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 "asymmetricus" 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.Cejchan'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 nektobenthic 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 optimalization, 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-

line of Siphonodella was accompanied by the diversification of nektobenthic Gnathodus and Protognathodus (see fig. 1). In this respect the situation was very similar to the uppermost Famennian when the final decline of "mesopelagic" Palmatolepis was accompanied by a diversification of nektobenthic Protognathodus.

In my interpretation the extinction of Siphonodella at the Middle-Upper Tournaisian boundary represents an important level of change in the composition of conodont fauna which subdivides the Tournaisian in two conodont evolutionary cycles The decline of Siphonodella seems to have been connected with two steps. The first step - a significant loss of diversity in the upper Siphonodella isosticha-Upper Siphonodella crenulata Zone was followed by the second step - the final extinction of the conservative stock which marks the Middle-Upper Tournaisian boundary (Sandberg et al., 1978).

According to Ziegler and Lane (1987) each low diversity episode followed an extinction event which was connected with a global event - usually of anoxic nature (Walliser, 1984, Aldridge, 1988). Jeppson (1990) distinguished a more humid low latitude and cooler high latitude climate (P episode) and dryer low latitude and warmer high latitude climate (S episode) in the Silurian. P episodes were characterized by a high conodont diversity and extinction events correlated with the transition from P episodes to S episodes. Kalvoda (1989b) stressed, however, that the most important Upper Devonian and Lower Carboniferous extinctions of conodonts were connected with the transition from thermal to "glacial" periods. It appears to be evident that both the transition from the P episode to the S episode and the transition from S episode to P episode produced unstable oceanographic conditions which may have profoundly influenced the distribution of biota. The Tournaisian evolutionary pattern of conodonts seems to support this assumption. A rapid conodont radiation connected with niche partitioning occurred in the Lower Tournaisian P episode and continued also in the lower part of the Middle Tournaisian , which may be regarded as S episode. The extinction interval Tn2c-Tn3a can be regarded as a P episode (see next chapter) and two major steps in the Siphonodella demise seem to have been connected both with the beginning of this interval and with the end of this interval. Nevertheless it is not clear to which extent the outlined scheme reflects the extrinsic environmental changes and to which extent the intrinsic evolutionary dynamism. Optimalization in the conodont mesopelagic ecospace may have resulted in shrinking variance(cf. Gould 1988) and low origination - extinctions rate making the group vulnerable to increased environmental stress.

It is interesting to note that the highest conodont diversity was achieved in the Upper Tournaisian (Ziegler, Lane, 1987) which represents evidently a S episode (cf. Kalvoda, 1989b) and the final Tn extinction was connected with the S-->P transition. It remains to be clarified why this pattern differs from the general Silurian scheme when the highest diversity of conodonts was always achieved in the P episodes (Jeppson, 1990).

The two major steps in the Siphonodella extinction seem to have been connected with oceanograophic changes both at the S-->P and at the P-->S transition. The lithological data don't support a worldwide rise of anoxic zone in the studied extinction interval (see next chapter) and so the above oceanographic changes may have been represented rather by some kind of advection of oxic or anoxic waters (Wilde, Quinby-Hunt, Berry, 1990) which destabilized the "mesopelagic" conodont habitats. The demise of Siphonodella may have been influenced both by the direct effects of this advections as well as by indirect effects reflecting the inner evolutionary dynamism. It is interesting to see that the Siphonodella niche had not been occupied by other conodonts untill the Upper Gnathodus typicus Zone and it is still puzzling why.

The demise of Siphonodella was accompanied by the diversification of gnathodids. Even though their habitats were different they overlapped. It seems possible that the decline of Siphonodella generated new empty ecospace favoring the diversification and dispersal of gnathodids.
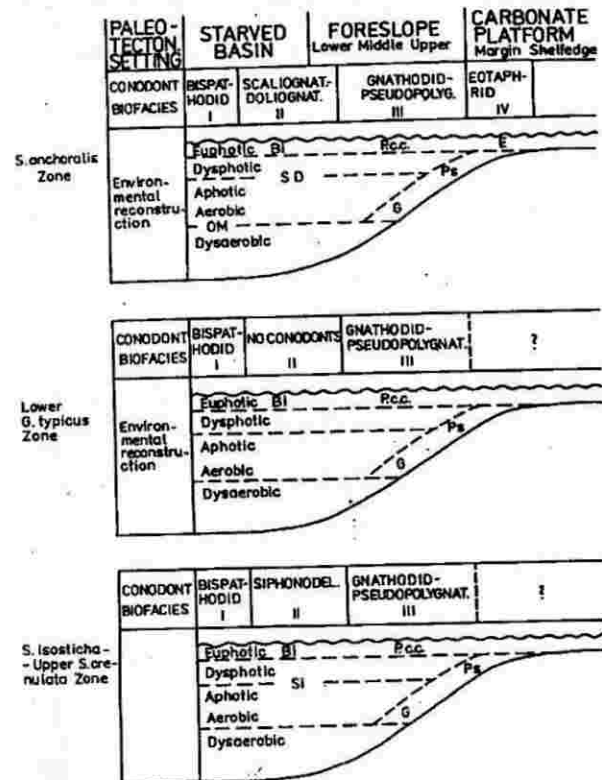

Fig. 1 – Conodont biofacies model showing interpreted palaeoecology of platform Pa conodonts of the Scaliognathus anchoralis, Lower Gnathodus typicus and Siphonodella isosticha – Upper Siphonodella crenulata conodont zone in open marine facies. Bi – Bispathodus P.c.c. – Polygnathus communis communis; E – Eotaphrus; S – Scaliognathus; D – Doliognathus; Ps – Pseudopolygnathus; G – Gnathodus; Si – Siphonodella. Modified according to Sandberg and Gutschick (1983, 1984).

Eustatic oscillations and lithological changes

The end of the Middle Tournaisian is marked by a widespread worldwide regression as well as by unconformities recognized in Western Europe (Paproth et al., 1983), Eastern Europe (Stepanov et al., 1975), North America (Lane 1974, 1978; Brenkle & Groves, 1987) and Siberia (Sweenen et al., 1986, Bushmina, Bogush & Kononova, 1984). This regression is also accompanied by profound lithological changes. In Eastern Europe they mark the boundary between the Cherepet or Kynov Horizon and Kizel Horizon, in Western Europe the boundary between the Landelies Limestone and Calcschistes de Maurenne or Hun. Similar lithological changes as in Western Europe can be recognized in Central Europe in Moravia. In Western Europe this level corresponds to the boundary of megasequences A and B (Paproth et al. 1983) while in Moravia it corresponds to the boundary of megacycles 8 and 9 (Kalvoda 1989a).

The mentioned lithological changes can be traced in shelf facies. A profound lithological change, however, can be recognized also in the basinal facies (e.g. in the Rheinische Schie-

fergebirge between the Liegende Alaunschiefer and Lydite Horizon - Voges 1959; Lane et al. 1980) where condensation, dissolution, erosion and reworking of fauna and paraconformities mark the Middle-Upper Tournaisian boundary.

The Tn2c-Tn3a interval represents a regressional period as unconformities occur worldwide and shallow water facies show only little distribution. An increased representation of shaly facies on shelves represents further characteristic feature. The regressional trend was reversed only during transgressions in the Gnathodus typicus Zone which can be seen both in Europe and in North America (Paproth et al., 1983, Lane, 1978, Sandberg et al., 1983, Kalvoda, 1989b). The initial transgression at the beginning of the zone appears to have increased up to the upper Gnathodus typicus Zone and it can have been connected with the restoration of carbonate sedimentation in shelf facies represented for example by the transition from Calcschistes de Maurenne and Hun to Calcaire d'Yvoir in Belgium (Paproth et al., 1983) or from Andrecito Member to Allamogordo Member in New Mexico (Lane & Ormiston 1982).

The increase in shale sedimentation and the drop of carbonate sedimentation in the extinction interval may be compatible with the decline of carbonate sedimentation during a cooler climatic P episode (Jeppson 1990).

Fig. 2 – Generalized correlation of foraminiferal, conodont and lithological cycles and climatic episodes at the Middle-Upper Tournaisian boundary.

Conclusions

The Middle-Upper Tournaisian boundary interval (Tn2c-Tn3a) correlates with important changes in biota (foraminifers, conodonts), lithology and climate (see fig. 2). In my interpretation the changes in the conodont fauna show a distinct offshore onshore trend - the largest impact on "mesopelagic" Siphonodella while shallow water gnathodids radiated in the new ecospace in the overlapping habitats. The pelagic to hemipelagic dysphotic to aphotic niche after the extinction of Siphonodella had not been occupied till the Upper Gnathodus typicus conodont zone.

The demise of "mesopelagic" Siphonodella reflects an interplay of both intrinsic and extrinsic factors. The biotic factors followed from the evolutionary dynamism - decreasing variance reflecting the general optimalization resulted in low morphological disparity and the low turnover rate of the end members making them vulnerable to environmental deterioration. The extrinsic factors were connected with climatic oscillations and accompanying oceanographic changes. We can recognize two events which seem to correspond to oceanographic changes at the transition from S to the P climatic episode (Jeppson 1990) and from the P to the S climatic episode (see

Fig.2). In this interpretation the extinction interval Tn2c-Tn3a corresponds to a cool P climatic episode. Lithologically it is characterized by the increased representation of shales as well as of anoxic and oxygen low facies on shelves even though the data don't support a worldwide long-term rise of anoxic zone.

Generally, the described pattern of biotic and lithologic evolution is a part of a broader Upper Devonian and Lower Carboniferous cyclic scheme (Kalvoda 1989a,b, 1990). It is still hard to decipher the driving force of this cyclic evlution as the resulting biotic and lithologic manifestation was modified by a multicausal nature of many nonrecurrent and cyclic processes involved.

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Some remarks from paleobotany and paleontology to adaptation of plants to the stress condition and survival

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Paleobotanical records may well contribute to the studies of plant taxa/biota adaptation to the short- or long-term stress and surviving during the geological history of plant kingdom by many examples. In following contribution an attempt is made to choose several examples for the brief demonstration. Some of them are derived from literary data, others are given from the own studies of microfossils or recent comparative material. Beside of macrofossils it is palynology that provides available evidence from the continuous records of plant fossils of various environments.

Several aspects significant for survival have been distinguished. They are arranged in the following paragraphs and discussed in the examples in more detail.

1. Change of the assemblage composition

due to the stress condition. The changes within the microfossil assemblages, corresponding to both favourable and unfavourable conditions in the marine environment can be traced as early as in Precambrian and Paleozoic. Their linkage with the changes of environment, e.g. from well oxygenated marine environment into inoxygenated is evident. For the flourishing planktonic unicellular algae (Acritarchs) the well oxygenated photic zone of the Ordovician (e.g. Ashgillian) sea may well be presumed as an excellent environment where Cyanobacteria (Cryptarchs) are absent or preserved only exceptionally. In contrary to it, the inoxic with depleting of oxygen, display only few rests of acritarchs in the assemblage (e.g. black shales) but it is rich in rests of Cyanobacteria or Bacteria (Cryptarchs). The change of the assemblage kin to the paleoenvironment is supported about the isotopic analysis (composition of organic carbon and sulphur content in Precambrian and Paleozoic shales). Chemotrophic Bacteria/Cyanobacteria were the favoured organisms that flourished in the extreme conditions of inoxic paleoenvironment due to their autotrophy and highly specialized metabolism. The other phytoplanktonic organisms disappeared or have been very supressed. Resistance and wide adaptation of Cyanobacteria to extreme environments enabled them to exist from the Precambrian up to the Recent. They are evidenced from Riphean (978 Ma) rocks up to recent muds of sea troughs and freshwater basins. (Demonstration of the main groups of these microfossils in Fig.1).

2. Higher production of organisms during stress

The higher production of plant organisms as one of the reaction stimulated by short- or long-term stress is known at the level of both, the lower and the higher plants. The short-term reactions to the stress environment have been evoked experimentally by the toxic input to the medium with living Rhodophyte specimen (for the comparative purposes). Very quick production of tiny reproductive bodies could be observed in