

SEDIMENTARY DYNAMICS OF COMPLEX SHELL
BEDS: IMPLICATIONS FOR ECOLOGIC AND
EVOLUTIONARY PATTERNS

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Abstract: The complex dynamics of shell accumulation by sediment aggradation, erosion, and omission (condensation) can proceed by three basic pathways, each having different implications for post-mortem bias and the ecologic response of living organisms to the accumulation of dead hardparts (taphonomic feedback). In evolutionary time scales, regimes of condensation can maintain shell gravel habitats for sufficiently prolonged periods to record microevolutionary changes in species, but morphometric trends through shell bed sequences can also reflect ecophenotypy in response to changing environments, e.g. during transgressive-regressive cycles. These implications are illustrated by complex shell beds from the Miocene of Maryland (U.S.A.) and the Eocene of Egypt.

INTRODUCTION

Internal complexity is a common feature of skeletal accumulations and is expressed (a) in the admixture of hardparts in different stages of degradation, (b) in the subdivision of single beds by discontinuity surfaces, and (c) in the admixture of hardparts from different environments or ages. However, aside from biostratigraphically complex condensed sequences and hardgrounds (HEIM, 1924; JENKYNS, 1971; FÜRSICH, 1971; WENDT, 1970), complex shell beds have received little attention from the perspective of their physical, sedimentary dynamics and their implications for ecological and evolutionary analysis.

Independent studies of complex shell beds from Miocene strata of Maryland (U.S.A.; KIDWELL, 1982, 1984) and from Eocene strata of Egypt (AIGNER, 1982) led us to similar conclusions regarding the dynamics of skeletal accumulation at two scales:

1. In terms of the small-scale, bed-by-bed processes of sediment aggradation and erosion, which can influence patterns of biotic colonization and faunal changes over short, ecological time scales. This is the significance of the dynamics of shell concentration for paleoecological patterns.
2. In terms of larger scale sedimentary regimes of stratigraphic condensation during transgressive-regressive cycles. Such regimes can maintain shell gravel habitats over

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evolutionarily significant periods of time, but can also confound the record of genetically controlled evolution with ecophenotypic changes in response to environmental changes. This is the significance of sedimentary dynamics for evolutionary patterns.

Both the Miocene and Eocene strata contain internally complex shell beds of wide distribution that rest on disconformities and serve as marker beds for regional correlation (KIDWELL, 1984; AIGNER, 1982; STROUGO, 1977). These skeletal accumulations lie at the base of disconformity-bounded depositional sequences of similar scale and are interpreted as the stratigraphically condensed records of minor transgressions. The six depositional sequences of the Miocene Calvert (Plum Point Member) and Chop-tank formations (SHATTUCK, 1904) together record ca 2.5 m.y. and 5 diatom zones in the late Burdigalian to Serravallian stages, they are each 5-10m thick (KIDWELL, 1984). The 6-7 complex shell beds in the Eocene Quasr-es-Sagha and Maadi formations subdivide about 1.5 m.y. in the Priabonian Stage (STROUGO, 1977); each transgressive-regressive cycle being 3-8 m thick.

The basal disconformities of these complex shell beds are marked by firmgrounds characterized by *Thalassinoides* burrows. The four Miocene shell beds can each be traced 2500 to 7600 km² along the basin margin. They vary from 0.5 to 10 m in thickness, depending on pre-existing relief on the basal disconformity, with shell beds thinnest over paleotopographic highs. Evidence for their stratigraphic condensation and primarily sedimentologic origin includes: (1) the lateral tracing of discrete shell horizons into amalgamated sections over paleohighs; (2) the winnowing of the fine sand matrix; (3) the reorientation and close-packing of parautochthonous infauna; and (4) the preservation of pods of original unworked silty sand. Eocene complex shell beds are thinner, ranging from 0.5 to 4 m, but exhibit similar patterns of amalgamation over a paleohigh, winnowed matrix, and evidence for hydraulic reworking and concentration. The fossil assemblages of both settings are dominated by molluscan species.

I. ECOLOGICAL-SCALE DYNAMICS

I.1. Pathways of Condensation and Ecologic Response

Dead hardparts can influence the structure of living benthic communities by providing substrata for attachment and by changing the mass properties of sedimentary substrata. Dead hardparts thus facilitate colonization by firm-bottom and epifaunal species while they inhibit the success of infaunal species through the reduction of suitable habitat space (Fig. 1). The entire spectrum of live/dead interactions in benthic communities has been termed "taphonomic feedback" (KIDWELL & JABLONSKI, 1983), since the living benthos not only contribute eventually to the dead assemblage but

TAPHONOMIC FEEDBACK

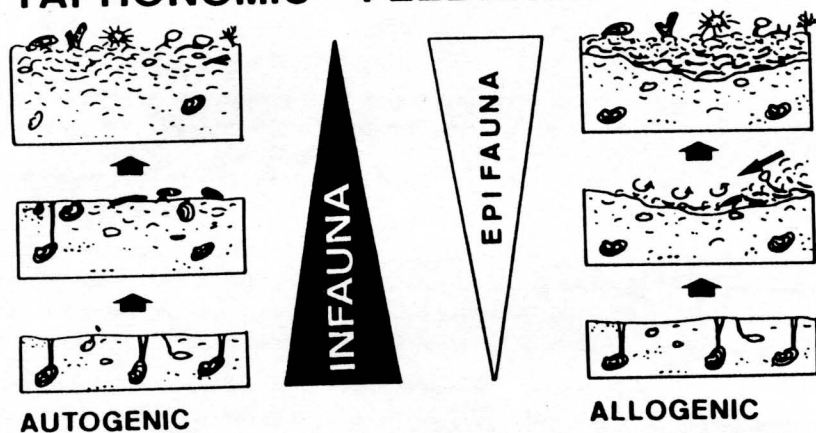


Fig. 1. Schematic diagram illustrating two principal modes of "taphonomic feedback" (KIDWELL & JABLONSKI, 1983) and resulting trends in the composition of benthic assemblages. In the autogenic mode (left), hardparts from the initial soft-bottom community transform the substrate into a progressively coarser, shell-rich substratum, thus facilitating firm-bottom and epifaunal species while inhibiting infaunal colonization. In the allogenic mode (right), changes in the physical environment (winnowing, shell introduction) produce shell concentrations that facilitate epifaunal colonisation.

are also influenced by it. Since sedimentary processes are to a large degree responsible for the availability of hardparts on and shallowly buried within the seafloor, sedimentary dynamics have direct significance for the ecology of benthic communities.

Stratigraphic condensation — the process of accumulating a relatively thin stratigraphic record under conditions of reduced net sedimentation — can proceed by several dynamic pathways of sediment aggradation, erosion, and omission. These are reduced here to three basic patterns (Figure 2). Each has different consequences for the taxonomic composition of the shell bed owing to differences in selective post-mortem destruction of skeletal elements and in pathways of taphonomic feedback.

Pathway 1 is the very simple situation of continuous accumulation of a shell gravel because sedimentation fails to keep up with hardpart accumulation. This can result (a) from negligible sediment supply (starvation) or bypassing of an appreciable supply, or (b) from high rates of biological production of autochthonous hardparts or (c) from an abundant supply of allochthonous hardparts from outside. Relatively infrequent and thin depositional increments (indicated by notches on the otherwise smooth

SEDIMENT DYNAMICS & ECOL. RESPONSE

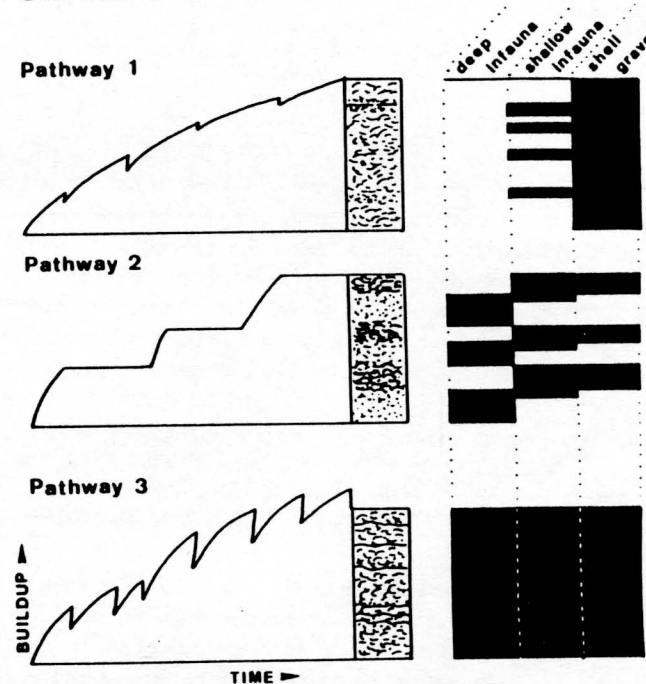


Fig. 2. Three basic pathways in the dynamics of complex skeletal accumulations and expected ecological responses. For further explanation see text.

curve, Fig. 2) permit the episodic colonization by shallow-burrowing infauna, but the community and final fossil assemblage will be dominated by the continued successful colonization of shell gravel species. The complex shell bed that results from pathway 1 will contain few discrete discontinuity surfaces and will have a winnowed, well-sorted sedimentary matrix.

Pathway 2 is characterized by a background condition of zero or low sedimentation relative to hardpart accumulation which is interrupted intermittently by the rapid accumulation of relatively thick depositional increments of muddy sediment. These increments provide an opportunity for colonization by deep- as well as shallow-burrowing infauna. After each "mud event", shell gravel conditions are gradually established as the hardparts from the initial soft-bottom community transform the substrate into a shell-rich and thus progressively coarser and firmer substratum (taphonomic feedback),

In which infauna is inhibited by the gradual exclusion of a suitable habitat. In the idealized situation illustrated in Fig. 2, each depositional increment records this temporal change in community composition in its sequence of assemblages, which contain an increasing diversity and abundance of shell gravel species. A complex shell bed built up by a series of such depositional events will contain a series of omission surfaces marked by shell gravel communities and will consist of the original sediment matrix, except where it was winnowed along the omission surfaces.

Pathway 3 is through alternating episodes of aggradation and erosional reworking: soft-bottom colonizers of depositional increments are reworked in-situ into a shell gravel lag, which provides opportunities for colonization by epifaunal taxa. This physically-driven mode of taphonomic feedback produces ecologically mixed assemblages of soft-bottom and shell gravel species which are both homogenized and then amalgamated onto older assemblages by reworking events. In addition to the mixed ecological character, the final complex shell bed should be characterized by a series of minor internal erosional surfaces and imperfectly winnowed sedimentary matrix.

1.2 Examples

1.2.1. Miocene

The different complex shell beds of the Miocene Calvert and Choptank formations exhibit similar vertical sequences: a basal fragmental shell hash, grading into the main body of the shell bed consisting of both whole and broken closely packed shells, and an upper interval of closely spaced but discrete shell horizons, by which the shell bed grades into less fossiliferous overlying strata (KIDWELL, 1984; KIDWELL & JABLONSKI, 1983). In detail, however, the four complex shell beds had very different histories of sediment accumulation and biotic response. For example, the Camp Roosevelt shell bed is dominated by molluscan taxa preferring shell gravel conditions as judged from species morphology, facies occurrence, and the ecology of modern congeners (KIDWELL & JABLONSKI, 1983). These include free-living bivalves (*Glycymeris*, *Chesapecten*) byssate nestlers (*Anadara*, *Cardita*), muricid gastropods, and a rich assortment of encrusting bryozoa, hydractinids, barnacles, boring polychaetes, and ctenid sponges. Discrete discontinuity surfaces within the shell bed are rare, the sedimentary matrix is extremely well-sorted, and infaunal species of the assemblages are almost all small-bodied, shallow burrowers (venerids, *Astarte*, *Bicorbula*, *Turritella*) that could inhibit the interstices of a shell gravel or could colonize thin, temporary sedimentary veneers and tolerate episodic exhumation. The low incidence of eptzoans (ca 5-6 % of all shells; high compared to other shell beds, but low in absolute terms) may itself be another indication for the existence of a shifting bottom such as might be produced by migrating ripple fields. These features indicate condensation under conditions of low total and net sedimentation (pathway 1 in Figure 2).

By contrast, the Drumcliff shell bed contains a diverse assemblage of soft-bottom, deeply burrowing infauna throughout most of its thickness, excluding only the basal 1 m thick shell hash, which is dominated by epifauna (*Crucibulum*, *Balanus*). Shell gravel species and shallow-burrowing species occur abundantly in those parts of the shell bed that are most densely packed (KIDWELL & JABLONSKI, in prep.) suggesting that the ecologically mixed fossil assemblages of the Drumcliff do record repeated conversion of soft-bottom sedimentary substrata into shell gravel habitats. An alternation of aggradation and seafloor reworking probably best describes the shell bed history (pathway 3 in Figure 2), accounting for the numerous scoured and burrowed discontinuity surfaces within the shell bed, the pods of silty sand representing the otherwise winnowed matrix, the thorough admixing of soft-bottom and shell gravel assemblages, and the lack of internal "successions" within the complex accumulation.

Individual reworking events were less effective in winnowing shells from sedimentary increments in the upper part of the shell bed, probably related to the nearing attainment of maximum transgression and maximum water depths for the depositional sequence. Thus, whereas the Camp Roosevelt shell bed records pathway 1 with shell gravel conditions maintained by taphonomic feedback during a period of sedimentary omission, the Drumcliff shell bed records only a short, initial interval of persistent shell gravel conditions, followed by an interval of condensation through pathway 3, with repeated reworking of depositional increments into shell gravel habitats. This presented a far more variable habitat to benthos on ecological time scales than did the pathway 1 dynamics of the Camp Roosevelt shell bed.

1.2.2. Eocene

The most striking feature of the Eocene complex shell beds is the frequently repeated change in faunal composition within the beds. Commonly, the basal firmground is overlain by a zone of mostly articulated, epifaunal anomid bivalves (*Carolia*), which are replaced upwards by *Plicatula* or by ostreid oysters that are partly cemented onto the large *Carolia* shells. In the *Ostrea* bed, the oysters are in turn encrusted by corals, leading to small coral banks. The larger coral colonies commonly show episodic growth restrictions with zones of borings, indicating an alternation of coral growth, anastrophic burial or growth slowdown due to turbidity, and recovery. These "systematic" vertical sequences in faunal composition are restricted to only the lower parts of some shell beds, and record taphonomic facilitation of benthic colonization during an initial period of low total sedimentation (pathway 1 in Figure 2). Most of each shell bed, however, is characterized by unsystematic shifts in assemblage composition. Assemblages include thick layers of (frequently glauconitic) shell hash with *Ophiomorpha*, and intercalations of muddy sand containing infaunal soft-bottom organisms such as *Turritella* and burrowing echinoids. Subsequent reworking of these infaunal assemblages is indica-

ted by post-mortem encrustation, for example of *Turritella* by bryozoa. Although these intercalations suggest episodic aggradation and omission (pathway 2 of Figure 2), erosional reworking of assemblages was a major factor in the condensation as evidenced by the internal discontinuities and erosion surfaces found within the bed sequences. These surfaces are commonly overlain by *Carolia* in a colonization pattern similar to that found on the basal firmground of the complex shell bed.

2. EVOLUTIONARY-SCALE DYNAMICS

2.1 Expected Patterns

Complex shell beds generated by stratigraphic condensation can record shell gravel habitats that persisted over evolutionarily significant periods of time. For example, each of the Miocene complex shell beds are estimated to have accumulated over thousands to tens of thousands of years (KIDWELL, 1982). Successive assemblages within complex shell beds may thus record changes in species morphometry produced by true genetic microevolution (e.g. BAYER & MCGHEE, this volume). However, morphometric trends may also reflect ecophenotypic variation in response to environmental changes, brought about both by the short-term dynamics of sedimentation during condensation events and by longer term cyclicity in condensation with transgression-regression.

2.1.1. Condensation and Information Loss

Samples collected from condensed shell beds will contain more kinds and greater degrees of post-mortem bias than those collected from non-condensed beds, owing to repeated events of hardpart reworking and to prolonged time-averaging (KIDWELL, 1982). For example, the dominance of robust forms (greater shell thickness, more compact shapes) in assemblages condensed through episodic erosion (pathway 3 in Fig. 2) may be a taphonomic artefact of the selective post-mortem destruction of less robust variants from a single genetic population. Prolonged time-averaging can also obscure original morphologic trends or compositions by mixing specimens from successive populations. Layer by layer dissection of complex shell beds might yield samples roughly equivalent in degree of time-averaging to those from a series of discrete, non-amalgamated concentrations. However, the admixture of assemblages by repeated events of reworking, omission, and colonization during the period of condensation will introduce to the samples an additional level of taphonomic bias. Thus it must diminish confidence in the direct comparison of samples between condensed and non-condensed beds as well as samples taken within a single condensed bed.

2.1.2. Condensation and Ecophenotypy

Many benthic species vary morphometrically with habitat parameters such as water depth, water turbulence, and substratum characteristics (EKMAN, 1953; ALEXANDER, 1974; CISNE et al., 1982). Consequently, a major concern in the evolutionary analysis of faunas from lithologically variable sequences is the problem of distinguishing true evolutionary change from ecophenotypic response to environmental change.

In sequences of alternating condensed and non-condensed strata, the condensed shell beds can look sufficiently similar to one another to be categorized as a single lithofacies type. However, treating complex shell beds as the expression of identical habitats in the hope of avoiding ecophenotypic variation among samples can be misleading on several scales.

1. On the scale of samples collected layer by layer through a single complex shell bed, ecophenotypic variation can be confounded with genetic morphologic change because of the alternation of soft-bottom, shell gravel, and ecologically mixed assemblages (Fig. 2).

2. A series of samples from a complex shell bed can record ecophenotypic variation among different bathymetric environments, since the shell bed may be the condensed record of transgressive shoreline migration.

3. Ecophenotypic variation among samples from successive complex shell beds in a stratigraphic sequence can be expected since the shell beds can record different pathways of condensation and condense a different spectrum of environments.

In addition to these problems of scale, several different patterns of morphometric variation can be expected from ecophenotypic responses to, for example, transgressive-regressive cycles (Fig. 3):

- A. Species exhibit an excursion in some aspect of morphometry through a transgressive-regressive cycle, tracking water depth or distance from shore.
- B. Species exhibit a directional shift in average morphometry through a transgressive-regressive cycle. The trend bears no relationship to water depth, but instead tracks substratum change as reflected in the lithofacies sequence.
- C. Morphometric variance of a species decreases upward through a transgressive-regressive cycle from a maximum value within the basal condensed shell bed. High morphometric variability early in the complex shell bed would reflect prolonged time-averaging and mixing of specimens from a series of bathymetric

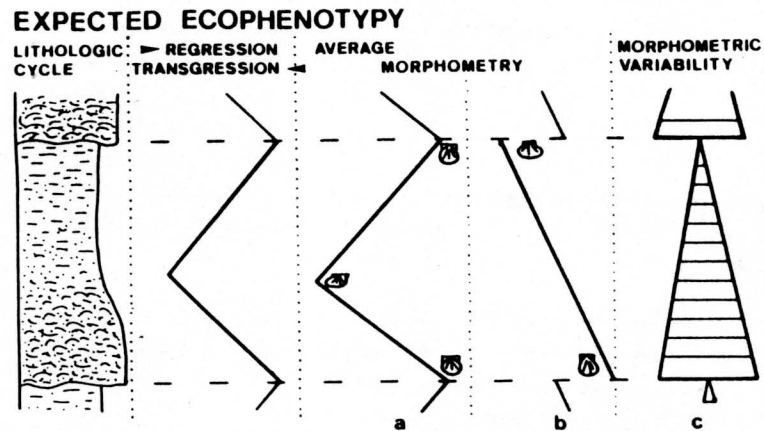


Fig. 3. Several patterns of morphometric variation can be expected from ecophenotypic responses to transgressive/regressive cycles that form asymmetric lithologic sequences. Further explanation see text.

environments through stratigraphic condensation. Morphometric variance decreases higher in the cycle because of the lesser time-averaging of fossil assemblages and the greater probability that specimens from a single sample represent the same environment.

2.2 Examples

The morphometric patterns expected from ecophenotypy are in fact apparent within complex shell beds of the Miocene Calvert and Choptank formations, as indicated by KELLEY's (1979; 1983) study of eight mollusk genera. *Lucina anodonta*, for example (Fig. 4), exhibits monotonic decreases in five out of eight measured features over a series of samples from the Camp Roosevelt shell bed (Zone 10 of SHATTUCK, 1904), which records deepening open marine waters (KIDWELL, 1984). This pattern is repeated through the Drumcliff shell bed (Zone 17) and Boston Cliffs shell bed (Zone 19), both also through transgressive deepening-up records. Although KELLEY (1983) interprets these patterns, which all range within 10 to 20% of the mean for the species, as microevolutionary in origin, they may as likely be ecophenotypic. If they are, the Miocene mollusks provide evidence of even greater morphometric stasis than previously thought.

Carolia placunoides, the characteristic bivalve of the Eocene shell beds, also varies in morphology, but on the scale of shell bed to shell bed through the regressive Qasr-es-Sagha Formation. This variation could similarly be interpreted as either a microevolutionary or an ecophenotypic phenomenon. The ecophenotypic explanation is supported by the occurrence of two basic colonization strategies. In most instances, *Carolia* forms dense in-situ pavements colonizing discontinuity surfaces at the base of, or within, complex shell beds. But in portions of the shell beds that are dominated by infaunal molluscs such as *Turritella*, *Carolia* commonly forms stacks of several individuals byssally attached on top of one another. Here, colonization by the stacking strategy seems to be the ecophenotypic response of the bivalve to a scarcity of other firm substrata in a soft-bottom habitat.

Unfortunately, information on morphometric variance is not available for either the Miocene or Eocene mollusks in these sections. However, the trend expected from ecophenotypy (Fig. 3c) is of evolutionary interest, because it mimics a pattern inferred by some workers (e.g. CARSON, 1975; WILLIAMSON, 1981; SYLVESTER-BRADLEY, 1977) for speciation — an initial burst of variation followed by a more narrowly-defined range of variation. The expected ecophenotypic trend reflects both ecophenotypic and time-averaging effects during stratigraphic condensation, and so should apply to sequences of shell beds condensed over any time scale.

2.3 Other Cyclic Patterns in Condensation

In the Miocene and Eocene sequences, fining-up depositional sequences, bounded by disconformities generate the basic cyclic pattern. Condensed intervals, marked by complex shell beds, lie at the base of each sequence and record transgressive events; they grade upward into shell-poor (i.e. carbonate-poor) muddy prograding facies. This pattern is opposite to that frequently observed in carbonate records, which are characterized by coarsening-up depositional sequences with condensed intervals at the top of the sequence marking the end of regression. Because discontinuity surfaces are used to define the depositional sequences in both situations, the different patterns in grain size and in the position of condensed intervals within cycles are not simply a problem of semantics or conceptual bias.

The timing of condensation during early transgression in the Miocene and Eocene situations can be explained in terms of the models of SWIFT (1968) and RYER (1977): during a rapid relative rise in sealevel, terrigenous sediment supplied by rivers is trapped in coastal estuaries owing to the rise in baselevel, thus starving the shelf. Seventy

MORPHOMETRY OF LUCINA ANODONTA

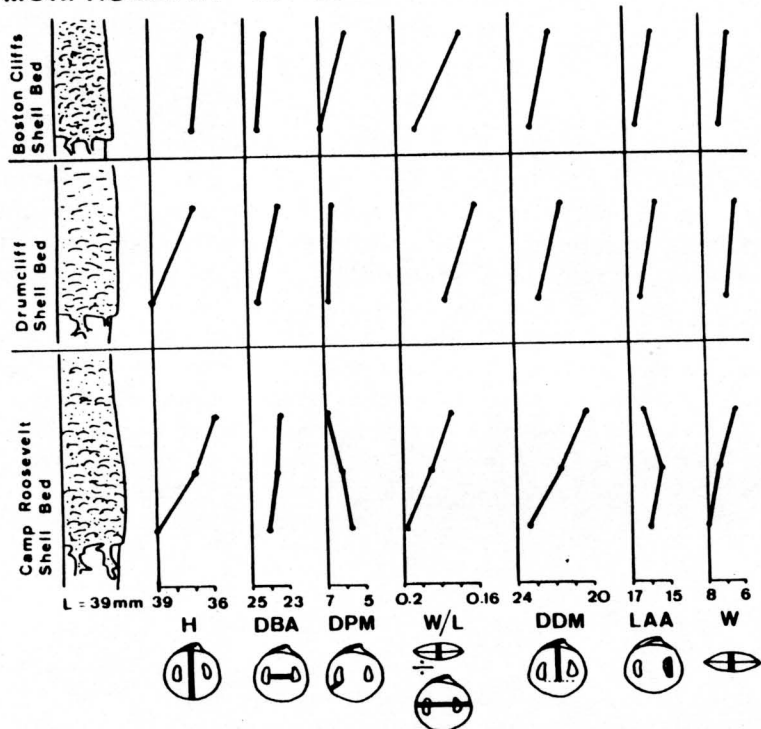


Fig. 4. Morphometric patterns of *Lucina anodonta* within complex shells beds of the Miocene Calvert and Choptank formations (from KELLEY, 1979, 1983). These patterns may be true genetic microevolutionary changes but they may just as well represent the ecophenotypic response to environmental changes.

percent of modern continental shelf areas have such starved regimes today as a consequence of the Holocene transgression (EMERY, 1968). The relatively thick regressive phase of the cycle records the resumption of terrigenous sediment supply to the shelf once estuaries and other coastal sediment sinks fill to grade, plus the effects of falling baselevel which permits erosional reworking and redistribution of older sediments.

By contrast, carbonate systems are largely fed by autochthonous sediment production, and can thus rapidly aggrade during initial baselevel rise. Hence, they generate a shallowing-up, regressive sequence (e.g. JAMES, 1980). Phases of baselevel still-stand and fall would be characterized by condensation of the upper part of the depositional sequence through winnowing. The lower (BAYER et al., this volume) and upper Muschel-

kalk (AIGNER, in press) of Germany provide excellent examples of subtidal shallowing-up cycles capped by complex, amalgamated, and condensed shell beds.

Early cementation of carbonate sediments on the seafloor impedes or prevents erosional destruction of the condensed record during latest regression and lowest base-level positions. In this way, not only is the end-regressive condensed phase preserved, but it can be utilized as a substratum by faunas of the following early transgressive phase, for instance as widespread hardground surfaces.

Thus, the opposite patterns in condensation through transgressive-regressive cycles -- base-of cycle shell beds in terrigenous systems and end-cycle shell beds in carbonate systems -- probably derive from qualitative differences in sediment supply between the largely allochthonous terrigenous and largely autochthonous carbonate systems.

CONCLUSIONS

Ironically, rich skeletal accumulations -- long perceived as bonanzas by paleontologists -- are among the most difficult subjects for ecological and evolutionary studies, owing to their complex biological and taphonomic histories.

In ecological analysis, the primary complexity involves the significance of ecologically mixed assemblages. Do they record:

- the admixing of allochthonous hardparts;
- condensation of successive, unrelated communities; or
- in-situ change in community composition due to biotically or physically driven taphonomic feedback?

This ambiguity can be resolved by the analysis of sedimentologic and stratigraphic features (e.g. matrix type, presence of discontinuity surfaces, proximity of appropriate source facies for allochthonous hardparts) as well as paleoecologic and taphonomic features (e.g. KIDWELL & JABLONSKI, 1983, in prep.). Understanding the ecology of ancient shell gravel habitats, however, is further complicated by the longer-term condensation of assemblages from migrating environments, as in the Miocene and Eocene examples. These patterns can usually be resolved by examining the larger stratigraphic and paleoenvironmental context of the complex shell bed.

Evolutionary analysis is also complicated by the several scales of complexity in shell bed accumulation. This ranges from the ecophenotypic variation among populations occupying successive soft-bottom and shell gravel substrata, to the complication of

each shell bed comprising populations from a bathymetric spectrum of environments. Even seemingly directional trends can be generated by an ecophenotypic response to progressive change in substratum type within an asymmetric cycle (Fig. 3). Factoring out such confounding effects depends on careful sampling along bathymetric gradients (e.g. CISNE et al., 1982) or, as GOULD & ELDREDGE (1977), emphasized, sampling among basins within a species geographic range but exhibiting different environmental histories (e.g. JOHNSON, 1982).

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