11

Evolution of the Fossil Record: Thickness Trends in Marine Skeletal Accumulations and Their Implications

SUSAN M. KIDWELL and PATRICK J. BRENCHLEY

The last two centuries of paleontological research have revealed extensive evolutionary changes in the composition of marine life. Major taxonomic groups have waxed and waned, sometimes to complete extinction, groups have shifted in their bathymetric and geographic distributions, and new lifestyles and biotic interactions have appeared. It is thus reasonable to ask whether patterns of fossil preservation have also changed, since organisms are important agents of postmortem destruction as well as objects of potential fossilization. Assessing such change is important because the quality of the fossil record is the ultimate arbiter of what can and cannot be inferred about biological processes and evolutionary relationships over geological time scales.

This chapter considers whether the taphonomic (i.e., preservational) quality of the shelly marine record has in fact changed over the Phanerozoic. We summarize and elaborate upon trends in bioclastic concentrations from Ordovician-Silurian, Jurassic, and Neogene strata first reported in Kidwell (1990) and Kidwell and Brenchley (1994), particularly the problems of (1) extracting meaningful characterizations of taphonomic features for past geological periods, given the tremendous variation among taxonomic groups and environments in the Recent and potential bias from sampling methods, (2) identifying driving mechanisms, and (3) assessing the consequences of changes in preservation for the quality of paleontological data. Our database, containing several hundred field observations supplemented by a literature survey and now including the microstructural composition of bioclasts, reveals significant expansion over the Phanerozoic in the physical scale and composition of noncrinoidal skeletal concentrations, and suggests that this expansion was driven by evolutionary and ecological changes among hardpart producers (that is, the supply side of the taphonomic equation) rather than by geological and biological "evolution" of postmortem conditions. An increase in hardpart durability, presumably driven by escalation, has evidently been one of the primary factors in this trend, as has increasing occupation of high-energy habitats favoring winnowing and physical concentration. Increased durability suggests greater potential for time averaging, and thus younger skeletal assemblages may provide poorer temporal resolution than their Paleozoic counterparts.

In: D Jablonski, D.H. Erwin, and J.H. Lipps, eds., Evolutionary Paleobiology. University of Chicago Press, p. 290-336 (1996)

Changing Patterns of Preservation?

Organisms as Hardpart Destroyers and Modifiers

There are many reasons to suspect that basic taphonomic budgets, and thus patterns of skeletal preservation, have changed over the Phanerozoic. Dramatic evolution among organisms that destroy or facilitate destruction of mineralized hardparts was an important part of the Mesozoic marine revolution (Vermeij 1977). Predators with structures specialized for shell crushing first appeared in the Early Devonian, and by the Late Devonian had attained a diversity plateau of about twelve families, which persisted through the Paleozoic (Signor and Brett 1984; Vermeij 1987; fig. 11.1a). Lungfishes, placoderms, and chondrichthyans were apparently the major durophagous predators at this time; contemporaneous cephalopods and arthropods exhibit few clear-cut morphological adaptations for durophagy. Shell crushers, shell breakers, and shell drillers diversified rapidly in the Mesozoic and Cenozoic. After the end-Permian extinction, durophagous morphologies appeared in cephalopods, placodont and ichthyosaur reptiles, and various actinopterygian fishes. By the Jurassic many groups that today contain molluscivores had either appeared for the first time or diversified rapidly, although not all had attained their specialized morphologies at the outset (asteroids, various gastropods, decapod crustaceans, stomatopod crustaceans, rays, skates, acanthopterygian bony fishes). New families of molluscivores appeared throughout the Cenozoic, especially among fishes, marine mammals, and shorebirds.

Borers and raspers of hard substrata were present throughout the Phanerozoic, as shown by traces in reefs (Vogel 1993), shells (Wignall and Simms 1990), and hardgrounds and other inorganic substrata (Palmer 1982), but the number of participating groups has increased over time (fig. 11.1b). Also, information on types of excavation (simple pits versus elaborately galleried systems; borehole diameters), levels of damage per hardpart, and percentage of infested hardparts per fossil assemblage suggest that some clades of bioeroders have become more effective destroyers over time, and these same groups are characterized by rapid rates of carbonate destruction today (Vogel 1993).

Several lines of evidence indicate that the depth and intensity of bioturbation have increased over the Phanerozoic, implying an increase in sediment irrigation with aerated seawater and thus a potential increase in acidification of porewaters. (Irrigation leads to acid production by promoting aerobic microbial decomposition of organic materials and by oxidizing reduced compounds produced in pockets of anaerobic microbial decay). Calibrating past bioturbation is difficult for several reasons: many organisms extend their burrows upward as the seafloor aggrades, so that the total preserved length of an individual burrow may be much greater than that occupied at any time; spacing of burrows (ichnofabric) is a complex function of sediment aggradation rate, abundance of burrowing individuals, and infaunal lifestyle (sessile versus mobile infauna; rate of sediment processing); infaunal activity decreases from shallow to deep water, thus requiring

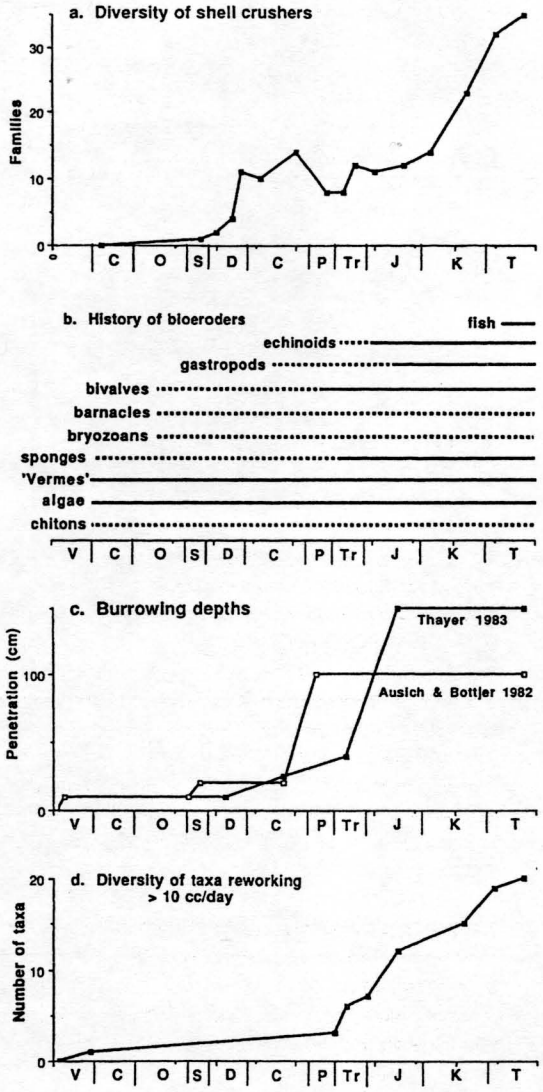

Fig. 11.1. The evolutionary history of taphonomic agents and processes of hardpart destruction, suggesting increasingly difficult postmortem conditions over geological time. In *b*, dashed lines indicate groups present, and solid lines indicate groups that have become highly effective. (*a*, data from Vermeij 1987; *b*, data from Vogel 1993; Wignall and Simms 1990; *c*, data from Thayer 1983 and Ausich and Bottjer 1982; *d*, data from Thayer 1983.)

an independent gauge of water depth; many important modern burrowers lack hardparts and thus have poor preservation potential as body fossils, making it difficult to extrapolate modern reworking rates into the past using phylogeny (Frey and Seilacher 1980; Sepkoski, Bambach, and Droser 1991; Miller and Byers 1984). Nonetheless, the consensus based on burrows observed in the fossil record is that the "average maximum" penetration depth of burrows was only 10–20 cm in Paleozoic rocks, but increased sharply to 100–150 cm in Permian to early Jurassic times (Frey and Seilacher 1980; Ausich and Bottjer 1982; Larson and Rhoads 1983; Brandt 1986; Droser and Bottjer 1989; Sepkoski, Bambach, and Droser 1991) (fig. 11.1c). A similar pattern emerges if one assumes on functional morphological grounds that ancestral members of modern groups (families, superfamilies, orders) had burrowing depths and activity rates similar to those of extant descendants (Thayer 1983) (figs. 11.1c and 11.1d). If bioturbation has increased over the Phanerozoic, then the potential for acidification should also have increased even if rates of organic supply per habitat remained constant (because available organics and reduced sulfides are more likely to be completely recycled when oxygen supply is increased); if rates of organic supply have increased over geological time, for example, due to increasing productivity, then we might expect a more pronounced increase in the global production of acid and thus the potential rate of shell carbonate destruction over time.

Bioturbators, especially conveyor-belt feeders such as callianassid shrimp, can also have a salutary effect on bioclast preservation by concentrating shells at the base of the burrowed zone (Rhoads and Stanley 1965; Meldahl 1987), thus reducing their vulnerability to burial-exhumation cycles and to porewaters with the greatest potential acidity. Combined with physical reworking by storms and other erosive processes, biogenic sorting of bioclasts can occur in both intertidal (Rhoads and Stanley 1965; Meldahl 1987) and subtidal settings (Wanless, Tedesco, and Tyrrell 1987) and has presumably increased in importance over the course of the Phanerozoic, for example, with the expansion of *Ophiomorpha*- and *Thalassinoides*-type burrows (Droser and Bottjer 1993; fig. 11.1c).

Organisms as Hardpart Producers

The diversity of marine metazoans with mineralized hardparts has increased dramatically over the Phanerozoic, and the taxonomic composition of these producers has shifted with the evolutionary waxing and waning of major groups: whereas trilobites, inarticulate brachiopods, and primitive mollusks were the most diverse hardpart producers in the Cambrian, these were soon exceeded by articulate brachiopods, crinoids, trepostome bryozoans, and cephalopods in the Ordovician and later Paleozoic, which were in turn progressively overtaken in diversity dominance by a "Modern" fauna of gastropods, bivalves, echinoids, cheilostome bryozoans, decapods, and bony fishes, which attained maximum diversities in the Mesozoic and Cenozoic (data in Sepkoski 1981; results not significantly changed in Sepkoski 1993 and Benton 1994) (fig. 11.2a). Important

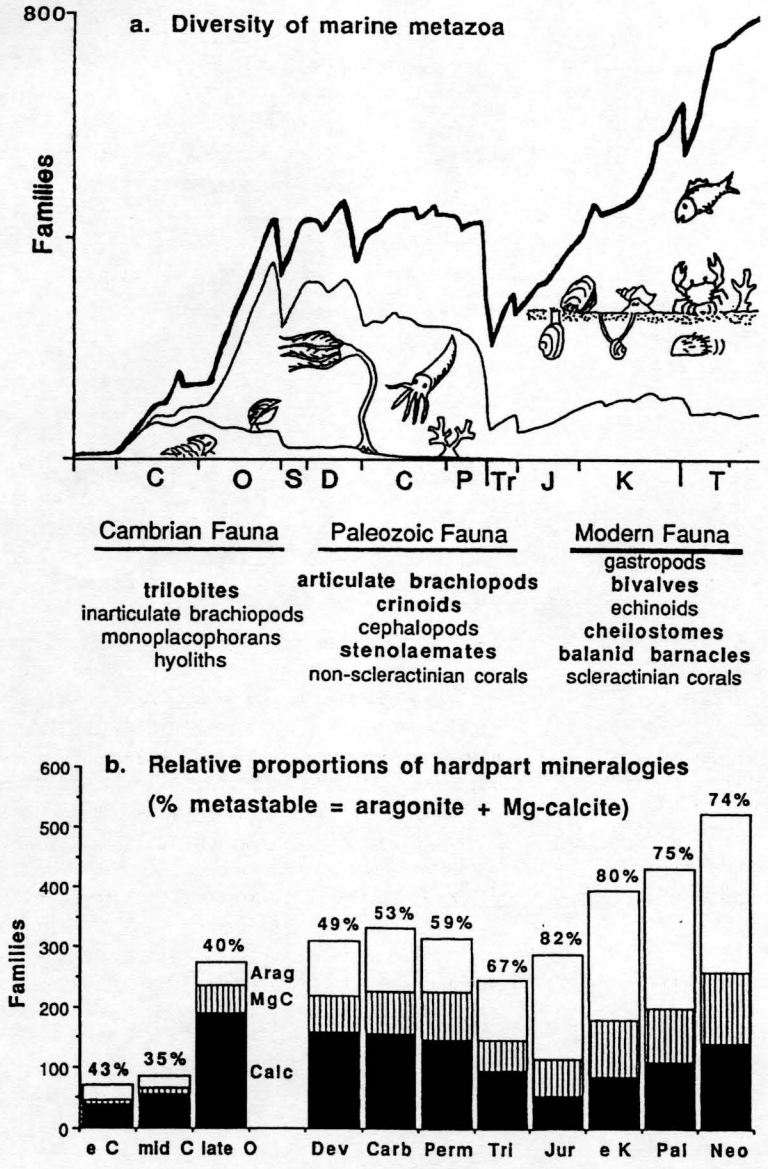

Fig. 11.2. The evolutionary history of hardpart producers, indicating changes in the composition of hardparts over time. *(a)* Diversity history of marine metazoan families; the most important bioclast producers are shown in boldface. *(b)* Increasing number and proportional diversity of families producing diagenetically metastable minerals (aragonite and high-magnesian calcite). (*a* after Sepkoski 1981; *b*, see text for sources.)

nonmetazoan producers of large (> 2 mm) mineralized hardparts include fusulinid foraminifera in the late Paleozoic and orbitolinid and nummulitid foraminifera and coralline algae in the post-Paleozoic (Benton 1993).

These taxonomic changes have been accompanied by an increase in the number of groups that form hardparts of aragonite and high-magnesian calcite, which are diagenetically more reactive minerals than low-magnesian calcite (Walter and Morse 1984; Dickson 1995). This shift should mitigate against shell preservation and accumulation. By our accounting based on diversity, the proportion of groups forming these metastable mineralogies increased from about 40% of the major groups present in the early Paleozoic to about 75% in the late Mesozoic and Cenozoic (based on diversity data for mollusks, brachiopods, bryozoans, echinoderms, corals, and arthropods from Sepkoski 1981; fig. 11.2b). Although many groups secrete a variety of accessory minerals, we tabulated all mollusks and scleractinian corals as aragonitic (fewer than 10% of molluscan families produce shells with significant calcite: e.g., belemnites (rostra), some "archaeogastropods," and scattered families in the Bivalvia produce low-Mg calcite). High-Mg calcite producers in this tabulation include all echinoderms and malacostracan arthropods, and low-Mg calcite producers include articulate brachiopods, all bryozoans, trilobites, ostracods, barnacles, and nonscleractinian corals.

Taxonomic diversity, although easily measured, is not necessarily the best estimate of changes in bulk composition of shelly material: taxa differ in numerical abundance of individuals, in skeletal mass, and in population size and turnover, all of which influence hardpart production and thus raw input to the fossil record. Van de Poel and Schlager (1994) quantified skeletal mineralogy in Mesozoic and Cenozoic carbonate platforms using published relative abundance data for benthic taxa, and suggested that metastable aragonites and high-Mg calcites were relatively abundant in Late Triassic and Jurassic time, decreased to a minimum in the Late Cretaceous, and rebounded to and maintained Triassic-Jurassic levels in the Cenozoic (their fig. 3B). These results are difficult to assess because, except for the 19 data points characterizing Recent carbonate platforms, geological periods were characterized using only 1–3 localities each (total N = 24) and were not compared statistically (e.g., whether past relative abundance values fall outside the envelope of variance for Recent platforms or other geological periods).

Although these changes are not always quantifiable, paleontologists have suggested that hardpart producers have changed in other ways over the Phanerozoic, including:

1. An increase in the diversity and burrowing depths of shelled infauna during the Mesozoic (irregular echinoids, predatory gastropods, suspension-feeding siphonate bivalves: Thayer 1983). Such infauna may have enhanced preservation because, upon death in their burrows, they are more protected from taphonomic

processes at the sediment-water interface. On the other hand, some infauna abandon their burrows under environmental stress or when morbid (e.g., some irregular echinoids: Smith 1984; Schäfer 1972), and even those that die in life positions are by definition still within the upper bioturbated part of the sedimentary column.

2. A sharp decrease in the diversity and ecological importance of nektonic hardpart producers (cephalopods) from the Mesozoic to the Cenozoic, thus reducing hardpart fallout in a range of environments (cf. Sepkoski 1981).

3. A shift among hardpart producers in the range of habitats occupied or in their abundance in various habitats, and thus the spectrum of physical environmental conditions faced by their hardparts. Well-documented shifts in habitat occupation or abundance include the offshore expansion of Paleozoic bivalves (Miller 1988) and the post-Paleozoic diversification of siphonate bivalves within nearshore shifting sands (Stanley 1968).

4. A probable increase in the robustness of body parts (massiveness, shell thickness) as a response to escalation of predation pressure in the Mesozoic and Cenozoic (e.g., Vermeij 1987; Harper and Skelton 1993).

5. A possible increase in maximum body size among hardpart producers, which should increase preservation potentials. There is almost certainly an increase in body size through the Paleozoic and into the Mesozoic (e.g., Bambach 1993). However, it is not clear that maximum sizes have increased monotonically to the present day: notwithstanding the existence of large species in many Recent groups (especially the bivalves, e.g., *Tridacna,* various scallops, oysters, spondylids, myids, venerids, lucinids), many Paleozoic and Mesozoic large-bodied shelled invertebrates have become extinct (e.g., nautiloids, ammonoids, productid brachiopods, and inoceramid, megalodontid, and rudist bivalves).

6. A possible increase in marine productivity over the Phanerozoic, inferred from the increasing fleshiness and body size of dominant organisms, and attributed to an increase in primary productivity (Bambach 1993). This could increase the total supply of hardparts to marine sediments if trophic resources were apportioned among shelly and nonshelly groups equally.

Changes in Shallow Marine Environments

This biological evolution has proceeded in the context of a dynamic physical world of shifting plates and fluctuating sea levels and climate, and thus "evolutionary paleogeography" alone might cause the quality of the fossil record to vary through geological time. Possible geological factors include:

1. Variation, but an overall decrease, in the area of shallow cratonic seas, as calculated from paleogeographic maps (Ronov 1994; fig. 11.3a).

2. Variation in the composition of lithofacies tracts and in the accommodation of sediment accumulation in shallow marine environments due to first-order (100-million-year duration) cycles in continental flooding; qualitatively, transgressive phases generate more abundant and diverse suites of authigenic and clastic-starved disequilibrial facies on continental margins and interiors, whereas regressive phases commonly lead to clastic-flooded conditions (fig. 11.3b).

3. Shifts in the latitudinal distribution of shallow seas due to continental drift; qualitatively, continents have drifted from primarily equatorial positions in the Cambrian to southern hemispheric in the Ordovician-Silurian, subtropical in the Triassic, equatorial and temperate in the Cretaceous, and northern hemispheric

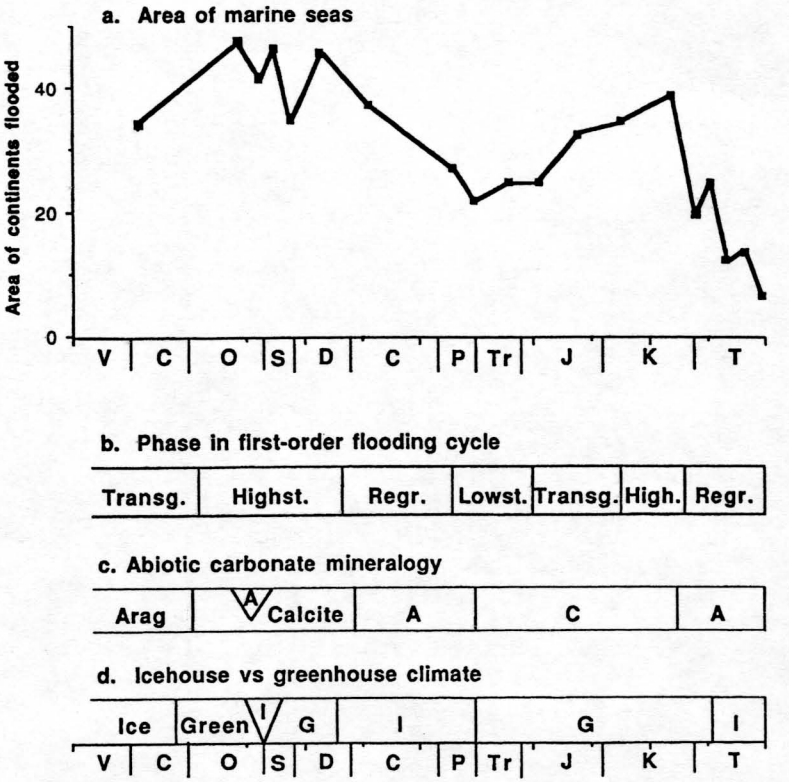

Fig. 11.3. Phanerozoic changes in global paleoenvironments, indicating shifting conditions for hardpart production and preservation independent of biological evolution. *(a)* Area of shallow marine seas, in units of 10^6 km^2. *(b)* Phase in relative sea level cycle, from transgression to highstand to regression to lowstand. *(c)* Alternation in carbonate saturation state of the world's oceans. A = aragonite cements present; C = calcite cements only. *(d)* Alternation in global climate from icehouse to greenhouse conditions. (*a* after Ronov 1994; *b* summarized from Ronov 1994 and Fischer 1984; *c* after Sandberg 1983; Wilkinson and Given 1986; *d* after Fischer 1984.)

in the Quaternary (Tardy, N'kounkou, and Probst 1989; Allison and Briggs 1994).

4. Possible variation in the carbonate saturation state and Mg/Ca ratios of world oceans, as inferred from the relative abundances of abiotic aragonite, calcite, and magnesian calcite (Sandberg 1983; Wilkinson and Given 1986; fig. 11.3c).

5. Variation in global climate and marine anoxia synchronized with (and possibly driven by) 400 my cycles of supercontinent accretion and breakup, which determine the first-order sea level curve (Fischer 1984; Worsley, Nance, and Moody 1986; fig. 11.3d).

The Effects of Cumulative Time

Finally, there are the consequences of elapsed time: the older the rocks, the greater the opportunities for tectonism, diagenesis, and erosion to have obliterated or obscured their fossil content (e.g., Raup 1979).

Net Results: Has Life after Death Become More Difficult?

The net result of these potential factors is difficult to predict because few of these historical trends—much less their interactions—have been sufficiently quantified. Moreover, actualistic studies demonstrate that taphonomic phenomena are highly specific to tissue type and environmental conditions, and that rates of destruction are commonly nonlinear and/or density dependent (e.g., Walter 1985; Cutler 1989). Writing an algorithm for preservation would thus be very difficult even for the Recent, given the current state of knowledge.

A simple listing of trends in these opposing preservational factors yields several contrasting scenarios. For example, increased infaunalization of shelled benthos, possible increases in maximum body sizes and hardpart robustness, possible increases in activity by conveyor-belt bioturbators, and less elapsed time all suggest that the likelihood of hardpart preservation, and thus the quality of the marine fossil record, might be better in younger rocks. On the other hand, there are as many or more reasons to suspect that some aspects of quality may have declined. Trends antagonistic to hardpart preservation include increased durophagous predation, more effective bioeroders, deeper and perhaps more intense bioturbation and irrigation, absolute and proportional increases in metastable mineralogies, and perhaps less shallow marine area. As a third alternative, these opposing factors might all balance out, producing no net trend.

Designing an Empirical Approach

What to Measure?

Given the tangle of taphonomic factors, the most promising strategy would seem to be assessing their net effects empirically in the fossil record. That said, however, it is not clear how to make this a tractable problem, and this may be why evolution in taphonomic quality has been so neglected since Efremov (1940) first raised the issue for the terrestrial vertebrate record.

TABLE 11.1 **Qualities of data of concern to paleontologists, and reasons why the geological record diverges from the biological signal**

		Aspect of quality	Reasons for divergence
Individual		Anatomic completeness	Disarticulation, dissociation, and selective destruction of soft tissues and mineralized hardparts
Assemblage		Spatial resolution	Transport out of life position, life habitat, or biogeographic province
		Temporal resolution	Mixing or time-averaging of noncontemporaneous elements within the sedimentary column
		Ecological fidelity	Selective destruction of species, morphs, and age-classes, affecting presence-absence and relative abundance; bias from exotics and noncontemporaneous elements
	Time series	Stratigraphic completeness	Erosion or nondeposition of sediments for intervals of time, producing gaps in the record
		Stratigraphic bias	Tendency for the deposits of some environments (basin types, eustatic phases) to be underrepresented because their records are initially thin, localized, or readily eroded

Some of the difficulties are logistic: for example, the sheer effort needed to test for any large-scale pattern through the Phanerozoic, even for a single biome. The greater challenge, however, is analytic design. Which aspect(s) of data quality should be tracked—anatomical completeness, spatial resolution, temporal resolution, ecological fidelity, stratigraphic completeness, stratigraphic bias (table 11.1)—and what can be measured in the record to make reliable estimates of these qualities? Can such data be compiled from the literature, to take advantage of many eyes, or can they be derived only from first-hand field experience? Also, in choosing features to measure, how do we maximize our ability to identify driving forces—that is, to isolate the effects of biological evolution from those of changing paleogeography and cumulative geological time—and to distinguish the effects of evolution in hardpart producers from those of hardpart destroyers?

The problem of what to measure is not trivial. Anatomical completeness is relatively straightforward: one might tabulate information on the presence of soft tissues or the degree of hardpart articulation for a particular group or for assemblages from a particular environment through the stratigraphic record (e.g., Greenstein 1992; Allison and Briggs 1994; Butterfield 1995). In contrast, actualistic studies have not yet provided clear guidelines for quantifying other important aspects of quality, such as whether fossils have been moved out of their original life habitat or time-averaged over a particular interval, or whether an observed species or age-class composition is taphonomically rather than ecologically derived. Simple proxies such as frequency of fragmentation or extent of disarticulation that were thought to correlate with distance of transport have proven to be more complicated: disarticulation depends more upon the condition of the carcass at the time of transport than on transport distance (Allison 1986; Kidwell and Baumiller 1990), and is highly sensitive to original morphology (e.g., Alexander 1990; Allison 1990); also, disarticulation and fragmentation can occur entirely within the life habitat, and can be caused by biological agents in low-energy settings as readily as by physical means in high-energy environments. As for temporal resolution, mineralized hardparts do disintegrate over time when exposed at the seafloor, but episodic shallow burial retards the process by protecting hardparts from some of the harshest taphonomic agents, as seen in Driscoll's (1970) elegant experiments. For shallow marine mollusks, short-term burial-exhumation cycles are so variable among individuals that most metrics of hardpart condition (e.g., rounding, boring, encrustation) do not increase monotonically with time since death over periods of time less than 100,000 years (Flessa 1993). The utility of "taphonomic grade" as a clock for time averaging probably varies substantially among nonmolluscan groups, but these have not yet been tested in detail (see papers in Kidwell and Behrensmeyer 1993). Finally, despite progress in establishing the ecological fidelities of death assemblages for major groups in modern environments (e.g., marine and freshwater mollusks, terrestrial mammals, pollen), guidelines for recognizing such bias in fossil assemblages are still nonquantitative, and rely primarily upon recognizing the environment of accumulation rather than on some distinctive taphonomic feature of the assemblage in question (reviewed in Kidwell and Flessa 1995).

A further complication in assessing long-term changes in data quality is that a measurable trend in one aspect of quality does not imply similar changes in other aspects, even within a single biome or taphofacies. For example, organisms preserved with high anatomical completeness in *Fossil-Lagerstätten* (Seilacher, Reif, and Westphal 1985) may be characterized by either high or low spatial resolution (specimens in life positions, versus specimens reoriented but still within the life habitat, versus specimens that are entirely exotic to the depositional site) and by either high or low ecological fidelity (catastrophic mortality focused on a single trophic group or age class rather than all organisms; diagenesis selective for a body size or mineralogy that is linked to particular ecological groups; mass mortality during times of extreme ecological stress, when community composition is unusual) (reviewed by Brett and Seilacher 1991; Whittington and Conway Morris 1985). Temporal resolution is generally thought to be very high for *Lagerstätten,* but can be lower, for example, in catastrophic burials of live infauna within a seafloor containing still-articulated remains from earlier generations (West, Rollins, and Busch 1990) and in fissure faunas (i.e., marine analogues of sinkholes). Also, faunal composition is time-averaged analytically for some *Lagerstätten* by pooling specimens from the entire formation rather than restricting faunal lists to the yield of single bedding planes (e.g., faunal characterizations of classic Solnhofen and Posidonienschiefer deposits). Stratigraphic completeness—that is, gappiness in paleontological time series due to erosion or nondeposition of sedimentary record (Sadler 1981)—and other stratigraphic bias (e.g., low recurrence interval of a specific physical environment) may be critical to the quality of *Lagerstätten* as an index of Phanerozoic diversity, but these factors are clearly independent of the other qualities of individual *Lagerstätten.*

An Approach to the Problem

Given these difficulties, our approach has been to start with a test for broad changes in the basic appearance of the shelly record—that is, changes in physical features that can be measured in outcrops with minimum subjectivity or inference. If such observable features have changed, then taphonomic factors that influence data quality have probably also changed.

Our initial focus has been on the shelliness of shallow marine deposits—the simple abundance of skeletal material—as a signal of change in taphonomic budgets over the Phanerozoic. This attribute is readily measurable in the field, even when hardparts are preserved only as molds; is commonly reported in the geological literature because of the exploration value of bioclastic rocks; and, most importantly, is the net product of all the major terms in the taphonomic equation, on both the production and destruction sides. A net trend might result from any number of underlying patterns and causes of credits and debits, but establishing the net trend should be the first priority and could be a useful guide to future research.

Because unfossiliferous and sparsely shelly sediments occur throughout the stratigraphic record, we focused on the other end of the abundance spectrum—that is, on concentrations of mineralized hardparts, or "shellbeds." A shellbed was defined operationally as a fossiliferous sedimentary deposit that is entirely bioclast-supported, with "bioclast" defined as any biomineralized particle 2 mm or more in maximum length. This size cutoff is arbitrary—bioclasts grade continuously in size from microscopic to meter-scale—but it was chosen, first, to eliminate the need for petrography in the description of basic shellbed characteristics, such as bioclastic fabric and taxonomic composition, and second, for con-

sistency with standard classification schemes for sedimentary rocks (e.g., sand vs. gravel size classes; calcarenitic vs. calciruditic limestones).

Bioclast-supported (= dense packed bioclastic fabric) deposits were defined as those in which bioclasts are so densely packed that, were intervening sediment to be removed, the bed would not collapse; this definition excludes reefs and other deposits constructed or bound by mutually attached benthos. Restriction of the analysis to densely packed, coarse bioclastic accumulations effectively focuses the analysis on a relatively narrow range of concentration processes, and on deposits that are heavily collected by paleontologists and that in some instances were distinctive habitats for benthic colonization (i.e., shellgrounds, shellgravels).

Finally, we stress that "shellbed" is shorthand for a densely packed bioclastic deposit; it does not imply that the concentration records a single depositional event as in the strict sedimentologic definition of a bed. In fact, the complex internal stratigraphy of most thick shellbeds indicates that many formed through the accretion or amalgamation of multiple true beds into a single densely packed interval. If bioclast-poor layers are intercalated, then the stratigraphic interval was described not as a single thick shellbed, but as a series of thinner shellbeds—by our operational definition, a shellbed cannot include any subsidiary increments that are not bioclast-supported.

Sediment shelliness varies among environments for many reasons unrelated to evolution (e.g., frequency of physical reworking, supply of allochthonous bioclasts, dilution by nonbiogenic sedimentary grains), so the analysis was restricted to a single suite of environments that we attempted to sample evenly in each geological period. We focused on marine *siliciclastic* records because these deposits can be found in all latitudes and tectonic settings, unlike pure carbonate platforms, and exhibit a wide spectrum of sediment shelliness. Shellbeds from micritic and bioherm-bearing successions ("pure carbonates") were excluded in order to minimize complications from boundstones, which intergrade with purely bioclastic deposits but are fundamentally different in physical behavior (due to the large effective grain size of cemented or encrusted seafloors), and in order to avoid comparing records with radically different diagenetic histories (e.g., the problems of pervasive pressure solution, dolomitization, and other obliterative diagenesis that are common even in very young pure carbonates). Shellbeds having a micritic matrix or interbedded with micritic units within the same facies were thus excluded, as were shelly flanking beds of boundstone reefs (since these might be compromised by boundstone fabrics in part, and because their physical dimensions would be determined in large part by the abilities of reef-building organisms to construct topographic relief on the seafloor at that time, rather than by other taphonomic factors).

Within siliciclastic records, sampled rock units were categorized paleoenvironmentally as coastal (lagoons, intertidal flats, beaches, deltas), shoreface (subtidal above fair-weather wave base), transition zone (between fair-weather and storm wave base), offshore shelf (below storm wave base), or offshore shoal (subtidal areas above fair-weather wave base but detached from the main shoreline), based on inferred geomorphology and tractive water energy. Shelly records were also classified according to the paleolatitude (30° divisions for low, mid- and high latitude) and rock accumulation rate of the basin (a product of tectonic subsidence and sediment aggradation that varies with tectonic setting). Rock accumulation rates were calculated for 1-million-year windows of the stratigraphic record in order to make tectonic categorization more objective and to average out shorter-term variation in sedimentation rate related to transgressive-regressive cycles. Rock accumulation rates ranged over three orders of magnitude: (1) 5–50 m/my (i.e., 10 m/my scale), where records from cratons, forebulges, and basin margins typically fall; (2) 50–500 m/my (100 m/my scale), dominated by foreland basins, relatively young passive margins, and backarc basins; and (3) 500–5,000 m/my (1,000 m/my scale), dominated by rift, strike-slip, and forearc basins. Siliciclastic records were also limited to those for which a full stratigraphic section or series of sections of the basin was available so that the full variety of shellbeds present could be documented, rather than isolated shellbeds of unusual thickness or composition. This protocol was adopted anticipating that records of different ages might differ only in the relative abundances of different kinds of shellbeds, rather than in the total range or abundance of shellbeds. Data are thus displayed as frequency distributions of shellbed attributes (e.g., thickness, taxonomic composition) and compared using the nonparametric Kolmogorov-Smirnov test (Sokal and Rohlf, 1981).

Comparable information was also gathered for beds with only loosely packed bioclasts (matrix-supported, but with bioclasts within a body length of each other). Many deposits reported as extremely shelly turned out on investigation to be only loosely packed or calcarenitic (supporting bioclasts < 2 mm), thus not meeting our operational definition of a shellbed. This parallel data set of loosely packed bioclastic deposits became a means of documenting our investigation of shellbeds reported in the literature or drawn to our attention by colleagues (= "candidate shellbeds") and of establishing when the absence of shellbeds from a stratigraphic unit was real: if a section contained siliciclastic sediments of shallow marine origin, and also contained dispersed or loosely packed bioclasts, then the absence of densely packed shellbeds in that section was interpreted as meaningful.

Each shellbed in a local record was counted as a separate data point, with the exception of shellbeds less than 10 cm thick. In that size class, each data point indicates a different *type* of concentration in a given lithostratigraphic unit; for example, bedding plane pavements of disarticulated corbulid bivalves and small clumps of life-positioned turritellid gastropods in the Calvert Formation were counted as two different types from this stratigraphic unit, and thus as two data points. This strategy was necessary in order to avoid being overwhelmed by the virtually uncountable shelly storm beds, turbidites, burrow fills, and so forth that

characterize some units, and in order to minimize artifacts related to the number of outcrops per stratigraphic unit: thicker shellbeds can usually be identified uniquely and traced confidently between outcrops, whereas very thin ones generally cannot, and are thus prone to double-counting. This procedure provides a highly conservative minimum value for the thinnest size class. Statistical comparisons were performed using both the full frequency distribution and one in which the thinnest size category was omitted (p values are denoted as full or truncated, respectively).

Finally, we focused data collection on three time intervals at key points in the evolutionary history of marine faunas: (1) the Ordovician-Silurian (Ord-Sil), which spans the dramatic early radiation of shelly families and is dominated by the Paleozoic evolutionary fauna; (2) the Neogene, at the opposite end of the Phanerozoic when marine communities were dominated by the Modern evolutionary fauna; and (3) the Jurassic, as a key intermediate period when Paleozoic groups were still a significant part of marine ecosystems (i.e., articulate brachiopods and crinoids), but Modern groups were radiating dramatically. Although the Ord-Sil and the Neogene provide time endpoints and faunal extremes, they both encompass icehouse climates, and the Jurassic avoids the problems of limited marine record that plague the Triassic as well as the maximum greenhouse conditions of the Cretaceous.

Figure 11.4 shows our data coverage by environment, paleolatitude, and geological age (see the appendix of Kidwell and Brenchley 1994 for a listing of stratigraphic units). Some cells in the matrix have proved difficult to sample—high-latitude records are a particular problem in the Neogene, as are coastal environments in the Ord-Sil. We have documented shellbeds from two or more stratigraphic units in each of the filled cells—"stratigraphic units" being mappable, usually formally named, lithostratigraphic members or formations. In some instances, a single unit may span several of our environmental categories (and thus be tallied in multiple cells in figure 11.4), but in many instances stratigraphic units comprise single facies. The Neogene and Ord-Sil data sets are the most robust, because in each we have extensive field experience in a number of basins. Unfortunately, neither of us specializes in the Jurassic, and that database represents two summers of field and library work on records in Great Britain and northern Europe with guidance from local experts (Kidwell 1990). This area drifted over only a few degrees of latitude during the Jurassic (database of Global Paleogeographic Atlas Project, University of Chicago; D. B. Rowley, pers. comm.), but the region nonetheless encompasses a considerable biogeographic range because the boundary between the Tethyan and Boreal provinces swung widely across it, based on the distribution of dasycladalean algae, corals, and Tethyan ammonites (see Kidwell and Brenchley 1994). Jurassic rock units have been categorized using these faunal criteria into biogeographic equivalents of low (all three Tethyan groups present), mid- ("ecotonal"; only corals present), and high paleolatitude (no Tethyan groups present) (fig. 11.4).

	No. of stratigraphic units	Bays, deltas, tidal flats	Shore-face	Transition zone	Offshore shoal	Below storm wavebase
Neogene						
High lat.	2	•	Literature	Literature	•	Literature
Mid-lat.	25	FIELD	FIELD	FIELD	Literature	FIELD
Low lat.	10	FIELD	FIELD	FIELD	FIELD	FIELD
	37					
Jurassic						
Non-Teth.	20	FIELD	FIELD	FIELD	Literature	FIELD
Ecotone	12	Literature	FIELD	FIELD	•	FIELD
Tethyan	14	FIELD	Literature	FIELD	Literature	•
	46					
Ord-Sil						
High lat.	4	•	FIELD	FIELD	•	FIELD
Mid-lat.	11	•	FIELD	FIELD	•	FIELD
Low lat.	19	FIELD	FIELD	FIELD	FIELD	FIELD
	34					

Fig. 11.4. Data coverage for the three study intervals used to assess changes in the thickness of bioclastic concentrations.

Results: An Expansion in Scale and Composition

The first set of analyses targeted shellbed thickness and taxonomic composition, as these are the most readily measured and commonly published features of dense bioclastic deposits. Most importantly, shellbed thickness should bear on the quality of the fossil record. Whereas very thin shellbeds commonly reflect a single, relatively brief, event of concentration and burial, virtually all thick shellbeds (> 50 cm) are the amalgamated or accretionary product of multiple concentration events. During this more complex (and in many instances more prolonged) history of stratigraphic accumulation, individual bioclasts commonly are processed through multiple burial-exhumation cycles (and/or diagenetic cycles), with each cycle presenting additional opportunities for degradation or outright destruction and thus additional opportunities for bias of the original input. This is not to say that all thin shellbeds have simple origins—skeletal lags at unconformities, for example, are typically thin and yet can be taphonomically complex—but rather that few thick shellbeds are *not* complex in origin (e.g., Seilacher 1985; Kidwell 1991). Trends in shellbed thickness thus might reveal something about the durabilities of hardparts to reworking, the rates of hardpart

introduction relative to siliciclastic dilution, or the spectrum of organisms capable of concentrating hardparts.

In the following discussion, we summarize and elaborate upon trends in shellbed thickness first reported in Kidwell (1990) and Kidwell and Brenchley (1994), and present new documentation on the effects of sampling methods and bioclast microstructure on thickness-frequency distributions.

Shellbed Thickness

The data exhibit a significant increase in the maximum thickness of densely packed bioclastic concentrations over time, from predominantly thin shellbeds in the Ordovician-Silurian (87% < 20 cm thick; maximum 65 cm), to a more right-skewed frequency distribution in the Jurassic (64% < 20 cm thick; maximum ~2 m), to a strongly right-skewed distribution in the Neogene (33% < 20 cm thick; maximum > 6 m; all differences significant at $p < .005$; figure 11.5; data excludes encrinites). Although maximum shellbed thickness does increase with sample size (*n*s are 85, 139, and 218 respectively), the histograms are effectively standardized by the number of entries in the thinnest category (shellbeds < 10 cm thick = 43, 46, and 49 respectively), and the statistical significance of the differences is borne out by pairwise tests of both the full and truncated distributions.

Sampling Effects

The robustness of each frequency distribution can be tested (1) by assessing the effect of removing subsets of data from the analysis (jackknifing) and (2) by treating each local record (generally a sedimentary basin) as a replicate sample of that geological interval. Within each data set, jackknifing shows that the frequency distributions do not vary significantly with field versus literature sources of data, tectonic setting, or paleolatitude ($p = .20$ or greater for all comparisons; fig. 11.5). The only effect of paleolatitude is that, proportionally, Ord-Sil and Neogene mid-latitudes yield about twice as many shellbeds per stratigraphic unit as do contemporaneous low and high latitudes; in the Jurassic, low-latitude records have twice the yield of other settings. We wondered whether shellbed *thickness* might vary with tectonic setting because previous work on Neogene records indicated that the relative abundances of shellbed *types* (i.e., single event, composite, condensed hiatal, and lag concentrations: Kidwell 1988; Kidwell 1993) vary, but our tests showed no significant variation in thickness within either Neogene or Ord-Sil distributions. Rock accumulation rates were difficult to calculate for many of the Jurassic records, which accumulated on the dynamic, irregular topography of the young eastern Atlantic margin, so we jackknifed those data along geographic divisions instead. Finally, the tail of each distribution is not produced by data from a single basin (fig. 11.5). However, variation does exist among basins, which serves as a caution against using a single basin to characterize a geological period taphonomically, regardless of how carefully that study is conducted.

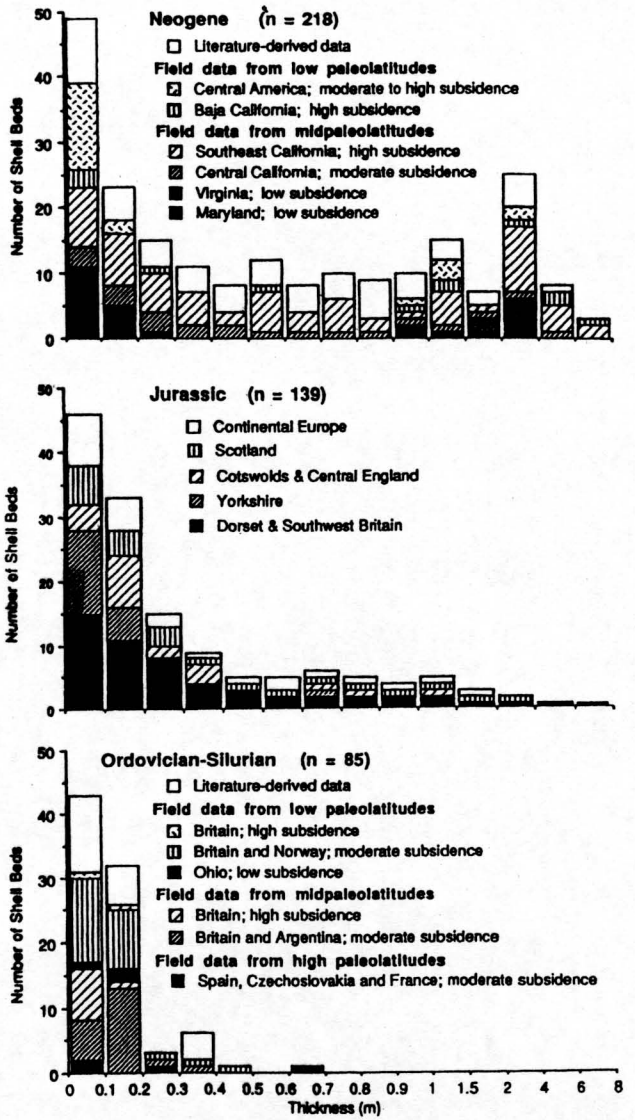

Fig. 11.5. Comparison of thickness-frequency distributions of Ordovician-Silurian, Jurassic, and Neogene shellbeds, showing no effect of data sources and paleogeography within each study interval and significant differences between study intervals. Note change in scale along x-axis in figures 11.5–11.7.

introduction relative to siliciclastic dilution, or the spectrum of organisms capable of concentrating hardparts.

In the following discussion, we summarize and elaborate upon trends in shellbed thickness first reported in Kidwell (1990) and Kidwell and Brenchley (1994), and present new documentation on the effects of sampling methods and bioclast microstructure on thickness-frequency distributions.

Shellbed Thickness

The data exhibit a significant increase in the maximum thickness of densely packed bioclastic concentrations over time, from predominantly thin shellbeds in the Ordovician-Silurian (87% < 20 cm thick; maximum 65 cm), to a more right-skewed frequency distribution in the Jurassic (64% < 20 cm thick; maximum ~2 m), to a strongly right-skewed distribution in the Neogene (33% < 20 cm thick; maximum > 6 m; all differences significant at $p < .005$; figure 11.5; data excludes encrinites). Although maximum shellbed thickness does increase with sample size (*n*s are 85, 139, and 218 respectively), the histograms are effectively standardized by the number of entries in the thinnest category (shellbeds < 10 cm thick = 43, 46, and 49 respectively), and the statistical significance of the differences is borne out by pairwise tests of both the full and truncated distributions.

Sampling Effects

The robustness of each frequency distribution can be tested (1) by assessing the effect of removing subsets of data from the analysis (jackknifing) and (2) by treating each local record (generally a sedimentary basin) as a replicate sample of that geological interval. Within each data set, jackknifing shows that the frequency distributions do not vary significantly with field versus literature sources of data, tectonic setting, or paleolatitude ($p = .20$ or greater for all comparisons; fig. 11.5). The only effect of paleolatitude is that, proportionally, Ord-Sil and Neogene mid-latitudes yield about twice as many shellbeds per stratigraphic unit as do contemporaneous low and high latitudes; in the Jurassic, low-latitude records have twice the yield of other settings. We wondered whether shellbed *thickness* might vary with tectonic setting because previous work on Neogene records indicated that the relative abundances of shellbed *types* (i.e., single event, composite, condensed hiatal, and lag concentrations: Kidwell 1988; Kidwell 1993) vary, but our tests showed no significant variation in thickness within either Neogene or Ord-Sil distributions. Rock accumulation rates were difficult to calculate for many of the Jurassic records, which accumulated on the dynamic, irregular topography of the young eastern Atlantic margin, so we jackknifed those data along geographic divisions instead. Finally, the tail of each distribution is not produced by data from a single basin (fig. 11.5). However, variation does exist among basins, which serves as a caution against using a single basin to characterize a geological period taphonomically, regardless of how carefully that study is conducted.

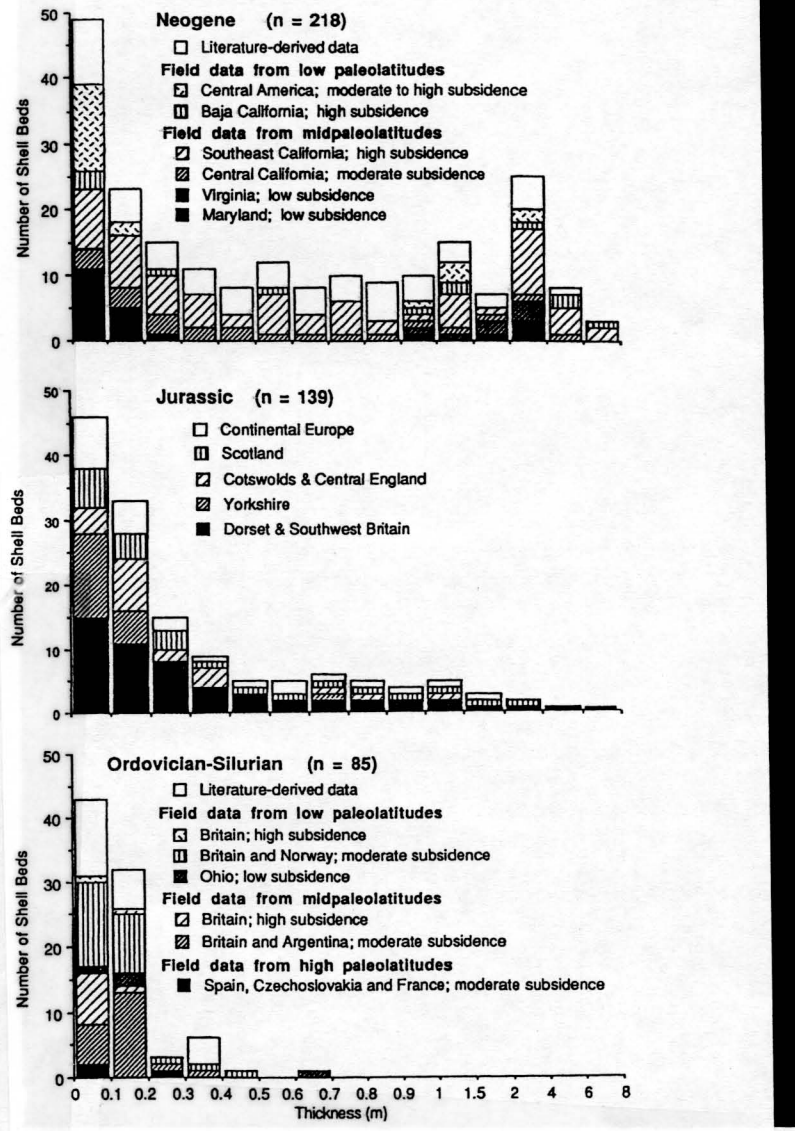

Fig. 11.5. Comparison of thickness-frequency distributions of Ordovician-Silurian, Jurassic, and Neogene shellbeds, showing no effect of data sources and paleogeography within each study interval and significant differences between study intervals. Note change in scale along x-axis in figures 11.5–11.7.

Taxonomic Composition

Shellbeds of different ages vary greatly in taxonomic composition. Mollusks are the most common dominant bioclast in the Neogene data set, but no single group is responsible for thick shellbeds in that time interval (fig. 11.6). Thick shellbeds vary in composition from entirely epifaunal bivalves (mostly monotaxic assemblages of pycnodont or ostreid oysters, pectinids, anomiids, chamids, massive isognomonids) to dominantly infaunal bivalves and gastropods (various monotaxic and polytaxic assemblages of anadarines, glycymerids, astartids, crassatellids, mactrids, venerids, corbulids, turritellids). Cheilostome bryozoans, balanid barnacles, irregular echinoids, hydractinians, solitary and small encrusting colonial corals, and various gastropods are common subsidiary elements. Most of these groups can also dominate thick shellbeds, especially cheilostomes (to 5.4 m: Balson 1990) and balanids (Kamp et al. 1988), but these are not included in the histograms because we lack information on the frequency distribution of any co-occurring, thinner shellbeds. Thin Neogene shellbeds can have virtually any taxonomic composition, but their maximum species richness tends to be lower than that of polytaxic thick shellbeds, which can contain a hundred molluscan species even in temperate settings (e.g., Middle Miocene of Maryland).

The Jurassic data set is also dominated by bivalve shellbeds, and the thickest shellbeds ($\geq$ 50 cm) are dominated by bivalves (fig. 11.6). Thick, virtually monotypic concentrations are formed by free-living gryphaeid oysters *(Praeexogyra, Liostrea, Nanogyra).* Gryphaeid and ostreid oysters are also important bioclastic contributors to polytaxic concentrations containing subequal numbers of other epifaunal (pectinid, entoliid, limid), byssate semi-infaunal (modiolid, pinnid, isognomonid, bakevelliid), and/or infaunal (trigoniid, crassatellid, corbiculid) bivalves. Encrusting serpulids and plicatulacean bivalves, deep-burrowing pleuromyid and pholadomyid bivalves, articulate brachiopods, and regular echinoids are subsidiary elements in these thickest shellbeds. We made a particular effort to find brachiopod shellbeds, but none exceeded a few dm in thickness. Brachiopods, especially terebratulides, are densely packed only in 10–20 cm "nests" and "huddles" in relatively fine-grained matrix, or in small lenticular shellbeds that appear to be slightly reworked nests. Nests can be common within meter-scale stratigraphic intervals (e.g., Marlstone Rock Bed), but such intervals are not densely packed with brachiopods throughout their thickness. Brachiopods, especially rhynchonellids, also occur as subsidiary elements within bivalve concentrations at various scales and in polytaxic shellbeds composed of infaunal and epifaunal bivalves, gastropods, ammonites, belemnites, echinoids, and bryozoans. Lingulids and terebratulides occur in these shellbeds less commonly, and thecideidine brachiopods have been found only in deposits with loosely packed bioclasts. Ammonites, belemnites, and the bivalve *Bositra* are common in monotypic, single-shell-thick pavements, especially in dark shale records. The Jurassic is also one of the youngest geological periods with abundant crinoids, which

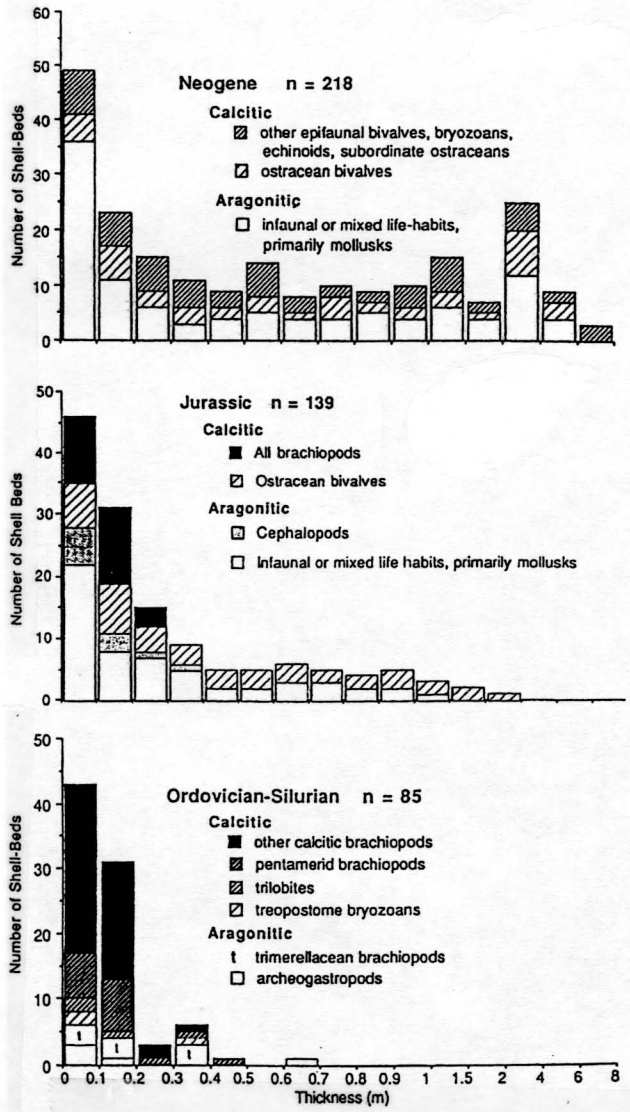

Fig. 11.6. Temporal trend in thickness-frequency distributions, with increasing right-skew through geological time; the tails of the Jurassic and Neogene distributions are not the product of a single hardpart mineralogy, life habit, or taxonomic group.

form encrinites up to 5 m thick within mid-Jurassic turbidites of the Carpathians (e.g., Birkenmajer 1977). The isocrinid ossicles are exclusively sand-sized (< 2 mm), however, and so are not sufficiently coarse to meet the criteria set for shellbeds here.

The Ord-Sil data set is dominated by brachiopod shellbeds (fig. 11.6), particularly those of orthid(e)s, strophomenides, pentamerides, and atrypids. Pentamerides and trimerellaceans also form 1–5 m thick multilayer buildups by repeated, opportunistic colonization of quiet seafloors (e.g., Johnson 1977; Webby and Percival 1983), but on close inspection these accumulations are not homogeneously densely packed. Instead, relatively thin, densely packed shellbeds up to 50 cm thick are separated by equivalent or thicker matrix-supported beds (loosely packed or dispersed bioclasts), so only the thickness of the densely packed bioclastic intervals is qualified for inclusion if we apply the same criteria as for the Jurassic and Neogene data sets: 50 cm is the maximum thickness we have found for entirely densely packed brachiopod bioclasts. Brachiopods also form dense polytaxic shellbeds up to 30 cm thick in combination with rugosan, trepostome, and trilobite bioclasts (e.g., Upper Silurian Aymestrey Limestone, Solvik Fm, and Pentamerus Sandstone, Upper Ordovician Bryn Fm). Trepostomes form dense, nearly monotypic bioclastic concentrations up to about 40 cm thick; thicker bioclastic intervals that we have checked have been only loosely packed (e.g., Upper Ordovician Martinsville Fm) or have been frameworks of some sort (e.g., Cuffey 1985). In general, we have found it difficult to extract reliable information on Paleozoic bryozoans from the literature because authors tend to focus on their reef-forming ability rather than on their bioclastic accumulations. We have found monotypic trilobite shellbeds to be exclusively less than 20 cm thick, whereas "archaeogastropod"-dominated shellbeds quite commonly range up to 40 cm, and an exceptional 65 cm interval of densely packed gastropods forms the outlier in the Ord-Sil data set (embedded within the Upper Ordovician Marble Hill Bed of Swadley 1980).

Encrinites—bioclastic concentrations composed almost exclusively of crinoid ossicles—are common in Ordovician-Silurian rocks and can be several meters thick (commonly 1–3 m, exceptionally up to 10 m) in both siliciclastic (S. M. Holland, pers. comm.) and carbonate platform records (Ausich 1990). Unlike Jurassic isocrinids, early Paleozoic groups produce ossicles of sizes greater than 2 mm, our operational cutoff for bioclasts, and so encrinites represent a potential exception to the frequency distribution of shellbeds formed by other Ord-Sil groups. However, large numbers of small ossicles are produced along with those greater than 2 mm, and as a consequence we have found that Ord-Sil encrinites tend to be either (1) so poorly sorted that the bed was supported by subcritical ossicles—that is, was calcarenitic—or (2) so obscured by syntaxial cementation or recrystallization, or so borderline in grain size, that the original biofabric was impossible to categorize confidently without petrographic analysis, which is impractical at this stage of the investigation. Some of these crinoid-rich deposits (or subsidiary layers within them) may prove to be sufficiently coarse-grained to be categorized as shellbeds; if so, they might shift the Ord-Sil frequency distribution to the right. However, owing to their porous stereom, crinoids have such low effective densities that their hydrodynamic mobility is much greater than that of other bioclasts of the same size (e.g., Cain 1968; Dodd et al. 1995), and so thick encrinites are not necessarily the functional equivalents of other thick shellbeds in the Phanerozoic data set. For all of these reasons, crinoid-dominated concentrations are excluded from the data set pending more work; also excluded are polytaxic concentrations in which crinoid ossicles constitute the matrix for the loosely packed bioclasts of other taxa.

Life Habit

The life habits of hardpart producers are not a significant factor in shellbed thickness; as noted above, thick Neogene and Jurassic shellbeds can be dominated by epifaunal, semi-infaunal, or infaunal taxa, or by a mixture of these habits (fig. 11.6). In addition, some thin shellbeds in the Jurassic are dominated by nektonic shelled cephalopods (ammonites, belemnites). Because fully infaunal *shelly* taxa are rare in the early Paleozoic, this comparison is trivial for the Ord-Sil data set. In all three data sets, suspension-feeding taxa are the overwhelmingly important hardpart producers.

Body Size

Nearly all the thick Ord-Sil brachiopod shellbeds are composed of large shells. Most of the thickest beds contain pentamerids, which are generally longer (*Pentamerus* to 6 cm in our data set) and more biconvex than other groups; other relatively thick shellbeds contain large and biconvex *Kirkidium* (up to 6 cm), *Holorhynchus* (up to 7 cm), and trimerellaceans (rarely), and we have unverified reports of thick shellbeds composed of atrypids (up to 4 cm). Thick concentrations of Ord-Sil bryozoans and gastropods, on the other hand, appear to be independent of body size.

Body size does not appear to play a major role in the thickness-frequency distributions of Jurassic and Neogene shellbeds. Some of the thickest shellbeds in the Neogene and Jurassic data sets are composed of very large bioclasts (for example, multimeter-thick Miocene concentrations of the 15–20 cm long articulated gryphaeid oysters *Pycnodonte heermani* [Imperial Fm] and *P. percrassa* [Calvert Fm]). However, the Neogene data set also includes meter-scale shellbeds composed of very small bioclasts (e.g., subtidal fans of 2–10 mm molluscan debris in subtropical Baja California; cross-bedded units of ≤ 8 mm disarticulated aragonitic bivalves *[Spisula]* in Maryland) and multimeter shellbeds composed of shells comparable in body size to those in Ord-Sil shellbeds (e.g., whole and broken valves from the relatively small-bodied ostreid oyster *Dendostrea vespertina* [3.5 cm; Imperial Fm]). Some of the thickest Jurassic shellbeds are 0.5–2+ m cross-bedded concentrations of the moderately sized

gryphaeid oysters *Preexogyra hebridica, P. accuminata,* and *Nanogrya virgula* (about 3.5 cm).

Multimeter-thick shellbeds of large free-living oysters have been reported from the Jurassic (Seilacher, Matyja, and Wierzbowski 1985), but these are embedded within micritic carbonate platform successions, as are various concentrations of relatively large-bodied nerineacean gastropods.

Thus, although some of the thickest shellbeds from each study interval are composed of bioclasts that are large, or at least large for their geological age, comparably thick shellbeds can also be constructed of much smaller bioclasts. Large body size thus no doubt contributes to the formation of thick shellbeds (and possibly to the Phanerozoic increase in maximum shellbed thickness), but it is neither a guarantee nor a requirement for thick shellbeds of any age.

Hardpart Mineralogy

For each geological interval, the frequency distribution of aragonite-dominated shellbeds is indistinguishable from that of exclusively calcite shellbeds: the tails of the distributions do not depend upon hardparts of a particular mineralogy (fig. 11.6). In Neogene shellbeds, bioclasts were usually unaltered, so mineralogy could be observed directly. The major exceptions were coarse-grained sediments of eastern Pacific records, where the original mineralogy of recrystallized shells and moldic specimens had to be inferred from taxonomy, assuming that extinct Neogene species had the same mineralogy as living congeners. Phylogenetic conservatism at the family level was assumed for Jurassic bioclasts, corroborated and expanded to extinct groups when possible using published surveys (Taylor, Kennedy, and Hall 1969, 1973; Carter 1990a,b). Assignment of mineralogy to Ord-Sil bioclasts used a variety of approaches, including both phylogeny and published petrographic studies. The calcitic composition of trilobites, trepostome bryozoans, and articulate and craniid brachiopods is well accepted; rugosans were probably also calcitic (Wendt 1990). An aragonitic composition has been inferred for trimerellacean brachiopods because they are invariably recrystallized or occur only as molds, even where co-occurring specimens of other, thinner-shelled brachiopods are unaltered calcite (Jaanusson 1966). "Archaeogastropod" shells are bimineralic with a calcitic outer shell layer, including the pleurotomariacean *Loxoplocus* that dominates the outlier shellbed in our Ord-Sil data set. Bivalves are minor contributors to Ord-Sil shellbeds; the major groups at this time were aragonitic or bimineralic (entirely aragonitic nuculoids, modiomorphids, cyrtodontids, lucinaceans; bimineralic pterineids, myalinids; unknown but probably aragonitic or bimineralic cycloconchids, lyrodesmatids: Carter 1990a,b).

Hardpart Microstructure

Although skeletal mineralogy does not vary with shellbed thickness, skeletal microstructure does. Microstructure is known for many living and fossil mollusks and brachiopods (e.g., Taylor, Kennedy, and Hall 1969, 1973; various

TABLE 11.2 Microstructural composition of macroinvertebrate hardparts

Microstructure type[a]	% organics	Major groups
Very high organic		
• Interlaminated organic and mineral layers, usually of high-organic prismatic C	40–50%	Lingulid brachiopods, trilobites, some pinnid bivalves
High organic		
• Nacreous A • Simple prismatic A • Simple prismatic C	0.7–5.3%	nuculoid, mytiloid, pteriacean, modiomorphoid, unionoid, trigonoid, pholadomyacean, most pandoracean, and most poromyacean bivalves; many "archaeogastropods"; ammonoid, nautiloid, and belemnoid cephalopods
• Fibrous C as composes secondary layer in brachiopods	1.5–5%	Punctate, impunctate, and pseudopunctate brachiopods with two-layered shells (craniaceans, orthides, stromphomenides, rhynchonellides, some terebratulides)
Low Organic		
• Homogeneous (granular) A • Composite prismatic A • Cross-lamellar A • Complex cross-lamellar A • Foliated C	0.0–0.6%	Arcoid, pectinacean, anominacean, limacean, ostreacean, many hippuritoid, veneroid, and myoid bivalves; patellid gastropods; all caenogastropods
• Prismatic C as composes tertiary layer in brachiopods	≤ 1%	Pentamerides, spiriferides, some terebratulides
• MgC stereom	< 1%	Echinoderms
Mixed Organic		
• Low-organic A inner layers and high-organic C outer layers		Some hippuritoid bivalves, some "archaeogastropods"

Note: Information on mollusks compiled from Taylor, Kennedy, and Hall 1969, 1973; Taylor and Layman 1972; J. D. Taylor, pers. comm.; Kennedy, Morris, and Taylor 1970; and Carter 1990a,b. Information on brachiopods compiled from Williams 1990; Williams and Rowell 1965[13]; Jope 1965; and Emig 1990.

[a]All microstructures refer to mollusks unless otherwise noted. A, aragonite; C, calcite; MgC, magnesium calcite.

chapters in Carter 1990c; Williams 1990), and can be combined with data on the arrangement and quantity of intercrystalline organic material, which varies over an order of magnitude in each phylum (Jope 1965; Emig 1990; Taylor and Layman 1972) and appears to influence rates of skeletal disintegration (e.g., Kennedy and Hall 1967; Collins 1986; Emig 1990; Glover and Kidwell 1993 and references therein) (table 11.2). We categorized each molluscan family or superfamily as high organic, low organic, or a combination of the two ("mixed"), taking into account that mollusk shells have several layers that may differ both in mineralogy and in organic content (table 11.2; a complete family listing is available on request). The myostracal layer in bivalves was ignored, as this is

volumetrically minor and always high-organic aragonite. The categories for brachiopod microstructures differ from those of mollusks, but are analogous in concept; the interlaminated organic and chitinophosphatic shells of noncraniacean inarticulate brachiopods are labeled as "very high organic" because their organic content was an order of magnitude greater than that in mollusks.

Each shellbed was then categorized according to its taxonomic composition. The only ambiguity involved some terebratulides, which can have an overall high or a low organic composition depending on the development of a low-organic, tertiary prismatic layer (Emig 1990); information on this layer is available for very few species. Trilobites were categorized as very high organic bioclasts, based on their petrographic similarity to chitinophosphatic brachiopods (Williams 1990). Echinodermal hardparts were classed as low organic; each hardpart is porous "monocrystalline" magnesian calcite (Smith 1990).

We found that shellbeds dominated by high or very high organic bioclasts are almost exclusively thin (fig. 11.7). High-organic shellbeds include in situ clusters of mytilid bivalves and pavements of isognomonid or pinnid bivalves in the Neogene (all have nacreoprismatic shells); "nests" of two-layered calcitic terebratulides and pavements of ammonites and modioloid, isognomonid, bakevelliid, posidoniid, and trigoniid bivalves in the Jurassic (all nacreous or nacreoprismatic); and very thin beds of trilobites and lingulids in the Ord-Sil (interlaminated organics and calcite).

High-organic taxa do occur in thicker shellbeds, but only where subordinate to taxa with less organic-rich microstructures. In the Ord-Sil data set, the thickest shellbeds (> 30 cm) contain groups of various compositions—for example, "archaeogastropods" (high-organic nacreoprismatic shells), pentamerids (which include lenses of tertiary low-organic prismatic calcite, and are thus among the least organic-rich Ord-Sil brachiopod groups), mixtures of pentamerids and rugosans (a probable low-organic calcitic group: Wendt 1990), and trepostomes (uncertain organic content). These shellbeds are still thin relative to Jurassic and Neogene "thick" shellbeds.

The sole exceptions to this pattern are relatively thick (50–100 cm), monospecific concentrations of high-organic (nacreoprismatic) isognomonid bivalves in the Neogene (Maryland Miocene) and Jurassic (Portugal; Fürsich 1981). These concentrations are dominated by articulated specimens, however, and so presumably have undergone a minimum of postmortem reworking, reflecting instead repeated gregarious settlement (i.e., a mode of concentration much like that of trimerellacean and pentameride brachiopods, which form some of the thickest Ord-Sil shellbeds). The Miocene examples are embedded within thicker, polytaxic intervals of densely packed shells, and thus are not discrete data points in the histogram; the Jurassic examples are not included because data on co-occurring thin shellbeds are not available.

There is little information available on bryozoan microstructures. Extinct stenolaemates (especially the trepostomes that are most common in our Ord-Sil data set) have few pores in zooid walls, but Williams (1990) indicates that they

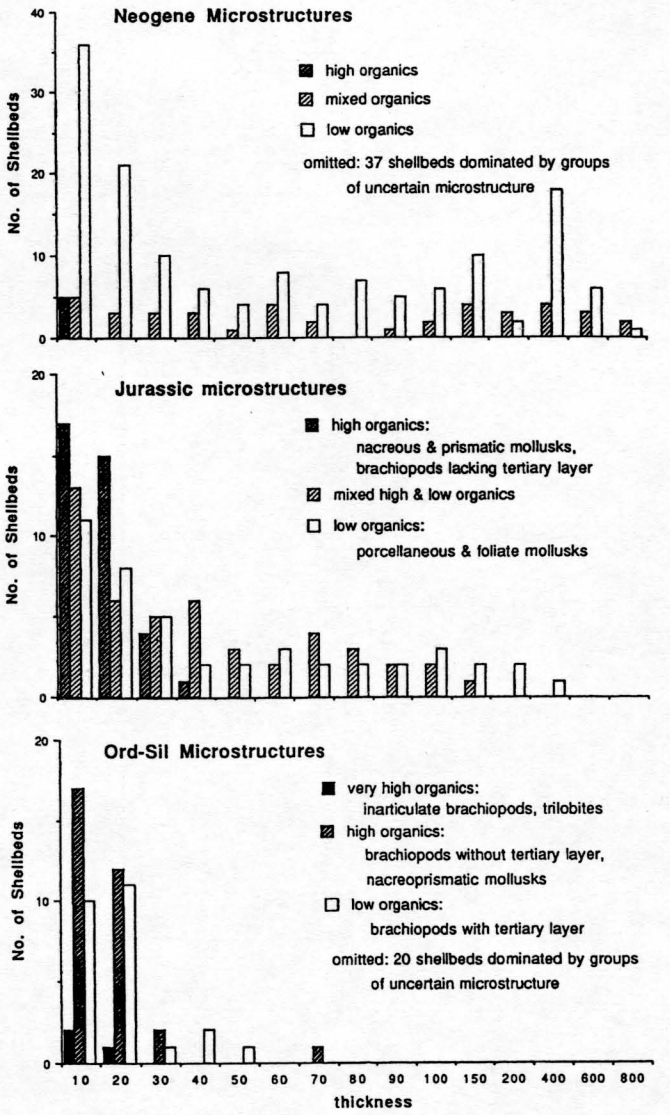

Fig. 11.7. Effect of hardpart microstructure on temporal trends in shellbed thickness. Shellbeds dominated by high or very high organic bioclasts are exclusively thin. (See table 11.2 for categorization of microstructures in terms of organic content.)

are characterized by a substantial secondary layer of laminated calcite analogous in crystallite form and arrangement to high-organic nacreous aragonite ("semi-nacre" of Carter 1990c). In cyclostomes, the only extant order in the class Stenolaemata, these calcite plates may be imbricated into a structure that is more foliate than nacreous (Taylor and Jones 1993; Taylor, Weedon, and Jones 1995), but the organic content is still unknown. The evidence is mixed for cheilostomes, the dominant Cenozoic order. On one hand, they have a low-organic secondary layer of prismatic calcite, which in some groups is supplemented with a tertiary layer of zero-organic prismatic calcite (Williams 1990). On the other hand, (1) thin organic sheets may be interleaved within the secondary layer (Williams 1990), (2) zooid walls tend to be porous, potentially providing access for microbial decomposers with a postmortem effect analogous to that postulated for punctae in brachiopods (cf. Emig 1990), and (3) zooids in series are commonly separated by organic sheets, which permit early postmortem disintegration of unilaminate colonies into single-zooid-wide strips (P. D. Taylor, pers. comm., 1995). The net effect of these features on overall organic content, and how cheilostomes rank relative to stenolaemates, is unclear. If cheilostome colonies are overall high-organic bioclasts, then they represent the major exception to the empirical trend that monotypic concentrations of high-organic bioclasts are exclusively thin. Fortunately for the analysis at hand, our data sets include few bryozoan-dominated shellbeds of any age, and therefore the uncertainties of bryozoan composition have little effect; however, this question must eventually be answered.

Shellbed Abundance

The data sets also suggest an increase in the overall abundance of shellbeds, independent of thickness-frequency distributions, with the average yield of shellbeds per stratigraphic unit being 5.9 in the Neogene and 2.5 in the Jurassic and the Ord-Sil. If the first column in each frequency distribution is excluded (i.e., shellbeds < 10 cm), the values are 4.6, 1.6, and 1.2. Although this abundance metric has its flaws, the results agree with our qualitative impression of the relative ease of finding records with shellbeds: Neogene siliciclastics seem more likely to yield shellbeds than Ord-Sil deposits from similar paleolatitudes and tectonic settings.

The lower than expected yields for the Jurassic may be real, but are more likely an artifact of sampling because this data set is drawn from a more limited number of exposures per lithostratigraphic unit, and often from a single "classic" section.

Discussion: Causal Factors

The data suggest a significant expansion in the thickness and possibly the abundance of densely packed bioclastic deposits over the Phanerozoic. To what extent, however, might this increase in bioclasticity be an artifact of our sampling rather than a real phenomenon? If real, is the pattern largely a by-product of geological factors or a direct consequence of biological evolution? To the extent that biology influences the pattern, which agents or sets of factors are most important? What additional data would allow us to test new hypotheses raised by these questions? What consequences do any of our present conclusions have for the reliability of paleontological data?

Artifact of Sampling?

We believe that our frequency distributions are reliable characterizations of the noncrinoidal bioclastic record in marine siliciclastics. We have made an effort to sample evenly from similar arrays of environments, but even if we failed in this, jackknifing shows that the frequency distributions are robust to tectonic and paleolatitudinal settings as well as to literature versus field sources of information. Moreover, although we have as yet unverified or unincorporated reports of additional shellbeds of all three ages, the thickest candidate shellbeds are still 5–10 m for the Neogene, 1–2 m for the Jurassic, and 1 m or less for the Ord-Sil (excepting encrinites). Additions are thus unlikely to change the pattern significantly. In an independent test of our Ord-Sil pattern, Li and Droser (1995; pers. comm.) found a very similar thickness-frequency distribution for shellbeds in Ordovician strata of the U.S. Great Basin (71% $<$ 20 cm thick, 60 cm maximum thickness), even though echinoderm-dominated shellbeds and deposits with only loosely packed bioclasts were also included.

In the absence of data on encrinites, we can only state that the pattern appears to be robust for the noncrinoidal skeletal record. At most, crinoids appear to be the only significant potential exception to the otherwise thin-bedded Ord-Sil bioclastic record, in contrast to the many groups that compose concentrations 50 cm or thicker in the Neogene. The rolling-stone fabric, low effective density, and monomineralic composition of high-Mg calcitic ossicles also contrasts qualitatively with the more interlocking fabrics, generally higher particle densities, and multimineralic natures of thick Jurassic and Neogene shellbeds. Thus, despite the unfortunate exclusion of encrinites from the analysis at this time, a qualitative difference would probably still hold between Ord-Sil and other shellbeds.

Diagenetic Residue?

One of the most intuitive explanations is that the pattern is simply the consequence of cumulative wear and tear on older fossil records. However, if differences in thickness-frequency distributions were a function of cumulative diagenesis, we would expect underrepresentation of the thinnest shellbeds in the oldest records: the relatively small mass of bioclasts in these should provide the least buffer against dissolution, against erosion before lithification, and against being smeared into oblivion by structural deformation and metamorphism. Instead, we observe the opposite trend, in which it is *thick* shellbeds that are in-

creasingly rare in older records. Because this would require preferential removal of the thickest shellbeds, we reject diagenesis as a significant shaper of frequency distributions. As a counterargument, one might postulate that thick shellbeds, by virtue of having greater lateral extents, might serve as fluid conduits once buried, and thus suffer disproportionate destruction by dissolution. However, interaction with fluids is as likely to enhance preservation as to reduce it, since fluids can lead to bioclast recrystallization or replacement and cementation of matrix (forming molds). Also, many thick shellbeds in our Neogene data set are lenticular rather than tabular bodies, and thus are not necessarily key paths of fluid flow.

Selective dissolution of aragonite is also unlikely to cause the differences in frequency distributions. The Ord-Sil data set is not exclusively calcitic in composition, but includes shellbeds composed of aragonitic and bimineralic bioclasts, and we did not exclude deposits where bioclasts are preserved only as molds. Moreover, if we exclude all aragonite-dominated and mixed mineralogy shellbeds from the Neogene data set, artificially degrading it to the stereotypic condition of early Paleozoic records, the Neogene frequency distribution still differs significantly from that of the Ord-Sil: 55% of Neogene shellbeds 1 m or thicker are composed entirely of calcitic taxa ($p < .001$; see fig. 11.6).

Compaction is another possible explanation for the exclusively thin shellbeds of the older record, but this too seems unlikely. One reason is that burial depth is not correlated with geological age. Shellbeds in the Neogene Imperial Formation of California, for example, are capped by about 5 km of younger strata and thus must have been buried to at least that depth, and several kilometers of burial is common for eastern Pacific records in our Neogene data set. Whereas some of our Ord-Sil successions are from old continental margins and thus have been deeply buried, others are cratonic. Nor is geological age accompanied by a shift in siliciclastic grain size, which is a major control on compaction. Shellbeds—especially thick shellbeds—commonly have a matrix of sandstone, which has low initial porosity (40–50%) and resists compaction. Mudstone is a common matrix among thin shellbeds of all ages and undergoes dramatic compaction within the first 5 km of burial (80%, using empirical formulas in Dickinson et al. 1987). Were we to decompact these mud-matrixed concentrations, they would expand in thickness, but bioclasts would also become less densely packed, possibly moving some out of our operational definition of shellbeds; however, this adjustment would affect the thinnest categories in all three data sets. Therefore, we do not expect that decompaction of shellbed-bearing records would significantly change the qualitative differences between the Ord-Sil and Neogene thickness-frequency distributions. Moreover, although we have not tabulated such data, we have not gotten the impression that compaction features are any more common among bioclasts in Ord-Sil shellbeds than in Neogene shellbeds (e.g., shells with crushed edges or collapsed vaults).

Finally, if the total abundance of skeletal material is a function of diagenesis, we would expect the older record to be poorer, and in fact the Ord-Sil record

does seem to yield fewer shellbeds and to be less shelly overall. However, this same trend might be as readily explained by biological phenomena, such as lower diversity of shelly taxa in the early Paleozoic (which is well known: e.g., Sepkoski 1981 in fig. 11.2a) and lower productivity (which has been suggested on independent grounds: Bambach 1993). Therefore, although we are convinced that the thickness-frequency distributions are not diagenetic in origin, the role of diagenesis in creating apparent changes in shellbed *abundance* remains equivocal.

By-product of "Evolutionary Paleogeography?"

Long-term changes in global paleogeography might drive long-term changes in bioclastic accumulation, but the observed trends are either opposite to those that would be expected or otherwise difficult to rationalize in these terms. For example, of our three study intervals, the area of shallow marine seas was greatest in the Ordovician-Silurian, intermediate in the Jurassic, and lowest in the Neogene (Ronov 1994; fig. 11.3a). The latitudinal distribution of these seas, which varied due to continental drift, shows no monotonic trend that might permit or drive the expansion of bioclastic concentrations, nor does phase in the flooding cycle, global climate ("icehouse" vs. "greenhouse" conditions), or the inferred carbonate saturation state of global oceans (figs. 11.3b, 11.3c, and 11.3d). Both the Ord-Sil and the Jurassic are described as having "calcite seas" of lowered Mg content (Sandberg 1983) and/or elevated pCO_2 (Wilkinson and Given 1986), conditions unfavorable for precipitation and preservation of aragonite, whereas Neogene seas are thought to have been above the "aragonite threshold" (fig. 11.3c). The history of ocean chemistry might help to explain the scarcity of original aragonite preserved within Ord-Sil and Jurassic shellbeds, but we have already documented that shellbeds dominated by aragonite-producing taxa were present in all three study intervals, and that their frequency distributions do not differ significantly from those of contemporaneous calcitic shellbeds. Therefore, the increasing breadth of the frequency distributions over time must be explained in terms of other factors.

Driven by Taphonomic Agents?

The evolutionary intensification of bioerosion, durophagous predation, and perhaps bioirrigation in the marine realm, especially during the Mesozoic (see fig. 11.1), should have increased taphonomic pressures on the survival of individual bioclasts, and thus decreased their likelihood of accumulating into thick concentrations with complex histories of reworking and event amalgamation. Instead, we observe the opposite pattern: an increase in both the numbers and the thickness of shellbeds in the Mesozoic and Cenozoic. Nor do we see evidence that taphonomic agents imposed any ceiling on shellbed thickness at a given time. In the Jurassic, for example, bivalve-dominated shellbeds (some composed exclusively of calcitic epifauna) attain thicknesses of 1–2 m, whereas

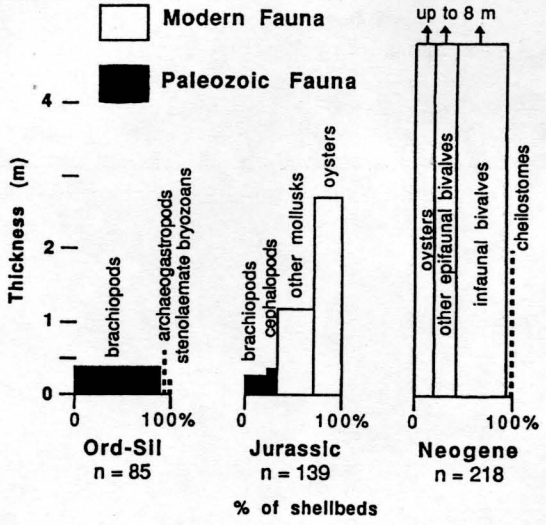

Fig. 11.8. Thickness data replotted (thickness on vertical axis) to illustrate the strong relationship between shellbed thickness and evolutionary affinities of hard part producers. Shellbeds dominated by members of the Paleozoic evolutionary rfauna of Sepkoski (1981) are exclusively thin regardless of geological age (crinoids, rnot plotted here, are the major potential exception). Thick (> 1 m) shellbeds are primarily a phenomenon of members of the Modern evolutionary fauna.

brachiopod shellbeds of the same age and occurring in some of the same lithofacies are exclusively less than 30 cm in thickness (Kidwell 1990) (fig. 11.8).

Conveyor-belt feeders are the only class of taphonomic agent that has an evolutionary trend consistent with increasing shellbed thickness: the intermediate burrowing depths and rates of sediment reworking inferred for the Jurassic by Thayer (1983; see fig. 11.1) might help to explain why the thickest molluscan shellbeds in the Jurassic are thinner than the thickest molluscan shellbeds in the Neogene (this comparison limits variation that might be due to differences in bioclast type and physical environment). Back-extrapolations of reworking rates are highly tenuous, however, and not all specialists believe that Jurassic burrowing depths diverge significantly from those of the Recent (see fig. 11.1). The positive influence of bioturbators on shellbeds is thus tantalizing, but still ambiguous.

Although the evolution of taphonomic agents does not seem to have been a direct driver of shellbed thickness, increased taphonomic intensity might be reflected in bioclast condition within shellbeds (Kidwell and Brenchley, unpublished data). In addition, the evolution of durophagous predation (and possibly of bioerosion) probably did have a strong *indirect* effect on shellbed thickness because many of the skeletal and behavioral attributes acquired in response to

these pressures (e.g., thicker shells and larger body sizes, infaunal life habits, metabolically cheap and thus faster-to-grow low-organic microstructures: Vermeij 1977; Harper and Skelton 1993; Palmer 1983) would also have favored the postmortem persistence and concentration of hardparts. It was in this way—through the evolutionary response of hardpart producers—that the evolution of taphonomic agents has probably most strongly influenced bioclastic accumulation in the shallow marine record (see next section). The increasing "bioclasticity" of the record reflects the history of hardpart producers, not that of hardpart destroyers.

Hardpart Producers Drive Bioclastic Expansion

The role of hardpart producers in the expansion of shellbed thickness is supported not only by the elimination of other geological and biological alternatives (discussed above), but by the relationship between shellbed thickness and taxonomic composition (fig. 11.8). Shellbeds composed of members of the Paleozoic evolutionary fauna are exclusively thin (dm-scale), whereas those dominated by members of the Modern fauna range up to a meter or more in thickness. Thick encrinites are a possible exception, but they are the *sole* potential exception within the Paleozoic fauna, and thus contrast with the diverse taxa within the Modern fauna that are capable of building thick deposits. The control exerted by hardpart producers is particularly clear in the Jurassic record, in which both brachiopods and bivalves were abundant but formed concentrations of significantly different scale. Jurassic remnants of the Paleozoic fauna (brachiopods) continued to produce exclusively thin shellbeds, whereas the diversifying bivalves and other members of the Modern fauna generated significantly thicker accumulations, similar to those seen in the Neogene (the Jurassic brachiopod distribution is significantly different from that of Jurassic bivalves, but not from that of Ord-Sil brachiopods; the Jurassic bivalve distribution is not significantly different from that of Neogene bivalves).

What makes some mineralized taxa so bioclastically proficient? Based on the evidence of our fossil data, the bioclastic disparity between Paleozoic and Modern groups is a function of three morphological/ecological factors. Taxa that form thick shellbeds have at least two of these favorable attributes.

1. Low-Organic Microstructures Increase Hardpart Durability.

A certain degree of durability is necessary for hardparts to survive the processes associated with concentration. It is particularly important in the formation of thick shellbeds, which generally form through repeated burial-exhumation cycles and time averaging. Durability might derive from several different morphological and ecological attributes. We have shown that some features suspected to be important, such as mineralogy and body size, are actually neutral in effect in that aragonitic and small bioclasts can both dominate thick shellbeds.

The compositional feature linked most closely with taxonomic dominance in

thick shellbeds (> 50 cm) is skeletal microstructure and, specifically, organic content (see fig. 11.7), and we believe that this is the Achilles' heel of bioclast durability. Actualistic studies indicate that microstructures with relatively large quantities of organic matrix disintegrate into crystallites relatively rapidly by hydrolysis and microbial degradation (loss occurs under anoxic as well as oxic conditions, and in supersaturated as well as undersaturated waters: Simon and Poulicek 1990; Collins 1986; Emig 1990; Glover and Kidwell 1993; Daley 1993; Heinrich and Wefer 1986); such microstructures characterize the members of the Paleozoic fauna and the Paleozoic-rooted members of the Modern fauna that form exclusively thin shellbeds (fig. 11.8, table 11.2). Organic-lined perforations such as punctae elevate organic content (e.g., 25% wt organics in micropunctate phosphatic shells of disciniscid brachiopods: Jope 1965), further undermining preservation. Groups such as noncraniid inarticulate brachiopods, trilobites, and pinnacean bivalves that interleave protein or chitin with (commonly high-organic) mineral layers have shells with even higher organic contents (35–50% wt: Jope 1965) and faster disintegration rates (e.g., Emig 1990). Unless stabilized diagenetically by mineral precipitation in the voids produced by organic decomposition (= "prefossilization": Gaspard 1989; Moir 1990), these bioclasts have a low likelihood of surviving repeated burial-exhumation cycles and disturbance by bioturbators. High-organic taxa are only subsidiary elements in thick shellbeds (see fig. 11.7) and in shellbeds of any thickness that have complex accumulation histories (Kidwell and Brenchley, unpublished data). Low-organic microstructures, on the other hand, disintegrate more slowly, and they are prevalent among the Modern fauna, especially the more derived clades that form thick shellbeds in the Jurassic and Neogene (fig. 11.8, table 11.2). It is probably not coincidental that crinoids, the potential bioclastic exception to this pattern among the Paleozoic fauna, are composed entirely of low-organic microstructure.

2. Occupation of Higher-Energy Habitats Favors Physical Concentration.

A second ecological change that appears to have represented a breakthrough for the accumulation of thick shellbeds was the evolutionary invasion by shelly fauna of shoreface and shoal habitats, where winnowing of fine matrix and amalgamation of storm event beds is more likely. The inability of pediculate brachiopods and stenolaemate bryozoans to colonize mobile shallow-water seafloors, and the low diversity and abundance of bivalves in these environments in the early Paleozoic (Thayer 1983; Miller 1988), are almost certainly major reasons why shellbeds are thin or absent in Ord-Sil nearshore facies, despite our search (but see unusual encrinite-dwelling spiriferaceans in the Mississippian: Carter 1967). Once again, crinoids are the ecological and potential bioclastic exception to this Paleozoic pattern.

In contrast, a variety of benthic mollusks (e.g., free-living scallops, siphonate

infaunal bivalves, active burrowing gastropods) and infaunal irregular echinoids became well established in these same habitats by the Mesozoic, possibly in response to predation pressure. In addition, colonization of very shallow subtidal and intertidal habitats by oysters and balanomorph barnacles (also in possible response to predation: Vermeij 1987; Harper and Skelton 1993) made their bioclasts especially subject to storm and tidal transport, commonly with redeposition in the nearshore as cross-bedded shellbeds and erosional lags (e.g., Kidwell 1988; Kamp et al. 1988; Kidwell and Brenchley, unpublished data). (Bryozoans have occupied shoalwater habitats since the Ordovician; their most important changes have been shifts in growth habit and perhaps in population growth rates: McKinney 1983, 1993; McKinney and Jackson 1989; Bishop 1989). Nearshore habitats of both high and low energy were simply a much larger source of hardparts in the Neogene than in the Ordovician-Silurian, and this must be a significant element in the bioclastic equation.

3. Has Bioclastic Expansion in the Face of Tougher Taphonomic Conditions Required Higher Productivity?

The increased durability of members of the Modern fauna and their invasion of shallow-water habitats may well explain the long-term increase in shellbed thickness and abundance. However, we wonder whether these changes are sufficient, given that advantageous factors must not only match, but must *exceed,* the increasingly antagonistic effects of taphonomic agents if the record is to become shellier over evolutionary time.

Kidwell (1990) considered gregarious behavior as a possible additional factor, but rejected it as fundamentally neutral in effect: although some gregarious hardpart producers, such as oysters and cheilostomes, produce major shellbeds, others, such as "huddling" rhynchonellids and terebratulids in the Jurassic, do not. On the basis of our larger database, we agree, but note that many of the thickest shellbeds of each age are monospecific or nearly so, which is consistent with gregarious behavior (table 11.3). Gregariousness seems especially important in the formation of the thickest Ord-Sil shellbeds (e.g., trimerellaceans and pentamerids).

High reproductive fecundity is a more probable additional factor (Kidwell 1990) that can be supported by analogy with living groups. For example, Recent bivalves in general, and oysters in particular, have some of the highest fecundities and growth rates among living shelled benthos, far outstripping those of living brachiopods (reviewed by Valentine and Jablonski 1983). In addition, higher metabolic and/or growth rates have been inferred for bivalves than for brachiopods (Rhodes and Thompson 1993) and for cheilostome than for cyclostome bryozoans (McKinney 1993). Although back-extrapolations of such rates are questionable, all of these physiological changes are consistent with higher rates of hardpart production, and thus are possible contributors to a Phanerozoic

TABLE 11.3 **Taxonomic distribution of ecological attributes favorable to highly bioclastic records**

Group	Low-organic microstructure	High-energy habitat	High productivity	Gregarious
COMMON DOMINANTS IN SHELLBEDS ≥ 1 M THICK				
Oysters	√	0	√	Common
Other epifaunal bivalves	√	Some	√	Some
"Modern" infaunal bivalves	√	√	√	Some
Cheilostome bryozoans	0?	√	√?	Some
Balanid barnacles	√	√	√	Common
CAN FORM SHELLBEDS 0.5–1 M THICK				
Crinoids (probable)	√	√	√	Some
"Archaic" bivalves	0	√	√?	Some
Caenogastropods	√	Some	√?	Some
ONLY FORM SHELLBEDS < 0.5 M THICK				
Inarticulate brachiopods	0	Some	0?	0
Brachiopods without layer	0	0	0?	Common
Brachiopods with layer	√	0	0?	Common
Stenolaemate bryozoans	?	√	?	Common
"Archaeogastropods"	0	Some	0?	Some
Shelled cephalopods	0	Nektonic	0?	Some
Echinoids	√	Some	0	Some

Note: Gregariousness appears to have little or no effect, whereas organisms that possess at least two of the remaining three attributes commonly form thick shellbeds.

expansion in shellbeds. Ausich (1990) has similarly attributed the development of thick regional encrinites in Paleozoic and Mesozoic carbonate platforms to the evolutionary waxing and waning of a few crinoid clades characterized by particularly high gregariousness and fecundity.

Our documented trend in shellbed thickness and abundance is also consistent with a broader increase in primary productivity postulated by Bambach (1993). In his view, the expanding bioclasticity of shallow marine (coast and shelf) siliciclastics reflects increasing productivity in just one segment of the complete environmental spectrum, with terrestrial habitats at one end (where land plants began a chain of events leading to increased resources in marine environments) and the deep sea at the other (where phytoplankton have increased in diversity and abundance over time as resources were released farther offshore). Vermeij (1995) suggests that the marine biological revolutions of the early Paleozoic and the Mesozoic, each marked by major ecological innovation and diversification, were linked to tectonic phases of supercontinent breakup that increased nutrient input and thus elevated marine productivity. These arguments are consistent with a mass of circumstantial evidence, including our data on Phanerozoic shellbeds, but will be difficult to test unequivocally until direct proxies for productivity are refined.

Summary and Implications for Paleontological Data: Quantity Is Up and Quality Is Down

Quantity

The shelly record of shallow marine siliciclastic seas thus seems to be one of increasing bioclasticity, shaped largely by the evolutionary ecology of hardpart producers rather than by the evolution of hardpart destroyers or physical environmental conditions. Thick bioclastic concentrations appear to be a fundamentally modern phenomenon, with shellbeds expanding in both thickness and (tentatively) abundance as evolutionarily Modern clades diversified taxonomically and shifted the global biota toward more durable microstructures, occupation of higher-energy habitats, and perhaps higher rates of carbonate production (see table 11.3). This bioclastic trend is not independent of the history of hardpart destroyers, because those organisms contributed to the Mesozoic arms race that drove hardpart producers to invade new habitats and acquire new morphologies. However, the increasing thickness of shellbeds is the more immediate result of the supply side of the taphonomic equation. We can now begin to rank the antagonistic trends introduced at the beginning of this chapter: taphonomic destructiveness has indeed increased over time, but skeletal input and durability have apparently increased even more, leading to a net increase in the shelliness of the fossil record.

These ideas can be further tested by gathering similar data for other geological periods. The few available studies of Cambrian siliciclastics indicate that the Cambrian fauna has a bioclastic potential as limited as that of the Paleozoic fauna. Most Cambrian shellbeds are dominated by or composed exclusively of trilobite debris, and they are overwhelmingly thin, with a maximum thickness of about 50 cm (90% < 20 cm thick in the U.S. Great Basin, including beds with only loosely packed bioclasts: Li and Droser, in press; and see Westrop 1986; Liddell et al. 1995; appendices in Kidwell 1991).

We expect the envelope of shellbed thickness and abundance to increase from the Ordovician-Silurian through the rest of the Paleozoic, essentially tracking the shifting relative diversities of the Paleozoic and Modern faunas (see fig. 11.2a). A characterization of late Paleozoic shellbeds would be extremely interesting; we have the impression that Permo-Carboniferous records have a more Jurassic aspect bioclastically. The Permo-Triassic extinction was a major taxonomic bottleneck for the Modern fauna and especially the Paleozoic fauna, and to our eyes marine Triassic records have a very early Paleozoic look to them. Shellbeds appear to have rebounded through the rest of the Mesozoic, probably attaining fully modern (i.e., Neogene) diversity levels by the Eocene at least. Based on our own observations and discussions with other paleontologists, we believe that the same basic patterns also pertain to nonreefal shellbeds (that is, calcirudites) in pure carbonate records, although this should be tested rigorously.

It is not possible at this point to tease apart the relative importance of microstructure, habitat, and hardpart productivity in generating the observed pattern, but this might be accomplished by tracking the bioclastic history of a few major hardpart-producing groups in greater detail and by determining more closely the timing of bioclastic expansion in relation to the acquisition of taphonomically important attributes.

Quality

The increase in the durability of bioclasts over time, inferred from the expansion in shellbed thickness, suggests that skeletal assemblages from the younger fossil record are more time-averaged than those from the older fossil record (excepting perhaps crinoid-rich deposits): the more durable the hardparts, the greater the probability that hardparts from successive generations and/or communities at a site will be mixed into a single fossil assemblage. Kidwell (1990) noted evidence supporting this view, including (1) the relatively fresh appearance of brachiopods in early Paleozoic assemblages compared with the highly uneven preservation seen among mollusks within time-averaged Neogene analogues (indicating that brachiopods may have disintegrated into crystallites faster than they accrued postmortem surface damage; exceptionally worn specimens are either exceptionally robust or composed of low-organic microstructures: e.g., Seilacher 1968; Holland 1988), and (2) field observations and experiments (Collins 1986; Daley 1993) suggesting that some Recent brachiopod shells do soften and disintegrate within months after death. We do not yet have sufficient data to test for differences in taphonomic grade, but we can document an increase in the diversity of bioclast sorting that is consistent with increased hardpart durability (Kidwell and Brenchley, unpublished data); and, as discussed above, recent experiments have shown that intercrystalline organics are a major factor in shell disintegration. A decrease in the temporal resolution of fossil assemblages toward the Recent has also been suggested on sedimentologic rather than taphonomic grounds, based on increased bioturbation and decreasing frequency of discrete storm beds (e.g., Brandt 1986).

The likely discrepancies between Ord-Sil and Neogene scales of time averaging are difficult to quantify, but we would estimate an order-of-magnitude difference. There have always been snapshot, census assemblages formed by sudden burial or other catastrophic events, but the scope for time averaging appears to have expanded significantly. Insights from stratigraphic context, compositional differences between modern life and death assemblages, and, more directly, radiocarbon dating and amino acid racemization indicate that time averaging in modern molluscan death assemblages is on the order of at least hundreds and commonly thousands of years in ordinary aggradational coastal environments, 5,000–20,000 years in condensed transgressive deposits of the open shelf, and about 100,000 years in erosional transgressive lags, in which shells from the preceding regression are reworked into sands of the succeeding

transgression (Kidwell and Bosence 1991; Flessa 1993; Wehmiller, York, and Bart 1995). Comparable information is urgently needed for modern brachiopods, but without stabilizing prefossilization (cement precipitation in intercrystalline voids), many brachiopods are unlikely to retain sufficient integrity to survive storm reworking or biological bulldozing in the same manner as low-organic molluscan materials after a few months of microbial attack.

This hypothesis might also be tested by a stratigraphic search for taphonomic differences in shellbeds associated with discontinuity surfaces of similar hiatal duration but different geological age. Kidwell (1990) suggested that hiatal concentrations in Paleozoic records should be thinner, less likely to develop, and less likely to show as much taphonomic variation between long and short hiatuses than post-Paleozoic analogues. Although we have abundant information on these relationships in the Neogene (Kidwell 1993), more data are needed on the sequence stratigraphic context of Jurassic and Ord-Sil shellbeds to test the hypothesis rigorously. What we have seen so far is consistent with the expected pattern (e.g., Kidwell 1990, 1991; Brett and Baird 1993), with modern-looking encrinites again providing the exception to the Paleozoic pattern.

We wonder whether fossil assemblages dominated by members of the Modern fauna might also suffer from greater bias in ecological fidelity. Based on actualistic studies of Recent mollusks, we expect preferential destruction of (1) small individuals within a given species (ontogenetically young specimens: cf. Cummins et al. 1986), (2) species dominated by high-organic microstructures, and (3) small-bodied species within a given microstructural type. If Modern communities of hardpart-producing organisms are microstructurally more heterogeneous than early Paleozoic communities—and this impression remains to be tested—then microstructural as well as size factors in differential destruction would come fully into play, and this could lead to more complex patterns of bias in ecological fidelity. On the other hand, comparisons of molluscan life and death assemblages in present-day habitats indicate that taxonomic composition and some aspects of ecological structure are captured by death assemblages despite taxonomic differences in microstructure, body size, and population turnover (Valentine 1989; metanalysis in Kidwell and Bosence 1991; Kidwell, unpublished data; and summarized in part by Kidwell and Flessa 1995). The question of possible long-term trends in the ecological fidelity of the fossil record (*sensu* table 11.1) thus remains unanswered.

The trend of increasing shelliness in the shallow marine macroinvertebrate record—and consequent trends in data quality—need not be paralleled in the records of other taxa and biomes. The frequency of soft-tissue preservation, for example, has evidently declined through the Phanerozoic (Allison and Briggs 1991, 1994; Butterfield 1995), and the quality of the marine microfossil record may have varied as well, owing to cyclic and secular variation in skeletal microstructures and ocean chemistry (Martin 1995). The quality of the terrestrial plant and vertebrate record has probably also changed through time, but this has

yet to be tested. As Behrensmeyer and Hook (1992) point out, the separation of true evolutionary effects from paleogeographically determined patterns of fossilization is difficult. However, the potential for secular change exists in virtually all segments of the fossil record, and we hope that our attempt to explore this possibility in the marine bioclastic record will stimulate others to approach this challenging problem elsewhere.

Acknowledgments

This chapter was written while visiting the Natural History Museum, London, whose staff we thank for generous discussion and access to collections, especially Paul D. Taylor, John D. Taylor, Ellis F. Owen, and Noel J. Morris. We are also grateful to Peter A. Allison, A. Kay Behrensmeyer, David Jablonski, Mary L. Droser, and three additional reviewers for their helpful comments, and to James W. Valentine, whose *Evolutionary Ecology of the Marine Biosphere* has been a long-standing influence. This project, begun in 1988, has been supported by NSF grant EAR 85-52411-PYI (to S. M. K.) and by the Research Development Fund of the University of Liverpool (to P. J. B.).

References

Alexander, R. R. 1990. Disarticulated shells of Late Ordovician brachiopods: Inferences on strength of hinge and valve architecture. *Journal of Paleontology* 64:524–32.

Allison, P. A. 1986. Soft-bodied animals in the fossil record: The role of decay in fragmentation during transport. *Geology* 14:979–81.

———. 1990. Variation in rates of decay and disarticulation of Echinodermata: Implications for the application of actualistic data. *Palaios* 5:432–40.

Allison, P. A., and D. E. G. Briggs. 1991. Taphonomy of nonmineralized tissues. In *Taphonomy: Releasing the data locked in the fossil record,* ed. P. A. Allison and D. E. G. Briggs, 26–70. New York: Plenum Press.

———. 1994. Exceptional fossil record: Distribution of soft-tissue preservation through the Phanerozoic. *Geology* 21:527–30.

Ausich, W. I. 1990. Regional encrinites: How can 5×10^9 m^3 of crinoidal limestone be accumulated? *Geological Society of America Abstracts with Programs* 22:A219.

Ausich, W. I., and D. J. Bottjer. 1982. Tiering in suspension-feeding communities on soft substrata throughout the Phanerozoic. *Science* 216:173–74.

Balson, P. S. 1990. The Neogene of East Anglia: A field excursion report. *Tertiary Research* 11:179–89.

Bambach, R. K. 1993. Seafood through time: Changes in biomass, energetics, and productivity in the marine ecosystem. *Paleobiology* 19:372–97.

Behrensmeyer, A. K., and R. W. Hook. 1992. Paleoenvironmental contexts and taphonomic modes. In *Terrestrial ecosystems through time,* ed. A. K. Behrensmeyer, J. D. Damuth, W. A. DiMichele, R. Potts, H.-D. Sues, and S. L. Wing, 15–136. Chicago: University of Chicago Press.

Benton, M. J., ed. 1993. *The fossil record 2.* London: Chapman and Hall.

Birkenmajer, K. 1977. Jurassic and Cretaceous lithostratigraphic units of the Pieniny Klippen Belt, Carpathians, Poland. *Studia Geologica Polonica* 45: 1–158.

Bishop, J. D. D. 1989. Colony form and the exploitation of spatial refuges by encrusting Bryozoa. *Biological Reviews* 64:197–218.

Brandt, D. S. 1986. Preservation of event beds through time. *Palaios* 1:92–96.

Brett, C. E., and G. C. Baird. 1993. Taphonomic approaches to temporal resolution in stratigraphy: Examples from Paleozoic marine mudrocks. In *Taphonomic Approaches to Time Resolution in Fossil Assemblages,* ed. S. M. Kidwell and A. K. Behrensmeyer, 250–74. Short Courses in Paleontology no. 6. Knoxville, Tenn.: The Paleontological Society.

Brett, C. E. and A. Seilacher. 1991. Fossil Lagerstatten: A taphonomic consequence of event sedimentation. In *Cycles and events in stratigraphy,* ed. G. Einsele, W. Ricken, and A. Seilacher, 283–98. Berlin: Springer-Verlag.

Butterfield, N. J. 1995. Secular distribution of Burgess-Shale-type preservation. *Lethaia* 28:1–13.

Cain, J. D. B. 1968. Aspects of the depositional environment and paleoecology of crinoidal limestones. *Scottish Journal of Geology* 4:191–208.

Carter, J. G. 1990a. Evolutionary significance of shell microstructure in the Palaeotaxodonta, Pteriomorphia, and Isofilibranchia (Bivalvia: Mollusca). In *Skeletal biomineralization: Patterns, processes and evolutionary trends,* vol. 1, ed. J. G. Carter, 136–296. New York: Van Nostrand Reinhold.

———. 1990b. Shell microstructural data for the Bivalvia. In *Skeletal biomineralization: Patterns, processes and evolutionary trends,* vol. 1, ed. J. G. Carter, 297–411. New York: Van Nostrand Reinhold.

———, ed. 1990c. *Skeletal biomineralization: Patterns, processes and evolutionary trends.* Vol. 1. New York: Van Nostrand Reinhold.

Carter, J. L. 1967. An unusual spiriferacean brachiopod from the Barnett Formation (Mississippian) of central Texas. *Journal of Paleontology* 41:587–94.

Collins, M. J. 1986. Post mortality strength loss in shells of the Recent articulate brachiopod *Terebratulina retusa* (L.) from the west coast of Scotland. In Les Brachiopodes fossiles et actuels, ed. P. R. Racheboeuf and C. C. Emig. *Biostratigraphie du Paléozoíque* 4 (1985):209–18.

Cuffey, R. J. 1985. Expanded reef-rock textural classification and the geologic history of bryozoan reefs. *Geology* 13:307–10.

Cummins, H., E. N. Powell, R. J. Stanton, and G. Staff. 1986. The rate of taphonomic loss in modern benthic habitats: How much of the potentially preservable community is preserved? *Palaeogeography, Palaeoclimatology, Palaeoecology* 52:291–320.

Cutler, A. H. 1989. Shells survive—loss, persistence, and accumulation of hard-

parts in shallow marine sediments. *Geological Society of America Abstracts with Programs* 21:A71.

Daley, G. M. 1993. Passive deterioration of shelly material: A study of the Recent eastern Pacific articulate brachiopod *Terebratalia transversa* Sowerby. *Palaios* 8:226–32.

Dickinson, W. R., R. A. Armin, N. Beckvar, T. C. Goodlin, S. U. Janecke, R. A. Mark, R. D. Norris, G. Radel, and A. A. Wortman. 1987. Geohistory analysis of rates of sediment accumulation and subsidence for selected California basins. In *Cenozoic basin development of coastal California,* ed. R. V. Ingersoll and W. G. Ernst, 1–23. Rubey Volume VI. Englewood Cliffs, N.J.: Prentice-Hall.

Dickson, J. A. D. 1995. Paleozoic Mg calcite preserved: Implications for the Carboniferous ocean. *Geology* 23:535–38.

Dodd, J. R., M. Savarese, K. Hagstrom, A. Krist, and K. Nell. 1995. Taphonomic implications of hydrodynamic behavior of crinoid columnals as determined by settling and entrainment experiments with modern specimens and plastic models. *Geological Society of America Abstracts with Programs* 27: A135–36.

Driscoll, E. G. 1970. Selective bivalve shell destruction in marine environments: A field study. *Journal of Sedimentary Petrology* 40:898–905.

Droser, M. L, and D. J. Bottjer. 1989. Ordovician increase in extent and depth of bioturbation: Implications for understanding early Paleozoic ecospace utilization. *Geology* 17:850–52.

———. 1993. Trends and patterns of Phanerozoic ichnofabrics. Annual Review of Earth and Planetary Sciences 21:205–25.

Efremov, J. A. 1940. Taphonomy: New branch of paleontology. *Pan-American Geologist* 74:81–93.

Emig, C. C. 1990. Examples of post-mortality alteration in Recent brachiopod shells and (paleo)ecological consequences. *Marine Biology* 104:233–38.

Fischer, A. G. 1984. The two Phanerozoic supercycles. In *Catastrophes and earth history,* ed. W. A. Berggren and J. A. Van Couvering, 129–50. Princeton, N.J.: Princeton University Press.

Flessa, K. W. 1993. Time-averaging and temporal resolution in Recent marine shelly faunas. In *Taphonomic Approaches to Time Resolution in Fossil Assemblages,* ed. S. M. Kidwell and A. K. Behrensmeyer, 9–33. Short Courses in Paleontology no. 6. Knoxville, Tenn.: The Paleontological Society.

Frey, R. W., and A. Seilacher. 1980. Uniformity in marine invertebrate ichnology. *Lethaia* 13:183–207.

Fürsich, F. T. 1981. Salinity-controlled benthic associations from the Upper Jurassic of Portugal. *Lethaia* 14:203–23.

Gaspard, D. 1989. Quelques aspects de la biodegradation des coquilles de brachiopods: Consequences sur leur fossilisation. *Bulletin de la Société Geologique de France* Ser 8, 5:1207–16.

Glover, C. P., and S. M. Kidwell. 1993. Influence of organic matrix on the post-mortem destruction of molluscan shells. *Journal of Geology* 101:729–47.

Greenstein, B. J. 1992. Taphonomic bias and the evolutionary history of the family Cidaridae (Echinodermata: Echinoidea). *Paleobiology* 18:50–79.

Harper, E. M., and P. W. Skelton. 1993. The Mesozoic marine revolution and epifaunal bivalves. *Scripta Geologica,* Special Issue 2:127–53.

Heinrich, R., and G. Wefer. 1986. Dissolution of biogenic carbonates: Effect of skeletal structure. *Marine Geology* 71:341–62.

Holland, S. M. 1988. Taphonomic effects of sea-floor exposure on an Ordovician brachiopod assemblage. *Palaios* 3:588–97.

Jaanusson, V. 1966. Fossil brachiopods with probably aragonitic shell. *Geologiska Foreningen i Stockholm Forhandlingar* 88:279–81.

Johnson, M. E. 1977. Succession and replacement in the development of Silurian brachiopod populations. *Lethaia* 10:83–93.

Jope, M. 1965. Composition of the brachiopod shell. In *Treatise on invertebrate paleontology,* part H, *Brachiopoda,* ed. R. C. Moore, 156–64. Lawrence, Kans.: Geological Society of America and University of Kansas Press.

Kamp, P. J. J., F. J. Harmsen, C. S. Nelson, and S. F. Boyle. 1988. Barnacle-dominated limestone with giant cross-beds in a non-tropical, tide-swept, Pliocene forearc seaway, Hawke's Bay, New Zealand. *Sedimentary Geology* 60: 173–95.

Kennedy, W. J., and A. Hall. 1967. The influence of organic matter on the preservation of aragonite in fossils. *Proceedings of the Geological Society of London* 1645:325–31.

Kennedy, W. J., N. J. Morris, and J. D. Taylor. 1970. The shell structure, mineralogy, and relationships of the Chamacea (Bivalvia). *Palaeontology* 13: 379–413.

Kidwell, S. M. 1988. Taphonomic comparison of passive and active continental margins: Neogene shellbeds of the Atlantic Coastal Plain and northern Gulf of California. *Palaeogeography, Palaeoclimatology, Palaeoecology* 63: 201–23.

———. 1990. Phanerozoic evolution of macroinvertebrate shell accumulations: Preliminary data from the Jurassic of Britain. In *Paleocommunity temporal dynamics: The long-term development of multispecies assemblies,* ed. W. Miller III, 309–27. Paleontological Society Special Publication no. 5. Knoxville, Tenn.: The Paleontological Society.

———. 1991. The stratigraphy of shell concentrations, In *Taphonomy: Releasing the data locked in the fossil record,* ed. P. A. Allison and D. E. G. Briggs, 211–90. New York: Plenum Press.

———. 1993. Taphonomic expressions of sedimentary hiatuses: Field observations on bioclastic concentrations and sequence anatomy in low, moderate and high subsidence settings. *Geologische Rundschau* 82:189–202.

Kidwell, S. M., and T. Baumiller. 1990. Experimental disintegration of regular

echinoids: Roles of temperature, oxygen, and decay thresholds. *Paleobiology* 16:247–71.

Kidwell, S. M., and A. K. Behrensmeyer, eds. 1993. *Taphonomic approaches to time resolution in fossil assemblages.* Short Courses in Paleontology no. 6. Knoxville, Tenn.: The Paleontological Society. 302 pp.

Kidwell, S. M., and D. W. J. Bosence. 1991. Taphonomy and time-averaging of marine shelly faunas. In *Taphonomy: Releasing the data locked in the fossil record,* ed. P. A. Allison and D. E. G. Briggs, 115–209. New York: Plenum Press.

Kidwell, S. M., and P. J. Brenchley. 1994. Patterns in bioclastic accumulation through the Phanerozoic: Changes in input or in destruction? *Geology* 22: 1139–43.

Kidwell, S. M., and K. W. Flessa. 1995. The quality of the fossil record: Populations, species, and communities. Annual Review of Ecology and Systematics 26:269–99.

Larson, D. W., and D. C. Rhoads. 1983. The evolution of infaunal communities and sedimentary fabrics. In *Biotic interactions in Recent and fossil benthic communities,* ed. M. J. S. Tevesz and P. L. McCall, 627–48. New York: Plenum.

Li, X. and M. L. Droser. 1995. Stop 5: Fossil Mountain, Section K. In M. L. Droser and P. M. Sheehan, Paleoecology of the Ordovician radiation and the Late Ordovician extinction event: Evidence from the Great Basin. In *Ordovician of the Great Basin, Pacific Section,* ed. J. D. Cooper, 88–93. Fullerton, Calif: Society of Economic Paleontologists and Mineralogists.

———. In press. Nature and distribution of Cambrian shell concentrations from the Great Basin (CA, NV, UT). *Palaios.*

Liddell, W. D., E. J. Wright, S. H. Wright, P. A. Allison, and C. E. Brett. 1995. A sequence stratigraphic model for Middle Cambrian trilobite assemblages from the eastern Great Basin. *Geological Society of America Abstracts with Programs* 27:A374.

Martin, R. E. 1995. Cyclic and secular variation in microfossil biomineralization: Clues to the biogeochemical evolution of Phanerozoic oceans. *Global and Planetary Change* 11:1–23.

McKinney, F. K. 1983. Asexual colony multiplication by fragmentation: An important mode of genet longevity in the Carboniferous bryozoan *Archimedes. Paleobiology* 9:35–43.

———. 1993. A faster-paced world?: Contrasts in biovolume and life-process rates in cyclostome (class Stenolaemata) and cheilostome (class Gymnolaemata) bryozoans. *Paleobiology* 19:335–54.

McKinney, F. K., and J. B. C. Jackson. 1989. *Bryozoan evolution.* Chicago: University of Chicago Press.

Meldahl, K. H. 1987. Sedimentology and taphonomic implications of biogenic stratification. *Palaios* 2:350–58.

Miller, A. I. 1988. Spatio-temporal transitions in Paleozoic Bivalvia: An analysis of North American fossil assemblages. *Historical Biology* 1:251–73.

Miller, M. F., and C. W. Byers. 1984. Abundant and diverse early Paleozoic infauna indicated by the stratigraphic record. *Geology* 12:40–43.

Moir, B. G. 1990. Comparative studies of "fresh" and "aged" *Triadacna gigas* shell: Preliminary investigations of a reported technique for pretreatment of tool material. *Journal of Archeological Science* 17:329–45.

Palmer, A. R. 1983. Relative cost of producing skeletal organic matrix versus calcification: Evidence from marine gastropods. *Marine Biology* 75:287–92.

Palmer, T. J. 1982. Cambrian to Cretaceous changes in hardground communities. *Lethaia* 15:309–23.

Raup, D. M. 1979. Biases in the fossil record of species and genera. *Bulletin of the Carnegie Museum of Natural History* 13:85–91.

Rhoads, D. C., and S. E. Stanley. 1965. Biogenic graded bedding. *Journal of Sedimentary Petrology* 35:956–63.

Rhodes, M. C., and R. J. Thompson. 1993. Comparative physiology of suspension-feeding in living brachiopods and bivalves: Evolutionary implications. *Paleobiology* 19:322–34.

Ronov, A. B. 1994. Phanerozoic transgressions and regressions on the continents: A quantitative approach based on areas flooded by the sea and areas of marine and continental deposition. *American Journal of Science* 294: 777–801.

Sadler, P. M. 1981. Sediment accumulation rates and the completeness of stratigraphic sections. *Journal of Geology* 89:569–84.

Sandberg, P. A. 1983. An oscillating trend in Phanerozoic non-skeletal carbonate mineralogy. *Nature* 305:19–22.

Schäfer, W. 1972. *Ecology and palaeoecology of marine environments.* Chicago: University of Chicago Press.

Seilacher, A. 1968. Origin and diagenesis of the Oriskany Sandstone (Lower Devonian, Appalachians) as reflected in its shell fossils. In *Recent developments in carbonate sedimentology in Central Europe,* ed. G. Muller and G. M. Friedman, 175–85. New York: Springer Verlag.

———. 1985. The Jeram Model: Event condensation in a modern intertidal environment. In *Sedimentary and evolutionary cycles,* ed. U. Bayer and A. Seilacher, 336–41. Berlin: Springer-Verlag.

Seilacher, A., B. A. Matyja, and A. Wierzbowski. 1985. Oyster beds: Morphologic response to changing substrate conditions. In *Sedimentary and evolutionary cycles,* ed. U. Bayer and A. Seilacher, 421–35. Berlin: Springer-Verlag.

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. 1981. A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology* 7:36–53.

———. 1993. Ten years in the library: New data confirm paleontological patterns. *Paleobiology* 19:43–51.

Sepkoski, J. J. Jr., R. K. Bambach, and M. L. Droser. 1991. Secular changes in Phanerozoic event bedding and the biological overprint. In *Cycles and events in stratigraphy,* ed. G. Einsele, W. Ricken, and A. Seilacher, 298–312. Berlin: Springer-Verlag.

Signor, P. W. III, and C. E. Brett. 1984. The mid-Paleozoic precursor to the Mesozoic marine revolution. *Paleobiology* 10:229–45.

Simon, A., and M. Poulicek. 1990. Biodegradation anaerobique des structures skeletiques en milieu marin: I. Approche morphologique. *Cahiers de Biologie Marine* 31:95–105.

Smith, A. B. 1984. *Echinoid paleobiology.* London: George Allen & Unwin.

———. 1990. Biomineralization in echinoderms. In *Skeletal biomineralization: Patterns, processes and evolutionary trends,* vol. 1, ed. J. G. Carter, 413–43. New York: Van Nostrand Reinhold.

Sokal, R. R., and F. J. Rohlf. 1981. *Biometry.* 2d ed. San Francisco: W. H. Freeman.

Stanley, S. M. 1968. Post-Paleozoic adaptive radiation of infaunal bivalve molluscs: A consequence of mantle fusion and siphon formation. *Journal of Paleontology* 42:214–29.

Swadley, W. C. 1980. *The Marble Hill Bed: An offshore bar–tidal channel complex in the Upper Ordovician Drakes Formation of Kentucky.* U.S. Geological Survey Professional Paper 1126–D. 18 pp.

Tappan, H. 1982. Extinction or survival: Selectivity and causes of Phanerozoic crises. Geological Society of America Special Publications 190:265–76.

Tardy, Y., R. N'kounkou, and J.-L. Probst. 1989. The global water cycle and continental erosion during Phanerozoic time (570 my). *American Journal of Science* 289:455–83.

Taylor, J. D., W. J. Kennedy, and A. Hall. 1969. The shell structure and mineralogy of the Bivalvia. Introduction. Nuculacea-Trigonacea. *Bulletin of the British Museum (Natural History), Zoology Supplement* 3:1–125.

———. 1973. The shell structure and mineralogy of the Bivalvia. II. Lucinacea-Clavagellacea, Conclusions. *Bulletin of the British Museum (Natural History), Zoology Supplement* 22 (9):253–94.

Taylor, J. D., and M. Layman. 1972. The mechanical properties of bivalve (Mollusca) shell structures. *Paleontology* 15:73–87.

Taylor, P. D., and C. G. Jones. 1993. Skeletal ultrastructure in the cyclostome bryozoan *Hornera. Acta Zoologica* 74:135–43.

Taylor, P. D., M. J. Weedon, and C. G. Jones. 1995. Skeletal ultrastructure in some cyclostome bryozoans of the family Lichenoporidae. *Acta Zoologica* 76:205–16.

Thayer, C. W. 1983. Sediment-mediated biological disturbance and the evolution of marine benthos. In *Biotic interactions in Recent and fossil benthic communities,* ed. M. J. S. Tevesz and P. L. McCall, 479–625. New York: Plenum Press.

Valentine, J. W. 1989. How good was the fossil record? Clues from the Californian Pleistocene. *Paleobiology* 15:83–94.

Valentine, J. W., and D. Jablonski. 1983. Larval adaptations and patterns of brachiopod diversity in space and time. *Evolution* 37:1052–61.

Van de Poel, H. M., and W. Schlager. 1994. Variations in Mesozoic-Cenozoic skeletal carbonate mineralogy. *Geologie en Mijnbouw* 73:31–51.

Vermeij, G. J. 1977. The Mesozoic marine revolution: Evidence from snails, predators and grazers. *Paleobiology* 2:245–58.

———. 1987. *Evolution and escalation: An ecological history of life.* Princeton, N.J.: Princeton University Press.

———. 1995. Economics, volcanoes, and Phanerozoic revolutions. *Paleobiology* 21:125–52.

Vogel, K. 1993. Bioeroders in fossil reefs. *Facies* 28:109–14.

Walter, L. M. 1985. *Relative reactivity of skeletal carbonates during dissolution: Implications for diagenesis.* Society of Economic Paleontologists and Mineralogists Special Publication no. 36:3–16. Tulsa, Okla.: Society of Economic Paleontologists and Mineralogists.

Walter, L. M., and J. W. Morse. 1984. Magnesian calcite stabilities: A re-evaluation. *Geochimica et Cosmochimica Acta* 48:1059–70.

Wanless, H., L. Tedesco, and K. Tyrrell. 1987. Production of subtidal tubular and surficial tempestites by Hurricane Kate, Caicos platform, British West Indies. *Journal of Sedimentary Petrology* 58:739–50.

Webby, B. D., and I. G. Percival. 1983. Ordovician trimerellacean brachiopod shell beds. *Lethaia* 16:215–32.

Wehmiller, J. F., L. L. York, and M. L. Bart. 1995. Amino acid racemization geochronology of reworked Quaternary mollusks on U.S. Atlantic coast beaches: Implications for chronostratigraphy, taphonomy and coastal sediment transport. *Marine Geology* 124:303–37.

Wendt, J. 1990. Corals and coralline sponges. In *Skeletal biomineralization: Patterns, processes and evolutionary trends,* vol. 1, ed. J. G. Carter, 45–66. New York: Van Nostrand Reinhold.

West, R. R., H. B. Rollins, and R. M. Busch. 1990. Taphonomy and an intertidal palimpsest surface: Implications for the fossil record. In *Paleocommunity temporal dynamics: The long-term development of multispecies assemblies,* ed. W. Miller III, 351–69. Paleontological Society Special Publication no. 5. Knoxville, Tenn.: The Paleontological Society.

Westrop, S. R. 1986. Taphonomic versus ecologic controls on taxonomic relative abundance patterns in tempestites. *Lethaia* 19:123–32.

Whittington, H. B., and S. Conway Morris. 1985. Extraordinary fossil biotas:

Their ecological and evolutionary significance. *Philosophical Transactions of the Royal Society of London* B 311:1–192.

Wignall, P. B., and M. J. Simms. 1990. Pseudoplankton. *Palaeontology* 33: 359–78.

Wilkinson, B. H., and R. K. Given. 1986. Secular variation in abiotic marine carbonates: Constraints on Phanerozoic atmospheric carbon dioxide contents and oceanic Mg/Ca ratios. *Journal of Geology* 94:321–33.

Williams, A. 1990. Biomineralization in the Lophophorates. In *Skeletal biomineralization: Patterns, processes and evolutionary trends,* vol. 1, ed. J. G. Carter, 67–82. New York: Van Nostrand Reinhold.

Williams, A., and A. J. Rowell. 1965. Morphology. In *Treatise on invertebrate paleontology,* part H, *Brachiopoda,* ed. R. C. Moore, 57–155. Lawrence, Kans.: Geological Society of America and University of Kansas Press.

Worsley, T. R., R. D. Nance, and J. B. Moody. 1986. Tectonic cycles and the history of the earth's biogeochemical and paleoceanographic record. *Paleoceanography* 1:233–63.