Fungi spike – an ecologic disaster?

Dirk Zamecnik, TU Bergakademie Freiberg

Abstract
Mass extinctions caused by catastrophic events were discussed very often during the last years. One of these events possibly happened at the Permian – Triassic transition. For possible reasons are volcanic activities and asteroid impacts in discussion. In context with the event at P/T-boundary (~251 Ma) are also a 'fungal event'[1] in discussion. A layer with abundance of fungi remains is still found worldwide and could be used for correlation between marine and terrestrial environments. On the other hand there is the point of view, that the fossils which were found are representatives of green algae. However, this fact is not necessary for usage for correlation, but important for the discussion of the reasons of mass extinction.

1. Introduction

The mass extinction at Permian – Triassic boundary was regarded for long time as only one event, but today several scenarios are in discussion: one catastrophic event, a stepwise change or a stepwise change with one or more culminations of extinction (Kozur 1998). A distinct variance in carbon isotope ratios implies a significant decrease of marine biomass production. This is simultaneously apparent in biodiversity of terrestrial life. For land plants a higher resistance was assumed, but terrestrial vegetation showed sensitivity for environmental worsening. Their production of biomass and the resulting remains in late Permian layers is eminent, hence they are in focus of investigations. However, today the disappearance of late Permian gymnosperms is accepted as a major event. This dieback is the cause for major accumulation of woody debris in sedimentary records close to the P/T-boundary. This is accompanied by a bloom of other organisms, predominantly fungis, which take over the function of decomposing the organic remains of late Permian landplants. The after-effect is a higher abundance of fungi remains in palynological assemblages in terrestrial and shallow marine deposits. In the fossil record single cells and chains of several cells are preserved, which are interpreted as relicts of ascomycetous fungi (Visscher et al. 1996), corresponding to *Reduviasporonites* as well as the zygnematalean green algae *Tympanicysta* (Afonin et al. 2001). However, as type location for establishing a correlation between marine and terrestrial facies an outcrop in South Africa's Karoo Supergroup is proposed by Steiner et al. because of its widespread occurrence of the 'fungal spike'[2] (Steiner et al. 2003).

2. Biotic crisis – causes and effects

In the discussion of possible causes of the extinction scenario is an asteroid impact, but the reported iridium spikes close the P/T-boundary have not later been confirmed. Another reason could be largescale volcanic activity. The Siberian Trap Basalts are up to 1000 m thick and cover an area of about 4,5 million km², other areas are widespread covered by volcanic ash falls. It is evident that such massive volcanic activity must have an influence on the climate, especially of the northern continents. Other consequences are acid rain and a conspicuous cooling in lower latitudes. The view of Kozur is that huge eruptions bring a large amount of dust and sulphate aerosols into the atmosphere above the cloud zone. Thus they cannot be rained out in a span of time of 3-6 months. The following decrease of solar radiation causes a cooling in low latitudes and mass extinctions in tropical and subtropical shallow marine facies but not so violent extinctions in ranges with seasonable changes of temperature. This pattern is apparent in the fossil record below the P/T-boundary. A cooling lasting for one month brings enough cool water by oceanic currents from lower latitudes to higher, to let the temperature descend below a critical value for reef growth. Moreover, a decreasing input of sunlight has a strong negative effect on the phytoplankton. Another aftereffect is a possible depletion of the ozone layer with consequences for terrestrial life. Admittedly the ' volcanic winter' could not cool down the central tropical realms of Panthalassa ocean and eastern Paleotethys. In these refuges elements of the tropical marine fauna could survive, but parts of these areas were later subducted. Thence a reconquest was possible. In Fig. 1. the paleogeographic situation of the late Permian is showed.

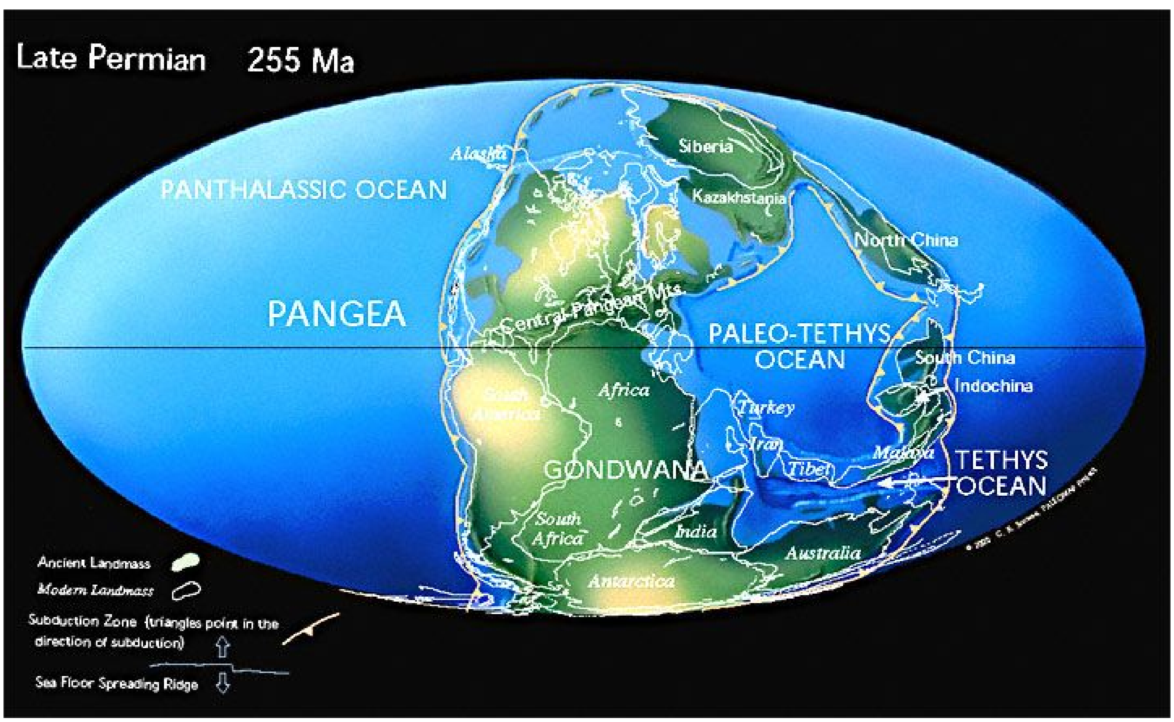

Fig. 1. Paleogeographic map of the late Permian by Scotese

Global warming, caused by volcanic CO_2 or global cooling associated with global darkness are also suggested, though still not acknowledged. The latter advisement includes glaciation, but there is no interlink between glaciation and mass extinction. Otherwise there is a record for cooling in the conchostracan data from Siberia, and a temporary cooling of lower latitudes could be too short for glaciation. Nevertheless in the sedimentary record are some hints of shallow and warm marine areas, where the accumulation of limestone is interrupted by a clay or tuff layer corresponding with the mass extinction. Such sequences have been reported from China, Iran and Europe (Kozur 1998).
The mass extinction of plankton is also correlated to this time segment. This could be due to strong global warming or cooling (Hallam and Wignall 1997, in Kozur 1998); if the mass extinction was based on warming, it would have been more fatal for terrestrial life and, moreover, for coldwater faunas than it is the case (Kozur 1998).
A global warming could immediately follow a global cooling, if it was the fact that the aerosols are fallen out after few months and accordingly a greenhouse effect triggered by volcanic CO_2 appeared. In addition to the large quantity of volcanic dust and aerosols in the atmosphere an increase of precipitation in both the higher cold latitudes and the lower hot latitudes occurred. The subsequent higher percentage of water vapour in the atmosphere might also have been triggered greenhouse warming, perhaps stronger than the atmospheric CO_2 because the amount of clouds have an essential influence on the amount of solar radiation which reaches the earth surface (Kozur 1998). A difficulty of the investigation of miscellaneous scenarios of the mass extinction at the P/T-boundary is to correlate between marine and terrestrial facies. This is important for establishing an interrelationship between both the marine extinction and the extinction of terrestrial plants and reptiles.
Admittedly should considered the significance of an terrestrial mass extinction different in comparison with the importance of the marine mass extinction.

3. The Fungal Spike Zone

3.1Worldwide appearance

Concerning its worldwide proliferation (Fig. 2.) in shallow marine, fluviatile and lacustrine environments the 'Fungi Spike' seems to be a good tool to correlate marine and terrestrial facies. The abundance is furthermore indepentent from climatic zonation and floral provinciality. But it could be that the significance decrease in high latitudes. In this case the 'Fungi Spike' must be handled carefully because there are other, not so clearly accumulations. The 'Fungi Spike' could be indistinct in comparison to the higher abundance which is detectable in lower latidudes. This would admit to connect chronological the marine extinctions and the terrestrial extinctions.
In some of the regions shown in Fig. 2. this fungal abundance horizon is used for the identification of the P/T-boundary. Indeed it is casually associated with the earliest Triassic rather than the latest Permian.

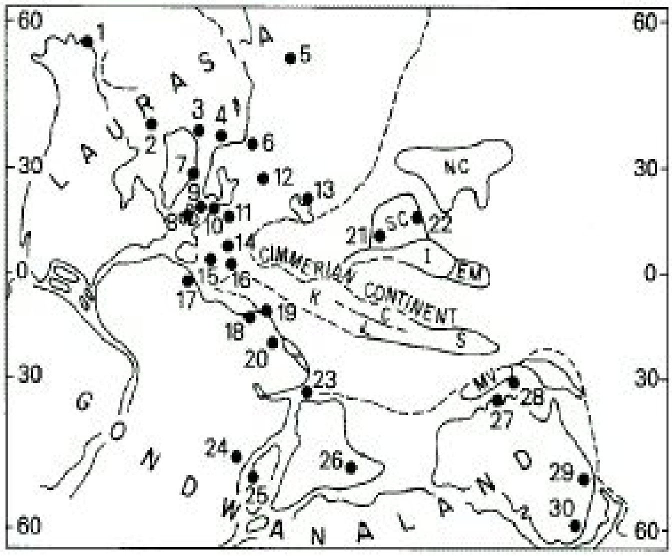

Fig. 2. Known occurrences of fungal remains in P-Tr transition sequences: 1 North Alaska; 2 Sverdrup Basin, Canada; 3 Svalbard; 4 Barents Sea; 5 Tunguska Basin, Siberia; 6 Pechora Basin, Russia; 7 East Greenland; 8 British Isles; 9, North Sea; 10 Zechstein Basin, Germany; 11 Zechstein Basin, Poland; 12 Moscow Basin, Russia; 13 Mangyshlak, Kazakhstan; 14 Transdanubian Mountains, Hungary; 15 Southern Alps, Italy; 16 Dinarides, Bosnia; 17 Tunisia; 18 Negev, Israel; 19 South Anatolia, Turkey; 20 Saudi Arabia; 21 Sishuan, South China; 22 Meishan, South China; 23 Salt Range, Pakistan; 24 Mombasa Basin, Kenia; 25 Morondova Basin, Malagasy; 26 Raniganj Basin, India; 27 Bonaparte Gulf Basin, Western Australia; 28 Banda Sea; 29 Bowen Basin, Queensland; 30 Sidney Basin, New South Wales. Paleogeography for terranes: NC North China, SC South China, I Indochina, EM East Malaya, K Kreios, C Changtang, L Lhasa, S Sibumasu, MV Mount Victoria Land

3.2 Karoo Supergroup

In the Karoo Supergroup of southern Africa are some prominent outcrops of the Permian–Triassic transition. One of them is Carlton Heights (Fig. 3.) with upper Permian and lower Triassic Beaufort Group. Here might be a good location to establish this correlation.

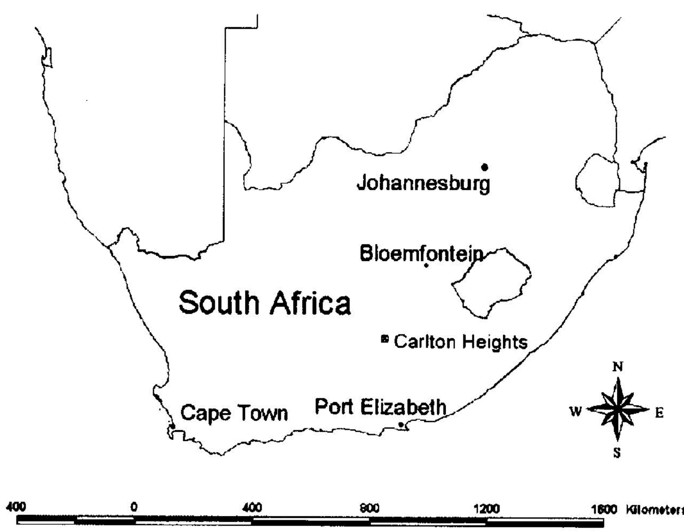

Fig. 3. Location map showing the Carlton Heights locality, Karoo Basin, South Africa (Steiner et al. 2003)

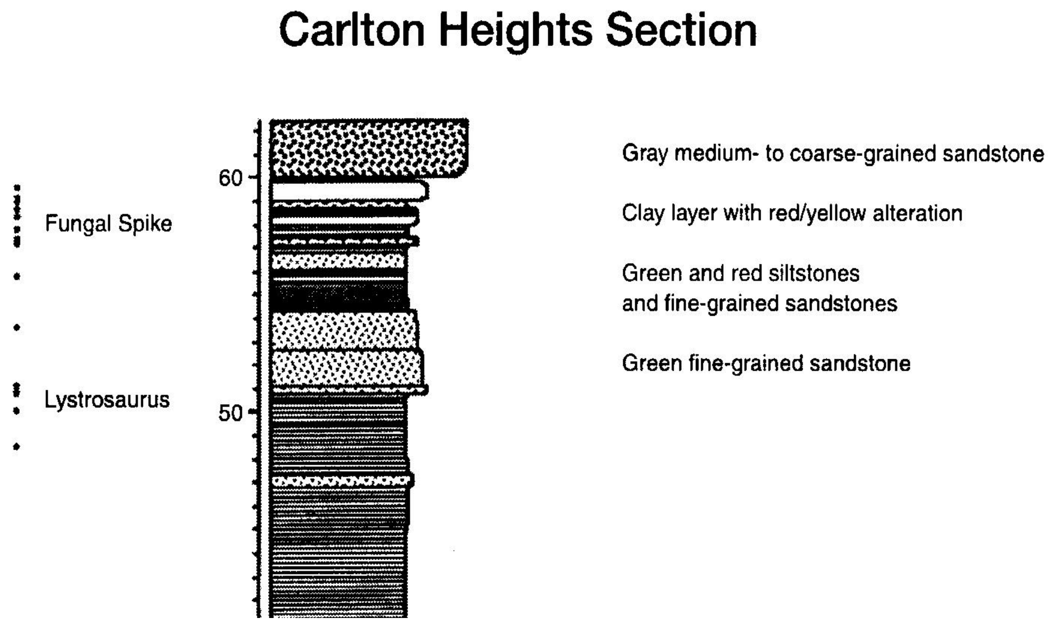

Fig. 4. Straticraphic section across the P/T-boundary in Carlton Heights, South Africa. Asterisks indicate samples analyzed for pollen and spores.

An up to 6 km thick sequence of lacustrine mudstones, fluvial overbank mudstones and channel sandstones dominated by a high sinuosity river system change to multistoried channel (Balfour Formation) and sheet sandstones with intermediate layers of mudstones, sedimented by a braided river system (Katberg Formation). The 1m thick layer of woody debris overlain by a layer with abundance of fungal remains – the ' FungiSpike Horizon' – is located about 0,5 m beneath the base of Katberg Formation. These sediments could represent a phase of ~2000y. For the P/T-boundary definition elements of the vertebrate faunal assemblage, e.g. *Lystrosaurus* are used (Steiner et al. 2003).

4. Fungi Spike or Algae Spike?

Steiner et al. have noted, that some researchers do not agree with the taxonomical interpretation of the supposed fungal remains. An overview of the discussion will be given. The following three notations are in common: *Reduviasporonites* Wilson, *Chordacysta* Foster and *Tympanicysta* Balme. *Reduviasporonites* is the older and *Tympanicysta* the more frequently used synonym. *Tympanicysta* is a genus of filamentous microfossils which are widely spread in Upper Permian and Lower Triassic, and became dominant close to the P/T-boundary. This bloom has been considered as an aftereffect of a mass extinction of late paleozoic floras (Visscher 1996).

The interpretation of *Reduviasporonites* in the original description is that it could be marine fungi. In his description wrote Balme, that *Tympanicysta* could be an encystment stage of algae or

fungi or an animal organism. In the aftermath *Reduviasporonites* and *Chordacysta* have been interpreted as fungal remains (hyphae and conidia of ascomycetes), fungal cysts or fungal spores by some researchers, thereupon implicated in the 'Fungi Spike' . Others have interpreted this fossil as
algae, and Foster denoted his interpretation (as fungi) as speculative and noted, that their circulation seems to be too large to make the assumption of a single event likely (Foster and Jones 1994). The fossils *Reduviasporonites, Tympanicysta and Chordacyste* seem to be congenerous, their taxonomical classification is in discussion. Based on Afonin (Afonin et al. 2001) an affinity to green algae is obvious because of its form and shape as well as its lenticuar connections between the cells (typical for this class of algae). He suggests for *Tympanicysta* a relationship with the *Zygnematales* , an order of green algae. This classification is based on the kind of the connection between the cells, conjugation (special form of reproduction, substitution of the cell cores of two ones of cells) and their zygotic character. Moreover their general morphology is similar to *Spirogyra* and *Mougeota;* two genera of *Zygnematales*, which also have unbranched filaments, cylindrical cells and thickened dormant cells or acinetes. The found thickened cells remind of acinetes; these are specialized cells with strong thickened cell walls and inclusions of nutrients (this kind of cells contradicts with an interpretation as fungi). The septa between the cells are smooth or, by thickened cells, wrinkled like those of *Spirogyra.* An important aspect are furthermore the contained chloroplasts, they are form and arrangement in dens granular masses or lining the cell walls. Latter are typical for an order of green algae (*Chladophorales*). The samples investigated by Afonin (Afonin et al. 2001) and the facies in which they were found implicate a freshwater or brackish environment, this fact is hardly conceivable for saprophytic fungi. Though *Tympanicysta* is close to zygnematalean green algae it has some attributes of other groups of green algae (common branching, chloroplasts lining cell walls), yet the derangement of characters is not uncommon for paleozoic forms (Afonin et al. 2001). The afterimages Fig. 5. and Fig. 6. are a comparison of investigated material of both Visscher (Visscher et al. 1996) and Afonin (Afonin et al. 2001).

Fig. 5. Sedimentary organic matter assemblage with extreme dominance of fungal remains from the Tesero Horizon, Southern Alps, at the level of last occurences of typical Late Permian faunal elements. (x 215)

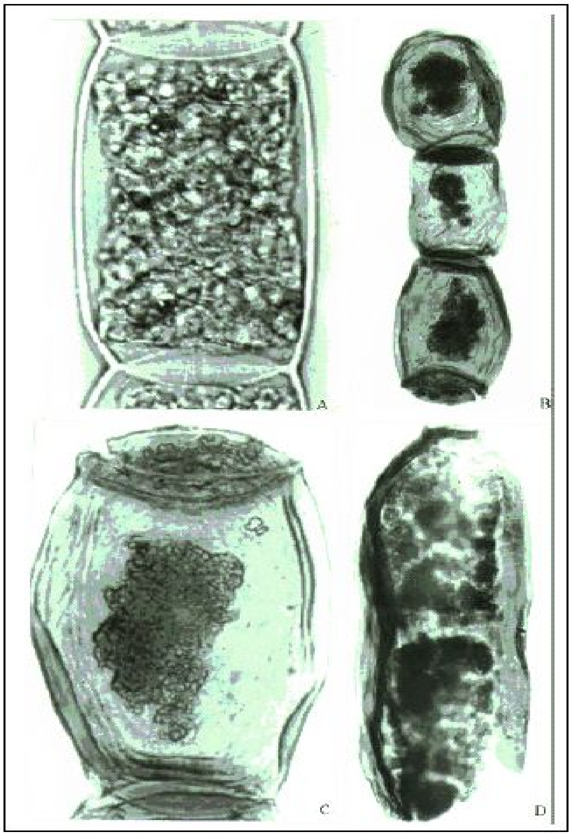

Fig. 6. Extant *Spirogyra* sp. (A. x600) from a flood plain pond of the Bitsa River, Moscow River Basin, and *Tympanicysta* sp. (B -filament with elliptical terminal cell, x246, C -folded septa, x620, D – acinete, x634) from the latest Permian to lowermost Triassic basal Vetlugian deposits of Nedubrovo, Vologda Region, Russian Plattform

In "A Revision of *Reduviasporonites* Wilson 1962" by (Foster et al. 2002) are *Reduviasporonites, Tympanicysta, and Chordacysta* have been carefully examined. The microbiological testings have been carried out using optical and electron microscopy and acknowledging the idendity of these genera. Anymore the character of the fossils, algae or fungi, has been ascertained. The results of geochemical analysis of carbon isotopic composition expel a saprophytic environment and therewith a possible role as a decomposer of woody remains. The same is appropriate for possible food sources of saprophytic fungi. Consequently *Reduviasporonites* may scarcely be related to the mass extinction at the P/T-boundary. The (algae) spike seems to exist, but the causes must be others. Though the algae spike exists, it does not appear to be related with the mass extinction but is likely to be in context with rising sea levels. But if there are no fungi to compose the remains of the dieback, there must be other saprophytic metaboliser.

References

Afonin et al. 2001	A bloom of Tympanicysta Balme (green algae of zygnematalean affinities) at the Permian–Triassic boundary, Geodiversitas 23, pp.481-487
Foster et al. 2002	A Revision of Reduviasporonites Wilson 1962: Description, Illustration, Comparison and Biological Affinitis, Palynology, 26, pp.35-58
Hallam and Wignall 1997	Mass extinctions and their aftermath, Oxford University Press, 320 pp.
Kozur 1998	Some aspects of the Permian-Triassic boundary (PTB)and of the possible causes for the biotic crisis around this boundary, Palaeo 143, pp. 227-272
Steiner et al. 2003	Fungal abundance spike and the Permian-Triassic boundary in the Karro Supergroup (South Africa), Palaeo 194, pp. 405-414
Visscher et al. 1996	The terminal Paleozoic fungal event: Evidence of terrestrial ecosystem destabilisation and collapse, Proc. Natl. Acad. Sci., Vol. 93, pp. 2155-21158

Additionaly literature

Eshet et al. 1995	Fungal event and palynological record of ecological crisis and recovery across the Permian-Triassic boundary, Geology, v. 23,,; no. 11; pp. 967-970
Hüssner, Hansmartin 1983	Die Faunenwende Perm/Trias, Geologische Rundschau 72, pp. 1-22
Kerp, Hans 2000	The modernisation of landscapes during the Late Paleozoic-Early Mesozoic, Paleontological Society Papers, V. 6
Krassilov et al. 1999	Floristic Evidence of Transitional Permian-Triassic Deposits of the Volga-Dvina Region, Permophiles 34, pp. 12-14
Krassilov et al. 1999	Tympanicysta and the Terminal Permian Events, Permophiles 35, pp. 16, 17
Looy et al. 1999	The delayed resurgence of equatorial forests after the Permian-Triassic ecologic crisis, Proc. Natl. Acad. Sci., Vol. 96, pp. 13857-13862
Looy et al. 2001	Life in the end-Permian dead zone, Proc. Natl. Acad. Sci., Vol. 98, pp. 7879-7883
Massari et al. 1999	Excursion 3: The Bletterbach Section (Val Gardena Sandstone and Bellerophon Formation), in Stratigraphy and facies Between Eastern Lombardy and Western Dolomites, Field Trip Guidebook

Racki, Grzegorz 2003	End-Permian mass estinction: oceanographic consequences of double catastrophic volcanism, Lethaia, Vol 36, pp 171-173
Rampino, M. R. & Adler, A. C.	Evidence for latest Permian mass extinction for Foraminifera: Results of tests for the Signor-Lipps effect
Twitchett et al. 2001	Rapid and synchronous collapse of marine and terrestrial ecosystems during the end-Permian biotic crisis Geology, v. 29; no. 4; pp. 351-354
Visscher et al. 2001	Permian Floras of the Southern Alps NATURA BRESCIANA, Ann. Mus. Civ. Sc. Nat. Monografia N. 25, pp. 117-123
Ward et al. 2000	Altered River Morphology in South Africa Related to the Permian-Triassic Extinction, Science vol. 289, pp. 1740-1742
Wignall, P. B. & Hallam, A. 1996	Facies Change and the End-Permian Mass Extinction in S. E. Sichuan, China PALAIOS, V. 11, pp. 587-596

Sources for illustrations

Fig. 1.	www.scotese.com
Fig. 2.	from Steiner et al. 2003 Palaeo 194, pp. 405-414
Fig. 3.	Adapted from Steiner et al. 2003 Palaeo 194, pp. 405-414
Fig. 4.	Adapted from Steiner et al. 2003, Palaeo 194, pp. 405414
Fig. 5.	from Visscher 1996, Proc. Natl. Acad. Sci. Vol. 93, pp. 215521158
Fig. 6.	from Krassilov, V. A. and Afonin S. A. 1999, Permophiles 35, pp. 16, 17