

TIME SCALES OF FOSSIL ACCUMULATION: PATTERNS FROM MIOCENE BENTHIC ASSEMBLAGES

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ABSTRACT--Fossils accumulate into enriched beds over an entire spectrum of time that includes the ecologic (10^0 to 10^2 years), subevolutionary (10^3 - 10^5), and evolutionary (10^6 and more) scales. These absolute time values have been inferred for Miocene Chesapeake Group shell beds using average species longevities of Neogene molluscs, diatom biostratigraphic data, analogy with modern processes of shell accumulation, and rank of shell beds within the lithostratigraphic hierarchy. Fine-scale evolutionary studies should stress samples from stratigraphic sections consisting of repeated ecologic scale accumulations, or microstratigraphic samples within subevolutionary or evolutionary scale accumulations. Because longer-scale accumulations can comprise considerable paleoecologic and taphonomic complexity, they are probably best suited to coarse-scale evolutionary studies in which ecophenotypic and biogeographic variation are unimportant factors.

INTRODUCTION

The time scales of fossil accumulation have received little attention as a problem in paleobiologic analysis or as a tool for geological interpretation. Implicit in the taphonomic literature though is the concept of a dichotomous record of fossil accumulation, in which many beds are identified as recording geologically brief processes, for example storms or mass mortalities, and many fewer are inferred to be geologically prolonged accumulations, including biostratigraphically condensed sequences. Only recently has Fürsich (1978) suggested that benthic invertebrates can indeed accumulate in soft substrata over periods of time of intermediate scale, more prolonged than that of most shell beds but clearly shorter than that required for condensed sequences.

The abundantly fossiliferous silts and sands of the Middle Miocene Chesapeake Group provide a wealth of examples of primarily molluscan shell beds from which some basic patterns in the mechanisms and consequences of varied time scales of shell accumulation can be inferred. These accumulations differ greatly in their physical scales, internal structures, paleontologic compositions and inferred taphonomies. The marine terrigenous clastic facies in which they occur are abundantly represented in the rock record and are among those most frequently sampled for evolutionary investigations. Conclusions drawn from an analysis of shell bed formation in these strata may thus find application in similar strata elsewhere in the stratigraphic record.

SHELL BEDS OF THE CALVERT AND CHOPTANK FORMATIONS

The gently dipping Plum Point Members of the Calvert Formation and the Choptank Formation are a cyclic series of disconformity-bound depositional sequences exposed in a broad belt throughout the eastern and western shores of the Chesapeake Bay estuary in Maryland and northern Virginia, U.S. Middle Atlantic Coastal Plain (Kidwell, 1982). All but one of the sequences comprise a basal well-sorted fine quartzose sand with abundant macroinvertebrate or vertebrate fossils that grades up into a less fossiliferous interval of silty fine sand or sandy mud. Bedding is thin to very thick. Within beds, primary physical structures are rare, and bioturbation is usually complete, consisting of vague

color or textural mottling to sharp-edged burrow systems of varied sizes and orientations. Inferred paleoenvironments range from intertidal to open shelf below storm wave base.

Shell beds of the Calvert and Choptank Formations can be readily categorized into two descriptive types based on their physical scale relative to contiguous facies and their internal complexity (Kidwell, 1979, 1982). These two types are termed minor simple and major complex shell beds.

Minor simple shell beds are relatively thin accumulations (cm to 10's cm thick) contained within the lateral bounds of a single facies (Table 1). Such shell beds usually can be traced only within single outcrops, rarely with concordance between outcrops (10's cm to km). They vary in geometry from irregular pods and lenses to persistent but discontinuous layers of pods, continuous single-valve stringers, and thicker beds of more than a few shells thick. These shell accumulations usually lack lateral or vertical variation in the composition or taphonomic character of their generally paucispecific fossil assemblages, or in the texture, mineralogy or structures of their sedimentary matrices. Exceptionally, they exhibit some simple variation, such as size grading of the terrigenous matrix or of shells, or a lateral change from a sharp erosional basal contact to a gradational one. Minor simple shell beds may or may not be associated with a depositional discontinuity: examples rest on bedding planes, beneath bedding planes, or "float" within a massive stratum.

All of the minor simple shell beds have simple taphonomic histories, being essentially one-event concentrations of specimens of autochthonous, parautochthonous, allochthonous or mixed origin. Biogenic concentrations were the product of the life habits of the shell producers, or the sorting activities of predators, scavengers and burrowers on live and dead shells (B in Table 1). For example, stringers of *Turritella plebeia* are identical in density and apical orientation to living aggregations of *Turritella communis* and *T. annulata* observed in muddy sediments of modern shelves (Bassindale, 1961; Holme, 1961). Densely packed and fragmental lenses of *Chione parkeria* and *Mercenaria rileyi* preserved in a different facies of the same sequence were probably created by the feeding activities of molluscivorous rays, whose modern traces are very similar in morphology and scale to the Miocene accumulations (Gregory et al., 1979).

DEPOSITIONAL SEQUENCE	DOMINANT SPECIES OR NAME	THICKNESS	LATERAL EXTENT	RELATIVE SCALE	GEOMETRY	ASSOCIATED DISCONTINUITIES	MICRO-STRATIGRAPHIC VARIATION	LATERAL VARIATION	FOSSIL ASSEMBLAGE	MODE OF FORMATION
MINOR SIMPLE SHELL BEDS										
PP-0	<i>Ostrea</i>	20cm max	1km	Wi/	discontinuous tongue	no	no	no	Par	SB
	<i>Ostrea</i>	1m	100m+?	=	tabular?	yes, on	packing only	no	Aut	B
	<i>Glossus</i>	2-8cm	m-10m	Wi/	stringer	yes, on	no	no	Par	SB
	<i>Turritella-Corbula</i>	8cm	m	Wi/	discontinuous stringer	yes, on	no	no	Par	S
	<i>Corbula</i>	15cm	cm-10cm	Wi/	pod horizons	yes, on	no	no	All/Par	S
	<i>Glossus-Ostrea</i>	15cm	10cm-m	Wi/	diffuse band	no	no	no	All/Par	SB
	<i>Glossus-Corbula</i>	13cm	m-10m	Wi/	stringer and pods in diffuse band	no	no	no	Par	SB
	<i>Corbula</i>	2-8cm	10m-km	Wi/	pods in thicker bed	yes, on	no	no	Par	SB
	<i>Corbula</i>	5cm	10m-km	Wi/	stringer	yes, on	packing only	no	All	S
	<i>Corbula</i>	30cm	10cm-m	Wi/	diffuse band	no	no	no	Par	B
PP-2	<i>Glossus</i>	3-8cm	10m-km?	Wi/	stringer	no	no	no	Par	SB
	<i>Glossus</i>	8-15cm	m-10m, km?	Wi/	stringer	yes, on	no	no	Par	SB
	<i>Chione</i>	120cm	km	Wi/	bed	yes, below	packing only	no	Par	B or SB?
	<i>Chione</i>	2-10cm	m	Wi/	stringer	yes, either on or below	no	no	Par	S or SB?
PP-3	<i>Turritella</i>	2-15cm	10m-km?	Wi/	stringer	yes, on	no	no	Aut/Par	B
	<i>Turritella</i>	2-8cm	m-10m	Wi/	stringer	yes, on	no	no	Par/All	S or SB
	<i>Pandora</i>	5-8cm	m-10m, 100m?	Wi/	stringer	yes, on	no	no	Par	SB
	<i>Isognomon</i>	5-8cm	10m+	Wi/	stringer	yes or no	no	no	Par	SB
	<i>Glossus</i>	5-8cm	10m-km?	Wi/	stringer	yes or no	no	no	Par	SB
	<i>Chione-Mercenaria</i>	10cm	10cm	Wi/	lenses	yes, on	no?	no	Par	B
CT-0	<i>Echinocardium</i>	10-13cm	10cm	Wi/	lenses	no	no	no	Aut	B
	<i>Scutella</i>	45-60cm	m-10m+?	Wi/	diffuse bed	yes, on	no	no	Aut	B
	<i>Mytilus</i>	10cm	10cm-m	Wi/	lenses	yes, on	no	no	Par	S
CT-1	<i>Anadara</i>	10-15cm	m-10m	Wi/	stringer	usually no	no	no	Par	SB?
MAJOR COMPLEX SHELL BEDS										
PP-1	Camp Roosevelt	3-3.6m	250 or 3800km ²	X	tabular	basal discontinuity, multiple discontinuities	yes, complex	slight	primarily Par	S
PP-3	Kenwood Beach	0.3-4.5m	2600km ²	X	wedge	"	yes, complex	yes	primarily Par	S
CT-0	Drumcliff	0.6-9m	7680km ²	X	roughly lensoidal	"	yes, complex	yes	primarily Par	S
CT-1	Boston Cliffs	0.6-3.6m	8960km ²	X	irregularly tabular	"	yes, complex	yes	primarily Par	S

TABLE-- Descriptive features and modes-of-formation of Miocene shell beds. Depositional sequences numbered sequentially through the Plum Point Member of the Calvert Formation (PP-) and the Choptank Formation (CT-). Wi/ = lateral extent of shell beds restricted to within the bounds of a single lithofacies, X = cross-facies distribution. Aut = autochthonous, Par = parautochthonous, All = allochthonous. S = sedimentologic, B = biogenic, SB = physically reworked biogenic accumulation.

Other examples of minor shell beds were primarily sedimentologic in origin (S in Table 1), produced by localized conditions of seafloor erosion or omission within a single environment, and/or the introduction of allochthonous shell. Great numbers of disarticulated specimens of the small bivalve *Corbula elevata* were passively washed into open burrow systems, and concentrated as winnowed lags. In contrast, dead specimens of the small bivalve *Pandora crassidens* suffered only minor within-habitat transport and, along with live specimens, were buried after accumulating on low energy intertidal flats (Allen, 1954; Allen and Allen, 1954).

Most of the minor simple shell beds probably formed by small-scale, in-situ reworking of initially biogenic accumulations (sedimentary overprint; SB in Table 1). These include stringers of reoriented *Atrina harriissi*, *Ostrea percrassa*, and *Isognomon maxillata*, and storm-reoriented, disarticulated and slightly enriched patches of *Glossus fraterna*.

In contrast, major complex shell beds can be quite thick (10's cm to 10 m) and extensive, exceeding the lateral extent of most vertically contiguous facies (Table 1). These tabular, wedge-shaped and lensoidal accumulations contain densely packed whole and fragmented shell either throughout their entire thickness or in closely spaced beds intercalated with slightly less fossiliferous sand. Shell packing densities are comparable to those of minor simple shell beds despite the great disparity in overall scale. A conservative estimate of the total volume of shell material in the Drumcliff shell bed alone is 6.2 km³, or 45 million boxcars (taking average thickness of 2 m and a 40% average biogenic carbonate content).

In addition to scale differences, major shell beds have complex internal microstratigraphies, consisting in any single outcrop of a series of fossil assemblages that differ in species relative abundances, size distribution, degree of fragmentation, shell packing, or sedimentary matrix. These assemblages vary in thickness and presence-absence between outcrops and, along with overall changes in bed thickness, constitute notable lateral variation within major shell beds. Also unlike minor simple shell beds, each of the four major shell beds is developed on a basal erosional disconformity and in addition incorporates many minor discontinuity surfaces that serve to separate microstratigraphic assemblages.

All four major shell beds of the study area are the stratigraphically condensed record of many minor simple shell beds. This sedimentologic origin is evidenced by the lateral tracing of individual shell layers, winnowed sedimentary textures, and post-mortem disruption and concentration of predominantly parautochthonous specimens. In the lowermost (Camp Roosevelt) example, reduced sedimentation conditions were achieved by the continuous, dynamic bypassing of sand and total passing of mud, fostering shell gravel ecologic conditions on the seafloor. In the other three examples, however, erosional removal of the appreciable sediment supply was only intermittent, so that shell gravel conditions existed only immediately after the reworking of sedimentary increments inhabited by infaunal and soft bottom species. Many initially biogenic, overprinted biogenic, and sedimentologic minor accumulations thus suffered an additional interval of sedimentologic reworking as they were vertically telescoped into

evolutionary

subevolutionary

ecologic

1 10¹ 10² 10³ 10⁴ 10⁵ 10⁶ 10⁷
 TEXT-FIG. 1--Range of absolute values for time scales of fossil accumulations.

larger, complex accumulations. In all examples, lateral variation in shell bed biofabric reflects paleotopographic relief on the basal disconformities, and molluscan biofacies record changing environmental conditions during the reduced sedimentation regimes.

TIME SCALES OF SHELL ACCUMULATION

Minor simple and major complex shell beds of the Miocene study area record two different temporal scales of shell accumulation. Minor simple shell beds record relatively short-term concentration events: they are inferred to be the product of biological and physical processes capable of concentrating shells rapidly, well within the total time represented by the sedimentary thickness of a single facies and often clearly in less time than a single generation or an individual invertebrate's lifespan. On an absolute scale, these events range in duration from minutes to months, years, and perhaps tens of years. Inasmuch as many are associated with bedding surfaces, the maximum duration of formation would be, to an order of magnitude, hundreds of years, the approximate upper time value of sedimentary diastems. This time range is here termed the ecologic time scale of shell accumulation (Fig. 1), because it brackets the time frame of most biological phenomena that would normally be considered as autecologic or synecologic in nature, and includes physical phenomena considered to be geologically instantaneous.

Major complex shell beds clearly represent a longer, supraecologic time scale inasmuch as they consist of many minor simple shell beds in microstratigraphic sequence or admixed within a single larger unit. An estimated lower limit for the duration of major complex shell beds would thus be thousands of years. An upper limit on the accumulation of major shell beds is imposed by molluscan biostratigraphic evidence. None of the major complex shell beds of the Calvert and Choptank Formations inarguably encompasses the entire duration of a molluscan species: species range zones extend beyond the upper bounds of any single shell bed and/or begin below their lower contacts (pers. obs.; also see data of Schoonover, 1941; Kelley, 1979). The shell beds are thus subevolutionary in scale.

An absolute value for this subevolutionary limit can be estimated from species longevities of

Neogene molluscs. Stanley, Addicott and Chinzei (1980) found mean longevities for Japanese and western North American Neogene molluscs of about ten million years, with gastropod species averaging about 8 m.y. and bivalves about 14 m.y. Average species durations are shorter for Neogene faunas of eastern North American, including Chesapeake Group assemblages, because of range truncation by regional extinction in the Plio-Pleistocene (Stanley and Campbell, 1981). The major complex shell beds of the Chesapeake fall within this subevolutionary scale, which would range from 10^3 to 10^5 or possibly 10^6 years (Fig. 1).

Time intervals in excess of 10^5 or 10^6 years are here assigned to the evolutionary time scale (Fig. 1). Although not known to be represented by any shell accumulations in the Chesapeake Group, this is the time scale required for the formation of classic condensed sequences¹ such as documented frequently by European workers in platform and pelagic sequences (Heim, 1934, 1958; Jenkyns, 1971; Geyer, 1973). In such deposits species of successive biozones are admixed or in microstratigraphic sequence within a thinned stratigraphic interval. Interestingly, few examples have been recognized in North America. One may be found in the Maestrichtian of eastern Wyoming, where species of *Coahuilites* and *Sphenodiscus* occur together in a 4 foot thick sandstone, whereas in Mexico and southern Texas these species occur separately through a section thousands of feet thick (K. M. Waage, pers. comm.; Böse, 1927; Cooper, 1971).

The 10^3 to 10^5 year estimate for the formation of major complex shell beds is strengthened by estimates derived from several other independent lines of evidence. These include diatom biostratigraphic evidence, carbon-14 dated rates for the accumulation of possible modern analogues, and the rank of major shell beds within the hierarchy of Chesapeake lithostratigraphic units.

Approximately one hundred Calvert-Choptank samples were examined for biostratigraphically significant diatoms and siliciflagellate species. All analyses were conducted by William H. Abbott of the South Carolina Geological Survey, who assigned assemblages to his concurrent range zonation for the Atlantic Coastal Plain (Abbott, 1978). One clear pattern in the data, documented in Kidwell (1982), is that the diatom biozones parallel the Calvert-Choptank depositional sequences. Two of the zones terminate against disconformity surfaces, but the others appear to terminate within the upper, less fossiliferous intervals of the sequences. (Abbott's Zone III is missing from the study area. This zone has previously been recognized in well cores only.)

The significance of this data is two-fold. One is that within the outcrop area, the depositional sequences represent events whose diachroneity is

¹The term stratigraphic condensation is used throughout this paper to denote the process by which a comparatively thin record accumulates through reduced sedimentation. Specifically, condensation here refers to the vertical telescoping of fossils of successive sedimentary increments of any scale into a single, thinner and more densely fossiliferous accumulation. The term condensed sequence is reserved strictly for those condensed deposits whose contained fossils are from successive biozones: that is, for biostratigraphically con-founded deposits.

less than what can be resolved by the biostratigraphic data; this has implications for some scales of sampling from these prolific strata. Secondly, the major shell beds along with their basal disconformities formed on some time scale less than the duration of a single diatom biozone. These zone durations can be estimated by the conventional method of division into total elapsed time, yielding a maximum estimation with the assumption that the zones record equal time increments. K-Ar dates are not available, but based on his correlation of Chesapeake diatoms with standard deep sea zones, Andrews (1978) suggests that the Plum Point - Choptank section studied here has an absolute duration of 2.5 million years, recording the Middle Miocene period from 14.7 to 12.25 m.y. B.P. (Langhian and Serravallian Stages, in part). The average duration of Abbott's five diatom zones would thus be less than 500,000 years each, providing a maximum order of magnitude estimation of the time for formation for any of the major shell beds. This estimate lies within the range of subevolutionary time estimated by molluscan data above, despite numerous factors acting to inflate it. The figure, however, does not improve the precision with which the time scale of shell accumulation can be estimated.

Similarly, using the historical, deductive method of estimating time from the hierarchy of lithostratigraphic units, if the total duration of Calvert-Choptank deposition was 2.5 million years, each of the depositional sequences represent hundreds of thousands of years, and each of the major shell beds within these sequences would record approximately tens of thousands of years (10^4 years) if all units within each hierarchical level were equal in length. Because some finite amount of time must be associated with the basal disconformities of the shell beds, the shell beds might be inferred to represent as little as 10^3 years by this method.

The most appropriate modern analogues for the Miocene major shell beds are the shell-rich pavements forming in modern continental shelves experiencing sediment starvation related to the rapid Holocene rise in sea level. Examples would include widespread and apparently continuous shell layers in the western New Zealand shelf (Norris, 1972), Gulf of Mexico (Coleman and Gagliano, 1965), and Gulf of California (Parker, 1964). Except that their matrix is usually of coarser terrigenous clastics and contains less abundant shell material than the Miocene accumulations, Holocene gravel lags found on almost all modern continental shelves away from actively prograding deltas could perhaps serve as analogues.

All of these shelly strata accumulated during the most recent Holocene transgression, and thus have periods of accumulation of 18,000 years or less. Perhaps the best analogue for the Miocene shell beds is found along the coast of Mauritania (Einsle et al., 1977) where an internally complex shell bed of great shell density and lateral extent comprises a much condensed record of fossil assemblages from coastal environments. Sediment supply to this region has been negligible. Interestingly, a single microstratigraphically complex part of the shell bed, the Nouakchottian, formed between 5,000 and 6,000 years B.P. during a high-stand of sea level. Both of these estimates, 10^3 and 10^4 years, are comparable with those inferred for the major shell beds.

DISCUSSION

The subdivision of time into ecologic and evolutionary scales is a not uncommon convention among biologists (for example, Osman and Whitlatch, 1978) and is implicit in the paleontological literature. One of the interesting results of the Chesapeake study has been the documentation of shell accumulation on an intermediate, supraecologic subevolutionary time scale involving stratigraphic condensation. Although derived for the Miocene shell beds, the absolute time estimates for ecological, subevolutionary and evolutionary time presented here may directly apply to the analysis of shell beds in other settings.

The boundaries of these time scales are not meant to be discrete, even though absolute time values are applied to them: the scales are intergrading over perhaps an order of magnitude interval. Additionally, the evolutionary-subevolutionary cut-off value should differ from situation to situation because of the different average species longevities of major taxonomic groups. The ecological-subevolutionary time boundary, however, should apply to any setting. Recently, Schindel (1980) compiled time estimates for various biological processes in the 10^0 to 10^4 year range that are in good agreement with values assumed in my own work (Kidwell, 1980). Processes he ascribes to 10^0 to 10^2 years include those inferred for the formation of Miocene minor shell beds, including colonization, population dynamics, competition and predation, ecological succession, resource partitioning, local extinction, and invasion. Those processes he ascribes to longer intervals of elapsed time are related to paleoenvironmental changes such as recorded in major complex shell beds, including habitat destruction and biogeographic changes. To avoid confusion, it should be noted that in his categorization of speciation, Schindel refers to the *event of speciation* (his estimate, possibly 10^0 to 10^2 or 10^3 years), whereas I refer to the *longevity of species*.

Complexity within a shell bed derives from the process of superposition, and thus is simply a consequence of elapsed time. It need not require subevolutionary scales of time to develop however, although it apparently did in the Miocene examples described here. In fact, the time required for the formation of a complex shell bed should be expected to vary among different depositional systems and different tectonic-eustatic settings by virtue of the dynamics of sediment accumulation and local benthic ecology. The minor simple and major complex shell beds observed in the Miocene can be considered end members of a continuous spectrum of shell bed types distinguished by physical scale (minor = within facies, major = cross facies distribution) and internal complexity (physical, paleoecological or biostratigraphic). Hypothetically, intermediate types of shell beds, specifically major simple and minor complex, are certainly possible. A major simple accumulation would have great lateral extent but no or only simple internal variation in composition and structure, for example some widespread storm beds, or shelf edge to deep basin turbidites. Minor complex shell beds, on the other hand, would be geographically conscribed to within a single facies but comprise features evident of multiple, shell concentrating events. The correlation of these shell bed types with the absolute time scales described for the Chesapeake examples is a next step

in establishing more general patterns in fossil accumulation.

IMPLICATIONS FOR EVOLUTIONARY STUDIES

In accumulations formed on an ecologic time scale, time-averaging can be advantageous to faunal sampling such as discussed by Peterson (1976). Treatment of complex fossil accumulations formed on longer time scales as time-averaged samples, however, obscures their ecological and taphonomic complexity, and undermines the validity of paleobiologic inferences.

The best possible situation for fine evolutionary sampling would, of course, be a sequence of identical minor simple shell beds, each formed over some period of brief, ecological time. Even here, there remains the problem of major breaks in the record between stratigraphic segments containing the shell beds, and of even smaller, innumerable breaks (diastems) dispersed between or associated with individual shell beds. Although Sadler (1981) provides us with a quantitative means of assessing this completeness factor, geological judgment is still required in the design of sampling schemes as he also points out.

A stratigraphic section comprising different kinds of minor simple shell beds presents the additional problem of how to distinguish morphologic features related to elapsed time from those that reflect changing environment. This is compounded in major complex shell beds, which are essentially the condensed record of such stratigraphic sequences. For example, the major shell beds of the Chesapeake Group each record marine transgression of biofacies as well as time, so that ecophenotypic as well as temporal variation in morphologies are included in any microstratigraphic series of samples. Although microstratigraphic dissection yields samples roughly equivalent to those from a series of distinct minor simple shell beds, admixture and repeated overprinting of older assemblages by successive taphonomic events during the condensation process can in some situations introduce an additional complication. Added to this must be the question of the degree to which the condensed record is a biased record of special events or particular assemblages only.

Further analysis of Chesapeake shell beds from this perspective will elucidate more of the practical limitations on evolutionary sampling imposed by shell bed mode-of-formation and temporal scale. It is clear, though, that subevolutionary and evolutionary scale complex accumulations will generally be most useful for fine-scale evolutionary studies if environmental conditions remained constant during their formation. For coarser scale studies where environmental changes and ecophenotypic variation are of secondary importance, complex shell beds can be treated as single data points if sampled thoroughly. A broad spectrum of evolutionary questions can thus be addressed in the fossil record, if fossil accumulations are chosen carefully and sampled appropriately.

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