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Taphonomy's contributions to paleobiology

Anna K. Behrensmeyer and Susan M. Kidwell

Abstract.—Taphonomy established itself in paleontology primarily as a subdiscipline of paleoecology, but it has evolved into a much broader study of the ways in which preservation affects the fossil record. The past decade has seen a change in emphasis from descriptive taphonomic studies of fossil assemblages to more experimental, process-oriented investigations of necrolysis, stratification, and diagenesis of organic remains in modern environments. These actualistic studies are increasing the sophistication of taphonomic analysis in the fossil record by sharpening the diagnosis of bias in paleontological data and by providing a baseline for quantitative modeling of preservational patterns. The analysis of bias is also expanding into the evaluation of temporal resolution in the fossil record (sample acuity, stratigraphic completeness), and taphonomic research is thus contributing to broad-scale problems in evolution, biogeography, and biostratigraphy. In addition, taphonomic studies are providing new insights into paleoenvironmental reconstruction and into the direct paleobiological significance of post mortem processes such as the behavior of scavengers and the role of dead hardparts in structuring benthic communities. One of taphonomy's most promising new frontiers is comparative analysis applied to different taxonomic groups within assemblages and across environments, tectonic settings, and climatic regimes. All of this currently active research is contributing to a better understanding of the fossil record as the result of a dynamic, evolving, integrated system of biological and sedimentological processes that have both limited and enhanced knowledge of Earth history.

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Introduction

Taphonomy is concerned with how organic remains are incorporated into the rock record and the fate of these materials after burial. It was originally described as the "study of the transition of organic remains from the biosphere into the lithosphere" (Efremov 1940) and has stressed the recognition and evaluation of the extent to which fossil assemblages are biased records of ancient life (Lawrence 1968, 1979). The analysis of bias has remained preeminent in the last decade and has become more quantitative and accurate, largely through increased emphasis on actualistic, process-oriented research. The nature of taphonomy has expanded beyond this focus on bias, however, because of the increasing number of paleontological and geological disciplines that utilize information on the post mortem history of organic remains. Our understanding of the fossilization process is rapidly accelerating owing in large part to constructive interactions among these fields (Fig. 1).

As the primary data concerning preservation become organized around stronger methodologies and focal problems, taphonomy is developing a clearer identity as a discipline within the natural sciences. Most paleontologists, however, would still define the field as the study of post mortem information loss, stressing the traditional cautionary role that taphonomic analysis has played particularly in paleoecological research. This characterization of taphonomy fails to communicate its broader concern with how fossil assemblages are changed during preservation by the addition and alteration of information as well as by its loss. We thus propose a new working definition for the field as *the study of processes of preservation and how they affect information in the fossil record.* This encompasses not only information loss and bias, but also the more positive contributions that taphonomy is now making to the study of organisms and environments through time.

A Brief History of Taphonomy

Although the field was named only 45 yr ago (Efremov 1940), the study of fossilization and the fidelity of the fossil record has a long history.

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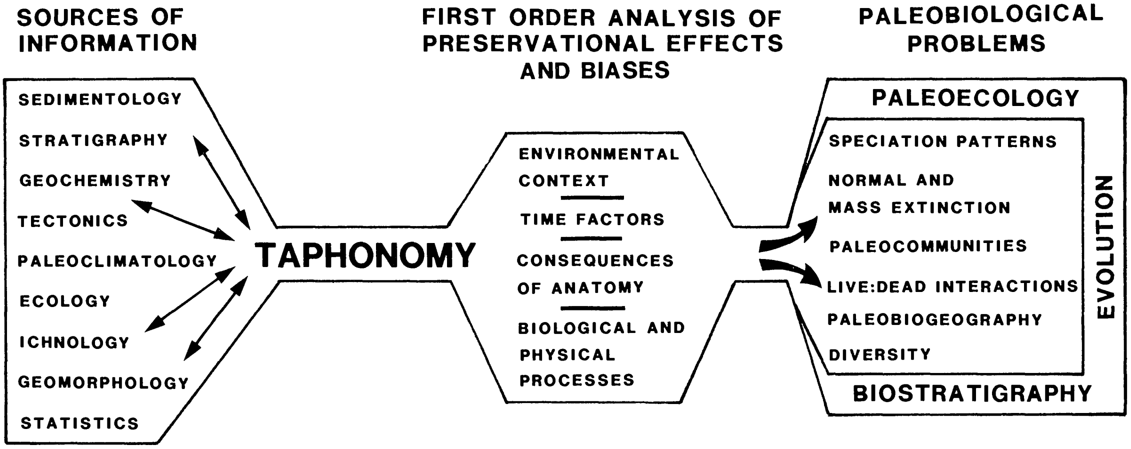

FIGURE 1. The present structure of taphonomic research, in terms of its interdisciplinary connections, primary first-order research objectives, and some of the paleobiological problems to which taphonomic information contributes.

The German workers Abel (1912), Wasmund (1926), Weigelt (1927), and Richter (1928) laid the foundations of the field in the first three decades of the twentieth century, interpreting both common and unusual fossil deposits in terms of post mortem processes that operate in modern environments. The strong reliance on actualism is traditionally a part of much taphonomic research, although the pros and cons of analogic reasoning and the validity of assumptions concerning the present as a key to the past are rarely discussed (but see Gifford 1981).

Efremov's (1940, 1953) concept of taphonomy was the earliest truly comprehensive view by modern standards, encompassing diagenetic as well as biostratinomic and necrolytic biases in vertebrate perservation (Fig. 2), and recognizing different scales of bias ranging from those affecting taxa in a single locality to those imposed by factors of continental scale. Although Efremov's clearly articulated concept of taphonomy soon had significant influence in vertebrate paleontology (Olson 1952, 1958, 1980), it failed to unify the diverse studies of preservation into one field. Interest in taphonomic problems has grown more or less independently within the traditional divisions of paleontology and, more recently, in archaeology.

During the 1950s and 1960s, the most influential taphonomic papers in the United States addressed post mortem bias in paleoecologic information. These included the work of Olson (1952, 1958) on Permian vertebrates, Johnson (1957, 1960, 1962) on fossil and recent shallow marine invertebrates, Lawrence (1968) on "information loss" in fossil marine communities, Clark et al. (1967) on Oligocene vertebrate paleoecology, and Voorhies (1969) on bone transport experiments and Pliocene vertebrate assemblages. Taphonomy became known in the United States as a prerequisite for paleoecologic research (Lawrence 1968), and was so firmly linked with paleoecology that its relevance to the question of bias in biostratigraphy and evolution was largely unappreciated. When the importance of studying preservational biases in such contexts was noted (e.g., Simpson 1960), it was not referred to as taphonomy.

The early 1970s saw an expansion of taphonomic research in Germany, spurred largely by the Sonderforschungsbereichs Project 53 on Paleoecology centered on Seilacher's group at the University of Tübingen (Seilacher 1976). The Fossil-Lagerstätten and Fossil-Diagenese programs funded a range of investigations into unusual fossil deposits and modes of preservation as a means of better understanding more normal types of occurrences (Seilacher 1970). These programs alone have produced approximately 100 papers to date (see listings in *Zentralbl. für Geol. und Paläont.*, Teil II, 1976; *Neues Jahrb. Geol. und Paläont.*, Abh. 157, 1979, and Abh. 164, 1982). The acceleration of interest in taphonomy in the United States during this same period and its broadening to include stratigraphic, sedimentologic, and actualistic approaches are due in part to the influence of this German work and a rediscovery of older pathfinding European

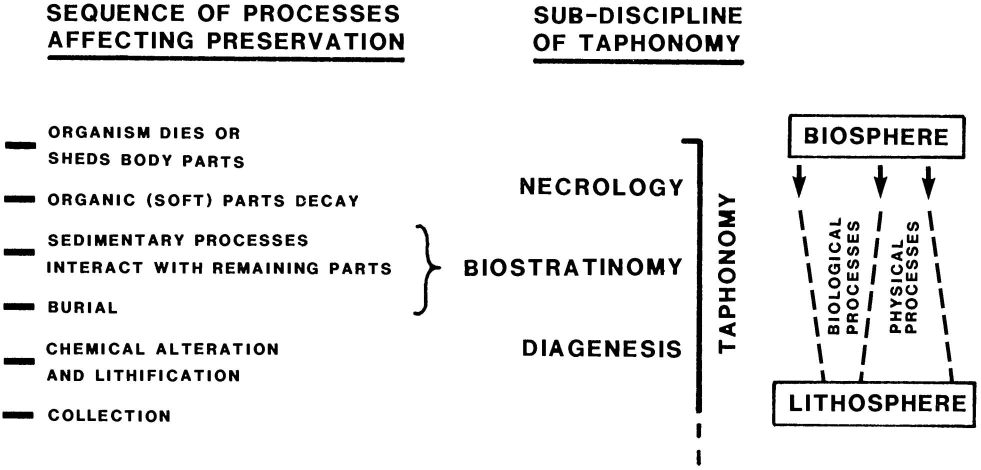

FIGURE 2. The subdisciplines of taphonomy address fossilization from the perspective of three phases of post mortem change: decay of softparts and organic matrix, other alteration of remains before burial, and post burial changes. The influence of biological processes wanes and the importance of physical (including chemical) processes increases through these phases.

studies, fostered by the translation of Schäfer's actuo-paleontologic opus into English (Schäfer 1972).

In the 1970s, taphonomy also expanded into paleoanthropology and archaeology with the work of Brain (1958, 1967, 1969), Behrensmeyer (1975, 1976a,b), and Hill (1975, 1978), which emphasized the paleoecological context of human evolution and human versus nonhuman agencies of bone modification. Taphonomy has been so enthusiastically incorporated into both the theory and the practice of archaeology (Gifford 1981) that many recent students in the field are unaware of its history and origins in paleontology. The application of taphonomy to archaeological problems has stimulated a great deal of rethinking of previous interpretations regarding early human behavior and resource utilization.

An early and continuing goal of taphonomic analysis has been to derive accurate estimates of species' relative abundances for paleocommunity reconstruction. In vertebrate paleontology, there were a number of attempts to develop methodologies for this, beginning with the work of Shotwell (1955, 1958) and Clark et al. (1967). In marine invertebrate faunas, pioneering work by a number of taphonomists led to understanding of differential preservation, time-averging effects, and the difficulties in obtaining accurate information concerning species abundances in the original communities (e.g., Johnson 1962, 1965; Cadée 1968; Lawrence 1971; Warme 1969, 1971; Levinton and Bambach 1975; Scott and West 1976; MacDonald 1976; Peterson 1976; Schopf 1978). During this same period, actualistic comparisons between life and death assemblages also became important in palynology (e.g., Havinga 1967; Davis 1969; Davis and Webb 1975; Bonnefille 1979), vertebrate paleontology (e.g., Zangerl and Richardson 1963; Schäfer 1972; Hill 1975; Behrensmeyer et al. 1979) and micropaleontology (e.g., Sliter 1975; Berger 1976).

The early to mid-1970s also witnessed the increased use of statistical techniques in taphonomy as workers sought to remedy "information loss," particularly in species diversity and relative abundance data. Rarefaction techniques developed by Sanders (1968) for living marine communities we applied to fossil assemblages. "Minimum numbers" estimates originated by Shotwell (1955) for vertebrate assemblages have been subject to reanalysis using statistical techniques (Grayson 1978; Holtzman 1979). The problems of large-scale biases in the fossil record have also been subjected to a wide range of innovative mathematical modeling techniques (e.g., Sepkoski 1975, 1976; Raup 1976, 1979).

Current Status and Scope of Taphonomy

From a traditional viewpoint, taphonomic processes begin when an organism loses control

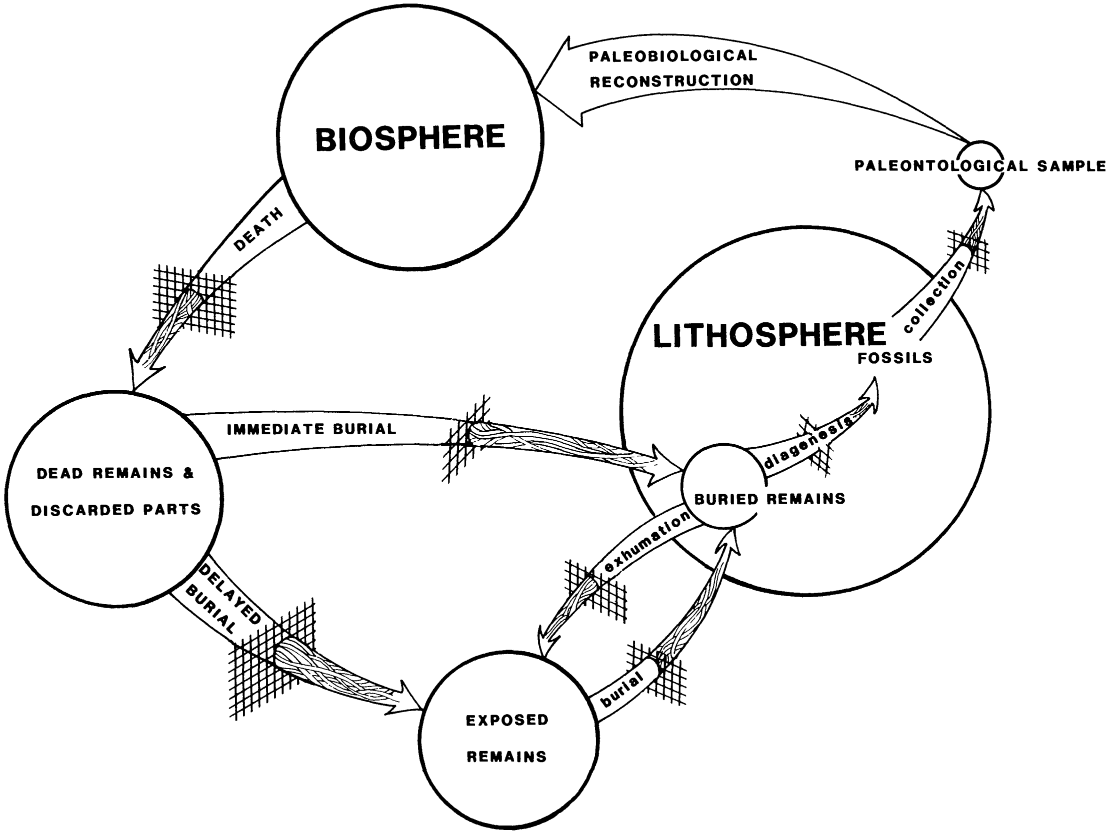

FIGURE 3. The progression of organic remains through distinct stages from death to final discovery, with intervening processes acting as filters on paleontological information, has become an accepted paradigm for the biosphere-lithosphere transition. Taphonomy is the study of how the different components in the system relate to one another and of the processes that effect the successive transformations.

over the organic components of its body, either through death or discard, and extend through the preburial interval of exposure and concentration through final burial and diagenesis (Fig. 3). Preservation is strongly affected by predeath circumstances such as habitat (e.g., nonaquatic vs. aquatic), however, and these can easily become part of a taphonomic study. Biases in paleontological data also inevitably result from outcrop patterns, collecting strategies, preparation, and even museum curation, hence these also may be included in taphonomic analysis. In practice, therefore, preservational effects extend well beyond the scope of the "biosphere to lithosphere" transition, and the perspective and methodologies of taphonomy can be applied throughout this expanded range of preservational effects.

Whether or not a problem is regarded as taphonomic (rather than paleoecological or statistical) is usually determined by the perspective of the researcher. For example, the strength of a cephalopod shell clearly has ecological significance for the animal but is also a critical factor in its potential for preservation and burial. In our survey of the last 10 years of research in taphonomy, we have included works with obvious application to taphonomic problems as well as those actually reporting taphonomic analyses.

Taphonomy varies in its importance to major topics in paleontological research. Many traditional problems relating to taxonomy and phylogeny either bypass obvious taphonomic biases or are chosen (often intuitively) to minimize such biases. Systematic description of species and functional morphology are usually based on well-preserved specimens whose structures were not affected significantly by taphonomic processes. In studies of populations, however, processes such as hardpart size sorting and time averaging can affect morphometric parameters. Differential preservation of species has important and well-recognized effects on paleocommunity reconstructions but also relates to problems in biostratigraphy. Phenomena such as the "Lazarus effect," in which species appear to become extinct but then reappear farther up a stratigraphic column (Jablonski 1983) can reflect taphonomic processes that therefore bias biostratigraphic correlations and patterns of speciation and extinction.

In the past decade, emphasis has changed from documenting biases in the records of ancient communities and "stripping off the taphonomic overprint," to focusing on biologically meaningful information that *is* contained in time-averaged, ecologically mixed assemblages, and to sampling designs aimed at these new goals. Biases themselves are now recognized as problem specific, and with the increase in knowledge concerning biasing processes, taphonomists can refine and simplify their studies by isolating and analyzing biases with respect to carefully defined problems. Moreover, processes that bias some types of evidence in fossil assemblages are now better appreciated as sources of other kinds of information. For example, bone samples with carnivore damage may have taxonomic biases owing to prey selection but at the same time reveal behavioral traits of the bone-processing agent. This positive trend is gradually replacing a commonly held view of taphonomic processes as obstructive rather than enlightening.

A Georef search of the past 10 yr of taphonomic literature (Appendix 1) reveals an average publication rate in taphonomy of nearly 50 articles per year since 1975. This is only a minimum estimate of the actual number of publications relating directly to the field and may be off by a factor of 2 or more since the Georef listing of 441 titles included only 19 of 40 articles in the first 9 volumes of *Paleobiology* which have taphonomy as a primary theme (Appendix 2). Taphonomy was mentioned by name in only 14 of the 150 *Paleobiology* articles of taphonomic significance, explaining in part the incompleteness of the Georef listing, which used "taphonomy" as the primary key word.

Of the articles found by Georef, vertebrate taphonomy is represented in about 30%, invertebrate taphonomy in another 30%, and the remaining 40% includes all other fields (e.g., paleobotany and palynology, micropaleontology, anthropology, sedimentology, ichnology). The vast majority of these publications are descriptive studies of specific fossil occurrences or stratigraphic intervals. Sedimentological papers pertaining to taphonomy are underrepresented in the Georef listing primarily because key words (e.g., taphonomy, fossilization, bias) often are not included in taphonomic articles published in geological journals. A similar situation exists with regard to biological literature on skeletal production, bioerosion, and ecological significance of organic remains (specifically for marine invertebrates). As a consequence, a great deal of information relevant to taphonomy is not easily accessible through presently available key word listings and library search procedures.

The Georef search suggests a significant expansion in taphonomic research in the United States relative to other countries since 1975. Of more than 20 other nations represented in the search, the Soviet Union appears to be the most active. Taphonomic publications in Europeran university journals and doctoral dissertations outside the United States are underrepresented in Georef, however, which obscures some of the research activity in other countries, particularly Germany. Even with its limitations, the Georef listing reflects generally available published work that influences the overall impact of taphonomy in paleontology, and there is little doubt of the increasing interest and involvement of U.S. researchers during the past decade.

The largest proportion of taphonomic articles in *Paleobiology* (Fig. 4; Appendix 2) are concerned with preservational and sampling biases, and these cover a variety of problems ranging from the effects of differential preservation of taxa (e.g., Lasker 1976; Koch and Sohl 1983) to representation of body size classes in mammal assemblages (Damuth 1982) and stratigraphic and area effects on local and Phanerozoic marine diversity (Sepkoski 1975; Flessa and Sepkoski 1978; Jablonski 1980). Theoretical as well as actualistic approaches have focussed on methodologies for analyzing bias in fossil assemblages (e.g., Schopf 1978; Behrensmeyer 1982a; Buzas et al. 1982).

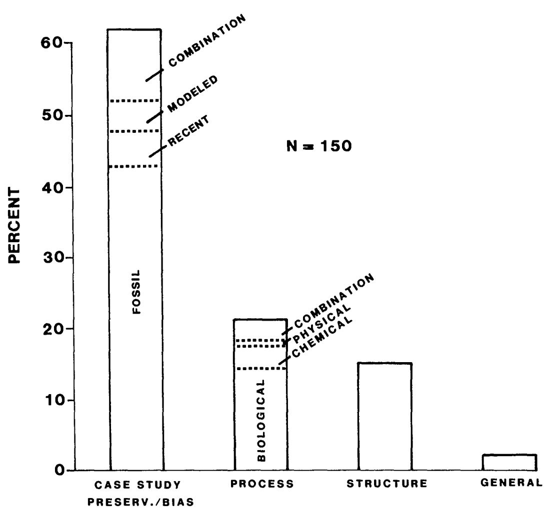

FIGURE 4. Types of taphonomic information contained in articles in *Paleobiology*. An article focusing on preservational patterns or biases was catagorized as 'Preserv./Bias.' Other central themes were classed as 'Process,' 'Structure' (e.g., affecting preservation) or 'General.' (See Appendix 2 for further explanation.)

Other themes in *Paleobiology* and in taphonomic literature in general include the analysis of skeletal architecture, growth habit, hydraulic behavior, and substrate attachment (see "Structure" in Appendix 2) and studies of biological and physical processes that leave identifiable traces on organic remains ("Processes" in Appendix 2). Some of these articles are written as studies in autecology but have important taphonomic implications (e.g., Schopf et al. 1980; Vermeij et al. 1980; Westermann and Ward 1980; Cheetham and Thomsen 1981). Publications focusing on vertebrate taphonomy have stressed processes (predators, scavengers, fluvial transport, weathering) that affect bone assemblages and leave recognizable evidence for their influence on the assemblages (e.g., Behrensmeyer 1978; Andrews and Nesbit Evans, 1983; Haynes 1983).

Not surprisingly, research in sedimentological aspects of biostratinomy and diagenesis has been underrepresented in *Paleobiology*. Analysis of post mortem histories of fossils is being used to reveal the dynamics of sediment deposition and erosion (evidence for cycles of exhumation and burial), porewater chemistry and timing of lithification (stage of decay, corrosion, mold formation, mineral replacement, and recrystallization), paleocurrent direction and regime (fossil orientation, geometry and alignment of fossil concentrations), substratum mass properties (bioclastic fabric, hardpart residence time on the seafloor), and hydraulic energy and sediment transport directions (fossil allochthony). While such data are often collected with sedimentological rather than paleobiological goals in mind, they are also a source of important information about taphonomic processes that affect paleoecological and evolutionary data.

New Directions in Taphonomy

The scope of taphonomy is increasingly broad, but it is also becoming more clearly focused on several major new areas of research.

Time resolution. The way in which time is represented in fossil assemblages determines how they can be used to address paleoecologic, biostratigraphic, and evolutionary questions. The temporal significance of paleontological samples can be examined on several scales. (1) What is the time represented in a single sample—how many years were required for its formation? This has been characterized as the problem of time averaging or temporal acuity (e.g., Schindel 1980, 1982). (2) How complete is a fossiliferous sequence—what percentage of increments of a given duration are represented in the rock record, and how does lithostratigraphic completeness relate to biostratigraphic completeness? (3) How are fossiliferous time increments distributed through the sequence—are beds (and paleontological samples) distributed evenly, randomly, or in other patterns that affect the record of paleontological change? Methodologies for studying acuity and completeness are now being developed for a variety of organisms and depositional settings (see review by Behrensmeyer and Schindel [1983]), but the analysis of sequence patterns (point 3) remains a frontier.

Although time averaging can obscure short-term paleobiological processes, it also has advantages for paleoecological and neontological surveys of community composition (Peterson 1976; Warme et al. 1976; Scott and Medioli 1980). Time averaging integrates "noise" from seasonal and other short-term spatial and temporal variations in species abundance (e.g. Johnson 1971), thereby enhancing longer-term patterns that may be of greater significance for the community as a whole. Badgley (1982a) used modern analogues to model time-averaging effects in the vertebrate fossil record. Comparison of two different types of samples from a recent vertebrate community in East Africa, representing 1 yr and 100 yr of time averaging of mammal populations, revealed how each might represent actual live populations in the fossil record. A similar approach to other types of communities would help define the limits to paleocommunity reconstruction using short-term time-averaged samples.

In the fossil record, time averaging has been evaluated on the basis of (*a*) the ecological comparability of the assemblage to a living community, using arguments based either on recent analogues or functional morphology, and (*b*) the taphonomic uniformity of the assemblage—whether features of the specimens themselves show comparable post mortem histories. More recently, the mode of formation of the sedimentary deposit containing a fossil assemblage has also been used to estimate the time it represents (Behrensmeyer 1982a, b; Kidwell 1982; Retallack 1984; Wing 1984). These estimates are based on analogy with modern processes that concentrate organic remains (e.g., storms, floods, predation, hydroseres) or on the stratigraphic context of the deposit (e.g., condensed marine transgressive lags, paleosol frequency, and distribution through a section).

Estimates of time averaging based on taphonomic history and other paleoenvironmental criteria may be at odds with estimates of acuity based on statistical treatment of sedimentation rates (e.g., Schindel 1980, 1982). Velbel (1984) has pointed out that discrepancies of as much as 6 orders of magnitude can arise because estimates of acuity based on average sedimentation rates do not take into account sedimentary processes responsible for the formation of individual beds. For example, Velbel's paleontological samples from a 1-cm-thick interval in a sequence of platform limestones have estimated acuities of 1,200 yr each if continuous sedimentation is assumed, yet actually may represent a single day's event (e.g., a storm) averaging remains from a few months or years of attritional death. Taphonomic analysis that draws upon knowledge of sedimentologic and ecologic processes can resolve time components more precisely than probabilistic methods and can also pinpoint samples of comparable temporal acuity by distinguishing essentially instantaneous (catastrophic) accumulations from longer-term ones. Jones (1980) demonstrated one method for doing this using molluscan growth lines to determine season of death, and catastrophic versus attritional histories for other types of assemblages can be deduced from other kinds of life-history parameters and taphonomic evidence.

The completeness of the fossil record is now being evaluated using the probabilistic method of Sadler (1981), which estimates the underlying stratigraphic completeness by comparing long- and short-term sedimentation rates. This method has been applied to questions such as how finely microevolution can be resolved in a particular stratigraphic section and how sedimentary increments are distributed in a given section with respect to an absolute time scale (Gingerich 1982; Sadler and Dingus 1982; see also NAPC Symposium, reviewed in Behrensmeyer and Schindel [1983]). The relation between bio- and lithostratigraphic completeness has been argued several ways: biostratigraphic completeness may be less (for a given time interval) because of unfossiliferous beds in the sequence (e.g., Dingus and Sadler 1982; Sadler and Dingus 1982), but the biostratigraphic record may also be more complete because of stratigraphic condensation of fossils during intervals of low sedimentation (Behrensmeyer 1982a,b; Kidwell 1982). In such instances, the intervals of time that are well represented by fossils are poorly represented by sediments, and these may alternate with other noncondensed increments in which biostratigraphic completeness is more a function of increased rates of sedimentation.

Megabiases.—Analysis of bias in large-scale paleobiologic patterns is another focal area for growth in taphonomy. "Megabiases" in relation to Phanerozoic diversity have already received considerable attention in a series of recent papers (Raup 1976; Sepkoski 1976; Sheehan and Raup 1977; Flessa and Sepkoski 1978; Lasker 1978; Signor 1978; Sepkoski et al. 1981). These confront many of the biases that affect the record of taxa through time, including the effect of exposure area and preserved thickness of strata of different ages, proportion of marine versus continental rocks, number of systematic studies and workers on groups and systems, and the biostratigraphic bias due to our more complete knowledge of Recent faunas relative to ancient faunas ("The Pull of the Recent" [Raup 1979]).

Further taphonomic work could contribute to the analysis of diversity patterns by (1) testing the effects of time averaging and other taphonomic processes on resolving immigration and extinction events, (2) providing a basis for assessing body size biases in the record, (3) estimating diversity biases due to loss of soft-bodied organisms in specified environmental settings, (4) examining the differences in large-scale preservation potential for stenotopic versus eurytopic organisms. Investigations into other types of large-scale, environmentally imposed biases could also prove fruitful. For example, land vertebrate deposits accumulate and are preserved under fairly specific combinations of tectonic, climatic, and sedimentologic conditions, and the best records may result from rapid infilling of continental basins in relatively dry or highly seasonal climates. If true, this would imply that much of land vertebrate paleoecology and evolution as we understand it is represented within a rather narrow, environmentally defined window through time. The same type of phenomenon could also apply to macrofloral and pollen records.

Taphonomy may play a larger role in structuring diversity patterns than is generally recognized, both in terms of differing post mortem biases among assemblages and in the changing role of dead hardparts on community dynamics. For example, to what extent do Bambach's (1977) estimates of within-habitat diversity reflect qualitatively different patterns of taphonomic bias in his samples? The Neogene data are derived largely from condensed shell beds of the Atlantic coastal plain, where fossil molluscan assemblages record prolonged time averaging and a mixture of habitat types within the nearshore setting. The condensed nature of these deposits would tend to increase apparent taxonomic diversity for the habitat. Moreover, because shell gravels provide opportunities for taphonomic feedback that are not available in communities from soft-bottom habitats of identical bathymetry, the two types of fossil assemblages are probably not comparable for biological reasons.

Another important taphonomic effect on community structure and evolution lies in differential preservation of taxa, which can strongly affect paleoecological interpretations. The genus *Hipparion* has been regarded as a dominant member of the mammal community in the Miocene of Pakistan after its abrupt appearance about 9.5 ma B.P. Yet through careful sampling and taphonomic analysis, Badgley (1982b) found that its apparent abundance was more likely due to the differential preservation and identifiability of its teeth. The reduced importance of *Hipparion,* a supposed grazer, in the paleocommunity changes interpretations of the habitats as open woodland or savanna and also affects hypotheses concerning its impact on the community structure and faunal turnover.

Differential preservation has also become an important consideration in distinguishing real from apparent extinction events and in placing confidence limits on paleontologic patterns near mass extinction boundaries (e.g., Lazarus effect [Jablonski 1983, 1985]; unconformity trunction effect [Birkelund and Hankasson 1982]). Although this applies directly to such currently debated extinctions as the end-Cretaceous event (Raup 1982; Van Valen 1984), there has been relatively little taphonomic evaluation of competing hypotheses. Ecological catastrophes that accomplish mass global extinction on the scale of days, weeks, and months (e.g., extreme versions of the asteroid impact hypothesis of Alvarez et al. [1980], such as Ahrens and O'Keefe [1983] and Pollack et al. [1983]) might leave a qualitatively different taphonomic record than more prolonged gradual or stepped extinctions. A change in the preserved record might be expected to result from a sudden increase in rate of hardpart supply to the record, enhanced by the swamping (or inactivity) of scavengers and decomposers.

What would be the taphonomic consequence of other factors in the final Cretaceous event, such as reduction in shallow marine sample area and possibly accelerated terrestrial erosion associated with deforestation, regression, and base-level fall? Additionally, is the stratigraphic record of the critical interval too time averaged or incomplete to resolve the short-term dynamics of a mass extinction? And what might be the effects of small sample size (e.g., for dinosaur remains) on interpretations of the observed record? The taphonomy of mass extinctions deserves further consideration, both in terms of the fidelity of the fossil record and as a potential source of direct information on the biological nature of the events.

Feedback systems.—Since taphonomic phenomena straddle the boundary between the biosphere and lithosphere, information on the post mortem fate of organic remains provides insights concerning interactions between biological and geological systems. Positive and negative feedback between these systems has become a productive line of new research. For example, although living organisms influence the composition of the death assemblage, the dead hardparts also have potential influence on the composition and dynamics of living benthic communities by altering the physical habitat. Dead hardparts provide attachment sites for organisms and, by changing the mass properties (firmness, texture, topography) of the substrate, facilitate colonization and survival for firm-bottom and shell-gravel taxa while inhibiting the success of soft-bottom, primarily infaunal groups.

The entire spectrum of interrelationships between living and dead hardparts has been termed taphonomic feedback (Kidwell and Jablonski 1983), which serves as a driving mechanism of community change that is highly dependent upon the physical sedimentary dynamics of hardpart accumulation (e.g., Kidwell and Aigner, 1985). Although recognition of the effects of hardparts on the marine benthos is not new (e.g., studies of encrusting and boring taxa in shell substrate [Walker and Parker 1976; Watkins and Hurst 1977]), a perspective stressing live : dead interactions as a dynamic feedback system provides the basis for a new look at benthonic marine ecosystems.

In addition to the ecological consequences of live : dead interactions, positive feedback probably operates as well between processes of hardpart concentration and their preservation potential. For example, buried hardparts in shallow marine settings are more likely to create favorable chemical microenvironments and thus survive early diagenesis when associated with other hardparts (e.g., MacCarthy 1977; Sepkoski 1978; Aller 1982; Fursich 1982). Vertebrate remains may reflect similar feedback systems in fluvial deposits, where dense primary bone concentrations and those associated with calcareous nodules have greater preservation potential than dispersed bone elements (A. Hill, pers. comm.). There is also growing evidence that rapid burial of soft tissues promotes geochemical changes that enhance pyrite and carbonate nodule formation and thus fossil preservation. It thus appears that early diagenesis may accentuate primary patterns in hardpart abundance created by physical and biological processes: the diagenetic filter on paleontologic information is not random, nor is it in opposition to the preservation of primary patterns in hardpart accumulation.

The role of organic remains in feedback systems that influence not only living organisms but also preservation potential offers fertile ground for future taphonomic research. One consequence of such feedback may be a bias toward massed organic remains and the ecological and sedimentary situations favoring these throughout the fossil record.

Comparative taphonomy.—Documentation of taphonomic features in fossil and recent case studies is building an essential data base for the field, and there is no question that such research will and should continue. There are also signs, however, that taphonomy is entering a more synthetic and theoretical phase in which the vast amount of information on preservation can be organized into a more coherent approach to the fossil record. In particular, there is fertile ground for comparisons of similar taphonomic phenomena that operate differently on major taxonomic groups both within assemblages and across different paleoenvironmental settings. For example, why are plants and vertebrates so seldom preserved in the same sedimentary bed? Are assemblages from biostratinomically identical storm lags in different latitudes and climates comparable in their early diagenesis? Have taphonomic pathways changed qualitatively or only quantitatively through the Phanerozoic as a consequence of biological evolution and Earth history?

A more integrated, comparative taphonomic approach to the fossil record will also help identify areas needing further research. For example, the taphonomy of microorganisms and macrofloral remains has received far less attention than that of vertebrates and macroinvertebrates. Furthermore, vertebrate taphonomy has focused primarily on preservation in terrestrial settings and invertebrate taphonomy has stressed marine settings in both actualistic and stratigraphic investigations. The characteristics and origin of marine bone beds and freshwater shell beds are thus less well understood despite their abundant representation in the record.

Taphonomic comparisons among major taxonomic groups are usually confounded by paleoenvironmental differences in the typical settings of fossil accumulation. Deposits of mixed composition such as shelly bone beds and stratigraphic sequences that are alternately rich in macrofloral remains and vertebrates are ideal for study because many potentially critical paleoenvironmental factors can be controlled. Nonetheless, because taphonomists almost always concentrate on a single major group, taxonomically mixed deposits are usually examined only from one perspective. The advantages of a comparative approach have been exemplified, however, by the results of Brett and others (Brett and Baird 1984; Speyer and Brett 1984; Brett et al., in press) on bathymetric trends in the preservation of different taxonomic groups in Devonian strata. Mode of death, history of hardpart concentration and interment, and porewater chemistries differ along the gradient as a function of sediment dynamics, water energy, and oxygenation. Through such investigations, taphonomic facies models are beginning to emerge.

Comparative taphonomy of depositional basins is another promising area for study. To the extent that rates of sedimentation govern the concentration of fossil hardparts, the distribution of fossil deposits and their degree of time averaging should differ among active margins, passive margins, and cratonic settings. On a smaller scale, condensed hardpart concentrations associated with unconformities and other breaks in the record should differ according to the history of deposition: starved condensed sequences have different dynamics of accumulation (and thus taphonomic attributes) than sequences condensed through alternating deposition and erosion (Kidwell 1981, 1983; Kidwell and Jablonski 1983). Patterns of sediment accumulation affect the distribution of shell gravels within cyclic transgressive-regressive sequences (Kidwell and Aigner, 1985). Tectonic setting may also determine the nature and distribution of bone accumulations in fluvial settings by controlling the balance of such processes as lateral versus vertical aggradation.

Climate is another controlling factor in the preservation of organic remains, and probably one of the least understood. Paleobotanists recognize a clear latitudinal gradient from low preservation potential in the tropics, where productivity is high but destruction rates are also high, to good macrofloral records in temperate settings where seasonality keeps production and destruction out of phase, to poor arctic records related to low overall production. Rates and patterns of net bone input may vary similarly. Probable latitudinal variation in net supply of marine invertebrate remains is not as apparent—how do rates of hardpart production, bioerosion, sedimentation, microbial decomposition, and dissolution correlate with climate?

Another target for comparative taphonomy (which we anticipate with considerble excitement) is the analysis of Phanerozoic trends in post mortem processes, including preservational biases and dynamic interactions between biological and geological processes. Opportunities and pathways for taphonomic feedback, for example, have no doubt changed through the Phanerozoic as a consequence of the evolution of hardpart producers, hardpart utilizers, and hardpart destroyers (Kidwell and Jablonski 1983) The preservation potential of physically concentrated fossil beds and the chemical diagenesis of fossils in general have probably also undergone qualitative changes through the Phanerozoic, as evidenced by the diminishing preservation potential of storm-generated beds (Sepkoski 1982; Larson and Rhoads 1983), shifting relative abundance of hardpart mineralogies, and increasing depth of penetration and bathymetric range of bioturbators and abundance of duraphagous predators (Vermeij 1977; Thayer 1983; Miller 1984). Actualistic models can play an important role in framing hypotheses for this comparative taphonomy of the Phanerozoic, complementing and explaining system-by-system patterns.

Conclusion

The expansion of taphonomy beyond its traditional role as the study of information loss and paleoecologic bias into broader problems in paleobiology has opened up a wealth of new avenues for research and interdisciplinary exchange. The past decade of growth in paleontology has generated new questions and demands on information contained in the fossil record, thus helping to stimulate more careful consideration of biases in this information. The increasingly rigorous approach to bias is, however, only half the story of taphonomy's new identity since taphonomic processes and effects are now seen as an important source of information about the interrelationships and dynamics of geological and biological processes throughout life's history. We are now looking more explicitly at the "information filters" as well as the remains and traces that passed through them to become the fossil record.

The new perspectives in taphonomy which we feel are likely to set the course for its immediate future are:

1) that taphonomic processes and biases cover the full range of scales in paleontological problems, from studies of single species to Phanerozoic diversity trends. There is a need for research in middle- to large-scale taphonomic phenomena that draws upon knowledge of smaller-scale patterns and looks for ways in which these are magnified or canceled out by longer-term, larger-scale processes.

2) that processes of preservation can be viewed as active forces which not only have affected the preserved record of biological evolution but which have the potential to directly influence biological evolution itself. The dynamic interactions between biological and geological processes in particular deserve more intensive research by paleontologists, biologists, sedimentologists, and geochemists.

Although continuing research in modern analogues and theoretical modeling is critical to the further growth of taphonomy, a more careful consideration of the limits of analogic reasoning is overdue, as is the development of methods for better understanding processes that are not represented in recent biological and geological systems. Practically speaking, however, perhaps the greatest challenge faced by taphonomy is to impose order on the vast body of multidisciplinary data that can contribute to its goals. This order is beginning to appear with the growing focus on broad-scale problems and more comparative, synthetic inquiries into processes of preservation and their consequences in the fossil record.

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Appendix 1.

Results of the Georef Database search

Computer access to the Georef Database was through the Dialog Information Retrieval Service, provided in conjunction with Smithsonian Institution Libraries. Georef's database includes over 4500 international journals plus books, dissertations, conference publications, and government publications. It is relatively comprehensive back to about 1970. Approximately 60% of the indexed publications originate from outside the United States. The keyword "taphonomy" was given for the search, with the specified period from 1975 to 1983.

The search resulted in 546 titles. After careful screening for duplications, dates from 1975 to 1983, and elimination of obvious misfits, about 440 of these were used for our analysis. These do not include some (such as a number of articles in *Paleobiology*) that are known to us as important taphonomic publications. Most omissions appear to be due to problems in coding particular subjects as taphonomy. For instance, studies of preservation potential in modern environments often were not picked up by the search unless their relevance to paleoecology was noted in the title. The total cataloguing for 1983 also was not available from Georef at the time of the search. Thus, the 440+ titles represent only part of the total output from taphonomic research over the last nine years. Nevertheless, we feel this reflects a generally valid overview of activities in the field based on literature that is available to the scientific community at large.

Country of publication is given for by Georef for most titles back to 1975. Doctoral dissertations, which do not have this information, were mostly from U.S. universities (probably from *Dissertation Abstracts*). Dissertations do not amount to a large proportion of the 440+ titles, but they do help to increase the apparent dominance of the United States in taphonomic productivity. Countries represented in the search included Venezuela, China, India, Romania, Czechoslovakia, Hungary, Poland, New Zealand, Norway, South Africa, and Japan in addition to the Western European block, Canada, and the United States.

Appendix 2.

Results of a review of *Paleobiology*

In terms of activity in different fields, invertebrate paleontology accounted for 41% of the 150 articles compared with vertebrate paleontology's 22%. Of those 40 primarily concerned with taphonomy, however, the percentages were reversed, IV with 23% and VP with 41%. Either way, this contrasts with the pattern presented by the Georef database. Also of interest is the large number of papers involving combinations of fields, for example, those dealing with such topics as differential preservation and ecological diversity (Lasker 1976) and biases in Phanerozoic species sampling (Signor 1978). Many of these are mainly concerned with marine invertebrates, but they also include other major groups of organisms and reflect the more interdisciplinary orientation of articles published in *Paleobiology*. A comparison of the first five and most recent four years of *Paleobiology* showed a relative increase in articles concerned with vertebrate taphonomy.

Articles were categorized according to the type of problem or information which was relevant to taphonomy. The categories were as follows:

1) Structural attributes of organisms influencing preservation
2) Post mortem proceses (including agencies of death)
    —biological
    —physical: primarily sedimentological
    —chemical
    —combination of the above
3) Patterns of preservation and bias (usually case studies)
    —based on knowledge of the fossil record
    —based on studies of recent analogues
    —based on models of natural systems
    —pertaining to a combination of the above
4) General: discussions of taphonomy as a field, etc.

The primary orientation of the article as presented by the author(s) was used to determine its category in the above scheme. Studies of specific fossil occurrence, for example, were placed in 3, even though processes were also a topic of discussion. Studies in which processes themselves were the primiary focus were placed in 2. The results of this analysis are shown in Fig. 4.

The alphabetical listing below shows the categorization of articles with taphonomic content. Primary concern with taphonomy is indicated as "Pri," indirect relevance as "ind," and incidental relevance as "Inc."

Author	Vol.	Num.	Category	Status
Ackersten et al.	9	3	Bias-fossil	Inc
Andrews & Evans	9	3	Process-biological	Pri
Andrews & Evans	5	1	Bias-combo	Ind
Antia	3	4	Bias-recent	Pri
Ashton & Rowell	1	2	Bias-fossil	Ind
Bambach	3	2	Bias-fossil	Ind
Behrensmeyer & Schindel	9	1	Bias-fossil	Ind
Behrensmeyer	8	3	Process-physical	Pri
Behrensmeyer	4	2	Process-combo	Pri
Behrensmeyer et al.	5	1	Bias-recent	Pri
Bell & Haglund	8	3	Bias-fossil	Ind
Berg & Nishenko	1	3	Process-biological	Ind
Bolt & Wassersug	1	3	Process-biological	Inc
Bretsky & Bretsky	1	3	Bias-fossil	Ind
Brett & Lindell	4	3	Bias-fossil	Ind
Buzas et al.	8	2	Bias-recent	Pri
Campbell & Valentine	3	1	Bias-combo	Pri
Chaloner	7	3	Bias-fossil	Ind
Chamberlain	4	4	Structure	Ind
Chamberlain & Wester	2	4	Structure	Inc
Chamberlain et al.	7	4	Process-biological	Pri
Cheetham & Thomsen	7	3	Structure	Ind
Cloud	2	4	Bias-fossil	Ind
Crick	7	2	Bias-fossil	Ind
Damuth	8	4	Bias-combo	Pri
Dodson	6	1	General review	Pri
Dodson & Wexlar	5	3	Process-biological	Pri
Dodson et al.	6	2	Bias-fossil	Pri
Dudley & Vermeij	4	4	Process-biological	Ind
Eldredge	2	2	Bias-fossil	Ind
Erben et al.	5	4	Structure	Inc
Farlow	9	3	Bias-fossil	Inc
Finney	5	1	Structure	Inc
Fisher	7	2	Process-biological	Pri
Fleagle	4	1	Bias-fossil	Inc
Flessa	1	2	Bias-combo	Ind
Flessa & Bray	3	4	Bias-fossil	Ind
Flessa & Jablonski	9	4	Bias-fossil	Ind
Flessa & Sepkoski	4	3	Bias-fossil	Pri
Gingerich	7	4	Bias-fossil	Inc
Gould & Calloway	6	4	Bias-fossil	Ind
Gould et al.	3	1	Bias-fossil	Ind
Grayson	4	1	Bias-fossil	Pri
Hallam	8	4	Bias-fossil	Inc
Hallam	4	1	Bias-fossil	Inc
Hallam	3	1	Bias-fossil	Inc
Hayami	4	3	Bias-fossil	Inc
Haynes	6	3	Process-biological	Pri
Haynes	9	2	Process-biological	Pri
Hill	5	3	Process-combo	Pri
Hoffman	5	4	Bias-fossil	Ind
Holtzman	5	2	Bias-combo	Pri
Hopson & Radinsky	6	3	Bias-fossil	Inc
Hulbert	8	2	Bias-fossil	Ind
Jablonski	6	4	Bias-fossil	Pri
Jones	6	3	Structure	Ind
Kanie et al.	6	1	Structure	Inc
Kaufman	7	4	Process-biological	Inc
Kellogg	9	4	Bias-fossil	Inc
Kier	3	2	Bias-fossil	Pri
Kippel & Parmalee	8	4	Bias-fossil	Ind
Kitchell et al.	4	2	Bias-recent	Inc
Kitchell et al.	7	4	Process-biological	Ind
Klein	8	2	Process-biological	Pri
Klein	8	2	General review	Pri
Klein & Cruz-Uribe	9	1	Structure	Ind
Kobluk et al.	4	2	Process-biological	Ind
Koch	4	3	Bias-combo	Pri
Koch	6	2	Bias-fossil	Ind
Koch & Sohl	9	1	Bias-fossil	Pri
Kohlberger	9	1	Bias-fossil	Ind
Kranz	3	4	Bias-modeled	Pri

Author	Vol.	Num.	Category	Status
Krohn	5	2	Bias-combo	Ind
Kurten	9	1	Bias-fossil	Ind
LaBarbera	7	4	Bias-combo	Ind
LaBarbera	3	3	Structure	Inc
Lasker	4	2	Bias-modeled	Pri
Lasker	2	1	Bias-combo	Pri
Levinton & Bambach	1	1	Bias-combo	Ind
Liddell & Brett	8	1	Process-biological	Ind
Lindberg & Kellogg	8	4	Process-biological	Pri
Lipps	7	2	General review	Ind
Malmgren et al.	9	4	Bias-fossil	Inc
Maynard	2	2	Bias-recent	Ind
Nichols & Pollack	9	2	Bias-modeled	Ind
Nicklas	7	1	Process-chemical	Ind
Noe-Nygaard	3	2	Process-biological	Pri
Oliver	6	2	Structure	Ind
Paine	9	1	General review	Ind
Peterson	9	4	Process-combo	Ind
Petry	8	1	Bias-recent	Ind
Pielou	5	4	Bias-combo	Inc
Radinsky	8	3	Process-biological	Ind
Raup	1	4	Bias-combo	Pri
Raup	8	1	Bias-fossil	Inc
Raup	9	2	Bias-fossil	Inc
Raup	2	4	Bias-fossil	Ind
Raup & Crick	8	2	Bias-fossil	Ind
Raup & Marshall	6	1	Bias-fossil	Ind
Richardson & Watson	1	4	Structure	Inc
Ronan	3	4	Process-biological	Ind
Sambol & Finks	3	1	Bias-fossil	Ind
Saunders & Wehman	3	1	Structure	Ind
Schindel	8	4	Bias-fossil	Ind
Schindel	6	4	Bias-fossil	Ind
Schindel & Gould	3	3	Bias-fossil	Inc
Schopf	4	3	Bias-recent	Pri
Schopf	7	2	Bias-fossil	Ind
Schopf	6	4	Bias-fossil	Ind
Schopf	5	3	Bias-fossil	Ind
Schopf et al.	6	4	Structure	Ind
Seilacher	5	3	Structure	Inc
Sepkoski	4	3	Bias-fossil	Ind
Sepkoski	1	4	Bias-fossil	Pri
Sepkoski	7	1	Bias-fossil	Ind
Sepkoski	5	3	Bias-fossil	Ind
Sepkoski	2	4	Bias-fossil	Ind
Sheehan & Raup	3	3	Bias-combo	Pri
Shipman & Walker	6	4	Process-biological	Pri
Signor	4	4	Bias-combo	Pri
Stanley	7	3	Structure	Ind
Stearn	8	3	Bias-combo	Ind
Strathmann	7	3	Structure	Inc
Thayer	1	1	Structure	Pri
Thayer	1	4	Structure	Inc
Thayer	3	1	Bias-combo	Ind
Thomas & Foin	8	1	Bias-modeled	Ind
Thomsen	3	4	Bias-fossil	Ind
Tipper	6	1	Bias-modeled	Ind
Valentine et al.	4	1	Bias-combo	Ind
Vermeij	3	3	Bias-fossil	Ind
Vermeij et al.	6	3	Process-biological	Ind
Walker & Alberstadt	1	3	Bias-fossil	Ind
Walker & Parker	2	3	Bias-fossil	Ind
Ward	7	1	Structure	Inc
Ward	6	3	Structure	Ind
Ward & Signor	9	2	Bias-fossil	Inc
Ward et al.	3	4	Structure	Inc
Watkins & Hurst	3	2	Bias-fossil	Ind
Weaver & Chamberlain	2	1	Structure	Pri
Webb	2	3	Bias-fossil	Ind
Weber et al.	1	2	Process-chemical	Inc
Weiner	6	1	Process-chemical	Ind
Weiner et al.	5	2	Process-chemical	Ind
Westbroek et al.	5	2	Process-chemical	Ind
Westerbroek	9	2	Process-combo	Ind
Westermann & Ward	6	1	Structure	Inc
Wise & Schopf	7	3	Bias-fossil	Ind
Wolff	1	2	Bias-fossil	Pri
Wolff	7	2	General review	Pri