

Cambrian explosion triggered by geosphere-biosphere feedbacks

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[1] A new hypothesis for the cause of the Cambrian explosion is presented. For that the evolution of the planet Earth is described by the co-evolution of the geosphere-biosphere system. Here we specify our previously published Earth system model for the long-term carbon cycle by introducing three different types of biosphere: procaryotes, eucaryotes, and complex multicellular life. They are characterized by different global temperature tolerance windows. The biotic enhancement of silicate weathering by complex multicellular life adds an additional feedback to the system and triggers the Cambrian explosion. The Cambrian explosion is characterized by a sudden increase of biomass and a rapid cooling, which amplified the spread of complex multicellular life. Cooling events in the Neoproterozoic, however, could force a premature appearance of complex multicellular life. *INDEX TERMS*: 0330 Atmospheric Composition and Structure: Geochemical cycles; 8125 Tectonophysics: Evolution of the Earth; 9699 Information Related to Geologic Time: General or miscellaneous; 3220 Mathematical Geophysics: Nonlinear dynamics; 0315 Atmospheric Composition and Structure: Biosphere/atmosphere interactions. **Citation**: von Bloh, W., C. Bounama, and S. Franck, Cambrian explosion triggered by geosphere-biosphere feedbacks, *Geophys. Res. Lett.*, 30(18), 1963, doi:10.1029/2003GL017928, 2003.

1. Introduction

[2] The Cambrian explosion is known as the Big Bang in biology. It began 542 million years ago and ended about 40 million years later. This period is characterized by the first appearance of abundant skeletonized metazoans, a sudden increase in biodiversity and the emergence of most modern lines. In the Vendian (0.56–0.54 Gyr ago) first animals with soft bodies appeared announcing the Cambrian explosion. Before the Vendian period life was microscopic, vegetative, and mainly procaryotic and eucaryotic.

[3] There is still a lot of speculation about what caused the Cambrian explosion and why it happened when it did after 3 billion years of potential evolutionary time. Its cause has been widely regarded as the foremost unresolved problem of paleontology [see, e.g., Zhuravlev and Riding, 2001] and even of astrobiology [Ward and Brownlee, 2000].

[4] The approaches that have been put forward to solve the puzzle of what triggered the explosion can be split into extrinsic (environmental) factors, intrinsic (biological) factors, or a mixture of both. Extrinsic factors are physical changes in the Precambrian environment. Among these changes are the breakup of the supercontinent Rodinia [see, e.g., Hoffman, 1999] and the Neoproterozoic glacia-

tions known as “snowball Earth” events [see, e.g., Schrag *et al.*, 2002]. The snowball Earth events and the continental breakup are associated with genetic isolation but also with a reorganization of oceanic flow patterns causing upwelling, with increasing primary production, and with a consequently higher atmospheric oxygen level [Zhuravlev and Riding, 2001]. Many authors have suggested rising atmospheric oxygen as a trigger of the Cambrian explosion [e.g., Nursall, 1959]. Intrinsic causes involve some mechanisms within the Precambrian biosphere itself, which enabled evolution and diversification to start. An example is the finding in developmental genetics that the mutation of just one hox gene in an ancestral metazoan could potentially initiate a large morphological change in the animal [Carroll, 1995].

[5] In the present paper we describe an extrinsic mechanism as a trigger of the Cambrian explosion. This mechanism is related to nonlinear geosphere-biosphere feedbacks. We show that gradual changes in environmental conditions, on passing a threshold, can cause abrupt changes in the composition of the biosphere and the state of the environment. To do this we apply our general model for the long-term co-evolution of the geosphere and the biosphere [Franck *et al.*, 2002]. Three different types of biosphere (procaryotes, eucaryotes, and complex multicellular life) have been incorporated. They differ in their environmental adaptation and additionally in their ability to increase life’s promotion of weathering over geologic time. Such a differentiation is in accordance with the concept of Schwartzman [1999] on the co-evolution of climate and life. Another question to be answered concerns the time interval in which the Cambrian explosion generally might have occurred. In this framework, we investigate the stability of the Earth system under environmental perturbations.

2. Model Description

[6] The global carbon cycle model of Franck *et al.* [2002] describes the evolution of the mass of carbon in the mantle, C_m , in the combined reservoir consisting of ocean and atmosphere, C_{o+a} , in the continental crust, C_c , in the ocean crust and floor, C_f , in the kerogen, C_{ker} , and in the different biospheres, $C_{bio,i}$ ($i = 1, \dots, n$), where n is the number of the distinct parameterized biosphere types. The equations for the efficiency of carbon transport between reservoirs take into account mantle de- and regassing, carbonate precipitation, carbonate accretion, evolution of continental biomass, the storage of dead organic matter, and weathering processes.

$$\begin{aligned} \frac{dC_{o+a}}{dt} = & \tau_f^{-1}(1-A)(1-R)C_f + S_A f_c d_m C_m / V_m + F_{\text{weath}} \\ & + (1-\gamma) \sum_{i=1}^n \tau_{\text{bio},i}^{-1} C_{\text{bio},i} + \tau_{\text{ker}}^{-1} - \sum_{i=1}^n \Pi_{\text{bio},i} \\ & - F_{\text{prec}} - F_{\text{hyd}} \end{aligned} \quad (2)$$

$$\frac{dC_c}{dt} = \tau_f^{-1} A C_f - F_{\text{weath}} \quad (3)$$

$$\frac{dC_f}{dt} = F_{\text{prec}} + F_{\text{hyd}} - \tau_f^{-1} C_f \quad (4)$$

$$\begin{aligned} \frac{dC_{\text{bio},1}}{dt} &= \Pi_{\text{bio},1} - \tau_{\text{bio},1}^{-1} C_{\text{bio},1} \\ &\vdots \end{aligned} \quad (5.1 \dots 5.n)$$

$$\frac{dC_{\text{bio},n}}{dt} = \Pi_{\text{bio},n} - \tau_{\text{bio},n}^{-1} C_{\text{bio},n}$$

$$\frac{dC_{\text{ker}}}{dt} = \gamma \sum_{i=1}^n \tau_{\text{bio},i}^{-1} C_{\text{bio},i} - \tau_{\text{ker}}^{-1} C_{\text{ker}} \quad (6)$$

The variable t is the time, τ_f the residence time of carbon in the seafloor, A the accretion ratio of carbon, R the regassing ratio, S_A the areal spreading rate, f_c the degassing fraction of carbon, d_m the melt generation depth, V_m the mantle volume, F_{weath} the weathering rate, F_{prec} the rate of carbonate precipitation, F_{hyd} the hydrothermal flux, γ the fraction of dead biomass transferred to the kerogen, $\tau_{\text{bio},i}$ the residence time of carbon in the type i biosphere, $\Pi_{\text{bio},i}$ the total productivity of the type i biosphere, and τ_{ker} is the residence time of carbon in the kerogen. The accretion ratio, A , is defined as the fraction of seafloor carbonates accreted to the continents to the total seafloor carbonates. The regassing ratio, R , is defined as the fraction of seafloor carbonates regassed into the mantle to the total subducting carbonates.

2.1. Parameterization of the Weathering Rates

[7] In the context of our basic model weathering is enhanced by the biosphere due to an increase of soil CO_2 partial pressure. This is valid only for vascular plants and corresponds to a rather weak functional dependence of the weathering rate on the biological productivity and underestimates the observed biotic amplification of weathering due to processes other than increased soil $p\text{CO}_2$. The total biotic amplification of weathering may even exceed a factor of 100 [Schwartzman, 1999]. Therefore, following Lenton and von Bloh [2001], we introduce an additional functional dependence of weathering on biological productivity by a factor β mediating the carbonate and silicate weathering rate, F_{weath}^c and F_{weath}^s , respectively:

$$F_{\text{weath}}^c = \beta (F_{\text{weath}}^{cc} + F_{\text{weath}}^{mc}), \quad (7)$$

$$F_{\text{weath}}^s = \beta (F_{\text{weath}}^{cs} + F_{\text{weath}}^{ms}), \quad (8)$$

where F_{weath}^{cc} denotes the weathering rate of CaCO_3 , F_{weath}^{mc} of MgCO_3 , F_{weath}^{cs} of CaSiO_3 , F_{weath}^{ms} of MgSiO_3 , and are parameterized according to Franck et al. [2002]. The

Table 1. Model Constants for the Three Different Biosphere Types: (1) Prokaryotes, (2) Eucaryotes, (3) Complex Multicellular Life

Biosphere type	$i = 1$	$i = 2$	$i = 3$
$T_{\min}$ (°C)	2	5	0
$T_{\max}$ (°C)	100	45	30
$\Pi_{\max}$ (Gt/yr)	20	20	20
$P_{\min}$ (10^{-6} bar)	10	10	10
$P_{1/2}$ (10^{-6} bar)	210.8	210.8	210.8
τ_{bio} (yr)	12.5	12.5	12.5
β	1	1	3.6

prefactor β reflects the biotic enhancement of weathering by the biosphere types, $i = 1, \dots, n$:

$$\beta = 1 - \sum_{i=1}^n \left(1 - \frac{1}{\beta_i}\right) \left(1 - \frac{\Pi_i}{\Pi_i^*}\right). \quad (9)$$

The factor β_i denotes the specific biotic amplification of weathering, Π_i the specific biological productivity, and Π_i^* the respective present-day value of biosphere type i . Following Berner [1997] the enhancement of weathering due to increasing soil $p\text{CO}_2$ by vascular land plants has been enabled at 350 Myr before present.

2.2. Parameterization of the Biological Productivity

[8] The photosynthesis-based biological productivity depends on the environmental parameters global surface temperature, T_s , and CO_2 atmospheric partial pressure, $p\text{CO}_2$:

$$\Pi_i = \Pi_{\max,i} f_{T_s,i}(T_s) f_{p\text{CO}_2,i}(p\text{CO}_2), \quad (10)$$

where $\Pi_{\max,i}$ is the maximum productivity of biosphere type i . The function describing the temperature dependence, $f_{T_s,i}$, is parameterized by a parabola:

$$\beta = 1 - \sum_{i=1}^n \left(1 - \frac{1}{\beta_i}\right) \left(1 - \frac{\Pi_i}{\Pi_i^*}\right) \quad (11)$$

and the function for the $p\text{CO}_2$ dependence is a Michaelis-Menten hyperbola:

$$f_{p\text{CO}_2,i}(p\text{CO}_2) = \frac{p\text{CO}_2 - p_{\min,i}}{p_{1/2,i} + p\text{CO}_2 - p_{\min,i}}. \quad (12)$$

$p_{\min,i}$ denotes the minimum CO_2 atmospheric partial pressure allowing photosynthesis of biosphere type i . $p_{1/2,i} + p_{\min,i}$ is the pressure resulting a productivity half its maximum value. The interval $[T_{\min,i} \dots T_{\max,i}]$ denotes the temperature tolerance window. It must be emphasized that this window is related to the mean global surface temperature. If the global surface temperature is inside this window a global abundance of biosphere type i is possible. The tolerance windows applied in this study are more restrictive than those given by other authors, e.g., Schwartzman [1999]. They define physiological tolerances for local temperatures of different organisms, which are 15°C to 20°C higher than our values given in Table 1. If the global surface temperature reaches the upper limit of this physiological

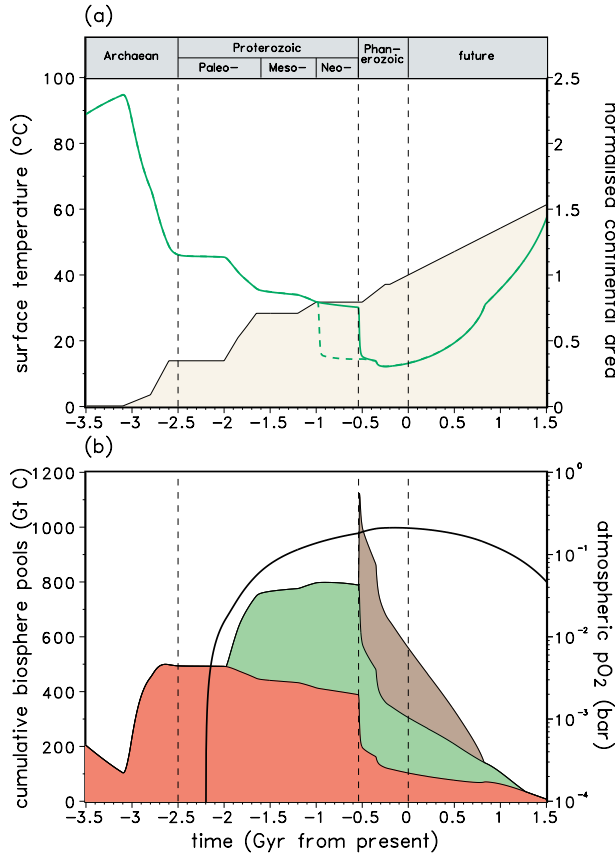


Figure 1. (a) Evolution of global surface temperature (solid green line). The green dashed line denotes a second possible evolutionary path triggered by a temperature perturbation in the Neoproterozoic era. The colored area indicates the evolution of the normalized continental area according to *Condie* [1990]. (b) Evolution of the cumulative biosphere pools for procaryotes (red), eucaryotes (green), and complex multicellular life (brown). The solid black curve denotes the evolution of atmospheric pO_2 .

tolerance, an emergence of a global abundant biosphere does not necessarily follow.

3. Results and Discussion

[9] The modified global carbon cycle model has been solved numerically for three biosphere types: procaryotes, eucaryotes, and complex multicellular life. The corresponding parameters for the biospheres are summarized in Table 1. All other parameters have been taken from *Franck et al.* [2002] for the favored model with spreading dependent hydrothermal flux and constant pH of the ocean. The biotic enhancement factor β_3 has been adjusted in such a way that complex multicellular life appears spontaneously first at -542 Myr. It must be mentioned that the first appearance of Ediacara 570 Myr ago might pre-date this event. Inferences from molecular phylogeny and problematic trace fossils suggest that metazoa emerged some 1 to 1.5 Gyr ago.

[10] In Figure 1 we have plotted in the upper graph the results for the evolution of the mean global surface temperature (solid green line) and in the lower graph the corresponding cumulative biosphere pools. The modeled

surface temperature curve is in good agreement with the ^{18}O chert thermometer [*Knauth and Lowe*, 2003]. According to their data, the ocean surface water has cooled from 70°C ($\pm 15^\circ C$) in the Archaean to the present value.

[11] From the Archaean to the future there always exists a procaryotic biosphere. 2 Gyr ago eucaryotic life first appears because the global surface temperature reaches the tolerance window for eucaryotes. This moment correlates with the onset of a rapid temperature drop caused by increasing continental area. The resulting increase in the weathering flux takes out CO_2 from the atmosphere. In contrast to the eucaryotes the first appearance of complex multicellular life starts with an explosive increase in biomass connected with a strong decrease in Cambrian global surface temperature at about 0.54 Gyr ago. The biological colonization of land surface by metaphyta and the consequent increase in silicate weathering rates caused a reduction in atmospheric CO_2 and planetary cooling. *Heckman et al.* [2001] have shown by protein sequence analysis that a first appearance of land plants at this time was already possible. According to *Logan et al.* [1995] metazoan faecal pellets supplied a new and important transport mechanism of organic carbon to the deep ocean. This provides an additional sink for CO_2 in the atmosphere-ocean system. After the Cambrian explosion there is a continuous decrease of biomass in all pools. At 0.35 Gyr ago there is a slight drop in all biomass pools connected with the rise of vascular plants. At present the biomass is almost equally distributed between the three pools.

[12] The evolution of the atmospheric partial pressure of oxygen, pO_2 , can be derived from the evolution of the kerogen pool, i.e., the long-term deposition of reduced organic carbon. According to *Rye and Holland* [1998] between about 2.2 and 2.0 Gyr ago there was a global oxidation event in which atmospheric pO_2 rose from <0.0008 bar to >0.002 bar. Under the assumption that before 2.2 Gyr all oxygen had been chemically bound we can make the following simple estimate:

$$pO_2(t) = pO_2^* \cdot \frac{C_{ker}(t) - C_{ker}(t = -2.2\text{Gyr})}{C_{ker}^* - C_{ker}(t = -2.2\text{Gyr})}, \quad (13)$$

where pO_2^* is the present atmospheric O_2 level and C_{ker}^* is the size of the present kerogen pool. The results for pO_2 shown in the lower graph of Figure 1 are in good agreement with data collected by *Lenton* [2003]. From the mid-Proterozoic onward there was sufficient atmospheric oxygen for the evolution of multi-cellularity and therefore, oxygen is not a limiting factor in our model.

[13] In order to show that the Cambrian explosion is driven by the nonlinear feedback between temperature-dependent productivity of complex multicellular life and their biotic enhancement of weathering we have performed a simulation without this feedback. This has been done by switching off the biotic enhancement of weathering by complex multicellular life. The results are shown in Figure 2. The red curves denote the complex multicellular life biomass (solid) and the corresponding global surface temperature (dashed dotted) in the case of a disabled weathering effect ($\beta \equiv 1 - 1/\beta_3$). Here biomass increases over a time interval of 300 Myr. For comparison the green curves show

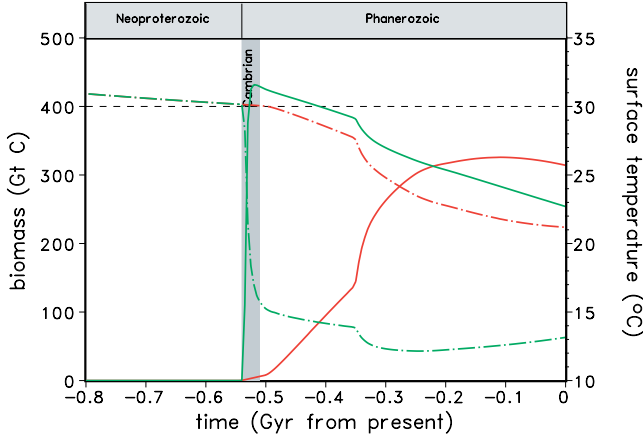


Figure 2. Evolution of the complex multicellular life biomass (solid lines) and the corresponding surface temperatures (dashed dotted lines). The green curves denote the results with enabled geosphere-biosphere feedback while the red curves denote the results for a disabled feedback. The horizontal dashed line indicates the upper temperature limit for the productivity of complex multicellular life ($T_{\max,3}$).

the results for an enabled geosphere-biosphere feedback. In contrast to the former results, the complex multicellular life biomass rises steeply within only 50 Myr in the Cambrian era. The temperature simultaneously drops to a value near to the optimum value of 15°C for complex multicellular life productivity. However, there is no evidence in the geologic record for such a cooling event but it cannot be dismissed. After the appearance of vascular plants 0.35 Gyr ago the surface temperature changes only slightly.

[14] In general, the Cambrian explosion is seen in the fossil record as a sudden increase in biodiversity where biodiversity is defined as the number of kinds of organisms within an ecologic unit [Sepkoski Jr., 1992]. Usually, an increase in biodiversity is connected with an increase of biomass and with changes in Earth's physical and chemical environment [Rothman, 2001]. As can be seen from Figure 2 both conditions are fulfilled. We find a rapid growth of biomass and a drastic change of environmental conditions in the Cambrian.

[15] Another important question is the timing of the Cambrian explosion, i.e., might it happened earlier? To examine this question, we performed a stability analysis of the Earth system model in the Proterozoic era. This was done by perturbing the system with artificial temperature drops, ΔT :

$$\Delta T(t) = \Delta T_p \cdot \exp\left(-\frac{(t - t_p)^2}{\sigma^2}\right), \quad (14)$$

where ΔT_p is the amplitude of the temperature perturbation at time t_p and σ determines its duration. We find that such perturbations can provoke a secondary stable solution. The second stable solution is shown in Figure 1a as a green dashed line for a perturbation of $\Delta T_p = -5^\circ\text{C}$ and $\sigma = 5$ Myr at $t_p = -1$ Gyr.

[16] In our model the timing of the first appearance of higher complex multicellular life depends on the value of the biotic enhancement factor, β_3 . In Figure 3 we have plotted the

time when complex multicellular life definitely appears and the time interval in which cooling events may trigger the first emergence prematurely. In the case of $\beta_3 = 3.6$ complex multicellular life could appear in principle at 1.7 Gyr ago. For realistic perturbations ($|\Delta T_p| < 5^\circ\text{C}$), however, this time interval is limited to the Neoproterozoic era. For $\beta_3 < 3.6$ complex multicellular life had to appear first before the Cambrian era. For $\beta_3 > 3.6$ a perturbation in environmental conditions is necessary to force the appearance of complex multicellular life in the Cambrian. For $\beta_3 > 16$ eucaryotes and complex multicellular life would appear simultaneously. Another important result is that for $\beta_3 > 6.38$ complex multicellular life cannot appear spontaneously but only due to cooling events, because the Earth surface temperature always remains above the upper temperature tolerance of 30°C for complex multicellular life.

[17] The results for β_3 depend on the applied continental growth model. In particular for a linear continental growth curve since -3.8 Gyr β_3 has to be slightly increased to 4.15 to fix the Cambrian explosion at -0.54 Gyr. Even for a model with substantial early continental growth with 60% of the present continental area 2.5 Gyr ago this value reaches only 4.4.

4. Conclusions

[18] The Cambrian explosion, i.e., the instantaneous increase of biomass, could have been triggered by nonlinear geosphere-biosphere interactions. The strength of these interactions can be described by the biotic enhancement factor of silicate weathering for complex multicellular life. In principle, there exist two stable model solutions for a certain interval of this biotic enhancement factor, one solution with and one without complex multicellular life. Cooling events can trigger a transition from one solution to the other. The

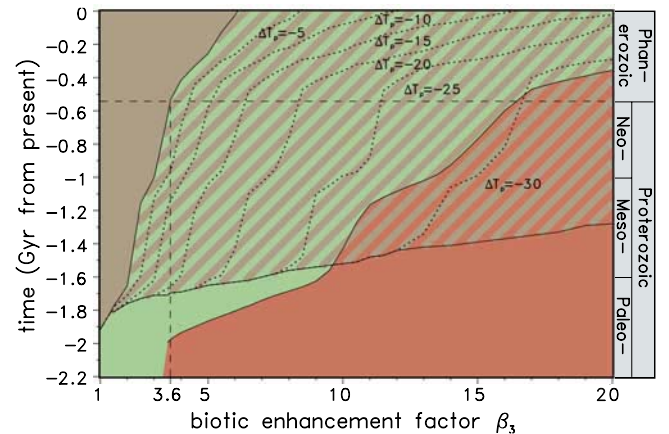


Figure 3. Stability diagram for the three types of biosphere as a function of the biotic enhancement factor, β_3 . In the red area only procaryotic life exists while in the green area eucaryotic and procaryotic life coexist. In the brown area complex multicellular life appears additionally. The dashed area indicates the time interval in which a cooling event may trigger the first emergence of complex multicellular life prematurely. The dotted lines denote the boundaries for certain amplitudes of temperature perturbations, ΔT_p .

Neoproterozoic snowball Earth events, e.g., could have initiated an earlier appearance of complex multicellular life. We have shown that the Cambrian explosion was mainly driven by extrinsic environmental causes, i.e., a gradual cooling of the Earth. The Cambrian explosion was so rapid because of a positive feedback between the spread of biosphere, increased silicate weathering, and a consequent cooling of the climate. The environment itself has been actively changed by the biosphere maintaining the temperature conditions for its existence. Therefore, our explanation of the Cambrian explosion is in line with the Gaia theory of the Earth as a self-regulating system [Lenton, 1998; Lovelock, 1995].

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