Towards an Evolutionary Stratigraphy

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SUMMARY

Event stratigraphy emphasizes the sedimentological and ecological effects of rare high-energy events episodically interrupting background conditions in many depositional environments. In response, corresponding background and post-event communities expand and contract alternatively, but in different proportions. Therefore the two communities might be expected to differ in the tempo and mode of evolution. Storm beds in epeiric seas, benthic horizons in bituminous shales and trace fossils in turbidite sequences are cited as potential test areas.

RESUMEN

La «estratigrafía de los acontecimientos» (event stratigraphy) pone de relieve los efectos sedimentológicos y ecológicos que se producen en algunos ambientes deposicionales como consecuencia de ocasionales episodios de elevada energía que perturban las condiciones ambientales existentes. Como resultado, las respectivas comunidades pre-existentes y las que se instalan posteriormente a dichos episodios se expanden y reducen alternativamente, si bien en diferentes proporciones. Asimismo, se puede esperar que las dos comunidades difieran en el ritmo y modo de evolución. Se han tomado como ejemplos ilustrativos las capas de tormenta en los mares epicoñtinentales, los horizontes con organismos bentónicos en las pizarras bituminosas y los ichnofósiles en las secuencias turbidíticas.

RESUM

L'estratigrafia dels esdeveniments (event stratigraphy) posa de relleu els efectes sedimentològics i ecològics que es produeixen en alguns ambients deposicionals com a conseqüència d'episodis ocasionals d'alta energia que torben les condicions ambientals existents. Com a resultat, les respectives comunitats preexistents i les que s'instal·len posteriorment a tals episodis s'expandeixen i redueixen alternativament, bé que en diferents proporcions. Així mateix, es pot esperar que ambdues comunitats difereixin en el ritme i forma d'evolució. S'han pres com a exemples il·lustratius les capes de tempestat dels mars epicontinentals, els horitzons amb organismes bentònics de les pissarres bituminoses i els icnofòssils de les seqüències turbidítiques.

INTRODUCTION

Biostratigraphy has been — and probably will remain— the most important contribution of paleontology to the development of earth sciences: Biological evolution as a measure stick for geologic history. A very useful method, to be sure. But what, in turn, do the stratigraphic data mean for paleontological theories beyond providing a convenient reference grit? We all know the examination question: «What would happen to biostratigraphy, if the whole evolutionary theory would collapse?» and the answer: «Nothing». In fact, non-biological features, such as the accidental variations in trace elements or in the crystallographic modifications of certain minerals within successive volcanic ash layers («tephro-stratigraphy»; Winter, in press) may in some cases be more valuable for correlation than associated index fossils. No wonder that many biologically minded paleontologists tend to turn away from a field, in which the ever increasing amount of observational data seems not to be balanced by new concepts beyond Steno's (1669) law of superposition and Gressly's (1840) notion of facies. In this essay I intend to show that this attitude towards stratigraphy is not justified.

During the last decades, earth scientists have been forced to revise their uniformitarian views in many instances. Not in the sense, that processes having acted in the past, or at least during the Phanerozoic, would be impossible to-day. But critical events — such as the collision of continental plates to form a Pangaea, or the impact of a large asteroid— that may have been the ultimate causes for major extinctions, are simply too rare to match our human experience. The same is true for less dramatic events, such as seismic shocks, volcanic eruptions, turbidity currents, storms or floods, for which our uniformitarian experience has sampled only the milder examples, while much higher intensities must be allowed for in view of geologic time scales. On a regional scale, these more common events do also disrupt biological systems and it is mainly a matter of scales whether or not they effect recognizeable evolutionary changes.

Due to advances in sedimentology, different kinds of rare-event deposits can now be recognized in marine sequences: Besides volcanic ashes *(tephra)* and *seismites* (Seilacher, 1969), there are the deposits of suspension currents (*turbidites*, Kuenen, 1951), storms (*tempestites,* Ager 1974) and floods *(inundites).* Because of differences in the kinds of turbulence, each kind of event beds shows a graded vertical sequence of distinctive erosional, depositional and deformational structures that may also grade laterally into more proximal or distal expressions along the paleoslope. Details will be published in the proceedings to a workshop on «Cyclic and Event Stratification» of the Tübingen SFB 53, held in 1980. (Einsele and Seilacher, in press).

In event stratigraphy, the *ecologic* aspect has so far been largely neglected: Strong turbulence events may disrupt the local bottom fauna. But commonly they also change bottom conditions (firmness, food content) in such a way that a different *post-event fauna* can establish itself and flourish for many generations, but for considerably shorter periods than

the *background-fauna* inhabiting the bottoms between successive events.

The distinction between background and post-event bottom faunas is essential for our further considerations: Both are subject to unpredictable but sometimes drastic expansions and reductions of habitat and population size, but the emphasis is different in the two groups. While the background community contracts only for short periods into fairly extended and continuous refuge areas deeper in the basin, the post-event community experiences short expansive booms and has to survive longer refuge phases confined to a narrow, patchy and time-instable zone closer to the shore.

According to current ecological and evolutionary models we should expect that the post-event fauna consists of more opportunistic species, that should also —if the punctated equilibrium idea (Gould and Eldredge, 1977) is correct— evolve more rapidly than those of the background fauna, because they spend most of the time in the bottleneck situation.

In order to study such effects, we should select small and faunistically isolated basins. They have the advantage (1) that faunas show some degree of endemism and may, as a whole, be expected to have evolved rather rapidly and (2) that their relief is commonly low enough to exaggerate the areal pulsations of bottom conditions. This is the case in epicontinental, or epeiric, seas, the deposits of which are commonly preserved in the continental crust; but similar conditions may be found on the continental rise, whose deposits (flysch facies) have a higher preservation potential than other deposits on the oceanic crust. Accordingly, we will discuss in the following chapters three examples in which our concepts can be put to test: (1) Storm-induced autochthonous coquinas (2) burrow horizons in bituminous shales (3) post-turbiditic trace fossil associations in flysch deposits, and compare them to the associated background faunas. In all cases it will be important that we know the ecology of the species implied.

STORM-INDUCED CHANGES IN THE BOTTOM FAUNAS OF EPEIRIC SEAS

In shallow marine environments, storms are the most common turbulence events. Their occurrence and intensity is unpredictable, but we may assume that there were always latitudinal gradients and that storms of increasingly higher intensity and extend have to be considered the more we extend the time scale of our observations. Since in a given situation the depth of storm wave base correlates with the energy level of the event, tempestite numbers within a given time interval can be used to contour the ancient basin morphology (Aigner, 1979). We can also use the varying degree of amalgamation, cannibalism and condensation of storm beds within a section as a measure of long-term fluctuations in sea level.

Sedimentologically, individual storm beds can be recognized by distinctive erosional and depositional structures (Aigner, in press) in graded succession. In contrast to similarly graded turbidites, these structures reflect wave rather than current activity.

With regard to the paleontological record, storm events concentrate shells of the organisms that inhabited the eroded soft muds (mainly infaunal molluscs). In fact, the resulting *parautochthonous coquinas* commonly preserve this background fauna better than the original shales, in which aragonitic shells are more likely to be diagenetically elimina-

ted. During times of reduced subsidence or dropping sea level, successive events commonly become cannibalistic to the extent that fossils from different chronological zones appear intermixed within a single *condensed* parautochthonous shell bed. The condensation process is enhanced by the tendency of previous erosional surfaces to consolidate diagenetically to form firm-or hard-grounds, which increasingly act as *reference horizons* during subsequent storm erosions.
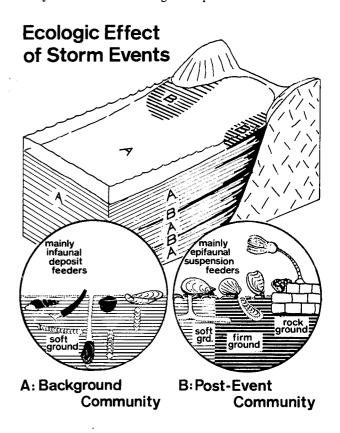
Ecologic Effect of Storm Events

A: Background Community   B: Post-Event Community

Fig. 1. In muddy deposits of shallow shelves, the post-event community (B) is confined to small and isolated populations during most of the time, but may extend over large parts of the basin after an extreme storm has changed bottom conditions. Faunal spectra (circles) are based on the Muschelkalk example. In addition, the background community (A) contained non-stalked brachiopods and primitive echinoderms in the Paleozoic and burrowing echinoderms after the Jurassic, while the rock ground community was enriched by pelecypod borers, but lost stalked crinoids, from the Cretaceous onwards.
Note that the background community has mainly aragonitic shells (drawn in black) with a reduced fossilization potential.

Storms do not only affect the background fauna and its preservation, but commonly create different bottom conditions. These allow the short-time establishment of a different *post-event* fauna, which occurs in three different ways: (1) burrows of the Glossifungites-association are characteristic for *firm grounds*. In contrast to the ichnocoenosis of the soft background muds, in which sediment feeding prevails, the Glossifungites association is dominated by burrows of suspension feeders. Their occurrence at the base of a shelly tempestite is a common indication that more than one event was involved in the formation of the bed. (2) If the process of erosion and reburial is repeated several times, the same reference horizon may diagenetically mature into a *hard ground*, which is documented by the burrows of borers

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(Trypanites association) and the incrustation by a cemented epifauna (oysters, echinoderms, barnacles, serpulids, bryozoans) of sessile suspension feeders.

(3) While post-event faunas of the types (1) and (2) are limited to intervals during which the storm-eroded surface remained exposed (which may have happened repeatedly), the species found in *autochthonous coquinas* are able to perpetuate the new habitat even though the founder surface (a firm ground, hard ground or shell lag) becomes covered by the shells of the own ancestors. Such shell beds are typically very low in diversity and contain forms of suspension feeders (oysters, brachiopods, epibyssate pelecypods or certain echinoderm species) which are attached loosely or only early in their ontogeny. Thus their remains may accumulate to beds of considerable thickness, before a heavy mud fall kills the whole population and re-establishes the softbottom habitat for the background fauna.

Autochthonous coquinas have long been used as marker horizons in regional stratigraphy, because they usually extend over large parts of the basin. Also they are commonly fingerprinted by characteristic differences, in size and shape, between the recurring populations of the same or closely related species. As examples, certain brachiopod and Myalina beds in the Paleozoic, Terebratulid beds in the Muschelkalk (Wagner, 1913), oyster beds in the Jurassic through Cenozoic and Carolia beds in the Eocene (Strougo, 1977) already suggest relatively fast evolutionary changes compared to the background fauna. This would agree with predictions from the punctuated equilibrium hypothesis. However, detailed comparisons of the different kinds of post-event communities, as opposed to the background communities, in continuous sections will be necessary to corroborate such a statement.

BENTHIC HORIZONS IN BITUMINOUS SHALES

Another type of epicontinental sedimentation is represented by bituminous shales, for which the Toarcian Posidonia Shales of Southern Germany with their well preserved fossils are a familiar example. In spite of recent challenges (Kaufman, 1978) we still adhere basically to an euxinic model with anoxic conditions at and near the bottom.

Lithologically, the Posidonia Shales appear to be rather continuous. On the other hand, vertical and lateral facies relationships as well as the occurrence of vertically embedded ammonite shells (Raup, 1973) indicate that the water was shallow enough for at least the stronger storms to have affected the bottom.

One expression of storm events may be seen in the *shell layers,* which are found at intervals throughout the section. They probably correspond to the previously discussed parautochthonous coquinas, but they are always very thin and contain mainly ammonite shells. Associated forms of pelecypods, articulate brachiopods, serpulids and bryozoa can be demonstrated to have lived not on «benthic islands» (Kaufman, in print), but attached to the ammonite shells before these sank to the bottom (Seilacher, in print). In other words, a benthic background fauna did not exist in this case. It should be mentioned, that measured azimuth shell orientations within these ammonite layers indicate unidirectional currents rather than the bipolar wave orientation that should be expected in true storm layers. But this deviation may be due to the transducing effect of the interface between the agitated surface waters and the oxygen-poor water body underneath.
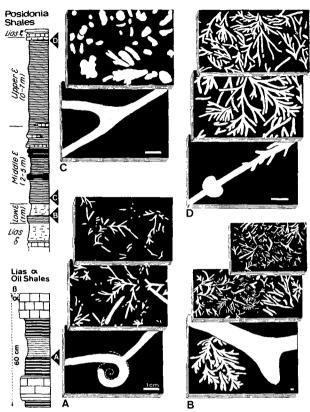
SEDIMENT FEEDER HORIZONS

Fig. 2. In the low energy environment of Liassic bituminous shales, anoxic conditions exclude benthic life during the background situation. Post-event communities, such as burrow horizons, consist of deposit rather than suspension-feeders and were so short-lived, that the original separation of burrowing levels (juvenile *Chondrites*/adult *Chondrites*/shrimp burrows) is still preserved (From Brenner & Seilacher, 1978).

A second, but rarer expression of turbulence events are horizons of truely benthic communities. We interpret them as analogues of the *post-event-faunas* in the more oxygenated facies; even though, corresponding to the quieter water conditions, they consist of deposit rather than suspension feeders. Since hard grounds are absent from this facies, we can distinguish only two types of post event faunas:

(1) *Bioturbation horizons* are a low energy version of the Glossifungites facies. They occur regularly at the tops of the bituminous units; but they are also found within the bituminous part of the section, more commonly so nearer to the margins of the basin. In both cases they indicate that oxygenation made the food-rich sapropelitic mud bottom accessible for sediment feeding worms (Chondrites) or crustaceans (Thalassinoides). In contrast to the feeding-burrows in the background fauna of the non-bituminous facies, these burrows still show a graded vertical distribution, reflecting the different levels, at which different age groups and different species exploited the mud underneath the contemporary sediment surface (fig. 2). This means that the community was only short-lived, since upward migration in response to sedimentation would have obscured the separation of the burrowing levels.

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(2) The Posidonia Shales also contain horizons with what seems to be true epibenthos. In contrast to the autochthonous coquinas of the higher energy regime, these *benthic horizons* are always very thin. Their fossils (minute echinoids and possibly Posidonia) are small, but very well preserved (echinoid spines still attached!), which indicates that this community became smothered soon after it had been established.

Another situation has been observed in the similar bituminous Lower Kimmeridge clay of England (Aigner, 1980). Here shell lags are encrusted by a single generation of small oysters, that seem to represent a reduced version of autochthonous coquinas. Possibly it was this type of poste-vent faunas that Kauffman (1978) observed in the Posidonia Shales.

Obviously in this case it was not so much a change in substrate consistency, but oxygenation that allowed the short-time establishment of specific post-event communities. Again, more comparative studies have still to be made, but already at this time we can say that the bed-to-bed changes are remarkable. This is most obvious in the bioturbation horizons, whose corresponding burrows are distinctive in size and behaviour for every horizon (fig. 2). But it is also known that Posidonia bronni is so different at different levels, that particular subspecies have been proposed for them.

POST AND PRE-TURBIDITIC TRACE FOSSIL COMMUNITIES IN FLYSCH DEPOSITS

Our third example refers to the bathyal or abyssal environments of the lower continental slope and the continental rise, where turbidity currents are the dominating events. For the question at hand this environment is in a way less suited, because its fauna is far from being endemic. On the other hand, the large numbers of turbidites and the high diversities of the trace fossil communities associated with them provide us with a unique opportunity to compare the evolutionary behavior of background and post-event faunas over longer periods of time.

The distinctive sedimentary structures of turbidites and their vertical and lateral gradations are well known (Bouma, 1962) and need not be repeated. Here we should only emphasize, that the sandy beds weathering out in the section represent only the lower part of the complete event deposit, which usually includes a «tail» of turbidity-reworked mud (Lingen, 1969). This means that the burrows impressed on the sandy tops are not made by sand-dwellers (Kern, 1980), but by mud burrowers that happened to penetrate the turbiditic top mud deep enough to reach the underlying sand.

In the shaly intervals, the boundary between turbiditic and hemipelagic mud may not be obvious lithologically; but it is commonly well marked by the burrows of the *post-turbidite community*. Like in the bioturbation horizons of the oil shales, these burrows are made by sediment feeders. They also preserve the original partitioning, between different species, of feeding levels below the surface of the turbiditic mud, which again means that this community existed only for a relatively short time after the event.

In contrast to the bituminous shales, flysch sequences also contain a background fauna of trace fossils distinct from the post-turbiditic ones. We call it the *pre-turbidite community*, because its burrows are found as erosional casts on the turbidite soles and not in the underlying hemipelagic muds, whose infauna they represent. This paradox, however, is a
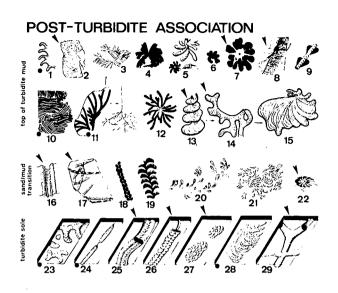

POST-TURBIDITE ASSOCIATION

Fig. 3. In the bathyal to abyssal flysch facies, the macrobenthos is almost exclusively represented by burrows of deposit feeders with highly differentiated search patterns. Nevertheless there is a sharp distinction between background and post-event communities.

The pre-turbidite association represents the background community and is dominated by open graphoglyptid tunnel systems (preserved as eroded sole casts), in which food was probably extracted from the mud by exosymbiotic microorganisms.

The post-turbidite community (this figure) is dominated by backfilled burrows indicating straight-forward sediment-ingestion. These burrows still preserve their ecological stratification (compare Fig. 2) below the surface of the turbidite mud. Some of them even reached, or penetrated, the sandy basal part of the turbidite.

Species from different parts of the world and from different levels in the Upper Cretaceous to Eocene are compiled in this figure, while rarely more than about half a dozen species are associated in an individual bed.

Formswith a dot are also known from pre-Cretaceous flysches. The rest are newcomers, of which the ones with a heavy arrow can be derived from shelf forms. Thin arrows indicate possible within-biotope speciations (from Seilacher, 1978).

List of trace fossils in Fig. 3

1. *Phycosiphon incertum* FISCHER-OOSTER
2. *Scolicia zumayensis* (GOMEZ DE LLARENA)
3. *Chondrites recurrens* FISCHER-OOSTER
4. *Zonarites alcicornis* FISCHER-OOSTER
5. *Gyrophyllites doblhoffi* LORENZ v. LIBURNAU
6. *Hydrancylus geniculata* (v. STERNBERG)
7. *Gyrophyllites kwassizensis* GLOCKER
8. *Granularia arcuata* SCHIMPER
9. *Muensteria fuggeri* LORENZ v. LIBURNAU
10. *Helminthoida labyrinthica* HEER
11. *Chondrites intricatus* BRONGNIART
12. *Taenidium fischeri* HEER
13-15. *Zoophycos* div. sp.
16. *Scolicia prisca* QUATREF.
    (Palaeobullia preservation)
17. *Gyrochorte comosa* HEER
18. *Caulerpites annulatus* ETTINGHAUSEN
19. *Polykampton alpinum* OOSTER
20. *Zonarites* sp.
21. Indet.
22. *Gyrophyllites* (*Palaeosemaeostoma* preservation)
23. *Phycosiphon incertum* FISCHER-OOSTER
24. *Uchirites triangularis* MACSOTAY
25. *Scolicia prisca* QUATREF.
    (*Subphyllochorda* preservation)
26. *Scalarituba missourensis* WELLER
27. cf. *Scalarituba*
28. *Lophoctenium ramosum* (TOULA)
29. *Granularia granulata* v. SCHLOTH.

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preservational artefact: Open tunnel systems, not filled with fecal material, can easily be eroded and sand-cast by a distal turbidity current; but otherwise they become wiped-out by compactional collapse (Seilacher, 1978). Since we also find tunnel systems from different penetration levels cast on the same bedding plane, we may assume that the pre-turbidite types of burrows were present throughout the long periods of hemipelagic mud sedimentation.

In the case of the flysch traces, the difference (with no species overlap) between a background and a post-event community is surprising, because
(1) there was probably no difference in consistency between the hemipelagic muds and the turbiditic muds;
(2) both communities are characterized by highly differentiated feeding burrows.

Probably this difference reflects the different nature and distribution of food in the two types of mud. In the background situation food comes as a continuous rain, but it is very much degraded. Therefore highly specialized feeding strategies, including farming, had to be developed by the macrobenthos living on this poor but reliable resource. Turbidity currents, in contrast, introduce less degraded detrital food, which becomes enriched in the top layers of the graded turbidite. This resource can be exploited by straight-forward sediment feeding, as it is expressed by the backfilled burrows of the post-turbidite community.

In both communities, overall diversity has increased considerably through Phanerozoic times (Seilacher, 1977 and 1978; conflicting evidence presented by Kern, 1980 and Pickerill, 1980 largely results from different standards of taxonomic distinction). New data show that this increase was not linear: After an initial burst in the Early Paleozoic, diversity seems to have levelled off. A second burst followed in the Cretaceous, coinciding with the angiosperm «revolution». Independent of the possible causal relationships, the stepwise increase suggests that the carrying capacity may have become a limiting factor for community evolution in this food-deprived but time-stable biotope. With respect to our theme it is interesting that the Cretaceous diversity burst seems to have affected both communities of flysch trace fossils, but in different ways. While the diversity of the pre-turbiditic background community is increased mainly by within-biotope radiation of one group (Graphoglyptida), the post-turbidite community becomes enriched mainly by evolutionary immigration of shelf forms, which adapt to the style of the new biotope by becoming miniaturized and by evolving specialized feeding behaviors.

While we have a certain idea about long term evolutionary trends, bed-by-bed changes of the two communities in turbidite sequences still need to be studied. Although trace fossils tend to be rather conservative, there may be minor changes on such a small time scale, which we expect to be more pronounced in the postevent association. There is also the chance, like in the previous examples, to include microfossils (Butt, 1980), provided their sampling follows the reference grit of event stratigraphy rather than lithologic bed units.

EPILOGUE

The catastrophic view of historical geology and paleontology is as old as the field itself. A few decades ago, this view focussed on orogenies and glaciations, neither of which coincide with the major changes in faunal history. More recently, plate tectonic events such as the formation of Pangaea in the Permian (Schopf, 1974) and an asteroid impact at the and of the Cretaceous (Alvarez et al. 1980) have been evoked for the eonic turnovers, global lowering of sea level for the minor turnovers at stage and series boundaries.

It is interesting to note, that in most «neocatastrophistic» theories emphasis has switched from the dramatic impact of the accident itself to its ecologic after-effects (reduction of shelf habitats by Pangaea formation; sunlight «switch-off» by dust shield after the asteroid impact). Our concept follows the same trend, though at a much more modest scale. The ecologic effects of even the most severe storms, floods and turbidity currents are much too local and too common to be responsible for macroevolutionary changes individually. But at the level of populations, particularly of the more endemic ones, such events and their ecologic bottle necks may be an important motor for evolutionary changes. At the same time the effects of individual events are still resolvable by sedimentological and paleoecological methods. In fact, event deposits constitute the grain of temporal facies recognition.

It seems to me that *event stratigraphy* is at the right spaciotemporal level, at which a link between the seemingly separated realms of micro and macro-evolution (sensu Stanley, 1977) should be sought. It also happens to be at the scale at which we study geologic sections and at which we should make our environmental interpretations. This field is thus open to all of us, irrespective of geographic, stratigraphic and taxonomic specialisations. Let us hope that future research in this direction will also reconcile the biogeological and the paleobiological viewpoints in our field and thereby help to overcome a schizophreny that is widely spread among the younger paleontologists of to-day.

ACKNOWLEDGEMENTS

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