

Global Bio-Events, Lecture Notes in Earth Sciences, 8, 1-4. Springer-Verl., Berlin, Heidelberg, New York, Paris, Tokyo.
WILLIAMS, G.C. (1992): Domains, Levels, and Challenges. - Oxford University Press, 208 pp. Oxford.

- * Examples of these reappearances have been seriously documented during the last years. For example: Urbanek (1992) - about the reappearance of true Silurian monograptids; Hladil & Kalvoda (1992) - about the reappearance of several Devonian scoliopods.
- ** Only two papers dealing with refugia were registered in Biological Abstracts, 1993 (BIOSIS, Philad.). Zink & Dittmann (1993) have suggested that roots of the haplotype cladograms on DNA data of song sparrow *Melospiza melodia* can be traced to Queen Charlotte Islands and Newfoundland. In my opinion, these places are again perspective for this sparrow. This is probably an example of a short-term expansion / consequent retraction of poor refugium. The authors of the second paper, Ravizza & Ravizza-Demateis (1993), have defined a refugium in a glacial valley of Pennine Alps of Italy. The refugium was defined in respect to populations of stone fly (Plecoptera, a very old-ancestor insects). The described phenomenon possesses some attributes of refugium but the other features speaks in favor of "step by step removed relict of glacial times".
- *** Philosophically, each of the system can possess some touch with the another system. These connections of any type are sources of instability because any "friction" generates some oscillating patterns. Recently, Drobnik (1993) has commented common oscillatory patterns within the biosystems. The problems of this type are solved by the science about non-linear waves, including their coincidence and magnification (chaotic jumps).

- **** The population density proper does not need to stimulate the emigration definitely. Coincidence of more factors is probable (compare Ostfeld et al. 1993; a study about meadow vole *Microtus pennsylvanicus*).
- ***** Contrary to it, the so-called Allee's rule speaks in favor of Boucot's approximation that populations with extremely small and/or big number of specimens are labile. These populations become easily extinct.
- ***** There is an analogy with early Farnennian relicts of marine reefs. Fishes (by scrapping) as well as fungi and bacteria (by poisoning and covering) attack the relicts of the reefs. This story bases on Devonian sections of Central Moravia. Another analogy can be found in relicts of recent spruce forests (for example in Krušné hory Mts. of western Bohemia). They experienced periodical damages by massive insect invasions.
- ***** Possibilities how can be the situation reflected by disparity is illustrated by Foote (1993) or by McShea (1993). The first paper shows that lower disparity is typical for the radiation, and once more later, during the extinction. The second paper comments discussion between S.J. Gould and M.Ridley whether morphology is perfectly plastic against the natural selection or whether the morphology is partly resistant, having simultaneously its own internal dynamics. A controversy rises whether the species is an active and/or a passive particle in evolutionary game. In my opinion the question is fruitless because each of the passive responses has some "active" face.
- ***** Kopta (1993) has introduced to Czech scientific public the story about the natural hybridization of *Balaenoptera musculus* and *B. physalus*. Despite the fact that both the species are well defined and they are separated as long as 3.5 Ma, there was observed a fertile female hybrid. The hybridization was probably started due to the drastic fall in population density.

High specialized organisms have ticket to death but some exceptions are allowed

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An idea that high specialization produces the extinction is probably right because all traditional paleontological experience corroborate this interpretation. The specialization of organisms, respectively the specialization within the whole group of related organisms (systagenesis according to Walliser 1992) take usually part at the end of the so-called progressive phase of the evolutionary cycle.⁽¹⁾

However, the all process does not completely fit to the most generalized model. For example, Allmon (1993) focused the investigation so that "Gould's heterochrony" is illustrated in modern gastropods. A new approach of heterochrony shows that evolution is full of variegated "spots" that each of them possesses some special rates and strategies of the evolution. Allmon agrees that heterochronical reaction reflects several environmental agents. He distinguishes several types of evolutionary patterns they can be involved in the heterochronical structure of the evolution: 1. Paedomorphosis - an appearance of ancestral features at younger ages in descendants. How we can realize it? For example, by progenesis = an early sexual maturation, or by neoteny = slowing of morphological development, or by postdisplacement = delayed onset of growth (see Allmon 1993).

My stromatoporoid and tabulate material reflects as the general pattern as the changes in detail but many of the reactions are so specific that I cannot describe them using a common evolutionary glossary.

Frasnian (Devonian) representatives of the genera *Alveolites* belonged to very specialized reef dwellers. The were ex-

emplary deteriorated by the Kellwasser crisis, totally to zero. Nevertheless, some specialists for non-specialization, i.e. *Amphipora*, passed the crises successfully being liquidated later - during the advanced recovery. *Amphipora tschussovensis* and *A. moravica* survived since Kellwasser datum (360 Ma) at least for 3.5 Ma.

Data on *Stachyodes* ex gr. *lagowiensis* are very specific. *Stachyodids* (one of the branched stromatoporoid clade) produced for 40 Ma-time interval within the Devonian period many forms they specialized exclusively to the reef environment. They have usually the same reactions as all the "clonal reef dwellers with probable 'zooxanthelid' symbionts". Nevertheless, the occurrences of *S. ex gr. lagowiensis* show an unusual possibility of switching: the populations are normally at the frontal reef edge but they can remove also exclusively to fore-reef slope and/or exclusively to backreef lagoon. Transitional stages of fluent dispersals are much more labile in comparison with the stability in selected niche (that is one selected from possible tree). Although the morphological response is not simple and we cannot easily outline it, the ecological fact of the switching among the several niches seems to be evident. I believe that nature of the "switching" depends on some behavioural, feeding or physiological mechanisms. The mechanisms activated the "switching" abruptly at distinct configuration of several agents. We can realize lot of accompanied processes. For example, a release or change of algal hostility in tissues of polyp is probable.

Although the knowledge about the nature of the "swit-

ching" is still poor, it seems that only the "switching" can explain a unique surviving of this stachyodid species after the very strong Kellwasser crisis. Inherited possibility to "switch" quickly among several strategies is a possible explanation how big specialists among the stromatoporoids may uniquely survive such a big crisis.

Another specific story is about late Devonian amphiporids. They were euryfacial during the crisis and still immediately after the crisis. They inhabited variety of niches. Nevertheless, later after the crisis, they gradually lost this ability. The amphiporids did not occupy any of offered empty niches although these niches look generally acceptable for them. The possible background was temperature, or still unknown chemical or biological inhibitors, or some of the hypothetical "internal factors"? We have no definite answer.

In 1993 we have redefined some common typical strategies they allowed to survive some Devonian organisms: 1. Sufficient tolerance. 2. Big dispersal possibility of spores, eggs, larval stages. 3. R-strategy of some accessory dwellers in the margins of collapse system. 4. Lazarus taxa they have minimized metabolism and evolution. 5. Supertramps – organisms they were jumping from niche to niche as "from the stone to another stone". 6. Organisms with higher rate of evolution when confronted the crisis.

Two rare but controversial examples were introduced by Hladil & Kalvoda (1993). The late Devonian icriodids (conodonts) and foraminifer species *Multiseptida corallina* survived in isolated reefoid shoals of very small dimensions. Typical refugium role is doubtful here although a hypothesis about commensalism on sharks (icriodids) and on stachyodids (foraminifers) may solve this controversy. Nevertheless, these unusual survivors were limited only to lower Famennian. Both survivors extinct during the main episodes of the upper Famennian recovery.

Neither the "switching" discussed here nor the probable heterochrony patterns support the one-cause explanations of the extinction and recovery episodes. This is more question

of philosophy. One approach says that a complicated trend configuration of background gradually has arisen but the start is a single agent even though it may be very small in intensity (J. Kříž - personal communication, 1992). Another approach says that only the simultaneously configured agents in distinct unusual proportions may effectively activate the system. Superimposition that led to randomly formed "jumps" is suggests an analogy to theory of composed non-linear waves (author - final conference of the IGCP Global Bioevents, 1992).

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* Evolutionary cycle was described, for example, by Walliser (1992). The first stage included there is the archaetypogenesis that forms the essential evolutionary structures. Consequent trends of evolution are more continuous and slower. This decelerated part of the evolutionary cycle is nomismogenesis. Consequently, some fluctuations due to the biological innovations occur and the process of biological radiation and diversification intensifies, having more and more the face of specialization. The process continues up to the top of the progressive phase. In this time, the background extinction starts = lowering of diversity in the background of diversified communities. Typical regressive phase begins by extinction of common taxa. The visible step-wise extinction foregoes the final collapse.

Intraspecific variability reduced before or during the extinction?

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First study about the relation between variability and crisis was free of any initial hypothesis. It was briefly a test about existence and quality of this relation. The study deals with Middle and Upper Devonian Alveolitinae (tabulate corals, Hladil 1989).

What is the result of this study? Evidently decreased values of several parameters characterized the times before the coming big crisis; i.e. for porosity (→ a trend to soliterization), and spinality (→ a trend to lesser activity & metabolism). Proportional volume of skeleton increased in contrast to the possible space for living tissues but the specific skeleton production simultaneously reduced in quantity (→ a trend to slim and starved organisms).

Variabilities in the all three parameters (porosity, spinality, and skeletization) displayed clearly decreasing trends toward the visible crisis followed by the visible extinctions. The decrease had to start earlier than any drastic diminishing of population densities developed. However, an assumption about a relation

"reduction of possible niches → reduction of variability ranges" seems to imply the data set without any apparent problems.

Nevertheless, all the variabilities decreased spontaneously neither within the whole group of Alveolitinae nor within the complete individual populations. When plotted, there was visible how the general decrease consisted of individual "wavy peaks & valleys" they alternated "with a specific phase shift". In my opinion this is an excellent illustration of a proper mosaic structure within the suffered system. New guilds replaced the previous, half-disintegrated guilds until the big Frasnian reef ecosystem approached the time of its depletion.

This study indicated that diversity & disparities do not rise simply from "poor crisis period" to "reef period". Surprisingly, the most diversified and flourished communities prominently appeared during advanced beginning but as well during early end of the reef period. The medium time that corresponds to maximum reef thickness as well as extension was the time