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Cover ilustration: inner cast of *Clypeaster* sp. (MJPV 78 L?) from Tertiary of Spain and *Turritella terebralis* (MPV 75 GF1) from Eocene of France, placed over a spanish mesozoic ammonite (Collection of the Natural Sciences Museum of Valencia, Spain) Photógraphy: Enrique Peñalver

CURRENT TOPICS ON TAPHONOMY AND FOSSILIZATION

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The stratigraphy of skeletal concentrations: Testing for broad-scale trends

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Concentrations of macroscopic skeletal material – whether invertebrate or vertebrate in composition – come in many forms and have diverse origins, ranging from small lenses created by predators to large clinoforms of current-swept debris and thin widespread beds punctuating transgressive-regressive cycles. This array has significance both to paleontologists (as sources of biological and biostratigraphic information) and to sedimentary geologists (e.g., as reservoirs and conduits of fluids). "Bone beds" and "shell lags" also have a long and primarily anecdotal use as marker beds for within-basin correlation and as criteria for unconformities. Moreover, among European geologists, diagenetically and paleontologically complex horizons are well-accepted clues to significant condensation.

To extract full value from such concentrations, however, including understanding their significance in terms of hardpart supply (biological productivity) and hardpart destruction (biogeochemical recycling), we need a more systematic and *quantitative* characterization of their distribution in the stratigraphic record, which will complement ongoing work on their genesis and reliability as archives of biological information. Examples of large-scale issues include:

THEME I

Concerning the most simple, objective aspects of skeletal concentrations that guide fossil prospecting and the exploration of bioclastic facies: How do the abundance (i.e., stratigraphic frequency, raw numbers) and physical scale (dimensions) of skeletal concentrations vary through the stratigraphic record? That is, along environmental gradients within basins, among major depositional systems, along latitu-

dinal/climatic gradients, through various orders of baselevel cycles, among tectonic settings (subsidence regimes), and over the course of evolutionary time? Information on stratigraphic variation in other objective taphonomic attributes—such as levels of disarticulation/fragmentation, biogenic damage, and details of bioclastic fabric and diagenetic state of preservation — would also yield data of value to paleobiologists and sedimentologists.

THEME II

To guide paleobiologic and biostratigraphic exploitation of skeletal concentrations: how fo *styles* of concentrations (e.g., hydraulic versus biogenic, single-event versus multi-event accumulations) vary stratigraphically (same list as above, e.g. along environmental gradients, among major depositional systems, etc). What are the consequences for the quality of (paleo)biological information, such as the biogeochemical fidelity of fossils (e.g., isotopic reliability), anatomical completeness of specimens, spatial and compositional fidelity of assemblages to their original living community, scales of time-averaging per assemblage, and completeness of time-series (including assemblage-to-assemblage homogeneity within those time-series; i.e., are assemblages "isotaphonomic"?).

THEME III

Of concern to evolutionary (paleo)biologists, biostratigraphers and basin-analysts: How consistently are stratigraphically important discontinuity surfaces—flooding surfaces, transgressive ravinements, surfaces of maximum transgression, stranding surfaces and sequence boundaries—mantled by skeletal material? Does the taphonomic nature of mantling skeletal material vary consistently with the nature of the hiatus (inferred duration, environment, magnitude of erosion)? Have such hiatal concentrations and lags changed over evolutionary time—for example, have they become progressively more common or more complex toward the modern world?

We have every reason to suspect that the quality of the record varies stratigraphically. But a quantitative approach is essential because broad-scale stratigraphic variation is more likely to be in degree (changing proportions in kinds of concentrations) rather than in type (shift from all one kind to all of a different kind). Thus, binary (presence/absence) data on various kinds of skeletal concentrations will probably not be sufficient to detect the variation that exists. Identifying and understanding this variation determines our strategies for paleobiologic sampling –how much care will be needed to sample isotaphonomically (i.e., acquire information of comparable taphonomic quality), and is isotaphonomic sampling even possible?

Gathering data on large-scale patterns does not necessarily require building huge, multi-authored databases. As I hope to illustrate in this talk, it is possible to break

the larger problem into smaller modules. However, undertaking such studies does challenge us –individually and as a scientific community— to quantify our methods of description and classification, and consider sampling methods more explicitly, including (a) our operational definitions of skeletal concentrations (or whatever taphonomic attribute we are targetting), (b) what constitutes a sample in stratigraphic analysis, and (c) what constitutes a unbiased and adequate sampling of the record (number and deployment of samples). Here I summarize some thoughts on how to quantify our analysis of the stratigraphic record, based on efforts in a number of different settings but focusing on two major studies as examples (Kidwell & Brenchley 1996; Rogers & Kidwell 2000).

(A) OPERATIONAL DEFINITIONS

This obviously depends on the question, but to detect variation in the stratigraphic record we need to focus on an aspect that is measurable. That said, semi-quantitative (ordinal) scales should be acceptable in many instances. For example, to test for secular trends in densely fossiliferous deposits in the marine macrobenthic record (Theme I above), Pat Brenchley and I defined a skeletal concentration as any deposit of bioclast-supported (densely-packed) sediment, where bioclasts are defined as skeletal particles =2 mm (i.e., coarser than sand; following Kidwell et al. 1986). For the micro/meiofaunal and vertebrate records, the operational definition would require adjustment (e.g., to include sand-sized bioclasts, or to include beds with only loosely-packed bioclasts). A completely different operational definition would be required if the target were Konservat Lagerstatten — e.g., does this require only a high proportion of articulated specimens (>10%?, >50%), or must soft-tissues be present?

For Theme III, the presence of any skeletal material in association with a discontinuity surface is of interest, and thus one might score all categories of skeletal close-packing (e.g., densely packed, loosely packed, dispersed, absent) and add categories for the state of preservation of that material (e.g., a semi-quantitative scale to record the degree of disarticulation-fragmentation-rounding, or the degree of diagenetic modification of skeletal structure and composition). Ray Rogers and I simply scored presence/absence of skeletal material associated with discontinuity surfaces in continental to shallow marine strata in the Campanian (Upper Cretaceous) of Montana. This was sufficient to estimate the frequency of occurrence of discontinuity-mantling deposits as a function of taxonomic group (vertebrate versus molluscan), facies (fluvial, estuarine, shallow marine), and discontinuity type (we developed an ordinal scale of discontinuity types).

Within the marine macrobenthic record, I tend to test for covariation between discontinuity type and the *genetic* type of skeletal concentration [single-event, multi-event composite, multi-event hiatal, and lag types, following Kidwell 1991; I found a close correspondence but on a sliding scale that varies with tectonic setting,

Kidwell 1993a]. Because the single-event/ composite/ etc distinctions imply different spectra of time-averaging in the skeletal assemblage (Fig. 1), this scoring system is also amenable to questions under Theme II above (e.g., how does the magnitude of time-averaging in assemblages vary stratigraphically?). [And see Rogers 1993 for a continental vertebrate example, where the proportions of high-resolution event-assemblages varied significantly from upland to lowland settings.]

(B) WHAT CONSTITUTES A SAMPLE?

To determine the relative abundance of shellbeds of different thicknesses (i.e., the proportions of shellbeds of various thicknesses in the total population of shellbeds), a sample will consist of a measured section: what is the frequency distribution of skeletal concentrations that are intersected by the measured section?

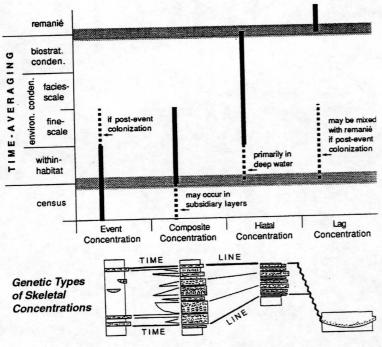


Figure 1. Range of scales of time-averaging expected for fossil assemblages as a function of the genetic type of skeletal concentration (adapted from Kidwell 1993b). Quantifying the relative proportions of these styles of concentration in different parts of the record thus permits those records to be ranked relative to each other in the likely quality of their paleobiologic data.

This is analogous to biological or petrographic sampling along a line-transect, with all those advantages. It is also analogous to quantitative bulk samples, as opposed to "surface picking" of fossils or the accrual of information via long periods of chance observations. The skeletal concentrations encountered in individual sections can eventually be pooled for a total "n" of concentrations. Importantly, however, each measured section is in itself an independent test of the shape of the frequency distribution, and thus an opportunity to reject the null hypothesis (null = no variation).

All of our data for the Phanerozoic shellbeds study (Kidwell & Brenchley 1996) are derived from measured sections, in which every concentration meeting our operational criteria was tallied (Fig. 2). Different formations yielded different total numbers of shellbeds, and qualitatively speaking, we had more difficulty accruing a large total number of shellbeds in the Ordovician-Silurian than in the Jurassic and Neogene records (for similar numbers of fossiliferous lithostratigraphic units examined). This suggests that skeletal concentrations are fundamentally less abundant in older rocks (soft, semi-quantitative result), in addition to having a lower maximum thickness (strong quantitative result; Fig. 2). For many reasons we concluded that this thickness trend was driven by the evolution of hardpart producers (supply side) rather than by other factors, and particularly by an overall evolutionary increase in the inherent durability (and possibly productivity) of hardparts, with the implication that the older record is a taphonomically less complex source of paleobiologic data than the younger record (less time-averaging per bed).

In our test of continental bone and shellbeds (Theme III), Ray Rogers and I also used measured sections as the unit of sampling: what percent of single-story fluvial channels were lagged with skeletal material, what % of such estuarine channels, of multi-story channels, of parasequence-bounding flooding surfaces, etc.? In this way we were able to detect significant previously unrecognized differences in the yield of estuarine versus fluvial channels (numbers of fossiliferous horizons, as well as types) and in the yield of progradational and retrogradational phases of sedimentation. We were also able to quantify the surprisingly the low absolute frequencies of skeletal concentration overall in the famously fossiliferous strata. Using such methods of scoring the quantity and quality of skeletal concentrations, it should be possible to rank different basins on a common taphonomic scale, and thus compare and predict their qualities as archives of paleobiologic data.

(C) UNBIASED & ADEQUATE SAMPLING

None of us believe that the stratigraphic record is taphonomically homogeneous, but rather that the abundances and types of skeletal concentrations—and other taphonomic aspects— vary non-randoml, at least at some scales and along some axes (stratigraphic variables). Thus, for example, in order to identify trends in the physical scale of densely-packed shellbeds, we need to control other possible sources of variation, such as variation as a function of bathymetric zone, depositional setting,

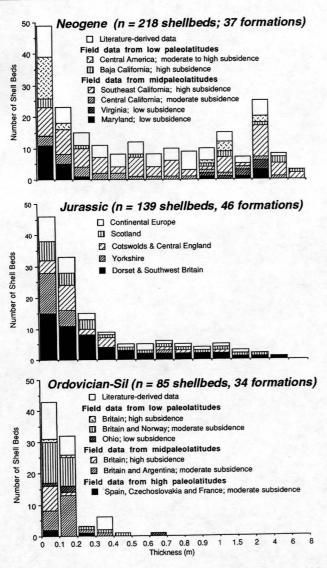


Figure 2. Histograms of the abundance of densely-packed shellbeds of various thicknesses (note change in scale on x-axis), based on tallies from measured sections of shallow-marine deposits, showing a secular increase in the maximum thickness of shellbeds (adapted from Kidwell & Brenchley 1996). Data are coded according to the latitude and tectonic setting of the sampled formations; neither of these variables affected the shape of the frequency distribution within a given period.

etc. This need is obvious –it is like controlling for temperature or tissue type in a laboratory experiments on the effect of oxygen-level on soft-tissue decay. However, I mention it explicitly because it is so important in framing an effective, modular test of the nature of the stratigraphic record, and because we have so little quantitative data concerning controls.

Pat Brenchley and I, for example, assumed that bathymetry and oceanographic facing mattered to the frequency distribution of shellbed thickness, but we had little quantitative data to extrapolate from (Aigner & Reineck 1982; Norris 1986). On the other hand, we were very uncertain about the effect of tectonic setting and latitudinal/climatic setting, even in the modern world. We thus tried to sample from a comparable spectrum of bathymetric zones in each of our 3 target geologic periods (Ordovician-Silurian, Jurassic, Neogene), and we explicitly tested the effects of paleolatitudal position and tectonic setting on the frequency distribution in each period. We discovered that these environmental variables had no effect on the frequency distribution for a geologic period (Fig. 2) - that is, we would not have biased our result if we had failed to keep these variables constant from geologic period to geologic period. This was a bit surprising but very fortunate, as it allowed us to pool all data from all samples in a geologic period ("n" of shellbeds in Fig. 2). However, to reach this conclusion we had to sample each of the cells in the multivariate matrix of geologic time (3 periods), bathymetric zone (5 categories), latitude (3 zones), and tectonic setting (3 categories based on rock-accumulation rates). Technically, the number of samples needed per cell will be determined by their homogeneity, which is something we discover in the process of doing the research or during a pilot study. Here, given the scope of the project, we simply tried to acquire measured-section data from more than one lithostratigraphic unit in each cell (that is, a sample size >1 Formation or Member). We were fairly successful, but have some empty cells, showing where future effort should be focused, and also where other kinds of paleontologic data (e.g., species richness, etc) might be biased by the available record. [We also tested the effect of gathering shellbedthickness data from the literature, versus from sections we had personally described or field-checked; coded in Fig. 2.]

CONCLUSIONS

These are not the only large-scale stratigraphic themes that might be pursued, of course, nor are these the only methodological issues that arise in testing for trends in the fossil record. However, I am convinced that our approach needs to become more quantitative:

Absolute numbers are fundamentally more valuable –they open more applications for taphonomic data, and in many instances are needed to recognize significant but subtle qualitative trends;

A quantitative approach generally forces a more rigorous consideration of test

design, including operationally defining the targets of the study, maintaining controls on variation, and setting levels for sampling; and

All of these procedures improve our ability to compare and combine results from studies in different settings and conducted by different workers, through which we will build a more robust model of how –and why– the taphonomic nature of the fossil record varies. If we do not want paleobiologists and sedimentary geologists to assume "no variation" or "random variation" in the taphonomic nature of the fossil record, then we must try to document the magnitude and significance of this variation, rather than being satisfied with qualitative assessments.

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Taphonomic data in paleoenvironmental reconstruction of shelly concentrations in a dune system

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INTRODUCTION

Although sedimentary structures are commonly outlined by shelly remains, these are still not fully exploited. Moreover, there have been few attempts to analyse fossil content in hypothesising some genetic or taphonomic models as supplement to the schemes used for shelly concentrations or fossil assemblages (Fagërstrom, 1964, Schäfer, 1972) which stress the biasing effects of hardparts desctruction, transport and time-averaging on paleoecological data. Kidwell et al. (1986) hypothesised a taphonomic model for skeletal concentrations in stratigraphic records, distinguishing three genetic processes: biogenic (mainly produced by the gregarious behaviour of skeletonised organisms), physical sedimentologic (produced by hydraulic displacing of hardparts as particles) and diagenetic (produced by significant post-burial physical and chemical agents).

In the present paper fossil concentrations within a Lower Pleistocene dune deposit, made up by mixed carbonate-siciliclastic sediments, are analysed.

MATERIALS AND METHODS

The sandy dune deposits, fall within a Plio-Quaternary succession infilling a graben located in the Barcellona Pozzo di Gotto area (NE Sicily), and crop out along the cliff of "Serra Maloto" (Fig. 1). They consist of mixed carbonate-siliciclastic coarse sands and calcarenites from Lower Pleistocene. Sandy deposits are whitish in