

Climate Change as a Driving Force for Evolution

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With 1 Figure

Abstract

Since there has been life on earth it has had to “adapt” to a changing environment driven by physiochemical exterior factors, such as geodynamic processes, cosmic radiation, the chemical composition of the sea and atmosphere, sea level, plate tectonics, volcanic activity and meteorites, which together have had an impact on the global and local climate. Environmental change can progress slowly, allowing for evolution by sequential adaptation, or rapidly, leading to drastic changes of the current flora and fauna, so called bioevents. These bioevents have often been followed by disastrous mass extinctions, which, however, paved the way for new evolutionary inventions and for significant spreading and radiation of existing organisms. Examples of bioevent-causing major global extinction events are the Precambrian/Cambrian, Ordovician/Silurian, Frasnian/Famennian, Permian/Triassic, Triassic/Jurassic and the Cretaceous/Paleogene events, in each of which more than 70 % of all living species became extinct. But these extinctions gave rise to evolutionary transitions – abruptly occurring new blueprints – and allowed the bloom of pre-adapted but until then unimportant groups. The following article is intended to give a brief and greatly condensed overview of major climate-related extinction events (Fig. 1), and current hypotheses on their origins and impacts.

Zusammenfassung

Seitdem es Leben auf der Erde gibt, musste dieses sich an eine veränderliche Umwelt „anpassen“. Exogene physiochemische Faktoren, wie geodynamische Prozesse, kosmische Strahlung, chemische Zusammensetzung der Ozeane und der Atmosphäre, Meeresspiegel, Plattentektonik, Vulkanismus und Meteoriten, verändern die Umwelt und dadurch das globale und das lokale Klima. Umweltveränderungen können sich langsam vollziehen und so eine Evolution durch fortlaufende Anpassung bewirken oder sehr rasch und dann zu einem drastischen Wechsel der Flora und Fauna führen, einem sogenannten Bioevent. Die Ursache für solche Bioevents waren oft dramatische Massenaussterben, welche aber letztlich neue evolutionäre Erfindungen und die Ausbreitung und Radiation bereits existierender Organismen nach sich zogen. Beispiele für solche globalen MasseneXTinktionen sind das Präkambrium/Kambrium-, Ordovizium/Silur-, Frasn/Famenne-, Perm/Trias-, Trias/Jura- und das Kreide/Paläogen-Event. In all diesen sind jeweils über 70 % aller lebenden Arten ausgestorben, jedoch ermöglichten sie einerseits evolutionäre Wechsel – abrupt auftretende neue Baupläne – und andererseits das Aufblühen präadaptierter, aber bis dahin unbedeutender Gruppen. Dieser Artikel soll eine kurze und kondensierte Übersicht über die großen klimabedingten Massenaussterben und die derzeitigen Hypothesen zu deren Entstehen und deren Folgen geben.

1. Introduction

The central fundament of climate change is the carbon cycle, which itself is largely dependent on tectonic energy (BERNER 2003). Today, carbon is primarily stored in the biosphere – it is the major constituent of all organic matter –, but of course also as carbon dioxide (CO₂) in

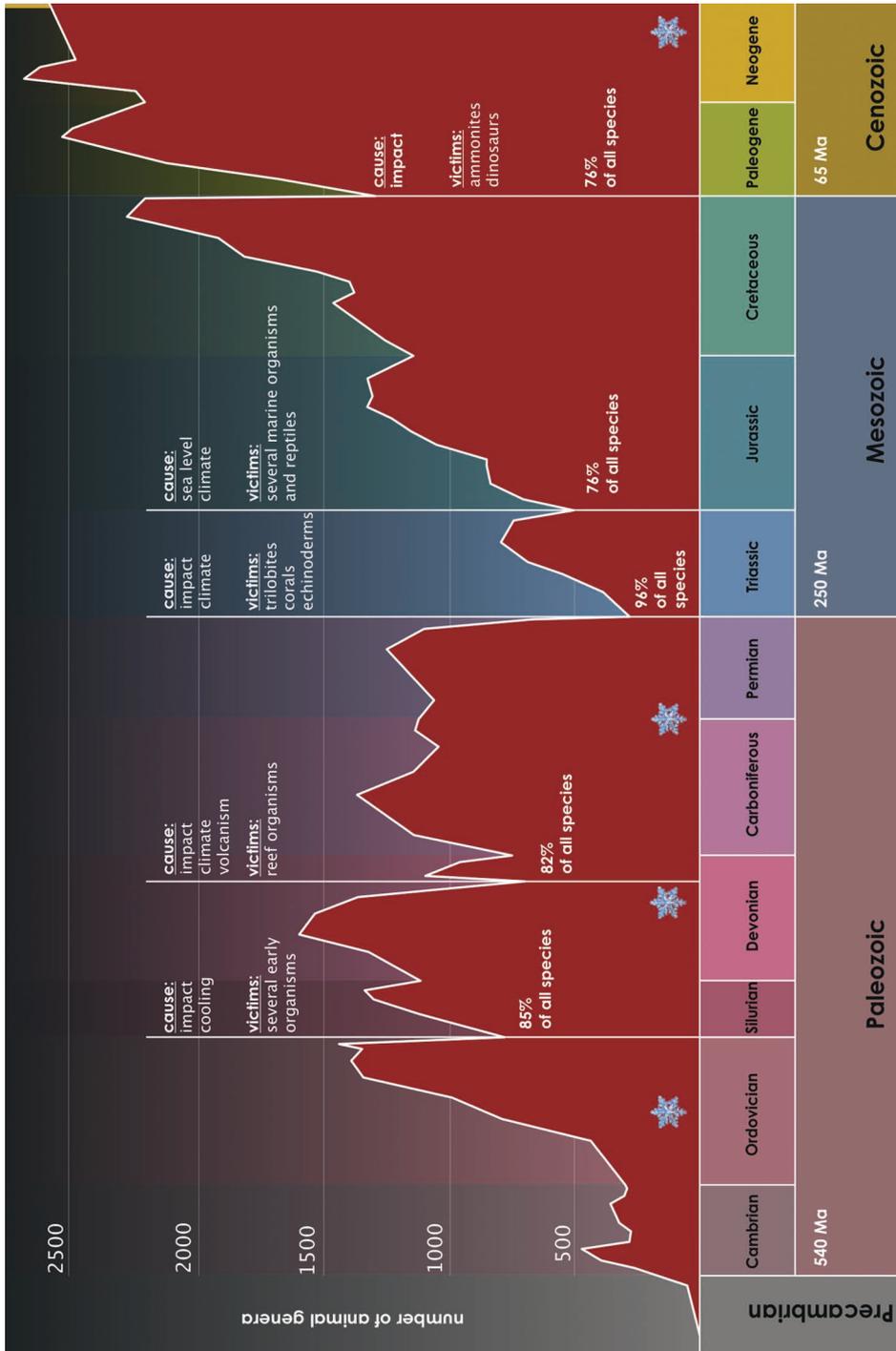


Fig. 1 Major impact events during evolution (modified after KROH and HARZHAUSER 2009)

the atmosphere¹, as dissolved atmospheric CO₂ in the hydrosphere, and as fossil fuels and sedimentary rocks (limestone, chalk etc.) in the lithosphere.

Organisms gain their CO₂ mostly from the atmosphere, either directly or dissolved in water. It enters the water by simple diffusion and then resides as CO₂ and converts into carbonate (CO₃⁻²) or bicarbonate (HCO₃⁻), respectively. The early earth had significantly higher levels of CO₂ in the atmosphere and it was the green-house effect of this CO₂ (in combination with CH₄) that finally provided moderate temperatures (from around -18 °C to +15 °C) in spite of an approximately 30 % weaker sun compared to today (TAJIKI 2003, PARIS et al. 2008 and references therein). This self-regulating carbon cycle has since then kept the Earth's global average temperature essentially constant, between +12 °C and +22 °C. The major driving forces for the cycle are tectonic movements leading to CO₂ release where plates drift apart and to carbonate metamorphism in the subduction zones (BERNER 2003). The melted crust contains carbon in the sediments and soils. Carbonate metamorphism finally results in the accumulation of magma and eventually volcanic eruptions, these being the source of atmospheric CO₂. High CO₂ levels in the atmosphere cause climate warming, which goes along with higher decomposition rates, bringing back the CO₂ and closing the cycle.

2. Pre-Conditions for Life

Besides carbon, all life on earth is dependent on water. The very early earth, however, most probably resembled a hot volcanic ball with no liquid water (temperatures >100 °C). A steady cooling and a slowly forming atmosphere eventually set the conditions for making life possible. Four and a half billion years ago (Gya) a large meteorite, Theia², is assumed to have hit the earth thereby splitting off the moon (HALLIDAY 2000, BELBRUNO and GOTT 2005). Then, around 4.1–3.8 Gya a rapid migration of the giant planets Jupiter and Saturn, and a short phase of close encounters between Saturn, Uranus and Neptune directed numerous comets at the earth (GOMES et al. 2005, BOTTKKE et al. 2007). According to a widely accepted hypothesis this so-called Late Heavy Bombardment led to a significant input of cosmic water, which – in addition to “homemade” volcanogenic water vapor – lay the foundation for large connected subaerial bodies of water (MOTTLE et al. 2007, JØRGENSEN et al. 2009).

The early water world was a reducing environment enabling the aggregation of small structural molecules. This period is termed the RNA World. RNA is characterized by not only self-replication, but also by catalytic, metabolic and coding capabilities. This paved the way for the synthesis of small peptides and nucleic acids utilizing reduced nitrogen (N) compounds (e.g. ammonia). It is likely that histidine (*his*) and other imidazole-containing compounds were present in this early environment and that simple peptides containing at least two imidazole groups acted as concerted acid-base catalysts. The most stable and still most abundant amino acids are glycine (GGC) and alanine (GCC). The formation of phospholipid bilayer membranes finally led to a compartmentalization of the continuously brewing “molecule soup”.

Among the early RNA, and later also DNA, molecules also selfish elements soon arose, first ribozymes incorporating themselves into other molecules (group I introns), later single

1 Presently >380 ppmv, the highest concentration for 650,000 years.

2 In Greek mythology the goddess Theia, daughter of Gaia, gave birth to the goddess of the moon, Selene.

strand and double strand RNA viruses, retrons and group II introns and finally DNA viruses and plasmids (KOONIN et al. 2006). This period, called the Virus World, was characterized by an extensive genetic exchange, such as horizontal gene transfer, recombination, fusion, fission and spread of mobile elements, altogether finally heralding the first arms race. Defense mechanisms became necessary, RNA interference (RNAi) as an early strategy to inactivate foreign RNA, and the “erection of walls” to generally keep foreign material out – the early compartments evolved into the first cells, covered with membranes, and in the case of bacteria even with cell walls. According to one of the many possible scenarios, two spin-offs of such small compartments “filled” with organic matter were evolutionary successful leading to the Archea and the Bacteria and an endosymbiotic event of an archeobacterium engulfing an eubacterium then gave rise to the first eukaryote, perhaps as soon as 2.7 Gya ago. However, the origin of life is still the subject of a most controversial debate. It is also possible – and many recent publications favor this hypothesis – that all three domains evolved at the same time, the so called biological big bang (BBB) (KOONIN 2007).

3. From Molecules to Cells

The last universal common ancestor (LUCA) is believed to have lived around 3.5 Gya and to have inhabited this system of compartments. Most probably LUCA was not the long believed hyper-thermophilic prokaryote³, but rather a community of protoeukaryotes with a RNA genome – possibly already surrounded by a “protonucleus” – living in a relatively broad but more moderate range of temperatures (GLANSDORFF et al. 2008). The RNA to DNA transition could have resulted independently for Bacteria and for Archaea/Eukarya from two “viral” invasions. Then both bacteria and archaeans would have emerged by reductive evolution, bacteria as the “non-thermophilic counterpart” to the archaeans, while the first eukaryote most probably was a mesophilic cell later adapting to the rising oxygen level by endosymbiosis (GLANSDORFF et al. 2008). One of the arguments corroborating the more or less synchronous evolution of Bacteria, Archaea and Eukarya is the histidine pathway. All three domains share a common gene fusion event in the *hisA* and *hisF* genes as the result of at least two elongation events followed by a paralogous gene duplication. However, in all three domains the *his* genes have since undergone major rearrangements in structure, organization, and order. Bacteria are assumed to have had at least two more gene fusion events, in *hisIE* and *hisNB*, and eukaryotes in *hisHF* and *hisIED* (FANI et al. 2007).

The very oldest indications of life – by chemotrophic evidence for autotrophy – derive from ~3.8 Gya old sediments in West Greenland (MOJZSIS et al. 1996). Early organisms may have lived in saline pools, and increasing oxygen toxification eventually promoted the evolution of photosynthesis, oxygenic photosynthesis evolving from anoxygenic photosynthesis (BJÖRN and GOVINDJEE 2008). As soon as sufficient oxygen had accumulated in the atmosphere, nitrification was outcompeted by de-nitrification, and a new stable electron “market” emerged. Photosynthesis and aerobic respiration ultimately spread via endosymbiotic events and massive lateral gene transfer to eukaryotic cells, allowing for the evolution of complex

3 The word prokaryote is epistemologically unsound, as the archaea and the bacteria do not seem to be a monophyletic group, and, moreover, nucleus-like structures with a double membrane and pores have been detected in representatives of the Planctomycetes (Domain: Eubacteria) (FUERST 2005).

organisms (FALKOWSKI and GODFREY 2008). The invention of oxygenic photosynthesis is credited to the cyanobacteria and subsequent extensive photosynthetic activity resulted in massive production of O₂. As photosynthetic organisms have a preference for light (¹²C) over heavy carbon (¹³C), a significant rise of ¹²C levels in sediment layers from 2.5 Gya is one of the strongest arguments for the origin of bacteria before this period (SCHIDLÓWSKI 2001, RASMUSSEN et al. 2008). Definitive fossil records for prokaryotes exist from around 1.9 Gya, from the Gunflint formation in Ontario, Canada (BARGHOORN and TYLER 1965).

The first indications of the existence of eukaryotes come from 2.8–2.5 billion years old sterane fossils in shale from Australia (BROCKS et al. 2003). Sterols, a cytoskeleton and an endomembrane are characteristic for eukaryotic cells. Moreover, eukaryotes “invented” an efficient intracellular transport system based on actin, myosin, tubulin, kinesin and dynein. With the further diversification of eukaryotic organisms, heterotrophy became the opposing strategy to autotrophy thereby establishing an early food chain. The permanent attack of mobile genetic elements probably quickly necessitated the development of the eukaryotic nucleus (possibly as an advancement over the “protonucleus” of LUCA) as a shelter for the genomic DNA. Early putative fossils include the ~1.85 billion year old large acritarchs from the Chuanlinggou Formation, China (PENG et al 2009) and the coiled alga-like *Grypania spiralis* (size: >1 cm!) found in North America, China and India (BUTTERFIELD 2009). Fossil proof is available from 1.7 Gya and from 1.4 Gya, both genera found, *Valeria* and *Tappania* (possibly a higher fungus), were already equipped with a nucleus (KNOLL et al. 2006). A recent study using continuous microfossil records inferred an early radiation of eukaryotes around 1.1 Gya (BERNEY and PAWŁOWSKI 2006). Among the oldest eukaryotic fossil material found are the testate amoebae, referred to as vase-shaped microfossils, and interestingly fossil isolates from 800–700 million years ago (Mya) are almost identical to today’s isolates. Examples are the species *Nebela penardiana* DEFLANDRE, 1936 and *Apodera vas* CERTES, 1889, the later being, although obviously populating the earth for almost 1 billion years, interestingly only found in the Southern hemisphere.

4. Sexual Reproduction and Multicellularity

One of the driving forces for eukaryotic diversification was the second formation of a supercontinent, called Rodinia, and the subsequent orogeny⁴ driven by tectonic movements (LI et al. 2008). Orogeny is generally followed by a cooling, as weathering is increased and atmospheric CO₂ is exhausted (GODDÉRIIS et al. 2007). These events were accompanied by significant changes in ocean chemistry and a rise of the atmospheric oxygen level (KUMAR et al. 2001, DONNADIEU et al. 2004). Within a relatively short period of time secondary endosymbiotic events occurred – the oldest record being the genus *Paleovancheris* from 1 Gya – eventually leading to the evolution of the 6 eukaryotic supergroups around 1.7–1.2 Gya: the Opisthokonta with the animals and the fungi, the Amoebozoa, the Archaeplastida, the Chromalveolata, the Rhizaria and the Excavata. Within the photosynthetic eukaryotes, secondary and also tertiary endosymbiotic events are very common (ARCHIBALD 2005). The diversification of the eukaryotes culminated in the Cambrian Explosion, the almost synchronic radiation of these 6

⁴ Large scale orogeny was not possible until 2.7 Gya, when the strength of the Earth’s mantle became sufficient to support high mountains.

eukaryotic supergroups, which also implicated the invention of sexual reproduction and multicellularity. Sexual reproduction became possible with rising communication between the cells, for which cell-cell adhesion was one of the crucial steps. Multicellularity, possibly triggered by sexual reproduction, evolved in at least 7 independent events, at least once in each of the supergroups and partly probably in the Proterozoic. Proof for multicellularity comes from 1.2 Gya fossils from the Hunting Formation, Canada (BUTTERFIELD 2001). *Bangiomorpha pubescens* BUTTERFIELD, 2000 is a multicellular plastid bearing red alga with sexual reproduction and 3 different types of cells. Multicellular organisms, typical in the Precambrian Ediacara fauna, not only allowed for a better exploitation of the environment and gain in size – and this was not insignificant in the early arms race – but can also protect their inner cells from the environment, giving them an evolutionary advantage in a changing environment, particularly with climate extremes. Favored blueprints and organisms after the Cambrian Explosion were the bilaterian animals and the green algae. Early records for the existence of animals are dated to around 630 Mya from the Doushantuo Formation in China (SHEN et al. 2008).

5. Major Extinctions and Bioevents

One of the possible triggers for the Cambrian Explosion might have been a geodynamic crisis, maybe a Slush Ball Earth (OLCOTT et al. 2005, MICHEELS and MONTENARI 2008), being the result of four (perhaps even five) discrete ice ages with intermittent episodes of heat within a relatively short period of time, between 720–600 Mya. This interval is characterized by an enrichment of ^{13}C in carbonates and organic matter (photosynthetic organisms having a preference for the light ^{12}C carbon), intercepted by unusually low rates of $\delta^{13}\text{C}$ indicating reduced green-house capacity and glaciation (KAUFMAN et al. 1997).

First, the break up of Rodinia, starting around 830 Mya, and a high sea level, led to high rates of organic carbon burial, and thus reduced the atmospheric green-house capacity. Increased rainfall took CO_2 out of the atmosphere thereby spurring the erosion of continental rocks. Massive flood basalt eruptions between 825–780 Mya in south China and in Canada caused a further decline of atmospheric CO_2 due to the rapid and CO_2 -consuming weathering (GODDÉRIIS et al. 2003, LI et al. 2008). This further reduced the CO_2 concentration in the atmosphere leading to a significant cooling and finally a glaciation possibly covering as much as 60% of the earth. Glaciation triggers further glaciation through the albedo effect, reflecting sun light and thus decreasing temperature, CO_2 levels then being less than 50% of the current values. At a certain stage, however, the process tips, the cold dry air caused the formation of deserts with almost no rainfall, so CO_2 released by volcanoes remained and accumulated in the atmosphere initiating a new green-house effect that eventually increased global temperature. The resulting deglaciation and rapid precipitation of calcium carbonate led to a decreasing oceanic carbon saturation and at the same time to an increasing O_2 level in the deep ocean. These higher O_2 concentrations brought elements acting as co-enzymes (Fe, Mo etc.) into solution and thus made N_2 fixation possible⁵, providing ammonium (NH_4) or nitrate (NO_3). The Cambrian explosion then, caused by significantly rising O_2 levels, resulted in an accelerated decomposition and more deposition into the ocean. At the same time the re-

5 All organisms depend on nitrogen, as an essential component of proteins and nucleic acids, however, in the form of N_2 gas it is almost inert, due to the triple bond.

sulting arms race between the more and more diverse and specialized organisms – for the first time there was a great variety of predators – also made carapaces and shells necessary, and the exoskeleton was invented. Apparently, evolutionary rates were highly accelerated after life's first, but almost fatal, bottle neck of Slush Ball Earth.

Around 440 Mya the Ordovician/Silurian Event, preceded by the Hirnantian glaciation, a resulting fall of the sea level and a subsequent deglaciation – with the elution of large amounts of nutrients into the sea (LAPORTE et al. 2009), algal bloom, reduction of O₂ levels and finally a toxification of the sea water –, caused a severe mass extinction among marine life, but at the same time paved the way for the first vertebrates and the first colonization of land. A gamma ray burst from a nearby supernova, destroying large parts of earth's atmosphere, is discussed as an additional trigger for this extinction event (MELOTT et al. 2004). The colonization of land was achieved synchronously by plants and arthropods. Early land plants were low, covered with wax as a strategy against desiccation and spread by wind (KENRICK and CRANE 1997). The first trees of the mid-Devonian dispersed to large forests during the Late Devonian (RETALLACK 1997) coinciding with the occurrence of the first wildfires (CRESSLER 2001). Animal life on land could only evolve “in the shade of plants”.

The Frasnian/Famennian or Kellwasser Event around 400 Mya, falling together with a sea-level height and global warming caused by submarine volcanic activity, was one of the biggest extinction events in earth history (PUJOL et al. 2006). It was preceded by an oceanic anoxic event⁶ and followed by a significant increase of oxygen levels. The spreading of continental vascular plants and the simultaneous enormously increased continental weatherability is a further factor causing a considerable increase of the burial of organic matter (GODDÉRIIS and JOACHIMSKI 2004). The subsequent cooling caused the collapse of the forests and a shut-down of the oxygen factory. Oxygen levels declined from around 25 % during Devonian times down to 10–15 % (WARD et al. 2006). Terrestrial metazoan life was severely hampered as reflected by the so-called Romer's Gap, a lack or scarceness of terrestrial vertebrate fossils in sediments from 360–345 Mya (WARD et al. 2006). This succession of crises, however, was followed by the second colonization of land and paved the way for the invention of active flight, for which high oxygen levels are necessary. With the second colonization of land, the era of insects and amphibians came. High O₂ levels, plenty of food and a lack of predators resulted in gigantism among early land arthropods (DUDLEY 2000).⁷ Orogeny was the cause for the first large fresh water biotopes and these again enabled a flourishing amphibian fauna. Towards the end of this period extremely high oxygen levels (>30 %) evoked auto-ignitions causing massive forest fires (e.g. UHL et al. 2004). This high oxygen level and a low CO₂ level, as revealed from stomata densities, allowed widespread Southern hemisphere glaciation (BEERLING 2002).

The scenario, however, changed distinctly during the Permian with the ongoing clustering of the continents into Pangea, coinciding with the establishment of a widespread dry continental climate (CHUMAKOV and ZHARKOV 2003). The Late Permian draught was the herald of the most dramatic extinction event, the Permian/Triassic Event, an extinction of > 90 % of all life and 96 % of all species. The trigger mechanisms are controversially discussed. Aside from the formation of the supercontinent, an asteroid impact (BECKER et al. 2001), increased volcanism (WIGNALL 2009) and the release of methane hydrates (KRULL and RETALLACK 2000)

6 Anoxia of the sea can be traced by black shale sedimentation.

7 The size of arthropods is limited by the exoskeleton and the open circulatory system with its relatively inefficient oxygen supply within the body.

may have amplified the catastrophe. The aridity exerted massive pressure on the amphibian world in favor of amniote-egg reptiles and thus paved the way for the origination of the mammals. The large land mass, also drove vertebrate evolution by allowing for an almost endless dispersal, colonization of all possible niches, and a long and efficient food chain with large carnivorous animals at the top. The endoskeleton was a significant advantage for gaining size and the amniote egg for a much higher offspring survival rate..

Certainly one of the most famous mass extinctions is the extinction of the dinosaurs, the Cretaceous/Paleogene Event (also often referred to as Cretaceous/Tertiary or C/T Event). In this period there was extensive volcanic activity causing environmental poisoning (GRACHEV et al. 2005, ZHAO et al. 2009) and a global warming followed by a drop of temperatures close to the Cretaceous/Paleogene boundary (WILF et al. 2002, RAVIZZA and PEUCKER-EHRENBRINK 2003). Then, around 65 Mya a large asteroid hit the earth resulting in the 40 km deep and 200–300 km wide Chicxulub Crater (its center lies near the coastal town of Puerto Chicxulub, Yucatan, Mexico) and a dramatic climate inter-linkage (KRING 2007). However, the extinction of the dinosaurs was the one big chance for the warm blooded animals, birds and also mammals, which now could fill the niches for large animals. The mammals with hair, a fatty layer under the skin, sweat glands and a four chambered heart had significant advantages over the reptiles in times of climate change. The dramatic climate change afflicted, however, also insects and induced new directions of evolution (ASPÖCK 1998).

In the mid-Miocene, tectonic movements resulted in the incremental closure of Tethys coinciding with the Mid-Miocene Climate optimum. Global mean surface water temperatures were about 3 °C warmer than present and atmospheric CO₂ concentrations rose to 460–580 ppmv (YOU et al. 2009). This warming resulted in speciation of terrestrial mammals and diversification of marine environments (BARNOSKY et al. 2003, HARZHAUSER and PILLER 2007). The subsequent cooling of surface waters and the expansion of the East-Antarctic ice-sheet approximately 14.2 Mya indicate the turning-point into the Middle Miocene Climate Transition (SHEVENELL et al. 2004). This trend was amplified by the uplift of Tibet between 40 and 26 Mya (DECELLES et al. 2007) which led to dramatically increased weathering rates and a drawdown of atmospheric CO₂ (GARZIONE 2008). Carbon fixation and water uptake is more efficient in C₄ than in C₃ plants when CO₂ levels and water supply are low, giving them an evolutionary advantage in the Late Miocene with declining rainfall. Most probably the C₄ pathway evolved independently in several plant groups. The global expansion of C₄ grasslands starting around 25 Mya – and the concerted evolution of ruminants, which now specialized on grass instead of fruits – has been attributed to this decrease in atmospheric CO₂ levels. In contrast, very recent studies suggest that continental aridity, seasonality of rainfall and increasing wind strength during the Late Miocene in association with frequent and intense wildfires caused the opening of landscapes and thereby favored the expansion of C₄ grasslands (TIPPLE and PAGANI 2007, OSBORNE 2008). In any case, the pre-adaptation of the digestive system coping with the changing diet was the reason for the enormous success of modern ruminants.

6. Hominisation

Finally, in the Late Miocene, hominids first appeared on the scene, probably triggered by a shrinkage of the rainforest and expansion of dry savannah and arid steppe which drove groups of primates out of the forest and onto their feet. Recent data suggest a pan-African

evolution of early hominids, with the oldest supposed hominid fossils from the period between 10–5 Mya (SCHRENK et al. 2004). The already bipedal australopithecines, an early lineage of the hominini, evolved around 5 Mya. According to isotopic records this was a period of a warm interglacial climate, with a temperature peak between 4–3.4 Mya. A climate shift around 2.5 Mya then was the driving force for more robust hominids, *Australopithecus africanus* and *A. garhi* became extinct and the genus *Homo* with *Homo rudolfensis*, *H. habilis*, *H. ergaster* and *H. erectus* arose, co-existing with the late australopithecines, *Australopithecus robustus* and *A. boisei*. The drop of the sea level due to the Northern hemisphere glaciation during this period probably was also the trigger for the migration out of Africa, first accomplished by *H. erectus*. Early fossil records exist from Java (1.9 Mya), Georgia (1.7 Mya) and Spain (1.4 Mya) (BULYGINA and CLOLS 2000, SCHRENK et al. 2004). Another dramatic climate shift with a Northern hemisphere glaciation around 1 Mya then promoted a more progressive group of hominids, the genus *Australopithecus* became extinct and finally *H. sapiens neanderthalensis* and *H. sapiens sapiens* populated the planet. The wandering humans, of course, also brought along their parasites, and the ability of humans to cope with almost any local climate – and to explore and to fill almost any niche – is probably also the reason why *H. sapiens sapiens* is the species harboring the highest number parasites (ASPÖCK and WALOCHNIK 2007).

Altogether, one can assume a biphasic evolution; rapid evolution – usually after an extinction event – characterized by extensive genetic exchange, followed by a slow radiation of “newly invented” blueprints mostly driven by natural selection. Both phenomena are intensively linked with climate change, and most probably these lines could not be written, if climate change had not had a significant impact on human evolution.

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