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Possible pitfalls in the procedure for paleobiodiversity-dynamics analysis

Pułapki analizy paleo-bioróżnorodności

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Abstract

The changes in the diversity of specific taxa during certain parts of the geological past (paleobiodiversity dynamics) can, in principle, be established by counting the number of the fossil taxa present (worldwide or in a specific study area) in rocks dated for the time interval under study. Numerous obstacles are present, however, for instance in the form of lacking field data, disappeared collections, ambiguous identifications, temporary 'disappearence' of taxa, and dating problems. One major problem is the fact that, particularly in regional studies in some countries, a local, regional or national chronostratigraphic terminology is used rather than the chronostratigraphy recommended by the International Stratigraphic Commision of the International Union of Geological Sciences. This hampers international correlation and makes precise global paleodiversity-dynamics analyses extremely difficult. A reliable insight into the true paleodiversity dynamics requires not only that the various problems are recognized, but also that their consequences are eliminated or, if this is impossible, minimized. This is particularly important if the effects of mass extinctions on fauna and flora are investigated. Each analysis of paleobiodiversity-dynamics analysis of phenomena related to mass extinctions should therefore try to quantify the impact that missing data or inaccuracies of any kind may have on the final results; such an analysis should, in addition, try to find a solution for the major problems, so as to avoid significant inaccuracies of the calculated values. Large electronic databases can help, since about a decade, to diminish possible errors in diversity estimates. Paleobiodiversity should preferably be expressed in the form of values with a certain band with, indicating the inaccuracy, rather than in the form of exact values.

Keywords: biodiversity, taxonomy, biostratigraphy, geochronology, Lazarus taxa

Streszczenie

Zmiany w zróżnicowaniu gatunków w pewnych przedziałach czasu przeszłości geologicznej (dynamika paleo-bioróżnorodności) są z zasady ustalane poprzez zliczanie liczby taksonów skamieniałości (na świecie lub na wybranym obszarze) w skałach datowanych na badany interwał czasowy. Tym niemniej procedura ta napotyka wiele przeszkód, np. w postaci braku danych z jakiegoś obszaru, zagubionych kolekcji, niejednoznacznych identyfikacji, czasowego „zaniku" taksonów czy problemów datowania. Jednym z głównych problemów, zwłaszcza w badaniach regionalnych w niektórych krajach, jest stosowanie lokalnej, regionalnej lub krajowej terminologii chronostratygraficznej, a nie chronostratygrafii rekomendowanej przez Międzynarodową Komisję Stratygraficzną przy Międzynarodowej Unii Nauk Geologicznych. Utrudnia to międzynarodowe korelacje i czyni niezwykle trudnym przeprowadzenie precyzyjnej globalnej analizy dynamiki paleo-bioróżnorodności. Wiarygodny wgląd w prawdziwą dynamikę paleo-bioróżnorodności wymaga nie tylko rozpoznania różnych problemów, ale również wyeliminowania ich konsekwencji, a gdy to niemożliwe, zminimalizowania ich. Jest to szczególnie ważne w przypadku, gdy badane są następstwa masowego wymierania fauny i flory. Dlatego każda analiza dynamiki paleo-bioróżnorodności zjawisk związanych z masowym wymieraniem powinna zawierać próbę ilościowego oszacowania wpływu, jakie brakujące dane lub niedokładności jakiegokolwiek rodzaju mogą wywierać na końcowe wnioski. Taka analiza powinna próbować znaleźć rozwiązanie dla głównych problemów, ażeby uniknąć znaczących niedokładności w obliczonych wartościach. Duże elektroniczne bazy danych, dostępne od około 10 lat, mogą pomóc w zmniejszeniu możliwych błędów przy szacowaniu różnorodności. Najlepiej, gdyby paleo-bioróżnorodność była wyrażana w formie wartości w pewnym zakresie, wskazującym na niedokładność, a nie w formie precyzyjnej wartości.

Słowa kluczowe: bioróżnorodność, taksonomia, biostratygrafia, geochronologia, taksony Łazarza

Introduction

Since the end of the 1970s, hundreds of articles and books have been devoted to changes in global biodiversity, mass extinctions and – more in particular – the changes in biodiversity patterns of numerous fossil groups. Regional patterns were also established for numerous regions worldwide. The studies by Sepkoski (1993, 1997) and his co-workers (Sepkoski *et al.* 1981; Raup & Sepkoski 1982) are of great importance in this context, as they have initiated new developments in historical geology and paleontology. This type of work coincided in time, to mutual benefit, with multidisciplinary studies that have led to the insight that exceptional events in the Earth's history have greatly affected biodiversity in time (e.g., Alvarez *et al.* 1980), but there exists no general agreement yet about extraterrestrial (e.g. impact of a bolide) or Earth-related (e.g. global environmental change) causes that must be held responsible for the various events (e.g., Courtillot 2007).

Most research on paleobiodiversity has concentrated on faunas, commonly marine ones, probably because of their higher preservation potential and because of the commonly lower number and the commonly shorter interruptions (hiatuses) in their record. Diversity changes in terrestrial floras have, in contrast, been studied in much less detail, and paleobotanical evidence for biotic crises is still scarce, which may be ascribed – at least partially – to the much less complete knowledge that is available nowadays about ancient terrestrial floras than marine biota. Attempts to estimate changes in the diversity of fossil plant assemblages have been undertaken by, particularly, Niklas *et al.* (1985), Boulter *et al.* (1988), Nishida (1991), Wing & DiMichele (1995), Tiwari (1996), Boulter (1997), and Philippe *et al.* (1999). The influences of mass extinctions on plants, including their diversity, were discussed by, among others, Tschudy & Tschudy (1986, Retallack (1995), Tiwari (2001), McAllister Rees (2002), and Wing (2004). Data about changes in paleobotanical diversity are still too scarce, however, to be reliable for statistically significant analyses. For instance, the highly interesting hypothesis of Guex *et al.* (2001) and Morard *et al.* (2003), later verified by Ruban (2004) and Ruban & Efendiyeva (2005) – which explains the end-Lias anoxia with the preceding plant growth – could not be supported by quantitatively sufficient data on changes in plant diversity, so that only qualitative and the simplest semi-quantitative data have been used. Most problems regarding the analyses of changes in paleobiodiversity (often referred to as 'paleobiodiversity dynamics') are similar for faunas and floras, although both groups have also their own specific problems because the evolution and preservation of both groups have their own specific aspects.

Some other aspects of paleodiversity-dynamics analysis have been reviewed and discussed by, among others, Benton (1995), Alroy

(2000, 2003), Foote (2000, 2007) and Hammer & Harper (2005). Several other works deal with the influence of differences in preservation potential and of the (in)completeness of the fossil record on diversity measurements and on the interpretation of the findings (e.g., Benton 1995; Peters & Foote 2001; Smith 2001, 2007; Twitchett 2001; Crampton *et al.* 2003; Vermeij & Leighton 2003; Bush & Bambach 2004; Boucot 2006; Peters 2006; Foote 2007). The present contribution is meant to present a brief overview of the more general problems related to the collection and compilation of data.

Collection of data

The first problem, met immediately when starting an analysis of taxonomic diversity dynamics, is how and where initial data (in their most simple form data regarding the stratigraphic range of a particular taxon) have to be collected. This information should, obviously, be as complete as possible; in addition, it should be representative and scientifically correct.

Data from literature can be found in two forms: (1) as dispersed information, spread over numerous publications, each of which is highly incomplete; and (2) as already compiled, fairly complete information on the stratigraphic distribution of the taxa being studied.

It is evident that – if sources of the second type are available – they should be chosen as a starting point. Their disadvantage is, however, that they are commonly outdated. This implies that, even if such compilations exist, additional collection of data from ‘dispersed’ sources remains essential. Thus, the search for data can be realized in the following three ways:

(1) if there are no sources with compiled data at all, a search for all possible publications and unpublished reports with „dispersed” information should be carried out [as an example: when the diversity studies of the Phanerozoic megaflora from the Northern Caucasus (Ruban 2003) was started, thousands of potential sources were checked, which took about a year];

(2) if there are several sources with compiled, but evidently incomplete or outdated data, they should be chosen as the basic ones, but the data found in them should be complemented with data from other sources with „dispersed” information (in exceptional cases, namely if the sources with compiled data seem neither incomplete nor outdated and if they seem sufficiently representative for the current knowledge, such basic sources may be used without additional search for complementary dispersed information);

(3) if there is only one source with previously compiled, but outdated information, it is necessary to search not only for complementary data in the literature that is devoted to the taxon/taxa under examination, but also for publications that might, as a ‘by-product’, contain information that might help to avoid shortcomings in the initial data (i.e., missing data, duplicate data).

Apart from carrying out the required literature search with great scrutiny, it is of utmost importance to decide carefully which of the three above approaches should be followed, as the choice of initial data is one of the most important factors that determine whether the inventory of data will result in a complete and reliable set of data that can form an adequate basis for the rest of the procedure.

Compilation of data

The compilation of data, which have commonly to be collected from numerous sources, is one of the most difficult, time-consuming and bothersome activities when preparing a quantitative analysis of paleodiversity dynamics. This holds for both global and regional studies.

Among the problems that are met during data compilation, one of the most important is taxonomical synonymy. Incorrect identifications of taxa, which are sometimes obvious (Sohn 1994; Benton 1995) but which are more often difficult to find out, strongly influence the results of diversity analysis. If the problem of synonymy is ignored, one taxon (e.g. a species, genus or family) may be counted for two or even more, suggesting a too large diversity; on the other hand, fossils that may represent different taxa may have been identified erroneously as identical, thus giving rise to an apparently too small number of taxa, and thus to an unduly low diversity. It is interesting in this context that DNA analysis becomes increasingly applicable to the establishment of taxonomic relationships [not only for fossils from the Pleistocene (see, among others, Rohland *et al.* 2007) but also for fossils that data back from tens of millions of years (see, among others, Wible *et al.* 2007)], thus suggesting that a DNA-based taxonomy may become feasible, as has been predicted already several years ago (Van Loon 1999). This might eventually help solving problems like those of synonyms and homonyms. In some cases (e.g., in the case of planktonic foraminifers), however, genetic explorations demonstrated that the available taxonomic classifications require fundamental re-consideration, which makes it difficult to measure diversity (Kucera 2007). The problems with synonymy should, indeed, be solved precisely, although sometimes (especially when „old" data are used) this cannot be realized due to a low quality of the initial information (e.g. the absence of the original fossil collections, of descriptions used for the taxonomic identification and/or classification, or of figures); it might in many cases even be better not to include such fossils in a paleodynamics-diversity study at all.

An example of synonymy

A characteristic example of a problem raised by synonymy is the confusion about two widespread Late Paleozoic plant genera, namely *Walchia* and *Lebachia*. According to Meyen (1987), *Lebachia* and *Lebachiaceae* are invalid taxa, which should be replaced by *Walchia* and *Walchiacae*; but he also states, remarkably enough, that these names may continue to be used "due to tradition". This 'taxonomic flexibility' is even more remarkable if one realizes that Carboniferous species are commonly indentified as *Lebachia*, whereas Permian remains with the same characteristics are commonly classified as *Walchia*. This 'tradition' is also followed in the Northern Caucasus: *Lebachia* species are found in the Pennsylvanian (Novik 1978), whereas *Walchia* has been described from Early Permian strata (Miklukho-Maklaj & Miklukho-Maklaj 1966). The 'Late Pennsylvanian' (i.e., Kasimovian and Gzhelian stages) assemblage consists of 34 genera, whereas the Permian flora contains only *Walchia* (Ruban 2003). An 'outsider' might conclude that – after the disappearance of the entire 'Late Pennsylvanian' flora – a new genus appeared in the Permian. The actual situation is, however, a sudden degradation of the flora at the end of the Carboniferous, with only one genus surviving into the Permian. This implies that a calculation of the rate of diversity dynamics on the basis of the disappearance of *Walchia* and the appearance of *Lebachia* would yield an incorrect value. Unfortunately, the name *Lebachia* still is found in recent publications, sometimes being even ascribed to the typical Permian *Walchia*, among others by Davydov & Leven (2003) who attempted, although they are not paleobotanists, to present a comprehensive overview for all kinds of stratigraphers/paleontologists.

An example of a problem raised by lack of correct data regarding distribution in time and space

Another significant problem is the frequent absence of clear indications regarding the exact position of taxa in time and space. For example, the presence of a particular taxon may be indicated for a specific study area, without exact data about the precise site or the age of the rocks in which the fossils under study were found; or the occurrence of a particular taxon may be indicated without information about its distribution in zones or even stages. It is, as a rule, highly questionable whether such data could be used, as diversity dynamics should based on "stage-by-stage" or "zone-by-zone" data.

A comparable problem is encountered if regional correlations become almost impossible by the use of different names for the same formation in sites far apart, or if different chronostratigraphic frameworks are used for different regions. A problem that is in many respects similar, but much more severe is posed by the frequent revisions of the geological time scale under the supervision of the International Commission on Stratigraphy (ICS) of the International Union of Geological Sciences (IUGS) (see, as an example, Gradstein *et al.* 2004). In a case of stage boundary re-definition, it may become uncertain whether the stage name has a former or present meaning.

Possible solutions

The above problems for data compilation may be (though sometimes only partly) solved in four ways:

(1) by revising the original data, for instance by re-examining the fossil collections;

(2) by recalculating data „as is", taking into consideration the possible impact of the insufficiently unambiguous data when interpreting the results of the fossil dynamics analysis (but it should be emphasized that such a recalculation almost inevitably reduces the scientific value of the analysis!); this type of recalculation of data was followed by, among others, Ruban (2005) in his discussion of paleontological data gathered in the middle of the 19th century;

(3) by adapting the objectives of the project, i.e. lowering the resolution of the analysis in time and/or space; as an example, the above-mentioned diversity of the Phanerozoic macrofloras from the Northern Caucasus was, as a result of such an adaptation, studied by estimating the number of taxa not per stage (as had been originally envisaged), but per series only (Ruban 2003); other examples have been provided by McGhee (1996);

(4) by using purposely developed numerical equations to predict or to minimize the errors linked to the compilation problems; these equations are similar to those used for evaluation of the preservation bias.

Which of the above approaches should be followed in order to obtain an optimum result, depends on the specifics of the initial data and of the project targets. Sometimes, however, the problems may be so large that the best solution may be to postpone the analysis until more and/or more reliable and unambiguous data become available. It is worthwhile mentioning in this context that the increasing number of electronic paleontological databases provides ever more data for a successful compilation process. The commonly not very clear original source of data from electronic data bases – and this holds even more for data found on internet – can, however, pose a problem; in addition, the reliability of data from not precisely known sources that cannot be trusted on the basis of peer review is dubious. Compilation of data on the basis of not generally recognized electronic sources is therefore not advisable.

Application of the compiled data

Even if data compilation has been successful and a range chart for the various taxa under study has been prepared, the application of the compiled data – for analysis of the fossil diversity dynamics – can meet severe problems. Some of these problems may be exemplified on the basis of a simple hypothetical chart with the stratigraphic distribution of 5 species (belonging to 2 genera) in the Triassic of an imaginary study area (Fig. 1). The data are complete, and, therefore, represent the actual situation. If the diversity dynamics (as defined on the basis of species) within the Early-Middle Triassic is to be analyzed, first the number of species present during each stage must be calculated. This is simple, but the calculating the diversity dynamics is less simple as will be shown here, because some new species appear for the first time, whereas other species become extinct.

To calculate the rate of the origination of new species in the lowermost part of the inves-

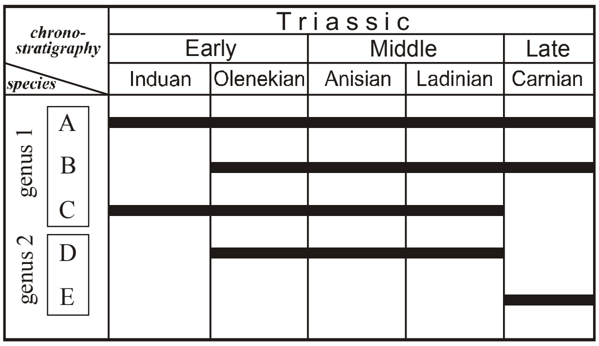

Fig. 1. Example of hypothesized ranges of taxa in the Triassic (see text for explanation)

Fig. 1. *Przykład hipotetycznych zakresów taksonów w triasie (objaśnienia w tekście)*

tigated stratigraphic interval, it is necessary to know how many taxa, absent in the previous stage, are present in this one. Commonly (as in this hypothetical case: Fig. 1) no data on fossils from the underlying strata are available. This implies that it is impossible to calculate the origination rate for the Induan stage, because the origination rate is the ratio between the number of new taxa in a chronostratigraphic unit and the number of new taxa in the immediately older chronostratigraphic unit of the same rank. Moreover, as the rate of change cannot be determined for the Induan, it is not possible to compare this ratio with that of the Olenekian.

In the example of Figure 1, the species A, B, and C belong to genus 1, whereas species D and E belong to genus 2. Genus 2 is represented by species during the Early, Middle and Late Triassic, but in the Carnian the earlier present species (D) was replaced by a new one (E), not present earlier. Data analysis of the Early and Middle Triassic should, obviously, take into account species A, B, C, and D. Species E should, however, also be taken into consideration: a calculation of the generic diversity on the basis of the abovementioned Early-Middle Triassic chart requires also an evaluation of the extinction rate for the last stage, i.e., for the Ladinian. It is therefore necessary to determine whether species that were present in the Early-Middle Triassic survived into the Late Triassic. In addition, it must be checked whether the other species belonging to genera 1 and 2 that did not exist earlier, appeared for the first time in the Carnian. Without such a check, conclusions about the extinction of genus 2 (as in this example) will be incorrect.

This example shows that even well-prepared data may be insufficient for a correct analysis, because lack of data from older and/or younger stages can induce errors. Before starting a quantitative diversity analysis, it is therefore necessary to look for such potential errors and to try to eliminate them.

The Lazarus taxa problem

A specific problem is formed by the so-called Lazarus taxa. The geological record shows frequent interruptions in the chronostratigraphic range of taxa. The re-appearance of a taxon after an interruption is called the Lazarus effect, and taxa showing such interruptions are known as Lazarus taxa. These terms became widely used after the studies by Flessa & Jablonski (1983) and Jablonski (1986). Although the Lazarus effect is linked by some workers to re-appearances after mass extinctions only, it is more logical to consider any re-appearance after interruption in the fossil record as a Lazarus effect (as suggested by Rickards & Wright 2002; and by Ruban & Tyszka 2005), even though the Lazarus effect seems, indeed, most commonly related to mass extinctions (Jablonski 1986, Fara 2001). Several questions related to the Lazarus effect and its influence on the calculation of fossil diversity have been discussed extensively (Flessa & Jablonski 1983; Jablonski 1986; Urbanek 1993, 1998; Senowbari-Daryan & Stanley 1998; Wignall & Benton 1999, 2000; Arz *et al.* 2000; Basov & Kuznetsova 2000; Fara & Benton 2000; Twitchett 2000; Fara 2001; Rickards & Wright 2002; Watkins 2002).

The temporal interruption of the stratigraphic range of a taxon may be due to one of the following causes:

- recurrence, i.e. the appearance of a morphologically similar taxon during evolution (this implies that the interruption is only apparent, as the original taxon is replaced by what is, in fact, another taxon);
- preservation of the taxon in refugia, for instance at times of a global environmental crisis (a widely accepted concept; see, among others, Fara 2001);
- an extreme decrease of the taxon's abundance during a mass extinction, so that the quantity of specimen became too low to trace them in the paleontological record (Wignall & Benton 1999); if the taxon was preserved in refugia, the case is identical to the previous one, but it is also possible that the taxon survived in numerous areas worldwide, but with few individuals;
- temporal disappearance of the taxon from the study area, for instance by migration to the adjacent areas;
- incompleteness of the paleontological record due to hiatuses as a result of non-deposition or erosion, a reduced preserva-

tion of fossils, or errors in sampling (see the review by Fara, 2001);

- taxonomic errors, i.e., incorrect identification of a taxon that appears after the interruption as the same taxon that was present before the interruption (such taxa are also referred to as Elvis taxa: Erwin 2006).

None of the above possibilities should be ignored, and pros and cons for each of these possibilities should be weighted in each particular case. Discussions on how to handle this are still going on (Wignall & Benton 1999, 2000; Rickards & Wright 2000; Twitchett 2000; Fara 2001). Ecological models explaining long survival of rare taxa (Yoshida 2002) support the concept of Wignall & Benton (1999). Meanwhile, refugia seem to play an important role, as suggested by paleoenvironmental studies of both of the geological past and the present (see, among others, Hladil 1994; Hladilova 2000; Riegl & Piller 2003). Possible other explanations for an apparent temporal interruption of the stratigraphic range of a taxon are a reduction in population size (resulting in less individuals that may be found in fossilized form) and a reduction in body size (resulting in less easily found fossil specimens) (Twitchett 2001).

False Lazarus taxa

It is possible to divide the Lazarus taxa into two groups: true and false (Fig. 2). The true Lazarus taxa are those the evolution of which was really interrupted for a particular time interval. In contrast, a false Lazarus effect is obtained if the collected data are incomplete or if taxonomic errors are made while the taxon under study was actually present during all the time span during which its occurrence was only seemingly interrupted. Both survival in refugia and extreme decrease in number are essentially the same in this context: the studied taxa did not really disappear, only no fossil remnants have been found.

A fundamental problem with respect to Lazarus taxa is how to determine whether species or genera before and after the interruption are actually the same, which would imply a true Lazarus effect. If, however, a morphologically similar taxon from before and after the interruption is erroneously considered as the same taxon, this is considered as a 'false Lazarus taxon', and the identification should simply be considered wrong. The fundamental paleontological problem in this context is on what basis species and genera should be distinguished from one another (see also Van Loon 1999; Kucera 2007). This question is closely related to another one: can convergence be so close that it becomes impossible to distinguish between different species (or genera) on the basis of morphology alone? This question is still under much debate, and an answer to this question is badly needed, if only to conclude how the Lazarus effect should be dealt with when determining the fossils' diversity. This is an important key to the systematic paleontology. Fortunately, it seems that application of genetic and other new approaches (such as microarchitectural analyses and investigations at even a molecular scale) may provide solutions for this key problem (see, e.g., Kucera 2007).

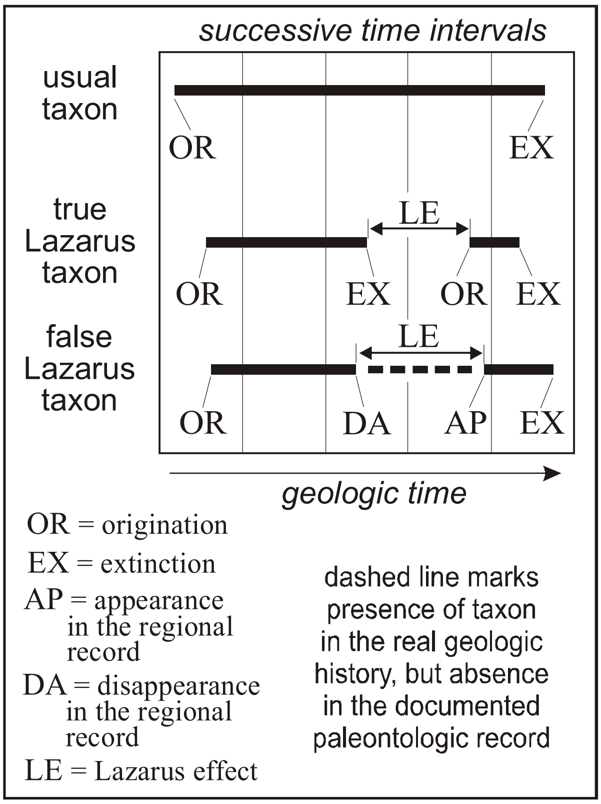

Fig. 2. True and false Lazarus taxa

***Fig. 2.** Prawdziwe i fałszywe taksony Łazarza*

Interruption of the stratigraphic range of a taxon increases the (apparent) extinction rate during the interruption interval and thus diminishes the (apparent) total fossil diversity. In contrast, the extinction rate during the next interval will be relatively low, because the 'extinct' taxon (re)appears (Fara 2001). A false Lazarus effect thus introduces a difference between the documented and the 'real' diversities, and therefore introduces erroneous values for the diversity dynamics. The fossil diversity and the diversity dynamics can therefore be estimated correctly only if the consequences of false Lazarus taxa are taken into account, and if the interruption of true Lazarus taxa is ignored. Dealing with a false Lazarus effect means that it is necessary to analyze the palaebiodiversity during the stratigraphic range as if the occurrence of the pertinent taxon or taxa had not been interrupted.

All Lazarus taxa in the *global* geological record are, following the above-mentioned causes, false ones, except for the case of recurrence, but even in that case one has to consider the possibility that there is only strong morphological resemblance of two different taxa. It seems therefore that the influence of the Lazarus effect cannot be neglected when evaluating global paleobiodiversity. Fara & Benton (2000) and Fara (2001) have indicated how to handle this.

If paleodiversity dynamics are analysed for a relatively small *region*, more complications arise than if a continental or even global analysis is made. The reasons are that (1) the Lazarus effect occurs much more commonly at a small scale than at a large scale (but note that this is true almost exclusively when false Lazarus taxa are involved), and (2) it is more difficult to distinguish between Lazarus taxa that migrated for some time to come back later (for instance as a result of shifting environments due to climate fluctuations), and taxa that are not documented due to an incomplete sedimentary record.

It is, obviously, possible to recalculate the fossil diversity for the possible presence of taxa during the intervals corresponding to their temporal absence in the fossil record. Only the highest probable value (HPV) of the Lazarus effect, which suggests the maximum possible extent of the latter, is thus obtained (Ruban & Tyszka 2005). In other words: the HPV represents the joint effect from both the true and the false Lazarus taxa. When an analysis of regional paleobiodiversity is made, the real diversity must be somewhere between the observed diversity curve and the curve corrected for the HPV (Fig. 3).

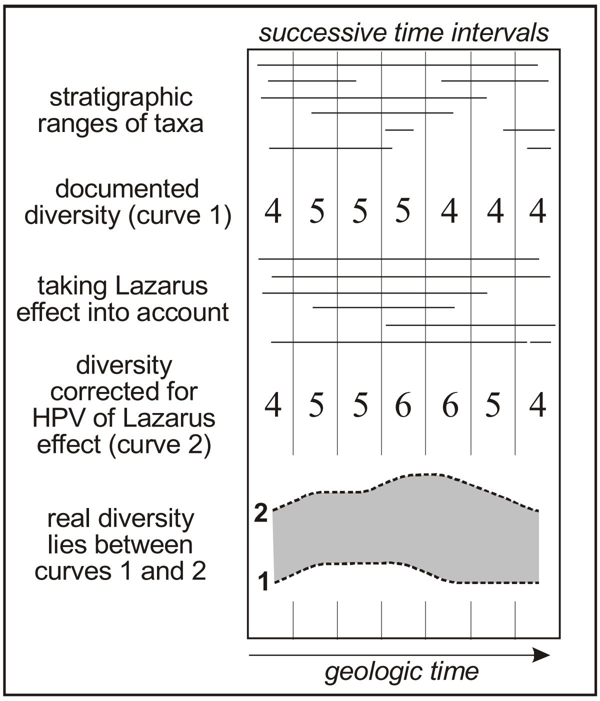

Fig. 3. Highest probable value (HPV) of the Lazarus effect and the estimation of regional fossil diversity.

Fig. 3. *Najbardziej prawdopodobna wartość efektu Łazarza i oszacowanie regionalnego zróżnicowania skamieniałości*

Geochronological problems

A highly important aspect when preparing a quantitative analysis of fossil diversity dynamics is the choice of an appropriate geological time scale. The calculations must be carried out for specific chronostratigraphic units, but the 'translation' of lithostratigraphic units into chronostratigraphic units remains a great problem. Recently a great step forwards has been made because the International Commission on Stratigraphy (ICS) has provided an excellent framework for chronostratigraphy (Gradstein *et al.* 2004), so that – in principle – the same geological time table can be used worldwide. This does not imply, however, that is has become easier to ascribe rock units to the correct chronostratigraphic unit. By far most datings of rock units are based on paleontological correlations, but if fossil diversity dynamics are investigated, it would be a vicious circle if the study would be based only on such paleontological data. Just like sedimentary facies shift in space with time, many fossils may show comparable diachronous occurrences. The first or last occurrence of a particular taxon at a certain place, where this occurrence coincides with a chronostratigraphically defined boundary, may therefore have a different age elsewhere in the world. Obviously, areas that are situated far from one another commonly are correlated through a number of intermediate correlations; the resulting inaccuracy of the correlation may be significant (Van Couvering 2000).

An entirely different problem is posed by the fact that the various chronostratigraphic units of one rank (e.g., stages) do not have an equally long duration. A stage that lasts twice as long as the previous one, has, obviously, a great chance to contain more species (and higher-order taxa) than its predecessor. It would be unjustified, however, to deduce that the longer stage is characterized by a higher biodiversity: at any given moment the biodiversity in both stages may be the same (within some band width), but the biodiversity in the longer-lasting stage may, at any given moment, also even be lower than the diversity at any given moment in the shorter stage! Biodiversity and the rate of fossil diversity dynamics should therefore preferably be determined for successive time-spans of approximately equal duration (Van Couvering 2000).

Such an approach may in practice turn out (almost) impossible with our present-day knowledge of correlations. Most areas are still described following a local or regional lithostratigraphic subdivision, and the duration of the time-span during which they were formed can often be estimated only roughly; in many cases attribution to an 'official' chronostratigraphic units is not even certain. This problem has to be solved, however, before reliable diversity dynamics can be determined. This implies (1) that the use of so-called "regional stages", representing a regional time scale, should be avoided whenever possible, and (2) that, more than was done previously, attention should be paid to defining the boundaries between chronostratigraphic units, so that at least a reasonable correlation is established with the recent ICS „International Stratigraphic Chart" (the most recent version is to be found at http://www.stratigraphy.org). Obviously, the decisions and recommendations of the ICS and its subcommissions should be followed. The presentation of data according to the International Stratigraphic Chart is, however, not yet always the case in a few countries (one of them being Russia), which should be regretted deeply as the use of any diverging stratigraphy prevents precise global paleodynamics analyses (or at least makes them more difficult and les reliable).

Geochronology vs. dating

The term 'geochronology' is often considered as a synonym of 'dating' (particularly radiometric dating) or another kind of absolute time estimation, but this is based on misunderstanding (Walsh 2001). It seems, at first sight, that several of the problems sketched above would be solved if all stratigraphic observations were complemented with data about their absolute ages. It is true that some types of fossils evolved so rapidly that they can be considered to represent (geologically) very short time intervals. This is, for instance, the case with Late Carboniferous fusulinids. Only few of such 'time-specific' taxa have been dated precisely, however, by radiometric or other means, but this does not imply that well-dated taxa can always be used as chronostratigraphic markers. Imagine that a marine succession is interrupted by two levels of volcanic ashes that can be dated precisely, and which differ 1,000 years in age. If a species is present in the entire interval between the two ash layers, but neither underneath the lower ash layer, nor above the upper one, this does not imply that the species can be used as a precise time marker: it may well be that the conditions between the deposition of the two ash layers were so different from before and after that the species found a good habitat in the region during the 1,000 'inter-ashes' years, but neither before nor afterwards. Elsewhere, however, the species may have occurred earlier or later. Using the well-dated time range once found for a particular taxon for all subsequent finds, is therefore in most cases without any doubt incorrect.

In addition, radiometric dating is not so absolute as sometimes believed. Much effort has been put by the ICS in establishing absolute ages for the boundaries between chronostratigraphic units (see the 'golden spikes' in the International Stratigraphic Chart), but new absolute ages for the various Devonian stages (Kaufmann 2006) were presented less than two years after the publication of the International Stratigraphic Chart of Gradstein *et al.* (2004). This is not amazing, as dating techniques become ever more refined, as expressed already much earlier by the successive editions of the Elsevier Geological Time Table [compare, for instance, the 4th edition (Haq & Van Eysinga 1987) with the recently published 6th edition (Haq, 2007)], where boundaries were changed sometimes for tens of millions of years. A comparison of the datings for the boundaries within the Mesozoic between the current International Stratigraphic Chart (ICS, 2006) and the 1999 GSA Geologic Time Scale (Palmer & Geissman, 1999) also shows that boundaries shifted in age sometimes more than the time-span of a stage. This means that the inaccuracies in absolute dating are sometimes larger than the duration of the chronological units themselves; it seems that such large changes do not – and will not – occur frequently anymore, but it should be a warning that adaptations of radiometric datings still take place. An example is the boundary (which is most important from a paleodynamics point of view because it is based on the largest mass extinction in the Earth history) between the Permian and the Triassic, which is indicated on the International Stratigraphic Chart (ICS, 2006) as 251.0 (± 0.1) Ma, but which has, shortly after the publication of the 2004 ICS, been found to be 252.6 Ma (± 0.2) (Mundi *et al*. 2004).

Similar conclusions have been drawn for other types of 'absolute datings'. There is, for instance, a gap of several hundreds of years between the varve countings and the C-14 datings for Late Pleistocene and early Holocene glaciolimnic deposits in Scandinavia (e.g. Schove 1977) and for comparable datings elsewhere (e.g. Grayson & Plater 2007). And the necessity to use several types of C-14 dating, is proof in itself that this method has to deal with numerous 'internal' problems (cf. Buck & Bard 2007).

Influence of changing astronomical parameters

Of academic interest only is the fact that paleodiversity dynamics is commonly calculated on the basis of diversity changes that occur in intervals of (usually) millions of years. These 'years' are, however, years with present-day length: ~365 days of 24 hours each. One should realize, however, that these parameters have changed in the course of the geological history. It has been calculated that in the Ediacaran (the end of the Neoproterozoic) a year lasted 444 days and 20.4 hours (Nesterov 1999) with the result that, for instance, the 88 million years that are attributed to the Ediacaran (according to the recent International Stratigraphic Chart it lasted from ~630 to 542 million years ago) lasted only 72 million years according to the astronomical years of the Ediacaran itself. As it is apparent that many organisms reproduce on the basis of yearly cycles, and that the rate of evolution depends (partly) on the velocity of reproduction (one of the reasons why *Drosophila melanogaster* is such a good 'guinea pig' for genetic research), it is obvious that the outcome of paleodiversity-dynamics analyses for Ediacaran (and other old) time intervals will give unduly low values. The change in the duration of a year had been deduced already much earlier, for instance for the Devonian (Wells 1963; Scrutton 1965). More recently, it has been concluded from the frequency modulation analysis of cyclic sedimentary successions that a Jurassic year had a duration intermediate between a Devonian and a recent one (Hinnov & Park 1998), and this confirms that a year on Earth has gradually become shorter. The gradual decrease in the number of days per year was probably compensated – at least in part – by lengthening of the days. This lengthening may, indeed, have had an adverse influence on the reproduction velocity and thus on the value of paleodiversity dynamics, but the net result is still far from clear. It is certain, however, that evolution goes faster with geological time; it even seems likely that more new species are formed per unit of time now than ever before, and probably even at a higher rate than species becoming extinct (Van Loon 2003). In contrast, the paleodiversity dynamics must have been low in the Proterozoic (lack of sexual reproduction will certainly have played a role during this era, but this cannot explain the acceleration of evolution during the Phanerozoic). The reason for the apparently ongoing acceleration of evolution is not well understood, but it means in fact that equal values of paleodiversity dynamics calculated for two time units indicate that the rate of change in the younger unit is *relatively* lower than that in the older unit.

Types of units for which the paleodiversity dynamics can be analysed

Paleodiversity dynamics can be determined for five types of units:

- non-diachronous lithostratigraphic units (results will be enforced by paleoenvironmental specifics);
- stages or epochs (results will be influenced by the uncertainties regarding the current chronostratigraphy);
- biozones (appropriate for particular fossil groups only);
- beds (appropriate only for the analysis of a given section; this is a common procedure particularly for microfossils);
- millions of years (not truly meaningful for fossils; moreover, fossils can rarely be dated within geologically restricted time boundaries).

It seems to us that events that affected biodiversity significantly, such as mass extinctions and sudden faunal explosions, can be used to establish time units that comprise the same number of biodiversity-affecting events (this extends the purpose of event stratigraphy as explained, particularly, by Walliser (1996) and Brett & Baird (1997). A possible alternative ecological approach in this context has been introduced by McGhee *et al.* (2004).

Conclusions

The above-mentioned problems concerning the quantitative analysis of paleodiversity dynamics (for both animals and plants) are presented in Fig. 4. All problems can commonly be solved, though often only in a time-consuming way. It is not uncommon, however, that the problems can be overcome only partly, because of insufficient, ambiguous and/or insufficiently accurate data. In some cases the lack or inaccuracy of information may be even so significant that a detailed paleodiversity-dynamics analysis is not worthwhile; in other cases the problems can be minimized or taken care of in one way or another.

Fortunately, ongoing work in this field, supported by large electronic databases (e.g. NMITA, PaleoTax, The Paleobiology Database,

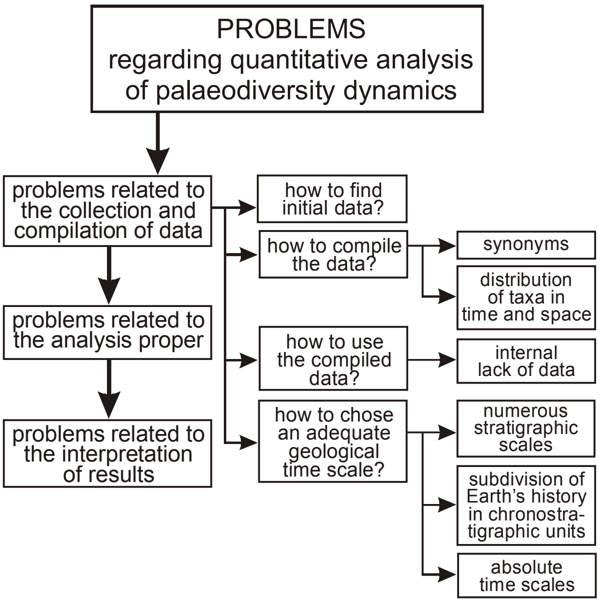

Fig. 4. Schematic overview of the problems related to the quantitative analysis of changes in paleobiodiversity

Fig. 4. *Schematyczne podsumowanie problemów związanych z ilościową analizą zmian w paleo-bioróżnorodności*

MIOMAP, FAUNMAP, Global Pollen Database, NOW, etc.) (Benton 1995; Budd *et al*. 2001; Alroy 2003; Löser 2004; Foote 2007), may help to diminish possible errors in the diversity estimates. Each analysis of paleodiversity dynamics or of phenomena related to the consequences of mass extinctions should, however, (1) try to quantify the impact that missing data or inaccuracies of any kind may have on the final results, and (2) try to find a solution for the major problems, so as to avoid significant inaccuracies of the calculated values.

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