

**Zeitschrift:** Eclogae Geologicae Helvetiae  
**Herausgeber:** Schweizerische Geologische Gesellschaft  
**Band:** 88 (1995)  
**Heft:** 3

**Artikel:** Shell concentrations  
**Autor:** Fürsich, Franz Theodor  
**DOI:** <https://doi.org/10.5169/seals-167692>

### **Nutzungsbedingungen**

Die ETH-Bibliothek ist die Anbieterin der digitalisierten Zeitschriften. Sie besitzt keine Urheberrechte an den Zeitschriften und ist nicht verantwortlich für deren Inhalte. Die Rechte liegen in der Regel bei den Herausgebern beziehungsweise den externen Rechteinhabern. [Siehe Rechtliche Hinweise.](#)

### **Conditions d'utilisation**

L'ETH Library est le fournisseur des revues numérisées. Elle ne détient aucun droit d'auteur sur les revues et n'est pas responsable de leur contenu. En règle générale, les droits sont détenus par les éditeurs ou les détenteurs de droits externes. [Voir Informations légales.](#)

### **Terms of use**

The ETH Library is the provider of the digitised journals. It does not own any copyrights to the journals and is not responsible for their content. The rights usually lie with the publishers or the external rights holders. [See Legal notice.](#)

**Download PDF:** 02.04.2025

**ETH-Bibliothek Zürich, E-Periodica, <https://www.e-periodica.ch>**

# Shell concentrations

FRANZ THEODOR FÜRSICH<sup>1</sup>

*Key words:* Taphonomy, shell concentration, review, biofabric, classification, genesis

## ABSTRACT

Shell concentrations, i.e. concentrations of biomineralized invertebrate remains >2 mm in size, are widespread features of the sedimentary record. They are formed by biological processes, physico-chemical processes, and time. Skeletal concentrations can be descriptively classified according to their taxonomic composition, biofabric, geometry, and complexity. On one hand their biostratigraphic and ecological value is often strongly reduced due to reworking and time-averaging. On the other hand, their biofabric and the taphonomic signatures of the individual components yield important information about the depositional environment and the final concentration process. Genetic classifications of shell concentrations are a useful tool for environmental analysis and the reconstruction of the history of sedimentary basins.

## ZUSAMMENFASSUNG

Schille, definiert als Konzentrationen biomineralisierter Invertebratenreste >2 mm, sind in der Erdgeschichte weit verbreitet. An ihrer Bildung beteiligt sind biologische Prozesse, physiko-chemische Prozesse und die Zeit. Schille lassen sich nach ihrer taxonomischen Zusammensetzung, ihrem Biogefüge, ihrer Geometrie, oder ihrer Internstruktur beschreibend klassifizieren. Einerseits ist ihr biostratigraphischer und ökologischer Wert häufig sehr gering, da Aufarbeitung und zeitliche Mitteilung die ursprünglich enthaltene Information stark verzerren können. Andererseits liefern das Biogefüge und die taphonomischen Merkmale der einzelnen Komponenten zahlreiche Hinweise auf den Ablagerungsraum und den letzten Konzentrationsprozess. Genetische Klassifikationen von Schillen sind ein wichtiger Beitrag für die Analyse von Ablagerungsräumen und die Rekonstruktion sedimentärer Becken.

## Introduction

Shell concentrations are products of a variety of taphonomic processes. They are ideal objects to illustrate the impact of such processes on organic hardparts and the consequences for palaeoecological and palaeoenvironmental interpretations. The purpose of this short review is to briefly discuss the various features and genetic aspects of shell concentrations, to illustrate ways of classifying them, and to outline their potential and limitations as geological and palaeoecological tools.

Shell concentrations have been defined by Kidwell (1991) as concentrations of biomineralized remains more than 2 mm in size from any invertebrate animal. The more familiar term shell bed refers to a particular geometric arrangement of shell concentration and is therefore less broadly applicable. The still more general term skeletal concentra-

---

<sup>1</sup> Institut für Paläontologie der Universität Würzburg, Pleicherwall 1, D-97070 Würzburg

tion (or fossil concentration; Kidwell et al. 1986) refers to concentrations of all biogenic hardparts regardless of size and taxonomic origin.

Although widespread in the sedimentary record, shell concentrations have received relatively little attention until recently. The pioneer work carried out by the Wilhelmshaven School since the 1920s (summarized in Schäfer 1966) was only taken up in the last two decades in the context of the resurgent interest in taphonomy. Recently, the state of the art has been extensively reviewed and the literature comprehensively compiled by Kidwell (1991).

### Descriptive classification of shell concentrations

Classifying shell concentrations in a descriptive way not only facilitates scientific communication, but hopefully also some basic factors, closely related to the genesis of the concentrations, become apparent during the classification process. From the numerous possibilities of descriptive classification, those based on the taxonomic composition, the biofabric, the geometry of the concentration, and on its complexity are particularly promising, as they reveal a variety of ecological, hydrodynamic, and topographic information (Fig. 1; Kidwell et al. 1986). For example, from the taxonomic composition of shell concentrations we get a glimpse of the communities which contributed hardparts and therefore obtain information on the ecological framework. In many cases the ecological information has been filtered by various taphonomic processes such as sorting according to size or shape. This provides information also on the hydrodynamic setting under which

### descriptive classification of shell concentrations

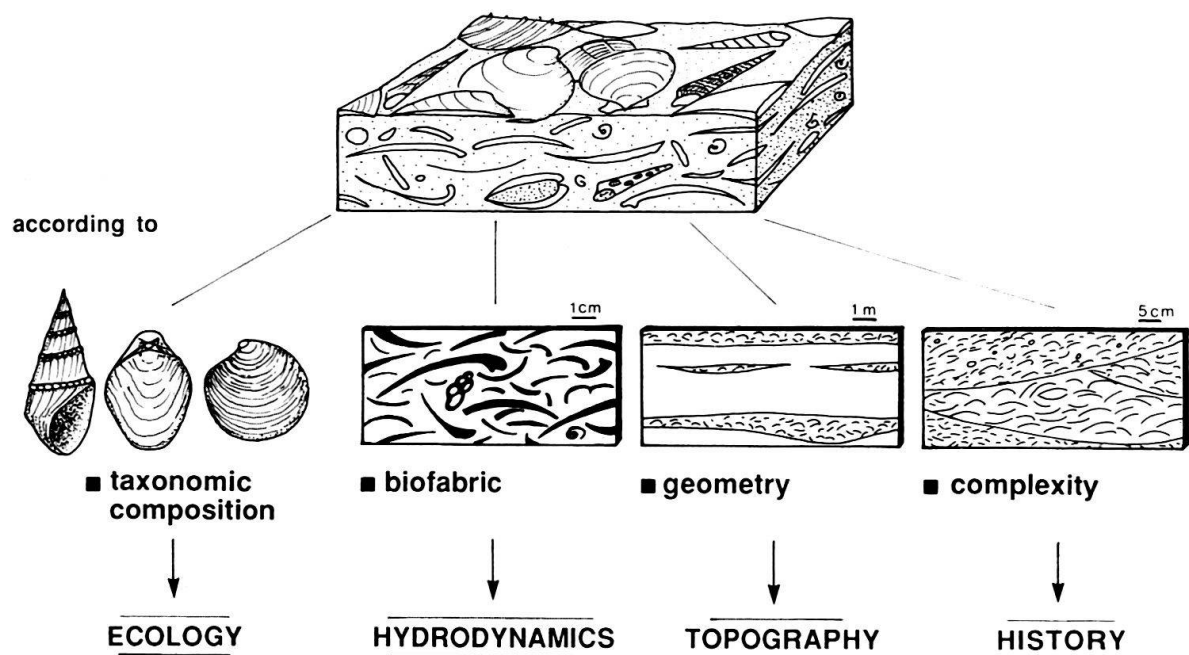


Fig. 1. Descriptive classification of skeletal concentrations.

the deposit formed. As a result we can distinguish between mono-, pauci- and polyspecific concentrations (Kidwell et al. 1986).

Similarly the biofabric, that is the three-dimensional arrangement of skeletal elements, yields information on the hydrodynamic regime and, to a lesser degree, on compaction and ecology by using orientation patterns, packing density and degree of sorting. A simple descriptive classification of biofabrics that can be easily used in the field was put forward by Kidwell & Holland (1991).

The geometry of shell concentrations (Fig. 3 in Kidwell et al. 1986) provides information on the topography and, to some extent, also on the concentration agents, be it organisms, waves, or currents.

Finally, the complexity of the internal structure of a shell concentration, e.g. the lateral and vertical changes in taxonomic composition, biofabric and matrix, tells us something about the history of the concentration process. For example, whether single or multiple events were involved and how much time is represented. Usually this will be no simple task, as the final concentration process tends to obliterate much of the earlier history of the shell concentration.

These descriptive approaches to classification of shell concentrations yield important clues as to the mode of their formation, although the information remains relatively general. For the more promising genetic classification we first have to answer the questions: how and why do shell concentrations form?

### Formation of shell concentrations

Three groups of factors play an essential role in the formation of shell concentrations: biological processes, physico-chemical processes, and time (Fig. 2).

Shell concentrations may be produced by the organisms whose remains are found in the concentration. Examples are gregarious settling behaviour (e.g. *Mytilus edulis* beds on modern tidal flats), high population densities due to opportunistic life strategies (e.g. Levinton 1970), high population densities due to optimal ecological conditions, and gregarious spawning behaviour (e.g. some belemnite "battlefields"; Doyle & MacDonald 1993). Another example is mass mortality of organisms, which is caused by a variety of biogenic or abiotic factors such as red tides, changes in water chemistry or temperature, or rapid sedimentation and which is ultimately a biological response to changing environmental conditions (e.g. Arntz 1985; Speyer & Brett 1985; Steimle & Sindermann 1978).

Alternatively, shell concentrations are formed by organisms that actively concentrate skeletal remains of other organisms. Most reflect particular feeding behaviour such as shell pockets formed by rays (e.g. Gregory et al. 1979), shell beds produced by the lug worm *Arenicola marina* (e.g. Van Straaten 1952), or other behaviour patterns (e.g. shell concentrations as backfills or used for wall construction of burrows).

Physical processes are the most important agents for the concentration of biogenic hardparts, whereas chemical processes, more or less restricted to compaction, play only a subordinate role. The main physical processes are waves, currents, and turbidity currents. They concentrate skeletal elements either by winnowing of finer material or by selective transport. Examples are countless and include shell pavements on the soles of tidal channels, storm shell beds, and shell bars. Before final burial it is hydraulic processes that act on the skeletal elements, whereas afterwards compaction and pressure solution operate

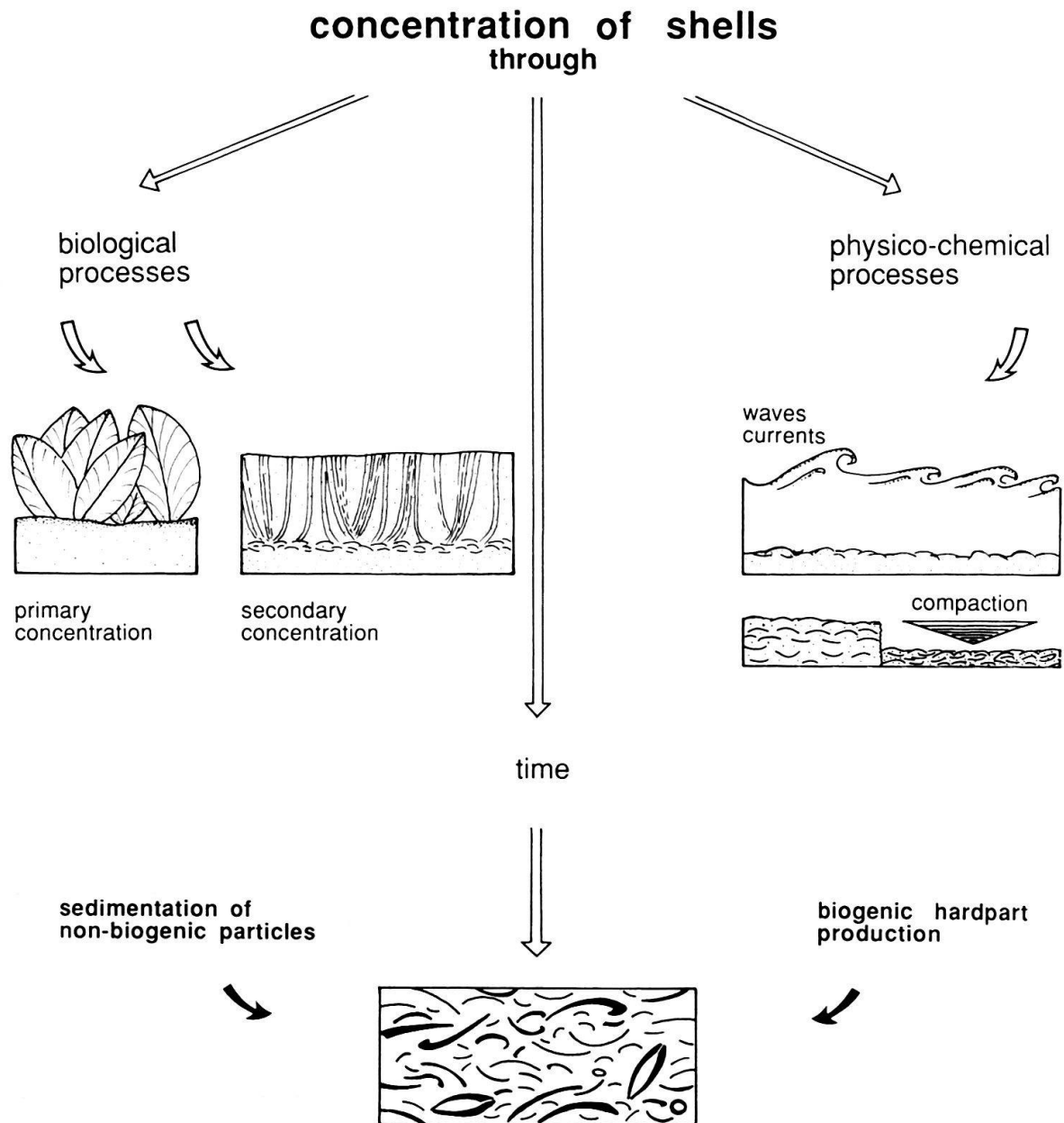


Fig. 2. Shell concentrations are formed by biological processes, physico-chemical processes, and by time.

as the two main diagenetic processes contributing to the formation of shell concentrations.

Time is also a decisive factor influencing the formation of shell concentrations either directly by the length of the concentration process, via the sedimentation of non-biogenic particles or else via production of biogenic hardparts (Fig. 2). A low rate of net sedimentation may lead to shell concentrations even when the production of biogenic hardparts is low. The result are condensed deposits (Heim 1958). Examples are the famous Bajocian (Middle Jurassic) oolithe ferrugineuse de Bayeux of Normandy (Fürsich 1971) or the cephalopod limestones so characteristic of Palaeozoic and Mesozoic pelagic platforms

### significance of shell concentrations

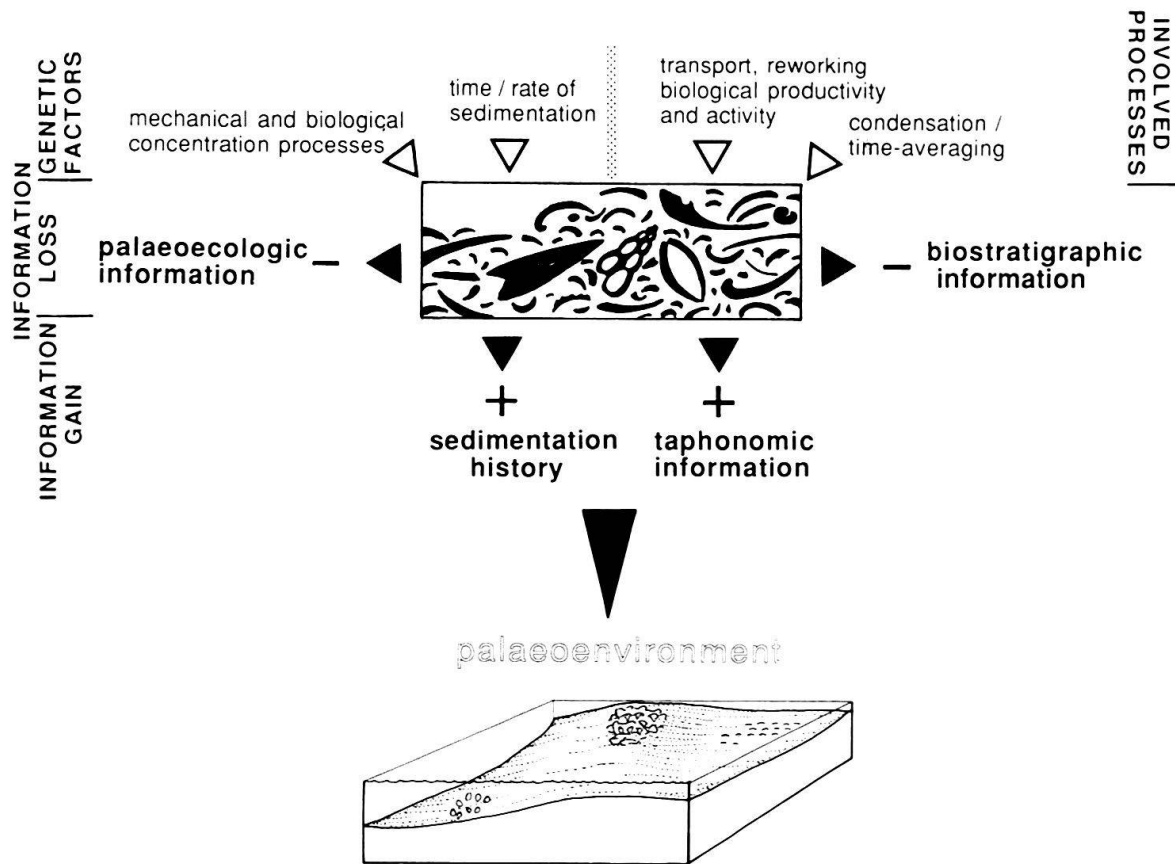


Fig. 3. Significance of shell concentrations. For further explanation see text.

(e.g. Wendt 1970; Wendt et al. 1984). Another example is the pteropod ooze that covers wide parts of present-day oceans.

In many cases more than just one group of factors will be involved in formation of shell concentrations. This aspect contributes to the difficulty in unraveling their often complex genetic history.

### Significance of shell concentrations (Fig. 3)

#### Information loss

Many shell concentrations are the product of reworking. As a rule, this entails a loss in biological information. Both autecological information, e.g. about growth position, fauna-substrate relations, and synecological information, e.g. about the composition of former communities, are lost. For this reason, many shell concentrations cannot be used for palaeoecological analysis, as the original data set is too heavily distorted. A similar

## Shell concentrations as information stores

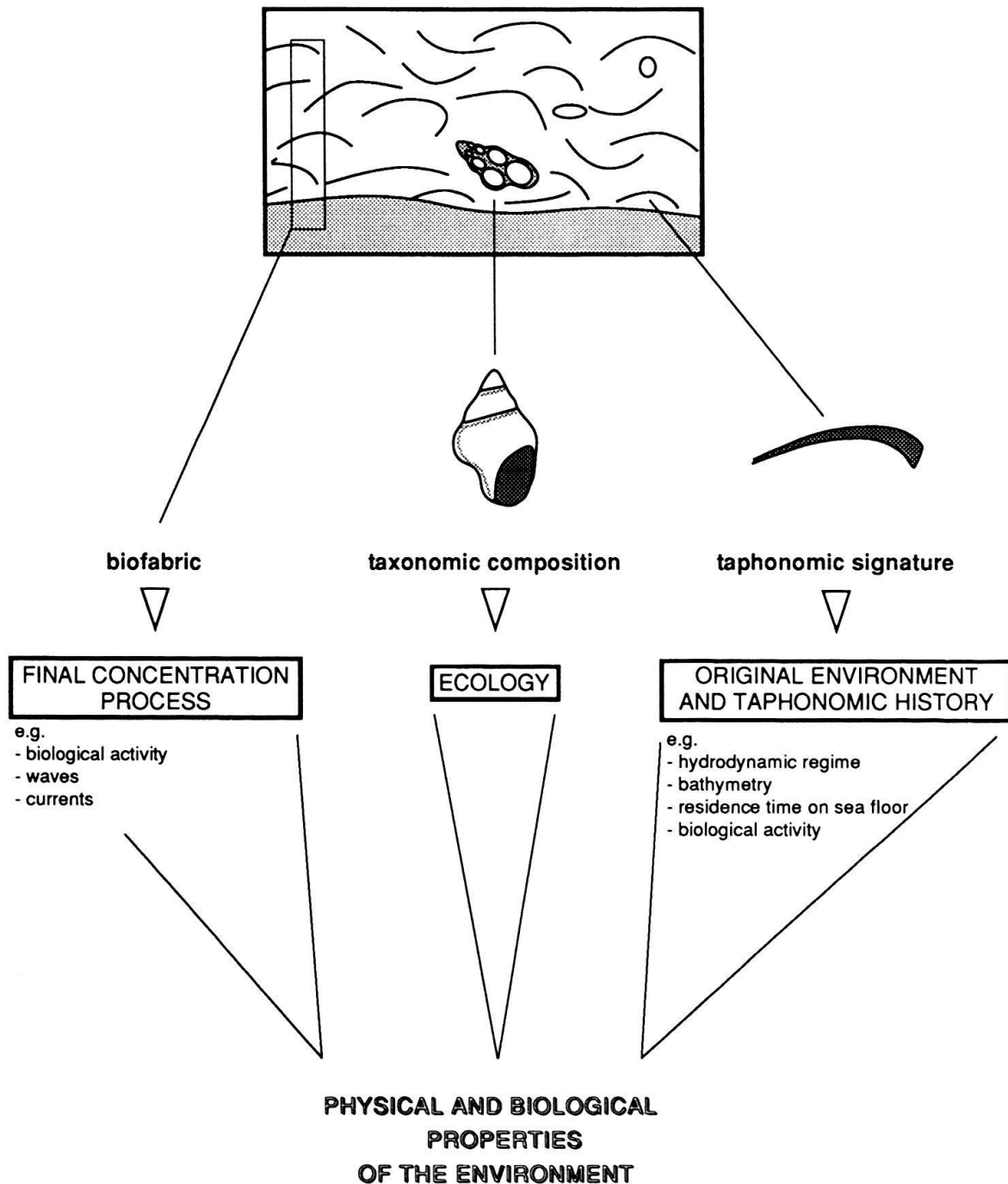


Fig. 4. Shell concentrations as information stores. For explanation see text.

loss concerns biostratigraphic information at a refined scale. Most shell concentrations are characterized by condensation of the time axis to a variable degree. This may have hardly any effect, e.g. when during a storm shells of the same age are concentrated, or else may have considerable consequences, when shells of different ages either accumu-

late together due to non-sedimentation or due to reworking of layers of different ages. In the latter two cases the resulting concentrations will be highly time-averaged and ecological attributes such as species diversity, species composition, or trophic group composition will no longer carry much significance (e.g. Fürsich & Aberhan 1990; Kidwell & Bosence 1991).

#### Information gain

On the other hand, shell concentrations offer a wealth of information both about the final concentration process and about preceding biological and physical parameters of the environment. The unraveling of this information has been the main aim of biostratigraphic studies in the last years and important progress has been made, based on studies of modern environments (e.g. Callender et al. 1990; Davies et al. 1989; Feige & Fürsich 1991) as well as on fossil ones (e.g. Beckvar & Kidwell 1988; Doyle & MacDonald 1993; Speyer & Brett 1988). The final concentration process is usually reflected by the biofabric (Fig. 4; Fürsich & Oschmann 1993). Thus the orientation of shells, presence or absence of grading and of an erosive base, and the modal distribution of skeletal elements and matrix will give us hints about the biological activity and the various hydrodynamic processes such as storm waves, storm flows and longshore currents. In contrast, the taphonomic signature imprinted on individual skeletal elements (Davies et al. 1989) carries information about the original environment, in which the organisms lived, and records, albeit in a fragmentary way, the history that led to their concentration. This includes information on the hydrodynamic regime, on the bathymetric setting, the residence time of the skeletal elements on the sea floor, and on the biological activity which affected them. Thus biofabric and taphonomic signatures, together with the taxonomic composition as a rudimentary ecological source, considerably contribute to the reconstruction of the physical and biological properties of ancient environments.

#### **Genetic classification of shell concentrations – a tool for environmental and basin analysis**

As the main importance of skeletal concentrations lies in their potential as environmental indicators, a genetic classification appears more appropriate than purely descriptive ones as outlined above. Such classification schemes exist on different levels of refinement. Very crudely, shell concentrations can be classified in ternary diagrams according to the relative importance of biological, sedimentological and diagenetic processes (Kidwell et al. 1986, Fig. 4). This approach can be used to characterize different environments according to prevailing shell concentrations, but the same type of shell concentration may appear in quite different environments.

A more refined classification scheme is that of Kidwell (1991), who distinguishes (1) event concentrations, caused by ecologically brief concentration episodes and preserved as discrete events; (2) composite concentrations, characterized by amalgamation or accretion of multiple events; (3) hiatal concentrations, in which slow net accumulation is the prominent feature; and (4) lag concentrations, in which erosion and/or corrosion plays the decisive role and significant stratigraphic truncation occurs (Fig. 5). These four types of shell concentrations too exhibit characteristic trends along onshore-offshore transects and within depositional sequences (Kidwell 1991).



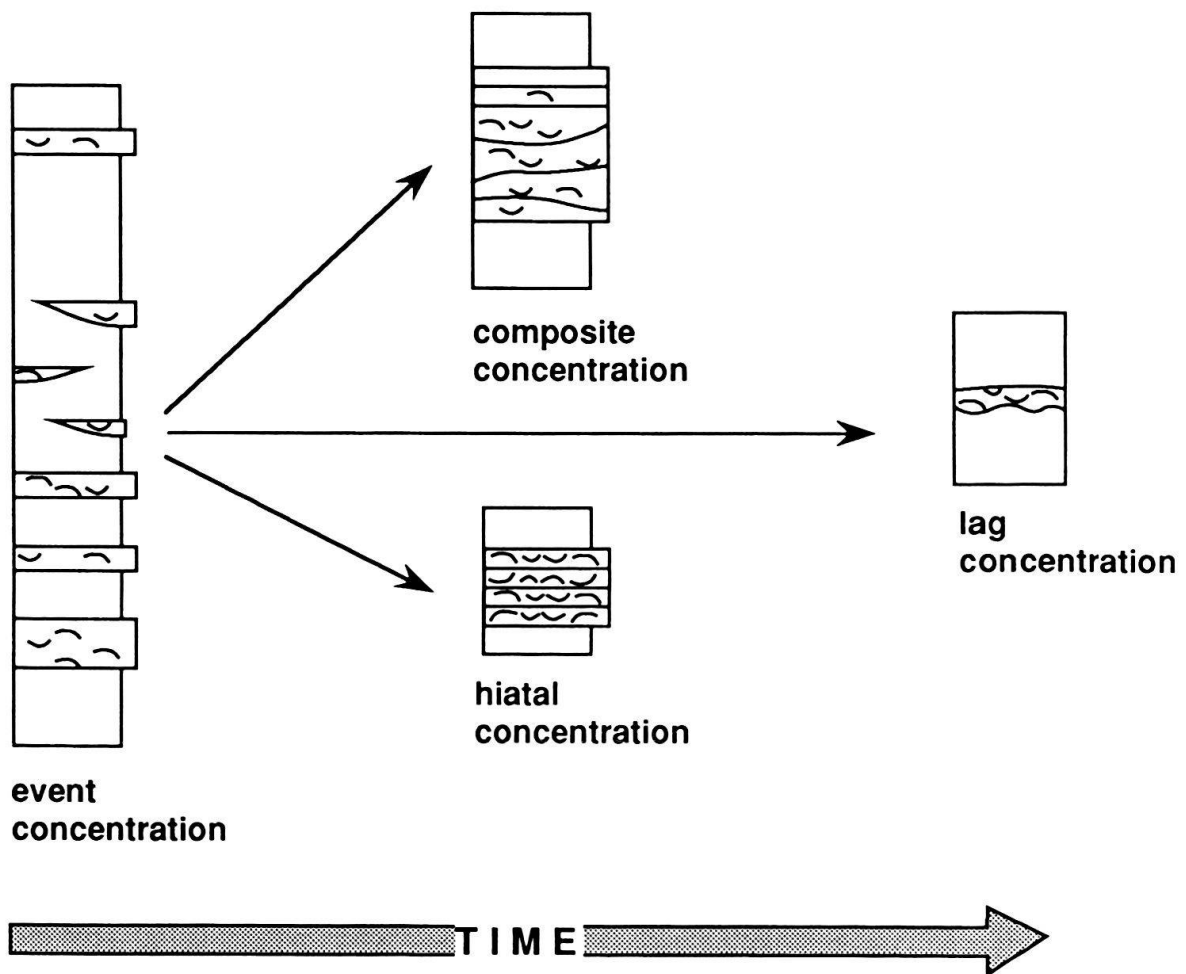
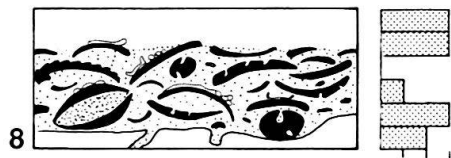
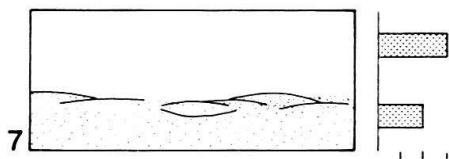
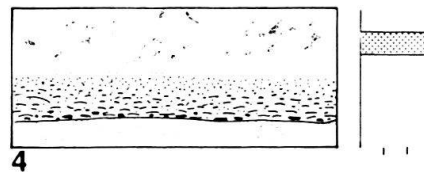
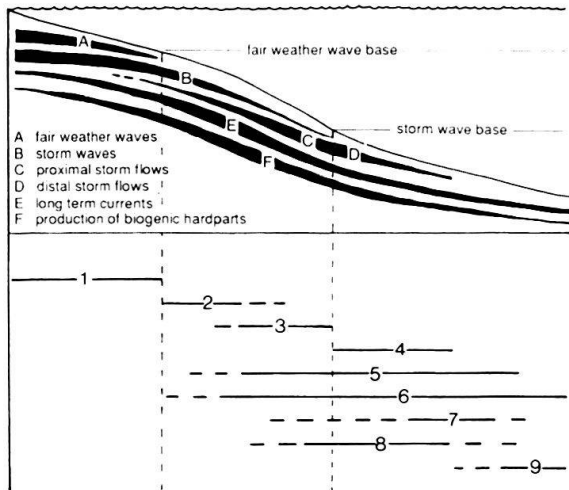
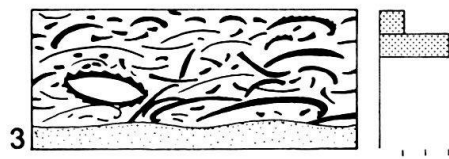
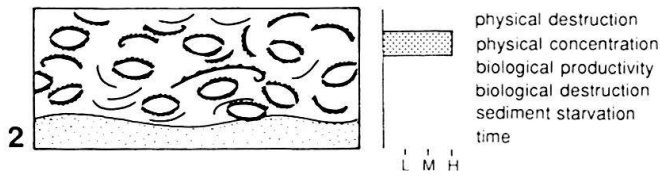
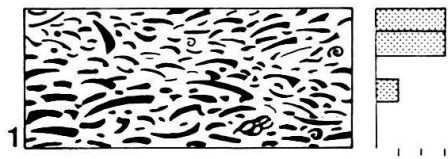


Fig. 5. Four categories of shell concentrations according to Kidwell (1991). Modified from Kidwell (1991, Fig. 5).

A still higher level of resolution is the classification scheme of Fürsich & Oschmann (1993), developed for shelf sequences in the Jurassic of the Kachchh Basin, Western India, but applicable to epicontinental seas in general (Fig. 6). Nine genetic types of shell concentrations, related to the relative importance of the main concentration processes (waves, currents, biological productivity, biological activity, net sedimentation, and time), can be distinguished. These types exhibit distinct bathymetric trends and thus serve as excellent tools in basin analysis (Fürsich & Oschmann 1993).

Fig. 6. Shell concentrations of epicontinental seas, their main controlling factors, and their distribution along an onshore-offshore transect. 1–9: Nine major types of shell concentrations. 1: Fair weather wave concentration; 2: storm wave concentration; 3: Proximal storm flow concentration (proximal tempestite); 4: distal storm flow concentration (distal tempestite); 5: current concentration; 6: primary biogenic concentration; 7: winnowed concentration; 8: transgressive lag concentration; 9: condensed concentration. A–F: Concentration processes. L: low; M: medium; H: high. After Fürsich & Oschmann (1993, Fig. 5).

### shell concentrations of epicontinental seas and their main controlling factors



The elements of fair weather wave concentrations (1) exhibit signs of abrasion and fragmentation due to the persistent wave exposure. Shells are invariably disarticulated; sorting is conspicuous. In plan view, a bimodal orientation pattern will be characteristic.

Storm wave concentrations (2) differ in being much better preserved, as reworking is only a brief event. Articulated shells may dominate, if a life assemblage is reworked. Signs of sorting are usually absent. Infaunal elements will lack signs of boring or encrustation.

Proximal tempestites (3) share many features with storm wave concentrations, but in addition exhibit signs of transport. As a rule they consist of reasonably preserved shells. Proximal tempestites have a sharp erosive base and grading is common. Disarticulated shells are preferentially in a convex-up orientation.

Distal tempestites (4) differ from proximal ones in being thinner and in the smaller size of their components. In addition they are graded and very well sorted.

In current concentrations (5), caused by tidal currents, longshore currents or any other type of shelf current, skeletal elements show a wide range of preservation qualities, depending on their residence time within the current regime, but poorly preserved shells prevail. Again most shells are convex-up oriented.

Primary biogenic concentrations (6) are the result of gregarious settling behaviour of larvae, but may also reflect low rates of sedimentation. Some shells may be preserved in life position and the original colonisation pattern (e.g. nests) may be preserved.

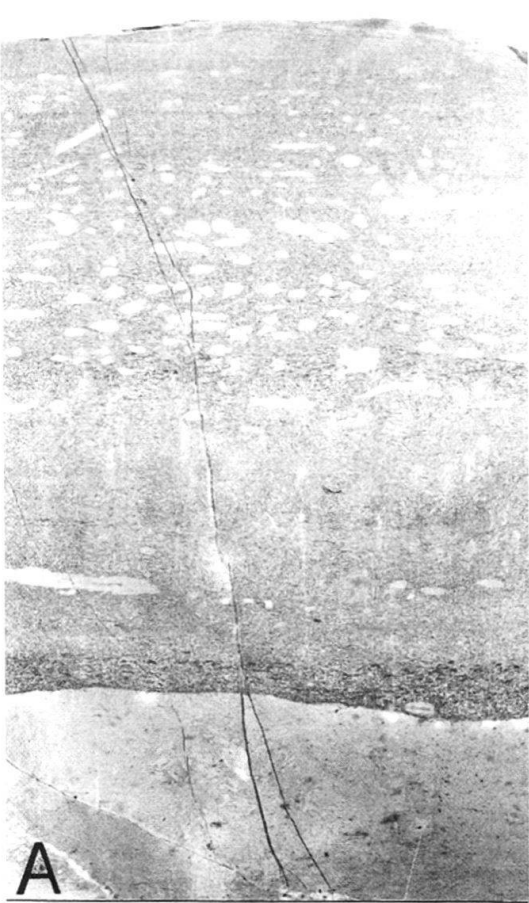
Winnowed concentrations (7) are pavements or thin accumulations of relatively well preserved shells, which formed by gentle winnowing of finer matrix due to currents too weak to transport larger skeletal elements.

In transgressive lag concentrations (8) the time factor becomes more prominent. As in Kidwell's (1991) lag concentrations, several phases of reworking and erosion are usually involved in addition to low net rates of sedimentation. In epicontinental seas, this scenario is characteristic of transgressive phases, during which exposure of formerly more restricted environments to open shelf currents and heavy storms lead to repeated reworking, while the sediment source retreats. Transgressive lag concentrations are therefore characteristically multi-event products and characterized by shells with a long residence time on the sea floor, complex taphonomic signatures and with moderate to poor preservation quality. Above all, many shells are bored and encrusted or at least show residual signs of such biogenic degradation.

Condensed concentrations (9) represent (in contrast to Kidwell's (1991)) hiatal concentrations with which they share most features) the longest time interval. Due to their long exposure time on the sea floor, the shells are often bored, encrusted, or corroded. The faunal composition may be heavily biased in favour of large, thick, sturdy shells, be-

---

Fig. 7. Examples of shell concentrations. A: Distal tempestite. Note erosive base, grading, and post-depositional bioturbation by *Chondrites*. Khavda Formation (Bathonian) of Jhura Dome, Kachchh, western India;  $\times 0.8$ . Strictly speaking, due to the small size of the biogenic hardparts ( $< 2$  mm), the bed should be termed skeletal concentration. B: Proximal tempestite. Habur Formation (Mid-Cretaceous), 5 km SW of Habur village, Rajasthan, India;  $\times 1$ . C: Nest of terebratulid brachiopods in growth positions (primary biogenic concentration); lower surface view. Chari Formation (Callovian) of Jara Dome, Kachchh, western India;  $\times 1$ . D: Current concentration; upper surface view. Note poor preservation of shells and belemnites; Chari Formation (Callovian) of Jumara Dome, Kachchh, western India.  $\times 1$ .



cause small and thin shells have been removed by bioerosion or chemical erosion. On the other hand, as fresh material is constantly added, some shells usually exhibit a very high preservation quality.

These brief characterizations of the various types of shell concentrations are supplemented by some examples in figure 7. The high variation in taphonomic signatures and biofabric corresponds to the wide range of environments represented. Analysed this way, shell beds are indeed useful environmental indicators, especially with regard to bathymetry, energy level and rates of sedimentation (e.g. Aigner 1983, 1985; Fürsich & Oschmann 1986, 1993; Kidwell 1988; Norris 1986).

Moreover shell concentrations appear to occupy characteristic positions within sequence stratigraphic frameworks. Banerjee & Kidwell (1991) in studying the Lower Cretaceous Mannville Group of Canada identified different types of shell concentrations at the base and at the top of parasequences as well as at the point of maximum flooding. Similarly, Fürsich & Oschmann (1993) recognized parasequences based on types of shell concentrations in the Jurassic of Western India and were able to correlate basin-wide shallowing-deepening cycles with the help of these shell beds. Clearly a useful tool for basin analysis, shell concentrations record even larger-scale trends in the geological record. As Kidwell & Brenchley (1994) showed, the increase in the thickness of shell concentrations through the Phanerozoic reflects evolutionary changes such as an increase in the reproductive and metabolic output in benthic communities over time.

For many years shell concentrations have been primarily viewed as products, in which palaeoecological information is preserved as distorted relicts. Today we know that this apparent disadvantage is more than compensated by the information on depositional environments and on the depositional history, which makes shell concentrations ideal geological tools.

### Acknowledgements

This short review formed the basis of a talk delivered at the Taphonomy Meeting of the Swiss Palaeontological Society in Aargau in October 1995. I would like to thank Jean-Pierre Berger for the invitation to take part in this meeting and Chris McRoberts for critically reading the manuscript.

### REFERENCES

- AIGNER, T. 1983: Facies and origin of nummulitic buildups: An example from the Giza Pyramids Plateau (Middle Eocene, Egypt). *N. Jb. Geol. Paläont. Abh.* 166, 347–368.
- 1985: Storm depositional systems. *Lecture Notes in Earth Sci.* 3, 1–174.
- ARNTZ, W. 1985: Zur Entstehung von Organismenansammlungen: «El Niño» 1982–1983 vor Peru. *Natur u. Museum* 115, 134–151.
- BANERJEE, I. & KIDWELL, S.M. 1991: Significance of molluscan shell beds in sequence stratigraphy: an example from the Lower Cretaceous Mannville Group of Canada. *Sedimentology* 38, 913–934.
- BECKVAR, N. & KIDWELL, S.M. 1988: Hiatal shell concentrations, sequence analysis and sealevel history of a Pleistocene coastal alluvial fan, Punta Chueca, Sonora. *Lethaia* 21, 257–270.
- CALLENDER, W.R., STAFF, G.M., POWELL, E.N. & MACDONALD, I.R. 1990: Gulf of Mexico hydrocarbon seep communities. V. Biofacies and shell orientation of autochthonous shell beds below storm wave base. *Palaios* 5, 2–14.
- DAVIES, D.J., POWELL, E.N. & STANTON, R.J. JR. 1989: Taphonomic signature as a function of environmental process: shells and shell beds in a hurricane-influenced inlet on the Texas coast. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 72, 317–356.
- DOYLE, P. & MACDONALD, D.I.M. 1993: Belemnite battlefields. *Lethaia* 26, 65–80.

- FEIGE, A. & FÜRSICH, F. 1991: Taphonomy of the Recent molluscs of Bahia la Choya (Gulf of California, Sonora, Mexico). *Zitteliana* 18, 89–133.
- FÜRSICH, F. 1971: Hartgründe und Kondensation im Dogger von Calvados. *N. Jb. Geol. Paläont. Abh.* 138, 313–342.
- FÜRSICH, F.T. & ABERHAN, M. 1990: Significance of time-averaging for palaeocommunity analysis. *Lethaia* 23, 143–152.
- FÜRSICH, F.T. & OSCHMANN, W. 1986: Storm beds of *Nanogyra virgula* in the Upper Jurassic of France. *N. Jb. Geol. Paläont. Abh.* 172, 141–161.
- 1993: Shell beds as tools in basin analysis: the Jurassic of Kachchh, western India. *J. Geol. Soc. Lond.* 150, 169–185.
- GREGORY, M.R., BALLANCE, P.F., GIBSON, G.W. & AYLING, A.M. 1979: On how some rays (Elasmobranchia) excavate feeding depressions by jetting water. *J. Sediment. Petrol.* 49, 1125–1130.
- HEIM, A. 1958: Oceanic sedimentation and submarine discontinuities. *Eclogae geol. Helv.* 51, 642–649.
- KIDWELL, S.M. 1988: Taphonomic comparison of passive and active continental margins: Neogene shell beds of the Atlantic Coastal Plain and northern Gulf of California. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 63, 201–223.
- 1991: The stratigraphy of shell concentrations. In: *Taphonomy: Releasing the data locked in the fossil record.* (Ed. by ALLISON, P.A. & BRIGGS, D.E.G.), 211–290, Plenum Press.
- KIDWELL, S.M. & BOSENCE, D.W.J. 1991: Taphonomy and time-averaging of marine shelly faunas. In: *Taphonomy: Releasing the data locked in the fossil record.* (Ed. by ALLISON, P.A. & BRIGGS, D.E.G.), 115–209, Plenum Press.
- KIDWELL, S.M. & BRENCHLEY, P.J. 1994: Patterns in bioclast accumulation through the Phanerozoic: Changes in input or in destruction? *Geology* 22, 1139–1143.
- KIDWELL, S.M. & HOLLAND, S.M. 1991: Field description of coarse bioclastic fabrics. *Palaios* 6, 426–434.
- KIDWELL, S.M., FÜRSICH, F.T. & AIGNER, T. 1986: Conceptual framework for the analysis and classification of fossil concentrations. *Palaios* 1, 228–238.
- LEVINTON, J.S. 1970: The paleoecological significance of opportunistic species. *Lethaia* 3, 69–78.
- NORRIS, R.D. 1986: Taphonomic gradients in shelf fossil assemblages: Pliocene Purissima Formation, California. *Palaios* 1, 256–270.
- SCHÄFER, W. 1966: *Aktuo-Paläontologie nach Studien in der Nordsee.* 666 pp., Waldemar Kramer.
- SPEYER, S.E. & BRETT, C.E. 1985: Clustered trilobite assemblages in the Middle Devonian Hamilton Group. *Lethaia*, 85–103.
- 1988: Taphofacies models for epeiric sea environments: Middle Paleozoic examples. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 63, 225–262.
- STEIMLE, F.W. & SINDERMAN, C.J. 1978: Review of oxygen depletion and associated mass mortalities of shellfish in the Middle Atlantic Bight in 1976. *Mar. Fish. Rev.* 40/ 12, 17–26.
- VAN STRAATEN, L.M.J.U. 1952: Biogenic textures and the formation of shell beds in the Dutch Wadden Sea. *I. Koninkl. Nederl. Akad. Wettensch. Ser.* 55, 500–516.
- WENDT, J. 1970: Stratigraphische Kondensation in triadischen und jurassischen Cephalopodenkalken der Tethys. *N. Jb. Geol. Paläont. Mh.* 1970, 433–448.
- WENDT, J., AIGNER, T. & NEUGEBAUER, J. 1984: Cephalopod limestone deposition on a shallow pelagic ridge: the Tafilalt Platform (Upper Devonian, eastern Anti-Atlas, Morocco). *Sedimentology* 31, 601–625.

