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Range-based biostratigraphy and evolutionary geochronology

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ABSTRACT - Ranges of fossils in rock sections, being controlled by environmental factors, have little to do with the biological evolution. Biostratigraphic methods of correlation rely thus indirectly on repeatable abiotic events and are related to the methods of event stratigraphy. The phylogeny of organisms, like radioactive decay, is a directional unrepeatable process well suited as a basis for a uniform geological time scale. To be reliable it should not refer to events of (allopatric) speciation that are not directly observable in fossil records but, instead, to biometrically documented phyletic transitions.

KEY WORDS: biostratigraphy, geochronology, evolution.

INTRODUCTION

After more than hundred years of steady development of paleontological methods of rock correlation there is still no agreement what the very concept of biostratigraphic correlation means. Despite of the great expansion, if not domination, of the view insisting on basic distinction between biostratigraphy and chronology opinions of biostratigrapher remain deeply split.

An interesting feature of the present state of the matter is that supposedly chronologically defined ("chronostratigraphic") units of higher rank (stages and, consequently, ages) have their boundaries generally defined by biostratigraphic units of lower rank (zones). This is an apparent logical inconsistency of the Hedbergian scheme of stratigraphic classification. Even if a "golden spike" is placed in the stratotype rock section it is invariably located at the base of a biostratigraphic zone. This seems to indicate that either proponents of these decisions believe in stability of biostratigraphic subdivisions in stratotypes (namely that the diagnostic species will not be found below the spike) or in a high time-correlative value of the zones (understood then as chronostratigraphic units).

Data on the distribution of the Jurassic ammonites were of basic importance in developing the basic ideas of biostratigraphy (see Callomon 1984). It seems therefore reasonable to discuss these problems here in Pergola. The crucial point of the discussion is the nature of correspondence between ranges of taxa recognized in the rock sections and actual time duration of evolutionary species. The question can be solved only with application of data from stratigraphically dense samples, large enough to allow biometrical treatment. This places micropaleontological methods in a privileged position. The micropaleontological fossil record is generally more continuous and complete in particular sections than that of macrofossils. Boundaries of many Jurassic ammonite zones in central Europe are known to coincide with sedimentary gaps (Bayer & McGhee 1985: p. 171). Therefore I shall use evidence derived from minute fossils rather than ammonites to discuss the problem. As there seems to be no reason to believe that the time and space distribution of small organisms was basically different from that of larger ones I hope it may be interesting also for ammonite workers to compare their own experience with that of Paleozoic micropaleontologists.

It is frequently assumed that the vertical distribution of fossil species is directly related to their evolution and that the first appearance of a species is more or less instanteous (in geological terms) over the whole area of its occurrence allowing thus delimitation of an isochrone with precision satisfactory for geological purposes (Teichert 1958: p. 111). Recent discussion concentrates on the question to what degree of precision is enough and how to estimate it (Scott 1985, Paul 1987, Martinez 1989). Even adherents of the American school of quantitative biostratigraphy, while denying chronological value of traditional biostratigraphic zones, believe that time correlation can be based on ranges of fossils determined in the rock sections.

CORRELATION BASED ON HOMOTAXY

Since the time when William Smith discovered that similarities in fossil content may serve for the correlation of rocks from different areas the concept of homotaxy continues to be a generally accepted basis of stratigraphy (i.a. Scott 1985). Within the continental European tradition the concept of assemblage zone (Oppel's zone) has been developed already in the middle of the nineteenth century while the twentieth century American quantitative approach has resulted, with publication of the influencial Shaw's (1964) book, in developing of the graphical method of correlation (Miller 1977). Both the assemblage zone concept and graphic correlation use ranges of taxa recorded in rocks as raw data. The assemblage zone concept assumes that ranges of taxa are generally correlated while the basic assumption of the graphic correlation method is that they are not. Even if they differ in these additional assumptions these concepts remain, in fact, direct derivatives of the idea of homotaxy. Somewhat paradoxically, while it is generally accepted that Oppel's zones are biostratigraphic units with boundaries not necessarily coeval in different places (Hancock 1977), the graphic correlation method still pretends to be a strict measure of time (Miller 1977: p. 166).

Known ranges of fossils are used to define units in biostratigraphic subdivisions either monothetically, when each zonal limit is defined at the apparent appearance of a single species, or polythetically, when more species are used to establish assemblage zones or to calibrate sections in graphic correlation plots. Units defined in this way may be understood strictly biostratigraphically, that is they are rock bodies with limits accepted to be diachronous. The general attitude of biostratigraphers is, however, to discover units with boundaries being as close to isochroneity as possible (Hedberg 1976). It is thus believed that ranges of fossils allow recognition of time correlation lines that are practically isochronous in geological terms. The actual meaning of ranges of fossils recorded in rock sections is therefore the most important issue.

RANGES OF FOSSILS AND DURATION OF SPECIES

To consider the problem of correspondence between ranges of fossils and durations of species let us consider an example of two species that enabled recognition of two celebrated biozones in the Ordovician, namely those of the conodonts *Prioniodus elegans* Pander 1856 and *Oepikodus evae* (Lindström 1955). Both are known from many localities all over the world, being almost always very abundant and frequently occurring in superposition within the same section, *O. evae* being the younger species. Despite of their abundance and wide distribution their direct ancestors remained unknown until recent work by Stouge & Bagnoli (1988) on the Arenig conodonts of Newfoundland (Fig. 1). Evidently, in both cases the first appearance in most known sections corresponded

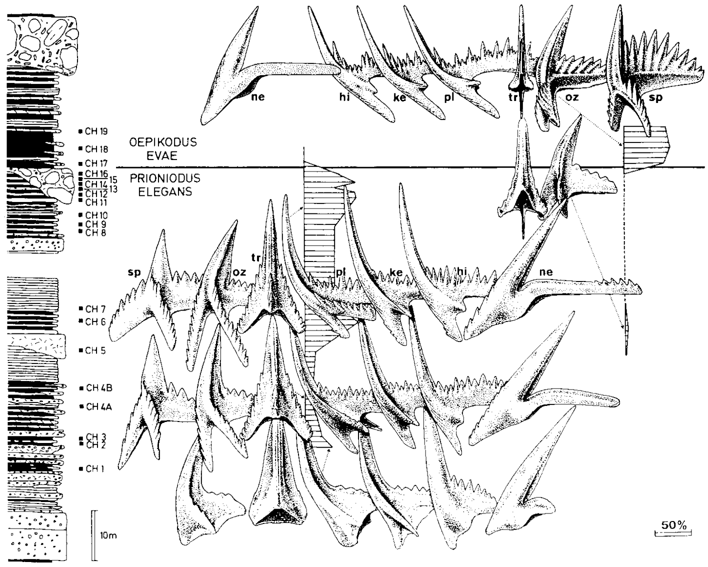

Fig. 1 - Succession of the *Prioniodus* and *Oepikodus* lineages in the Arenig of the Cow Head Peninsula, Newfoundland. Logs of percent contribution to samples and semidiagrammatic drawings of apparatuses given. Based on Stouge & Bagnoli (1988).

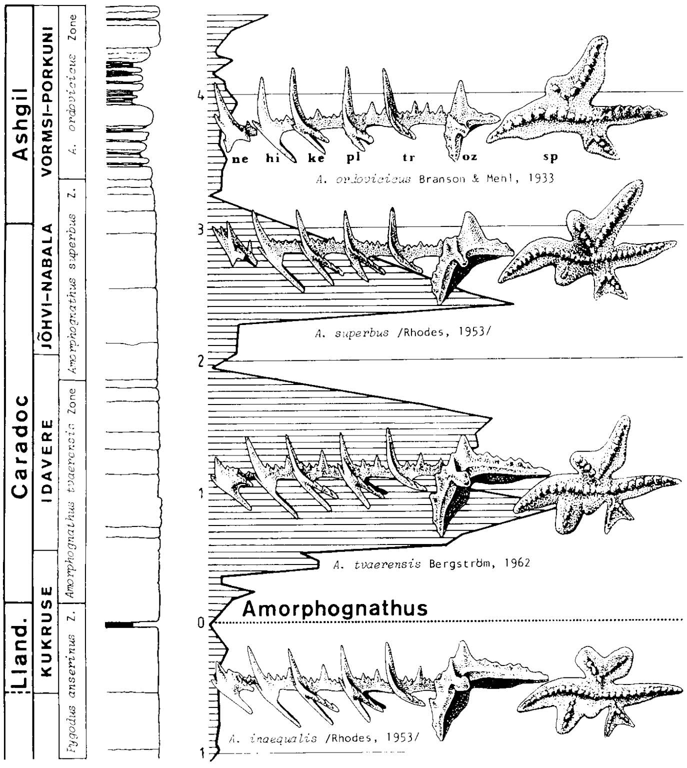

Fig. 2 - Distribution of the *Amorphognathus* lineage in the Mojcza Limestone, Holy Cross Mts., Poland. Log of percent contribution to samples and drawings of apparatuses given. Modified from Dzik (1990b).

to worldwide expansions of the species. In the case of *O. evae* this was a transgressive event (Stouge & Bagnoli 1988, Bergström 1988), and rare specimens of its direct ancestor are associated in Newfoundland with a minor transgressive event preceding the zonal one. Such an expansion does not need to be instanteous as the transgression is also extended in time. There is hardly any evidence for a correspondence between the expansion events and evolutionary origins of the species even if available data are too sparce to exclude this completely.

A better documented example presenting lack of any correspondence between migration and evolution is provided by one of the best known lineages of conodonts, that of *Amorphognathus*. Its species have been used to define several zones in the Middle and Late Ordovician (Bergström 1971, 1983). In the Baltic area and the Appalachians the lineage invaded the area suddenly, approximately at the base of the Caradoc, and this is the base of a zone named after *A. tvaerensis* Bergström 1963. However, in the Holy Cross Mts., Poland the lineage is known to occur already well before the transition within the conodont lineage of *Pygodus* that marks the base of Llandeilo (Dzik 1990b). The time horizon at which *Amorphognathus* expanded to the Baltic region seems to correspond to a great increase in numerical abundance of the species (Fig. 2), clearly connected with a world-wide environmental change (the *Nemagraptus gracilis* transgression event). Biometrical study on the lineage shows no apparent change in the rate or direction of the evolution at this change in abundance (Fig. 3). *Amorphognathus* evolved smoothly not only at this zonal boundary but also during other radical changes in its distribution.

The *Amorphognathus* lineage was by no means unique in this respect, nor is it a feature of the conodonts only. The Brinkmann's (1929) ammonite lineages, even if disputable in details, represents another example of a morphologic transformations recorded in a single section, thus probably without any influence of migration as a possible factor increasing the rate of evolution. A lot of papers presenting empirical evidence for far-reaching morphological transfor-mations in the course of evolution within the same area has been published in the last decade. The most impressive one seems to be the Rose & Bown's (1984) description of a gradual

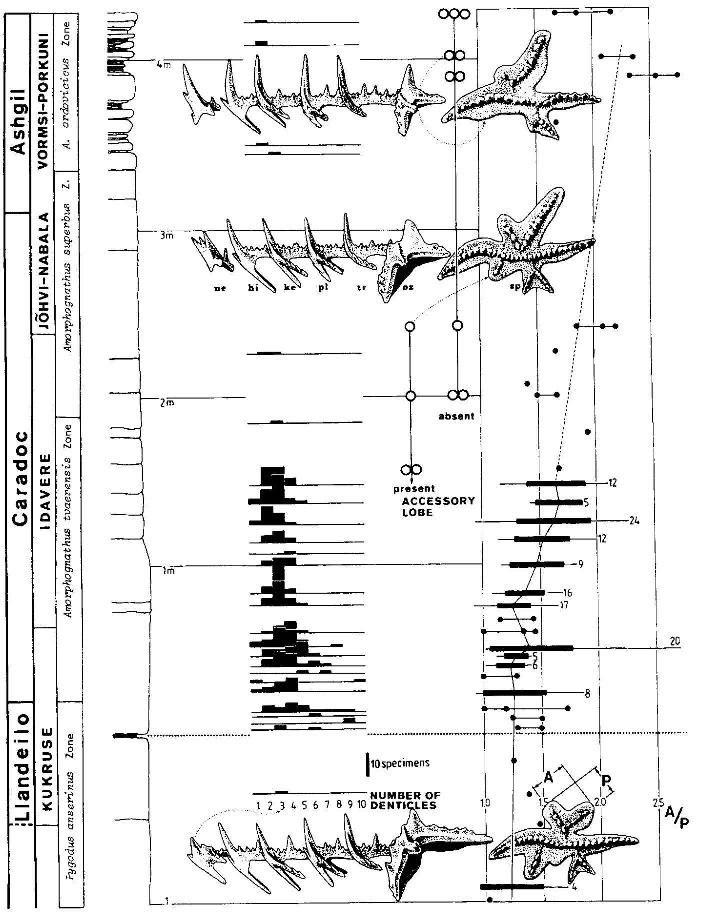

Fig. 3 - Evolution of *Amorphognathus* in the Mójcza Limestone. Particular characters of the ne and sp elements have been measured. Slightly modified after Dzik (1990b).

disappearance of teeth in mammals that resulted in differences generally accepted to be of generic level in taxonomic value. This shows also how discontinuous distribution of morphologies may be associated with a gradual evolution. In transitional populations when a tooth reaches critical minimum size, presumably that of the morphogenetic field, some specimens were apparently not able to develop its germ. In the Olempska's (1989) biometrical study on the evolution of moulting stages in ostracods it was possible to show how an evolutionary novelty expands in the ontogeny during evolution. A character initially occurring only among adult specimens gradually spreads towards earlier and earlier stages. Paradoxically, this well known feature of evolution has been there shown for the first time in paleontologically documented evolutionary succession of species. Several attempts to study the same feature in ammonite conchs, with their complete record of ontogeny, have been published, among most recent ones that of myself (Dzik 1986) and Dommergues (1987). Most unfortunately, unlike arthropods, molluscs do not have anything in the morphology of their conches that would allow strict identification of particular stages in ontogenetic development and this makes any quantitative presentation quite unclear leaving too much room for subjectivity in evaluation (see Dzik, this volume).

Such well documented evolutionary transitions between morphologically distinct populations are not as common in rock sections as one would expect if more or less complete parts of ranges of species are recorded in them. The fossil record is obviously highly discontinuous both in respect to time represented in rocks (Kitts, 1965, Dott 1983, McKinney 1985, Sadler & Strauss 1990) and durations of species represented in ranges of fossils (see Dzik, in press, for discussion). Some paleontologists prefer rather to assume that evolution is discontinuous than to accept this obvious feature of paleontological data.

Relatively good and well recognized fossil documentation of the time distribution of ancient organisms is known from the Ordovician of Europe and North America. One of the best is the record of time distribution of conodont assemblages there (see Dzik 1983, 1990b). It shows that only rarely and in special environments a complete range of a chronospecies can be established. Most commonly only insignificant part of its total range is recorded in sections. If some evolutionary changes are recognized they almost invariably concern quickly evolving lineages with short range species that have greater chance to be preserved within the time span occupied by the lineage in a studied area (see Bergström 1971). Only in extremely stable, usually cold-water, environments long ranging lineages can be studied (Fig. 4) and relatively low rates of evolution appear then to be generally typical for them (Dzik 1990b).

Conclusions can be drawn from the reviewed evidence that

(1) there is no correspondence between migration events and the evolution and

(2) ranges of species observed in particular sections represent generally only a minor part of their actual durations.

Both the base and top of a species range recognized in a rock section almost invariably correspond to its immigration to the area and local extinction. This may result from processes of two kinds. Either a quite new ecosystem with its complete set of species establishes in the area and after some time of persistence disappears being replaced by another species assemblage or, instead, a smooth change in ecological conditions takes place resulting in a gradual replacement of one species by another in the area in effect of horizontal shifts in their distribution.

In the first of these cases a more or less sudden appearance and disappearance of the ecosystem enables recognition of some characteristic assemblages of fossils different from these below and above in sections. A clear-cut assemblage zone can be distinguished there. The boundaries of the zone may or may not be synchroneous over the whole area occupied by the ecosystem. To be isochronous a sudden environmental change is necessary to control incursion of the ecosystem to the area.

The second case requires a smooth environmental change that may be synchroneous in the whole area or, as well, polarized geographically, especially when trangressive-regressive processes are involved. Similar stages in the evolution of the ecosystem can be precisely correlated by means of the graphic correlation method. The correlation horizons (lines) may then appear iso- or diachronous, respectively.

In both cases the correlation procedure relies thus actually on environmental events, whether they are instanteous in time and extended in space or, quite oppositely, extended in time and restricted in space. Only provided the change is instanteous and widespread geographically the biostratigraphic correlation horizon (line) would represent an isochrone. The method of biostratigraphy, being based on recorded ranges of species, is thus closely related, if not identical, to the method of event stratigraphy. The only difference is not in methods of inference but in the source of data: while biostratigraphy restricts its interests to studying the ranges of fossils, event stratigraphy uses all the available evidence of environmental changes, both biotic and sedimentary in nature, to recognize geographically extended synchronous events. In both these areas of stratigraphy the major problem is how to exclude polarized spatially events to avoid diachronous correlation (Scott 1985).

Stratigraphy bases thus its inference generally on expressions of abiotic events in distribution of organisms. Unlike evolutionary processes or radioactive decay those are processes that are recurring in time. Even if these events are as brief in time and distinct as bentonite layers, to be sure that proper horizons from different areas are matched one has to refer to independent time scale based on non-recurrent processes. The biotic evolution provides the general scheme of geochronological subdivisions. This time scale is actually in use since the William Smith's observations although its evolutionary connotations are rarely explicitly expressed. Even if the distinction between biostratigraphic and chronological (chronostratigraphic) methods of inference is now attempted generally to be strictly obeyed, these two areas of research are deeply interfingered. If any zonal species are unique it is a result of the general feature of the evolution, its unrepeatability. Especially when referring to units of higher rank one undirectly must refer to the evolution that made fossils from different epochs so different. There is thus no problem with distinguishing any Oxfordian ammonite assemblage from those of the Tithonian. This is quite obvious and the present paper is not intended to discuss ways of correlation at this level. The real methodological problem concerns distinction between biostratigraphy and chronology when boundaries of zonal and subzonal units are considered.

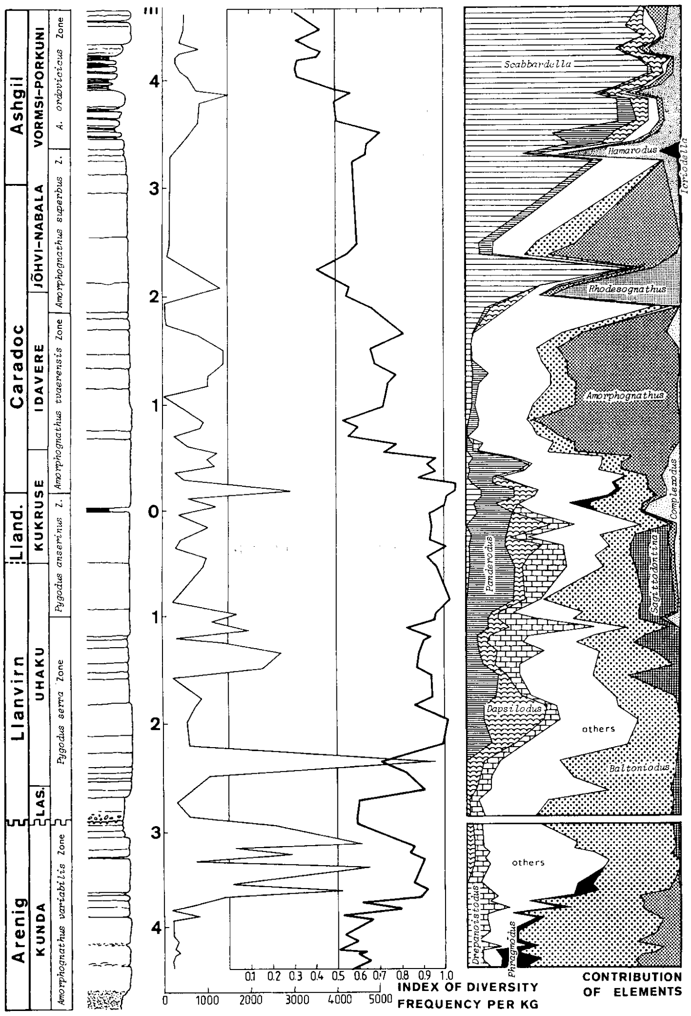

Fig. 4 - Succession of conodont assemblages in the Mojcza Limestone showing extremely complete record of evolving lineages. After Dzik (1990b).

EVOLUTIONARY ZONE

The tendency to establish a clear-cut distinction between biostratigraphy and chronology results from a belief that names of fossils represent observable facts while anything that refers to biological or sedimentological interpretations is considered to belong to another level of pure speculations (Krumbein & Sloss 1963). The relationship between these two aspects of paleontological research is, nevertheless, not so simple. Fossils represent remnants of living organisms and any reliable taxonomic identifications is a conclusion of a long line of inference (see Dzik 1990a). Applying empty names of fossils to biostratigraphic correlation one makes all the inference hidden behind them instead of exposing it. In effect the whole procedure becomes hard to be tested and thus, in fact, unscientific. All the inference in biostratigraphy is based on interpretations of biological and sedimentary processes and both have to be considered in full extend in any attempt to solve a time correlation problem.

Followers of the German stratigraphic tradition assume that the basic units of biostratigraphy are *actually* time units (Schindewolf 1954: p. 32). It is expected that their boundaries are based on evolutionary events of speciation. If strictly understood this would mean that boundaries of such zones cannot be indicated in any rock section as an allopatric speciation event cannot be identified unequivocally in any rock section (Dzik, in press). They are then purely theoretical units that refer to reconstructions of the course of evolution. Nevertheless, another possibility remains to make paleontologically defined time units strictly connected with the fossil record and testable. Namely, one may define boundaries of a time unit at a phyletic evolutionary transition identified in a section ("Autochronologie" of Richter 1956: p. 339).

It remains well known how limited is fossil record of evolutionary transitions at the population level. Is it then realistic to introduce any units based on the evolutionary events of this kind? I believe that it is. First of all, it seems quite clear that only insignificant part of easily accessible fossil evidence has been interpreted in evolutionary terms. However limited, available paleontological data suggest that the phyletic evolution is by no means rare in the fossil record. The main reason for its poor knowledge is a plain lack of interest among paleontologists. Brief periods of increased interest in microevolutionary paleontological studies have invariably resulted in publication of large number of valuable biometric descriptions of evolutionary processes. Classic works by Bettenstedt (1958) and Grabert (1959) mark such an epoch in the development of German micropaleontology, during the last decade we experience even greater increase in productivity of papers on biometrically documented phyletic evolution.

It seems thus possible to provide evidence for evolutionary origin of at least some chronospecies of fossil pelagic organisms and in some periods of geological time the number of such known transitions is large enough to establish a standard evolutionary time scale. Among the most successful attempts to do it is the standard zonation proposed for the North Atlantic faunal province of the Ordovician by Bergström (1971). Most of his zones are defined on well established evolutionary transitions within some lineages of the conodonts and it is possible to establish time relationships between these transitions recorded in the Baltic area with evolutionary changes in lineages occurring in other zoogeographic provinces (Dzik 1983, 1990). The Baltic scheme may thus serve as a global standard of time subdivisions for the Ordovician. Another attempt to establish such a global evolutionary based chronology is that of Ziegler & Sandberg (1990) proposed for the Late Devonian. In this case transitions that serve to define time boundaries are unfortunately not precisely identified and it is not quite clear whether they do not represent ecologically controlled shifts of related species rather than phyletic changes within lineages, but at least this is a good basis for further testing and discussion. Actually many of the Jurassic ammonite zones may appear to represent good time units, if based on populationally defined evolutionary transitions within particular lineages.

An evolutionary zone, defined as a time span between two evolutionary transitions (within the same or in different lineages), do not allow precise time correlation, unless the transitions are identified in different sections within the area occupied by the lineage. It is even usually not possible to say that all the strata containing the diagnostic species are coeval with some part of the zone as defined in its type area. Because of the diverging nature of evolution the ancestral species, even if completely transformed into the successive one in some areas, may survive in another places for long time. Only what one may state with certainty is that all the strata containing particular species are not older than the time of its evolutionary origins. If the origins is recorded in a rock section it may allow to establish its position in respect to evolutionary changes in cooccurring species. This is not much but the most important advantage of this kind of inference is that it is testable and quite safe.

CONCLUSIONS

During last decades we have experienced a great progress in developing radiometric methods of absolute time dating as well as event-based methods of time correlation. Paleontological methods of dating have not been improved so much and are more and more commonly believed to be not competitive. Paleontologists seem to be rather in retreat, frequently declaring interest only in narrowly understood biostratigraphy. I think that this is unnecessarily defeatist attitude. The fossil record of the evolution is good enough to allow presentation of a complete time scale based on population-level evolutionary events. However, this would require quite a deep shift in approach to the fossil record. Instead for being interested only in discontinuities in the distribution of fossils, that so commonly appear to have little to do with evolution, being ecologically controlled or even resulting from an incompleteness of the geological record, we should concentrate on studying complete sections with full record of the evolution.

Ranges of fossils have little to do with the evolution of species they represent. They cannot thus be used to establish any precise paleontologically based time scale. Such a time scale can be calibrated only with phyletic evolutionary transitions identified in continuous rock sections. This cannot give results as strict as correlations based on abiotic events but it provides the necessary frame for more precise event and biostratigraphic subdivisions. To be reliable the transitions have to be defined populationally (horizontally), preferably with application of biometrics. Although there were already some attempts to develop evolutionary time scale in some periods of geological time a lot remains to be done in this area.

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