5. Broad ecological plasticity (see also paragraph 1)

is also one of the phenomena enabling survival and reproduction under the stress condition. It has been probably the reason of survival of several very ancient families rooting in Paleozoic and living up to Recent. The representatives of the family Schizeaceae emerging in the Late Paleozoic and spreading almost globally in Mesozoic and Early Tertiary are a good example. Schizaea, Lygodium, Aneimia and Mohria are living in disjunct areals up to Recent. The continuity in existence of the family is recorded in the fossil remains of these ferns and their spores, known also in situ in the connection with the mother plants.

References

REYRE, Y. (1973): Palynologie du Mésozoique saharien. – Mém. Mus. Natl. Hist. Nat., C, 27, 8–284. Paris.

KONZALOVÁ, M. (1991): Palynological studies in the Mesák Formation (Central Libya). – M.J. Salem, O.S. Hamuda, B.A., Eliagoubi, Edts., The Geology of Libya IV, 1229–1241. Elsevier Publ. Co., Tripoli, Amsterdam, Tokyo, London.

NĚMEJC, F. (1963): Paleobotanika. II. – Nakladatelství ČSAV, 259 pp. Praha.

Ideas about an interaction between sea-level changings, biogeographic patterns, global extinction events, and recovery – exemplified by the Devonian

Andreas MAY, Friedrich-List-Str. 66, D–59425 Unna 1, BRD

Prior to the recovery is the extinction, and therefore it is important to understand the patterns and causes of global extinction events. In this paper I want to present some ideas exemplified by the Devonian. The Upper Devonian Kellwasser Event at the Frasnian/Famennian boundary caused the extinction of many animal groups as well as the end of the mid-Paleozoic reef era. Before the Kellwasser Event there were some other, less important extinction events in the Devonian - e.g. the jugleri-Choteč Event in the lower Eifelian and the otomari-Kačák Event in the upper Eifelian. Furthermore there is an intensified "background extinction" well before the Kellwasser Event.

In my view there is an interaction between sea-level changings, biogeographic patterns and global extinction events: In the late Early Devonian the marine fauna has a maximum of provincionality caused by a world-wide lowstand of the sea-level. Accompanying to the sea-level rise a lowering of the global climatic gradient can be observed. Both together lowered the provincionalism in the Frasnian nearly to zero and only one of three biogeographical realms (+- tropical Old World Realm) remained. The transgressions destroyed important barriers against faunal exchange by opening gateways for the fauna and lowering climatic gradient. The co-existence of former separated organisms resulted in an intensified competition and selection. This conducted to an extinction of the less fit species. The extinction of species as a result of intensified faunal exchange is the cause for the intensified "background extinction" in the (higher) Middle Devonian and lower Upper Devonian. Maybe also some minor extinction events can be explained fully by suddenly intensified faunal exchange (opening of gateways!), but more important events - like the Kellwasser Event and the Kačák Event - need further explanations.

The detailed investigation of extinction events in the passed years has shown that they are combined with important regressions/transgressions and/or global anoxic events. E.g. the Kellwasser Event (or better: "Crisis") consists of two global anoxic events and important regressions. The Kačák Event is often interpreted as a transgressive event. The remarkable acme of pelagic organisms within the Kačák Event resembles much to the Kellwasser Event, so that an anoxic event is possible.

The normal explanation of anoxic events are changings in the circulation of the ocean water. Circulation changings can be caused by re- or transgressions (closing or opening of gateways) and/or climatic changes. Climatic changes can result of sea-level changings. Direct effects of sea-level changings on the fauna (esp. the shallow marine fauna) are: 1. Transgressions produce faunal mixing leading to intensified selection and disturbing of ecosystems. 2. Regressions reduce the living space.

The rapid changings of the sea-level and their effects are better explanations for extinction events than meteorite impacts is confirmed by following observation - which are among other extinctions made by the Kellwasser Event, too (see e.g. Boucot and Schindler in Kauffman & Walliser 1990): 1. Decoupling in the history of ecologically different parts of the fauna. 2. Stepwise extinction. /Note esp. the idea of Boucot (in Kauffman & Walliser 1990: 20) that "there are certain keystone taxa that when finally eliminated cause the whole community structure to crash"./

These considerations can explain the causes of one extinction event but they do not explain, why, as an example, the Kellwasser Event was much more important than the Kačák Event and the other Devonian extinction events. An explanation may give an evolution of provincionalism in the Devonian: Before the Upper Devonian was a remarkable degree of provincionalism and the destroying effects on the fauna of a sea-level & anoxic event similar to the Kellwasser Event would have been less serious, because: 1. The diversity of the total fauna was larger and therefore the probability of the existence of species which can resist. 2. The collapse of one ecosystem would not be so serious for the fauna of the whole world, because there are much more ecosystems (more provincionalism!). 3. The interaction between the different oceans (or parts of one ocean) was not so great, and therefore remarkable changings (esp. anoxic events) in one ocean (or part) need not to be so serious in other oceans (or parts). This can be shown by the minor extinction events of the fauna: 1. It seems to be so, that the Kačák Event has a great effect to the shallow water faunas of the Eastern Americas Realm but not to the fauna of the Old World Realm. 2. In the Old World Realm the shallow marine equivalent of the jugleri-Choteč Event (lower Eifelian) is marked by the extinction of Paraspirifer, but in the Northern America Paraspirifer becomes extinct not before the Upper Eifelian!

Just before the Kellwasser Event (1) the marine fauna was nearly identical all over the world and (2) the marine fauna had had some million years time to adapt itself to a tropical climate with low climatic gradient. Therefore the Kellwasser Event was a very large extinction event and the other Devonian extinction events are less important.

In similar way differences of recovery can be explained: Within Lower and Middle Devonian extinction events affected only limited areas of the world. In consequence there existed several potential refugia and several source ecosystems for substitutes. The Frasnian shallow, +/- tropical sea had only few (or no?) potential refugia and source ecosystems for substitutes. Therefore the source area of the recovering Famennian shallow marine fauna were colder and/or deeper (=colder, too!) water. That would give a good explanation for the remarkable impoverished shallow marine fauna of the Famennian, because of the low climate gradient and low provincionalism of the Frasnian there can not have been large areas with cold water faunas. This also may explain the "Lazarus" taxa (e.g. the reappearance of "ancient" stromatoporoids in the Famennian).

Selected references

BOUCOT, A.J. (1988): Devonian Biogeography: An Update. – In: McMillan, N.J., Embry, A.F. & Glass, D.J. (eds): Devonian of the World, Candian Society of Petroleum Geologists, Memoir, 14 (Vol. III), 211–227, 3 figs. Calgary.

HLADIL, J. & KREJČÍ ,Z., et al. (1991): Carbonate ramp environment of Kellwasser time-interval (Lesní lom, Moravia, Czechoslovakia). – Bull. Soc. belge Géol., 100 (1–2), 57–119, 15 pls. Bruxelles.

KAUFFMAN, E.G. & WALLISER, O.H. (eds.) (1990): Extinction Events in Earth History. – Lecture Notes in Earth Sciences, 30. Springer Verl., Berlin.

MAY, A. (1994): Palaeoecology and palaeobiogeography of corals and other reef-builders from the Middle Devonian of the Sauerland (Germany). – In: Proceedings of the 6th International Symposium on Fossil Cnidaria. – Courier Forsch.–Inst. Senckenberg, Frankfurt a.M. (in print).

McGHEE, G.R., BAYER, U. & SEILACHER, A. (1991): Biological and Evolutionary Responses to Transgressive-Regressive Cycles. – In: Einsele, G., Ricken, W. & Seilacher, A. (eds.): Cycles and Event Stratigraphy: 696–708, 7 figs., Springer Verl., Berlin.

Using of "semi-fossil" sources of energy: a successful strategy in crises of biota?

Radek MIKULÁŠ, Geological Institute, Academy of Science, Rozvojová 135, 165 02 Praha 6 – Suchdol, Czech Republic

What living strategies are successful in periods of crises and recovery? The study of fossil traces (ichnology) gives (or may give) the explicit answers in some cases, because the traces are a direct record of behaviour (see further contribution in this bulletin, Mikuláš 1994). This proposition is documented by the following case.

A specific assemblage of feeding traces (fodinichnia), represented namely by the ichnogenera Chondrites and Zoophycos, often occurred after events reducing the marine benthic assemblages by decreasing of oxygen volume in water and in sediment. As example of such redox event, documented also in the Bohemian Massif, the Kačák event in the Middle Devonian could serve (see, e.g., Chlupáč 1992). The ichnoassemblage, representing a suite of specific activities of benthic organisms, has been designated by Bromley (1990) as Chondrites – Zoophycos ichnoguild. After Bromley, these traces resulted by activity of non-agile feeders of deeper deposits within the substrate; they are characteristic by mass occurrence in oxygen-deficient settings. In oxygenated settings, their occurrence is characterized usually by less density and by the presence in the deepest tiers of the substrate (where the oxygen volume is also reduced). The position of the Chondrites - Zoophycos ichnoguild and scheme of morphology of the main representatives is on Fig. 1; for idealized example of dysoxic event and joined ichnological demonstration see Fig. 2; a model case of the ichnoassemblages put across the oxygenation gradient is shown in Fig. 3. The topic of Chondrites - Zoophycos ichnoassemblages is very frequent at present (Bromley 1990, Ekdale and Mason 1988, Ekdale and Lewis 1991, Savrda and Bottjer 1987, 1989, 1991, Savrda and Seilacher 1991, Wetzel 1991, and others). Summary of the results was given by Savrda (1992).

Chondrites consists of a root-like branching system of tunnels. Burrow fills are usually structureless and often differ in colour from surrounding rock (Häntzschel 1975 a.o.). Origin of the burrow infill is problematic; evidence for both active and passive fillings has been reported. However, the fill usually derived from above and is not a result of reworking of the neighbouring substrate (Savrda 1992).

Despite the general ubiquity and long geological range of the occurrence (Precambrian to Holocene), taxonomic affinities of the producers are unknown. Considering the morphological variability of Chondrites, Osgood (1970) suggested that various organisms as polychaetes, sipunculids or arthropods could be the tracemakers. The most traditionally held model of function of the Chondrites systems is that of Simpson (1957), who explained them as fodinichnia. Newly Seilacher (in Savrda et al. 1991) suggested an alternative that explains better the morphology of the ichnogenus: the "well systems" made to extract H_2S or methane from reducing sediments. These gases were used to culturing endosymbiotic bacteria. Seilacher has found the analogy in behaviour of Recent chemosymbiotic bivalves (Solemya and Thyasira) and polychaetes (Nereis diversicolor).

The ichnogenus Zoophycos is a complex structure composed namely of spreite. Individual components of the structure are lamellae that form the spirally coiled plane - lamina, and a cylindrical tunnel in the axis and along the margins of the lamina (see Fig. 1; after the summary of the problem by Savrda 1992).