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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 very short time after input in embedded medium. The reproductive bodies were produced in large amount and spread with relatively great energy. High productivity in the stress condition or under very special condition of environment, where only one type of plants/organisms may live, is also known from the fossil state. The assemblages are often represented by many specimens of one species. The examples are known from paleoplanktonic and palynological studies of assemblages of different age and environment. Calcareous nannoplankton, cycts and colonies of fossil algae, as well as fossil pollen of halophytes (Chenopodiaceae) recorded in Miocene and Pliocene spectra can be mentioned.

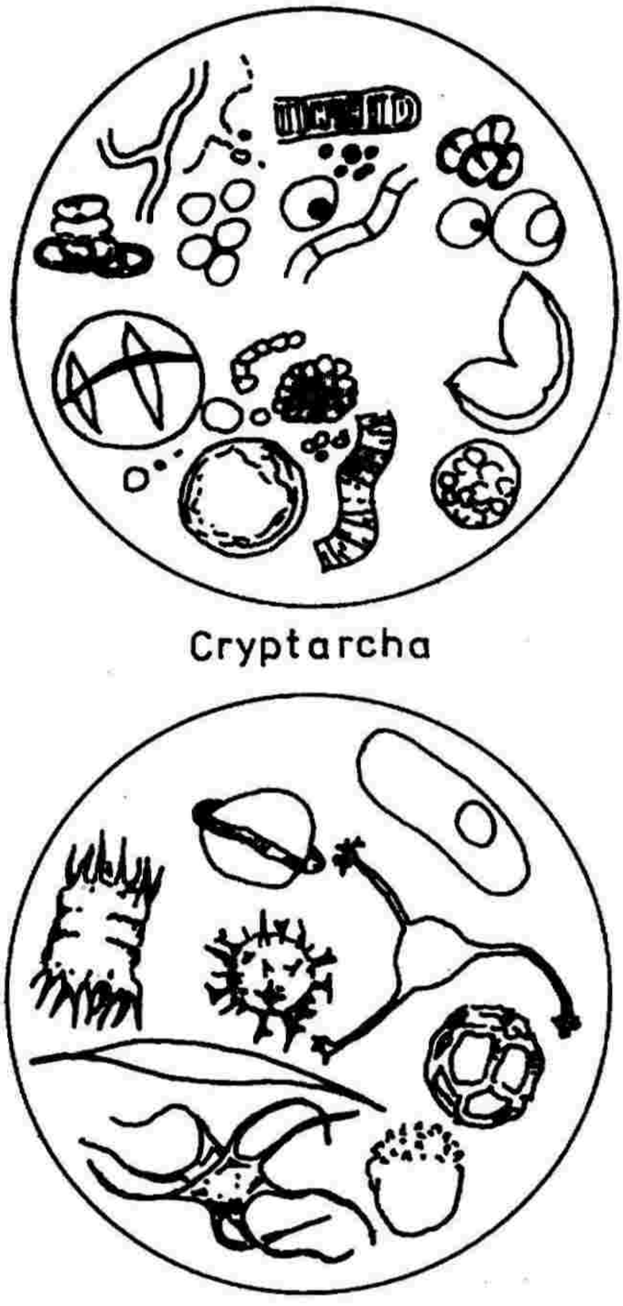

Fig. 1 – Illustrations of various cryptarchs (Cyanobacteria/Bacteria) and acritarch species from Paleozoic, after Peat ex A. Traverse, 1988.

3. Morpological and ecological plasticity

is one of the other marks that enables survival and competitive life under the stress conditions of extreme habitats (rocky slopes, nival belt, salt soils, higher solar activity, sudden alteration of temperature and others).

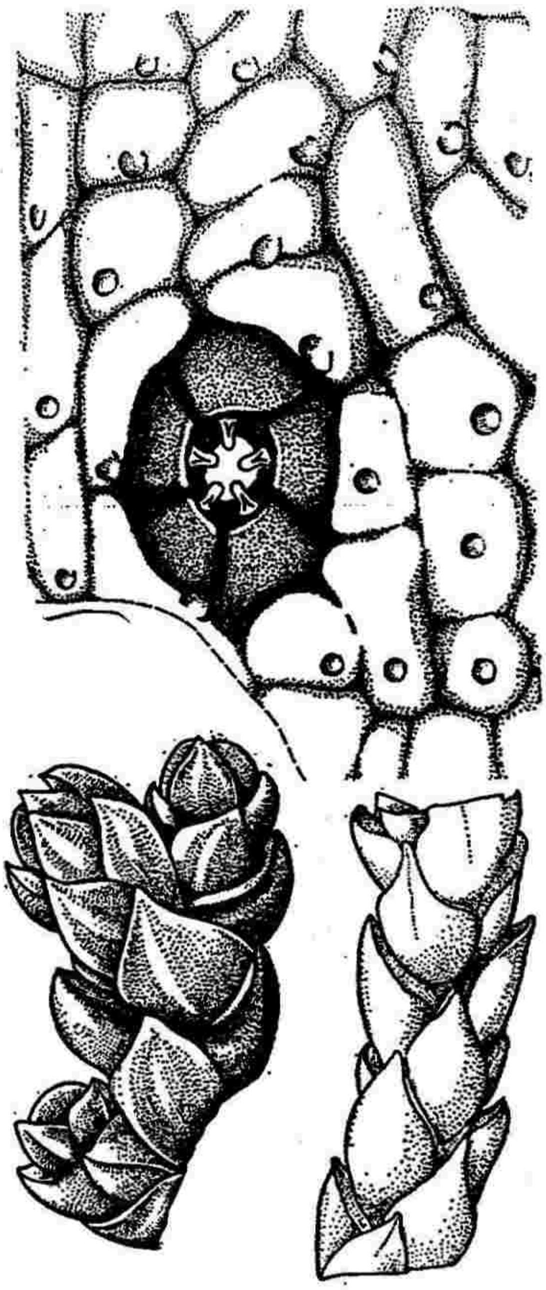

Fig.2 – Brachyphyllum negevensis Lrch., from Lorch, 1968. Portion of thick cuticle with one stoma protected by papillae. An example of adaptive reaction to subhumid/semiarid conditions.

Mesozoic sweep-like cheirolepidaceous conifers growing probably along shore side and at the rims of ephemeral lakes on salt soils, may be given as an example from the group of extinct conifers. Some of their representatives display the markers typical for the plants of extreme habitats: thick epidermal cover, i.e. thick cuticle (up to 30 mm; manytimes thicker than posses other plants), scale- or cushion-like, reduced leaves with submersed stomata, often protected by papillar outgrowths. All these anatomic and physiologic markers characterize the fossil conifer Brachyphyllum negevensis Lrch. (Cheirolepidaceae), known from the Mesozoic of the Negev Desert (Fig.2). This dressing hindered the plant from transpiration and may be interpreted as the morphological protection (functional morphology) known from modern plant taxa growing under subhumid and semiarid/arid conditions, linked ofted with salt soils. Such conditions are too unfavourable for most of the other plants.

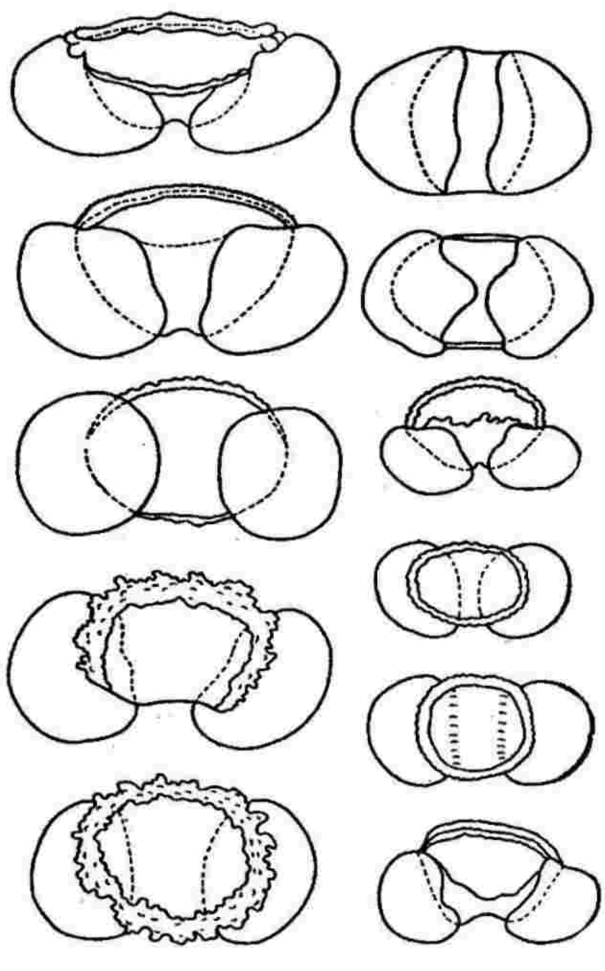

Fig.3 – Paleogene Pinaceae pollen from Priaralian area ex Zaklinskaya, 1963. The illustrated shapes demonstrate thick proximal part of pollen that may be explained as protection of pollen content.

To the functional morphology belongs also variable dressing of fossil pollen. It si well demonstated within pollen morphotypes of cheirolepidaceous conifers too. It was recognized that they have possessed Classopollis pollen, very common in Mesozoic. Their exines displays striking differnces in coating. For example, Classopollis pollen ornamented with dense hairs and provided distinct granular layer are known from Sahara Mesozoic (Reyre 1973). The purpose of dressing is to protect the cell content, probably under the condition of lower humidity/higher aridity. Similar markers display stoutly ribbed and corrugated spores of some schizeaceous ferns (Aneimia, Mohria, Schizaea) or Welwitschia and Ephedra pollen of desert/arid and semidesert/semiarid plants. Also the thick proximal exine cap (Fig.3) of the Paleogene pollen of Pinaceae (Section Strobus) from the Priaralian area may be of interest from this view.

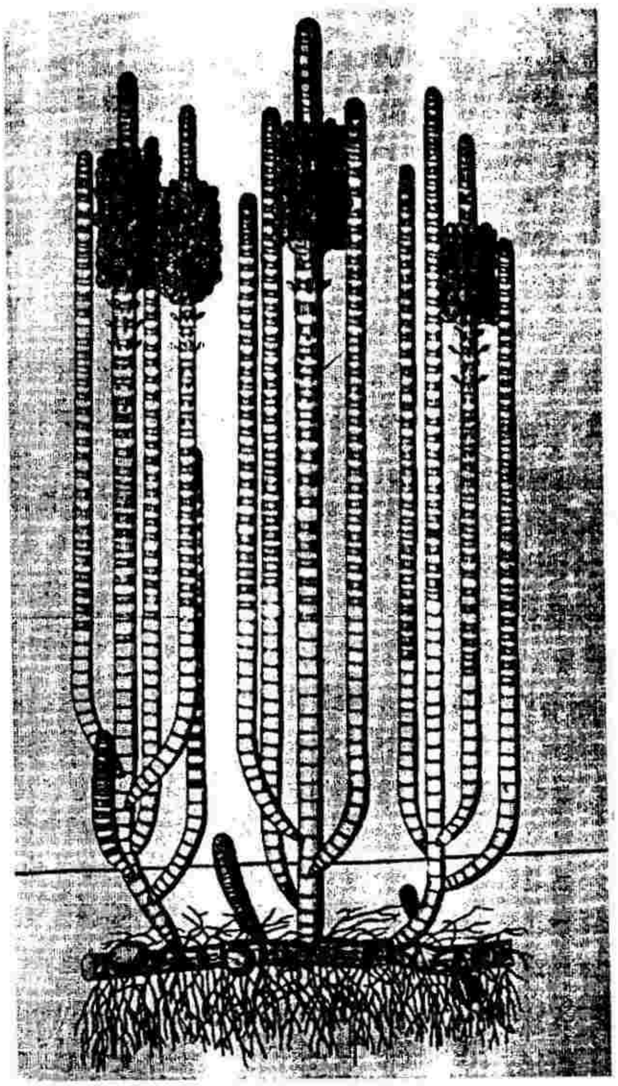

Fig.4 – Equisetaceae: Equisetites arenaceus from Triassic of Germany. Example of diminishing of the representatives of the family Equisetaceae during geological history. After Frentzen, 1934 ex Mägdefrau, 1953.

4. Diminishing of the habitus

In the connection with conifers, the diminishing of the tree habitus under the stress condition (wind, rocky slopes, desertification and others) is long time known and may well be supposed in the geologic times. The phyllogenetic lines from trees to shrubs and herbs have been supposed by many authors and demonstrated often within lycopods and sigillarids from Carboniferous via Mesozoic up to today representatives of Lycopodiaceae and Sellaginellaceae. The size differency between Triassic Equisetites Sternb. (e.g. E. areanaceous (Jaeger) Schenk) and modern Equisetes L. species is striking (Fig.4). Diminishing of habitus may be seen as one of reactions to the stress phenomena, practically on all the levels - known from unicellular organisms (foraminifers, radiolarians and others) up to multicellular highly organized organisms.

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.

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

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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