



## Did Surface Temperatures Constrain Microbial Evolution?

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# Did surface temperatures constrain microbial evolution?

**I**n what may prove a dramatic example of multiple discovery with major implications for the earth sciences and biology, scientists recently have proposed that some, if not all, ancient glacial deposits are really impact deposits, the material ejected by large impacts (Marshall and Oberbeck 1992, Oberbeck and Marshall 1992, Rampino 1992). The cited evidence includes the great volume of the deposits, thought inconsistent with a glaciomarine origin, and their incongruous association with indicators of warm climates. Evidently, even the classic evidence of glaciation—the polished and striated bedrock surfaces—can be produced by debris flows triggered by large impacts, because these features are associated with debris flows of nonglacial origin. Furthermore, Oberbeck et al. (1993) have calculated the areal extents and different depths of impact debris predicted by the impact rate over the last two billion years, and this curve reproduces the global area-depth data from the presumed glacial deposits.

The proposition that glaciation may not have occurred before the Cenozoic—albeit not yet a consensus position—nevertheless raises for reconsideration the surface temperature history of the earth. Glacial episodes, from the Huronian (2.3 billion years ago; BYA) through the late Paleozoic (320 to 250 million years ago; MYA) have been critical constraints on estimation of the upper bounds of temperature (Crowley 1983, Kasting and Toon 1989). Once removed, few if any constraints on the upper temperature limit other than life remain. Walker (1982) recognized that life provides an upper limit to tempera-

ture in the Precambrian. We propose a more radical concept: the upper temperature limit for viable growth of a given microbial group corresponds to the actual surface temperature at the time of the group's first appearance. In particular, we propose here that two major evolutionary developments—the emergence of cyanobacteria and aerobic eukaryotes—can be used to determine surface temperature in the Precambrian, and that only subsequent cooling mediated by higher plants and then angiosperms permitted what may possibly be the earth's first glaciation in the late Cenozoic.

The Huronian and late Precambrian (850–600 MYA) glaciations have been taken as evidence that the mean surface temperature on Earth hovered near 20°C through the Proterozoic, 20°C being the apparent upper temperature limit for glaciation to occur (Kasting and Toon 1989). For this reason, estimates of higher surface temperatures for the Precambrian, derived from the oxygen isotope record of coexisting cherts and phosphates (Karhu and Epstein 1986), ranging from 40 to 80°C (from 1.0 to 3.5 BYA), have been generally dismissed as being burial temperatures (i.e., surface equilibria reset by subsurface heating).

Kasting (1992) put it as follows in his contribution to the monumental survey of the Proterozoic, referring to the Karhu and Epstein study: "Unfortunately the temperatures inferred from the isotopic data exhibit no correlation with the climate history suggested by the glacial record. It therefore seems likely that the isotopic data reflect temperatures during diagenesis rather than during deposition" (p. 165). Although diagenesis may well have partially reset the surface system, we suggest that Karhu and Epstein's paleotemperatures should now be taken more seriously, because the assumed glacial record may be

spurious.

One other upper limit on surface temperature has been cited. From evidence for primary evaporitic gypsum precipitation, Walker (1982) provided a limit of 58°C for 3.5 BYA, because anhydrite is stable above that temperature in fresh water; in sea water the temperature is still lower. However, this constraint appears tenuous given the metastable precipitation of gypsum in nature and in laboratory experiments, above its stability field in place of anhydrite (Berner 1971, Gunatilaka 1990). Metastable precipitation of gypsum above its stability field may also undercut the claim that evidence of possible coexisting evaporitic gypsum and halite in the Proterozoic gives an upper temperature limit of 18°C (Walker 1982). When anhydrite does form from a gypsum precursor, it often inherits the gypsum crystal form, the very evidence (in the form of pseudomorphs or molds) that is cited for the 58 and 18°C temperature limits. If both the glaciation and gypsum-derived constraints are removed, then life itself may provide the best limits for the Precambrian.

The Archean is of particular interest, with cyanobacteria and the earliest aerobic eukaryotes (Eukarya with mitochondria) appearing at 3.5 BYA (Schopf 1992) and at 2.0–2.8 BYA (Chapman 1992, Knoll 1992) respectively. Anaerobic Eukarya may well have emerged even earlier (Sogin et al. 1989, Woese 1987). The thermophilic character of primitive microbes is apparently ancient, with the phylogeny of both eubacteria and archaebacteria consistent with their upper temperature limits (see Woese 1987).

In light of the above arguments in favor of a hotter Archean, we propose that the upper temperature limit for viable growth of both cyanobacteria (70–73°C) and eukaryotes (60–62°C; Brock 1978) corresponds to the sur-

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face temperatures at the time of the first appearance of each group, thus providing critical points on the surface temperature trajectory of the Archean. Further, with the emergence of eukaryotes in the late Archean or beginning of the Proterozoic, the upper temperature limit for the Proterozoic and some of the Phanerozoic is now 50–60°C, the upper temperature limit for eukaryotes, with additional constraints arising from the paleotemperature record of the Mesozoic and Cenozoic and the recent glaciations of the Cenozoic. If, indeed, no glaciations occurred until the Cenozoic then the lower temperature limit may be 20°C, the highest mean global temperature compatible with glaciation (Kasting and Toon 1989).

Regarding the temperature at the emergence of cyanobacteria, one piece of evidence does appear to directly support an estimate of 70°C or more at 3.5 BYA. It is the lack of fractionation of sulfur isotopes between coexisting sulfide and sulfates in sediments of that age. Knoll (1990) reviews possible explanations for this observation, concluding: “[P]erhaps almost all sulphate in pore fluids was reduced biologically to sulphide in an essentially closed system with little fractionation because of high ambient temperatures (70°C or more)—a theory for which the geological record provides little supporting evidence. A generally acceptable solution to this

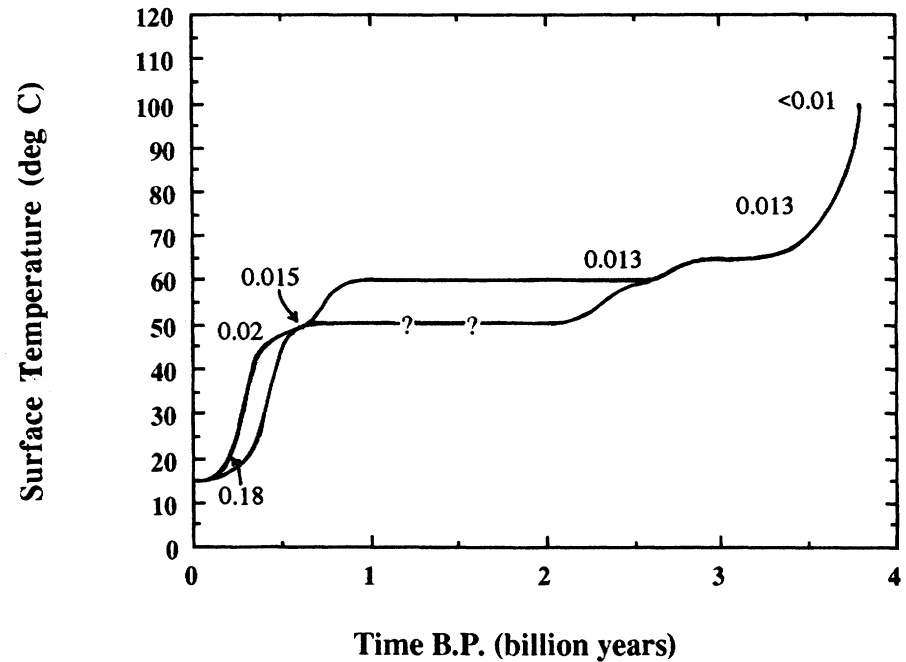


Figure 1. Proposed surface temperature of the earth as a function of time. The numbers on curves are the  $B_R$  values whose computation is described in Table 1.

problem has not yet been proposed” (p. 12). Other workers have similarly argued for high surface temperatures in the Archean (Ohmoto and Felder 1987).

If cyanobacteria emerged even earlier than 3.5 BYA, a possibility consistent with a now-absent or undiscovered sedimentary record, then 70°C would be an upper limit for 3.5 BYA rather than the actual surface tem-

perature. However, Knoll’s constraint is consistent with the emergence of cyanobacteria close to 3.5 BYA. Aerobic eukaryotes may have emerged in microenvironments with significant oxygen levels, such as cyanobacterial mats, before the rise of atmospheric oxygen. The occurrence of sparse Archean redbeds (2.0–2.1 BYA; Twist and Cheney 1986), indicators of local oxic conditions, is consistent with this

Table 1. Summary of scenario shown in Figure 1.

Age (BYA)	Global mean surface temperature (°C)*	Model $B_R$ †	Soil community (new land biota)
3.8–3.5	~100–70	<0.01–0.013	Extreme thermophiles
3.5–2.6‡	70–60	0.013	Cyanobacteria
2.6–2.3	60>→50		Cyanobacteria mats with eucaryotes <sup>§</sup>
2.3–1.0	60>→50		Eukaryotic/prokaryotic mats <sup>  </sup>
1.0–0.65	60>→50		Algal mats, lichens? (primitive fungi)
0.65–0.4	50>→45	0.015<–<0.023	First Metazoa
0.4–0.2	45>→20	0.023<–≤0.18	Vascular plants, fungi, lichens
0.2–0	≥20–15	0.18–1.00	Angiosperms

\*The temperatures are only first approximations to global mean values because probable latitudinal variation is ignored.

† $B_R$  is the ratio of the biotic enhancement of weathering at any time to the enhancement at the present. The biotic enhancement of weathering is itself the ratio of the chemical weathering rate contributing to the sequestering of carbon from the atmosphere with biota present to the rate under abiotic conditions at the same carbon dioxide level and temperature (Schwartzman and Volk 1989, 1991). The biotic weathering rate implicitly incorporates the extent of biotic colonization of land, along with the actual acceleration of weathering under biotic cover, as well as global factors (such as frost wedging, itself a result of global cooling and possibly oxygen level in the atmosphere) that affect the weathering rate. Model  $B_R$  values were computed from “preferred model b” for the variation of volcanic outgassing rate and continental land area, with  $\alpha = 0.3$ ,  $\alpha$  being the exponential factor affecting the influence of the atmospheric carbon dioxide level on the weathering rate (Schwartzman and Volk 1991).

‡For modeling purposes, we assume aerobic eukaryotes appear at 2.6 BYA.

§This likely community can be viewed as an antilichen by the reversal of the prokaryote/eukaryote spatial relation, that is, prokaryotic matrix with embedded eukaryotic cells, the inverse of lichen with cyanobacteria as the phycobiont. Perhaps modern microbial mats (Brown et al. 1985) are in some ways a model of ancient antilichens.

||For example, possibly the actinolichen, a symbiosis of actinobacteria and green algae. Actinolichens have been synthesized in the laboratory, and one example has been reported in nature (Hawksworth 1988).

scenario. Of the organellar membranes, that of the mitochondria is particularly thermolabile (Brock and Madigan 1991). Thus, anaerobic eukaryotes, thought to have preceded aerobic eukaryotes, may have emerged at somewhat higher temperatures than the assumed limit for eukaryotes. It would be interesting if any living anaerobic eukaryotes are viable above 62°C.

Consistent with the above discussion, we propose the following scenario:

- Just before the origin of life at 3.8 BYA, the earth had a high carbon dioxide pressure-cooker atmosphere, inherited from the vigorous degassing and cometary impacts on early Earth, with surface temperatures close to 100°C (Chyba et al. 1990, Kasting and Ackerman 1986, Walker 1985). Soon after the origin of life, extreme thermophiles colonized the land, enhancing weathering rates, and sequestering carbon dioxide into limestone deposits, thereby cooling Earth's surface (Schwartzman and Volk 1989, 1991).

- Subsequent cooling was in part a result of microbial evolutionary developments, with each innovation in the microbial soil community producing greater biotic enhancement of weathering, the latest being the angiosperm rhizosphere (Robinson 1991, Volk 1989). Progressive biotic colonization of the land through time would also contribute to a growing enhancement of weathering, first involving microbes alone and then vascular plants (see Robinson 1991 on the expansion of land plants in the last 400 million years).

A temperature history consistent with this scenario is shown in Figure 1 and Table 1. A speculative (at least for the Precambrian) history of soil communities on land, which is consistent with inferred timing of evolutionary innovation, is also indicated in Table 1. The model calculation is not proposed as a unique solution, only to show the required progressive increase in biotic enhancements of weathering to the present, as temperatures drop.

The Archean scenario outlined above is consistent with the following possibilities: The present biotic enhancement of weathering is high (more

than 100; Schwartzman and Volk 1989, 1991), with either steady-state or transiently high atmospheric carbon dioxide levels inherited from the pre-biotic pressure-cooker atmosphere; or a methane and ammonia greenhouse (Kasting et al. 1983, Kasting and Grinspoon 1990, Zahnle 1986) achieved atmospheric carbon dioxide steady-state by high surface temperature alone before the rise of atmospheric oxygen in the Proterozoic.

Several abiotic factors—impact-derived soil (regolith) and greater volcanic activity (volcanics weather faster than other silicate rocks)—would have favored a higher weathering intensity, relative to the present, and lower temperatures, strengthening the requirement for a high present biotic enhancement of weathering to keep temperatures high in the Archean. The plausibility of a methane greenhouse during the Archean may be diminished if there was present an additional sink, with respect to the atmosphere, aside from photochemical dissociation of methane (Kasting et al. 1983). Because aerobic microenvironments probably existed in the Archean, both aerobic and anaerobic (sulfate reduction) methane-oxidizing microbes may have provided such a sink (Large 1983, Strauss et al. 1992).

The indicated trajectory is a first approximation, not including temperature perturbations arising from factors likely to affect mean global temperature, such as variations in organic carbon burial and continental drift. Nevertheless, given the state of current knowledge, the temperature trajectory is consistent with the geologic constraints on paleoclimates, imposed by life-constraining temperature, assuming pre-Cenozoic glaciation did not occur. A lower temperature limit of 50°C is proposed for the Proterozoic, 50°C being the upper limit for Metazoa (Brock 1978), which first appear at 0.65 BYA (McMenamin and McMenamin 1990). An upper temperature limit of 45°C (Brock 1978) is assumed at 0.4 BYA, corresponding to the first known appearance of vascular plants. Whether an actual temperature record can be inferred from the emergence of plants and animals needs further study.

Even if the ancient glacial record is valid, the above argument for the

Archean may be robust, because the earliest well-established glaciation has been assumed to be the Huronian (2.3 BYA). In this scenario, surface temperatures during the Precambrian would describe a step function, with significant cooling coinciding with the rise of atmospheric oxygen at approximately 2.3 BYA.

Our proposed temperature history of the earth's surface is subject to test from determinations of paleoatmospheric levels of carbon dioxide (Cerling 1992, Yapp and Poths 1992). It may also be considered in relation to other possible indicators of levels of greenhouse gases, particularly in the Precambrian.

## Conclusions

In conclusion, the Archean was apparently much warmer than previously assumed. If the ancient tillites are indeed confirmed as impact deposits, a critical upper limit to surface temperature will be eliminated for most of the rest of Earth history. Then, the possibility arises that temperatures were much higher for most of Earth history than heretofore assumed. The timing of major evolutionary innovation could then be determined by the temperature of the surface system of Earth, itself determined by the evolution of the biosphere, constrained by abiotic boundary conditions (e.g., the luminosity of the sun). A Gaian feedback is implied between temperature and the biosphere (Barlow and Volk 1992). The genetic potentiality for rapid evolution is realized as soon as—relative to a geologic time scale, of course—external conditions allow its expression. This conclusion would have major implications for evolutionary biology and understanding of the evolution of the biosphere.

## Note added in proof

A number of additional references have come to our attention that support our main argument. Spooner (1992) argues for high surface temperatures and atmospheric carbon dioxide levels in the early Archean on the basis of the phylogeny and environmental requirements of living extreme thermophiles. Knauth and Epstein (1976) point out the consistency between the warm Precambrian

temperatures, derived from oxygen and hydrogen isotopic composition of cherts, and the upper temperature limits for different organismal groups. They cite Hoyle (1972), who suggested that hot surface conditions on Earth may have held up the emergence of complex life, an argument based on the correspondence of the sequence of appearance of life forms in the Precambrian to their upper temperature limits.

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