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A consideration upon macrobenthic assemblages of the Korytnica Clays (Middle Miocene; Holy Cross Mountains, Central Poland)

ABSTRACT: Paleocology of macrobenthic assemblages of the Korytnica Clays (Middle Miocene; Holy Cross Mountains, Central Poland) is considered basing upon two contrasting neoecological theories. Comparison of the results shows that what is to be regarded as distinct communities in the light of one of the theories, appears as a product of resilient responses of a single benthic community type according to the other theory. This conclusion undermines validity of each paleo-environmental inference based solely upon the ecological structure of paleocommunities. The derivative nature of community-paleoecological analyses does, however, not affect any evolutionary-paleoecological argument.

INTRODUCTION

The Korytnica Clays were deposited in a shallow and protected small basin formed by the Middle Miocene (Badenian) marine transgression onto the southern slopes of the Holy Cross Mountains, Central Poland (Radwański 1969, Bałuk & Radwański 1977). Paleocology of their abundant and excellently preserved macrobenthos was recently studied by the present author (Hoffman 1977). In that paper, distributional patterns of forty dominant taxa were analysed with the use of a multivariate technique and shown to indicate the occurrence of some distinct fossil assemblages (derived from originally distinct ecological communities) controlled by a few environmental and biotic factors as well; the latter were identified as mostly those involved in a process of ecological succession leading from pioneer colonization of a barren muddy substrate up to eventual development of a mature seagrass-associated community. The whole argument was based upon a modern ecological theory (Margalef 1968, Odum 1971).

One may, however, ask how strongly does this community-paleoecological interpretation depend upon its neoecological theoretical background, and how heavily does this dependence affect the paleobiological and paleoenvironmental

inference. In fact, the nature of both ecological-succession process and ecological communities themselves is in hot dispute among the scientists. The present paper is therefore aimed to reconsider the previously studied data set using somewhat different descriptive terms (namely, those following a system-analytic approach to the community paleoecology; cf. Hoffman & al. 1978) and in the light of another ecological theory (Holling 1973, Horn 1976).

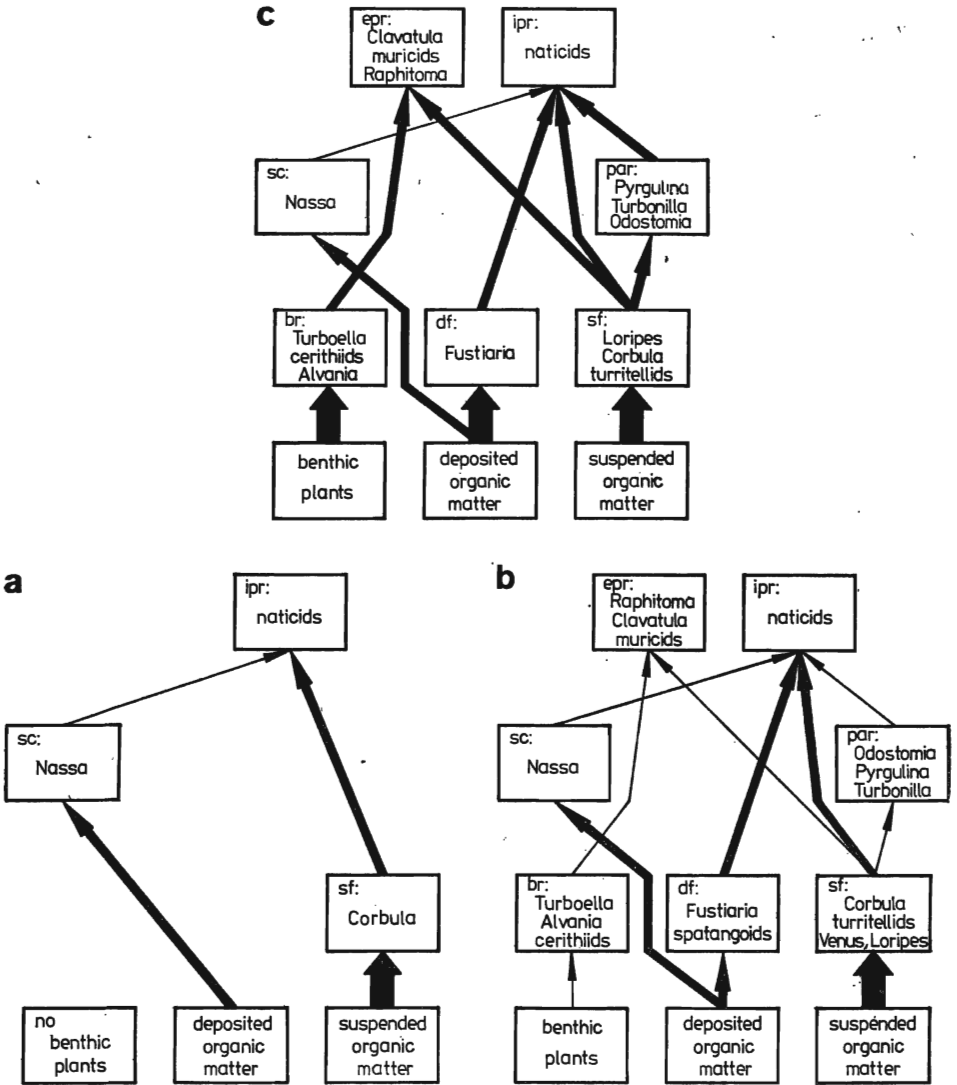


Fig. 1. Simplified trophic webs of *Corbula* to *Turboella-Loripes* ecological continuum

Width of the arrows indicates relative significance of the paths; only dominant taxa are shown
epr epifaunal predators, *ipr* infaunal predators, *sc* scavengers, *par* parasites, *br* browsers, *df* deposit feeders, *sf* suspension feeders

a — *Corbula* community, b — *Corbula*-scaphopod community, c — *Turboella-Loripes* community

KORYTNICA FOSSIL ASSEMBLAGES

As judged from a *Q*-mode factor analysis of relative-abundance data on distribution of the lithothamian algae and 39 dominant macrobenthic (mostly mollusk) animal taxa, some distinct fossil assemblages occur in the Korytnica Clays. These assemblages were called (Hoffman 1977) after their most important organic constituents as follows: (i) *Corbula*, (ii) *Corbula*-scaphopod, (iii) *Corbula*-spatangoid, (iv) *Turboella-Loripes*, (v) turritellid, (vi) *Pteromeris*-coral, and (vii) *Ostrea* assemblages.

Both the *Pteromeris*-coral and *Ostrea* assemblages are insofar known from but singular samples (there is, however, some evidence for their commonness in the basin; Dr. W. Bałuk, *pers. communication*) and represent clearly distinctive and unique in the Korytnica basin environments and biota. The other assemblages share usually most dominant macrobenthic animal taxa, the relative abundances of which appear, however, widely variable among the assemblages. The variation in inferred ecological structure (Figs 1—2) among the Korytnica communities reflects a variation in their

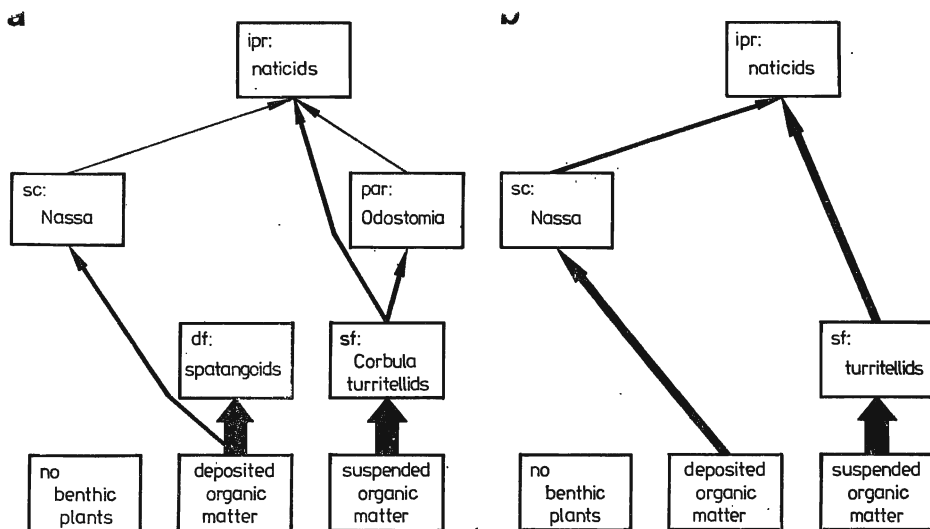


Fig. 2. Simplified trophic webs of the Korytnica bay-marginal communities; for explanation of the symbols see Text-fig. 1

a — *Corbula*-spatangoid community, b — turritellid community

biotope which may be briefly summarized as follows: The *Corbula* community lived under conditions of very high water turbidity. Both the *Corbula*-scaphopod and *Turboella-Loripes* communities inhabited fairly quiet- and clear-water areas; the latter community was, however, associated with a more or less dense seagrass cover. The turritellid community settled marginal muddy flats characterized by an unstable bottom microrelief and salinity fluctuations. Finally, the *Corbula*-spatangoid community inhabited some shelters with rather poor water circulation and low redox potential at the sediment-water interface.

The samples from within the *Corbula*, *Corbula*-scaphopod, and *Turboella-Loripes* assemblages change in their taxonomic composition and the original ecological structure almost continuously

from the extreme *Corbula* endmember to the other extreme of *Turboella-Loripes* endmember. In fact, there are samples consisting almost exclusively of *Corbula gibba* itself and on the other hand, ones comprising much more than a hundred mollusk species with *Corbula gibba* lacking at all. This trend in taxonomic composition and diversity is also paralleled by a distinct increase in complexity of the original trophic webs (cf. Fig. 1). As seen from the comparison of a dozen samples taken approximately along a vertical section, these changes displayed a more or less oscillatory pattern in time (Fig. 3). The *Corbula* to *Turboella-Loripes* continuum was therefore interpreted

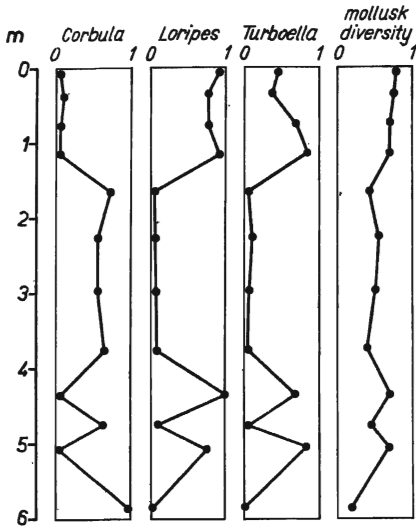


Fig. 3

Oscillatory changes in sample composition (relative abundance of three dominant taxa, and mollusk diversity) of the *Corbula* to *Turboella-Loripes* ecological continuum (from: Hoffman 1977, Text-fig. 41)

(Hoffman 1977) as reflecting a true, short-term ecological succession leading from an initial colonization of a barren muddy bottom up to development of a mature seagrass-associated community. The oscillations in composition are then to be regarded as temporary degradations caused by such local physical disturbances as an increase in water turbulence, turbidity, or sedimentation rate. This conclusion permits also a reconstruction of the order of ecological succession in the Korytnica seagrass-associated macrobenthic community (Fig. 4).

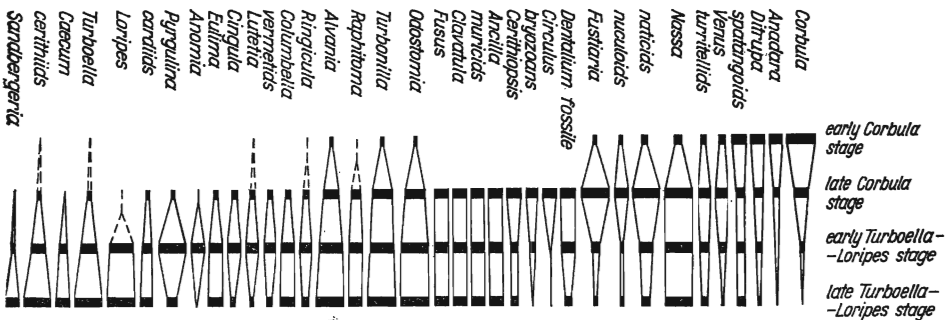


Fig. 4. Ecological succession leading to development of a mature seagrass-associated macrobenthic community; for each taxon changes in its relative abundance at successive seral stages are shown (from: Hoffman 1977, Text-fig. 42)

BETWEEN-COMMUNITY RELATIONSHIPS

One may, however, wonder whether the above summarized interpretation of changes in the Korytnica seagrass-associated community as a process of the community regeneration after an episodic devastation or disturbance is adequate or not. In fact, one can hardly say that the early successional species did actually transform their biotope in such a way as to permit the later species to flourish; unless the very concept of biologically controlled ecological succession reduces to the obvious banality that a herbivore needs always a plant to graze, and a predator needs prey species to feed upon.

The *Corbula*-dominated stage is not necessary to permit development of a seagrass cover. At best, it may result in stabilization of an initially fluid muddy bottom and thus, in a decrease in bottom-sediment resuspension. This may in its turn accelerate a drop in turbidity of the nearbottom water layers down to the point below which more efficient suspension feeders are able to persist. Then, the pioneer *Corbula gibba* would be gradually outcompeted from the environment. One may thus suppose that the ideal *Corbula* community (composed almost exclusively of *Corbula gibba* itself) represents an explosion of the opportunistic species (*cf.* Levinton 1970, Hallam 1972) displaying an extremely high intrinsic rate of reproduction, very short generation time, and large migration ability.

This early portion of the inferred ecological succession leading to development of a complex benthic community (*viz.* *Corbula*-scaphopod one) is probably to be best represented as a Markovian replacement process. This is meant that it can be adequately described in purely statistical terms of a table showing the probabilities that particular organisms will be in a specific time replaced with other organisms conspecific with them or not. The basic assumption of such a succession model is that the table of replacement probabilities remains constant through time. Actually, however, this is rarely (if ever) the case in the nature. Unique historical events affect episodically communities hindering them from returning to their initial steady states (Paine 1974, Horn 1976). One may claim that introduction of seagrass stands to a benthic ecosystem represents just such an unexpected, purely historical event changing entirely the original table of species replacement probabilities.

The Korytnica bay-marginal communities (*viz.* turrnellid and *Corbula*-spatangoid ones) can also be interpreted in terms of historical vagaries of a disturbance and subsequent succession process. In fact, both the communities are distinctly dominated by very early successional species of the *Corbula* to *Turboella-Loripes* ecological continuum. Their divergent compositions and structures may thus reflect shifts to dominance of species playing usually but subordinate roles in the mature structure, triggered by some severe physical disturbances and maintained subsequently by purely biological, interspecific relationships. The turrnellid community could form owing to a rapid increase in population density of those semi-infaunal, largely sessile, suspension feeding gastropods excluding usually most infauna and sessile epifauna from an otherwise suitable environment due to their gregarious habits and high competitive potential for space at and just below the sediment-water

interface. Such an initial explosive increase in turrnellid relative abundance and density may be explained by some episodic environmental fluctuations (e.g. in salinity, turbulence, or bottom microrelief) that the turrnellids were able to resist. Causal mechanisms of a similar type may also be claimed to explain the formation of the *Corbula*-spatangoid community. Then, the variation in original dominance hierarchy and ecological structure among the most important Korytnica fossil assemblages (Figs 1—2) could actually represent an example of multiple stable points (Fig. 5) reached by benthic ecosystems of a single type (cf. Connell 1972, Sutherland 1974), instead of an effect of preponderant environmental controls upon the ecological organization of Korytnica macrobenthos as it was claimed in the original interpretation (Hoffman 1977).

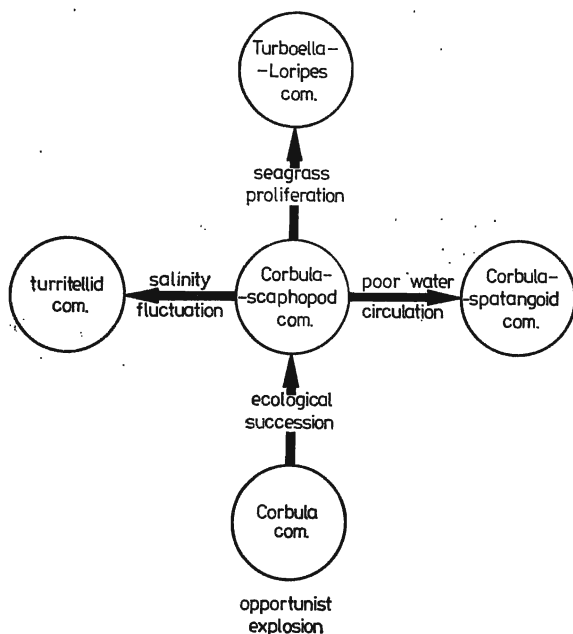


Fig. 5

Multiple-stable-point interpretation of between-community relationships in the Korytnica basin

When the main Korytnica communities are conceived in terms of alternative steady states of a benthic ecosystem, the system itself is to be considered as a rather resilient one. The term ecological resilience was introduced by Holling (1973) for the ability of communities to absorb disturbances and still maintain the same web of biological interactions; it is contrasted to the ecological stability meant as the ability of communities to return to the original equilibrium after a temporary disturbance. In fact, the constituent populations of the Korytnica communities and their interrelationships did generally remain the same but some peculiarities of the particular kinds of succession (i.e. leading to development of the *Turboella-Loripes*, turrnellid, and *Corbula*-spatangoid communities) resulted in the population sizes and hence, the patterns of energy flow having been widely variable among the ma-

ture communities. In other words, the communities underwent structural changes even though they preserved their taxonomic identity.

It is important to note at this point that there are no objective criteria to distinguish clearly between a resilient response of a community to disturbance and an upgradation of a newly introduced community. (This is especially clear when expressed in system-analytic terms; cf. Weinberg 1972). Therefore, the author is unable to ultimately recognize the nature of the relationship of the Korytnica bay-marginal communities to the *Corbula* to *Turboella-Loripes* ecological continuum. Either the bay-marginal communities were actually distinct communities occupying bottom areas adjacent to the area covered with seagrasses; or they were merely products of the ecosystem resilient responses to various environmental disturbances.

CONCLUSIONS

All the above argument permits a conclusion that because of their very nature community-paleoecological interpretations do strongly depend upon the underlying neocological theories, which dependence does heavily affect paleoenvironmental inferences. In fact, one can never determine whether one deals with distinct but intergrading communities of Johnson (1972) or with resilient reactions of a single ecosystem; whereas the attribute of ecological resilience may occur quite commonly among soft-bottom benthic communities. Hence, one can hardly conclude with any reasonable degree of certainty about the biotope characteristics on the sole basis of the ecological structure of a community. The structures of the Korytnica bay-marginal communities may reflect some permanent restrictive environmental conditions or just historical vagaries of the ecosystem development, as well.

Invariant in both the above discussed paleoecological interpretations of the Korytnica macrobenthic assemblages are at least three steady-static ecological structures (viz. *Turboella-Loripes*, turritellid, and *Corbula*-spatangoid ones). No matter whether they do actually represent intergrading communities or merely distinct stable points of a single ecosystem, they are recurrent in ecological time and therefore, can be justifiably treated in terms of community types. While it is just a community type, which is here meant as a pool of species or a range of taxonomic variability within a constant framework of ecological structure, that makes the true subject of the evolutionary paleoecology. Then, the derivative nature of community-paleoecological conclusions appears negligible for research in the latter field.

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A. HOFFMAN

PRÓBA REINTERPRETACJI ANALIZY EKOLOGICZNEJ MAKROBENTONICZNYCH ZESPOŁÓW ORGANICZNYCH Z IŁÓW KORYTYNICKICH

(Streszczenie)

Przedmiotem pracy jest próba odmiennej interpretacji ekologicznej makrobentonicznych zespołów organicznych rozpoznanych wśród fauny iłów korytyńskich. W poprzedniej pracy poświęconej ekologii tych zespołów rozważono je (Hoffman 1977) w świetle najbardziej, jak się zdawało, adekwatnej teorii ekologicznej. Obecnie zaś zinterpretowano je w kategoriach innej, konkurencyjnej teorii. Okazuje się przy tym, że zróżnicowanie pierwotnej struktury ekologicznej zespołów (*patrz* fig. 1—2) jest za małe, by można było owe zespoły uznać za odrębne biocenozy, a i zrekonstruowana poprzednio sukcesja ekologiczna (*patrz* fig. 3—4) nabiera innego, przede wszystkim statystycznego charakteru. Poszczególne zespoły trzeba w świetle tych rozważań traktować jako odmienne, lecz trwałe stany ekosystemu jednego tylko rodzaju, tj. jako skutki elastycznej reakcji ekosystemu bentonicznego na zaburzenia środowiska (*patrz* fig. 5).

Dyskutowana rozbieżność interpretacji paleoekologicznych zależy od założonej podstawy teoretycznej podważa wiarygodność wszelkich wnioskowań o środowisku opartych jedynie na analizie ekologicznej biocenoz kopalnych. Nie ma ona natomiast większego znaczenia dla wywodów z dziedziny paleoekologii ewolucyjnej.