

Fig. 2. Distribution of agglutinated foraminifera and diversity of different microfossil groups in Blatnička Section. Abbreviation used for sedimentology: H - hemipelagite, Te - turbidite claystone (Te interval).

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Refugia in ecology: a question of their existence and their basic attributes

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Introduction

An explanation about possible source-areas or biological sources represents one of the most promising views to the recovery game that superimposes over the global crisis.

Major categories are suggested here: refugia and relicts. Both subjects display two faces - they are as the biotope as the joined biological system. We cannot dissect the structures exclusively even favoring a holistic approach.

As clearly visible from the name, the refugium is a place that is convenient for coming "refugees" that is such a pla-

ce that can adsorb a partial biota stressed in neighborhood. The refugium, as a biotope, is settled by migrants they are coming from marginal of previously flourishing ecosystems. Various types can be distinguished among these settlements or colonizations: from random or passive dispersals, through changed-reproductive but still "passive" ways, up to an "active or aimed" invasion. The beginning crises have to be reflected by "a flow in" on the fluctuating margins of the refugium.

Contrary to this scenario, a relict of formerly flourishing ecosystem is never characterized by any important "flow in"; that means no large-spectrum immigration can be detected.

The relict usually consists of reduced frame of dominant connections they survived from the ancestral flourished structure. Highly specialized and long living organisms are typical here. However, these organisms regularly possess only small chance of further continuity. Some of these organisms may survive but these possible survivors usually fall within the drastic competition during the advanced recovery. Evaluating the scenario needs some source that lies beside. The existence of this source is an essential precaution why refugia have to be defined.

Good indications of refugia are the Lazarus-taxa. The Lazarus-taxa are allowed to vanish from our paleontological observance sensibility for significant time-intervals. The barren intervals fluctuate from several up to several tens of Ma. Both the vanishing and reappearance of Lazarus are bounded to global crises. The same clade is allowed to vanish during one crisis and reappear during the next crisis. A super-evidence is provided by those Lazarus they were hidden through several crisis-limited intervals. ()

Besides the Lazarus, also other taxa suggest that their recovery source is somewhere outside the main crisis/recovery field. They can be hardly traced in the field where an inflexible system is deteriorated; where background extinction is overprinted by step-wise collapse. Explicitly, they can be also placed to some hypothetical refugia.

I cannot and I would not totally exclude the sources inside the collapse systems. Such a step is not sufficiently based on data. Any preliminary assumption that has been given until now does not reasonably introduce this source. Structures of this doubtful type, if any, may form only some marginal structures, despite they are approximated in geography and/or structure-hierarchy.

The prominent role of refugia among the bio-reservoirs as well as possible sources for recovery seems to be strongly indicated.

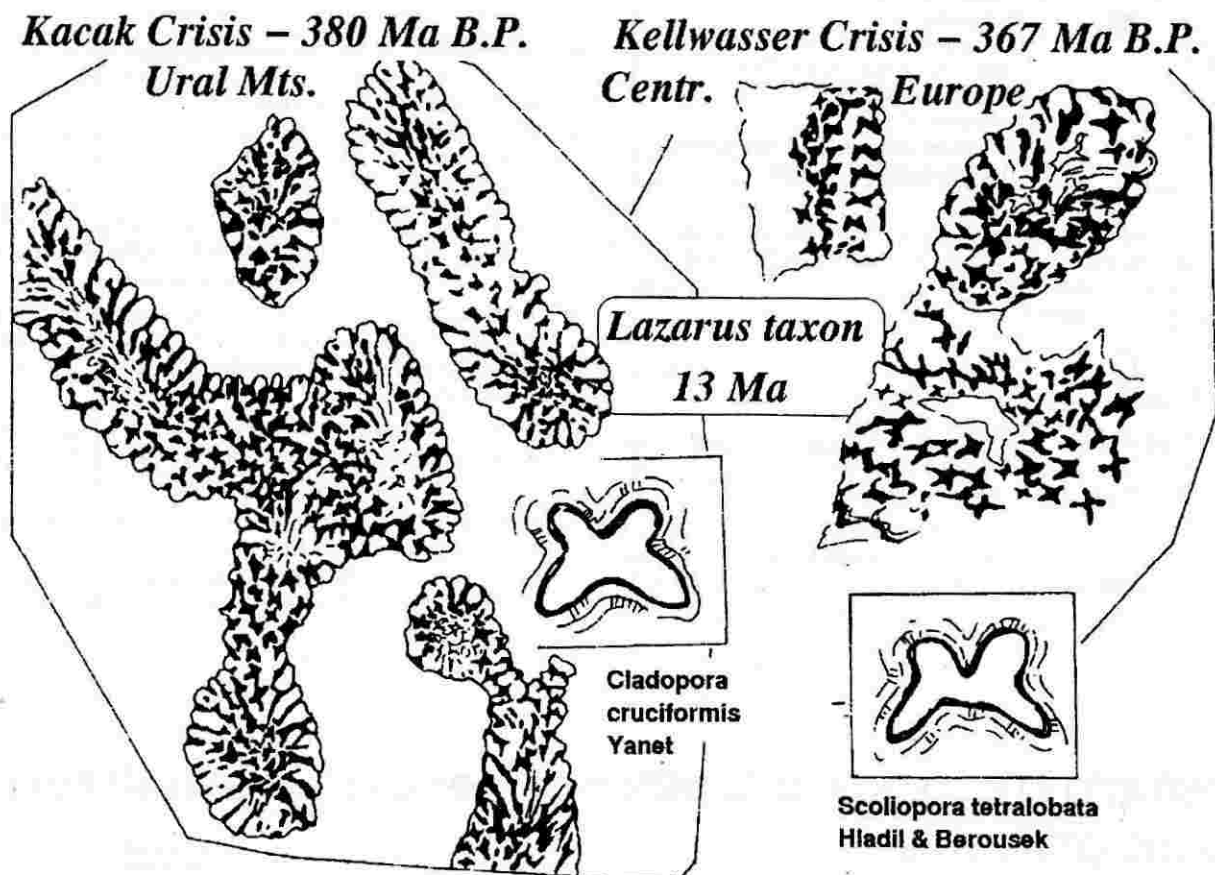


Fig. 1 – Eifelian "Cladopora cruciformis" and Frasnian Scoliopora tetralobata. Both fossils belong to one Lazarus taxon. Duration of this taxon is at least 13 Ma but real duration is probably longer. These corals belong to rare fossils that perform only during ecosystem disturbances.

Refugia in real world

There is still discussed whether refugia form real segments of environment, biotopes and ecosystems, or, they are dissolved within the ecosystems on variety of hierarchical levels. Briefly said, a question rises whether refugia can be considered as a real subject or they can be rather approximated as a chimerical category, respectively a tool.

In my interpretation, the first of the approaches has been involved in Walliser's (1986) formulation: "formerly unaffec-

ted biotopes which were only secondarily influenced from these neighborhood biotopes where big bio-event (thought crisis) happened".

The second of the approaches can be approximated "as and exchange of cubes": One of the species is removed into other system so that be returned by the same way. These "cube" or "diffusive" theories are generally valid but they can be preferentially used in slow-changed interactions of roughly adequate systems. No validity is documented for vast and dras-

tic changes and no validity is assumed for strongly inadequate systems.

Expression "refugium" is handled for long time but the definition of the term is still (or already?) vagrant and ambiguous. Refugia are sporadically used in paleontology. Low frequency of the term is typical also for information flow in biology.^()

Model 1 – Stable refugium: The refugium can be realized as quasi-opened, vast object, having quasi-stable environment but possessing controversially also a structure of low density. It can be hardly refused that refugium environment must be less touched by the killing stress of the global crisis in comparison with the main field of the crisis. This fact appears to be an essential postulate. Consequently, the reasons of this situation certainly corroborate with a primordial high refugium-resistance against the global crisis agents. Organisms that have extinct within specialized but more and more and then catastrophically collapsed systems are incorporated in refugia. Heavy discussions performed about the time when the refugium was allowed to receipt these inhabitants. Main discrepancy is between two ideas; that is between "older" and "simultaneous" occupation of the refugium, in respect to the peak-crisis datum. The refugium displays both the periods of receipt and periods of release. It must join three functions they have to be switched: temporal protection, temporal receipt, and releasing of organisms. It possesses through the whole time ambiguous valences and connections, and conditions of well structured or quickly evolved systems are not permitted.

Model 2 – Stationary refugium: The refugium is quasi-stable only in internal parameters. Essential imagination speaks about the moving system that has been derived from some marginal system before the collapse of the main structures. Reflectance of the crisis is considered as power of the movement. Physical center of the structure significantly exceeds the previous outlines of the structure. Model 2 easy corresponds to necessity that empty niches, gaps or ambiguity of valences must be persistently generated.

One common but simultaneously striking feature has to be deduced: "Worse conditions" are actually the conditions they govern the refugia. The refugium-environment is not normally favored by main bulk of the organisms, at least at normal conditions of nomismogenesis. At least one of the common parameters (e.g. temperature, light, possibility of feeding) have to be shifted to marginal position.

Discussion to some basic attributes of the refugia

Trying to understand the extinction-recovery game in larger complexity a discussion of refugium attributes appears to be a useful tool.

1. Physical and chemical properties differ from those they dominate in the flourishing diversified systems before the beginning of their collapses. The difference cannot be bigger than accessible ranges for any type of adaptive capabilities (for example the genetical, constructional, physiological, and behavioral limits). Unfortunately, we cannot recognize this capability in sufficient measure of reliability, except for such predictions "that hippopotamus cannot live in boiling water".
2. An existence of free or insufficiently occupied niches. What are the main controls they are responsible for continuously "immature system state"? Some of them are assumed; for example the conditions at the limits of acceptance, decrease in metabolism, right intensities of stress & movement. These configurations can probably generate. Briefly we

can operate with an idea of "stable refugia" or "stationary refugia". Periodical and mosaic events of niche opening are good topic for sophisticated case studies - an interplay of various oscillating factors with local random jumps (micro-crisis).^()

3. Permeability of margins. At least in some intervals of crises the refugia have open very well so that organisms can make some massive colonization attempts. Controversially, if highly diversified systems form dense structures (that is in the time-span between the crises), the margins of those structures may represent some walls against a recurrent infiltration. In this play, the refugia look like temporal traps.
4. Colonization flow takes usually an advantage of the inclined density pattern. The migrants go "toward the open niches". This situation is probable also in function of refugium. Rare migrants they perhaps go "from less dense to more dense" have to experience hard stress & competition that ends, as a rule, by total liquidation, or luckily by an evolutionary jump. The pattern is partly controversial. The organisms look always for better food. It does not matter whether they do it actively or by selection during their passive migration. The transition into the refugium can process in variety of ways; for example through the feeding strategies, breeding frequencies, changed quantity & quality of cysts, spores, eggs, or changed larval stadia. The colonization flow is much more complicated than we can judge only on the base of the density and "open niches" models.^()
5. Diversity is low but disparity is big. Massive populations of few solitary species are typical. Nevertheless, some less abundant organisms also appear. The latter ones disperse or locally aggregated in the refugium. Both the situations introduced above represents typical low diversity patterns. Nevertheless, the filters of physical & chemical conditions allow strikingly quite high disparity. Boucot's 1986 general approximation on short live of rare species appears to be inadequate in the refugia because the inhabitants of the refugia are typically decreasing the metabolism, skeletization, dependence on synhabitants. All these inhabitants are "rare species". There are evident "refugium-affiliated" corals (for example *Scoliopora cruciformis* – tetralobata HL. & BER.) which are typical "short-range" fossils but they look so only due to their preservation properties. The refugia lying usually outside the continental seas own only poor chance of preservation in orogenes. Boucot's approximation speaks rather about the fact that "short-range" organisms only occasionally fossilized than about any other consequences.^()
6. During the crisis, as many times documented (opinion that pointed out by J.Krhovský), the state of the system approach more the entropy. Formerly individual systems acquire more simple & spatially unified patterns. This crisis pattern results from many examples. For example, Urbanek (1992) speaks about "post-crisis syndrome". He has found lilliput but common populations of graptolites, with big lateral dispersals, but they belong only to few clades. Here is an interesting point. There is spoken that some unity rises during the crisis. It may be assumed that "worse conditions" of the crisis field approach the hypothetical "worse conditions" of refugia. This is a crucial moment that indicates as the character of environment in refugium as the mechanism how can be refugium opened. Openings they performed only during the crises can be easily illustrated by inputs and outputs of Lazarus taxa. Some of them were hidden for two or more crises-limited intervals before their reappearance. The reappearance of these "ancient & conserved" taxa is clearly bound to the crisis.
7. Refugia against relicts. Many naturalists & conservators jud-

ge that relict is identical to any remnant ecosystem while its biotope is refugium. So, in this view, a remnant part of damaged forest is based on "refugium". This approach clearly apologize a continuous pattern of big ecosystem that can be cut by crisis/refugium level. Dispersal pattern without any induced changes is, in fact, also apologized. Briefly the dispersal of organisms was semi-constant but crisis amputated only the best part. All right. But we must explain the structure of this relict in situ. The structures of relict reefs or wild-forests are true relicts. They are similar to mother structure being only simplified along the main structures and connections. All the relict ecosystem bases on the long-living organisms they have been specialized since the times of flourished system. Danger of collapse is big. Small relict possesses only small reserves for the flexibility of reactions.^() Particular some "disaster-taxon" may attack the relict with catastrophically consequences. The taxon of this type is usually solidarity in connections, abundant in number of specimens, and very aggressive. The taxon invades abruptly from the field of the crisis. But this is a totally another story than about the refugium. In my explanation, the refugia significantly differ from relicts. The subjects of both the refugia and the relicts possess simultaneously two faces – as the ecosystem one, as the biotope one.

8. Typical inhabitants of refugia. Our marine Devonian data suggest that typical inhabitants displayed low requirements in feeding, both in total amount and quality. Inhabitants of refugium usually recruited from organisms they were quite tolerant to environmental factors, at least to several of them. Their connections in the previous ecosystem never fixed definitely. Some Paleozoic *Amphipora* or *Scoliopora* may exemplify this situation very well. Species they are feeding nearly all but in good quantity appear, too. They are usually very flexible in niches, or in the environment at all. Shark populations of late Frasnian and early Famennian can exemplify the latter case. Stasis of these organisms does not reflect any "genetical conservation". Controversially, this type of stasis results actually from large scale of niches and tolerances. These very exciting and important conclusions have been recently introduced by Williams (1993) and commented by Ridley (1993). The latter type of organisms is not restricted only to refugia. Some people call them as "specialists for non-specialization". These organisms pass the refugia living simultaneously in other systems. Some episodes of global crises look like right time for them. An interesting analogy to crisis syndrome was found by Moore (1993) among seeding plants. The large seeding plants live in "richer" conditions while the small seeding ones live in "poorer" conditions. There is a parallel so that the large seeding plants are probably typical for flourishing systems while the small seeding ones are typical for crisis. The bigger seeding plants possess bigger amount of photosynthesis but the small ones are more effective when calculated per unit of organic mass (compare Moore).
9. Appropriate situations when organisms can enter or leave the refugium: Several scenarios can be introduced. The prominent ones are: # When organism lives in large range of conditions; in the touch, or, partly also within the refugium. # A "Supertramp" who can easily jump from one type to another type of niches, in variable series. # Possibility to switch behavioral and physiological patterns. # An excessive but applicable mutation (as a rule, only very small group of organisms, at the "advanced" organisms a couple of "Adam & Eve"). Gould & Eldridge (1993) show that good examples of gradualism are not so numerous as people commonly judge. They exist, however, but they are in minority. The origination that is a jump from ancestor clade to new clade is not so puzzling as in the past.

Some tools how understand this jump are provided by the quasi-species concept by Max Eigner. Very exciting, although still poorly tested, is the hypothesis on possible information-unity decay under the specifically strong stress (Doskočil 1993). Phylogenesis, filtration by extinction, and consequently the proper parameters of the entering and leaving of the refugium – all these questions can be effectively viewed by a restored tool of disparity.^()

10. Origination of "progenitor taxa" (a category given by E. Kauffmann & D. Erwin, 1993). These very prospective organisms originate at the end of the crisis. The power of their success is the relatively early evolution that started during late time of the crisis when other organism was still a little bit late in the developing "applicable" trends. These species or clades were probably always a little bit ahead. The first position in the front of the migrants is often the right, small but significant reason for the success in colonization. Nevertheless, there is an essential question why this early evolution actually started and how could start this evolution in refugium? Despite this uncertainty, this late crisis evolutionary activation is a quite probable scenario. The origination of progenitors based probably on two essential controls. Either the all refugium experienced some adequate portion of the stress or the field of the origination was actually in the marginal part of the refugium. Also the hypothesis on hybridization at low density conditions is not totally out of the speculations.^()

Several remarks to special, shortly persisting, and possible recent refugia

"Town effect" = an attraction of animals into the vicinity of the civilization centers. This is a quite common trend explained as an example of commensalism. We may approach one of the latest examples when jays (*Garrulus glandarius*) entered the inner Prague during 1992. The migrants were originally a couple "Adam & Eve" but nowadays they consist of several big and very fearless specimens. Birds are entering an environment with worse physical background but with incompletely occupied niches. They are clearly coming for food. Simultaneously, jays belong among tolerant, "intelligent" and relatively all-feeding birds. This situation partly resembles the story about the refugia. A question rises whether the margins of the towns are actual types of refugia. If they fit to refugia then we remember some crazy speculations from science-fiction literature (= dark visions of recovery when big rat deviants colonized the ruins of civilization).

"Trash-heap effect". Accumulated rubbish attracts some of the organisms in the same way as the "town" accumulations. The trash-heap itself is typically a subject of new colonization because there is a new catastrophically opened space. Additionally, this space provides extremely variegated conditions "rich in food and rich in poisons". Scenario of small trash-heap differs from the scenario of big one. Total trash-heap is also something another. The small trash-heap resembles small temporal refugium formed in the place that experienced the local crisis. Controversially, the overall trash-heap represents a critical turnover when the field previously damaged by the waste is subjected to new recovery. This stage accelerates from very restricted biological sources but this is a stage that accelerates the evolution more than any other which can be realized.

Both special effects are typical for the recent global crisis of biota. Both are probably significant for contemporaneous evolution of, even much more than recently accepted. Sophisticated monitoring may provide us significant data.

Where are natural refugia today? We may expect placing of them in relatively worse conditions. They should be protected against the biggest dispersal maxima of the crisis agents. Deeper continental slopes, hidden steppe-valleys or abandoned caves play probably this role. An idea about possible refugia in off-shore was supported by Molyneux & Rushton (1988). The authors (M. & R.) documented that Ordovician cratonic interior ... experienced change with a taxonomical jump which is not visible in open sea surrounding. Unfortunately, the basinal records are often damaged in tectonic processes.

Our knowledge about the nature and function of refugia is still incomplete. Many of the tasks have to be solved if we would reflect or control the recent global biological crisis. The recent crisis is evidently accelerated by industrial pollution. Despite the fact that civilization changed the ecosystem overall the planet, there are indications that these crisis agents only superimposed over the natural global-crisis agents.

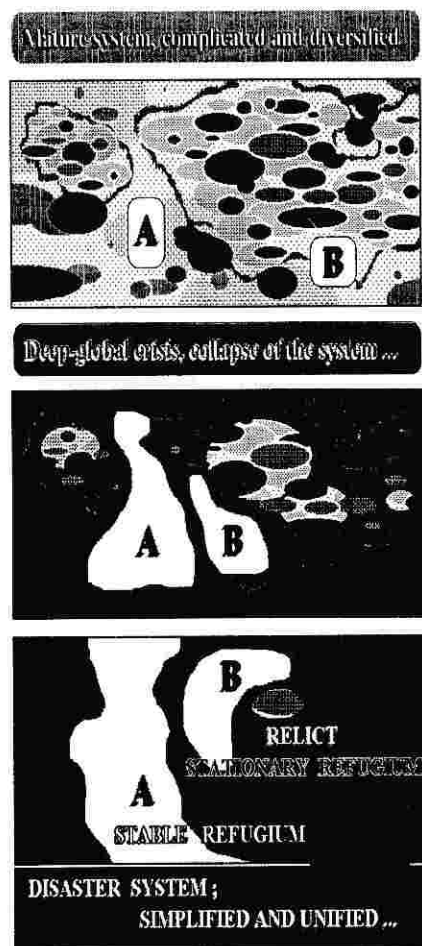


Fig.2 – Approximation of ecosystem displacements. Mature system is complicated and diversified. The crisis fields are small and strongly fluctuating (black patches). Embryonic refugia are bounded to stable places (A = stable refugia), or the others are bounded to migrating set of ecosystem disturbances (B = stationary refugia).

Deep global crisis, collapse of the system. The mature systems of shoals are deteriorated. Disaster system occupies significant part of areas. The stable refugia are bigger and the stationary refugia begin to move. Finally, the disaster system embraces majority of the area [black field]. The refugia reach major dimensions (A and B types). The formerly flourishing ecosystems are extinct with an exception of some local relicts.

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- * 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-