The Lilliput Effect – a response of life to increasing gravity?

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Abstract. According to Harries & Knorr (2009) "the Lilliput Effect represents a pronounced reduction in the size of the biota associated with the aftermath of mass extinctions". It is commonly attributed to environmental perturbations due to primary (abiotic) factors like CO_2 and O_2 contents of the atmosphere, temperature, salinity of seawater, soil composition a.o., and to secondary (biotic) factors, mainly reduction in primary productivity and its corollary, nutrient scarcity. However, if mass extinctions are triggered, as commonly assumed, by short and violent events like volcanic outbursts or meteorite impacts, the understanding of the Lilliput Effect becomes problematic, as it predates in some instances these ecologic catastrophes. Notably the best example is provided by the most dramatic mass extinction of the Phanerozoic that took place at the end of the Permian. Here I show that a better explanation of the Lilliput Effect may be rendered by the assumption of jumps in gravity as an effect of Earth growth in accord with increasing SN-rates.

Preamble. The impulse to advance into new, untouched realms of knowledge usually implies the necessity to tackle a problem from a completely new, unconventional perspective. This often means to integrate knowledge of certain scientific domains which at first sight seem to have nothing in common. Here I am about to start an excursion on the Lilliput Effect by bringing together two apparently unrelated topics, namely *mass extinctions* and *gravitational biology*. If someone is not aware of the possibility that the Earth may really increase in size, meaning in mass *as well as* in gravity, he or she seemingly will never conceive of such connections. However, as will be seen, such connections may offer the possibility of finding feasible answers to scientific questions that are presently considered unsolved or unsatisfactory resolved.

The Lilliput Effect. This effect which surprisingly did not make its entry into Wikipedia up to the present, refers to a distinctive size reduction of living organisms that occurs during or in the aftermath of a mass extinction (Harries & Knorr, 2009). In a way it represents the reverse to the tendency to gigantism, known as Cope's rule. The cause of this effect is currently debated. Basically it is assumed that deteriorated environmental conditions are responsible for it. These include in particular low oxygen levels of the atmosphere, mostly coupled with high contents of CO_2 (*hypoxia*). Elevated surface and water temperature is likewise taken into account. Reduced oxygen levels in the

seawater and standstill of sea currents that prevent water exchange and oxygenation bring about the onset of an euxinic environment, extremely hostile to life due to high H_2S contents. Such conditions may result in reduced bioproductivity at the bottom of the food chain and thus in overall food shortage. It is expected that particularly taxa of large dimensions are impaired by it because of their higher food requirements. Their smaller populations and reduced reproductive rates due to food shortage predispose them to be the most affected during mass extinctions. Among specialists it is highly disputed if the Lilliput Effect is due primarily to a filtering or sorting process whereby smaller taxa preferentially survive, or to a real size reduction ("miniaturization" according to Harries & Knorr, 2009) of initially larger taxa. In the last case it must be further distinguished between simple dwarfism and real "miniaturization" implying also variation of morphological traits, leading to the occurrence of new species or genera. In order to perform such detailed investigations large numbers of well-preserved fossils would be needed, a demand which is rarely fulfilled.

The Lilliput Effect can be remarked to a variable extent on land as well as in the sea, equally among plants (Chatterjee et al., 2014) and animals (Fürsich et al., 2001; Twitchett, 2007; Harries & Knorr, 2009; Sallan & Galimberti, 2015; Botha-Brink et al., 2016). This aspect raises some doubts on the assumption that the contents of O_2 and CO_2 respectively may be held responsible for its operation. Because elevated levels of CO_2 would certainly disadvantage animals but not plants; the situation would be reverted in the case of raised O_2 contents. Incidentally Sallan & Galimberti (2015) do not believe that oxygen contents or raised temperature might have prompted the Lilliput Effect at the end of the Devonian, whereas Twitchett (2007) and Fürsich et al. (2001) admit only a subsidiary role of oxygen contents relative to the Lilliput Effect manifested at the end of the Permian and respectively during the lower Toarcian mass extinctions. In the sea the salinity of water may likewise be questioned as a factor contributing to the Lilliput Effect as it could hardly explain why both shelly fauna and non-mineralized burrowing infauna were affected (Twitchett, 2007). On the other hand food shortage may well lead to dwarfism, but in most cases it seems that we are dealing with more than just size reduction.

Of interest are in this respect some conclusions of Botha-Brink & Angielczyk (2010), Huttenlocker & Botha-Brink (2014), and Botha-Brink et al. (2016), reached after examination of bone microstructure of different therapsid genera (particularly *Dicynodontia* and *Therocephalia*) that lived before and after the Permian-Triassic mass extinction event. Bone microstructure reveals that the Triassic species grew generally faster and probably reached reproductive age earlier than their Permian ancestors. Concurrently their size diminished. Botha-Brink et al. (2016) opine that this happened as a response to the "unpredictable, resource-limited" environmental conditions that established at the Permian-Triassic boundary and lasted all along the early Triassic. According to them, the results are "consistent with truncated development, shortened life expectancies, elevated mortality rates and higher extinction risks amongst post-extinction species". Although size diminution, shortened life expectancies or elevated mortality are not by themselves hinting at altered gene expressions, some of the observations made by Huttenocker & Botha-Brink (2014) regarding limb bone structures certainly are, as is the finding of Kemp (1978; 1986) that "the primitive therapsid hindlimbs could operate in either a sprawling mode, or in a more advanced, parasagittal mode". According to Kemp (2005), this dual gait is compatible with the anatomy of the hind limb bones of basal therapsids and represents the link between the sprawling gait of "primitive" pelycosaurs and the parasagittal gait of "modern" mammals. The dual gait possibly developed gradually beginning with the Late Permian and is not an "innovation" that occurred during the mass extinction aftermath. Ideas on the relatively

rapid "mammalization" of therapsids during the Late Permian were also expressed by Sloan (1985), concurring with Kemp's conclusions. Whereas Sloan considers the rapid development of the therapsids as an attempt to keep up their respiratory system with the critical drop of the oxygen level throughout the Permian, I assume that the observed evolution is a response to increased gravity, or more precisely, gives evidence of a frenetic search for the best mode to cope with increased gravity, which culminated with the adoption of the parasagittal gait of mammals during the Triassic. This evolution presupposes high mutation rates, which are assumed also for the attendant Lilliput Effect. In this respect my hypothesis is in agreement with the statement of Harries & Knorr (2009), who emphasized that *"the 'Lilliput Effect' has the potential to … reflect profound morphologic, physiologic, and behavioral changes within taxa"*. Such profound structural modifications are inconceivable without alteration of the genetic material.

> *"Gravity is an important environmental cue that has shaped biological responses"*
> (Plaut et al., 2003)

> *"Cells cannot be considered <<blind>> with respect to gravity"*
> (Bizzarri et al., 2015)

Influence of Hypergravity on Living Organisms.

What do we know about this influence at the moment? Very little indeed, but what has been ascertained is essential with reference to the topic under discussion. In the chapter "Effects of prolonged hypergravity on the anatomy and behaviour of small animals" of his thesis, Sondag (1996) gives an overview of the warranted data at the time of his writing obtained by experiments under hypergravity conditions. It was found out that under hypergravity small test animals (mice, hamsters and rats) lose weight and reduce their size[1], whereupon weight varies inverse to gravity. The weight loss results in part by the reduction of adipose tissue. At the same time it was observed that bones become shorter, but thicker and denser. The musculature accordingly changes. Although the total bone mass decreases, the ratio between the mass of limb bones and the total mass increases. In pregnant rats exposed to 2*G* up to one third of pregnancies were interrupted and stillbirths were much more abundant than in control animals. Practically all organs are affected and are subject to transformations, including the vestibular system, which was the object of the study. Plaut et al. (2003) came to similar conclusions regarding the weight of pregnant rats and fetuses under hypergravity. Howes (2014), who investigated the behavior of *Xenopus laevis* tadpoles under hypergravity, found that they actually lost weight but that their heart, particularly the ventricle, grew bigger. He explained this by the increased mechanical stress and the resulting raised metabolic rate as a consequence of the adaptation to enhanced gravity. In fact, it appears that the increased activity of the heart which induces its enlargement is exactly the reverse to the cardiovascular deconditioning syndrome which occurs in weightlessness.

Different organic modifications have been observed within tissues, suggesting that enhanced gravity induces an increase in the ageing rates (Sondag, 1996 and references herein). In the Howes (2014) experiments animals exposed to higher than 15*G* died during the runs. Contrariwise it could be remarked, however, that surviving animals which were brought back to normal gravity conditions could compensate their weight losses after some time and readapt successfully. All experiments

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[1] Likewise, Vernos et al. (1989) had shown that experiments with *Drosophila melanogaster* caused larger sizes of embryos under weightlessness and smaller ones under higher than normal gravity as compared to controls.

show concordantly how quickly organisms react on hypergravity[2]. They all lose weight and reduce their size whereas the heart apparently increases due to the excess work which it is forced to do. Limbs become smaller but sturdier because their density increases. The birth-rate falls down and pup mortality is high as compared to controls. There is, as well, evidence that life expectancy is reduced. Beyond these large-scale physiological changes, it is long since known that the effect of altered gravity can be traced down to the cellular level, influencing cell shapes and sizes as well as cytoskeletal structures (Moroz, 1984). Analysis of the STS-90 Space Shuttle Mission had revealed for the first time that reduced gravity can affect a wide range of genes (Becker & Souza, 2013). This strongly suggests that similar alterations of gene expression must occur under hypergravity. All these biological characteristics described and inferred to be triggered by a changing gravity force are strikingly matching the features which we meet in conjunction with mass extinctions.

Discussion. Under the assumption of a stepwise increase of gravity on Earth large-size animals would be most endangered and among the first to die. However, some would survive if they could adapt- according to the Lilliput Effect – by "miniaturizing". This means more than just dwarfing, involving alteration of gene expression and thus mutation. The heart must be adapted in order to tackle the additional load. In this regard Mardfar (2012) points out that the whole evolution of the heart of tetrapods since their first steps on land becomes explainable under the premise of a steady increase of gravity.
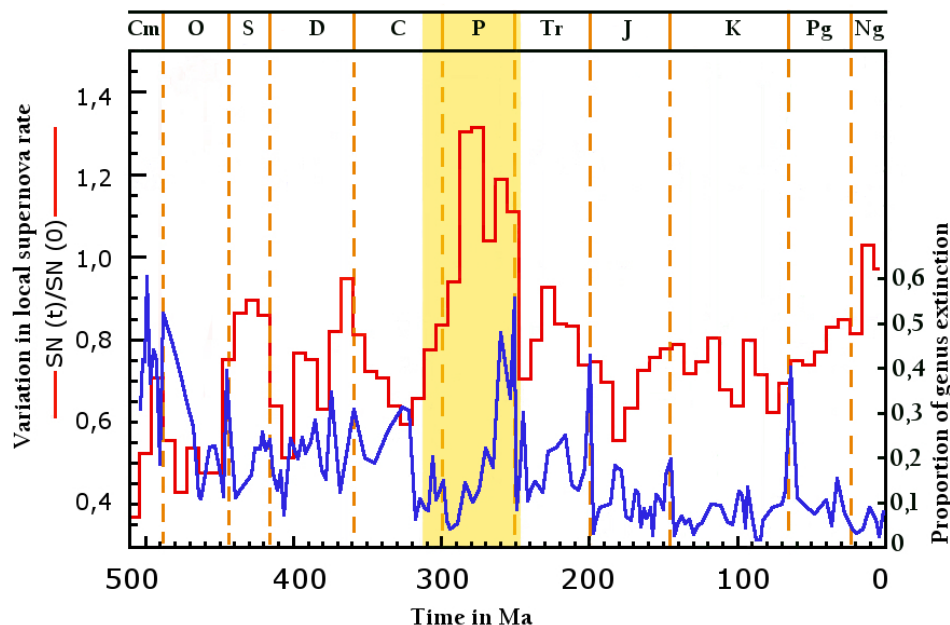

Figure 1 Correlation between the SN-rate (after Svensmark, 2012) and proportion of genus extinction (after Melott & Bambach, 2010) with emphasis on the Late Carboniferous-Permian age interval (shaded area).

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[2] The experiments are conducted mostly over days, much rarer over a year or longer.

I hypothesize (Strutinski, 2015 and in prep.) that the increase took place stepwise and that it happened in correlation with rises of supernova (SN)-rates[3] (Svensmark, 2012; Figure 1). Svensmark's diagram shows a steep rise of SN-rate beginning with the Late Carboniferous and an unprecedented high level of the rate during much of the Permian. Even the short-term low at the end of the Lower Permian stands higher than all other highs from the Phanerozoic. This unique situation is expected to have had far-reaching consequences on the Earth. The timespan between the Late Carboniferous and the end of the Permian actually comprises the longest glaciation of the last 600 Ma and along its length four important turnovers in the evolution of the biosphere occurred: the Carboniferous rainforest collapse, the Olson extinction at the end of the Early Permian, the Capitanian extinction between the Middle and Late Permian and the great end-Permian extinction. It is commonly considered that this last extinction was the most dramatic during the evolution of life and that it erased over 90 % of all marine species and about 75% of terrestrial life. However, Sengör & Atayman (2009) question this statement, emphasizing the far less diminution of biodiversity rate before the end-Permian extinction compared to that at the end-Cretaceous event. To attest this they recall some earlier findings of Stanley (1987), writing:

"Stanley (1987, p. 97) pointed out that great transitions had taken place on land and at sea and that these were not confined to the very end of the Permian, but spread over a time interval of some ten million years and perhaps more. […] the time interval becomes even longer as more research results accrue, effectively disposing of explanations involving fast events such as meteorite impact and catastrophic vulcanicity confined to a million years or less."

Hence, according to Sengör & Atayman it is unrealistic to make a short-time cataclysm (an asteroid impact or a volcanic event like the Siberian trap) responsible for the end-Permian extinction, knowing that a long biological crisis extending at least over the Late Permian preceded that event.

Twitchett (2007) yields statistical evidence showing that the general trend to decreasing dimensions of molluscs began in the Middle Permian (gastropods) or even in the Lower Permian (bivalves), 20-30 Ma before the end-Permian mass extinction. Moreover, the lowest point on the decreasing trend of large-sized bivalves was attained already during the Late Permian (Fig. 2). These data evidently contradict the assumption that the Lilliput Effect was triggered by the end-Permian extinction. Huttenlocker & Botha-Brink (2014) likewise show that "body size reductions occurred early during the evolution of eutherocephalians" (already during the Middle Permian, according to their Figure 7) and are not strictly confined to the post-Permian taxa. Moreover, referring to specimens of the *Hofmeyriidae*, a family that went extinct before the end of the Permian, the authors had to admit that even "small-bodied taxa exhibited unexpectedly thick bone walls" and that "bone wall thickness correlates poorly with size and growth proxies, suggesting that bone robusticity is not necessarily tied directly to growth." The 'unexpected' finding of robust bones in small-bodied taxa is, however, in consonance with the results of the hypergravity experiments: it may be tentatively assumed that thicker bones are an off-the-cuff reaction to increased gravity, implying adaptation by using higher amounts of already existing building material. The fast-growing bones of Triassic *Akidnognathidae* (Huttenlocker & Botha-Brink, 2014) may serve as examples. In a more advanced evolutionary stage, with the checking out of "new", more resistant materials or structures (e.g. parallel-fibred instead of

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[3] High SN-rates are equated with high fluxes of galactic cosmic rays from supernova shock fronts. In my hypothesis high energy protons originating from supernovae are captured at the core-mantle boundary and contribute by "cold fusion" to the growth of the Earth (for details see Strutinski, 2015).

woven bone structure), the chunky bones may be replaced by slender ones, such as has been found in the more derived *Baurioidea*.
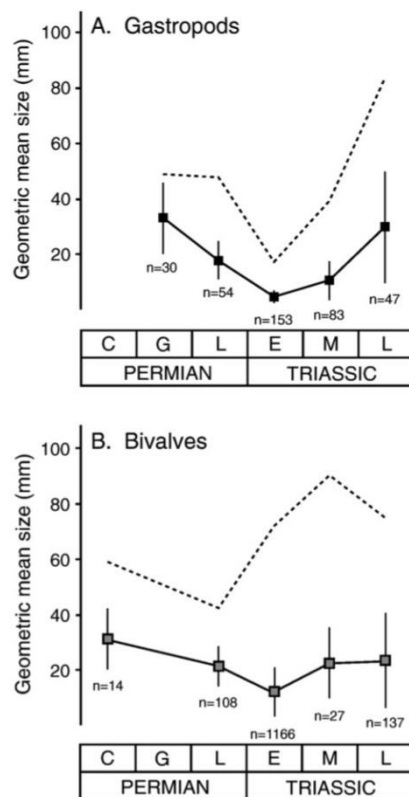

Figure 2 Size change through the Permian and Triassic in gastropods (A) and bivalves (B). Mean size (square symbols – continuous line) and maximum size (dashed line) are represented. "n"= number of measured fossils. . C-Cisuralian, G-Guadalupian, L-Lopingian, E-Early Triassic, M-Middle Triassic, L-Late Triassic. For details, see text (From Twitchett, 2007).

Sahney & Benton (2008) mentioned that the Olson extinction wiped out 2/3 of the land vertebrates. These recovered only to be battered again during the Capitanian extinction, and then, once more at the end of the Permian. The authors produced a graphic representation showing the respective proportions of large, middle-sized and small-sized tetrapods during successive stages of the Permian and Triassic (Fig. 3). As can be observed, large forms show successive ups and downs during the Permian. These may be due to the alternation of governance of Cope's rule and the Lilliput Effect respectively, as an illustration of the rapid succession of extinction and recovery phases. Beginning with the Triassic, small-sized taxa push down the ratios of both large and medium-sized forms. However, the tendency of decreasing size was set during the Permian. Other authors who presented paleontological evidence in support of an earlier onset of the end-Permian extinction were Algeo et al., 2012, and Ward et al., 2005. The latter characterize the situation as follows:

"The pattern that we observe for the P-T is consistent with a *long-term deterioration of the terrestrial ecosystem* [emphasis added, C.S.], with a heightened pulse of both extinction and origination approximately coincident with the P-T boundary."

As regards the evolution of the flora, Erwin (1990) pointed out that it was also affected by a long period of diversity drop by which Paleophytic taxa were successively replaced by Mesophytic taxa. The change lasted 25-30 Ma. Likewise, relying on different sources, Erwin stated that the marine fauna of the Middle Permian, characterized by a high specific diversity assigned to twelve faunal provinces or even more, was replaced during the Early Triassic by a cosmopolitan yet abundant fauna of low diversity pertaining to only six provinces. In a newer report on the distribution of foraminifers

during the Early and Middle Triassic, Payne et al. (2011) endorse the conclusion of Early Triassic cosmopolitanism. Typically, though, the majority of taxa that transgressed the Permian-Triassic boundary, or occurred immediately after the turnover, went extinct by the Early Triassic or during the Middle Triassic. Thus, most of the "successful" foraminifers (cf. Payne et al., 2010) or therapsids (cf. Botha-Brink et al., 2016) living in the aftermath of the Permian-Triassic extinction died out very
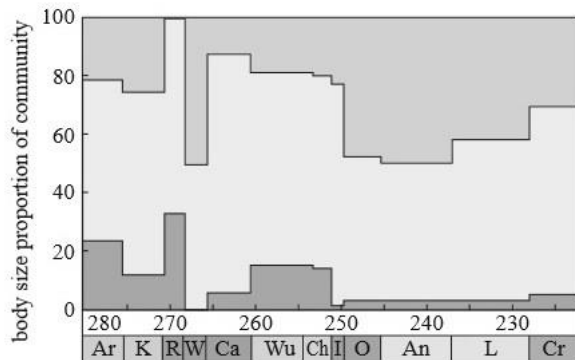

Figure 3 Body size proportion of large, medium and small tetrapods between the Artinskian (Ar) and the Carnian (Cr). The large tetrapods (dark grey) are shown at the bottom of the graph, the small ones at the top (simplified after Sahney und Benton, 2008).

early after the cataclysm. Only four of eleven foraminifer genera outlived the earliest Triassic (Payne et al., 2010) and out of the Early Triassic therapsids apart from a few exceptions only the lineage of Cynodonts passed the "trial and error" barrier of the post-extinction recovery time. According to Huttenlocker & Botha-Brink (2014), although the adopted "strategies were apparently common in the post-extinction environment, their success was temporary." This is conceivable under the consideration that under high environmental stress it is not the best strategies that are regularly adopted, but "the first that come along" (Wickler, 2014).

Authors that assume that the Triassic was – from the point of view of environmental conditions –a more "extreme" or at least highly "unpredictable" period as compared to the Permian (e.g. Chatterjee et al., 2014; Botha-Brink et al., 2016) are in part contradicted by their own data. Twitchett (2007) showed that the "microgastropods … are so common in Lower Triassic rocks that they may reach rock-building densities". This seems hardly reconcilable with inferred inhospitable conditions. The carbon cycle incursions occurring at the Permian-Triassic boundary, considered by Retallack et al. (2006) as indications of a hostile biotic environment, may be related directly or indirectly to the formation of the Siberian Traps and may have consistently deepened the crisis that provoked the mass extinction. However, they did not trigger it. In accord with my interpretation of SN-rates (Strutinski, 2015 and in prep.), I assume that beginning with the Late Carboniferous and lasting over the entire Permian a highly pronounced multiphase increase of gravity took place. It dramatically affected life, took a terrible toll on biota (several extinctions in close succession), but at the same time provoked a fast, unprecedented biologic revolution. The quick evolution of tetrapods from the temnospondyls of the Carboniferous through the pelycosaurs of the Early Permian to the therapsids of the Late Permian may be explained in this way. As a consequence, the amphibian era lasted only about 70 Ma, less than half the time over which dinosaurs were about to reign. Compared to the Permian, the Triassic was most likely a time during which the environmental conditions have been more predictable than usually assumed. Gravity seems to have remained at a constant level for a time. The high strain undergone during the Permian and the transition period into the Triassic could be overcome only step by step by the flora and fauna. This may be the reason why the evolution almost stopped for some million years and Lilliput forms continued to exist to the end of the Early Triassic. The survival of a few antiquated temnospondyls measuring 5-6 meters (*Mastodonsaurus*)

may be a consequence of their living in shallow waters, taking advantage of buoyancy (Strutinski, 2016). They could be considered the exception that confirms the rule.

Conclusion. Diverse evidence coming from paleontology, statistical distribution of taxa and bone histology suggests that the Lilliput Effect manifest on land and at sea before as well as after the end of the Permian was not due to some unfavorable "new" environmental conditions installed in connection with the end-Permian extinction but to the long-lasting instability of the Permian period. In accordance with a postulated mass and gravity increase of the Earth, I assume that the Lilliput Effect was a consequence of repeated jumps of gravity in dependence to raised SN-rates, which took place during the Late Carboniferous and the Permian. The characteristics of 'Lilliput fauna' are strikingly reminding of morphological and physiological changes undergone by animals exposed to hypergravity, thus substantiating the gravity-linked hypothesis. Moreover, it is assumed that every increase of gravity may stimulate variation and beyond the risks of getting extinct offers the opportunity for elevated levels of biodiversity. From this point of view, it was not the Triassic that offered "unpredictable" provocative environmental conditions to life, but instead, the Permian.

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