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SOME NOTES TO THE PERMOTRIASSIC CLIMATE IMPLICATIONS FROM MAMMALOGENESIS

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Összefoglalás - A terapsida hüllők késő ókori és középkori evolúciója bizonyos adatokat szolgáltat e korszak őséghajlati feltételeire. Összevetjük a terapsidák által elért fejlődést az őshőmérsékleti becslésekkel, és bizonyos javításokat sugallunk a permi eljegesedés befolyására.

Summary - Late Paleosoic and Mesosoic evolution of therapsid reptiles gives some constraints on paleoclimatic conditions during these periods. We compare the basic achievements of therapsides during this period with the paleoclimatic estimations and suggest some improvements on the profile of the Permian glaciation.

Key words: paleoclimatology, P/T boundary, therapsids, anoxia.

1. INTRODUCTION

Permian (and Triassic) times converted some synapsid reptiles into mammals, a very important grade development. In addition the Permian showed repeated glaciations, absent in the next 200 Ma. There was a big but obscure catastrophic event too on the P/T boundary. So Permotriassic was an interesting period for climate/environment. Some reconstructions do exist, but the era is more than thrice older than the popular C/T boundary about which there is still controversy. Therefore the reconstructions are not so reliable.

But the development of synapsids towards a mammal stage must imply something for climate/environment, as seen from the fact that later reptilian diapsids returned and dominated mammals and mammal-like reptiles for some 120 Ma ("the dark age of mammals"). So mammals were not "optimal" then; they were better adapted to *some* climate/environment. If so, then comparisons between environmental reconstruction and therogenesis may help fill holes of both. The present paper is such an attempt.

The problem may seem simple. If cold climate (present in some Permian times) is sufficiently long, then outside the tropical regions all reptiles are converted finally into endothermic animals with high metabolic rate, developed feeding apparatus etc. This suggests as if hair, dominant dentale, secondary jaw articulation, vivipary and lactation had all been responses to the challenge of cold, in which case the success of mammals would have been predetermined. But the paleontologic finds do *not* support such a simple picture: the cold climate ended when the therogenesis was only halfway. Maybe this explains the subsequent long "mammalian dark age" too. We think that at least 2 environmental data must be compared to facts of therogenesis: temperature *and* atmospheric oxygen content. (The CO_2 level seems redundant: it was never high enough to affect animals directly, onto them it acted via temperature as a greenhouse gas.)

In addition, the evolution must have been once interrupted (disturbed?) by a catastrophe of obscure origin at the Perm-Triassic boundary. In the seas this catastrophe killed life almost globally; on lands it was less lethal but still serious. The Permotriassic evolution seems rather involved.

In Chapt. 2 we recapitulate a detailed reconstruction for paleotemperatures. In Sects. 3-6 we follow therogenesis in the Permian, at P/T boundary, in Triassic and in Jurassic times, respectively; at the end of Jurassic mammals are practically ready albeit still obscured by dinosaurs, and according to many authors split into the present eutherians, metatherians and atherians happened in the uppermost Jurassic or in basal Cretaceous. Sect. 7 tells about a possible (albeit unproven) solar mechanism for an oscillation of Sun between a "normal" and a "cool" mode of operation (then we would now be in the "cool" one), and Sect. 8 recapitulates the reconstruction for the oxygen content. The emerging picture is uncertain but coherent. Chapt. 9 gives some brief conclusions.

2. RECONSTRUCTIONS FOR THE PERMIAN GLACIATIONS

Since the time of the First World War it has been known that on the southern hemisphere substantial territories were permanently covered by ice roughly in the Permian. While the involved areas seem almost random on a recent map, global tectonics gives a very clear picture: the subpolar territories of the southern supercontinent Gondwana was then glacial.

Maybe in 1912 Wegener was the first who took seriously the traces of Permian glaciation. As an explanation he tried with the shift of continents and regrouped all parts of Gondwana to the neighbourhood of the South Pole. The mechanical model behind the continental shifts was quite wrong, therefore the idea was rejected. However in the 30's Du Toit, a Boer with thorough knowledge about South African layers, collected many data about Permian glaciers, determined the directions of ice "flows", and the facts clearly indicated touching continental shores. What is more, it seemed that the pole was somewhere in South Africa.

However recently we have learnt that a polar or subpolar location in itself is not enough for permanent ice cover. E.g. it turned out that the Antarctic permanent ice is not older than 5.5 Ma. Instead of complicated arguments let us use a simple one. The Milankovic theory of repeated glaciations is based on quasiperiodic changes of eccentricity and axial tilt of Earth by gravitational perturbations. The scale time can be calculated as several myriad years. Some combinations of orbital parameters result in small seasonal changes, e.g. with small eccentricity and minimal possible tilt the seasons are not too expressed. Then on the moderately cold winters snowfall is substantial, the subsequent tepid summer cannot melt *all* the snow and therefore around (at least one of) the pole(s) the white ice cover starts to expand. This cover has a high albedo and therefore the global terrestrial temperature starts to decrease. So obviously quasiperiodic glacial eras indicate permanent ice at least at the pole.

Recently (at least in the last 2-3 Ma) glaciations are repeated. But not it was so before mid-Pliocene. Therefore before mid-Pliocene the annual mean temperature of Earth must have been so high that even at the poles practically all the ice and snow melted in summers. Now there is a circumpolar continent on the southern hemisphere, which is optimal for permanent ice. Hence one guesses a mean terrestrial temperature definitely not higher than the present one, for Permian during the glaciations. Now, *Budyko et al.* (1987) reconstructed paleotemperatures, with the result that during practically all the Permian temperature had a local minimum compared to end-Carboniferous and Lower Triassic but with some global mean temperature 21°C. *Budyko et al*'s temperature curve is redrawn on *Fig. 1*; absolute times, for comparison, are everywhere in this paper rescaled to the averages of the 2 timescales in *Farquhar* (1967).

This temperature is cca. the same as for the Paleogene/Neogene border in the same reconstruction. Now at that time there were definitely no glaciations. As told above, during quasiperiodic glaciations the average temperature drops several °C; and, as an experimental fact we know that the mechanism cannot start at that temperature. Therefore, if we use Pleistocene as an analogy

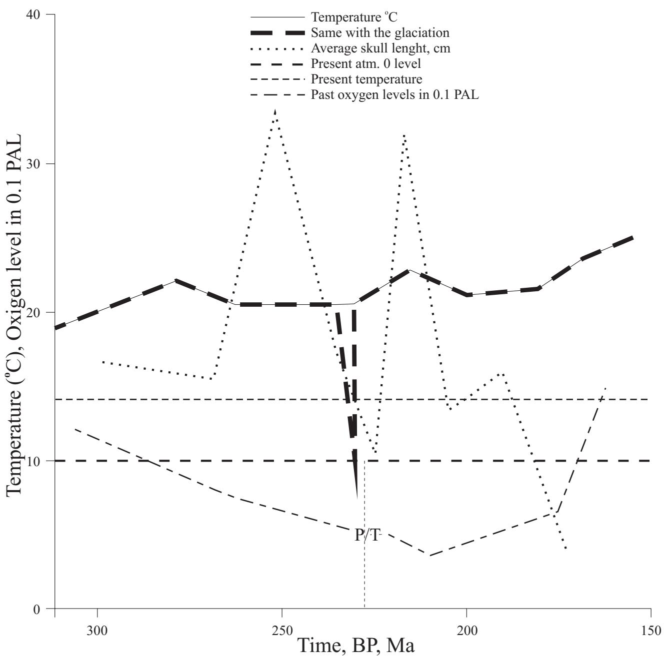

Fig.1 Reconstructed paleotemperatures, oxygen levels and average synapsid skull sizes. Climatic data are from *Budyko et al.*, skull sizes from *Kemp*, and timescales from *Farquhar*.

(*Woldstedt*, 1969), we guess a further cooling somewhere in the Permian to cca. 16°C, and then an oscillation down to at least 11°C, again shown as a guess on *Fig. 1*. Of course the numbers are based on a similarity between meteorologic processes in eras 300 Ma apart from each other.

3. PERMIAN THEROGENESIS

According to fossil evidences the Permian was very important in the genesis of mammals (therians and relatives). During the Permian synapsid reptiles arrived at advanced therapsid (i.e. mammal-like) stage from a rather primitive stage (*Kemp*, 1982), at the end with diaphragm, endothermy, differentiated teeth, 7 cervic vertebre and the final digital formula (*Kemp*, 1982; *Bérczi et al.*, 1997). As a matter of fact, vivipary, lactation and maternal care cannot be documented from Permian, but it seems that all the advanced synapsids were already on the march toward true mammals at the end of Permian. This fact implies that the evolution of pelycosaurs and therapsids may give further data for the atmospheric conditions in Permian (and Triassic).

But the fact also gives a temptation to explain the evolution of *all* mammalian characteristics with the Permian glaciation. Such an argumentation goes as follows.

Let us assume a prolonged cold and snowy environment in Southern Gondwana when the most advanced vertebrates are reptiles. Then such an environment forces several correlated processes as: thermoregulation (endothermy, hair), higher temperature needing better eating apparatus (differentiated and fitting teeth, stronger mastication therefore a single, rigid bone in the lower jaw, so atrophy of postdentales, dentale/squamosum articulation) and retention of the premature young and feeding later (viviparity, lactation, etc.). I.e. *all* mammalian characteristics might be simply answers to the challenge of cold.

However the facts do not support this monistic explanation. Some important mammalian features seem to have appeared after the glacial times, at or just after the P/T boundary (femur in the parasagittal plane, hair, double circulation), and the true mammals appeared only in the Upper Triassic (*Kemp*, 1982), when the temperature was so high that glaciation was absent. So some other challenge must have been present in the Triassic.

4. THE P/T BOUNDARY

Some disrupting events definitely took place at the Permian/Triassic boundary. First, there was a Great Extinction, quite catastropic in the seas; for aquatic life the greatest up to now. Second, in many places, e.g. at Sasayama, Japan, a definite "dead" layer is seen between end-Permian and basal Triassic (*Ishida et al.*, 1992). Third, the sea level oscillates just at the boundary. Fourth, it seems that at the boundary the spherule content of layers has a peak; although statistical data are accumulating just now, it is sure that a specific "Miono-type" FeO kind of spherules peaked just at the P/T (*Tóth et al*., 1997). Many analyses showed anoxic and superanoxic conditions at least in seas (e.g. *Erwin*, 1993; *Isozaki*, 1994; *Géczy,* 1996) which may explain the "dead" separating layer.

We do not yet know, what put an end to the good old Paleozoic times. As a working hypothesis, one may think about, e.g., a cosmic impact, disturbing the atmospheric conditions, maybe triggering the activity of volcanoes of whole Siberia (*Kemp*, 1982), causing strange chemistry in the air; the spherules may have come with the impactor, from its surface as droplets, and from the terrestrial matter thrown up by the impact. This is the simplest scenario, because it goes parallelly with the most popular C/T one (when the Deccan volcanoes started) only on a larger scale. The details are still obscure, but spherule counting and analyses may help. E.g. if anoxia was caused by the impact as trigger, then the spherules must be slightly earlier than the anoxia. In addition, if the impact was made by asteroid-sized bodies, then the overwhelming majority of the spherules must be of terrestrial composition according to the phenomenology of impacts. The necessary analyses are going on.

Anything had been the reason, we know from the extinctions that the P/T boundary was hard for life. Synapsid fossil data do *not* show very marked extinction (they show some other signal to which we will return in due course), but some branches died out about the boundary.

Paleotemperature reconstruction (*Budyko et al.*, 1987) does not show anything dramatic at the boundary; it is a starting-point of a temperature increase, to cca. 23°C during Lower Permian. This may have been caused by the volcano activity (emission of greenhouse gases as CO_2 and H_2O), but not necessarily so; the Permian cold may have been simply the previous Fowler cycle (see in Chap. 7), which possibility will be treated later. Of course, if there was an impact, the dust certainly must have caused an "impact winter". However the estimated length of such a cold period is only several years, and already endothermic synapsids, trained by the Permian cold, were probably not too much disturbed by it. The preceeding cold is the only qualitative difference between this P/T scenario and the popular C/T one.

At or just after the P/T boundary advanced synapsids reached the stage of good insulation (hair) and complete double circulation, plus femur in the parasagittal plane. The first advance may have been the proper answer to cold. The second one made possible high peak power of activity. The third one is the present status of locomotion of recent Australian monotremes. It increased the speed of walking and "running" and the double circulation system, with highly oxygenised arterial blood, could yield the necessary higher power.

5. TRIASSIC TEMPERATURES

For Triassic times the temperature reconstruction shows first a relatively fast temperature increase, some 3 centigrades above the Permian level in the Lower Triassic, then a cooling, and a final short heating up (*Koppány*, 1996). The end-Triassic temperature was not much above the Permian level, but it must have been enough to break the Milankovic cycle, because no trace of cyclic glaciation is seen.

The real temperature increase was, of course, higher. Pleistocene reconstructions give cca. 5 centigrades amplitude oscillation between glacials and interglacials. On this basis, as told in Sect. 2, we must guess the global terrestrial time averages at end-Permian not higher than 11°C; and the end-Triassic one can be guessed from the reconstructions as cca. 22°C.

Therefore *for temperature* the driving force towards mammalian stage was absent during Triassic. Still the evolution did not slow down substantially. During the Lower Triassic the leading therapsids reached a therian stage in the differentiation of hind teeth to premolars vs. molars, produced a proper occlusion of molars, and a secondary lower jaw hinge. During Upper Triassic, in addition, they reached qualitatively the therian dentition and molar cusp pattern, diphyodonty and the characteristic mammal prismatic enamel, triangular motion during mastication, the fundamental structure of skull, completely therian locomotion, brain structure, milk secretion plus hypertonic urine. In some points recent monotremes did not follow the uppermost Triassic innovations.

Some of the Triassic advances simply continue earlier ones; but if we do not want to refer to orthogenesis, driving forces must have still been present. In 2 points the driving force is clear. Diphyodonty is necessary to keep the precise occlusion, and the hypertonic urine may have been forced by aridity. However the majority of other advances (better feeding system plus milk for the young) seem to have been answers to the challenge of generally "hard conditions" in a situation when low temperatures did not pose any challenge anymore.

We must analyse the locomotion in slightly more details. For a long time it was believed that vertical femur *and* humerus are energy conserving. But recently it turned out that it is so only if the feet are the only contact points with the ground. Spiky anteaters traverse the same distance with less energy consumption than recent therian mammals of the same mass do it (*Edmeades and Baudinette*, 1975). Now, the recent spiky anteater is at Lower Triassic level for locomotion. The vertical femur gives the momentum at the starting- point of step, then the forelegs with horizontal humerus roll forward the body; then transiently the foreregion of the rump is resting on the ground and the new cycle starts again from behind.

This is indeed an energy conserving way of locomotion, but not so fast as with a vertical humerus. If both meat-eater and prey are therapsids, there is a natural selection force for "erect" quadrupedal gait, provided the environmental conditions are not forcing too much energy conservation. Observe that present Australian monotremes, in the Lower Triassic state of locomotion, are insect-eaters.

6. JURASSIC SITUATION

For completeness' sake we finish this sequence of Chapters with Jurassic. For temperature, Jurassic was hot and uneventful. In the mid-Jurassic the global temperature average was cca. 24 °C, some 10 centigrades higher than the present one.

At the end of Jurassic the therian mammals, albeit primitive and minute, are ready.

But the Jurassic innovations seem rather logical consequences of earlier changes. E.g. the atrophied primary "reptile" Ar/Q joint vanishes, so giving a possibility that both of them go to the ear as malleus and incus, generating much more acute hearing. Also the atlas and axis fuse, giving more possibility for head movements. In these points the Australian monotremes, probably evolving already independently, follow the therians.

So there is no trace of "hard conditions". Indeeed, Jurassic is the beginning of the golden days of large diapsid reptiles. Very probably mammals remained small only for filling niches completely different from those of dinosaurs.

Tritylodonts died out in mid-Jurassic with Stereognathus (*Kemp*, 1982). But this is not necessarily a signal for "hard conditions". Tritylodonts, the last non-mammal therapsids, were specialised herbivores, and still not too different from contemporary mammals. Maybe they concurred with herbivorous mammals and were not so successful.

Diapsid birds separate from dinosaurs sometime in the Jurassic, and they are now homoiotherm with double circulation. But they need high body temperature for flying.

7. FOWLER CYCLES

It is possible that the relatively low temperature of Permian may have had an extraterrestrial, namely solar, explanation. The mechanism was first suggested by *Fowler* (1972) for explaining the present solar neutrino deficiency. For details see the original article, but the scheme is simple enough.

The present solar energy output is very well known. Assume that all of it comes from H > He fusion. Then, with some uncertainty from chemical composition etc., one can count the fusion rate, and for an Ó nucleus formation 2 neutrinos leave Sun. One can detect at least the high energy tail of the neutrino flux by a reaction

$$Cl^{37} + \text{neutrino} \rightarrow Ar^{37}$$

Ar^{37} being radioactive. But when Davis tried to detect the neutrinos, he was first unsuccessful, and finally found some 1/30 part of the first prediction (*Davis et al.*, 1971 vs. *Abraham and Iben*, 1971).

Now, Fowler explained the surprisingly low neutrino flux with a mechanism causing global cooling by several centigrades on a cca. 30 Ma scale. He called attention to the fact that the (Cl, Ar) reaction rate steeply increases with energy, and the highest energy neutrinos come from side reactions as proton capture by B and Be. There the Coulomb barrier is substantial, so their neutrino rates increase with high powers of the central temperature. So an 5-10% decrease of the central temperature may completely explain the very low detection rate. (Later measurements started with Ga as detector material: it is much less energy-dependent and still some 1/3 of the rate is missing.)

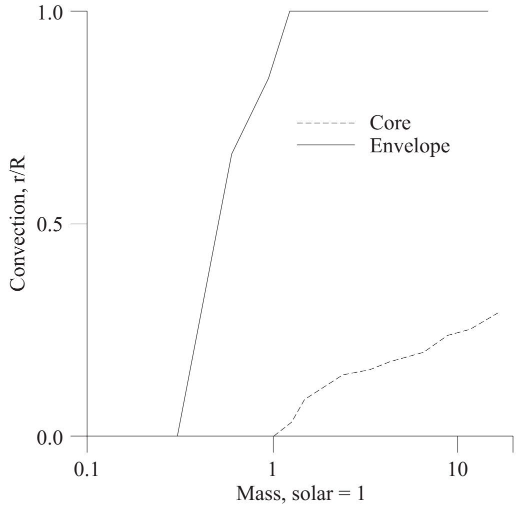

Fig. 2 The borders of envelope and core convections, respectively, vs. stellar mass, after *Schwarzschild and Novotny*. The actual values moderately depend on stellar age too.

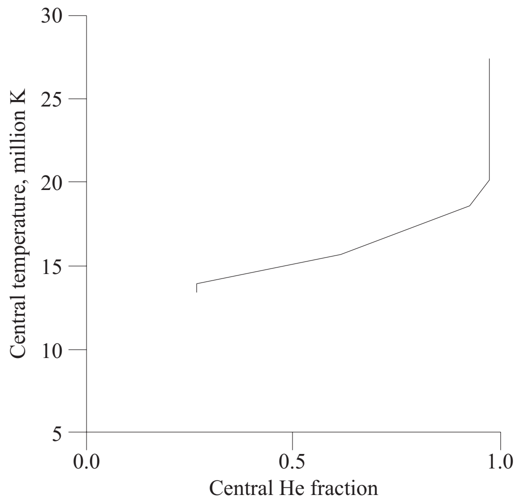

Fig. 3 Solar central temperature vs. central He fraction from a sequence of non-cyclic evolutionary calculations collected by *Novotny*

So there would be no problem *with neutrinos* if the central solar temperature were slightly lower than given by the best simulations. Fowler observed that the Sun of best available calculations (based on slow evolution and primordial chemical composition outside) is not too far from convectional instability at the outer boundary of the core, while convection is present at the surface. Less massive stars are stable for convection inside and convective at the surface, much more massive ones are convective at the core and not at the surface, and in a narrow mass range, in present, non-cyclic simulations starting at 1.1 solar mass, the two convection zones can coexist. (For the borders of the convective zones some stellar interior calculations are shown on *Fig. 2*).

Now take a star with proper mass. First the core is not convective. By the advancing fusion H is converted to He, and during that the particle number of the core is decreasing. Let us start with a given number of NH and NHe, and neglect the heavier elements, practically unchanged. Then the total particle number, being atoms fully ionised, can be obtained by taking the electrons into account as

$$N(t_o)\text{, } 2N_H + 3N_{He} \qquad (7.1)$$

After some time dt the formula is the same but with changed numbers

$$N_H(t_o+dt)=N_H-4rdt; \quad N_{He}(t_o+dt)=N_{He}+rdt \qquad (7.2)$$

r being the creation rate of He; resulting e^+'s annihilate with some e^-'s. So

$$N(t_o+dt) = N(t_o) - 5rdt \qquad (7.3)$$

But the pressure in the core must not change too much, because it supports the unchanged layers above the core. Then the average core temperature must increase inversely with N, i.e. at least for short periods

$$T_c(t_o+dt) \approx T_c(t_o)\{1 + (5r/N(t_o))dt) \qquad (7.4)$$

Indeed, evolutionary calculations show that T_c will increase with the central He weight concentration. But with increasing core temperature the rate r goes up first as T_c^4, then the CNO fusion starts too with T_c^{20}, and with the increase of the He concentration in the core this process has a positive feedback. This makes the temperature gradient at the border of the core (outside of which the fusion is negligible) more and more negative. When the absolute value of the gradient is too large, "bubbles" of hot gas can ascend by the Archimede Law, being thinner at the same pressure. The condition *against* convective instability for fully ionised gas is

$$-2d\ln P/dr > -5d\ln T/dr \qquad (7.5)$$

(*Schwarzschild*, 1958); note that by the - signs both sides are positive.

Now the left hand side is governed by gravitational equilibrium and so remains more or less the same while the right hand one is by the evolution of core material, as seen above. So the right hand side is continuously growing, and at a moment the core boundary may become convective (if there is enough time).

If so, then convection mixes matter inside and outside the core; the core helium will be washed out, and N will go up again. Then T_c drops, the fusion rate drops too, not to the original value, because the total He content of the star is already higher, but near to. With the fusion rate the total energy output drops too, and on astronomic time scales the star's fusion energy output is a saw-toothed curve superimposed on a slow increase. The gravity equilibrium cannot be instantaneous, so there is a slow expansion during the nonconvective evolution, while there is a contraction just after convection, making the decrease of energy output more gradual.

We emphasize that the calculations for solar interior can reproduce quite good bulk Suns from cca. 1968, but this fact and the stability against core convection at 1 solar mass does *not* rule out a quasicyclic Sun. Namely one initial condition has been chosen by assuming a priori the lack of core convection, and there is no valid theorem against core convection at 1 solar mass.

Namely, for performing an evolutionary calculation we need initial conditions, e.g. for chemical composition. Starting from a galactic gas cloud, it was of course homogeneous in space, and we may assume that the concentrations beyond He were the same as the present values; but some part of the present He was produced in the Sun. However if we *assume* the lack of the core convection *in the whole past*, then the initial He concentration was the same as now on the surface. The non-cyclic solar model is self-consistent, except for neutrino flux.

However if one accepts Fowler's suggestion then the present surface He content is higher than it was in the presolar nebula. In addition, the present solar luminosity contains a non-fusion component too, practically neglected in the non-cyclic calculations. So a whole series of calculations should be started from various initial conditions to see if any of them runs into core convection and after 4.5 Ga into the present Sun with the present luminosity from fusion + contraction. We do not know sufficient methodical and detailed such analyses.

So much about the Fowler cycles qualitatively. But what is the amplitude and timescale of the changes?

Since detailed calculations remained only partly successful, no reliable result exists for the amplitude. However with great uncertainty the 2 timescales can be guessed, and then from the longer timescale the amplitude of the oscillation of central He concentration too. As for the ascending part of the saw-tooth, for a star of one solar mass all simulations give some 10 billion years to consume the majority of core H. Then 1% H depletion needs 200 Ma, and means 1.3% temperature increase. At the present status of art we do not know how near the Sun is to convective core instability (at 1.1 solar mass the timescale must be short); one may tell then that perhaps some 200-1000 Ma would be the ascending slope for 1 solar mass.

For the descending slope the estimations are more qualitative. *Schwarzschild* (1958) guesses that the velocity of convective cells in the interior of a Sun-like star is about 0.03 km/s. Such a cell can traverse substantial part of the star in a year (!), so the mixing times are short on geological or astronomical timescales. However this is *not* the timescale of *luminosity* drop.

Namely, if the whole scenario holds for the Sun, we are now in the low fusion rate so low luminosity phase; however the luminosity fits to the old, non-cyclic models. But not all the luminosity comes from fusion. When the fusion power drops, the Sun starts to cool, the average pressure of the whole body drops too, and gravitational contraction starts. (See, as an example, such stages of *long* timescale in stars in Iben's calculations, cited by *Novotny* (1973).) But this latest process is energy deliberating, so the luminosity does not decrease so much as the reaction rate does. The Sun is an energy buffer, and the characteristic time of this effect is the so called Kelvin-Helmholtz time, the Sun's gravitational energy divided by the normal luminosity. With some minor uncertainties for the internal structure this time is guessed as 30 Ma (*Schwarzschild*, 1958).

From the temperature reconstructions we may guess that the necessary temperature decrease from normal to periodic glaciations is 6-8 centigrades, so 2%. That means a 8% decrease in solar luminosity, or less if the changes of atmospheric CO_2 and H_2O concentrations, with positive feedback to temperature, help. Such changes are not dramatic at all. That needs cca. 2% drop of T_c, i.e. cca. 1.5% of H depletion, which would need slightly more time than 200 Ma. The argumentation is slightly circular, but not impossible.

So, *if* this model works for the Sun, then we can predict several hundred Ma's of normal high temperatures for Earth, separated by, say, 30 Ma's of temperatures continuously

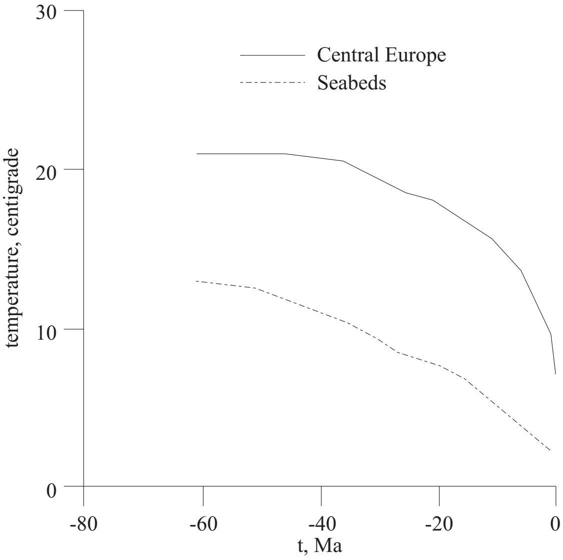

Fig. 4 Tertiary temperatures after *Emiliani and Woldstedt*

decreasing, at the end lower by several centigrades and then quasiperiodic glaciations. What is really interesting is the well known neogenic cooling (*Fig. 4*) which is appearing on all temperature reconstructions, started just 30 Ma ago (*Emiliani*, 1958), as noted by Fowler himself too. The cycles must shorten as the Sun is filled up by He.

Therefore there is a possibility that the cool Permian was the end of the previous Fowler cycle some 250 Ma ago; and if so the second previous one can be guessed to the end of Precambrian.

The picture is full of holes, but the skeleton is coherent. Detailed astrophysical calculations will decide in the future if this mechanism can work for the Sun, but it is viable for stars with 1.05-1.1 solar mass. This picture was the reason that i) we did not rule out a cooling in Permian from "Paleogenic" temperatures to "Neogenic" ones and that ii) we guessed that the Permian glaciation would have ended even without the P/T catastrophe. But then we can conclude that therapsids did not get enough time to replace the other reptiles without mammalian trends.

8. "HARD CONDITIONS": THE OXYGEN CONCENTRATION

However the therogenesis did *not* stop with the Lower Triassic heating; and the therapsid evolution went by as if therapsids needed the efficient feeding mechanisms, endothermy etc. even in the returning benign climate. And there is indeed one more environmental characteristics which may have meant "hard conditions" for them, and not for the conservative diapsid reptiles.

As we remember, Permian ended with anoxy. It may or may not be connected with the P/T catastrophe, but it certainly existed. *Budyko et al.* (1987) reconstruct the oxygen concentration too. Until Devonian it is always below 1 PAL, there is a local maximum at cca. 1.7 PAL in Lower Carboniferous, it is cca. 0.9 PAL at C/P, and it remains near to 0.8 PAL for the major part of Permian. Then it decreases again, with 0.5 PAL at P/T, still dropping. The minimum is cca. 0.4 PAL in mid-Triassic. There is a rapid increase from T/J, and the concentration is almost 3 PAL in Lower Cretaceous. This is the absolute maximum, going back to 1 PAL in Paleogene. The oxygen concentration from Carboniferous to Jurassic is included too into *Fig. 1*. Now let us see if this curve is coherent with the Triassic and Jurassic therogenesis.

It seems so. At end-Permian the synapsid strategy, spread in many parallel branches of therapsids, was an active adaptation to *cold*. The animals maintained "constant" temperature higher than outside; this was energy-consuming but the feeding apparatus was becoming more and more efficient too. The differentation and occlusion of teeth made new prey, herbs or seeds available and real cutting dentition made them more digestible. Diaphragm made the oxygen intake more efficient and so metabolic rate higher. At Southern Gondwana this was the leading strategy: there were no real opponent land animals during the cold (*Kemp*, 1982). Anapsid or diapsid reptiles retreated to tropic climates.

However from the P/T boundary this strategy was not necessary, was not enough advantage to the returning conservative reptiles; and was difficult to be maintained with the decreasing O_2 concentration.

There was however a way to adapt to the decreasing oxygen level without giving up the higher level of organisation. Oxygen is taken through the "surface" of lungs (which is not a surface but rather a fractal with an index between 2 and 3) and is used in metabolism in the volume of the body with fractal index 3. So one can guess that the halving of oxygen concentration is balanced by more than halving the linear sizes. Of course, shrinking sizes may increase the heat loss, but the environment was hot and insulation by hair developing. For any case the shrinking bodies did not permit to relax the need of endothermy, high metabolism, etc.

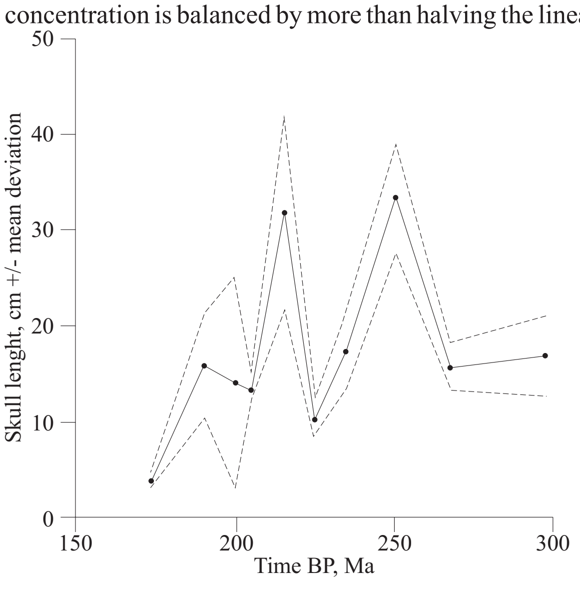

Fig. 5 Average synapsid skull lengths with standard deviations calculated from Figures of Kemp.

Now the shrinking can be seen in fossil data. We used the drawings of *Kemp* (1982), first all of them with complete skeleta. By measuring them it turns out (*Bérczi et al*., 1997) that, apart from some early pelycosaurs, during the synapsid evolution the ratio of body length (including skull but excluding tail) and skull length is continuously cca. 4, as well for therapsids as for old and recent mammals. Then skull pictures with precise magnification factors can be used as first approximations instead of full bodies. In *Kemp* (1982) we found 6 dozen such figures and *Fig. 5* gives the averages and mean deviations for 10 aggregated times as follows: Upper Carboniferous, Lower Permian, Upper Permian till Tapinoceras horizon, Upper Permian later, the Lystrosaurus level (just after P/T), Lower Triassic after the Lystrosaurus level, Middle Triassic, the Santa Maria formation (from South America), Upper Triassic after the Santa Maria age, and the South Welsh fissures (uppermost Triassic or basal Jurassic) and some other mainly Jurassic skulls. Absolute ages were needed to draw the diagram, but the geologic ages are more reliable; in numbers we took the averages of 2 reliable chronologies in *Farquhar* (1967). The average skull lengths are also shown on *Fig. 1*.

As we see, skulls (so animals) were biggest in the first half of Upper Permian (cold climate and still 0.8 PAL O_2); the maximum skull size in the analysis was 80 cm, corresponding to cca. 320 cm body length. The first serious diminution happened just after the P/T catastrophe. Then first the sizes regenerated but there was another shrinking in Middle Triassic, at the minimum of oxygen level. The final dwarving to Jurassic may have been already the effect of the big concurrent diapsids than that of the environment.

At the same time the low oxygen level was much less problem to the returning diapsids than to the synapsids. Diapsids were not endothermic at that time, so sizes were thermodynamically irrelevant for them. They did not have energy-consuming strategies, not only for heat equilibrium: the gait in the Triassic was generally lizard-like. When the oxygen-concentration went up in the Jurassic, no hard limits existed either for thermal balance or for fast motion: Jurassic mammals were "erect" quadrupeds and some big dinosaurs erect bipeds.

9. CONCLUSIONS

We collected evolutionary advances and their stamps on therapsid reptiles achieved during the Permian-Mesosoic periods and on the basis of their constraints we can conclude the following assertions about Permotriassic climate:

1) In the light of the better documented Pliocene/Pleistocene glaciation the temperature of the Permian glaciation must have been lower than that values estimated by Budyko et al. 1987.

2) In mammalogenesis cold could not have been the only constraint and challenge for therapsid reptiles during late Permian and early Triassic.

3) Further studies and documentations of the P/T boundary events will play important role in clarifying the nature of constraints at the boundary. These studies may also emphasize the roles of both the cosmic event and mammalogenesis in paleoclimatologic reconstructions of the terrestrial atmosphere.

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REFERENCES

Abraham, Z. and Iben, I., 1971: More Solar Models and Neutrino Fluxes. *Ap. J. 170*, 157-163.

Bérczi, Sz., Holba, Á., Lukács, B. and Papp, É., 1997: Notes on the mammalian evolution. KFKI-1998-12/C. (in press).

Budyko, M. I., Ronov, A. B. and Yanshin, A. L., 1987: *History of Earth's Atmosphere*. Springer, Berlin

Davis, R., Rogers, L. C. and Radeka, V., 1971: *Bull. Amer. Phys. Soc. 16*, 631

Edmeades, R. and Baudinette, R. V., 1975: Energetics of Locomotion in a Monotreme the Echidna Tachyglossus aculeatus. *Experientia 31*, 935-936.

Emiliani, C., 1958: *Sci. Amer. 198*, 54

Erwin, D. H., 1993: *The Great Paleozoic Crisis. Life and Death in the Permian*. Columbia Univ. Press, N. Y.

Farquhar, R. M., 1967: Radioactive Geochronology. In *Runcorn, S. K.* (ed.), *International Dictionary of Geophysics*, Pergamon Press, Oxford.

Fowler, W. A., 1972: What Cooks with Solar Neutrinos? *Nature 238*, 24-26.

Géczy, B., 1996: Extinctions and Astroblemes. *Annales Univ. Sci. Budapestiensis, Sect. Geophysica & Meteorologica 12*, 13-16.

Ishida, K., Yamashita, M. and Ishiga, H., 1992: P/T Boundary in Pelagic Sediments in the Tanba Belt, Southwest Japan. *Geol. Rept. Shimane Univ. 11*, 39-57.

Isozaki, Y., 1994: Superanoxia across the Permian-Triassic Boundary: Record in Accreted Deep-Sea Pelagic Chert in Japan. Canadian Society of Petroleum Geologists. Memoir 17, 805-812

Kemp, T. S., 1982: *Mammal-like Reptiles and the Origin of the Mammals*. Academic Press, London.

Koppány, Gy, 1996: Mutual evolution of terrestrial atmosphere and biosphere. *Acta Climatologica 30*, 31-40.

Novotny, É., 1973: *Introduction to Stellar Atmospheres and Interiors*. Oxford University Press, Oxford.

Schwarzschild, M., 1958: *Structure and Evolution of Stars*. Princeton University Press, Princeton.

Tóth, I. et al., 1997: A Possible Nearby Supernova Explosion in the Permo-Triassic Boundary &c. TISS, ed. by Miura, Y. et al., Yamaguchi University, pp. 18-19.

Woldstedt, P., 1969: *Quarter*. Encke, Stuttgart.