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Great Revolutions in the History of Life*

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Evolution is a historical process. Like human history it's course is unpredictable, because it results from the response of organisms and their biographies to changing outside conditions. Yet it makes perfect sense in retrospect, because every move was conditioned by the previous one.

Another characteristic of historical changes is that they proceed gradually on the one hand, but are accentuated by events on the other. With regard to human history, one has always emphasized the events, such as wars and political revolutions; only recently historians got also interested in the more gradual changes in everyday life during the intervening periods. In evolutionary biology, emphasis was reversed. Darwinian theory focuses in gradual transformations, because this is what we can directly observe in natural and domesticated populations. Therefore the breaks that paleontologists noted in the fossil record were for a long time considered as preservational artifacts. Today we know that they reflect real evolutionary cascades induced by environmental perturbations of higher order. We are also becoming aware that the impact of our own species on the global environment could mark such a break, which a few million years later will be taken as the end of the Cenozoic and the beginning of a new era, the "Anthropozoic". With such perspectives in mind we shall now study the patterns of the great revolutions in the history of life, back to the greatest of all, the "Cambrian Explosion".

The End-Cretaceous Extinction

Because it happened only 65 million years ago, the events connected with the mass extinction at the end of the Cretaceous period are known in most detail. A large number of previously dominating groups of animals (dinosaurs, belemnites, ammonites, inoceramid and rudist bivalves etc.) became extinct during a very short time interval. This allowed minority groups, which had previously been held in check by the rulers, to gain dominance by radiating into the evacuated niches. The mammals, which had been in existence since 200 million years ago, well represent this phenomenon.

We also know the main culprit: an asteroid about ten kilometers in diameter hit the earth, producing a giant crater in the Yucatan area of Mexico and the Caribbean. It also ejected dust rich in "cosmic" elements into the air, which became deposited all over the earth in the Cretaceous/Tertiary boundary layer. Although this catastrophe itself must have been destructive enough, its longer-term consequences were probably even more pervasive. By perturbing the delicate balance in most ecosystems (but not on deep sea bottoms!), it resulted in the extinction of probably more than 50% of the species in the wake of the impact.

Yet, was the impact the only cause of the end-Cretaceous extinction? Other perturba-

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tions, such as unusually high levels of volcanism or sea level changes are still being discussed as alternative explanations. Also, some of the victim groups appear to have dwindled already during the upper Cretaceous and some (e.g. rudists) may actually have become extinct a few million years before the impact.

At this point we should remember that history is a non-linear process. The French Revolution may have been triggered by the storm on the Bastille; but it had its roots in the socio-economic developments of decades before. Equally we must consider the state of the biosphere before the asteroid impact in order to understand its effects.

As we know from geochemical evidence, the Cretaceous (particularly the Middle Cretaceous) has been a period, in which the climate was unusually equitable. This meant that the diversification in many groups of animals could proceed without being called back by minor extinctions. So dinosaurs on land and aquatic reptiles, as well as ammonites and rudist bivalves in the sea, could exceed the limits of their respective bauplans with regard to size and shape. In earlier times, this phenomenon has been interpreted as a kind of phyletic "decadence" (Schindewolf, 1950), heralding the demise of those groups in the end-Cretaceous extinction. Today we can not accept such an orthogenetic view. In fact, the "bizzare" dinosaurs, ammonites and rudists were probably no less fit than their more normal relatives: but their specializations made them more vulnerable towards environmental perturbations.

If we see mass extinction as a synergetic (Haken, 1983) rather than a linear process, we do not have to search for a single culprit, such as the asteroid impact, because after a "Golden Age" any kind of perturbation would result in unusually high levels of extinction.

The End-Permian Extinction

At the turn of the Permian to the Triassic period, about 200 million years ago, the number of species that became extinct was probably even higher. What interests more in this context: among the victims were not only the last survivors of trilobites (which had their best time earlier in the Paleozoic) and the rugose corals that had been prominent Paleozoic reef builders. We also see the extinction of extravagant groups having evolved only during the Permian. Among them are the Alaticonchia, a group of thick-shelled and giant bivalves that reached almost 2 m in size (Hamish Campbell, personal communication, 1995). Their shapes and fibrous shell structures suggest that they housed photosymbiotic algae like the rudists of Cretaceous times and the giant cockle Tridacna of the present. In the deposits of warm shallow seas in Southeast Asia Alaticonchia are locally the dominant kinds of fossils.

Another example are derived groups of productid brachiopods. While standard productids are recliners with a highly convex and often spiny ventral, and a slightly concave dorsal, valve; richthofeniids and lyttoniids modified this shell shape by first attaching their ventral valves by cementation to hard substrates. From such a starting point, the richthofeniidds and a few other groups switched to a "coralliform" elevator growth of the ventral valve, while the lid valve became completely flat and deeply sunk into the ventral one in *Richthofenia*. Lyttoniids, in contrast, transformed the dorsal valve into a digitate structure that fits snugly into a corresponding ridge pattern on the inside of the lower valve. Since both valves of *Leptodus* participated in the elevator growth in a reef environment, muscular opening and closing of the long valves became a problem. It was solved by the introduction of an openig ligament near the umbo—a structure of which all other brachiopods were deprived. That this design was successful is shown by the related genus *Oldhamia*, which secondarily invaded soft bottoms by transforming the shell into a deep bowl rather than the elongate tongue of the reel-dwelling *Leptodus*.

In summary, the Permian fauna again shows the evolutionary consequence of a climatically "golden age" that followed the Permo-Carboniferous ice age and allowed evolution to proceed in various groups beyond usual standards. But the higher levels of specialization also increased vulnerability towards environmental perturbations of any kind.

The Extinction at the End of the Proterozoic

The most profound break in the fossil record happened at the beginning of the Cambrian period, about 540 million years ago. It is marked by the "sudden" appearance of most animal phyla living today. Therefore this boundary has been chosen to mark not only the beginning of the Paleozoic Era, but also of the Phanerozoic Eon, which lasts until today. For a long time, this boundary has been a paleontological dead end. Older rocks are in most parts of the world crystalline "basement" without the hope to find any fossils. But even when non-metamorphosed sedimentary rocks of Precambrian age were discovered, they only rendered algal stromatolites and a variety of "Pseudofossils"—forms that have the appearance of organisms, but are formed by physical processes.

This situation changed with the discovery of the "Ediacaran fossils". They were first found in Namibia, then in Australia (where they received their name from a locality in the Flinders Ranges north of Adelaide) and are now known from more than 30 localities all over the globe. Ediacaran fossils are preserved as mere impressions. Nevertheless, their regular shapes and sculptures leave no doubt that we deal not with pseudofossils, but with the remains of true, yet soft bodied, organisms of considerable size and complex morphologies. All occurrences correspond to the latest, Vendian, phase of the Proterozoic, 600 to 540 million years ago.

It is a consequence of the research history that Precambrian paleontology proceeded, like Precambrian stratigraphy, by pushing the dead end of the fossil record back beyond the base of the Cambrian. This rearward perspective is also expressed in the original interpretation of the Ediacaran fossils: because the Precambrian evolutionary "explosion" of skeleton-bearing animals could not have taken place without predecessors, one considered the Ediacaran organisms as the soft-bodied ancestors of later animal phyla, which their shapes happened to resemble (Glaessner, 1984). Recently, this view has changed.

In spite of their morphological diversity, the Ediacaran fossils share the preservation as mere impressions in sandy sediments, in which soft-part preservation is unknown from later periods. Closer examination also showed that the similarities of Ediacaran fossils with worms, sea pens, jellyfish, arthropods and echinoderms are fortuitous and that these organisms could not have functioned like the animals to which they have been compared. One also fails to see organs, such as mouths or appendages. On the other hand, many of the Ediacaran organisms shared—across their morphological dissimilarity—a strange "quilted" structure. In this way the bodies became foliate with an highly incresed surface area. But quilting, in an either serial or fractal mode, had also the effect that the living material inside the outer skin became increasingly compartmentalized during growth. This principle is well known from larger foraminifera, in which it is the hard skeleton instead of a flexible skin that compartmentalizes the protoplasm inside. Foraminifera are unicellular organisms; but the protoplasm of the larger forms is syncytial, i.e. it contains many nuclei. Physiologically, subdivision of a multi-nucleate protoplasm by the shell wall has the same effect as multicellularity: the distance of the nuclei from the surface does not exceed a certain critical level.

It is because of this analogy that I consider most Ediacaran fossils as an extinct group of organisms (Vendobionta), unrelated to animals of later times. Even more: in spite of their considerable sizes (*Dickinsonia* gets almost a meter long and several decimeters wide, but only a few millimeters thick), these organisms were probably unicellular "dinosaurs"! In this view the Vendobionts solved the problem of reaching large body sizes without becoming multicellular. Metazoans, in contrast borrowed the process of cell division (which was also neccessary in Vendobionta for subdividing their protoplasm into spores during reproduction) for a building-block type of body construction. The metazoan alternative, of course, proved to be much more successful, because it allowed the differentiation into specialized tissues and organs that account for the great diversity of metazoan bauplans and modes of life.

If the Ediacaran organisms (which also comprise forms different from the quilted type, but no more similar to animals) were a failed experiment of evolution, the Cambrian Explosion looses some of its uniqueness: like the radiations in the early parts of the Mesozoic and Cenozoic it was preceded by a major extinction. This extinction seems to also fall after a climatically golden age: like the end-Paleozoic diversification took place after the Permo-Carboniferous ice age, the beginning of the Vendian is marked by the end of the last Proterozoic glaciation.

But where are the Precambrian roots of the true multicellular animals, from which the explosive evolution of skeletonized phyla at the beginning of the Cambrian originated? Here, another parallel emerges to what we observe in later evolutionary turnovers.

In addition to the Ediacaran body fossils, there is another kind of paleontological documents in clastic rocks of the Precambrian: trace fossils. In contrast to the immobile Vendobionta, which must in a way have lived like plants by absorbing their energy through the whole body surface, these traces attest for the presence of worm-like animals that actively burrowed through the sediment in search for particulate food. Their locomotion seems to have been peristaltic, like in earthworms. This suggests that they already had a coelomatic construction. By Vendian time, some of them had also aquired systematic search behaviors, such as meandering. This would have been impossible without a well developed central nervous system.

In Vendian sandstones, burrows are usually small and suggest that their worm-like makers browsed along the decaying zone underneath ubiquitous microbial biomats. But the trace fossil record of unquestionable bilaterian animals goes much farther back than Ediacaran body fossils. Recently, probable worm burrows have been discovered in sandstones of North-India that are more than 1.1 billion years old—double as old as the lowermost Cambrian!

If these discoveries substantiate, bilaterian animals have a much longer history than expected. But during the first half of their existance, or longer, they lived as a minority group—just like the mammals did in the shadow of the Mesozoic dinosaurs. Only after multicellular animals (metazoans) acquired hard skeletons, did bilaterian animals manage to raise to dominance and to transform the biosphere into a new state. In the new view the extinction of the strange Ediacaran biota does not require an extrinsic catastrophy, but resulted from evolution itself. Nevertheless the Cambrian revolution marks not only the replacement of old guilds by new ones, but the beginning of a world, in which evolution is driven by the "struggle for survival" and by the arm's race between predator and prey species. The peaceful "Garden of Ediacara" (McMenamin, 1986) ended 540 million years ago!

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生命史における大変革

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白亜紀末の大絶滅，二畳紀末の大絶滅そして原生代の大絶滅という 3 つの生命史の大事件には，共通のパターンが存在する．すなわち，これらの大絶滅は，気候が比較的長く安定した時期の後に起きており，またそこで絶滅した生物は，この安定期のある特定の環境に適応した特殊な形態やサイズを有する型の生物であった．これらの大事件の謎を解明するには，生命史が本質的に非線形過程であるという点を認識する必要がある．