

Two essays on an annotated edition of Darwin's *ORIGIN OF SPECIES*

Or

An Expansionist's alternative to Gould, Dawkins & Co

by

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Abstract. Without disclaiming the role of natural selection and allopatry in speciation, the author implies that the appearance of new species is predominantly induced under high environmental stress in a process called spotted sympatry. Such high-level stress frequently causes mass extinctions and, according to the author, is mainly triggered by abrupt increases of gravity. That gravity is the main culprit in this tandem process of extinction-speciation is demonstrated by the longevity of some clades that produced "living fossils" like *Latimeria* and *Nautilus*. These clades outlived several mass extinctions due to key innovations that permitted them to successfully adapt to the stepwise increase of gravity.

1.

Key words: Isolation, allopatric speciation, sympatric speciation

From: Chapter IV: Natural Selection

Circumstances favourable to natural selection (p. 105-107)

Darwin: Lastly, isolation, by checking immigration and consequently competition, will give time for any new variety to be slowly improved; and this may sometimes be of importance in the production of new species. If, however, an isolated area be very small, either from being surrounded by barriers, or from having very peculiar physical conditions, the total number of the individuals supported on it will necessarily be very small; and fewness of individuals will greatly retard the production of new species through natural selection, by decreasing the chance of the appearance of favourable variations.

If we turn to nature to test the truth of these remarks, and look at any small isolated area, such as an oceanic island, although the total number of the species inhabiting it, will be found to be small, as we shall see in our chapter on geographical distribution; yet of these species a very large proportion are endemic, - that is, have been produced there, and nowhere else. Hence an oceanic island at first sight seems to have been highly favourable for the production of new species. But we may thus greatly deceive ourselves, for to ascertain whether a small isolated area, or a large open area like a continent, has been most favourable for the production of new organic forms, we ought to make the comparison within equal times; and this we are incapable of doing.

Although I do not doubt that isolation is of considerable importance in the production of new species, on the whole I am inclined to believe that largeness of area is of more importance, more especially in the production of species, which will prove capable of enduring for a long period, and of spreading widely. Throughout a great and open area, not only will there be a better chance of favourable variations arising from the large number of individuals of the same species there supported, but the conditions of life are infinitely complex from the large number of already existing species; and if some of these many species become modified and improved, others will have to be improved in a corresponding degree or they will be exterminated. Each new form, also, as soon as it has been much improved, will be able to spread over the open and continuous area, and will thus come into competition with many others. Hence more new places will be formed, and the competition to fill them will be more severe, on a large than on a small and isolated area... Finally, I conclude that, although small isolated areas probably have been in some respects highly favourable for the production of new species, yet that the course of modification will generally have been more rapid on large areas; and what is more important, that the new forms produced on large areas, which already have been victorious over many competitors, will be those that will spread most widely, will give rise to most new varieties and species, and will thus play an important part in the changing history of the organic world.

Costa: Isolation was clearly more important to Darwin's early thinking than to his later thinking. In *Natural Selection* (Stauffer, 1975, p. 255) he wrote: "I infer that some degree of isolation would generally be almost indispensable." In the *Origin*, however, Darwin gives the distinct impression that he does not think isolation is the only or even the primary means of species evolution. In fact, he discounts its importance in favor of a selection-driven mechanism. Note that he suggests here that oceanic islands might seem "at first sight" to have been favorable for the formation of new species in comparison to similar continental areas, but that "we may thus greatly deceive ourselves." Darwin suspects that "largeness of area" is more important than isolation.... The modern take on speciation, first cogently argued by Mayr (1942), is that isolation nearly always plays a role, and thus oceanic islands are veritable crucibles of evolutionary change.

Darwin (continued): We can, perhaps, on these views, understand some facts which will be again alluded to in our chapter on geographical distribution; for instance, that the productions of the smaller continent of Australia have formerly yielded, and apparently are now yielding, before those of the larger Europaeo-Asiatic area. Thus, also, it is that continental productions have everywhere become so largely naturalised on islands. On a small island, the race for life will have been less severe, and there will have been less modification and less extermination...

Costa: Here Darwin makes an observation to back up the argument that largeness of area is more important than isolation: when "continental productions" (i.e., continental species) are introduced into islands or similar isolated areas, they tend to handily outcompete the native species, displacing them and not infrequently even driving them to extinction. Darwin takes

this as an indication of the superior competitive ability of continental species, superiority derived from the intense history of competition they experienced.

My comments: In his early considerations on evolution Darwin assumed that speciation takes place very slowly over long time periods and that *isolation* represents a basic requirement for it to happen. This idea was probably influenced by the study of the fauna from the isolated Galapagos Islands and his awareness on the results of breeders with artificial selection. According to him, a less well isolation of the island of Madeira from Europe and Africa prevented or at least hindered the origination of new species of birds on this island (Stauffer, 1975, p. 256-257). In the first annotation to the Darwinian text, quoted herein, Costa alludes to the fact that in the *Origins* Darwin evidently refrains from his earlier idea regarding the importance of isolation. At the same time Costa emphasizes that according to modern interpretations (e.g. Mayr, 1942), "isolation nearly always plays a role" in speciation, a statement which may be assumed as a slight criticism of Darwin's change of mind. That is because the concept of isolation is indispensable to the principle of *allopatric speciation* still considered the principal means of speciation. According to it, populations should first split and then isolate, before beginning to evolve separately and differentiate. It is evident that allopatric speciation had a dominant role when continents rifted apart and were separated by oceanic spreading. This may best explain how Australia got its status as a peculiar natural habitat. It is much more difficult to explain why the aboriginal fauna and flora of Australia could/can so easily be supplanted by the euro-asiatic ones. According to Darwin, the explanation is that the euro-asiatic taxa were more evolved than the Australian ones, due to the higher selection pressure operative on a super-continent as compared to a small landmass like the Australian one. This argument may be valid; however there may also contribute other factors to explain this situation. For instance, it should not be overlooked that the immigration of an invasive species always produces a disturbance of the ecosystem into which it intrudes, and as initially it has no enemies there, it can evolve undamped, pushing the native forms aside or even exterminating them.

A much less importance for speciation is acknowledged to *sympatric speciation* because it is usually considered that in sympatry gene flow, which must be cut off in order to permit diversification, never decreases dramatically. This seems fully unjustified, as I will show. Sympatric speciation takes place in the area of the parent population without splitting. Under which circumstances could gene flow be blocked, in order to permit variation leading to speciation? We should remember that allopatric speciation implies physical separation of a population, without any possibility for individuals from one of the resulted sub-populations to mate with individuals from another one. However, other environmental factors (e.g. temperature, salinity, O₂ and CO₂ contents of the atmosphere and hydrosphere, most of the existing ecosystem interrelations) remain more or less unaltered, at least for a while, almost as if physical separation would not have occurred at all. Under such circumstances it is conceivable that only second-order stress factors like intra- and interspecific competition may exert selection pressure in order to drive allopatric speciation.

However, if catastrophic environmental changes abruptly occur within a territory occupied by a population, possibly leading to mass extinctions, the adaptation pressures on individuals expectedly shoot up, leading to mutation “avalanches” akin to models imagined by Bak (1996) and Sneppen and Zocchi (2005). These soon create reproductive incompatibilities within the population (reproductive barriers, acc. to Nei and Nozawa, 2011; Nei, 2013), which, however, *do not prevent mating*, yet activate postzygotic isolation mechanisms, gene flow being almost totally interrupted. Consequently, mere nonviable or sterile offspring will be born. This is hardly preserved in the stratigraphic record, which is the cause why fossil links between parent and daughter species are generally missing. Nonetheless, random mating between genetically compatible positively transmuted individuals (“hopeful monsters”, according to Goldschmidt, 1940) may give birth in short time (meaning thousands or tens of thousands of years) to one or even more new species. Most of these would go extinct as well, but some will be viable under the new environmental conditions and will thrive and disseminate, eventually replacing their ancestors. I assume that this might be the mode by which recovery after mass extinctions takes place (see also Strutinski, 2016). This viewpoint seems to conform best to the facts; it also includes the alternatives of survival or, on the contrary, extinction of parent species, and successfully integrates the hypothesis of punctuated equilibrium (Eldredge and Gould, 1972), according to which evolution takes place in short boosts separated by long intervals of evolutionary stasis. Indeed, Eldredge and Gould’s conclusion that “most evolutionary changes occur in a short period of time” equally applies to the great biotic turnovers, better known as mass extinctions. However, Gould (Glen, 1994) considered that the hypothesis of “punctuated equilibrium is about the extinction and origination of species; mass extinction is a different scale of event within the punctuational model”; a link between the two concepts would be a “misapplication” (Gould, 2007)¹. This view may possibly be maintained when speciation demonstrably takes place under the condition of allopatry. Nevertheless, during mass extinctions and in their aftermath we have to deal with the spot-like appearance of new species *inside the territory of the parent ones*, or, as I call it, with *spotted sympatry*, in which case the statement: “new fossil species do not originate in the place where their ancestors lived” (Eldredge and Gould, 1972) does not apply. Moreover, the whole process of extinction/speciation is linked to a deep ecological catastrophe and not to the struggle for new ecological niches. In other words, the former case implies *reaction* to, whereas the latter assumes *action* upon the environment.

I am fully aware of the fact that with my hypothesis I come unwantedly near to Couvier’s catastrophism or to creationism. However, at the same time I am refuting them on scientific grounds. Thus, according to the hypothesis, the pursuit of *missing links*, which are falsely assumed to have existed during the transition from the ancestor species to the descendant

¹ It should be mentioned, however, that recently Eldredge (2013) acknowledged that „much, if not all, evolution occurs only after episodes of ecosystem disruption, sufficiently widespread and severe to cause the extinction of entire species – and in the most dramatic and easily seen cases – of higher taxa“. This statement is very near to that advocated herein.

one, becomes superfluous and sidelines the creationists' "heavy artillery" against evolution. My solution of the "missing links" problem does not even require "marginalization" or migration of the mini-population that gives rise to a new species from the range of its ancestors, as implied by Eldredge and Gould (1972).

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2.

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From: Chapter IV: Natural Selection

Circumstances favourable to natural selection (p. 107)

Darwin: All fresh-water basins, taken together, make a small area compared with that of the sea or of the land; and, consequently, the competition between fresh-water productions will have been less severe than elsewhere; new forms will have been more slowly formed, and old forms more slowly exterminated. And it is in fresh water that we find seven genera of Ganoid fishes, remnants of a once preponderant order: and in fresh water we find some of the most anomalous forms now known in the world, as the *Ornithorhynchus* and *Lepidosiren*, which, like fossils, connect to a certain extent orders now widely separated in the natural scale. These anomalous forms may almost be called *living fossils* [my emphasis]; they have endured to the present day, from having inhabited a confined area, and from having thus been exposed to less severe competition.

Costa: Here Darwin gives examples to support the assertion that island forms are less well adapted than continental forms. ... [A]rchaic animal forms are often found on islands or in island-like habitats (like lakes) – shelters where relictual variants or species hold out. The argument is that such groups are found on islands or island-like environments because they were outcompeted and driven to extinction in continental areas. There is, of course, some truth to both of Darwin's assertions: island species often cannot compete with introduced species, and taxonomic relicts are disproportionately found in island environments (e.g. tuataras of New Zealand, the last remnant of once-flourishing rhychocephalian reptiles).

Note the origin of the phrase "living fossil" which Darwin coined to describe anomalous or relictual species that have apparently persisted far past their heyday when the groups to which they belong were dominant. This is a slightly different meaning from that often used today, which typically refers to species like horseshoe crabs or ginkgo trees that have apparently changed little from their distant ancestors known from the fossil record.

The groups Darwin mentions here are all considered representatives of basal lineages. Ganoids are a primitive fish group with thick, bony, diamond-shaped scales. They are best represented in the fossil record (e.g., all Sarcopterygii and some Actinopterygii), but some actinopterygids such as gars (Lepisosteidae) and the bizarre bichirs of Africa (Polypteridae) still exist. *Ornithorhynchus* is the duck-billed platypus of eastern Australia, and *Lepidosiren* is the South American lungfish, represented by the sole species *L. paradoxa* in the family Lepidosirenidae.

My comments: I remember that for tens of years I lived with the impression that Darwin's *living fossils* became our contemporaries only because they lived over tens or even hundreds of millions of years under "anomalous" environmental conditions, meaning conditions that did not change, and consequently did not force these "anomalous forms" (Darwin, 1859) to change too. It was the only mode I could reconcile the existence of "living fossils" with Darwin's theory of evolution. According to Werth and Shear (2014) the preservation in some extant taxa (of fauna as well as flora) of "archaic" morphologies over tens of millions of years or more is still a "mystery that has long plagued biologists" These authors are not very far away from my former belief, when they suppose:

"Ecological stasis might reward morphological stasis, and species that are well adapted face little need to change without the spur of an environmental alteration".

Does this mean that "living fossils" thrived in environments that did not change for eons? Today I am convinced that this cannot be true. At least during the "big five" mass extinctions no habitat on Earth should have been left undisturbed. However, small changes occur more or less continuously. So organisms are forced to adapt permanently and the rate of their evolution depends mainly on the degree of the environmental stress. Low environmental stress or "background stress" may be equated with *stasis* and as it may last for millions or sometimes tens of millions of years, organisms and their whole ecosystems would accordingly show some kind of stasis, as assumed by the hypothesis of punctuated equilibrium (Eldredge and Gould, 1972). However, according to Dawkins and Krebs (1979), it is not the "static" environment that detains a species from evolution, but the inexistence of competition: "lineages that evolve slowly do so precisely because they are not involved in severe arms races". This is a more general conclusion than that of Darwin (1859) who assumed that in restricted, isolated areas "the race for life will have been less severe", giving Australia's less evolved "productions" as an example. I do not question these arguments, though I give preference to Darwin's weaker "race for life" instead of the bellicose "arms race". There is, however, a problem, when referring to intraspecific competition between individuals as the "primary driving force of Darwinian evolution" (Dawkins and Krebs, 1979). Firstly, because, were this the case, then even under "static" environmental conditions gradual evolution should be expected to occur which is not supported by the fossil record; and secondly, because in an ever changing world intraspecific competition and "archaic" traits as presented by "living fossils" could hardly be reconciled. Without denying some sort of race between different species in their fight for ecological niches or inside the predator-

prey escalation, I assert that the fossil record generally favors the hypothesis of punctuated equilibrium which leads to the conclusion that “primary <<struggles>> are with changing climates, geologies, geographies, not with each other” (Gould, 1985). This means that higher-than-background environmental stress most probably is the primordial factor in evolution, thus assigning to “arms races” only an accessory role, possibly restricted to allopatric speciation and internal ecosystem feuds. Likewise, an *automatic* tendency towards diversity and complexity increasing with time within the biosphere, as asserted by McShea and Brandon (2010), is at least doubtful considering diverse arguments to the contrary which cannot be just considered as exceptions that prove the rule. I refer especially to the evidence of “living fossils” with their ancestral traits, to so-called retrogressive evolutions within different lineages and to the fact that there is a great disparity between groups as regards diversification. It is at least confusing to realize that the propensity for diversifying is indeed very high in some cases (different groups of ray-finned fishes, dinosaurs, mammals), but medium in others (e.g. sponges, cnidarians, sharks) and extremely low in still others (e.g. comb jellies, hagfish, coelacanths; lungfish; bichirs). Typically most of the latter two categories seem to have passed all the bottlenecks of mass extinctions with negligible losses, in spite of their extremely low diversity. Many “living fossils” belong to these groups. As remarked by Werth and Shear (2014), “it is not simply luck ... but often a *key innovation that renders living fossils successful in persisting for long stretches of time* [my emphasis]”. However, this interpretation is at variance with the contemporary use of the key-innovation concept, according to which “a key innovation is an evolutionary change in individual trait(s) that is causally linked to an *increased diversification rate* in the resulting clade [my emphasis]” (Heard and Hauser, 1995). The incompatibility resides in the fact that “living fossils” mostly belong to clades that are characterized by extremely low diversification rates. Therefore, I prefer the original view of Miller (1949), who spoke of “key adjustments in the morphological and physiological mechanism which are essential to the origin of new major groups”. Even this definition does not exactly conform to “living fossils”, as they show very little improvement (if at all) in their morphology. The dilemma created by the “living fossils” is additionally illustrated by the fact that some biologists regard them as generalists, while others consider them to be specialists (Werth and Shear, 2014; Strutinski, 2016a). Thus, the “mystery” of “living fossils” and the low diversity of the clades to which most of them belong continue to “plague” biologists. Obviously, the idea that high diversification rates within clades guarantee a high survivability and thus suggest “progress” seems to be wrong. To the contrary, my firm impression is that “living fossils” tell us that high survival rates, particularly if extinction events are comprised, are inversely proportional to diversification rates. To put it another way, *Homo sapiens* may be, in the long term, less adapted than, say, *Latimeria*! Coelacanths at least crossed through several mass extinctions to the present, while hominids did not pass a corresponding test until now. *Latimeria* is not incidentally mentioned here. If we are looking for key innovations that enabled coelacanths to survive for more than 400 Ma, we should not think of innovations permitting high diversification and implicitly good adaptation to ecological niches, but of means to overcome great ecological catastrophes leading to mass extinctions. In this respect, the story that coelacanths tell us is remarkable

(Strutinski, 2016a). The first coelacanths that lived during the Lower Devonian, shortly after their divergence from bony fishes, most probably continued to share with the latter a bony skeleton and an air-filled swim bladder. However, already in the aftermath of the Late Devonian mass extinction and during the remainder of the Carboniferous coelacanths decisively diverged from bony fishes by successively replacing their bony skeleton with lightweight cartilage, and protecting their swim bladder with an ossified integument, considered by Williamson (1849) as “an anomaly which ... has hitherto *presented no parallel in nature* [my emphasis]”. This “bony” air-filled swim bladder was maintained during the whole of the Mesozoic, or possibly straight to the Tertiary, but was finally abandoned and replaced by an oil-filled bladder without a protecting encasement. The result: *Latimeria* has neutral buoyancy (Adamicka and Ahnelt, 1976), in contrast to most teleosts which have to counterbalance their negative buoyancy hydrodynamically by swimming. It is striking that such remarkable “anomalies” within the realm of fishes, as witnessed by the “bony” and then oil-filled swim bladder of coelacanths, have not been considered as key innovations until now, in spite of the fact that other features of coelacanths are clearly ancestral and can give no indication as to why representatives of this order managed to do so well during four of the “big five” mass extinctions on Earth. However, there might be a simple explanation for this bias in paleobiological investigations: no one takes into consideration that *during Earth’s evolution gravity might have increased!* Otherwise the “mystery” of coelacanths would have long ago been solved, because a “bony” and then an oil-filled bladder make sense only by assuming adaptation to an increasing hydrostatic pressure induced by a gravity increase. Moreover, I suspect that there have been jumps in the increase of gravity, occurring at about the times when most of the great mass extinctions took place (Strutinski, 2016a; Strutinski, in prep). On the other hand, less effective innovations in most orders of bony fishes² forced them to “invest” in diversification, to compensate their thinning out during mass extinctions. It should not be overlooked that the key innovations of *Latimeria* caused the regression of its brain (involution!), making it a “dull” fish compared to teleosts. Yet, as regards the survival probability during mass extinctions, it seems that the brain is only a poor substitute, if it is of any help at all. We may thus doubt with Gould (1996) that there is any directionality³ in the biologic evolution, despite virulent criticisms coming particularly from the field of sociobiology. However, as stressed by Davies (2013), “evidence for a systematic directionality in biology is not well founded”, particularly if we account for the fact that the most evolved organisms, i.e. animals including humans, represent only 0.2% of the total quantity of biomass on Earth.

Another “living fossil” that seems to point out that its capacity of maintaining neutral buoyancy in the pelagic domain was essential to outlive mass extinctions is the invertebrate *Nautilus*. As noted by Greenwald and Ward (2009), “*Nautilus* is somehow sensitive to its

² After all, bony fishes improved their swim bladder only by partially abandoning the physostomous bladder in favor of the physoclistous one, or by getting entirely rid of it (Strutinski, 2016a).

³ Directionality may be defined as the tendency of evolution to build more complex and intelligent animals over time. See Robert Wright “The Accidental Creationist” (<http://www.nonzero.org/newyorker.htm> - retrieved on 30th of July, 2016).

buoyancy and can make appropriate *compensatory adjustments*. [my emphasis]" In fact Jordan et al. (1988) have experimentally demonstrated that *Nautilus* senses instantly changes in hydrostatic pressure as small as $1 \times 10^5 \text{Nm}^{-2}$ (almost 1 atmosphere) owing to mechanisms that are not well understood. Eventually this key innovation may be the real "survival secret" (cf. Switek, <http://www.wired.com/2012/05/the-secret-of-ammonoid-success/>, retrieved on 6th of August, 2016_) of nautiloids as compared to their more evolved cousins, the ammonoids. It is not clear why the latter apparently did not have the same capability and finally went extinct at the end of the Cretaceous⁴. My assumption is that ammonites may have invested only in speed to counterbalance increasing pressure, as most bony fishes did. Here too we have an example of a "progressive" group of animals which, being less well adapted than "primitive" nautiloids to overcome a bottleneck, does not support directionality. In this respect, Prothero's (2013) remark regarding bivalves is also suggestive:

"Bivalves may not be smart or fast or have heads with many sense organs, but they are well adapted for their niches and have survived many crises that wiped out much faster, more intelligent groups of animals (such as the ammonites)".

Likewise, whatever we may think about the brain of dinosaurs, it cannot be ignored that it probably was the highest evolved among terrestrial tetrapods during the Mesozoic. However, except birds, their direct descendants, they all went extinct at the end of the Cretaceous and their brain was obviously of no use to them.

Assuming increasing gravity to be an important stress factor to living organisms, it appears that, apart from a greater unpredictability (Lavers, 2000) the freshwater realm as well as the littoral zone of the seas offer the highest possible protection against upward stepping of gravity. This is because locomotion as well as other physiological processes of animals living on land or in the pelagic zone are badly vitiated under a raised gravitational attraction, yet are still possible where hydrostatic pressure remains manageable and buoyancy is still effective as is the case in shallow marine and freshwater environments. I think that it is for this reason why even large animals like crocodiles and turtles, along with a great number of small amphibians, reptiles and mammals managed to cross the Cretaceous-Tertiary boundary without great losses. Statistical data show that 90% of the "freshwater" vertebrates from Montana broke the bottleneck at the end of the Cretaceous, while the survivor rate among "land-dwelling" faunas was only 12% (Sheehan and Fastovsky, 1992). Other explanations of this fact, like the "sheltering" hypothesis of Robertson et al. (2004) are

⁴ An explanation may be the different functionality of the siphuncle (central in nautiloids and ventral in ammonoids). As noted by Kennedy and Cobban (1976), "many ammonites lack all sign of a siphuncular tube in the last few chambers ... and it may be that these last chambers were flooded in life and that lack of a supporting siphuncular tube rendered the animal unable to pump out cameral fluid." This fact may have been highly inconvenient under the assumption of a stepping rise of gravity, explaining the discontinuous evolution of ammonoids. According to Wiedmann (1973), "times of evolution were repeatedly interrupted by periods of explosive revolution together with sudden extinction".

unlikely or only apply to some big animals like crocodiles and turtles (Lavers, 2000)⁵. Practically all of the “living fossils” cited by Darwin also fall in the category of freshwater-dwelling animals: ganoid fishes, *Ornithorhynchus* and *Lepidosiren*. It seems quite possible that ancestors of the “old-fashioned” tuataras, mentioned by Costa, as well as of Komodo dragons or Galapagos iguanas also survived in shallow water habitats during the last big mass extinction at the end of the Cretaceous. The same applies for the horseshoe crabs. Likewise the lungfishes and ganoid fishes (sturgeons, paddlefishes, bichirs, bowfins and gars) also inhabit predominantly freshwater and brackish environments. According to Darwin, they survived to our days because “the competition between fresh-water productions will have been less severe than elsewhere”.

All the primitive-looking animals mentioned above (except coelacanths and nautiloids) and probably some diadromous fishes belonging to the more evolved orders of *Anguilliformes*, *Clupeiformes* and *Salmoniformes* (Strutinski, 2016a) appear to have crossed without casualty the Cretaceous-Tertiary boundary due to the fact that they lived, at least intermittently, in shallow water environments. However, it was not the less severe competition in such environments that caused the conservation of their morphology and their survival, as Darwin assumed, but, as I hypothesize, the fact that in these environments *the impact of gravitational stepping is less severe experienced*. The evidence that in many presently known isolated ecosystems high diversification rates occur (e.g. the East African lakes with their abundance of cichlid forms) clearly argues against isolation as a cause of species conservatism. On the contrary, it seems that conservatism and low diversification rates are the rule whenever a key innovation randomly occurring as a response to a major environmental stress is near to its optimal level⁶. The materialization of this principle is illustrated herein by the “living fossils” *Latimeria* and *Nautilus*, as representatives of clades (coelacanths and nautiloids) that crossed several mass extinction events without great losses, compared to some of their more evolved sister clades which were seriously harmed or even went extinct. In both cases I consider that relevant, yet different key innovations permitted the animals to optimally adapt to upward jumps of the hydrostatic pressure presumably triggered by a stepwise increase of gravity. As I showed elsewhere (Strutinski, 2016a), these are not exceptions within the marine environment because entire classes of sea inhabitants, as are chondrichthyans among fishes and four out of five classes of cnidarians (jellyfish), are better adapted to hydrostatic pressure variations than the great majority of fishes. Chondrichthyans suffered some losses during the Paleozoic mass extinctions, but fared quite well during the Mesozoic ones. According to Kriwet and Benton (2004), out of 41 families of sharks living in the Cretaceous only seven went extinct at the

⁵ According to Robertson et al. (2004), the Chicxulub impact triggered a heat pulse which destroyed all life on land excluding mainly small-sized animals which managed to shelter underwater and/or in underground cavities. On the other side, Lavers (2000) saw in the “unsurpassable ecological design” of crocodylians the explanation for their 200 Ma survival.

⁶ According to Wickler (http://www.seniorenstudium.uni-muenchen.de/forschung/publikationen/pub_pdf/wickler_darwin.pdf, retrieved on 29th. of May, 2012) it is not the best possible but the first available solution to a problem that normally occurs during evolution.

end of the Mesozoic. Today more than 500 species of sharks are known, representing, however, only about 2 per cent of the equivalent number of bony fishes. This may be a further argument in favor of the hypothesis that better key innovations are probably the main cause for low diversification rates. Another indication that gravity increase might be the principal stress factor during times of mass extinction is the tendency of organisms to firstly respond by size diminution, a phenomenon commonly known as “Lilliput Effect” (Strutinski, 2016b). Size diminution has also been noticed to take place in hypergravity experiments (Sondag, 1996; Howes, 2014). Many plants and animals reduced their sizes significantly during evolution and particularly old lineages seemed to have it fixed in their genes that small size is the only way to prevent extinction. On the contrary, apart from some big representatives of older clades which are restricted to freshwater environments (e.g. the amphibian *Mastodonsaurus* in the Triassic, crocodylians today) it is always within newly originated clades that the tendency to gigantism, known as Cope’s rule, is manifested. Thus, in the Early Paleozoic arthropods, brachiopods and echinoderms were the clades which most significantly showed size increases (Novack-Gottshall, 2008). A noticeable size increase was then successively performed by amphibians (in the Late Paleozoic), reptiles (during the Mesozoic), and birds and mammals (during the Tertiary). So it seems that lineages need time and the devastating experience of more than just one mass extinction to “learn” to invest in adaptations successfully counterbalancing increasing gravity or, otherwise, to resort to size reduction. The improvement of locomotion of animals living in the pelagic domain is usually considered to have been accomplished in order to enhance their ability to capture prey or, conversely, to escape from being captured (in other words, to drive competition or “arms races”). However, it is known that pelagic fishes are dependent on swimming to attain hydrodynamic lift necessary to prevent sinking. Therefore, assuming growing gravity and hydrostatic pressure, it is possible that their costly investment⁷ in locomotion was primarily caused by these factors and not by the necessity to improve their hunting-escaping capacities. The same may apply to other “high energy” predators like ammonoids. Relevant to an increase in gravity during the Early Paleozoic may be the so-called nekton revolution that took place during the Devonian (Klug et al., 2010) and according to which the “sluggish predators” of pre-Devonian times, like nautiloids, eurypterids and starfish, were successively replaced by “active swimmers” (ammonoids and jawed fishes) (Bambach, 1999). Nevertheless, under the condition of a growing gravity, enhancement of speed alone to maintain buoyancy is not quite the optimal solution and the final extinction of ammonoids (but not of nautiloids!) (MacLeod et al., 1997) and fast swimming fishes (Friedman, 2009) at the end of the Mesozoic may be regarded as arguments favoring my hypothesis.

Conclusion. As concisely shown above, the assumption of a (stepwise) growth of gravity as a consequence of Earth’s mass increase allows for a better explanation of some of the biological enigmas, like Darwin’s “living fossils” or particular features defining mass extinctions, which continue to “plague” biologists and paleobiologists. From an astrophysical

⁷ According to Dyson (2003), up to 20 percent of the energy consumed by continuously swimming fishes is assigned to ensure neutral buoyancy.

standpoint, the assumption of Earth's gravity increase is not so far-fetched, as it conforms well to the general increase of entropy of the gravitational field of the Universe, which drives aggregation into celestial bodies on all scales (Davies, 2013) and relieves on Earth the energies spent in creating the diversity of processes and structures we are surrounded by. If some readers may argue that my hypothesis is wholly unfounded, as measurements actually do not show any evidence of Earth growth and increase of gravity, I simply remind them that there have been periods lasting several millions of years during which the growth of the Earth was obviously too small to impact on the biosphere (the stasis intervals). So what relevance could have geodetic measurements conducted over some decades – merely a bat of eyelashes in the history of the Earth – about changes in its radius?

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