PALEOCLIMATOLOGY AND PALEOECOLOGY

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Contents

Summary

This chapter is intended to provide a synthesis of current questions about the links between paleoclimates, paleoenvironments, and life on our planet throughout the geological time. An attempt is made to cover some milestones on the journey of evolution based on some corner-stone or "classical" publications in the respective

sections. The latest trends are referred to some of the most recent relevant publications, to enable the reader to explore further the several issues outlined here.

1. Prelude: Aim and Scope of the Chapter

Our aim is not to provide the reader with an exhaustive document, but to offer a synthesis of ongoing questions about the links between paleoclimates, paleoenvironments, and life throughout geological time. Regarding the enormous bibliographic resources, choices had to be made whether to deal or not to deal with specific periods and subjects. Attempts were made to cite the corner-stone or “classical” papers for each of the sections and sub-sections, as well as the most recent relevant publications (up to 2012), so that the reader can refer easily to them and explore further the several debates and issues depicted here.

2. Concepts and History

2.1. Basic Definitions

Paleoecology and paleoclimatology are derived from climatology and ecology, and one can approach the definition of the former by first defining the latter. Ecology can be defined as the study of interactions of organisms with one another and with their environment. Thus paleoecology refers to the study of these interactions in the geological past. Climatology is obviously the study of climate. However, as noted by McGuffie & Henderson-Sellers in 2005, it is difficult to describe *climate* with a single satisfactory definition. These authors suggest that climate can be defined as “*all of the statistics describing the atmosphere and ocean determined over an agreed time interval, computed for the globe or possibly for a selected region*”. Thus climatology can be viewed as the study of physical processes that explain mean states of the ocean-atmospheric system, typically 30-year averages of meteorological variables such as temperature or precipitation or wind fields. Climate can also be defined as a system comprising physical compartments (atmosphere, oceans, cryosphere and vegetation) interacting and influencing each other. As the study of ancient climates, paleoclimatology aims at describing and understanding these interactions in the past, prior to the period of instrumental measurements.

The time dimension makes paleoecology and paleoclimatology very distinct from ecology and climatology, respectively. Ecologists and climatologists deal with processes and mechanisms taking place during intervals of several years or decades at most, whereas this information is almost never available in the fossil and paleoclimatic records. Typically paleoclimatology can cover abrupt cooling events occurring 40,000 years ago as well as long-term trends of climate variables at the million-year timescale.

2.2. Early Links between Paleoclimatology and Paleoecology and General Context

Until recent connections that are mostly due to the impact of human-induced climate change on ecosystems, climatology and ecology have been two major scientific fields almost totally disconnected. The study of climate has been the world of physicians and applied mathematicians, while ecology was mostly done by biologists and statisticians.

Interestingly, this assertion turns out to be wrong for their "*paleo*" counterparts. Paleoclimatology was initiated first by scientists wishing to understand the environments in which ancient life now found in fossils, had evolved, and has been intimately linked to paleoecology, the study of relationships between past animals and plants and their surroundings.

The roots of the sciences of paleoclimatology are clearly linked to those of paleoecology and belong to the late seventeenth and early eighteenth centuries. Giving an exhaustive list of the early scientists who published about past life and climates is out of the scope of this chapter; readers should refer to either modern or ancient syntheses to grasp the extraordinary dynamics of these scientific fields at that time. Here we will cite a few names of scientists who added stepping-stones to these disciplines. In his famous "*Principles of Geology*" Charles Lyell (1797-1875) dedicates a whole chapter ("*History of the progress of Geology*") to previous works on geology, citing numerous scientists and explorers who had contributed to the field. Although the terms did not exist yet, several scientists cited by Lyell in this chapter had been actually dealing with paleoclimatology and paleoecology issues *at the same time*. Among them, Lyell acknowledges the work of Robert Hooke (1635-1703), a "great mathematician and natural philosopher". Hooke had observed giant ammonites and turtles in the Jurassic of England and suggested that "*England once lay under the sea within the torrid zone*" and explained this phenomenon by speculating about "*a shifting in the Earth's centre of gravity*". In the same chapter, Lyell describes also the work of Buffon (1707-1788) who had depicted his theoretical views about a former hotter Earth, the crucial roles of rivers and who, like several contemporaneous scientists, had to make an official revision of his "Theory of the Earth" as it was "*reprehensible, and contrary to the creed of the church*". Lyell himself dealt a lot with paleoclimatology and paleoecology, and the relationship between ancient climates and ancient flora and fauna is the center of several of his "*Principles*" chapters. In "*Doctrine of the discordance of the ancient and modern causes of change controverted*", Lyell illustrates the connection between fossil ecosystems differing from the present ones and hypotheses about changing climate. The interest of Lyell for paleoclimate and paleoecology is clearly linked to his uniformitarism theory, which considers that the same geological processes that operate today also operated in the distant past (" *the present is the key to the past* "). To him, the driving mechanisms of climate change were linked to continuous changes in the distribution of land and sea. In turn, the variations of species distribution through time were due to these changing climatic and geographical conditions, and not any catastrophic event, as Lyell rejected Cuvier's ideas on catastrophic mass extinctions occurring episodically.

Nowadays, the links between paleoecology and paleoclimatology are also interesting regarding macro-evolutionary processes. There are two views of evolution that mostly depend on the scale at which evolutionary processes are studied. The Red Queen model refers to Lewis Caroll's Through the Looking-Glass, in which Alice encounters the Red Queen who has this statement: "*It takes all the running you can do, to keep in the same place.*". The Red Queen hypothesis suggests that continuing adaptation is needed in order for a species to maintain its relative fitness amongst other species. It originates in Darwin's theory and was popularized by Leigh van Valen, who stated that species diversity is a response of biotic interactions and pressures, especially competition, and is based mostly on short time spans and local scales. Conversely, the Court Jester model, based on large and long-scale patterns, proposes that speciation and extinction occur only rarely, "*except in response to unpredictable changes in the physical environment, recalling the capricious behavior of the licensed fool of Medieval times* ", as stated by Benton in 2009. As a consequence, it is crucial to gather long-term paleoecological information (fossils, phylogenies) as well as having constraints on the geological-scale evolution of abiotic factors, namely climate and tectonics.

3. Precambrian: Changing Climates of Early Ecosystems

3.1. Hadean-Archean (4.6–2.5 Ga)

In 2004, E. Bard wrote, in order to illustrate the lack of knowledge of Quaternary glaciations during the 18th century, that it "*was, at that time, about equivalent to our present-day knowledge of Precambrian climatic fluctuations.* ". Conversely, this statement summarizes our rather poor understanding of the first 4 billion-years (Ga) of Earth's climate history. However, numerous geological and geochemical records, as well as recent climate modeling works and phylogenetics, have shed new light on early life and climate on Earth.

We do not know of any rocks that have witnessed the first 500 Ma of Earth's history, but techniques developed in the 1980s allow identifying and dating detrital zircon crystals, which are found in meta-sedimentary rocks from western Australia. Latest discoveries are zircons from the Jack Hills region with an age of 4.4 Ga. The fractionation between two stable isotopes of the oxygen (^{16}O and ^{18}O), noted $\delta^{18}O$, can be measured on these crystals and compared to the primitive ratios of the Earth's mantle. $\delta^{18}O$ values are rather high, which indicates low-temperature interaction between the rocks that contained the Zircons and water at the surface of the Earth. This ultimately indicates that liquid water was present on early Earth and that, unlike what the "Hadean" term suggests, temperatures were not "hell-like" at that time, but rather cool. Such findings make plausible, but still conjectural, the hypothesis of a very early life between 4.4 and 4.0 Ga. No fossil record exists for these hypothetical early ecosystems as no rocks are preserved from that time. Furthermore, the organisms that may have inhabited these ecosystems have presumably left no descendants, as they would have been wiped out by the Late Heavy Bombardment that struck Earth, vaporized its oceans, and cratered the moon at 3.9 Ga.

The earliest evidence for life on Earth is indirect, as it comes from a typically low carbon isotope ratio ($\delta^{13}C$) recorded in turbiditic and pelagic sedimentary rocks of the Isua terrane (fragment of crustal material), west Greenland. These rocks are dated at 3.7-3.9 Ga. The $\delta^{13}C$ signature in the reduced carbon of these rocks is inferred to be related to biological pathways, and then to be a fingerprint of early life. Direct fossil evidence for early life comes from stromatolites. Although often debated, the biogenicity of these structures is more and more constrained. The earliest stromatolites are found in the Dresser formation, Australia, and are dated at ca. 3.5 Ga.

Views about climate at that time are contradictory. Oxygen isotopes ratios from cherts, a rock in which silica precipitates directly from fluid, from Barbeton, South Africa, have first suggested hot surface temperatures of 70±15°C. These estimates have been widely contradicted by geological materials indicating moderate to cool temperatures from 3.5 to 3 Ga. New measurements combining $\delta^{18}O$ et δD suggest that Archean ocean temperatures ranged between 26 and 35°C, values close to present-day and more consistent with geological indicators. Other clues suggest a cool climate on Earth by 2.9 Ga. Breccias found in Zimbabwe and diamictites from South Africa have been inferred to be from glacial origins, evoking a possible ice age at that time. However there is no evidence for glaciations in the following 400 million-years, which suggests a rather warm late Archean. As the Sun is estimated to have been 20 % less luminous than the present in Archean times, these observations of a temperate Earth led to the “Faint Sun Paradox”, as one needed to reconcile very low energy coming from outer space with present-day-like temperatures. This paradox has been partly explained by studying the greenhouse gases balance of the Archean. It is now widely admitted that methane (CH_4), produced by volcanic activity and biological activity (early methanogen archeabacteria), played a pivotal role in warming Earth’s early atmosphere. In an anoxic atmosphere such as the one of the Archean, methane lifetime was 1000 times longer than today, allowing this gas to increase the greenhouse effect and warm the atmosphere.

3.2. The Proterozoic (2.5-0.54 Ga): Global glaciations, warm climates and rise of atmospheric O_2

The long Proterozoic eon is characterized by two periods of widespread glaciations separated by a long, supposedly ice-free, equable climate period. Contrary to the Archean, evidence (diamictites and dropstones) for these glaciations is abundant and found on different continents (Western Australia, North America, South Africa and NW Europe).

The first period of Proterozoic glaciations occurs during the Paleoproterozoic, precisely during the Huronian, between 2.45 and 2.2 Ga, with three successive glaciations, culminating with the Makganyene glaciation, considered as a “snowball-Earth event” as it involves a totally ice-covered Earth. Evidence comes from glaciogenic rocks found in a thick sedimentary succession close to Lake Huron, Ontario, South Canada. The Huronian glaciations correlate with a period of massive increase in O_2 in the atmosphere called the Great Oxidation Event (GOE), dated at 2.4 Ga. The rise of O_2 would have strongly shortened the lifetime of methane in the atmosphere, leading to its collapse and thereby cooling the atmosphere and triggering glaciation. The 300 million-year lag between earliest evidence of the start of biogenic O_2 producing and the GOE is still a matter of debate. Some scientists suggest that the release of oxygen-consuming gases by volcanic activity decreased at 2.4 Ga, allowing atmospheric O_2 to rise. Others invoke a complex balance with atmospheric CH_4.

Atmospheric O_2 rise is considered to result from O_2-producing photosynthetic activity of cyanobacteria , but the exact time of origin of the latter is still highly debated. Some authors suggest cyanobacteria evolved before the Makganyene snowball whereas others infer that they postdate the Archean.

Huronian glaciations have been followed by a long period of equable climate, for which no evidence for any glaciation has been found. Authors suggest that, at ca. 2.1 Ga, O_2 peaked at values between 0.02 and 0.04 atm, and was maintained at these levels until 0.8 Ga. This period was sometimes called the ‘boring billion’, as the global ocean was supposed to have been mildly oxygenated and no major climate event occurred. Conversely, on a paleoecological point of view, the 2-0.8 Ga interval is far from being a “boring billion”. The oldest fossil eukaryote, *Grypania spiralis*, is dated at 2.2 Ga (see Chapters 3 & 4) while the earliest putative (although controversial) multicellular life, as suggested by fossils recently found in Gabon by Albani, has been dated at 2.1 Ga.

Constraining O_2 concentration in the atmosphere and in the ocean is a major challenge to understand Proterozoic climate changes. This can at least partly be done using Banded Iron Formations (BIFs). BIFs result from the gradual oxidation of Fe^{2+} gathered in the ocean during the Archean. Their frequency through time is typically interpreted as a response to variations of O_2, and their absence after 1.8 Ga was long viewed as the evidence of total oxidation of the deep oceans, which prevented the persistence of dissolved Fe. This view changed in 1998, when Canfield suggested that increased oxygen levels favored higher concentrations of seawater sulfate and subsequent sulfate production *via* sulfate reduction, ultimately turning Fe-containing oceans into sulfidic oceans. According to this author, aerobic deep-ocean waters did not expand until the Neoproterozoic, and atmospheric O_2 concentrations remained in the range of 5% to 18% PAL during the Proterozoic.

But the most striking pre-Cambrian period in terms of tectonics, paleoclimate and paleoecological fluctuations is definitely the Neoproterozoic. The Neoproterozoic (1 Ga- 542 Ma) encompasses the most intense orogenic activity in the history of the Earth, with the long (> 250 Ma) break-up of the Rodinia supercontinent, also called Paleo-Pangea (Fig. 1). Three major glacial episodes, separated by warm periods, have been recorded during the Neoproterozoic: the Sturtian (750-670 Ma), Marinoan (635 Ma), and Gaskiers (584-582 Ma) glaciations. These three glaciations were evidenced by geological materials including marine diamictites, striated pavements, and laminated mudstone with dropstones. The Sturtian and Marinoan glaciations are considered to be snowball-Earth events. The carbon isotopic fractionation ($\delta^{13}C$) measured in carbonates lying beneath and above the glacial deposits of these glaciations depicts strong fluctuations in the carbon cycle. Modeling studies have suggested that changes in paleogeography, involving the fractionation of the supercontinent Rodinia, would have enhanced the silicate weathering which is a sink for atmospheric carbon. Higher weathering rates would have in turn strongly decreased the atmospheric pCO_2, explaining the global glaciations. Indeed, at geological timescales pCO_2 values result from a sharp balance (paleothermostat) between the sources (mostly volcanic degassing) and the sinks (CO_2 consumption through silicate weathering and organic carbon burial). A recent study has interpreted the high values of $\delta^{13}C$ recorded in preglacial deposits as indicating an enhanced export of organic matter from the upper ocean into anoxic subsurface waters and sediments. This export, which would in turn lead to lower atmospheric pCO_2 and enhance the ice ages, may be linked to the diversification of marine eukaryotes. Conversely, the drop of $\delta^{13}C$ after each glaciation has been interpreted as a lowering of organic activity, and a “near extirpation of life” during the Snowball Earth events. However this interpretation, as well as the whole concept of fully ice-covered Earth, is still a matter of debate, as many life forms happened to survive through these glaciations and radiate afterwards. Indeed these events have likely played both negative and positive roles on the evolution of life. On the one hand, glacial conditions over the whole planet may have led to some extinctions, but on the other hand, biological diversification may have been favored by the opening of immense ecological niches that occurred when Earth escaped from snowball events. This latter mechanism, along with the deep-ocean oxygenation after the Glaskiers glaciations, likely explains the rise of the Ediacara fauna (Ediacaran radiation), the first architecturally complex life form, which occurred 575 Ma ago.

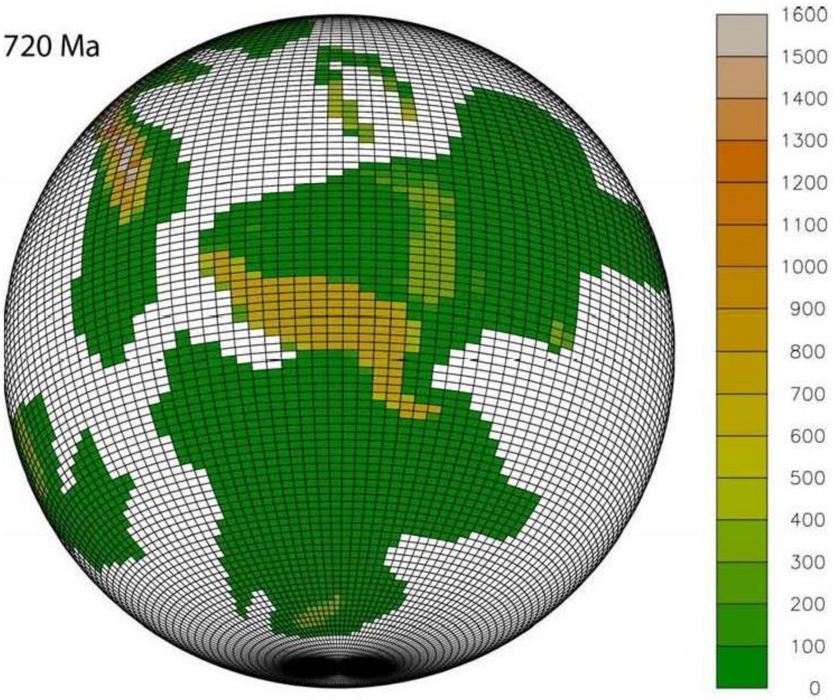

Figure 1. Continental configuration and hypothesized paleoaltitude reconstructed for the Neoproterozoic, 720 million-years ago, and projected on the grid of the FOAM climate model.

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Bibliography

References

1. Albani, A. E., S. Bengtson, et al. (2010). "Large colonial organisms with coordinated growth in oxygenated environments 2.1[thinsp]Gyr ago." *Nature* 466(7302): 100-104. [Description of the oldest putative multi-cellular organisms.]

2. Algeo, T. J. and S. E. Scheckler (1998). "Terrestrial-marine teleconnections in the Devonian: links between the evolution of land plants, weathering processes, and marine anoxic events." *Phil. Trans. R. Soc. Lond*. B 353: 113-130. [Paper describing the possible links between geological processes, environmental change, and the evolution of land plants.]

3. Alvarez, L. W., W. Alvarez, et al. (1980). "Extraterrestrial cause for the Cretaceous-Tertiary extinction." *Science* 208(4448): 1095-1108. [The first paper on the Iridium anomaly, the extraterrestrial impact and the K/T extinction]

4. Barnosky, A. D., N. Matzke, et al. (2011). "Has the Earth/'s sixth mass extinction already arrived?" *Nature* 471(7336): 51-57.[A comparison of fossil record and modern data that evaluates the ongoing extinction rates as abnormally high, highlighting the need for effective conservation measures]

5. Benton, M. J. (2009). "The Red Queen and the Court Jester: species diversity and the role of biotic and abiotic factors through time." *Science* 323(5915): 728-732.[This synthesis paper presents the two classical views of evolution and how they interact.]

6. Brunet, M., F. Guy, et al. (2002). "A new hominid from the Upper Miocene of Chad, Central Africa." *Nature* 418(6894): 145-151.[This paper describes the fossil of Tumaï, the earliest hominid known from Africa.]

7. Courtillot, V. and F. d. r. Fluteau (2010). "Cretaceous Extinctions: The Volcanic Hypothesis." *Science* 328(5981): 973-974.[This paper stresses the impact of the Deccan Traps on the Earth system, and its contemporaneity with the K/T extinction, suggesting that it could be the ultimate trigger.]

8. DeConto, R. M. and D. Pollard (2003). "Rapid Cenozoic glaciation of Antarctica induced by declining atmospheric CO2." *Nature* 421(6920): 245-249. [Through numerical modeling, this paper shows that the atmospheric CO2 was the most important factor triggering the onset of Eocene-Oligocene glaciation.]

9. Edwards, E. J., C. P. Osborne, et al. (2010). "The origins of C4 grasslands: integrating evolutionary and ecosystem science." *Science* 328(5978): 587-591.[This paper reviews fossil and genetic data about the latest vegetation transition, namely the rise of C4 plants.]

10. Kasting, J. F. and S. Ono (2006). "Palaeoclimates: the first two billion years." *Philosophical Transactions of the Royal Society* B: *Biological Sciences* 361(1470): 917-929.[A synthesis of knowledge of Earth's early climates.]

11. Kerr, R. A. (2005). "The Story of O2." *Science* 308(5729): 1730-1732.[A review about O2 long-term evolution]

12. van Valen, L. (1973). "A new evolutionary law." *Evolutionary theory* 1: 1-30.[This is the "classic" paper formalizing evolutionary theory and presenting the "Red Queen" analogy.]

13. Zachos, J. C., M. Pagani, et al. (2001). "Trends, rhythms, and aberrations in global climate 65 Ma to present." *Science* 292: 686-693.[This study computes marine fossil data and isotopic measurements to reconstruct a long-term trend of Earth climate during the Cenozoic.]

Biographical Sketch

P. Sepulchre received the Agronomic Engineer degree from AgroParisTech in 2003. He also received a MSc. In Paleontology, Phylogeny, and Paleoenvironments from Université Montpellier II. In 2007, he obtained a PhD on paleoclimate modeling of Africa during the Miocene, supervised by Prof. Michel Brunet and Gilles Ramstein. PS was a postdoctoral fellow in Prof. Lisa Sloan's laboratory of climate modeling in UC Santa Cruz during one year and a half. In 2010, he was appointed as a permanent researcher by the CNRS, and has been based at Laboratoire des Sciences du Climat et de l'Environnement (LSCE), Gif-sur-Yvette, France. He is working at understanding the links between tectonics, climate and evolution at geological timescales. Most of his work focuses on the Neotropics and Africa during the Cenozoic.