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 H2S 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).

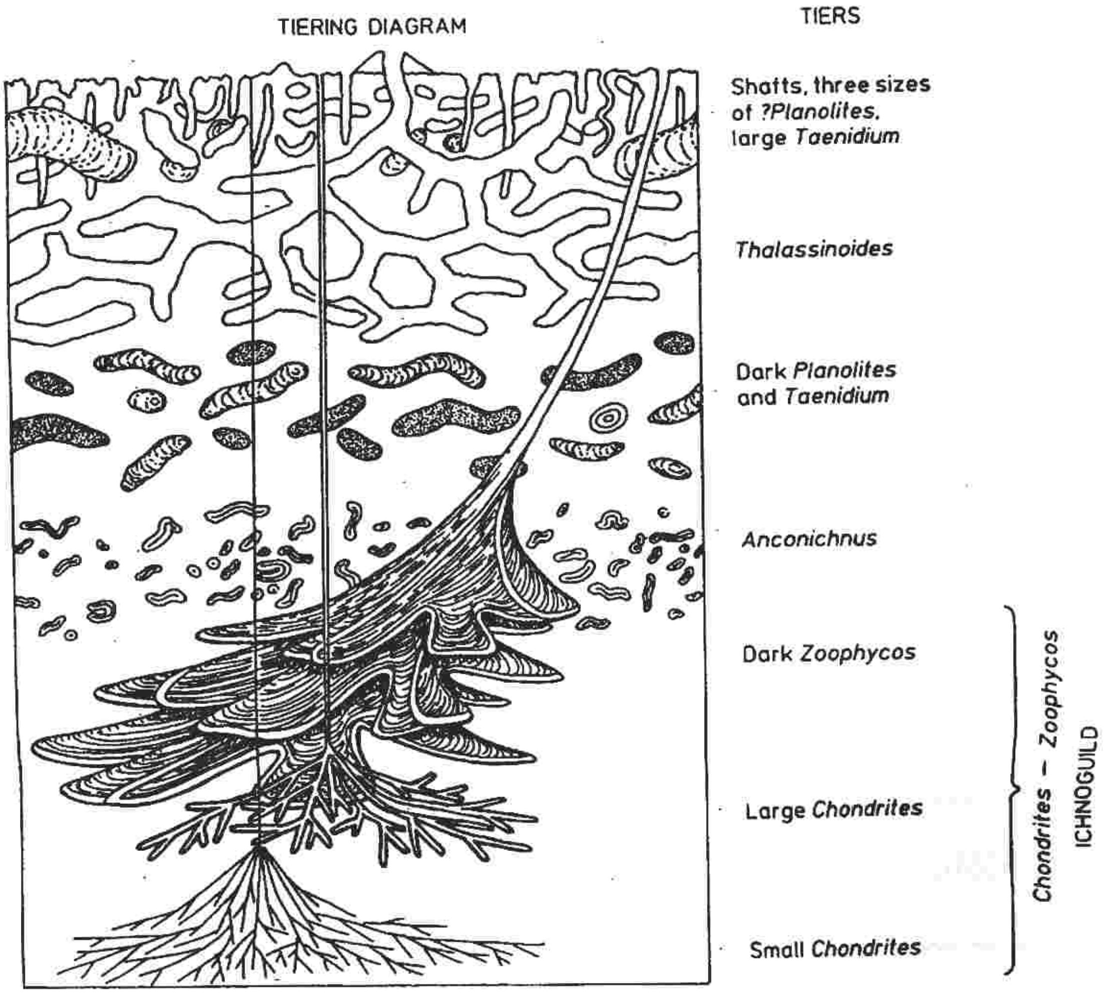

Fig. 1 – Tiering diagram showing the position and basic morphology of the members of Chondrites – Zoophycos ichnoguild. Upper Cretaceous, Denmark. After Ekdale and Bromley (1991).

In the Paleozoic, Zoophycos occurred both in nearshore and in basinal settings. Through the Mesozoic and Cenozoic it was gradually restricted to deeper facies (Bottjer et al. 1988). The occurrence of Zoophycos in oxygen-deficient settings is similar to that of Chondrites. Zoophycos is common often in organic-rich marine mudrocks. Where it is present in ichnocoenoses representing more oxygenated substrates, it occupies deeply in the substrate (Savrda 1992 a.o.).

Taxonomic appurtenance of the Zoophycos producer (or producers) is unknown (similarly as in Chondrites). The ethological sense of the Zoophycos traces is also a complicated question (see, e.g., Ekdale and Lewis 1991). Zoophycos is most often considered to be a fodinichnion produced by sediment feeders, e.g. annelids, sipunculids, phoronids (Savrda 1992).

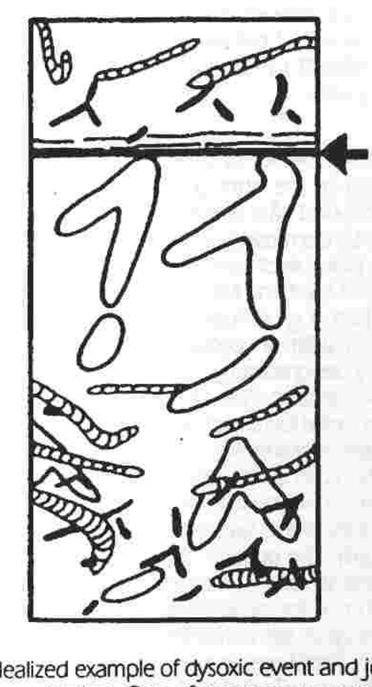

Fig. 2 – Idealized example of dysoxic event and joined ichnological demonstration. One of numerous examples given by Savrda and Bottjer (1989). The event is marked by arrow. Black oblique tunnels = Chondrites; spreiten structures = Zoophycos; large traces = Thalassinoides or similar ichnogenera.

The ichnogenera Teichichnus and Trichichnus are further potential members of the Chondrites - Zoophycos ichnoguild (Savrda 1992). In my opinion, the ichnofossil Pragichnus fascis Chlupáč, 1987 is also a "full-value" member of this ichnoguild. It consists of the tunnel system somewhat similar to the Chondrites system, but showing the passages much steeper; overall vertical dimension is up to 40 cm (Fig. 4). Pragichnus is known from pale quartzites from the Ordovician of the Barrandian area and from the Central Bohemian roof pendants ("islet zone") (Chlupáč 1987). These quartzites, however, contanin thin intercalations of black clay shales that could be a source of CH_4 and H_2S; the gases could penetrate to overlying sandy material and there extracted.

It cannot be the aim of this short paper to contribute to a knowledge of the Chondrites - Zoophycos ichnoguild traces; the aim is only to look at their evidence thorough the questions put to the participants of the workshop. It is obvious that the producers of the Chondrites - Zoophycos ichnoguild were extraordinarily resisting to dysoxia. The evidence also offers to test the proposition that the producers of the Chondrites - Zoophycos ichnoguild were successful during dysoxic (and not only dysoxic) crises, because they were able to employ the substances "conserved" in the substrate to feeding (and therefore they were not so distressed by fluctuation and reduction of feeding possibilities following the state of biosphere of the moment). If the interpretation of Chondrites as "wells" extracting H_2S and CH_4 is correct, it perhaps can be recognized as obtaining of "semifossil energy". This activity may show as not solitary strategy of surviving the crises of biota.

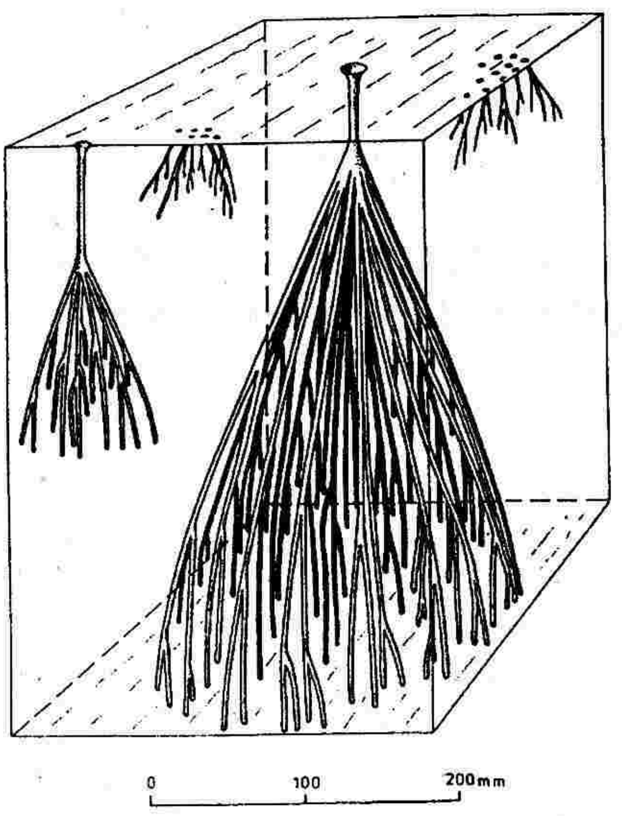

Fig. 4 – Pragichnus fascis Chlupáč, 1987. Reconstruction of the burrow system. Ordovician, Czech Republic. After Chlupáč (1987).

References

BOTTJER, D.J. – DROSER, M.L. – JABLONSKI, D. (1988): Paleoenvironmental trends in the history of trace fossils. – Nature, 333, 252–255.

BROMLEY, R.G. (1990): Trace Fossils – Biology and Taphonomy. – Unwin-Hyman, 280 p. London.

CHLUPÁČ, I. (1987): Ordovician ichnofossils in the metamorphic mantle of the Central Bohemian Pluton. – Čas. Mineral. Geol., 32, 3, 249–260. Praha.

– (1992): Pražská pánev. Devon. In I. Chlupáč et al.: Paleozoikum Barrandienu (kambrium – devon), p. 148–198. – Ústř. Úst. geol. Praha.

EKDALE, A.A. – BROMLEY, R.G. (1991): Analysis of composite ichnofabrics: an example in uppermost Cretaceous chalk of Denmark. – Palaios, 6, 232–249.

EKDALE, A.A. – Lewis, D.W. (1991): The New Zealand Zoophycos revisited: morphology, ethology, and paleoecology. – Ichnos, 1, 183–194.

EKDALE, A.A. – Mason, T.R. (1988): Chracteristic trace fossil associations in oxygen-poor sedimentary environments. – Geology, 16, 720–723.

HÄNTZSCHEL, W. (1975): Trace fossils and problematica. In: C. Teichert (ed.): Treatise on Invertebrate Paleontology, W, 2nd ed. – Geol. Soc. Amer. and Kansas Univ. Press, 269 p. Boulder-Lawrence.

MIKULÁŠ, R: (1994): Ichnology and its possibilities in the study of crises of biota. – This bulletin, p. xx–xx.

OSGOOD, R.G. (1970): Trace fossils of the Cincinnati area. – Palaeontographica amer., 6, 41, 281–444.

SAVRDA, C.E. (1992): Trace Fossils and Benthic Oxygenation. In: C.G. Maples and R.R. West (ed.): Trace fossils. – Short Courses in Paleontology, Paleontological Society, 5, 172–196.

SAVRDA, C.E. and Bottjer, D.J. (1987): Trace fossils as indicators of bottom-water redox conditions in ancient marine environments. In: D.J. Bottjer (ed.): New concepts in the use of biogenic sedimentary structures for paleoenvironmental interpretation. – Soc. Econ. Paleontologists Mineralogists, Pacific Section, 52, p. 3–26.

SAVRDA, C.E. and Bottjer, D.J. (1989): Trace fossil model for reconstructing oxygenation histories of ancient marine bottom waters: application to Upper Cretaceous Niobrara Formation, Colorado. – Palaeogeogr. Palaeoclimatol. Palaeoecol., 74, 49–74.

SAVRDA, C.E. and Bottjer, D.J. (1991): Oxygen-related biofacies in marine strata: an overview and update. In: R.V. Tyson and T.H. Pearson (eds.): Modern and ancient continental shelf anoxia. – Geol. Soc. London, Spec. Publ. 58, p. 201–219.

SAVRDA, C.E., BOTTJER, D.J. and SEILACHER, A. (1991): Redox-related benthic events. In: G. Einsele, W. Ricken, and A. Seilacher (eds.): Cycles and Events in Stratigraphy, p. 524–541. Springer-Verlag. Berlin.

SIMPSON, S. (1957): On the trace fossil Chondrites. Geol. Soc. London, Quaterly Journal, 112, 475–499.

WETZEL, A. (1991): Ecologic interpretation of deep-sea trace fossil communities. – Palaeogeogr. Palaeoclimatol. Palaeoecol., 32, 185–212.