

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

of relatively lesser diversity. Why? At least two ways allow to explain the middle-diversity valley: 1. The valley corresponded to high temperature when the reef communities reduced in diversity while the cyanobacteria appeared. 2. The best reef community needs the best intensity of the stress. That means, whenever stress is too big the situation is wrong. This is a crisis scenario of induced crisis. Whenever the stress is too small the situation is wrong again. This is a crisis scenario of internal crisis.

Recent studies project both data and interpretation. We are studying the variability that decreases before the extinction of the species looking carefully to many accompanied phenomena in physical and biological background. One of the studies deals with *Caliapora battersbyi*, a Devonian coral having an onset at the Kačák crisis and vanishing before the "asymmetric" radiation event. We examine several tens of *Caliapora* populations. The study is difficult due to extremely large material base. Preliminary results indicate that decrease of the variability started about 0.7 Ma before extinction. Some negligible positive peaks appeared only within the latest interval of several Ka.

Mutual dependence among the variability, population density, mean age of colony, guild diversity, and all reef di-

versity were preliminary evaluated. Typical positive or negative correlation is absent or weakly expressed only. However, the last three parameters show some measure of the correlation. Poor correlation is typical also for the exposition against the waves. More over, the attacks of predators, competitors and diseases are also imperfectly correlative (!). Also an assumption that variability is simply dependent on the number of simultaneously occupied niches is not in accordance with our documents (!). When the preliminary calculations will corroborate with P.Čejchan's computing of probability in sequences then we must consider up to enigmatic independence of the discussed variability fall. When the independence of the diversity fall would not confirm then, at least, a majestic complexity of this phenomenon is very probable. We encourage our colleagues that produce more studies that deal the relation between the variability parameters and extinctions.

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The conodont extinction at the Middle - Upper Tournaisian boundary

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Abstract

The Middle-Upper Tournaisian boundary broadly correlating with the Kinderhookian-Osagean boundary in North America represents a level of a conspicuous lithological as well as biotic change. In the evolution of conodonts we can recognize an apparent offshore-onshore trend. The decline of *Siphonodella* inhabiting the pelagic to hemipelagic dysphotic to aphotic environment is accompanied by a widespread dispersal and diversification of nektonic gnathodids and characterizes the end of the first Tournaisian conodont cycle. The demise of *Siphonodella* may have reflected both the intrinsic evolutionary dynamism resulting in optimization, decreasing variance and low turnover rate and the extrinsic environmental changes. A major regression associated with important sedimentological changes marks the boundary between the middle and upper Tournaisian megasequences. The above changes in fauna and lithology seem to be connected with climatic oscillations and accompanying oceanographic changes. They are a part of the broader Upper Devonian - Lower Carboniferous cyclic scheme which appears to have been modified by a complicated interplay of cyclic and nonrecurring processes.

Introduction

The Middle-Upper Tournaisian boundary interval seems to represent a level of important changes in fauna and lithology. The global nature and climatic causes of these changes have been already outlined by Kalvoda (1989b). In this study we' d

like to elucidate in greater detail the patterns of evolution of two stratigraphically important group of conodonts, as well as to examine the character of lithologic and eustatic oscillations and changes.

Conodonts

The evolution of conodonts at the Middle-Upper Tournaisian boundary has been summarized in the studies by Sandberg et al. (1978) and Lane et al. (1980). Ziegler and Lane (1987) distinguished several conodont evolutionary cycles in the Devonian and Lower Carboniferous. They suggest a possible extinction event at the Middle-Upper Tournaisian boundary, however, they prefer to distinguish only one conodont evolutionary cycle within the Tournaisian.

In my opinion the changes in conodont diversity should be studied not only in shortest time-intervals as possible but also separately in different facies as the conodont biosphere had a considerable facial range and conodonts showed different life strategies (Sandberg, Gutschick, 1984). When we examine the conodont evolution at the Middle-Upper Tournaisian boundary from this viewpoint, the differentiated offshore - onshore trend can be traced in the pelagic to hemipelagic facies and in the shallow water facies. The most influenced are the pelagic to hemipelagic dysphotic to aphotic nektonic *Siphonodella* facies. This niche seems not to have been occupied by conodonts at all in the Lower *Gnathodus typicus* Zone. Little influenced was euphotic bispathodid facies while in the foreslope *Gnathodus-Pseudopolygnathus* facies the dec-