acta
geologica
polonica

Vol. 30, No. 1 Warszawa 1980

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Ecostratigraphy: the limits of applicability

ABSTRACT: Chronostratigraphy recalls a set of arbitrarily chosen reference time-planes. In turn, ecostratigraphic time-scale refers to remarkable events recorded in the stratigraphic distribution of species. Biotic evolution appears as the model of the geologic time as conceived in terms of both the chronostratigraphic and ecostratigraphic time-scale. The basic assumption about the evolution, required by ecostratigraphy, is that either there is the process of community evolution, or co-evolution among large groups of species plays an important role in the biotic evolution. There is no community evolution in the nature because ecological communities themselves are merely an epiphenomenon of species evolution. Empirical data show that co-evolution is insignificant among planktic organisms; but it is important among shallow-marine benthic organisms. This observation sets the limits of applicability to the ecostratigraphic time-scale which appears adequate to that part of the fossil record that represents shallow-marine realm, but not to the record of pelagic realm.

INTRODUCTION

Ecostratigraphy (Hedberg 1958; Martinsson 1973, 1978) is among the most modern stratigraphic methods. Actually, it is something more than merely a method; it is an approach to (Cisne & Rabe 1978), or even a philosophy of stratigraphy (Krassilov 1978). Nevertheless, its theoretical background and its relationships to other stratigraphic and biologic theories are thus far fairly cloudy. The limits of its applicability are unknown. This is probably why there are so few doubtless achievements of ecostratigraphy. One is therefore tempted to analyse the theoretical justification for ecostratigraphy in some detail. This is the aim of the present paper.

CHRONOSTRATIGRAPHIC *VERSUS* ECOSTRATIGRAPHIC TIME-SCALE

The concept of chronostratigraphy as proposed by Hedberg (1948, 1954, and a dozen later papers) recalls a set of arbitrarily chosen reference time-planes making up the internationally agreed geologic

time-scale. The reference time-planes are entirely abstract and marked each merely by a designated reference point in the type section. Thus, the Silurian/Devonian boundary is marked by a golden spike hammered in the rock at Klonk, Czechoslovakia (Chlupáč & *al.* 1972). A chronostratigraphic unit comprises all the rocks formed at the time between two successive reference time-planes and hence, it may lack and indeed most commonly lacks any internal unity or homogeneity. The chronostratigraphic time-scale consists therefore of divisions, not units (Harland & *al.* 1972). The reference time-planes must not have anything to do with remarkable features of the fossil record; they must not refer to any remarkable events in the geobiologic history of the earth. Nevertheless, time-correlation of rocks is most commonly approached through biostratigraphic methods intended to recognize ancient deposits accumulated at moments equidistant from the nearest time-plane. It is so because the time-planes are defined in terms of evolutionary events in the biotic history of the earth, and considefed as falling usually within the limits of biostratigraphic-correlation confidence intervals. In this context, the evolution of organic species appears as the model of the geologic time as conceived in terms of the chronostratigraphic time--scale; and the only assumption about the evolution of organic species, required to validate the biochronostratigraphic approach to the earth history, is that all the species are of monophyletic origin.

No doubt that the chronostratigraphic approach is valid. In fact, it offers an excellent common language for geologists and paleontologists all over the world. However, the resulting classification of rocks is entirely artificial and gives by itself no valuable information about the earth history. As seen from the chronostratigraphic perspective, the geobiologic history of the earth appears as a sequence of disorderly, randomly arranged events; while the science in general is aimed just to find out the order of the nature or to impose an order onto the chaos of perceived natural phenomena. In other words, the ideal time--classification of rocks should reflect a geologic time-scale consisting of units, not divisions (*sensu* Harland & *al.* 1972). This ultimate goal will be achieved with attainment of the ecostratigraphic time-scale. In fact, the concept of ecostratigraphy recalls a set of reference time-planes representing each a remarkable geobiologic event recorded in the stratigraphic distribution of organic species (Martinsson 1973, 1978; *cf.* also Krassilov 1978).

Actually, the higher order chronostratigraphic units (erathems, systems, most series, and several stages) approximate commonly ecostratigraphic units because the traditional way to recognize a chronostratigraphic reference time-plane was to point to phenomena reflecting some remarkable events in the geobiologic history of the earth. Thus, the Precambrian/Cambrian boundary was intended to co-incide with

the time of skeletal-life explosion, and the Permian/Triassic boundary was marked by the evidence of a great extinction. At the level of chronozone, the chronostratigraphic and ecostratigraphic time-scales become, however, completely discrepant. In biochronostratigraphy, there are many kinds of zones based upon time ranges of single species and their partial overlaps (Henningsmoen 1961). Ecostratigraphy is in turn concerned with remarkable evolutionary events and hence, ecostratigraphic zones (coenozones) are to be based upon time ranges of communities, taxocoenes, large species groups, and their partial overlaps (Krassilov 1974, 1978). Thus, the biotic evolution appears as the model of the geologic time as conceived in terms of the ecostratigraphic time-scale (just as it is in the case of chronostratigraphy). The basic assumption about the evolution, required by the ecostratigraphic approach to the earth history, is that either there is indeed the process of community evolution reflected in the fossil record by cliseres (*i.e.*, sequences of climax ecosystems replacing each other in response to physical disturbances; Krassilov 1974) divided into coenozones; or at least co-evolution among various species co-occurring in a single macrohabitat plays an important role in the evolution of species. Were both these assumptions about the organic evolution invalid, a sequence of coenozones would be merely an epiphenomenon of the evolution, migration, and extinction of several species evolving as mutually independent lineages. The boundaries of coenozones would then not reflect any remarkable evolutionary events but merely some random associations of quite usual phenomena; in such a case, one should consequently conclude that the only valid geologic time-scale to be achieved through biostratigraphic methods is the chronostratigraphic one.

THEORETICAL BASIS FOR ECOSTRATIGRAPHY

The present author was deeply involved in the study of community evolution (Hoffman & Szubzda 1976; Hoffman 1977, 1978a, 1979a) which is certainly among the main topics of community paleoecology. However, the present author's opinion is now that community paleoecology as a whole is merely an epiphenomenal science because ecological communities themselves are merely an epiphenomenon of the overlaps in distributional patterns of various organisms controlled primarily by the environmental framework (Hoffman 1979b). Three lines of argument can be developed to support the latter conclusion. Firstly, the actual degree of community integration is in general insufficient to induce any driving force of a structural development predicted by the ecological theory. Secondly, the assumption that natural communities achieve with time an equilibrium state, representing an optimum habitat and resource partitioning among the component species, is invalid at least as a generalization. Thirdly, the concept of biologic reality and distinctness of the community level of biotic organization implies assignment of a significant role to the group selection, while the latter idea is largely falsified

and refuted by the modern biology. One may thus conclude that the concept of ecostratigraphic coenozones based upon the record of community evolution is unjustified.

The only possible justification for ecostratigraphy would then be a commonness of co-evolution among large species groups associated in a single macrohabitat. However, the absence of any considerable niche partitioning from highly diverse tropical rain forests, recognized usually for the model of perfect climax communities, points to the weakness of co-evolutionary mechanisms arising from competitive interactions (Connell 1978). In fact, discarded the assumption that ecological communities are commonly in equilibrium, co-evolutionary buffering of interspecific competition in large niche complexes may appear improbable. The scope of co-evolution seems to be restricted mostly to predator-prey, parasite-host, and herbivore-plant interactions involving each a negative feedback loop. The problem that remains to be solved is, however, the common co-occurrence in a single macrohabitat of a large number of closely related species, reflecting certainly a minute niche partitioning such as those recorded among rodents by Mares (1976) and among bryozoans by Winston (1977) or predicted from the aerosol model for various filter feeders (*e.g.* bivalves) by LaBarbera (1978). To account for this taxonomic diversity and corresponding niche specialization in some groups, one may refer to either stochastic patterns of diversification arising from entirely opportunistic speciation in independent evolutionary lineages (*cf.* Raup & *al.* 1973, Anderson 1974, Gould & *al.* 1977); or co-evolution among ecologically related species at a single trophic level. To determine the relative importance of both these modes of diversity production is crucial for analysis of the theoretical validity of ecostratigraphic approach to the earth history.

NICHE PATTERNS AND CO-EVOLUTION

One may argue that even despite the apparent prevalence of communities non-equilibrated in ecological time, a co-evolution leading to niche subdivision among related species is possible within a community type (*sensu* Whittaker 1970, Hoffman 1979b) in equilibrium in evolutionary time. Evolutionary equilibrium of a community type (or community permanence; Hoffman 1979a) is here meant as a long-term persistence of the component lineages permitted by a sufficient constancy in the environmental framework. This notion widely differs from that one derived from the theory of island biogeography (*see* Wilson 1969; Webb 1969, 1976; Strong 1974; Rosenzweig 1975; Bretsky & Bretsky 1976; Mark & Flessa 1977) in that the latter concept refers to a steady-static species number limited by the carrying capacity (be it set by biotic or abiotic parameters) of a geographic region or bioprovince; while under the conditions of community permanence, an increase in species number may well occur through optimization of niche dimensions among the taxa that filled initially up an ecological vacuum. (Whether outcompetition of a species or lineage from a persistent community type is possible or not, may be disputable.)

When a co-evolution among ecologically related species of a single trophic level is invoked to account for a niche subdivision, the basic assumption is that under conditions of long-term maintenance of a sufficiently constant (or at least predictable) environmental framework the ergonomic nature of organic evolution should eventually result in optimization of the niche pattern (Schopf 1973, 1977) predetermined in a sense by the very nature of a macrohabitat or biotope (*cf.* Hutchinson 1968). To claim that niche partitioning arises just from an universal trend to optimize niche dimensions, appears reasonable because a decrease in interspecific competition is obviously of advantage to the individuals. This may indeed be the cause for the apparent commonness of divergent character displacement (*see* Eldredge 1968, Kellogg 1975, Schindel & Gould 1977, Hoffman 1978b; to cite but a few examples from the fossil record). It is however to be noted that under certain ecological conditions it is a character convergence that gives the optimum solution to the problem in minimization of interspecific competition (MacArthur & Levins 1964, Grant 1972, Cody 1973). Therefore, one can only assess that there are macrohabitats, mostly those with a constant supply of diversified resources, where specialists are more fit than opportunists because of their higher efficiency, which should in average result in prevalence of niche subdivision in those environments.

Thus far, paleocommunity descriptions are usually much too vague to permit estimation of the actual frequency of community permanence in evolutionary time and recognition of its relationship to physical environment. The data available indicate only that community permanence as defined above (or rather preservable niche-complex permanence) occurs quite commonly in nearshore, high-stress marine habitats (*cf.* Wright 1974, Watkins & Boucot 1975, Hoffman 1977). This may however well be an artifact of considerable methodologic problems involved in analysis of more complex ecosystems. In the latter case, a large number of coeval paleocommunities are to be sampled in order to reconstruct the actual composition of an ancient community type, prior to any attempt to analyse its evolutionary longevity; furthermore, a sound but independent evidence of environmental limits to the ecospace realized by a community type is also necessary. One can thus merely cite those few authors that may indeed have some evidence that complex subtidal community types do also show a community permanence (*see* Berry 1974, Watkins 1974, Boucot 1975). In addition, Krassilov (1978) claims a considerable community permanence for the Mesozoic deciduous forests of Siberia. It is to be concluded that much precise community-oriented paleoecologic work is needed before one will be able to tell finally whether community permanence occurs commonly or not; whether the precondition to co-evolution among several ecologically related species of a single trophic level was ever met; and if so, under what environmental conditions.

Fortunately, there is also another approach to the problem. The basic assumption is that a community type in evolutionary disequilibrium should show much higher rate of evolutionary turnover of species than an equilibrated one (or close to equilibrium), regardless of the mode of ecological reorganization or rate of environmental change. This assumption appears trivial because an increase in both speciation and extinction rate is obviously to be expected under conditions of a major change in environmental framework. Time distribution of speciation events (no matter, of anagenetic or cladogenetic type) in the macrohabitat specific for a community type may thus make basis for recognition in the fossil

record of community permanence, evolution, and reorganization. The latter two terms are here meant very imprecisely, intended merely to point out that a change in composition of a community type may be gradual or jerky, respectively, depending mostly upon the rate of environmental change and the average virtual eurytopy of the component taxa. Speciation rate can be expected to be a stochastic constant under conditions of community permanence and evolution; whereas most new species should arise in bunches or clusters in a macrohabitat the geologic development of which permits periodically achievement of an evolutionary equilibrium disturbed by community evolution or reorganization. Much analogy should be shown by distribution of specific extinction rates in various environmental settings (*cf.* Van Valen 1973, Salthe 1975, Raup 1978).

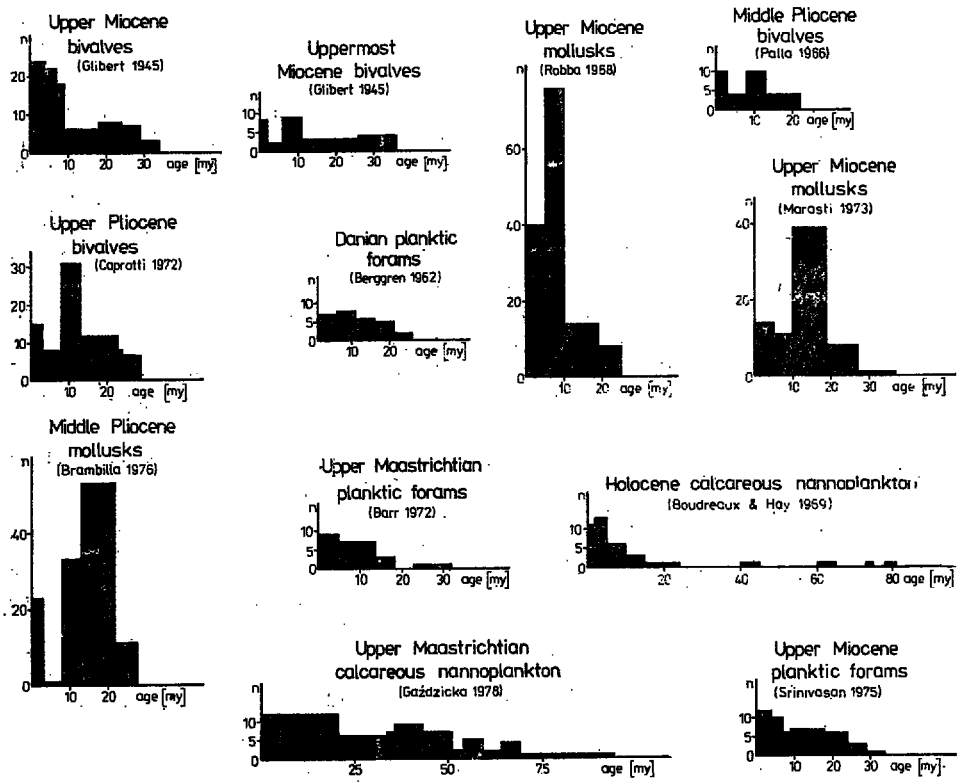

Fig. 1. Chronospecies-longevity histograms in samples of co-existing species from shallow-marine benthic and pelagic habitats (cf. Table 1)

Stratigraphic correlation was taken to the level of geologic stage or substage, with the samples and chronospecies originations dated at the midpoint of a time interval. Origination dates given by the original taxonomic works referred to in the figure were often considerably modified with up-to-date paleontologic research taken into account

Time-scale used for the Neogene *after* Berggren & Van Couvering (1974) and Van Couvering & Berggren (1977); for the Paleogene *after* Berggren (1972); for the Cretaceous and Late Jurassic *after* Van Hinte (1976a, b)

One is hardly able to find in paleontological literature data adequate to determine precisely the time distribution of species originations for a large niche complex in a single macrohabitat persistent over a considerable span of geologic time. The problem can however be reverted and approached with the use of a method similar to that introduced recently by Stanley (1978). In order to recognize the mode of speciation in a macrohabitat, one may study a longevity-frequency-distribution of chronospecies found living together and thus, forming supposedly a consistent niche complex (no matter, with overlapping or non-overlapping niches). There is obviously an unavoidable taxonomic bias inherent in data set of this type. Basic data should therefore be always critically evaluated and judged on their own prior to their actual use in analysis.

Table 1

Chronospecies-longevity distributions in samples of co-existing species from shallow-marine benthic and pelagic habitats; for explanation of the nature of the data *see* Text-fig. 1

Organic group	Geologic age	Sample size	Longevity distribution (at .95 confidence level)	Source of data
bivalves	uppermost Miocene	42	non-linear	Glibert (1945)
bivalves	Upper Miocene	88	linear	Glibert (1945)
bivalves	Middle Pliocene	28	non-linear	Palla (1966)
mollusks	Upper Miocene	138	non-monotonic	Robba (1968)
bivalves	Upper Pliocene	73	non-monotonic	Caprotti (1972)
mollusks	Upper Miocene	73	non-linear	Marasti (1973)
mollusks	Middle Pliocene	121	non-monotonic	Brambilla (1976)
planktic foraminifers	Danian	28	linear	Berggren (1962)
calcareous nannoplankton	Holocene	38	linear	Boudreaux & Hay (1969)
planktic foraminifers	Upper Maastrichtian	28	linear	Barr (1972)
planktic foraminifers	Upper Miocene	45	linear	Srinivasan (1975)
calcareous nannoplankton	Upper Maastrichtian	75	linear	Gaździcka (1978)

Given constant rates of chronospecies origination and extinction, the survivorship curve of species is obviously linear, as well as the longevity distribution. Therefore, non-linearity of a chronospecies-longevity distribution appears indicative of significant fluctuations in the origination and/or extinction rates which may point to the niche-complex permanence punctuated by niche-complex evolution or reorganization. A change in extinction rate should, however, not cause any deviation from the monotonic nature of longevity distribution.

Non-monotonic longevity distribution among a large set of co-existing species suggests that the species originated in bunches. Distribution of this type does not prove that the niche complex did indeed achieve evolutionary equilibrium because it may be produced by alternation of niche-complex evolution and reorganization as well. The longevity-distribution approach is therefore to be supplemented with a classic community-oriented paleoecologic research. This is

why the recent demonstration of a fluctuating origination rate of the Silurian graptolites (Rickards 1977) does not necessarily imply any long-term permanence of the respective niche complex. This is also the case with the Pleistocene mammals of Europe (*cf.* Kurtén 1968).

The data presented (Text-fig. 1 and Table 1) demonstrate clearly that there is a sharp difference in longevity distribution between subtidal benthic mollusks and planktic microorganisms. One can hardly assume a constant extinction rate for inhabitants of the Neogene Tethyan and East-Atlantic shelves. Nonetheless, the chronospecies-longevity distributions of some analysed Tertiary mollusk faunules are so far from monotonic that the origination rates were certainly subject to considerable fluctuations. Shallow-marine benthic biota have indeed been demonstrated by community paleoecologists to show sometimes a niche--complex permanence. In turn, Van Valen (1973) demonstrated an apparent constancy in extinction rate of planktic forams; this may also hold true for calcareous nannoplankton. A hypothesis that the pelagic realm underwent no change at all throughout the time spans covered by the analysed data seems implausible (*cf.* Fischer & Arthur 1977). The present preliminary analysis may therefore indicate a gradual evolution (as defined above) of marine planktic niche complexes, contrasting with periodically disturbed permanence of shallow-marine benthic niche complexes. In other words, the precondition to optimization of niche dimensions through co-evolution among related species at a single trophic level was indeed met in benthic habitats but not in pelagic ones.

This is obviously not to imply that there is no niche subdivision among planktic organisms. In fact, there is some convincing evidence that such a niche partitioning does exist (Steele 1970, 1976). However, to account for it, one cannot refer to co-evolutionary mechanisms but rather to a stochastic pattern of speciation consistent with the Wright's Rule proposed by Gould & Eldredge (1977).

The apparent discrepancy between the modes of niche subdivision permitted by shallow-marine benthic and pelagic habitats may be due to a difference in either environmental predictability (*cf.* Levinton 1974), or environmental inertia (susceptibility *versus* resistance to environmental reorganization).

CONCLUSIONS

The above discussion and preliminary analysis of the role of co--evolution among species of a single trophic level shows that there is no way to achieve a natural stratigraphic classification of sedimentary rocks representing pelagic realm. Any coenozones cannot be reasonably established in those rocks because the pattern of speciation, as reflected

by the fossil record, is most probably stochastic. Therefore, the only geologic time-scale that can be attained through a biostratigraphic study of planktic organisms is the artificial chronostratigraphic one.

In turn, shallow-marine depositional environments are inhabited by benthic biota the evolution of which can be adequately described in terms of an ecostratigraphic time-scale. It is so because the evolutionary history of shallow-marine benthic community types recalls the model of punctuated equilibria. One may suppose that there exists a real continuum of patterns of speciation between the two endmembers described in the present paper.

These conclusions greatly undermine the validity of ecostratigraphy as a philosophy of natural classification of sedimentary rocks. In fact, the applicability of coenozonal patterns is, even in theory, much more limited in space and time than the applicability of chronozones. The latter are applicable to the whole fossil record, whereas the former are adequate merely to a part of the record. It is however to be noted that where ecostratigraphic units can be successfully applied, the resulting time-scale is much more informative about the course of the geobiologic evolution than the traditional chronostratigraphic one.

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GRANICE STOSOWALNOŚCI EKOSTRATYGRAFII

(Streszczenie)

Chronostratygrafia posługuje się zbiorem arbitralnie wybranych powierzchni czasu definiowanych i w praktyce identyfikowanych przede wszystkim za pośrednictwem metod biostratygraficznych. Natomiast ekostratygraficzna skala czasu wyznaczona ma być przez zespół istotnych wydarzeń w dziejach Ziemi. Wydarzenia te zapisane są w postaci zasięgów stratygraficznych rozmaitych gatunków organizmów kopalnych. Ewolucja organiczna jest zatem modelem czasu geologicznego zarówno dla chrono-, jak i dla ekostratygrafii. Taka koncepcja ekostratygrafii zakłada jednak, że albo istnieje w przyrodzie proces ewolucji biocenoz i ekosystemów, albo też poważną rolę w ewolucji świata organicznego odgrywa proces koewolucji wielkich grup gatunków. Ewolucja biocenoz i ekosystemów jest jednak tylko złudzeniem, gdyż same biocenozy to tylko przejaw, a więc epifenomen ewolucji poszczególnych gatunków. Wstępna analiza danych empirycznych (patrz fig. 1 oraz tab. 1) wskazuje natomiast, że koewolucja jest nieistotna pośród organizmów planktonicznych, ale gra ona poważną rolę wśród płytkomorskiego bentosu. Obserwacja ta ustanawia granice stosowalności ekostratygrafii, która może być wprawdzie adekwatna do badań nad utworami płytkomorskimi, ale nie nadaje się do badania facji pełnomorskich.