. *Philosophical Transactions of the Royal Society of London B* 354:77–87.
- Badgley, C. E. 1982. How much time is represented in the present? The development of time-averaged modern assemblages as models for the fossil record. In B. Mamet and M. J. Copeland, eds. *Proceedings of the Third North American Paleontological Convention* 1:23–28.
- . 1986. Counting individuals in mammalian fossil assemblages from fluvial environments. *Palaios* 1:328–355.
- Badgley, C. E., and A. K. Behrensmeyer. 1995. Preservational, paleoecological and evolutionary patterns in the Paleogene of Wyoming–Montana and the Neogene of Pakistan. *Palaeogeography, Palaeoclimatology, Palaeoecology* 115:319–340.
- Baird, G. C., S. D. Sroka, C. W. Shabica, and G. J. Kuecher. 1986. Taphonomy of Middle Pennsylvanian Mazon Creek area fossil localities, northeast Illinois: significance of exceptional fossil preservation in syngenetic concretions. *Palaios* 1:271–285.
- Bambach, R. K. 1977. Species richness in marine benthic habitats through the Phanerozoic. *Paleobiology* 3:152–167.
- Barry, J. C., M. E. Morgan, A. J. Winkler, L. J. Flynn, E. H. Lindsay, L. L. Jacobs, and D. Pilbeam. 1991. Faunal interchange and Miocene terrestrial vertebrates of southern Asia. *Paleobiology* 17:231–245.
- Bartels, C., D. E. G. Briggs, and G. Brassel. 1998. *The fossils of the Hunsrück Slate: marine life in the Devonian*. Cambridge University Press, Cambridge.
- Barthel, K. W., N. H. M. Winburne, and S. Conway Morris. 1990. *Solnhofen: a study in Mesozoic paleontology*. Cambridge University Press, Cambridge.
- Bartley, J. K. 1996. Actualistic taphonomy of cyanobacteria: implications for the Precambrian fossil record. *Palaios* 11:571–586.
- Bartram, L. E., Jr., and C. W. Marean. 1999. Explaining the “Klaesies pattern”: Kua ethnoarchaeology, the Die Kelders Middle Stone Age archaeofauna, long bone fragmentation and carnivore ravaging. *Journal of Archaeological Science* 26:9–29.
- Baumiller, T. K., G. Llewellyn, C. G. Messing, and W. E. Ausich. 1995. Taphonomy of isocrinoid stalks: influence of decay and autonomy. *Palaios* 10:87–95.
- Behrensmeyer, A. K. 1978a. Taphonomic and ecological information from bone weathering. *Paleobiology* 4:150–162.
- . 1978b. Correlation in Plio-Pleistocene sequences of the northern Lake Turkana Basin: a summary of evidence and issues. Pp. 421–440 in W. W. Bishop, ed. *Geological background to fossil man*. Scottish Academic Press, Edinburgh.
- . 1982. Time resolution in fluvial vertebrate assemblages. *Paleobiology* 8:211–227.
- . 1987. Miocene fluvial facies and vertebrate taphonomy in northern Pakistan. In F. G. Ethridge, R. M. Flores, and M. D. Harvey, eds. *Recent developments in fluvial sedimentology*. SEPM Special Publication 39:169–176.
- . 1988. Vertebrate preservation in fluvial channels. *Palaeogeography, Palaeoclimatology, Palaeoecology* 63:183–199.
- . 1990. Transport/hydrodynamics of bones. Pp. 232–235 in Briggs and Crowther 1990.
- . 1991. Terrestrial vertebrate accumulation. Pp. 291–335 in Allison and Briggs 1991.
- . 1993. The bones of Amboseli: bone assemblages and ecological change in a modern African ecosystem. *National Geographic Research* 9:402–421.
- Behrensmeyer, A. K., and R. E. Chapman. 1993. Models and simulations of time-averaging in terrestrial vertebrate accumulations. Pp. 125–149 in Kidwell and Behrensmeyer 1993.
- Behrensmeyer, A. K., and D. E. Dechant Boaz. 1980. The Recent bones of Amboseli Park, Kenya, in relation to East African paleoecology. Pp. 72–92 in A. K. Behrensmeyer and A. P. Hill,

- eds. Fossils in the making. University of Chicago Press, Chicago.
- Behrensmeyer, A. K., and R. W. Hook. 1992. Paleoenvironmental contexts and taphonomic modes. Pp. 15–136 in A. K. Behrensmeyer, J. D. Damuth, W. A. DiMichele, R. Potts, H.-D. Sues, and S. L. Wing, eds. *Terrestrial ecosystems through time*. University of Chicago Press, Chicago.
- Behrensmeyer, A. K., and S. M. Kidwell. 1985. Taphonomy's contributions to paleobiology. *Paleobiology* 11:105–119.
- Behrensmeyer, A. K., N. E. Todd, R. Potts, and G. E. McBrinn. 1997. Late Pliocene faunal turnover in the Turkana Basin, Kenya and Ethiopia. *Science* 278:1589–1594.
- Bell, M. A., M. S. Sadagursky, and J. V. Baumgartner. 1987. Utility of lacustrine deposits for study of variation within fossil samples. *Palaios* 2:455–466.
- Bell, M. A., C. E. Wells, and J. A. Marshall. 1989. Mass-mortality layers of fossil stickleback fish: catastrophic kills of polymorphic schools. *Evolution* 43:607–619.
- Bengtson, S. 1994. Early life on Earth (Nobel Symposium No. 84). Columbia University Press, New York.
- Bennington, J. B., and S. D. Rutherford. 1999. Precision and reliability in paleocommunity comparisons based on cluster-confidence intervals: how to get more statistical bang for your sampling buck. *Palaios* 14:506–515.
- Benton, M. J. 1998. The quality of the fossil record of the vertebrates. Pp. 269–300 in S. K. Donovan and C. R. C. Paul, eds. *The adequacy of the fossil record*. Wiley, New York.
- Berner, R. A. 1991. A model for atmospheric CO₂ over Phanerozoic time. *American Journal of Science* 291:339–376.
- Berner, R. A., and D. E. Canfield. 1989. A new model for atmospheric oxygen over Phanerozoic time. *American Journal of Science* 289:333–361.
- Best, M. M. R., and S. M. Kidwell. 1996. Bivalve shell taphonomy in tropical siliciclastic environments: preliminary experimental results. In J. E. Repetski, ed. *Sixth North American paleontological convention, Abstracts of papers*. Paleontological Society Special Publication 8:34.
- . 2000a. Bivalve taphonomy in tropical mixed siliciclastic-carbonate settings. I. Environmental variation in shell condition. *Paleobiology* 26:80–102.
- . 2000b. Bivalve taphonomy in tropical mixed siliciclastic-carbonate settings. II. Effect of bivalve life habits and shell types. *Paleobiology* 26:103–115.
- Best, M. M. R., S. M. Kidwell, T. C. W. Ku, and L. M. Walter. 1999. The role of microbial iron reduction in the preservation of skeletal carbonate: bivalve taphonomy and porewater geochemistry in tropic siliciclastics vs. carbonates. *Geological Society of America Abstracts with Programs* 31:419–420.
- Bishop, J. D. D. 1989. Colony form and the exploitation of spatial refuges by encrusting bryozoa. *Biological Reviews* 64:197–218.
- Blob, R. W. 1997. Relative hydrodynamic dispersal potentials of soft-shelled turtle elements: implications for interpreting skeletal sorting in assemblages of non-mammalian terrestrial vertebrates. *Palaios* 12:151–164.
- Blumenshine, R. 1986. Carcass consumption sequences and the archaeological distinction of scavenging and hunting. *Journal of Human Evolution* 15:639–659.
- . 1988. An experimental model of the timing of hominid and carnivore influence on archaeological bone assemblages. *Journal of Archaeological Science* 15:483–502.
- . 1991. Hominid carnivory and foraging strategies and the socio-economic function of early archaeological sites. *Philosophical Transactions of the Royal Society of London B* 334:211–221.
- Bonnichsen, R., and M. H. Sorg. 1989. Bone modification. Institute for Quaternary Studies, University of Maine, Orono.
- Bosence, D. W. J. 1979. Live and dead faunas from coralline algal gravels, Co. Galway. *Palaeontology* 22:449–478.
- Bottjer, D. J., and D. Jablonski. 1988. Paleoenvironmental patterns in the evolution of post-Paleozoic benthic marine invertebrates. *Palaios* 3:540–560.
- Boulton, A. J., and P. I. Boon. 1991. A review of methodology used to measure leaf litter decomposition in lotic environments: time to turn over an old leaf? *Australian Journal of Marine and Freshwater Research* 42:1–43.
- Bown, T. M., and K. C. Beard. 1990. Systematic lateral variation in the distribution of fossil mammals in alluvial paleosols, lower Eocene Willwood Formation, Wyoming. *Geological Society of America Special Paper* 243:135–151.
- Brandt, D. S. 1986. Preservation of event beds through time. *Palaios* 1:92–96.
- Brandt, D. S., and R. J. Elias. 1989. Temporal variation in tephrite thickness may be a geologic record of atmospheric CO₂. *Geology* 17:951–952.
- Brett, C. E. 1995. Sequence stratigraphy, biostratigraphy, and taphonomy in shallow marine environments. *Palaios* 10:597–616.
- Brett, C. E., and G. C. Baird. 1986. Comparative taphonomy: a key to paleoenvironmental interpretation based on fossil preservation. *Palaios* 1:207–227.
- Brett, C. E., and A. Seilacher. 1991. Fossil Lagerstätten: a taphonomic consequence of event sedimentation. Pp. 283–297 in G. Einsele, W. Ricken, and A. Seilacher, eds. *Cycles and events in stratigraphy*. Springer, Berlin.
- Brett, C. E., A. J. Boucot, and B. Jones. 1993. Absolute depths of Silurian benthic assemblages. *Lethaia* 26:25–40.
- Brett, C. E., T. E. Whiteley, P. A. Allison, and E. L. Yochelson. 1999. The Walcott-Rust quarry: Middle Ordovician trilobite Konservat-Lagerstätten. *Journal of Paleontology* 73:288–305.
- Briggs, D. E. G. 1993. Fossil biomolecules. *Bulletin of the Biochemical Society* 15:8–12.
- . 1995. Experimental taphonomy. *Palaios* 10:539–550.
- Briggs, D. E. G., and E. N. K. Clarkson. 1990. The late Palaeozoic radiation of malacostracan crustaceans. In P. D. Taylor and G. P. Larwood, eds. *Major evolutionary radiations*. Systematics Association Special Volume 42:165–186. Clarendon, Oxford.
- Briggs, D. E. G., and P. R. Crowther, eds. 1990. *Palaeobiology, a synthesis*. Blackwell Science, Oxford.
- Briggs, D. E. G., and A. J. Kear. 1994a. Decay of *Branchiostoma*: Implications for soft-tissue preservation in conodonts and other primitive chordates. *Lethaia* 26:275–287.
- . 1994b. Decay and mineralization of shrimps. *Palaios* 9:431–456.
- Briggs, D. J., D. D. Gilbertson, and A. L. Harris. 1990. Molluscan taphonomy in a braided river environment and its implications for studies of Quaternary cold-stage river deposits. *Journal of Biogeography* 17:623–637.
- Briggs, D. E. G., P. R. Wilby, B. P. Pérez-Moreno, J. L. Sanz, and M. Fregenal-Martínez. 1997. The mineralization of dinosaur soft tissue in the Lower Cretaceous of Las Hoyas, Spain. *Journal of the Geological Society, London* 154:587–588.
- Briggs, D. E. G., B. A. Stankiewicz, D. Meischner, A. Bierstedt, and R. P. Evershed. 1998. Taphonomy of arthropod cuticles from Pliocene late sediments, Willershausen, Germany. *Palaios* 13:386–394.
- Briggs, D. E. G., R. P. Evershed, and M. J. Lockheart. 2000. The molecular paleontology of continental fossils. In D. H. Erwin and S. L. Wing, eds. *Deep time: Paleobiology's perspective*. *Paleobiology* 26(Suppl. to No. 4):169–193.
- Buatois, L. A., A. G. Mángano, J. F. Genise, and T. N. Taylor. 1998. The ichnologic record of the continental invertebrate invasion: evolutionary trends in environmental expansion, ecospace utilization, and behavioral complexity. *Palaios* 13:217–240.
- Budd, D. A., and E. E. Hiatt. 1993. Mineralogical stabilization of

- high-magnesium calcite: geochemical evidence for intracrystalline recrystallization within Holocene porcellaneous foraminifera. *Journal of Sedimentary Petrology* 63:261–274.
- Burnham, R. J. 1989. Relationships between standing vegetation and leaf litter in a paratropical forest: implications for paleobotany. *Review of Palaeobotany and Palynology* 58:5–32.
- . 1990. Paleobotanical implications of drifted seeds and fruits from modern mangrove litter, Twin Cays, Belize. *Palaios* 5:364–370.
- . 1993. Reconstructing richness in the plant fossil record. *Palaios* 8:376–384.
- . 1994. Patterns in tropical leaf litter and implications for angiosperm paleobotany. *Review of Palaeobotany and Palynology* 81:99–113.
- Burnham, R. J., and R. A. Spicer. 1986. Fossil litter preserved by volcanic activity at El Chicón, Mexico: a potentially accurate record of the pre-eruption vegetation. *Palaios* 1:158–161.
- Burnham, R. J., S. L. Wing, and G. C. Parker. 1992. The reflection of deciduous forest communities in leaf litter: implications for autochthonous litter assemblages from the fossil record. *Paleobiology* 18:30–49.
- Butterfield, N. J. 1990. Organic preservation of non-mineralizing organisms and the taphonomy of the Burgess Shale. *Paleobiology* 16:272–286.
- . 1995. Secular distribution of Burgess Shale-type preservation. *Lethaia* 28:1–13.
- Cadée, G. C. 1984. Macrobenthos and macrobenthic remains on the Oyster Ground, North Sea. *Netherlands Journal of Sea Research* 18:160–178.
- . 1991. The history of taphonomy. Pp. 3–21 in Donovan 1991.
- . 1994. Eider, shelduck, and other predators: the main producers of shell fragments in the Wadden Sea—paleoecological implications. *Palaeontology* 37:181–202.
- . 1999. Bioerosion of shells by terrestrial gastropods. *Lethaia* 32:253–260.
- Calleja, M., M. Rossignol-Strick, and D. Duzer. 1993. Atmospheric pollen content off West Africa. *Review of Palaeobotany and Palynology* 79:335–368.
- Callender, W. R., E. N. Powell, and G. M. Staff. 1994. Taphonomic rates of molluscan shells placed in autochthonous assemblages on the Louisiana continental slope. *Palaios* 9:60–73.
- Carroll, R. L. 1997. *Patterns and processes of vertebrate evolution*. Cambridge University Press, Cambridge.
- Cate, A. S., and I. Evans. 1994. Taphonomic significance of the biomechanical fragmentation of live molluscan shell material by a bottom-feeding fish (*Pogonias cromis*) in Texas coastal bays. *Palaios* 9:254–274.
- Chafetz, H., and C. Buczynski. 1992. Bacterially induced lithification of microbial mats. *Palaios* 7:277–293.
- Chatterton, B. D. E., and S. E. Speyer. 1997. Ontogeny. Pp. 173–247 in H. B. Whittington et al. *Arthropoda 1, Trilobita*, revised. Part O of R. C. Moore and C. Teichert, eds. *Treatise on invertebrate paleontology*. Geological Society of America and University of Kansas, Boulder, Colo.
- Claassen, C. 1998. *Shells*. Cambridge Manuals in Archaeology. Cambridge University Press, Cambridge.
- Clark, G. R., II. 1999. Organic matrix taphonomy in some molluscan shell microstructures. *Palaeogeography, Palaeoclimatology, Palaeoecology* 149:305–312.
- Clyde, W. C., and P. D. Gingerich. 1998. Mammalian community response to the latest Paleocene thermal maximum: an isotaphonomic study in the northern Bighorn Basin, Wyoming. *Geology* 26:1011–1014.
- Collinson, M. E. 1983. Accumulations of fruits and seeds in three small sedimentary environments in southern England and their palaeoecological implications. *Annals of Botany* 52:583–592.
- Cook, E. 1995. Taphonomy of two non-marine Lower Cretaceous bone accumulations from southeastern England. *Palaeogeography, Palaeoclimatology, Palaeoecology* 116:263–270.
- Crowley, S. S., D. A. Dufek, R. W. Stanton, and T. A. Ryer. 1994. The effects of volcanic ash disturbances on a peat-forming environment: environmental disruption and taphonomic consequences. *Palaios* 9:158–174.
- Cruz-Uribe, K., and R. G. Klein. 1998. Hyrax and hare bones from modern South African eagle roosts and the detection of eagle involvement in fossil bone assemblages. *Journal of Archaeological Science* 25:135–147.
- Cummins, H. 1994. Taphonomic processes in modern freshwater molluscan death assemblages: implications of the freshwater fossil record. *Palaeogeography, Palaeoclimatology, Palaeoecology* 108:55–73.
- Cummins, H., E. N. Powell, R. J. Stanton, and G. M. Staff. 1986a. The size frequency distribution in palaeoecology: effects of taphonomic processes during formation of molluscan death assemblages in Texas bays. *Palaeontology* 29:495–518.
- . 1986b. The rate of taphonomic loss in modern benthic habitats: how much of the potentially preservable community is preserved? *Palaeogeography, Palaeoclimatology, Palaeoecology* 52:291–320.
- Cunningham, C. R., H. R. Feldman, E. K. Franseen, R. A. Gastaldo, G. Mapes, C. G. Maples, and H.-P. Schultze. 1993. The Upper Carboniferous Hamilton fossil Lagerstätte in Kansas: a valley fill, tidally influenced deposit. *Lethaia* 26:225–236.
- Cutler, A. H. 1989. Shells survive—loss, persistence and accumulation of hardparts in shallow marine sediments. *Geological Society of America Abstracts with Programs* 21:A71.
- . 1991. Nested faunas and extinction in fragmented habitats. *Conservation Biology* 5:496–505.
- . 1993. Mathematical models of temporal mixing in the fossil record. Pp. 169–187 in Kidwell and Behrensmeier 1993.
- Cutler, A. H., and A. K. Behrensmeier. 1996. Models of vertebrate mass mortality events at the K/T Boundary. In G. Ryder, D. Fastovsky, and S. Gartner, eds. *The Cretaceous-Tertiary Event and other catastrophes in earth history*. Geological Society of America Special Paper 307:375–380.
- Cutler, A. H., and K. W. Flessa. 1990. Fossils out of sequence: computer simulations and strategies for dealing with stratigraphic disorder. *Palaios* 5:227–235.
- . 1995. Bioerosion, dissolution and precipitation as taphonomic agents at high and low latitudes. *Senckenbergiana Maritima* 25:115–121.
- Cutler, A. H., A. K. Behrensmeier, and R. E. Chapman. 1999. Environmental information in a recent bone assemblage: roles of taphonomic processes and ecological change. *Palaeogeography, Palaeoclimatology, Palaeoecology* 149:359–372.
- Daley, G. M. 1993. Passive deterioration of shelly material: a study of the Recent eastern Pacific articulate brachiopod *Terbratalia transversa* Sowerby. *Palaios* 8:226–232.
- Daley, R. L., and D. W. Boyd. 1996. The role of skeletal microstructure during selective silicification of brachiopods. *Journal of Sedimentary Research* 66:155–162.
- Damuth, J. 1982. Analysis of the preservation of community structure in assemblages of fossil mammals. *Paleobiology* 8:434–446.
- Davies, D. J. 1993. Taphonomic analysis as a tool for long-term community baseline delineation: taphoanalysis in an environmental impact statement (EIS) for proposed human seafloor disturbances, Alabama continental shelf. *Geological Society of America Abstracts with Programs* 25:A459.
- Davies, D. J., E. N. Powell, and R. J. Stanton. 1989. Taphonomic signature as a function of environmental process: shells and shell beds in a hurricane-influenced inlet on the Texas coast.

- Palaeogeography, Palaeoclimatology, Palaeoecology 72:317–356.
- Davies-Vollum, K. S., and S. L. Wing. 1998. Sedimentological, taphonomic, and climatic aspects of Eocene swamp deposits (Willwood Formation, Bighorn Basin, Wyoming). *Palaios* 13: 28–40.
- Davis, P. G., and D. E. G. Briggs. 1998. The impact of decay and disarticulation on the preservation of fossil birds. *Palaios* 13: 3–13.
- Dawson, J. W. 1882. On the results of recent explorations of erect trees containing animal remains in the coal formation of Nova Scotia. *Philosophical Transactions of the Royal Society of London B* 173:621–659.
- Dechant Boaz, D. 1994. Taphonomy and the fluvial environment. Pp. 377–413 in R. S. Corruccini and R. L. Ciochon, eds. *Integrative paths to the past: paleoanthropological advances in honor of F. Clark Howell*. Prentice-Hall, Englewood Cliffs, N.J.
- Demko, T. M., and R. A. Gastaldo. 1992. Paludal environments of the Lower Mary Lee coal zone, Pottsville Formation, Alabama: stacked clastic swamps and peat mires. *International Journal of Coal Geology* 20:23–47.
- Demko, T. M., R. F. Dubiel, and J. T. Parrish. 1998. Plant taphonomy in incised valleys: implications for interpreting paleoclimate from fossil plants. *Geology* 26:1119–1122.
- Dent, S. R. 1995. A taphofacies model of the Recent South Florida continental shelf: a new perspective for a classic, exposed carbonate environment. Ph.D. dissertation. University of Cincinnati, Cincinnati, Ohio.
- D'Hondt, S., P. Donaghay, J. C. Zachos, D. Luttenberg, and M. Lindinger. 1998. Organic carbon fluxes and ecological recovery from the Cretaceous-Tertiary mass extinction. *Science* 282: 276–279.
- DiMichele, W. A., and R. B. Aronson. 1992. The Pennsylvanian-Permian vegetational transition: a terrestrial analogue to the onshore-offshore hypothesis. *Evolution* 46:807–824.
- DiMichele, W. A., and R. W. Hook. 1992. Paleozoic terrestrial ecosystems. Pp. 205–325 in A. K. Behrensmeier, J. D. Damuth, W. A. DiMichele, R. Potts, H.-D. Sues, and S. L. Wing, eds. *Terrestrial ecosystems through time*. University of Chicago Press, Chicago.
- DiMichele, W. A., S. H. Mamay, D. S. Chaney, R. W. Hook, and W. J. Nelson. In press. An early Permian flora with Late Permian and Mesozoic affinities from north-central Texas. *Journal of Paleontology*.
- Dodson, P. 1987. Microfaunal studies of dinosaur paleoecology, Judith River Formation of southern Alberta (Canada). *Palaeogeography, Palaeoclimatology, Palaeoecology* 10:21–74.
- Dominguez-Rodrigo, M. 1999. Flesh availability and bone modifications in carcasses consumed by lions: palaeoecological relevance in hominid foraging patterns. *Palaeogeography, Palaeoclimatology, Palaeoecology* 149:373–388.
- Donovan, S. K., ed. 1991. *The processes of fossilization*. Columbia University Press, New York.
- Donovan, S. K., and C. R. C. Paul, eds. 1998. *The adequacy of the fossil record*. Wiley, New York.
- Downing, K. F., and L. E. Park. 1998. Geochemistry and early diagenesis of mammal-bearing concretions from the Sucker Creek Formation (Miocene) of southeastern Oregon. *Palaios* 13:14–27.
- Doyle, P., and D. I. M. Macdonald. 1993. Belemnite battlefields. *Lethaia* 26:65–80.
- Droser, M. L., and D. J. Bottjer. 1993. Trends and patterns of Phanerozoic ichnofabrics. *Annual Review of Earth and Planetary Sciences* 21:205–225.
- Duncan, I. J., D. E. G. Briggs, and M. Archer. 1998. Three-dimensionally mineralized insects and millipedes from the Tertiary of Riversleigh, Queensland, Australia. *Palaeontology* 41: 835–851.
- Eberth, D. A. 1990. Stratigraphy and sedimentology of vertebrate microfossil localities in uppermost Judith River Formation (Campanian) of Dinosaur Provincial Park, south-central Alberta, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology* 78:1–36.
- Eberth, D., R. Rogers and T. Fiorillo, convenors. 1999. Bonebeds: genesis, analysis, and paleoecological significance (program for a symposium). *Journal of Vertebrate Paleontology* 19(Suppl. to No. 3):7A.
- Efremov, J. A. 1940. Taphonomy: new branch of paleontology. *Pan American Geologist* 74:81–93.
- Elder, R. L., and G. R. Smith. 1984. Fish taphonomy and paleoecology. *Geobios Mémoire Spécial* 8:287–291.
- Elias, S. A., T. R. Van Devender, and R. De Baca. 1995. Insect fossil evidence of late glacial and Holocene environments in the Bolson de Mapimi, Chihuahuan Desert, Mexico: comparisons with the paleobotanical record. *Palaios* 10:454–464.
- Emig, C. C. 1990. Examples of post-mortality alteration in Recent brachiopod shells and (paleo)ecological consequences. *Marine Biology* 104:233–238.
- Evans, S., and J. A. Todd. 1997. Late Jurassic soft-bodied wood epibionts preserved by bioimmuration. *Lethaia* 30:185–189.
- Farley, M. B. 1987. Palynomorphs from surface water of the eastern and central Caribbean Sea. *Micropaleontology* 33:254–262.
- Fedonkin, M. A. 1994. Vendian body fossils and trace fossils. Pp. 370–388 in Bengtson 1984.
- Feige, A., and F. T. Fürsich. 1991. Taphonomy of the Recent molluscs of Bahía la Choya (Gulf of California, Sonora, Mexico). *Zitteliana* 18:89–113.
- Feldmann, R. M., T. Villamil, and E. G. Kauffman. 1999. Decapod and stomatopod crustaceans from mass mortality Lagerstätten: Turonian (Cretaceous) of Colombia. *Journal of Paleontology* 73:91–101.
- Ferguson, D. K. 1995. Plant part processing and community reconstruction. *Eclogae Geologicae Helvetiae* 88:627–641.
- Fernández-Jalvo, Y., C. Denys, P. Andrews, T. Williams, Y. Dauphin and L. Humphreys. 1998. Taphonomy and paleoecology of Olduvai Bed-I (Pleistocene, Tanzania). *Journal of Human Evolution* 34:137–172.
- Fernández-López, S. 2000. Ammonite taphocycles in carbonate epicontinental platforms. Fifth international symposium on the Jurassic System (Vancouver, B.C.). *GeoResearch Forum* 6: 293–300.
- Fiorillo, A. R. 1988. Taphonomy of Hazard Homestead Quarry (Ogallala Group), Hitchcock County, Nebraska. *Contributions to Geology University of Wyoming* 26:57–97.
- . 1989. An experimental study of trampling: implications for the fossil record. Pp. 61–72 in R. Bonnicksen and M. H. Sorg, eds. *Bone modification*. Institute for Quaternary Studies, University of Maine, Orono.
- . 1991. Taphonomy and depositional setting of Careless Creek Quarry (Judith River Formation), Wheatland County, Montana. *Palaeogeography, Palaeoclimatology, Palaeoecology* 81:281–311.
- Flessa, K. W. 1998. Well-traveled cockles: shell transport during the Holocene transgression of the southern North Sea. *Geology* 26:187–190.
- Flessa, K. W., and M. Kowalewski. 1994. Shell survival and time-averaging in nearshore and shelf environments: estimates from the radiocarbon literature. *Lethaia* 27:153–165.
- Flessa, K. W., A. H. Cutler, and K. H. Meldahl. 1993. Time and taphonomy: quantitative estimates of time-averaging and stratigraphic disorder in a shallow marine habitat. *Paleobiology* 19:266–286.

- Foote, M. 1996. On the probability of ancestors in the fossil record. *Paleobiology* 22:141-151.
- . 1997. Sampling, taxonomic description, and our evolving knowledge of morphological diversity. *Paleobiology* 23:181-206.
- . 2000. Origination and extinction components of taxonomic diversity: general problems. In D. H. Erwin and S. L. Wing, eds. *Deep time: Paleobiology's perspective*. *Paleobiology* 26(Suppl. to No. 4):74-102.
- Foote, M., and D. M. Raup. 1996. Fossil preservation and the stratigraphic ranges of taxa. *Paleobiology* 22:121-140.
- Foote, M., J. P. Hunter, C. M. Janis, and J. J. Sepkoski Jr. 1999. Evolutionary and preservational constraints on origins of biologic groups: divergence times of Eutherian mammals. *Science* 283:1310-1314.
- Franzen, J. L. 1985. Exceptional preservation of Eocene vertebrates in the lake deposits of Grube Messel (West Germany). *Philosophical Transactions of the Royal Society of London B* 311:181-186.
- Frison, G. C., and L. C. Todd. 1986. The Colby Mammoth Site: taphonomy and archaeology of a Clovis kill in northern Wyoming. University of New Mexico Press, Albuquerque.
- Fürsich, F. T. 1978. The influence of faunal condensation and mixing on the preservation of fossil benthic communities. *Lethaia* 11:243-250.
- Fürsich, F. T., and M. Aberhan. 1990. Significance of time-averaging for paleocommunity analysis. *Lethaia* 23:143-152.
- Fürsich, F. T., and W. Oschmann. 1993. Shell beds as tools in basin analysis: the Jurassic of Kachchh, western India. *Journal of the Geological Society, London* 150:169-185.
- Gastaldo, R. A. 1988. A conspectus of phytotaphonomy. In W. A. DiMichele and S. L. Wing, eds. *Methods and applications of plant paleoecology: notes for a short course*. *Paleontological Society Special Publication* 3:14-28.
- . 1992. Taphonomic considerations for plant evolutionary investigations. *The Palaeobotanist* 41:211-223.
- . 1994. The genesis and sedimentation of phytoclasts with examples from coastal environments. Pp. 103-127 in A. Traverse, ed. *Sedimentation of organic particles*. Cambridge University Press, Cambridge.
- Gastaldo, R. A., and D. K. Ferguson. 1998. Reconstructing Tertiary plant communities: introductory remarks. *Review of Palaeobotany and Palynology* 101:3-6.
- Gastaldo, R. A., and A. Y. Huc. 1992. Sediment facies, depositional environments, and distribution of phytoclasts in the Recent Mahakam River delta, Kalimantan, Indonesia. *Palaios* 7:574-591.
- Gastaldo, R. A., and J. R. Staub. 1999. A mechanism to explain the preservation of leaf litter lenses in coals derived from raised mires. *Palaeogeography, Palaeoclimatology, Palaeoecology* 149:1-14.
- Gastaldo, R. A., D. P. Douglass, and S. M. McCarroll. 1987. Origin, characteristics, and provenance of plant macrodetritus in a Holocene crevasse splay, Mobile Delta, Alabama. *Palaios* 2:229-240.
- Gastaldo, R. A., T. M. Demko, and Y. Liu. 1993a. Application of sequence and genetic stratigraphic concepts to Carboniferous coal-bearing strata: an example from the Black Warrior Basin, USA. *Geologische Rundschau* 82:212-226.
- Gastaldo, R. A., G. P. Allen, and A. Y. Huc. 1993b. Detrital peat formation in the tropical Mahakam River delta, Kalimantan, eastern Borneo: formation, plant composition, and geochemistry. In J. C. Cobb and C. B. Cecil, eds. *Modern and ancient coal-forming environments*. Geological Society of America Special Paper 286:107-118.
- Gastaldo, R. A., H. Walther, J. Rabold, and D. Ferguson. 1996. Criteria to distinguish parautochthonous leaves in Cenophytic alluvial channel-fills. *Review of Palaeobotany and Palynology* 91:1-21.
- Gastaldo, R. A., W. Riegel, W. Püttmann, U. H. Linnemann, and R. Zetter. 1998. A multidisciplinary approach to reconstruct the Late Oligocene vegetation in central Europe. *Review of Palaeobotany and Palynology* 101:71-94.
- Gehling, J. G. 1999. Microbial mats in terminal Proterozoic silticlastics: Ediacaran death masks. *Palaios* 14:40-57.
- Gifford-Gonzalez, D. 1991. Bones are not enough: analogues, knowledge, and interpretive strategies in zooarchaeology. *Journal of Anthropological Archaeology* 10:215-254.
- Gilinsky, N. L., and J. B. Bennington. 1994. Estimating numbers of whole individuals from collections of body parts: a taphonomic limitation of the paleontological record. *Paleobiology* 20:245-258.
- Gilinsky, N. L., and P. W. Signor, eds. 1991. *Analytical paleontology. Short Courses in Paleontology No. 4*. Paleontological Society, Knoxville, Tenn.
- Glover, C. P., and S. M. Kidwell. 1993. Influence of organic matrix on the post-mortem destruction of molluscan shells. *Journal of Geology* 101:729-747.
- Goldstein, S. T., P. Van Cappellen, A. Roychoudhury, and C. Kortschy. 1997. Preservation of salt-marsh foraminifera in experimental arrays deployed below the sediment-water interface, Sapelo Island, Georgia (USA). *Geological Society of America Abstracts with Programs* 30:A383.
- Grayson, D. K. 1989. Bone transport, bone destruction, and reverse utility curves. *Journal of Archaeological Science* 16:643-652.
- Greenstein, B. J. 1989. Mass mortality of the West-Indian echinoid *Diadema antillarum* (Echinodermata: Echinoidea): a natural experiment in taphonomy. *Palaios* 4:487-492.
- . 1991. An integrated study of echinoid taphonomy: predictions for the fossil record of four echinoid families. *Palaios* 6:519-540.
- . 1992. Taphonomic bias and the evolutionary history of the family Cidaridae (Echinodermata: Echinoidea). *Paleobiology* 18:50-79.
- . 1993. Is the fossil record of regular echinoids really so poor a comparison of living and subfossil assemblages? *Palaios* 8:587-601.
- . 1999. Taphonomy of reef-building corals II: shallow and deep reef environments of the tropical western Atlantic. *Geological Society of America Abstracts with Programs* 31:A420.
- Greenstein, B. J., and H. A. Moffat. 1996. Comparative taphonomy of modern and Pleistocene corals, San Salvador, Bahama. *Palaios* 11:57-63.
- Greenstein, B. J., and J. M. Pandolfi. 1997. Preservation of community structure in modern reef coral life and death assemblages of the Florida Keys: implications for the Quaternary fossil record of coral reefs. *Bulletin of Marine Science* 61:431-452.
- Greenstein, B. J., L. A. Harris, and H. A. Curran. 1998. Comparison of Recent coral life and death assemblages to Pleistocene reef communities: implications for rapid faunal replacement of recent reefs. *Carbonates and Evaporites* 13:23-31.
- Grotzinger, J. P. 1994. Trends in Precambrian carbonate sediments and their implication for understanding evolution. Pp. 245-258 in Bengtson 1984.
- Hadly, E. A. 1999. Fidelity of terrestrial vertebrate fossils to a modern ecosystem. *Palaeogeography, Palaeoclimatology, Palaeoecology* 149:389-410.
- Hageman, S. J., N. P. James, and Y. Bone. 2000. Cool-water carbonate production from epizoic bryozoans on ephemeral substrates. *Palaios* 15:33-48.
- Haglund, W. D., and M. H. Sorg, eds. 1997. *Forensic taphonomy*,

- the post-mortem fate of human remains. CRC Press, New York.
- Haynes, C. 1985. On watering holes, mineral licks, death, and predation. Pp. 53-71 in D. Meltzer and J. I. Mead, eds. *Environments and extinctions in late glacial North America*. Center for the Study of Early Man, University of Maine, Orono.
- . 1988. Mass deaths and serial predation: comparative taphonomic studies of modern large-mammal deathsites. *Journal of Archaeological Science* 15:219-235.
- . 1991. *Mammoths, mastodonts and elephants*. Cambridge University Press, Cambridge.
- Henderson, S. W., and R. W. Frey. 1986. Taphonomic redistribution of mollusk shells in a tidal inlet channel, Sapelo Island, Georgia. *Palaios* 1:3-16.
- Henwood, A. A. 1992a. Exceptional preservation of dipteran flight muscle and the taphonomy of insects in amber. *Palaios* 7:203-212.
- . 1992b. Soft-part preservation of beetles in Tertiary amber from the Dominican Republic. *Palaeontology* 35:901-912.
- Holland, S. M. 1995. The stratigraphic distribution of fossils. *Paleobiology* 21:92-109.
- . 1996. Recognizing artifactually generated coordinated stasis: implications of numerical models and strategies for field tests. *Palaeogeography, Palaeoclimatology, Palaeoecology* 127:147-156.
- . 2000. The quality of the fossil record: a sequence stratigraphic perspective. In D. H. Erwin and S. L. Wing, eds. *Deep time: Paleobiology's perspective*. *Paleobiology* 26(Suppl. to No. 4):148-168.
- Holland, S. M., and M. E. Patzkowsky. 1999. Models for simulating the fossil record. *Geology* 27:491-494.
- Hudson, J. 1993. From bones to behavior. Occasional Paper No. 21. Center for Archaeological Investigations, Southern Illinois University, Carbondale.
- Hughes, N. C., and D. L. Cooper. 1999. Paleobiologic and taphonomic aspects of the "granulosa" trilobite cluster, Kope Formation (Upper Ordovician, Cincinnati region). *Journal of Paleontology* 73:306-319.
- Hughes, N. C., and C. C. Labandeira. 1995. The stability of species in taxonomy. *Paleobiology* 21:401-403.
- Hunter, J. 1994. Lack of a high body count at the K-T boundary. *Journal of Paleontology* 68:1158.
- Jablonski, D. J. 1988. Estimates of species durations. *Science* 240:969.
- . 1999. The future of the fossil record. *Science* 284:2114-2116.
- . 2000. Micro- and macroevolution: scale and hierarchy in evolutionary biology and paleontology. In D. H. Erwin and S. L. Wing, eds. *Deep time: Paleobiology's perspective*. *Paleobiology* 26(Suppl. to No. 4):15-52.
- Jablonski, D. J., S. Lidgard, and P. D. Taylor. 1997. Comparative ecology of bryozoan radiations: origin of novelties in cyclostomes and cheilostomes. *Palaios* 12:505-523.
- Jackson, S. T. 1989. Postglacial vegetational change along an elevational gradient in the Adirondack Mountains (New York): a study of plant macrofossils. *New York State Museum Bulletin* 465.
- . 1994. Pollen and spores in Quaternary lake sediments as sensors of vegetation composition: theoretical models and empirical evidence. Pp. 253-286 in A. Traverse, ed. *Sedimentation of organic particles*. Cambridge University Press, Cambridge.
- Jackson, S. T., and J. T. Overpeck. 2000. Responses of plant populations and communities to environmental changes of the late Quaternary. In D. H. Erwin and S. L. Wing, eds. *Deep time: Paleobiology's perspective*. *Paleobiology* 26(Suppl. to No. 4):194-220.
- Jackson, S. T., and D. R. Whitehead. 1991. Holocene vegetation patterns in the Adirondack Mountains. *Ecology* 72:641-653.
- Janzen, D. H. 1977. Why fruits rot, seeds mold, and meat spoils. *American Naturalist* 111:691-713.
- Jodry, M. A., and D. J. Stanford. 1992. Stewart's Cattle Guard Site: an analysis of bison remains in a Folsom kill-butcherery campsite. Pp. 101-168 in D. J. Stanford and J. S. Day, eds. *Ice Age hunters of the Rockies*. Denver Museum of Natural History and University Press of Colorado, Denver. 378 pp.
- Johnson, R. G. 1960. Models and methods for analysis of the mode of formation of fossil assemblages. *Geological Society of America Bulletin* 71:105-1086.
- Kah, L. C., and A. H. Knoll. 1996. Microbenthic distribution of Proterozoic tidal flats: environmental and taphonomic considerations. *Geology* 24:79-82.
- Kendricks, P., and P. R. Crane. 1997. The origin and early diversification of land plants: a cladistic study. Smithsonian Institution Press, Washington, D.C.
- Kennish, M. J., and R. A. Lutz. 1999. Calcium carbonate dissolution rates in deep-sea bivalve shells on the East Pacific Rise at 21°N: results of an 8-year in-situ experiment. *Palaeogeography, Palaeoclimatology, Palaeoecology* 154:293-299.
- Kerbis Peterhans, J. C., R. W. Wrangham, M. L. Carter, and M. D. Hauser. 1993. A contribution to tropical rain forest taphonomy: retrieval and documentation of chimpanzee remains from Kibale Forest, Uganda. *Journal of Human Evolution* 25:485-514.
- Kershaw, P. J., D. J. Swift, and D. C. Denoon. 1988. Evidence of recent sedimentation in the eastern Irish Sea. *Marine Geology* 85:1-14.
- Kidston, R., and W. H. Lang. 1920. Old Red Sandstone plants showing structure, from the Rhynie Chert bed, Aberdeenshire, Part 2. *Transactions of the Royal Society of Edinburgh* 52:603-627.
- Kidwell, S. M. 1991. The stratigraphy of shell concentrations. Pp. 211-290 in Allison and Briggs 1991.
- . 1993. Taphonomic expressions of sedimentary hiatus: field observations on bioclastic concentrations and sequence anatomy in low, moderate and high subsidence settings. *Geologische Rundschau* 82:189-202.
- . 1998. Time-averaging in the marine fossil record: overview of strategies and uncertainties. *Geobios* 30:977-995.
- . 1999. High fidelity of species relative abundances in marine molluscan death assemblages. *Geological Society of America Abstracts with Programs* 31:A419.
- . In press. Ecological fidelity of molluscan death assemblages. In S. A. Woodin, J. Y. Aller, and R. C. Aller, eds. *Organism-sediment interactions*. Belle Baruch Institute Volume. University of South Carolina Press, Columbia.
- Kidwell, S. M., and T. Aigner. 1985. Sedimentary dynamics of complex shell beds: implications for ecologic and evolutionary patterns. Pp. 382-395 in U. Bayer and A. Seilacher, eds. *Sedimentary and evolutionary cycles*. Springer, Berlin.
- Kidwell, S. M., and T. Baumiller. 1990. Experimental disintegration of regular echinoids: roles of temperature, oxygen and decay thresholds. *Paleobiology* 16:247-271.
- Kidwell, S. M., and A. K. Behrensmeier, eds. 1993. *Taphonomic approaches to time resolution in fossil assemblages*. Short Courses in Paleontology No. 6. Paleontological Society, Knoxville, Tenn.
- Kidwell, S. M., and D. W. J. Bosence. 1991. Taphonomy and time-averaging of marine shelly faunas. Pp. 115-209 in Allison and Briggs 1991.
- Kidwell, S. M., and P. J. Brenchley. 1994. Patterns in bioclastic accumulation through the Phanerozoic: changes in input or in destruction? *Geology* 22:1139-1143.
- . 1996. Evolution of the fossil record: thickness trends in marine skeletal accumulations and their implications. Pp.

- 290–336 in D. Jablonski, D. H. Erwin, and J. H. Lipps, eds. *Evolutionary paleobiology*. University of Chicago Press, Chicago.
- Kidwell, S. M., and K. W. Flessa. 1995. The quality of the fossil record: populations, species, and communities. *Annual Review of Ecology and Systematics* 26:269–299.
- Kidwell, S. M., and D. Jablonski. 1983. Taphonomic feedback: ecological consequences of shell accumulation. Pp. 195–248 in M. J. S. Tevesz and P. L. McCall, eds. *Biotic interactions in recent and fossil benthic communities*. Plenum, New York.
- Knoll, A. H. 1985. Exceptional preservation of photosynthetic organisms in silicified carbonates and silicified peats. *Philosophical Transactions of the Royal Society of London B* 311: 111–122.
- Knoll, A. H., and V. N. Sergeev. 1995. Taphonomic and evolutionary changes across the Mesoproterozoic-Neoproterozoic transition. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 195:289–302.
- Knoll, A. H., K. Niklas, P. G. Gensel, and B. Tiffney. 1984. Character diversification and patterns of evolution in early vascular plants. *Paleobiology* 10:34–47.
- Knoll, A. H., I. J. Fairchild, and K. Swett. 1993. Calcified microbes in Neoproterozoic carbonates: implications for our understanding of the Proterozoic/Cambrian transition. *Palaios* 8:512–525.
- Kondo, Y., S. T. Abbott, A. Katamura, P. J. J. Kamp, T. R. E. Naish, T. Kamataki, and G. S. Saul. 1998. The relationship between shellbed type and sequence architecture: examples from Japan and New Zealand. *Sedimentary Geology* 122:109–127.
- Kotler, E., R. E. Martin, and W. D. Liddell. 1992. Experimental analysis of abrasion and dissolution resistance of modern reef-dwelling Foraminifera: implications for the preservation of biogenic carbonate. *Palaios* 7:244–276.
- Kowalewski, M. 1996a. Taphonomy of a living fossil: the lingulide brachiopod *Glottidia palmeri* Dall from Baja California, Mexico. *Palaios* 11:244–265.
- . 1996b. Time-averaging, overcompleteness, and the geological record. *Journal of Geology* 104:317–326.
- . 1997. The reciprocal taphonomic model. *Lethaia* 30:86–88.
- Kowalewski, M., and K. W. Flessa. 1996. Improving with age: the fossil record of lingulide brachiopods and the nature of taphonomic megabiases. *Geology* 24:977–980.
- Kowalewski, M., G. A. Goodfriend, and K. W. Flessa. 1998. High-resolution estimates of temporal mixing within shell beds: the evils and virtues of time-averaging. *Paleobiology* 24: 287–304.
- Kranz, P. M. 1974. The anastrophic burial of bivalves and its palaeoecological significance. *Journal of Geology* 82:237–265.
- Kristensen, E., S. I. Ahmed, and A. H. Devol. 1995. Aerobic and anaerobic decomposition of organic matter in marine sediment: which is fastest? *Limnology and Oceanography* 40: 1430–1437.
- Labandeira, C. C. 1998. Early history of arthropod and vascular plant associations. *Annual Review of Earth Planetary Sciences* 28:153–193.
- Labandeira, C. C., and D. M. Smith. 1999. Forging a future for fossil insects: thoughts on the First International Congress of Paleontomology. *Paleobiology* 25:154–157.
- Labandeira, C. C., K. R. Johnson, and P. Lang. In press. Insect herbivory across the Cretaceous/Tertiary boundary: major extinction and minimum rebound. In J. H. Hartman, K. R. Johnson, and D. J. Nichols, eds. *The Hell Creek Formation and the Cretaceous-Tertiary boundary in the northern Great Plains—an integrated Continental record at the end of the Cretaceous*. Geological Society of America Special Paper.
- Lask, P. B. 1993. The hydrodynamic behavior of sclerites from the trilobite *Flexicalymene meeki*. *Palaios* 8:219–225.
- Lescinsky, H. L. 1993. Taphonomy and paleoecology of epibionts on the scallops *Chlamys hastata* (Sowerby 1843) and *Chlamys rubida* (Hinds 1845). *Palaios* 8:267–277.
- . 1995. The life orientation of concavo-convex brachiopods: overturning the paradigm. *Paleobiology* 21:520–551.
- Li, X., and M. L. Droser. 1997. Nature and distribution of Cambrian shell concentrations: evidence from the Basin and Range province of western United States (California, Nevada and Utah). *Palaios* 12:11–1126.
- Llewellyn, G., and C. G. Messing. 1993. Compositional and taphonomic variations in modern crinoid-rich sediments from the deep-water margin of a carbonate bank. *Palaios* 8: 554–573.
- Llona, A., C. Pinto, and P. Andrews. 1999. Amphibian taphonomy and its application to the fossil record of Dolina (middle Pleistocene, Atapuerca, Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology* 149:411–430.
- Lupia, R. 1995. Paleobotanical data from fossil charcoal: an actualistic study of seed plant reproductive structures. *Palaios* 10:465–477.
- Lyell, C., and J. W. Dawson. 1853. On the remains of a reptile (*Dendroperpeton acadianum*, Wyman and Owen), and of a land shell discovered in the interior of an erect fossil tree in the coal measures of Nova Scotia. *Quarterly Journal of the Geological Society of London* IX:58–63.
- Lyman, R. L. 1985. Bone frequencies: differential transport, in situ destruction, and the MGUI. *Journal of Archaeological Science* 12:221–236.
- . 1994. *Vertebrate taphonomy*. Cambridge Manuals in Archaeology, Cambridge University Press, Cambridge.
- Lyman, R. L., and G. L. Fox. 1989. A critical evaluation of bone weathering as an indication of bone assemblage formation. *Journal of Archaeological Science* 16:293–317.
- Malinky, J. M., and P. H. Heckel. 1998. Paleoecology and taphonomy of faunal assemblages in gray “core” (offshore) shales in Midcontinent Pennsylvanian cyclothems. *Palaios* 13: 311–334.
- Maliva, R. G., A. H. Knoll, and R. Siever. 1989. Secular change in chert distribution: a reflection of evolving biological participation in the silica cycle. *Palaios* 4:519–532.
- Marean, C. W. 1991. Measuring the post-depositional destruction of bone in archaeological assemblages. *Journal of Archaeological Science* 18:677–694.
- . 1992. Captive hyaena bone choice and destruction, the Schleppe effect and Olduvai archaeofaunas. *Journal of Archaeological Science* 19:101–121.
- Markwick, P. J. 1998. Crocodylian diversity in space and time: the role of climate in paleoecology and its implications for understanding K/T extinctions. *Paleobiology* 24:470–497.
- Marshall, C. R. 1990. Confidence intervals on stratigraphic ranges. *Paleobiology* 16:1–10.
- . 1994. Confidence intervals on stratigraphic ranges: partial relaxation of the assumption of randomly distributed fossil horizons. *Paleobiology* 20:459–460.
- Martill, D. M. 1985. The preservation of marine vertebrates in the Lower Oxford Clay (Jurassic) of central England. *Philosophical Transactions of the Royal Society of London B* 311: 155–165.
- . 1988. Preservation of fish in the Cretaceous Santana Formation of Brazil. *Palaeontology* 31:1–18.
- . 1990. Macromolecular resolution of fossilized muscle tissue from an elopomorph fish. *Nature* 346:171–172.
- Martin, R. E. 1993. Time and taphonomy: actualistic evidence for time-averaging of benthic foraminiferal assemblages. Pp. 34–56 in Kidwell and Behrensmeier 1993.
- . 1995. Cyclic and secular variation in microfossil biom- ineralization: clues to the biogeochemical evolution of Phanerozoic oceans. *Global and Planetary Change* 11:1–23.

- . 1999. Taphonomy, a process approach. Cambridge University Press, Cambridge.
- Martin, R. E., J. F. Wehmiller, M. S. Harris, and W. D. Liddell. 1996. Comparative taphonomy of bivalves and foraminifera from Holocene tidal flat sediments, Bahía la Choya, Sonora, Mexico (Northern Gulf of California): taphonomic grades and temporal resolution. *Paleobiology* 22:80–90.
- Martin, R. E., R. T. Patterson, S. T. Goldstein, and A. Kumar, eds. 1999a. Taphonomy as a tool in paleoenvironmental reconstruction and environmental assessment. *Palaeogeography, Palaeoclimatology, Palaeoecology* 149(special issue).
- Martin, R. E., S. P. Hippensteel, D. Nikitina, and J. E. Pizzuto. 1999b. Artificial time-averaging and the recovery of ecological signals preserved in the microfossil record: linking the temporal scales of ecology and paleoecology. *Geological Society of America Abstracts with Programs*: A356.
- Martinez-Delclos, X., and J. Martinell. 1993. Insect taphonomy experiments: their application to the Cretaceous outcrops of lithographic limestones from Spain. *Kaupia (Darmstädter Beiträge zur Naturgeschichte)* 2:133–144.
- Massé, H. L. 1999. Les carbonates associés à la macrofaune des sables fins littoraux en Méditerranée nord-occidentale. *Oceanologica Acta* 22:413–420.
- Maxwell, W. D., and M. J. Benton. 1990. Historical tests of the absolute completeness of the fossil record of tetrapods. *Paleobiology* 16:322–335.
- McGree, H. 1984. On food and cooking: the science and lore of the kitchen. Scribner, New York.
- McIlroy, D., and G. A. Logan. 1999. The impact of bioturbation on infaunal ecology and evolution during the Proterozoic-Cambrian transition. *Palaios* 14:58–72.
- McKinney, F. K. 1996. Encrusting organisms on co-occurring disarticulated valves of two marine bivalves: comparison of living assemblages and skeletal residues. *Paleobiology* 22:534–567.
- McKinney, M. L. 1991. Completeness of the fossil record: an overview. Pp. 66–83 in Donovan 1991.
- Meldahl, K. H. 1990. Sampling, species abundance, and the stratigraphic signature of mass extinction: a test using Holocene tidal flat molluscs. *Geology* 18:890–893.
- Meldahl, K. H., and K. W. Flessa. 1990. Taphonomic pathways and comparative biofacies and taphofacies in a Recent intertidal/shallow shelf environment. *Lethaia* 23:43–60.
- Meldahl, K. H., D. Scott, and K. Carney. 1995. Autochthonous leaf assemblages as records of deciduous forest communities: an actualistic study. *Lethaia* 28:383–394.
- Meldahl, K. H., K. W. Flessa, and A. H. Cutler. 1997a. Time-averaging and postmortem skeletal survival in benthic fossil assemblages: quantitative comparisons among Holocene environments. *Paleobiology* 23:209–229.
- Meldahl, K. H., O. G. Yajimovich, C. D. Empedocles, C. S. Gustafson, M. M. Hidalgo, and T. W. Reardon. 1997b. Holocene sediments and molluscan faunas of Bahía Concepción: a modern analog to Neogene rift basins of the Gulf of California. *Geological Society of America Special Paper* 318:39–56.
- Meyer, D. L., and K. B. Meyer. 1986. Biostratigraphy of Recent crinoids (Echinodermata) at Lizard Island, Great Barrier Reef, Australia. *Palaios* 1:294–302.
- Meyer, D. L., W. I. Ausich, and R. E. Terry. 1989. Comparative taphonomy of echinoderms in carbonate facies: Fort Payne Formation (Lower Mississippian) of Kentucky and Tennessee. *Palaios* 4:533–552.
- Miller, A. I. 1988. Spatial resolution in microfossil molluscan remains: implications for paleobiological analyses. *Paleobiology* 14:91–103.
- . 1997. Dissecting global diversity patterns: examples from the Ordovician radiation. *Annual Review of Ecology and Systematics* 28:85–104.
- Miller, A. I., and H. Cummins. 1990. A numerical model for the formation of fossil assemblages: estimating the amount of post-mortem transport along environmental gradients. *Palaios* 5:303–316.
- . 1993. Using numerical models to evaluate the consequences to time-averaging in marine fossil assemblages. Pp. 150–168 in Kidwell and Behrensmeier 1993.
- Miller, A. I., and M. Foote. 1996. Calibrating the Ordovician radiation of marine life: implications for Phanerozoic diversity trends. *Paleobiology* 22:304–309.
- Miller, A. I., G. Lewellyn, K. M. Parsons, H. Cummins, M. R. Boardman, B. J. Greenstein, and D. K. Jacobs. 1992. Effect of Hurricane Hugo on molluscan skeletal distributions, Salt River Bay, St. Croix, U. S. Virgin Islands. *Geology* 20:23–26.
- Mirsky, S. 1998. I shall return. *Earth* 7:48–53.
- Morales, M., ed. 1996. The continental Jurassic. *Museum of Northern Arizona Bulletin* 60.
- Nebelsick, J. H. 1992. Echinoid distribution by fragment identification in the northern Bay of Safaga, Red Sea, Egypt. *Palaios* 7:316–328.
- . 1995. Comparative taphonomy of clypeasteroids. *Eclogae Geologicae Helveticae* 88:685–693.
- . 1999. Taphonomy of *Clypeaster* fragments: preservation and taphofacies. *Lethaia* 32:241–252.
- Noe-Nygaard, N. 1987. Taphonomy in archaeology, with special emphasis on man as a biasing factor. *Journal of Danish Archaeology* 6:7–62.
- Norris, R. D. 1986. Taphonomic gradients in shelf fossil assemblages: Pliocene Purisima Formation, California. *Palaios* 1:256–270.
- Oliver, J. S., and R. W. Graham. 1994. A catastrophic kill of ice-trapped coots: time-averaged versus scavenger-specific disarticulation patterns. *Paleobiology* 20:229–244.
- Oliver, J. S., N. E. Sikes, and K. M. Stewart, eds. 1994. Early hominid behavioural ecology. Academic Press, London.
- Olson, E. C. 1966. Community evolution and the origin of mammals. *Ecology* 47:291–302.
- Olshewski, T. D. 1999. Taking advantage of time-averaging. *Paleobiology* 25:226–238.
- Olshewski, T. D., and R. R. West. 1997. Influence of transportation and time-averaging in fossil assemblages from the Pennsylvanian of Oklahoma. *Lethaia* 30:315–329.
- Oost, A. P., and P. L. de Boer. 1994. Tectonic and climatic setting of lithographic limestone basins. *Geobios Mémoire Spécial* 16:321–330.
- Orr, P. J., D. E. G. Briggs, and S. L. Kearns. 1998. Cambrian Burgess Shale animals replicated in clay minerals. *Science* 281:1173–1175.
- Palaios. 1999. Unexplored microbial worlds (theme issue). Vol. 141 *Palaios*. 1999. Unexplored microbial worlds (theme issue). Vol. 14, No. 1.
- Palmqvist, P. 1991. Differences in the fossilization potential of bivalve and gastropod species related to their life sites and trophic resources. *Lethaia* 24:287–288.
- . 1993. Trophic levels and the observational completeness of the fossil record. *Revista Española de Paleontología* 8:33–36.
- Pandolfi, J. M., and B. J. Greenstein. 1997a. Taphonomic alteration of reef coral: effects of reef environment and coral growth form. I. The Great Barrier Reef. *Palaios* 12:27–42.
- . 1997b. Preservation of community structure in death assemblages of deep-water Caribbean reef corals. *Limnology and Oceanography* 42:1505–1516.
- Parsons, K. M. 1989. Taphonomy as an indicator of environment: Smuggler's Cove, St. Croix, U.S.V.I. In D. K. Hubbard, ed. *Terrestrial and marine ecology of St. Croix, U.S. Virgin Islands*. West Indies Laboratory Special Publication 8:135–143.
- Parsons, K. M., and C. E. Brett. 1991. Taphonomic processes and

- biases in modern marine environments: an actualistic perspective on fossil assemblage preservation. Pp. 22–65 in Donovan 1991.
- Parsons, K. M., C. E. Brett, and K. B. Miller. 1988. Taphonomy and depositional dynamics of Devonian shell-rich mudstones. *Palaeogeography, Palaeoclimatology, Palaeoecology* 63:109–140.
- Parsons-Hubbard, K. M., W. R. Callender, E. N. Powell, C. E. Brett, S. E. Walker, A. L. Raymond, and G. M. Staff. 1999. Rates of burial and disturbance of experimentally-deployed molluscs: implications for preservation potential. *Palaios* 14:337–351.
- Paul, C. R. C. 1992. How complete does the fossil record have to be? *Revista Española Paleontología* 7:127–133.
- . 1998. Adequacy, completeness and the fossil record. Pp. 1–22 in S. K. Donovan and C. R. C. Paul, eds. *The adequacy of the fossil record*. Wiley, New York.
- Perry, C. T. 1996. The rapid response of reef sediments to changes in community composition: implications for time averaging and sediment accumulation. *Journal of Sedimentary Research* 66:459–467.
- . 1999. Reef framework preservation in four contrasting modern reef environments, Discovery Bay, Jamaica. *Journal of Coastal Research* 15:796–812.
- Peterson, C. H. 1977. The paleoecological significance of undetected short-term temporal variability. *Journal of Paleontology* 51:976–981.
- Plummer, T., and A. M. Kinyua. 1994. Provenancing of hominid and mammalian fossils from Kanjera, Kenya, using EDXRF. *Journal of Archaeological Science* 21:553–563.
- Potts, R. 1986. Temporal span of bone accumulations at Olduvai Gorge and implications for early hominid foraging behavior. *Paleobiology* 12:25–31.
- . 1988. *Early hominid activities at Olduvai*. Aldyne de Gruyter, New York.
- Potts, R., A. K. Behrensmeyer, and P. Ditchfield. 1999. Paleolandscape variation and early Pleistocene hominid activities: Members 1 and 7, Olorgesailie Formation. *Journal of Human Evolution* 37:747–788.
- Poulicek, M., G. Goffinet, C. Jeuniaux, A. Simon, and M. F. Voss-Foucart. 1988. Early diagenesis of skeletal remains in marine sediments: a 10 years study. *Actes Colloque Recherches Océanographiques en Mer Méditerranée, Université Etat, Liege* 107–124.
- Powell, E. N., and D. J. Davies. 1990. When is an "old" shell really old? *Journal of Geology* 98:823–844.
- Powell, E. N., G. Staff, D. J. Davies, and W. R. Callender. 1989. Macrobenitic death assemblages in modern marine environments: formation, interpretation and application. *CRC Critical Reviews in Aquatic Science* 1:555–589.
- Powell, E. N., R. J. Stanton Jr., A. Logan, and M. A. Craig. 1992. Preservation of Mollusca in Copano Bay, Texas. The long-term record. *Palaeogeography, Palaeoclimatology, Palaeoecology* 95:209–228.
- Prager, E. J., J. B. Southard, and E. R. Vivoni-Gallart. 1996. Experiments on the entrainment threshold of well-sorted and poorly sorted carbonate sands. *Sedimentology* 43:33–40.
- Pratt, B. R. 1998. Probable predation on Upper Cambrian trilobites and its relevance for the extinction of soft-bodied Burgess Shale-type animals. *Lethaia* 31:73–88.
- Rasmussen, K. A., and C. E. Brett. 1985. Taphonomy of Holocene cryptic biotas from St. Croix, Virgin Islands: information loss and preservation biases. *Geology* 13:551–553.
- Raup, D. M. 1975. Taxonomic diversity estimation using rarefaction. *Paleobiology* 1:333–342.
- Raymond, A., and C. Metz. 1995. Laurussian land-plant diversity during the Silurian and Devonian: mass extinction, sampling bias, or both? *Paleobiology* 21:74–91.
- Retallack, G. J. 1990. *Soils of the past: an introduction to paleopedology*. Unwin Hyman, London.
- Retallack, G. J., and D. L. Dilcher. 1986. Reconstructions of selected seed ferns. *Annals of the Missouri Botanical Garden* 75:1010–1057.
- Rich, F. J. 1989. A review of the taphonomy of plant remains in lacustrine sediments. *Review of Palaeobotany and Palynology* 58:33–46.
- Richmond, D. R., and T. H. Morris. 1996. The dinosaur death-trap of the Cleveland-Lloyd Dinosaur Quarry, Emery County, Utah. Pp. 533–546 in Morales 1996.
- Rigby, J. K., Jr., K. R. Newman, J. Smit, S. Van Der Kaars, R. E. Sloan, and J. K. Rigby. 1987. Dinosaurs from the Paleocene part of the Hell Creek Formation, McCone County, Montana. *Palaios* 2:296–302.
- Rivas, P., J. Aguirre, and J. C. Braga. 1997. *Entolium* beds: hiatal shell concentrations in starved pelagic settings (middle Liassic, SE Spain). *Eclogae Geologicae Helveticae* 90:293–301.
- Robinson, J. M. 1990. Lignin, land plants, and fungi. Biological evolution affecting Phanerozoic oxygen balance. *Geology* 15:607–610.
- . 1991. Phanerozoic atmospheric reconstructions: a terrestrial perspective. *Palaeogeography, Palaeoclimatology, Palaeoecology* 97:51–62.
- Rogers, R. R. 1990. Taphonomy of three dinosaur bone beds in the Upper Cretaceous Two Medicine Formation of northwestern Montana: evidence for drought-related mortality. *Palaios* 5:394–413.
- . 1993. Systematic patterns of time-averaging in the terrestrial vertebrate record: a Cretaceous case study. Pp. 228–249 in S. M. Kidwell and A. K. Behrensmeyer, eds. *Taphonomic approaches to time resolution in fossil assemblages*. *Short Courses in Paleontology* 6 (Paleontological Society).
- Rogers, R. R., and S. M. Kidwell. 2000. Associations of vertebrate skeletal concentrations and discontinuity surfaces in continental and shallow marine records: a test in the Cretaceous of Montana. *Journal of Geology* 108:131–154.
- Rolfe, W. D. I., E. N. K. Clarkson, and A. L. Panchen, eds. 1994 (1993). *Volcanism and early terrestrial biotas*. *Transactions of the Royal Society of Edinburgh (Earth Sciences)* 84.
- Roopnarine, P. D. 1999. Breaking the enigma of stratophenetic series: a computational approach to the analysis of microevolutionary mode. *Geological Society of America Abstracts with Programs* 31(7):A42.
- Roopnarine, P. D., G. Byars, and P. Fitzgerald. 1999. Anagenetic evolution, stratophenetic patterns, and random walk models. *Paleobiology* 25:41–57.
- Roy, K., J. W. Valentine, D. Jablonski, and S. M. Kidwell. 1996. Scales of climatic variability and time averaging in Pleistocene biotas: implications for ecology and evolution. *Trends in Ecology and Evolution* 11:458–463.
- Sadler, P. M. 1981. Sediment accumulation and the completeness of stratigraphic sections. *Journal of Geology* 89:569–584.
- Sander, P. M. 1989. Early Permian depositional environments and pond bonebeds in central Archer County, Texas. *Palaeogeography, Palaeoclimatology, Palaeoecology* 69:1–21.
- Sanders, H. L. 1968. Marine benthic diversity: a comparative study. *American Naturalist* 102:243–282.
- Schaal, S., and W. Ziegler, eds. 1992. *Messel: an insight into the history of life and of the Earth*. Translated by M. Shaffer-Fehre. Clarendon, Oxford.
- Schäfer, W. 1972. *Ecology and paleoecology of marine environments*. University of Chicago Press, Chicago.
- Scheihing, M. 1980. Reduction of wind velocity by the forest canopy and the rarity of non-arborescent plants in the Upper Carboniferous fossil record. *Augumenta Palaeobotanica* 6:133–138.
- Scheihing, M. H., and H. W. Pfefferkorn. 1984. The taphonomy

- of land plants in the Orinoco Delta: a model for the incorporation of plant parts in clastic sediments of late Carboniferous age of Euramerica. *Review of Palaeobotany and Palynology* 41:205-240.
- Schmude, D. E., and C. J. Weege. 1996. Stratigraphic relationship, sedimentology, and taphonomy of Meilyn, a dinosaur quarry in the basal Morrison Formation of Wyoming. Pp. 547-554 in Morales 1996.
- Schopf, T. J. M. 1978. Fossilization potential of an intertidal fauna: Friday Harbor, Washington. *Paleobiology* 4:261-270.
- Schubert, J. K., D. L. Kidder, and D. H. Erwin. 1997. Silica-replaced fossils through the Phanerozoic. *Geology* 25:1031-1034.
- Scoffin, T. P. 1992. Taphonomy of coral reefs: a review. *Coral Reefs* 11:57-77.
- Scott, A. C. 1990. Anatomical preservation of fossil plants. Pp. 263-266 in Briggs and Crowther 1990.
- Scott, R. W. 1978. Approaches to trophic analysis of paleocommunities. *Lethaia* 11:1-14.
- Seilacher, R. W. 1984. Late Precambrian and Early Cambrian metazoa: preservational or real extinctions? Pp. 159-168 in H. D. Holland and A. F. Trendall, eds. *Patterns of change in earth evolution*. Springer, Berlin.
- . 1985. The Jeram Model: event condensation in a modern intertidal environment. Pp. 336-341 in U. Bayer and A. Seilacher, eds. *Sedimentary and evolutionary cycles*. Springer, Berlin.
- . 1994. Early multicellular life: late Proterozoic fossils and the Cambrian extinction. Pp. 389-400 in Bengtson 1984.
- Seilacher, A., W. E. Reif, and F. Westphal. 1985. Sedimentological, ecological, and temporal patterns of fossil Lagerstätten. *Philosophical Transactions of the Royal Society of London B* 311:5-23.
- Sepkoski, J. J., Jr. 1978. A kinetic model of Phanerozoic taxonomic diversity: I. Analysis of marine orders. *Paleobiology* 4:223-251.
- . 1990. The taxonomic structure of periodic extinction. In V. Sharpton and P. Ward, eds. *Global catastrophes in earth history*. Geological Society of America Special Paper 247:33-44.
- . 1993. Ten years in the library: new data confirm paleontological patterns. *Paleobiology* 19:43-51.
- Sepkoski, J. J., Jr., and C. F. Koch. 1996. Evaluating paleontological data relating to bio-events. Pp. 21-34 in O. H. Walliser, ed. *Global events and event stratigraphy in the Phanerozoic*. Springer, Berlin.
- Sepkoski, J. J., Jr., R. K. Bambach, D. M. Raup, and J. W. Valentine. 1981. Phanerozoic marine diversity and the fossil record. *Nature* 293:435-437.
- Sepkoski, J. J., Jr., R. K. Bambach, and M. L. Droser. 1991. Secular changes in Phanerozoic event bedding and the biological overprint. Pp. 298-312 in G. Einsele, W. Ricken, and A. Seilacher, eds. *Cycles and events in stratigraphy*. Springer, Berlin.
- Sept, J. M. 1994. Bone distribution in a semi-arid riverine habitat in eastern Zaire: implications for the interpretation of faunal assemblages at early archaeological sites. *Journal of Archaeological Science* 21:217-235.
- Silva de Echols, C. M. H. M. 1993. Diatom infestation of Recent crinoid ossicles in temperate waters, Friday harbor Laboratories, Washington: implications for biodegradation of skeletal carbonates. *Palaaios* 8:278-288.
- Simões, M. G., A. C. Marques, L. H. C. Mello, and R. P. Ghilardi. 2000a. The role of taphonomy in cladistic analysis: a case study in Permian bivalves. *Revista Española de Paleontología* 15:153-164.
- Simões, M. G., M. Kowalewski, F. F. Torello, R. P. Ghilardi, and L. H. C. Mello. 2000b. Early onset of modern-style shell beds in the Permian sequences of the Paraná Basin: implications for the Phanerozoic trend in bioclastic accumulations. *Revista Brasileira de Geociências* 30:495-499.
- Smith, A. M., and C. S. Nelson. 1994. Selectivity in sea-floor processes: taphonomy of bryozoans. Pp. 177-180 in P. J. Hayward, J. S. Ryland, and P. D. Taylor, eds. *Biology and palaeobiology of bryozoans*. Proceedings of the ninth international bryozoology conference, 1992. Olsen and Olsen, Fredensborg, Denmark.
- Smith, D. M. 2000. Beetle taphonomy in a recent ephemeral lake, southeastern Arizona. *Palaaios* 15:152-160.
- Smith, G. R., R. F. Stearley, and C. E. Badgley. 1988. Taphonomic bias in fish diversity from Cenozoic floodplain environments. *Palaeogeography, Palaeoclimatology, Palaeoecology* 63:263-273.
- Smith, R. M. H. 1993. Vertebrate taphonomy of Late Permian floodplain deposits in the southwestern Karoo Basin of South Africa. *Palaaios* 8:45-67.
- . 1995. Changing fluvial environments across the Permian-Triassic boundary in the Karoo Basin, South Africa and possible causes of tetrapod extinctions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 117:81-104.
- Smith, R. M. H., and J. Kitching. 1996. Sedimentology and vertebrate taphonomy of the Tritylodon Acme Zone: a reworked palaeosol in the Lower Jurassic Elliot Formation, Karoo Supergroup, South Africa. Pp. 531-532 in Morales 1996.
- Solomon, S., I. Davidson, and D. Watson. 1990. Problem solving in taphonomy. *Tempus: archaeology and material culture studies in anthropology*, Vol. 2. University of Queensland, St. Lucia, Queensland, Australia.
- Speyer, S. E., and C. E. Brett. 1986. Trilobite taphonomy and Middle Devonian taphofacies. *Palaaios* 1:312-327.
- . 1991. Taphofacies controls: background and episodic processes in fossil assemblage preservation. Pp. 501-545 in Allison and Briggs 1991.
- Spicer, R. A. 1980. The importance of depositional sorting to the biostratigraphy of plant megafossils. Pp. 171-183 in D. L. Dilcher and T. N. Taylor, eds. *Biostratigraphy of fossil plants*. Dowdon, Hutchinson, and Ross, New York.
- . 1991. Plant taphonomic processes. Pp. 71-113 in Allison and Briggs 1991.
- Stachowitsch, M. 1984. Mass mortality in the Gulf of Trieste: the course of community destruction. *Marine Ecology (Publicazioni della Stazione Zoologica di Napoli)* 5:243-264.
- Staff, G. M., E. N. Powell, R. J. Stanton Jr., and H. Cummins. 1985. Biomass: is it a useful tool in paleocommunity reconstruction? *Lethaia* 18:209-232.
- Staff, G. M., R. J. Stanton Jr., E. N. Powell, and H. Cummins. 1986. Time averaging, taphonomy and their impact on paleocommunity reconstruction: death assemblages in Texas bays. *Geological Society of America Bulletin* 97:428-443.
- Stankiewicz, B. A., H. N. Poinar, D. E. G. Briggs, R. P. Evershed, and G. O. Poinar Jr. 1998. Chemical preservation of plants and insects in natural resins. *Proceedings of the Royal Society of London B* 265:641-647.
- Stanley, S. E., and L. A. Hardie. 1998. Secular oscillations in the carbonate mineralogy of reef-building and sediment-producing organism driven by tectonically forced shifts in seawater chemistry. *Palaeogeography, Palaeoclimatology, Palaeoecology* 144:3-19.
- Stewart, K. M., L. Lebranc, D. P. Matthiesen and J. West. 1999. Microfaunal remains from a modern east African raptor roost: patterning and implications for fossil bone scatters. *Paleobiology* 25:483-503.
- Stoner, A. W., and M. Ray. 1996. Shell remains provide clues to historical distribution and abundance patterns in a large seagrass-associated gastropod (*Stombus gigas*). *Marine Ecology Progress Series* 135:101-108.

- Strauss, D., and P. M. Sadler. 1989. Classical confidence intervals and Bayesian probability estimates for ends of local taxon ranges. *Mathematical Geology* 21:411–427.
- Sutcliffe, A. J. 1990. Rates of decay of mammalian remains in the permafrost environment of the Canadian High Arctic. Pp. 161–186 in C. R. Harrington, ed. *Canada's missing dimension: science and history in the Canadian Arctic Islands*, Vol. 1. Canadian Museum of Nature, Ottawa.
- Tappan, M. J. 1994a. Savanna ecology and natural bone deposition: implications for early hominid site formation, hunting and scavenging. *Current Anthropology* 36:223–260.
- . 1994b. Bone weathering in the tropical rain forest. *Journal of Archaeological Science* 21:667–673.
- Tardy, Y., R. N'Koukou, and J.-L. Probst. 1989. The global water cycle and continental erosion during Phanerozoic time. *American Journal of Science* 289:455–483.
- Taylor, P. D. 1990. Preservation of soft-bodied and other organisms by bioimmuration: a review. *Palaeontology* 33:1–17.
- . 1994. Evolutionary paleoecology of symbioses between bryozoans and hermit crabs. *Historical Biology* 9:157–205.
- Thayer, C. W. 1983. Sediment-mediated biological disturbance and the evolution of marine benthos. Pp. 479–625 in M. J. S. Tevesz and P. L. McCall, eds. *Biotic interactions in recent and fossil benthic communities*. Plenum, New York.
- Thomasson, J. R. 1991. Sediment-borne "seeds" from Sand Creek, northwestern Kansas: taphonomic significance and paleoecological and paleoenvironmental implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 85:213–225.
- Traverse, A. 1990. Studies of pollen and spores in rivers and other bodies of water, in terms of source-vegetation and sedimentation, with special reference to Trinity River and Bay, Texas. *Review of Palaeobotany Palynology* 64:297–303.
- , ed. 1994. *Sedimentation of organic particles*. Cambridge University Press, Cambridge.
- Trueman, C. N. 1999. Rare earth element geochemistry and taphonomy of terrestrial vertebrate assemblages. *Palaios* 14:555–568.
- Trueman, C. N., and M. J. Benton. 1997. A geochemical method to trace the taphonomic history of reworked bones in sedimentary settings. *Geology* 25:263–266.
- Underwood, C. J., and S. M. Bottrell. 1994. Diagenetic controls on multiphase pyritization of graptolites. *Geological Magazine* 131:315–327.
- Valentine, J. W. 1989. How good was the fossil record? Clues from the Californian Pleistocene. *Paleobiology* 15:83–94.
- Valentine, J. W., D. Jablonski, and D. H. Erwin. 1999. Fossils, molecules, and embryos: new perspectives on the Cambrian explosion. *Development* 126:851–859.
- Vaughan, A., and G. Nichols. 1995. Controls on the deposition of charcoal: implications for sedimentary accumulations of fusain. *Journal of Sedimentary Research A* 65:129–135.
- Vermeij, G. J. 1977. The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology* 2:245–258.
- . 1987. *Evolution and escalation: an ecological history of life*. Princeton University Press, Princeton, N.J.
- Voorhies, M. R. 1992. *Ashfall: life and death at a Nebraska waterhole ten million years ago*. University of Nebraska State Museum, Museum Notes 81.
- Vrba, E. S. 1995. On the connections between paleoclimate and evolution. Pp. 24–45 in E. S. Vrba, G. H. Denton, T. C. Partridge, and L. H. Burckle, eds. *Paleoclimate and evolution, with emphasis on human origins*. Yale University Press, New Haven, Conn.
- Wagner, P. J. 2000a. The quality of the fossil record and the accuracy of phylogenetic inferences about sampling and diversity. *Systematic Biology* 49:65–86.
- . 2000b. Phylogenetic analyses and the fossil record: tests and inferences, hypotheses and models. In D. H. Erwin and S. L. Wing, eds. *Deep time: Paleobiology's perspective*. *Paleobiology* 26(Suppl. to No. 4):341–371.
- Waisfeld, B. G., T. M. Sanchez, and M. G. Carrera. 1999. Biodiversification patterns in the Early Ordovician of Argentina. *Palaios* 14:198–214.
- Walker, K. R., and R. K. Bambach. 1971. The significance of fossil assemblages from fine-grained sediments: time-averaged communities. *Geological Society of America Abstracts with Programs* 3:783–784.
- Walker, K. R., and W. W. Diehl. 1985. The role of marine cementation in the preservation of lower Paleozoic assemblages. *Philosophical Transactions of the Royal Society of London B* 311:143–153.
- Walker, S. E. 1988. Taphonomic significance of hermit crabs (Anomura: Paguridea): epifaunal hermit crab—infaunal gastropod example. *Palaeogeography, Palaeoclimatology, Palaeoecology* 63:45–71.
- . 1989. Hermit crabs as taphonomic agents. *Palaios* 4:439–452.
- . 1995. Taphonomy of modern and fossil intertidal gastropod associations from Isla Santa Cruz and Isla Santa Fe, Galapagos Islands. *Lethaia* 28:371–382.
- Walker, S. E., and J. R. Voight. 1994. Paleoecologic and taphonomic potential of deepsea gastropods. *Palaios* 9:48–58.
- Walker, S. E., P. Van Cappellen, A. Roychoudhury, and C. Kortschy. 1997. Preservation of experimentally deployed molluscan carbonate below the sediment-water interface. *Geological Society of America Abstracts with Programs* 30:266.
- Walker, S. E., K. Parsons-Hubbard, E. N. Powell, and C. E. Brett. 1998. Bioerosion or bioaccumulation? Shelf-slope trends for epi- and endobionts on experimentally deployed gastropod shells. *Historical Biology* 13:61–72.
- Walter, M. R., J. J. Veevers, C. R. Calver, and K. Grey. 1995. Neoproterozoic stratigraphy of the Centralian Superbasin, Australia. *Precambrian Research* 73:173–195.
- Walters, L. J., and D. S. Wetthey. 1991. Settlement, refuges, and adult body form in colonial marine invertebrates: a field experiment. *Biological Bulletin* 180:112–118.
- Warren, R. E. 1991. Ozarkian fresh-water mussels (Unionoidea) in the upper Eleven Point River, Missouri. *American Malacological Bulletin* 8:131–137.
- Wayne, R. K., J. A. Leonard, and A. Cooper. 1999. Full of sound and fury: the recent history of ancient DNA. *Annual Review of Ecology and Systematics* 30:457–477.
- Webb, T., III. 1993. Constructing the past from late-Quaternary pollen data: temporal resolution and a zoom lens space-time perspective. In Kidwell and Behrensmeier 1993.
- Wehmiller, J. F., L. L. York, and M. L. Bart. 1995. Amino acid racemization geochronology of reworked Quaternary mollusks on US Atlantic coast beaches: implications for chronostratigraphy, taphonomy, and coastal sediment transport. *Marine Geology* 124:303–337.
- Westall, F., L. Boni, and E. Guerzoni. 1995. The experimental silicification of microorganisms. *Palaeontology* 38:495–528.
- Whittington, H. B., and S. Conway Morris, eds. 1985. *Extraordinary fossil biotas: their ecological and evolutionary significance*. *Philosophical Transactions of the Royal Society of London B* 311:1–192.
- Wilby, P. R., and D. E. G. Briggs. 1997. Taxonomic trends in the resolution of detail preserved in fossil phosphatized soft tissues. *Geobios Mémoire Spécial* 20:493–502.
- Wilby, P. R., D. E. G. Briggs, P. Bernier, and C. Gaillard. 1996. Role of microbial mats in the fossilization of soft tissues. *Geology* 24:787–790.
- Wilf, P., and C. Labandeira. 1999. Response of plant-insect associations to Paleocene-Eocene warming. *Science* 284:2153–2156.

- Wilf, P., K. C. Beard, K. S. Davies-Vollum, and J. W. Norejko. 1998. Portrait of a Late Paleocene (Early Clarkforkian) terrestrial ecosystem: Big Multi Quarry and associated strata, Washakie Basin, southwestern Wyoming. *Palaios* 13:514-532.
- Williams, M. E. 1994. Catastrophic versus noncatastrophic extinction of the dinosaurs: testing, falsifiability, and the burden of proof. *Journal of Paleontology* 68:183-190.
- Wilson, M. V. H. 1988a. Taphonomic processes: information loss and information gain. *Geoscience Canada* 15:131-148.
- . 1988b. Reconstruction of ancient lake environments using both autochthonous and allochthonous fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology* 62:609-623.
- . 1988c. Predation as a source of fish fossils in Eocene lake sediments. *Palaios* 2:497-504.
- . 1993. Calibration of Eocene varves at Horsefly, British Columbia, Canada, and temporal distribution of specimens of the Eocene fish *Amyzon aggregatum* Wilson. *Kaupia (Darmstadtter Beitrage zur Naturgeschichte)* 2:27-38.
- Wilson, M. V. H., and D. G. Barton. 1996. Seven centuries of taphonomic variation in Eocene freshwater fishes preserved in varves: paleoenvironments and temporal averaging. *Paleobiology* 22:535-542.
- Wing, S. L., and W. A. DiMichele. 1995. Conflict between local and global changes in plant diversity through geologic time. *Palaios* 10:551-564.
- Wing, S. L., L. J. Hickey, and C. C. Swisher. 1993. Implications of an exceptional fossil flora for Late Cretaceous vegetation. *Nature* 363:342-344.
- Wolff, R. G. 1975. Sampling and sample size in ecological analyses of fossil mammals. *Paleobiology* 1:195-204.
- Xiao, S., and A. H. Knoll. 1999. Fossil preservation in the Neoproterozoic Doushantuo phosphorite Lagerstätte, South China. *Lethaia* 32:219-240.
- Yang, H., and S. Yang. 1994. The Shanwang fossil biota in eastern China: a Miocene Konservat-Lagerstätte in lacustrine deposits. *Lethaia* 27:345-354.
- Zuschin, M., and J. Hohenegger. 1998. Subtropical coral-reef associated sedimentary facies characterized by molluscs (northern Bay of Safaga, Red Sea, Egypt). *Facies* 38:229-254.
- Zuschin, M., J. Hohenegger, and F. F. Steininger. 2000. A comparison of living and dead molluscs on coral reef associated hard substrata in the northern Red Sea—implications for the fossil record. *Palaeogeography, Palaeoclimatology, Palaeoecology* 159:167-190.

