Neoproterozoic 'snowball Earth' simulations with a coupled climate/ice-sheet model

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Ice sheets may have reached the Equator in the late Proterozoic era (600–800 Myr ago), according to geological and palaeomagnetic studies, possibly resulting in a 'snowball Earth'. But this period was a critical time in the evolution of multicellular animals, posing the question of how early life survived under such environmental stress. Here we present computer simulations of this unusual climate stage with a coupled climate/ice-sheet model. To simulate a snowball Earth, we use only a reduction in the solar constant compared to present-day conditions and we keep atmospheric CO_2 concentrations near present levels. We find rapid transitions into and out of full glaciation that are consistent with the geological evidence. When we combine these results with a general circulation model, some of the simulations result in an equatorial belt of open water that may have provided a refugium for multicellular animals.

Some of the most dramatic events in the Earth's history occurred at the end of the Proterozoic era (this era was about 1,000–540 Myr ago). This epoch was characterized by formation of the supercontinent of Rodinia from about 1,000 to 800 Myr ago, the later breakup of this landmass and eventual reassembly into a different configuration by ~550 Myr ago, during the final phase of the pan-African orogeny[1,2]. There were also major changes in strontium, sulphur and carbon isotopes[3], together with the most extensive glaciation of the past billion years. At least two main phases of ice advance occurred, with glaciers apparently extending to the Equator at sea level[4–8]. The first phase from ~760 to 700 Myr is generally termed the Sturtian ice age, while the second, which occurred in the interval ~620–580 Myr ago, is often termed the Varanger (or Marinoan) ice age.

The late Proterozoic also marked the first appearance of metazoans (multicelled animals), perhaps as early as 700–1,000 Myr ago[9–12], while the Varanger ice age was almost immediately followed by the time interval (Vendian) featuring the first fossil remains of multicelled animals—the Ediacaran fauna. If metazoans are pre-Varanger, extensive glaciation may have exerted a significant stress on biota during a critical interval in their evolution.

Recent work[4] has focused attention on the Neoproterozoic by interpreting new carbon-isotope data to indicate that biological productivity of the oceans virtually ceased for perhaps millions of years during the glacial era. These authors concluded from this and other evidence that the planet entered a snowball Earth state, in which it was completely covered by ice until CO_2 outgassing produced a sufficiently large greenhouse effect to melt the ice. In this scenario the sudden warming caused a rapid precipitation of calcium carbonate, producing the cap carbonate rocks often observed in strata of this era. The repetition of such formations suggests that this sequence of events occurred at least twice in the Neoproterozoic.

Although this provocative hypothesis has stimulated considerable interest, it remains to be shown that the physical climate system can respond in the proposed manner. For example, although the concepts of the snowball Earth 'attractor', and rapid exits therefrom, are a feature of energy balance models (EBMs)[13], it is not at all clear to what degree the slow dynamics of ice-sheet physics would modify this model. Previous simulations with EBMs[14] and general circulation models (GCMs)[15,16] indicated that plausible changes in solar luminosity, the Earth's rotation rate and ocean heat transport were

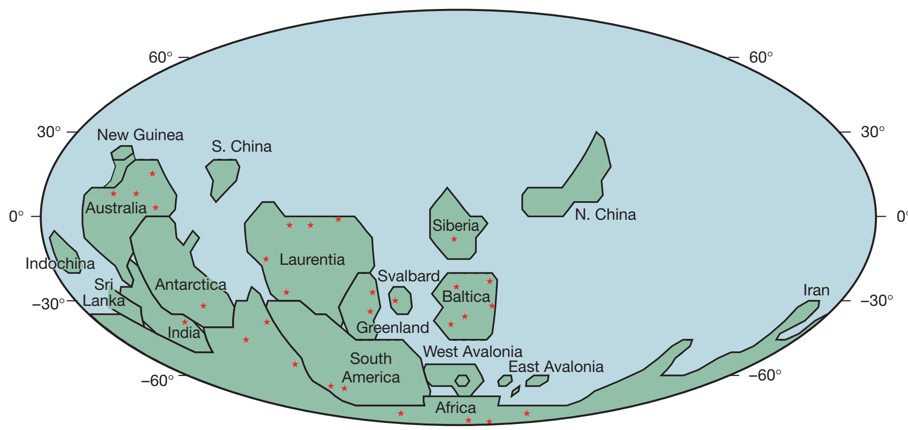

Figure 1 Late Precambrian geography. The figure shows the input geography[2] (Mollweide projection) used in our late Precambrian simulation. Red asterisks indicate the location of Neoproterozoic glacial deposits[7].

insufficient to produce a snowball Earth unless CO_2 is lowered to less than half the present value. Simulations with a radically increased planetary obliquity—which has been suggested as an explanation for equatorial glaciation[17]—preferentially produce snow in low but not high latitudes[18], and their seasonally extremely warm polar areas are in direct conflict with evidence for glaciation in these regions (see, for example, Fig. 1).

None of the above simulations included an ice-sheet model, and few evaluated the effects of orbital insolation variations or used 'realistic' geography. Here we demonstrate that a coupled EBM/ice-sheet model using realistic boundary conditions can successfully predict land ice at the Equator. We further demonstrate that a stand-alone general circulation model experiment with ice-covered continents predicts open water in equatorial regions, thereby creating a refugium for metazoans in this extreme climate.

Ice-sheet model and boundary conditions

The climate/ice-sheet model that we use was introduced by Deblonde and Peltier[19,20]; here, we will use the version described fully by Tarasov and Peltier[21]. Its physical basis consists of four submodels, which predict ice flow, mass balance, temperature and bedrock sinking. In brief, ice is assumed to flow subject to a temperature-independent rheology based on the Nye[22] formulation. Precipitation/ablation is computed according to statistical models[23,24] which themselves take as input monthly temperatures from a nonlinear, two-dimensional (latitude–longitude) diffusive seasonal EBM[25]. Bedrock sinking is assumed to occur with a time constant of 4,000 years. The EBM has been validated against many different GCMs[26], while the coupled EBM/ice-sheet model reproduces many features of climate change over the past 120,000 years and predicts ice for about 80% of the known glacial deposits for the radically different geography of the Carboniferous ice age[27]. The flexibility of the model lends itself to extensive sensitivity testing and long runs; for example, here we have run approximately 20 million years of model simulations.

Model inputs include palaeogeography, atmosphere CO_2 concentrations, precipitation, Milankovitch forcing, and the solar constant. Our baseline palaeogeography for the ~590-Myr Varanger glaciation is taken from Dalziel's reconstruction for 545 Myr ago[2]. Although data suggest that at 590 Myr ago amalgamation was not as great as it was at 545 Myr, the latitudes of important glacial sites in Namibia and Australia are close to their Varanger positions. However, interior seaways existed before the final joining of Africa and South America, and Baltica was closer to Laurentia before the opening of the Iapetus Ocean. We will later discuss a number of experiments that examine the sensitivity of our conclusions to uncertainties in palaeogeography. For convenience we initially assume that the continents are at sea level; adding freeboard is nearly equivalent to reducing the solar constant. We employ a solar constant appropriate to the era in question, that is, about 6% below present[14]. Precipitation and CO_2 values are varied to test the snowball Earth hypothesis. In our initial simulations, ice sheets were driven by a uniform precipitation of 0.6 mm d^{-1}, which declines with height and decreasing temperature. This value is characteristic of current Northern Hemisphere mid-latitude land areas. Given the important role which the tropics play in our simulations, a lower value cannot be justified for our (initially ice-free) Neoproterozoic simulations. The model is relatively insensitive to higher precipitation rates[27]. The model is driven with Milankovitch variations appropriate to the Pleistocene epoch[28], although the very cold climates we investigate are relatively uninfluenced by this forcing. The model makes predictions of temperature, sea ice, and ice volume that can be tested for consistency against the snowball Earth hypothesis and other geological evidence.

Neoproterozoic simulations

Our first experiment, with the above inputs and present-day atmospheric CO_2 concentration resulted in a large ice sheet (not shown) that in coastal areas approaches 40° latitude, but which is restricted by summer warming on the supercontinent to about 50° S in the interior. Sensitivity experiments with the alternative reconstruction of Bond *et al.*[29] yield similar results, but the smaller amount of land area in middle to high latitudes leads to ice growth to 30° palaeolatitude (not shown).

Neoproterozoic CO_2 levels are not known, but may have been very variable due to large carbon reservoir shifts as indicated by $\delta^{13}C$ changes[3,4,30]. We therefore conducted a series of sensitivity tests in which CO_2 levels were varied by adding or subtracting infrared forcing. For CO_2 levels approximately half that of the Holocene epoch (that is, ~130 p.p.m. or a cooling of roughly 5 W m^{-2}) the entire land surface is glaciated (Fig. 2), while for higher levels (slightly over twice the Holocene value) the ice volume approaches that of the Last Glacial Maximum. The transition from a cold state to a fully snow-covered one (snowball Earth) is abrupt (~2,000 years; Fig. 3), as conjectured by Hoffman *et al.*[4] and consistent with other EBM[31], GCM[32] and EBM/ice-sheet studies[27]. It occurs at a CO_2 level equivalent to an infrared cooling of 4.75 to 5.0 W m^{-2}. The exact location of this discontinuity is not particularly important, given the known uncertainty in solar constant and—for example—the different land albedo of a world without vascular plants. The

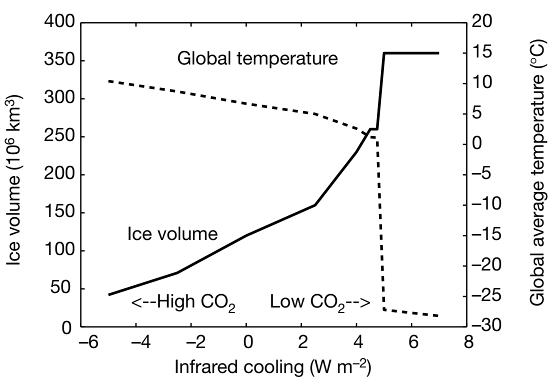

Figure 2 Operating curve for the climate/ice-sheet model. Ice volume and global sea level temperature are shown as a function of CO_2 level and of infrared forcing. A bifurcation occurs at a cooling of ~5 W m^{-2}, beyond which all land surfaces are ice-covered and global temperature drops considerably: the snowball Earth.

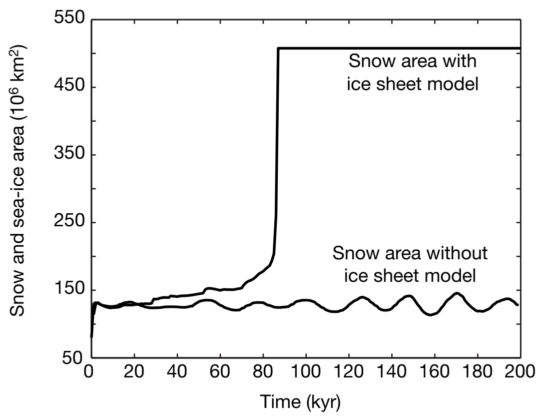

Figure 3 The effect of ice dynamics on model results for an experiment with −5 W m^{-2} of infrared forcing. Without the ice sheet, the climate model predicts a climate in which only about one-quarter of the planetary surface is covered in snow or sea ice. If the ice sheets are allowed to grow, however, they flow into areas originally too warm for year-round snow, but the ice-sheet's thermal inertia and elevation prevent it from melting.

transition is associated with an abrupt drop in globally averaged surface temperature, from approximately zero to about −27 °C.

Continental freeboard and atmosphere CO_2 concentrations (or luminosity) play complementary roles in determining ice volume—the higher the freeboard, the greater the level of CO_2 consistent with ice-covered continents. Sensitivity experiments (not shown), in which we raised baseline continental topography by 100-m increments, indicate that for a 500-m baseline, the snowball Earth solution occurs with CO_2 levels approximately 50–100% greater than present. These are reasonable freeboards for the interval (800–550 Myr ago) associated with the pan-African orogeny.

A number of additional experiments (not shown) were run to determine the sensitivity of our results to continental configuration. For example, most of the Neoproterozoic glaciation occurred in an era of dispersed geography[4]. In the absence of a reliable 590-Myr geography, we tested the effect of continental dispersion by using a Cenomanian (94 Myr ago) geography[33]. No qualitative difference was observed—although total ice volume was approximately one-third less than in our supercontinent runs, and the bifurcation point for the transition between cold and 'snowball' conditions occurred at a higher CO_2 level, equivalent to about $1\,W\,m^{-2}$ more infrared forcing. Runs with alternative Neoproterozoic reconstructions[2,29] yielded similar results, although the critical CO_2 level again differed slightly ($<1\,W\,m^{-2}$) for different geographies.

To determine what difference the ice sheet makes to our solution,

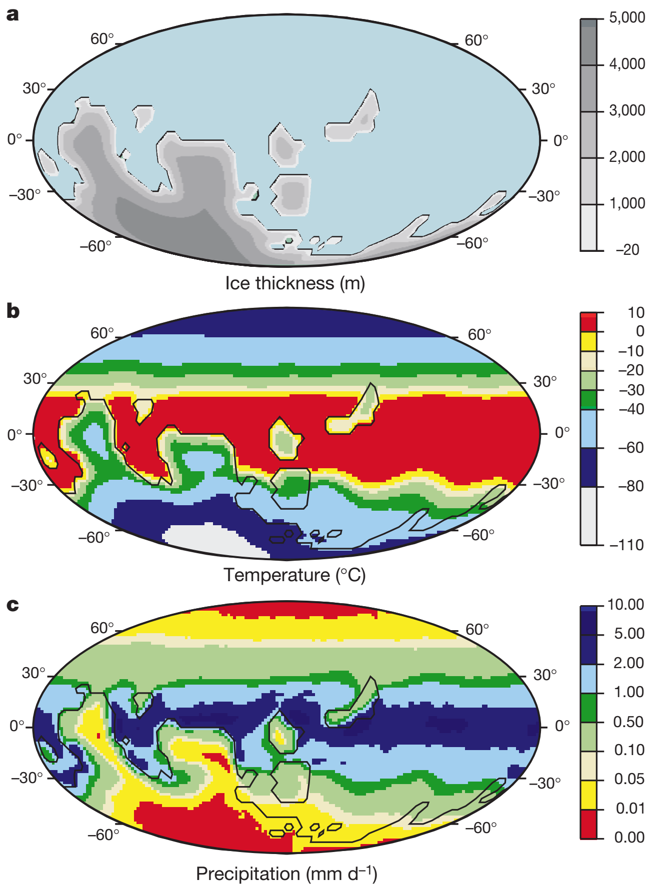

Figure 4 Late Precambrian (Neoproterozoic) climate simulations. **a**, Ice extent at equilibrium (Mollweide projection) for a 'snowball Earth' simulation. **b**, Annually averaged temperature for a GCM Neoproterozoic simulation using the above ice sheets as a lower boundary condition. A considerable area of open water exists in the tropics, though the ice sheets are almost everywhere below the melting point. **c**, Annually averaged precipitation in the GCM experiment. The cold temperatures and restricted area of open water result in a precipitation field which is less than $0.06\,mm\,d^{-1}$ over the ice-sheet accumulation zone.

we ran the EBM with the same luminosity and CO_2 values used to obtain the ice-covered land-mass solution (note that snow and sea ice are still predicted). A comparison (Fig. 3) of the EBM alone and EBM/ice-model solutions indicates that an interactive ice sheet leads to a qualitatively different result. Ice elevation, and the long time constant associated with melting thick ice, allows the ice to 'weather' warm summer orbital configurations[14,34] without deglaciating. Whereas ice growth is restricted by the time constants inherent in ice flow and precipitation, snow area can grow rapidly. A CO_2 increase equivalent to a $69–70\,W\,m^{-2}$ warming is required to melt the ice (not shown). This is approximately equivalent to one-third of a bar of CO_2. The deglaciation is very rapid, requiring less than 2,000 years to complete. Both of the above results are in agreement with ref. 4. This rapid and large warming would also explain the unusual configuration of tropical carbonates resting on diamictites—a characteristic feature of Neoproterozoic sediment sequences.

Although the coupled model generates a snowball Earth solution with sea-ice albedos greater than 0.5, the highly idealized sea-ice parameterization[25] raises questions about the validity of the oceanic component of the model simulation. In addition, the EBM's diffusive heat transport mechanism is not as good a representation of tropical dynamics as it is of mid-latitude eddies. We therefore ran an additional set of stand-alone GCM mixed-layer ocean experiments (that is, without oceanic dynamics) with the fixed ice sheet obtained from our coupled run. We employed the GENESIS 2 GCM[35] which has diurnal forcing, interactive clouds, semi-lagrangian water vapour transport, and a six-layer sea-ice model. The sea-ice albedos vary between 0.7 and 0.8 (at visible wavelengths) and 0.4 to 0.5 (infrared) depending on whether temperatures are at the melting point, 5 °C below the melting point, or in between. The total albedo at each ocean point is based on sea-ice fraction, itself dependent on the sea-ice thickness. The model was run at T31 resolution (approximately 3.75° × 3.75°). The initial conditions involved a zonally averaged state with an average temperature of 0 °C. Simulations[36] used CO_2 values ranging from 0.5 to 2.5 times present levels, and the same luminosity decrease as in our coupled runs.

Simulations[36] with 0.5 and 1.0 times CO_2 (not shown) quickly yielded ice-covered oceans whereas a doubled CO_2 experiment resulted in ice-free tropical oceans but with a very slow drift to lower temperatures. We illustrate the last three years of the more stable 2.5 × CO_2 run (Fig. 4). An important feature of this experiment is that sea ice extends to only about 25° palaeolatitude (Fig. 4b), with sea-ice thickness varying from ~1 m near the ice

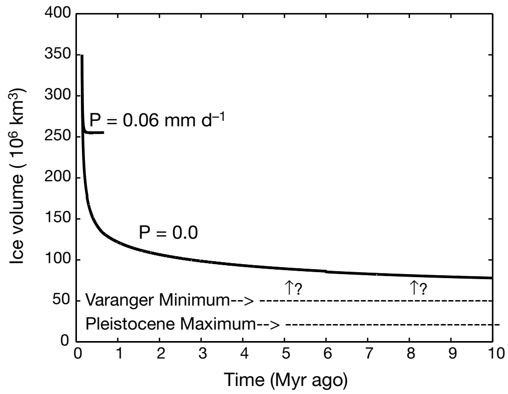

Figure 5 The effect of precipitation on global ice volume. When precipitation is reduced by a factor of ten, the ice sheets quickly achieve a slightly thinner equilibrium state. When precipitation is reduced to zero, the decline in ice volume is continuous. After 10 Myr the volume is about double that of the Pleistocene maximum, but comparable to some sea-level estimates[43] for the late Precambrian (Varanger) glaciation.

edge to 10 m in higher latitudes (the model cut-off limit). Open water can exist despite extensive ice sheets for two reasons—the ~1,500-km length scale of the influence of ice sheets on temperatures[37–39], and an important negative feedback in the GCM that is not included in the EBM. Reduced absolute humidity in a colder world reduces cloudiness by about 35%, and hence the reduction in insolation due to the younger Sun is somewhat compensated by a lower equatorial albedo (compare ref. 40). Dynamical feedback between sea-ice formation and ocean circulation might further affect the equatorial extent of sea ice. Additional model simulations with the fully coupled climate/ice-sheet model (W. T. Hyde *et al.*, manuscript in preparation) mimicking this negative feedback yield open water in the tropics. However, in this open-water case isolated land masses in equatorial regions are ice-free. This problem will be examined further in subsequent work.

Even with this large area of open water zonally averaged precipitation over much of the ice sheet is less than 0.05 mm d^{-1}; this is because most of the precipitation rains out over the open water, with very little transport into continental interiors. Temperatures below zero over most of the ice sheet indicate that open water is consistent with a mainly ice-covered land area (except for those ice sheets confined to small land masses in the equatorial ocean). Such open-water conditions near the ice are consistent with peritidal deposits[41] for the south Australia (Fig. 1) glacial sequence.

The near-snowball climate, which was first conjectured by Kirschvink[42], is qualitatively different from that of a true snowball Earth. This result is also not consistent with the interpretation[4] of $\delta^{13}C$ records as indicating a near-abiotic ocean. However, if metazoans are found to have evolved by that time, and if the $\delta^{13}C$ record is shown to be open to alternative interpretation (see further comments below), then the open-water solution represents a straightforward reconciliation of these possibilities with equatorial glaciation.

Although the model can rather easily generate ice-covered continents with plausible changes in boundary conditions, the model-generated ice volume (nearly 10 times Pleistocene values) is in excess of estimated sea-level changes due to Precambrian glaciations[4,7]. Such a change would also increase mean ocean salinities by about 20%. The very large ice sheet raises the question of whether the model produces reasonable ice volumes for a given ice area. Several lines of reasoning lead us to believe that our ice sheets are not unrealistically thick. For example, our ice sheets are considerably thinner than predicted by one published area/volume relation[44]. The model's predicted Pleistocene ice volumes are in line with observations[21]. Although our single-domed Neoproterozoic simulation tends to exaggerate ice volume as compared with a more realistic multidomed reconstruction, a comparison between this model's single-domed Laurentide simulation[21] and a multidomed simulation[45,46] implies that this exaggeration is not large. The latter effect would also to some degree be offset by the fact that we do not allow ice to accumulate on continental shelves or epicontinental seas.

As our GCM results indicate (Fig. 4c), a radical reduction in precipitation should occur[4] as a result of decreased temperatures and increased sea ice extent. However, the continued ablation of the ice sheet (largely due to calving of icebergs) would decrease ice volume. This would in turn allow sea level to rise, partially reversing the initial large sea-level drop. We tested this possibility through a series of runs in which the precipitation was lowered from 0.6 to 0.06 mm d^{-1}, and further to a limiting case of 0.0 mm d^{-1}, starting from the glaciated state of Fig. 4. The 10-Myr duration of our zero-precipitation run should be regarded as a minimum estimate for the time required to produce this sea-level drop, as the model uses a temperature- and pressure-independent rheology, and ice velocities would be much slower in the very cold snowball Earth, particularly as the ice sheets thinned, resulting in a slower rate of mass loss at the coast. When precipitation is reduced the ice sheets initially decay quite rapidly, slowing as the ice surface slopes decrease (Fig. 5). A drop in precipitation by a factor of 10 decreases the equilibrium ice amount by about 30%, while a complete shut-off of moisture reduces the ice volume by 70%, but only after ~5–10 million years. Although our 0.06 mm d^{-1} run predicts a sea-level decline far greater than a recent estimate[43] of 160 m for the Neoproterozoic, the magnitude of the observational constraint is still open to question. For example, it took more than a century to narrow down the sea-level decrease for the Last Glacial Maximum[47]. The larger ice volume we simulate could explain the thickness of postglacial carbonates (>300 m) precipitated on continental shelves. Such an amount could be accommodated by the degree of isostatic subsidence (~300 m) accompanying a 1,000-m ice sheet at the coast (Fig. 2a); overdeepening of continental shelves due to ice-sheet scouring would further enhance such accommodation (for reference, shelf depth is several hundred metres in places around Antarctica).

Discussion

An ice-covered Neoproterozoic land mass is predicted by our coupled climate/ice-sheet model with only two significant changes in boundary conditions from present values—a solar luminosity decrease consistent with estimates from solar physics, and a CO_2 level within about 50% of the present value. The final phase of the glacial advance, and the subsequent deglaciation, are consistent with the hypotheses proposed by Hoffman *et al.*[4]. These conclusions are relatively robust, in that they hold true for different land–sea configurations and continental freeboard. The results were obtained without any retuning of a model developed to explain the last glacial cycle.

A major finding of this study is that an area of open water in the equatorial oceans—which could have allowed for the survival of metazoans—is consistent with the evidence for equatorial glaciation at sea level. Although this result requires more model testing, it does not seem to be completely at variance with $\delta^{13}C$ data. Several studies suggest $\delta^{13}C$ values of −3‰ to −4‰ in deposits flanking the Varanger glaciation[4,48,49]; such values are not consistent with a near-abiotic ocean, but would be consistent with the low level of ocean productivity that might have occurred in an ocean refugium of the size we simulate. Because of the need by early metazoans for a shallow water substrate, such an area could only be a true refugium if it contained ice-free continental shelves during the otherwise near-total glaciation. Identification of such sites would be a critical test of our open-water result (some of the equatorial land masses illustrated in Fig. 1 could have been in different locations 590 Myr ago). Length-scale arguments discussed above suggest that these sites would probably be isolated equatorial land masses at some distance from the main land mass (Fig. 1). If such sites are found, they should provide information about metazoa during one of the most significant 'bottlenecks' in the evolution of life. For example, selection pressure exerted on biota by the extreme climates may have led to rapid development of new forms during glaciation and afterwards, with the sea-level rise and expansion of biota into the large number of new and unpopulated habitats. Although there is clearly a need for more climate modelling and additional geological data (for example, clarification of the $\delta^{13}C$ and sea-level evidence, and more high-quality palaeomagnetic sites), our results indicate that inclusion of explicit ice-sheet physics significantly closes the gap between models and data for the largest glaciation of the past billion years and for one of the most critical intervals of evolution in Earth history. □

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Loophole for snowball Earth

Bruce Runnegar

The snowball Earth hypothesis posits an ice-covered planet. New climate simulations of 'snowball' conditions allow ice-free equatorial oceans that may be crucial for a theory about early animal evolution.

Snowball Earth is a script for global catastrophe that rivals giant-impact theories in the severity of its postulated environmental effects. In the 'hard' version of this hypothesis[1], low concentrations of atmospheric carbon dioxide (around 150 μbar) and fainter sunlight (by some 6%) allowed polar ice caps to grow until reflected sunlight cooled the Earth and the oceans froze to a depth of about one kilometre. According to proponents, this happened at least twice during the Cryogenian period of the late Precambrian (850–590 million years ago) and perhaps more frequently a billion-and-a-half years before that[2,3]. Recovery from these episodes depended on CO_2 emissions from volcanoes, and consequent greenhouse warming.

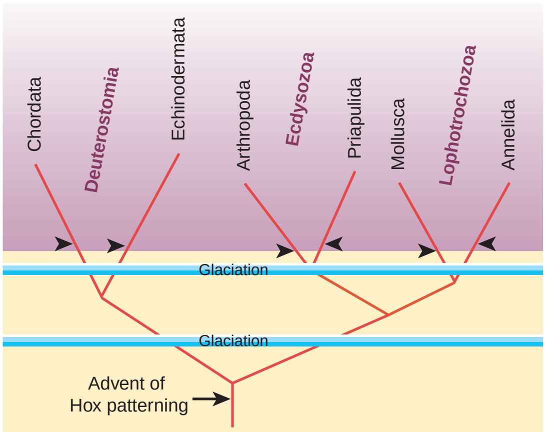
The effect on the biosphere of snowball events is thought to have been catastrophic. Carbonates immediately below and above the glacial deposits record carbon-isotope ratios characteristic of Earth's mantle[1,4], rather than of life processes, implying that oceanic photosynthesis was effectively eliminated during each snowball event. The result of this and anoxic conditions beneath the ice should have annihilated most kinds of eukaryotic life — that is, almost everything except bacteria. So successive snowball Earths should represent bottlenecks in the evolutionary history of eukaryotes through which comparatively few organisms passed. Conversely, the final disappearance of snowball conditions may have permitted and even stimulated the Cambrian explosion of complex multicellular life that began some 565 million years ago.

On page 425 of this issue, Hyde *et al.*[5] challenge the 'hard' snowball Earth hypothesis. Their energy-balance and general-circulation climate models allow open water in equatorial regions to coexist with snowball Earth conditions elsewhere. According to their calculations, massive continental ice sheets up to 5 km thick flowed outwards into low latitudes. However, providing that atmospheric CO_2 was above a plausible level (roughly double the present amount), these flows did not create global oceanic ice shelves. Instead, they calved and melted to leave a narrow circum-equatorial refugium that might have included some access to coastal zones.

This 'softer' picture of a snowball Earth is similar to the original version proposed by Kirschvink a decade ago[6], and it allows for the evolution of the biosphere to proceed in a more orderly fashion than does the 'hard' alternative. But which of those views is likely to be correct?

A key question not addressed by Hyde *et al.* is whether enough CO_2 could accumulate in an atmosphere in contact with the global ocean to end a snowball Earth event. Hoffman *et al.*[1] assumed that more than a tenth of a bar of CO_2 would be required to overcome the increased reflectivity of an ice-covered Earth, so it is not a trivial matter. Presumably, all continental silicates and shallow-water carbonates were protected from chemical weathering by very cold ice cover, so the usual controls on CO_2 build-up would not have applied[7]. If total alkalinity remained relatively constant, only a fraction of the carbon that needed to accumulate in the atmosphere could have been absorbed by the ocean. However, such an ocean would have been acidic, freezing, undersaturated in calcium carbonate, and inimical to the formation of mineral skeletons. This is one possible reason why the

Box 1 How to make an animal — indirectly



In a provocative series of articles, summarized in ref. 9, Peterson, Cameron and Davidson have proposed a new model for the origins of the disparate body plans of the various bilaterian metazoan phyla — primitively mobile animals that have an anterior–posterior axis, a central nervous system, and tissues and organs derived from a middle body layer. Molecular phylogenies segregate all bilaterian phyla into three large groups: deuterostomes, ecdysozoans and lophotrochozoans, shown in the figure here with some distinctive component phyla. The last two are sister groups and they jointly share the last common ancestor of all living bilaterians with the deuterostomes. That animal, argue Peterson *et al.*, had a free-living larval stage that bore little or no resemblance to the adult. The adult body was built from undifferentiated 'set-aside' cells that were free of growth constraints imposed on all other parts of the embryo. These cells could thus participate in a more sophisticated developmental process, involving Hox gene expression patterns, that is characteristic of all bilaterian phyla.

The key point here is that similar bilaterian larvae are thought to have given rise to very different adult body plans. A classic case is the dissimilarity of adult molluscs and sipunculan worms and the great similarity of their larvae. But here lies the difficulty. Molluscs and sipunculans are lophotrochozoans, so their origins lie well above the common bilaterian ancestor in the metazoan tree. Somehow, deployment and patterning of pre-existing set-aside cells had to be delayed until the various lineages leading to the bilaterian phyla had been separated for long periods of time. For example, distantly related members of the three bilaterian groups appear abruptly in the fossil record at the beginning of the Cambrian around 545 million years ago (arrows). However, molecular clocks[10] suggest that the common ancestor of all three groups lived before the Cryogenian glaciations. Early-diverging bilaterians may therefore have been kept in 'larval mode' after the invention of set-aside cells and Hox cluster patterning by being forced to survive one or more snowball Earth glaciations in open-ocean environments. **B.R.**

Cambrian explosion might have been postponed (Box 1).

But there is another outcome of the work of Hyde *et al.*[5]. Let us accept, tentatively, that there were two global glaciations that occurred about 200 and 50 million years before the beginning of the Cambrian[4]. If so, each could have had one of three effects on the biosphere, in decreasing order of severity.

A snowball bottleneck. Conditions: global oceanic ice cover for around ten million years; anoxic oceans; almost complete loss of photosynthesizing biomass; extinction of all but a few lineages of eukaryotes, which survived mainly in geothermal oases on the continents. Probable consequences: a massive bottleneck in eukaryotic lineages; survivors that were predominantly terrestrial in origin.

A blue-water (pelagic) refugium, such as emerges from the paper of Hyde *et al.* Conditions: massive continental ice sheets and marginal ice shelves, but an open-water circum-tropical ocean with unglaciated volcanic islands; almost complete destruction of terrestrial biota and shallow-water, bottom-dwelling life; oxygenated oceans; prolific pelagic biomass in the nutrient-rich equatorial waters. Probable consequences: snowball episodes filtered eukaryotic lineages by allowing the survival of organisms that inhabited either the pelagic, open-ocean realm, or ocean-floor hydrothermal vents.

A uniformitarian outcome. Conditions: global refrigeration, but minimal impact on the biosphere because habitat loss was offset by positive effects such as the increased solubility of oxygen in sea water. Probable consequences: little or no evidence for snowball episodes in the evolutionary histories of post-Cryogenian marine eukaryotes.

The possibility that early metazoan (multicellular animal) lineages went through a pelagic filter may help to overcome a fundamental difficulty with one explanation for the origin of metazoan body plans[8,9]. According to this view, described in more detail in Box 1, a unique innovation — the evolutionary origin of larval 'set-aside' cells — provided the canvas on which a wide range of animal body plans could ultimately be sketched. But to generate the main metazoan groups by this method it is necessary to separate lineage-splitting in time from body-plan specification. In other words, some environmental filter was required to maintain early metazoans in 'larval mode' after they had invented set-aside cells. This enabled them to diversify into well-separated lineages that ultimately became the independent sources of radically different body plans. A blue-water refugium could have served this purpose. If so, the Cambrian explosion might have begun with pelagic organisms discovering or rediscovering the sea floor. ■

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Cancer

New link in a web of human genes

Jean Y. J. Wang

Biologists have solved complex problems through genetics for more than a century. The simple approach of cataloguing genetic mutants often reveals interesting and important relationships between genes. By applying this principle, several groups[1–4], including two whose reports appear on pages 473 and 477 of this issue[2,3], have now established a functional link between *ATM* and *NBS1* — two genes involved in human diseases.

ATM is mutated in the disease ataxia telangiectasia (AT), the symptoms of which include degeneration of a particular brain region (the cerebellum), immune dysfunction, sterility, sensitivity to radiation, and increased risk of cancer. *NBS1* is mutated in a rare disease called Nijmegen breakage syndrome (NBS). Patients with NBS have symptoms similar to those seen in AT. Although AT and NBS can be distinguished by clinical criteria, cells of AT and NBS patients show striking similarities, including the increased breakage of chromosomes.

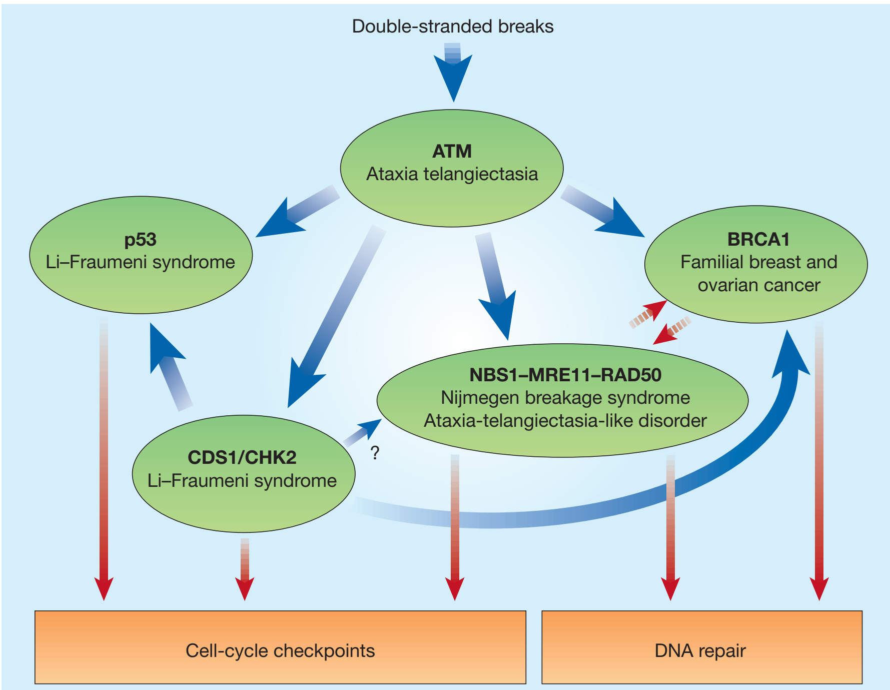

Figure 1 **A network of proteins, implicated in human cancer, that regulate cellular responses to DNA damage. Double-stranded breaks (DSBs) in chromosomal DNA can activate a network of phosphorylation events to regulate DNA repair and progression through the cell-division cycle. Phosphorylation events are indicated by blue arrows. The protein kinase ATM is activated by DSBs to phosphorylate p53 (refs 1, 5, 6), CDS1/CHK2 (ref. 7), NBS1 (refs 1–4) and BRCA1 (ref. 9). (Mutations in the genes encoding these proteins are characteristic of the diseases indicated.) Further phosphorylation of p53 (refs 13–15) and BRCA1 (ref. 16) by CDS1/CHK2 might reinforce the actions of ATM. It will be interesting to know whether CDS1/CHK2 might also phosphorylate NBS1. The NBS1–MRE11–RAD50 complex also interacts with BRCA1, perhaps to coordinate DNA repair (dashed red arrows). Phosphorylation of p53, CDS1 and NBS1 activates cell-cycle checkpoints, which prevent the duplication and propagation of damaged DNA. Phosphorylation of NBS1 and BRCA1 may regulate the repair of DSBs. Together, the genes in this network protect the integrity of the genome, and mutations in the network predispose people to cancer.**

Geophysics

Life, geology and snowball Earth

According to the 'snowball Earth' hypothesis, a series of global glaciations occurred 750–580 million years ago, each lasting for millions of years and ending in a scorching heat caused by an extreme enrichment of atmospheric greenhouse gases. Hyde *et al.*[1] have used climate models to simulate this global glaciation, finding in one case an alternative climate scenario in which a partially frozen Earth has ice-free oceans equatorward of 25° latitude. We do not believe that this 'slushball' Earth is consistent with the most striking geological and palaeomagnetic observations explained by the snowball Earth hypothesis.

Palaeomagnetic and geological data from Neoproterozoic glacial deposits indicate that glaciations were long-lived (lasting for millions of years)[2,3] and locally associated with iron formations. The glacial deposits are covered by extraordinary sequences of carbonate sediments called 'cap' carbonates, which have unusual textures and low $\delta^{13}C$ values. The snowball Earth hypothesis can explain all these observations[3], whereas a semifrozen (slushball) Earth does not.

In the snowball Earth hypothesis, a runaway ice–albedo feedback leads to a planet frozen to the Equator[4]. Extremely large increases in carbon dioxide are required to terminate the glaciation and overcome the climate stability imposed by the high planetary albedo[5]. In Hyde *et al.*'s model[1], with all the continents covered in ice, volcanic emissions without chemical weathering would cause atmospheric CO_2 levels to rise. But with ice-free tropical oceans, even a modest rise in CO_2 would cause the tropical glaciation to be short-lived. The exact duration would depend on the extent of chemical equilibration between sea water and calcium carbonate in the deep ocean, but it would be far less than the roughly 10 million years estimated from analysis of basin subsidence[3]. It is also unclear how iron could accumulate in sea water to produce banded iron formations if tropical oceans were ice-free. Moreover, the model of Hyde *et al.* predicts a progressive deglaciation from the Equator to the poles occurring at much lower CO_2 concentrations, no higher than during the Cretaceous period.

Support for extreme increases in CO_2 in the aftermath of the glaciations comes from cap carbonates, which are nearly ubiquitous features of Neoproterozoic glacial deposits. These carbonate rocks have distinctive features, including "knife-sharp" contacts with glacial deposits and unusual textures indicative of rapid precipitation on the sea floor[6]. The cap carbonates, which have been singled out as a climate paradox of Neoproterozoic geology[7], are predicted by the snowball Earth hypothesis to be a consequence of intense carbonate and silicate weathering in the aftermath of the deglaciation. It is hard to reconcile the global occurrence of such a pulse of intense carbonate precipitation immediately after the termination of the ice ages with the progressive retreat of ice at moderate CO_2 levels predicted by the Hyde *et al.* model.

Excitement over whether a semifrozen Earth might explain the geological observations stems from concern for the survival of eukaryotic life in such extreme and extended glaciations[8]. The critical feature is the survival of groups of photosynthetic algae that evolved before the glaciations. The survival of metazoans, as discussed by Hyde *et al.*, is less problematic because such organisms (if they existed) could live wherever primary producers (photosynthetic or chemosynthetic) were still active. Photosynthetic algae could survive a series of glaciations in refugia near volcanic islands, such as Iceland and Hawaii, or beneath thin equatorial ice cover[9]. Evolution might well be stimulated by this prolonged genetic isolation, and by perturbations of biogeochemical cycles during the postglacial, ultra-greenhouse climate. This is consistent not merely with the survival of eukaryotic life, but also with the coincident radiation of metazoa and other groups[8].

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Hyde et al. *reply* — We are not convinced that the data discussed by Schrag and Hoffman can be interpreted in only one way. With respect to the duration of glaciation, calculations[1] suggest that the open-water solution could have persisted up to CO_2 levels of about four times those at present. With buffering from the reactive ocean carbonate reservoir, the time required for degassing to raise atmospheric concentrations to this level would be about 0.2–0.6 million years (L. A. Derry, personal communication). As ice sheets would still discharge ground carbonate into the ocean, the buffering time would be extended. This timescale is consistent with range estimates derived from palaeomagnetic data[2] and geochemical calculations[3].

Our open-water results also agree with the environment of deposition of some glaciomarine sediments[4]. Iron is not a consistent feature of Neoproterozoic glacial sequences[5]. Meltwater from glacial calving could suppress water-column convection and decrease deep-sea oxygen; overturn[6] could contribute to the low $\delta^{13}C$ in postglacial sequences.

The idea that a modest CO_2 increase would eliminate tropical glaciation in the open-water solution assumes a linear response, which is in contrast to many examples in the Pleistocene and the model used in our study[1,7]. Increases in CO_2 produce virtually no meltback until a threshold level is reached[1], whereupon a small increase causes rapid melting. Calculated ice-sheet retreat times of tens of thousands of years agree with sedimentological estimates[8]. Isostatic depression from the large ice sheets we describe could accommodate a thick layer of postglacial carbonate (only the thin bottom layer of which is cap rock in the strictest sense).

We are not as sanguine as Schrag and Hoffman about the ability of metazoans to survive under the extreme conditions of a hard snowball Earth. Whether life could survive on a few scattered volcanic islands is a matter of conjecture. A "thin-ice" scenario[9] is not consistent with results[10] indicating that such regions have temperatures substantially colder than those estimated in ref. 9 (with implications for sea-ice thickness). Although evidence for life extends almost to the oldest rocks, three billion years transpired before the appearance of metazoans. This vast time interval suggests that the environmental tolerance of metazoans is much narrower than that of their simpler and hardier colleagues. If deep waters were anoxic, they could not survive on deep-sea chemosynthetic communities either, as these organisms still require free oxygen.

Future data may call for the reassessment of our open-water scenario, but we consider that the hard-snowball scenario is not yet proven. We believe that the open-water solution is much more favourable for the survival of metazoans, allowing their remote progeny to continue this discussion.

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