Low-latitude glaciation in the Palaeoproterozoic era

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One of the most fundamental enigmas of the Earth's palaeoclimate concerns the temporal and spatial distributions of Precambrian glaciations. Through four billion years of Precambrian history, unequivocally glacial deposits have been found only in the Palaeoproterozoic and Neoproterozoic record[1]. Nonetheless, some of these deposits are closely associated with tropical—rather than just polar—palaeolatitudinal indicators such as carbonate rocks, red beds, and evaporites[1,2]. These observations are quantitatively supported by palaeomagnetic results indicating a ~5° latitude for Neoproterozoic glaciogenic rocks in Australia[3–5]. Similarly reliable palaeolatitudes for the older, Palaeoproterozoic glaciogenic rocks have not yet been obtained, as such deposits commonly suffer from poor preservation and secondary magnetic overprinting. The Archaean–Palaeoproterozoic 'Transvaal Supergroup' on the Kaapvaal craton in South Africa is, however, exceptionally well preserved, and is thus amenable to the palaeomagnetic determination of depositional palaeolatitudes. Within this supergroup the ~2.2 billion-year old Ongeluk lavas are a regionally extensive, largely undeformed and unmetamorphosed, extrusive volcanic succession[6], which conformably overlies glaciogenic deposits (the Makganyene diamictite). Here we report a palaeomagnetic estimate of 11 ± 5° depositional latitude for the lavas, and hence for the underlying contemporaneous glacial rocks. The palaeoclimate enigma is thus deepened; a largely ice-free Precambrian world was apparently punctuated by two long ice ages, both yielding glacial deposits well within tropical latitudes.

The Ongeluk Formation comprises ~500–1,000 m of extrusive, basaltic-andesitic lavas deposited in the marine facies succession of the Transvaal Supergroup[7], exposed in the Griqualand West region of the Northern Cape Province (Fig. 1). A correlative volcanic unit, the Hekpoort Formation, occurs in the Chuniespoort region to the northeast (Fig. 1). Isopach trends[8] indicate that the two volcanic units were deposited in a single, contiguous basin across the Kaapvaal craton[9]. The Ongeluk lavas have been Pb/Pb-dated at 2,222 ± 13 Myr old[10], and the Hekpoort Formation has a recalculated Rb–Sr age[11,12] of 2,177 ± 21 Myr. Studies using the U–Pb system in zircon give ages of 2,432 ± 31 Myr for the underlying Griquatown Iron Formation[13] and ~2,050 Myr for the Bushveld complex[14] which intrudes the Transvaal sequence; these results firmly bracket the age of the Ongeluk–Hekpoort formations between about 2.4 and 2.1 Gyr. The Hekpoort andesites were studied palaeomagnetically by Briden[15], who obtained near-present-field directions by alternating-field demagnetization of samples from only four sites. Of all other penecontemporaneous rocks (2.0–2.4 Gyr) on the Kaapvaal craton, only the Bushveld complex has palaeomagnetic constraints, yielding a range of palaeolatitudes from ~25° to ~60° (ref. 16).

Palaeomagnetic investigations of other Palaeoproterozoic successions have not conclusively demonstrated primary magnetic remanence. For example, the partly glaciogenic Huronian succession (2.45–2.22 Gyr) in North America has been the object of several palaeomagnetic studies[17–19], but those results vary greatly, and a more recent study of the 2.22-Gyr Nipissing diabase and other early Palaeoproterozoic intrusive rocks of the Superior craton casts doubt upon the established apparent polar wander path for the Huronian interval[20]. Huronian palaeolatitudes thus remain unresolved, partly because of greenschist- or higher-grade regional metamorphism, multiple magnetic components within and among sampling sites, and a lack of unequivocal tests for determining the ages of those components.

In the Northern Cape Province, autochthonous sedimentary rocks of the Transvaal Supergroup are better preserved. Warped into broad, open folds with bedding dips usually less than 5°, the Ongeluk Formation is exposed in several structural troughs in this area. From the mineralogy of the underlying Kuruman Iron Formation, maximum metamorphic temperatures of <170 °C were estimated[21]. All localities discussed herein are road-cut exposures of fresh, fine-grained, massive or pillowed, green-grey lava, except for two sites ("OLL") whose coarse grain size may indicate that these rocks are intrusive, perhaps feeder dykes for subsequent flows. The remarkably low degree of deformation, low metamorphic grade, and fresh exposures of the Ongeluk lavas provide an ideal opportunity for preservation of primary magnetic directions from the Palaeoproterozoic.

The stratigraphic succession in the Griqualand West region was widely misinterpreted for many years[6,22] because a large thrust fault was not recognized. In its place, some chose to assign unconformities between virtually all of the formations to account for their juxtapositions; this view has been rejected by subsequent observations and geological syntheses[23] that incorporate the thrust fault and only one major unconformity within the Transvaal sequence, between the Ghaap and Postmasburg groups (Fig. 1).

We present the following field evidence in support of the results outlined by Beukes and Smit[23], that no significant hiatus separates the Ongeluk lavas and the underlying, glaciogenic Makganyene Formation. First, although thicknesses of individual members of the Makganyene Formation vary considerably, this is to be expected in a glacial deposit[24], where thickness variations may be due to original facies variability rather than subsequent removal by erosion. Indeed, the lower sections of the Makganyene Formation have widely variable lithology, as seen in boreholes[25]. Second, the Hekpoort andesite is intercalated with the underlying Boshoek Formation, partly glaciogenic and correlative with the Makganyene Formation, at several localities[26]. Third, we and other workers[25,27] have observed, in borehole cores, apparently conformable contacts with no palaeo-weathering between the diamictite and the Ongeluk lava. Fourth, volcanic shards are abundant within the upper strata of the Makganyene Formation[25], indicating that volcanism had already commenced during late-stage glacial times. From the above arguments we contend that no significant plate motion could have occurred between deposition of the diamictite and the lava, and that palaeolatitude estimates of the latter should apply equally to the former.

Visser[28] demonstrated a glacial origin for the Makganyene diamictites, citing abundant striated and pockmarked clasts in the Griqualand West region. In addition, during our field work we found cobbles with multiple polished facets and several directions of striations from Makganyene-derived colluvium. Such textures are unlikely to have formed within non-glacial debris flows, but are common in subglacial or glaciomarine environments[24]. The glacial

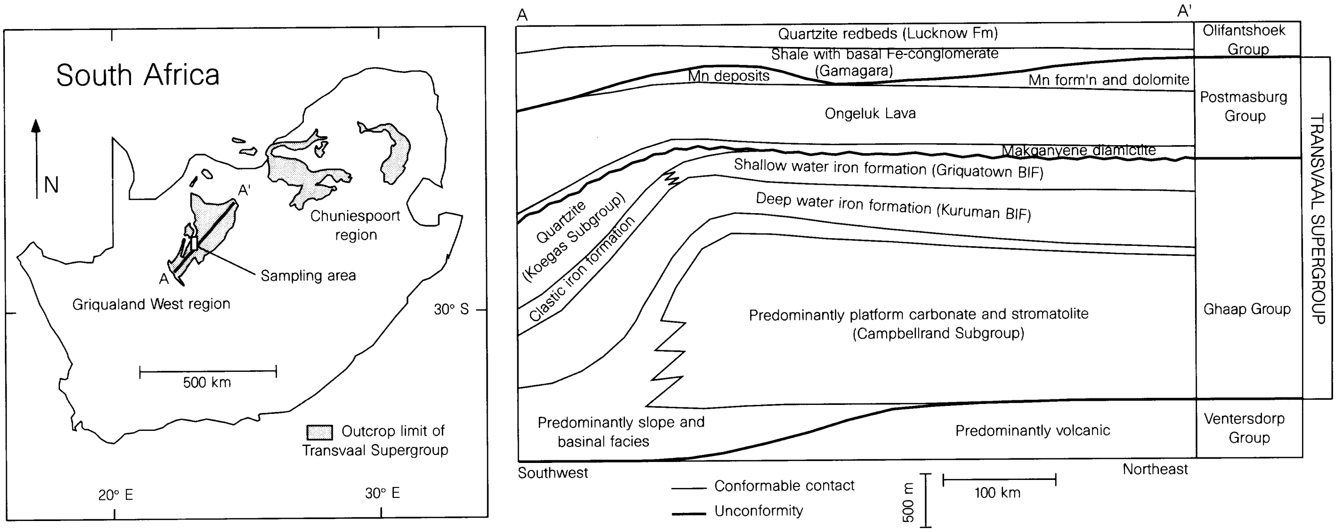

Figure 1 Regional map (left) and schematic stratigraphic overview of the Transvaal Supergroup in the Northern Cape Province[7] (right). BIF, banded iron formation.

units are fluvial–deltaic throughout the Chuniespoort region, whereas glaciomarine conditions existed in the Griqualand West region[9]. In the latter region, rafted pebbles within mudstone imply a distal environment with input from floating icebergs, and sandstone beds between diamictite bodies are interpreted as subaqueous debris flows[25]. The sub-Makganyene unconformity involves gentle warping of the lithosphere, less than 1° in the Griqualand West region, which was followed by sheetlike sedimentation over virtually all of the Kaapvaal craton (Fig. 1). Sedimentary indicators all across the craton point to a continental (northeastern or eastern) source for the deposits, ultimately the Limpopo belt or some other subsequently rifted craton[9]; thus the Makganyene Formation cannot be ascribed to local alpine glaciation sourced from either an advancing (offshore to the present west) mountainous terrain or the so-called "Vryburg arch"[8] which is a post-Transvaal anticlinal flexure now separating the once-contiguous Griqualand West and Chuniespoort 'sub-basins' (Fig. 1). The vast regional extent of the Makganyene and equivalent formations in the Chuniespoort region also suggests proximity to a continental ice sheet rather than a local montane source.

Twenty flow-units of the Ongeluk lavas were sampled from 12 localities in the Griqualand West region. Virtually all of the Ongeluk specimens exhibited two magnetic components (Fig. 2). The first to be removed, at the low alternating-field and thermal steps, is directed moderately-to-steeply up and north, coincident with the present local field (PLF) at the sampling sites (Fig. 3a). The coercivity/unblocking spectrum of this component, which is undoubtedly of Recent age, suggests that it is held partly as a viscous-remanent magnetization by multidomain grains, and partly as a chemical-remanent magnetization by goethite, which is visible along fractured surfaces within a few of the samples.

The higher-coercivity, high-temperature component, observed in 114 of 122 samples of pillow lava or massive andesite, is westerly and of shallow negative (up) inclination (Fig. 3a). Five samples of the coarse-grained rock at a single site ("OLL2") are oppositely directed; as this site may be intrusive to and slightly younger than the others, its opposite polarity is not surprising. The broad, 30–80 mT coercivity of the westerly component, as well as a narrow ~580 °C unblocking temperature spectrum, suggests that it is carried by single-domain magnetite. Most samples yielded extremely stable, linear demagnetization behaviour (Fig. 2a), conducive to principal-component analysis[29]. For some of the samples which did not demagnetize to the origin, the trajectories tended towards the present field direction, probably indicating incomplete removal of a haematitic (coercivity >80 mT) component of the Recent chemical-remanent magnetization.

A palaeomagnetic breccia test at one locality ("OVG") places a constraint on the relative ages of the magnetic components. The hyaloclastic breccia at this site is thought to have formed by explosion of the partly solidified lava on entering shallow water[30]. The larger clasts have the same megascopic lithology as the overlying and underlying pillowed and massive lavas exposed in the same road-cutting, and in some instances can be identified as fragments of chilled-rim pillows[30]. Thus, if the large volcanic clasts entrained in the breccia show similar magnetic behaviour to our samples taken from *in situ* flows, then magnetization is primary in the clasts if and only if it is primary in the flows.

As distinct from a conglomerate, whose rounded clasts imply

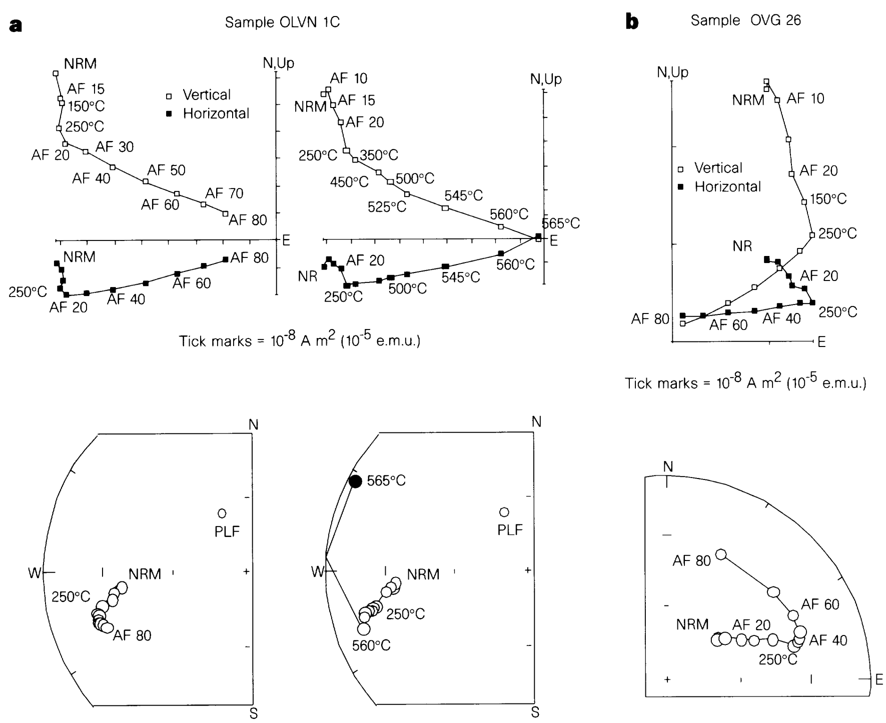

Figure 2 Representative sample demagnetization behaviour. **a**, Sample from *in situ* flow-unit. **b**, Sample from breccia clast. Orthogonal projection diagrams (top): open (solid) symbols depict projection onto the vertical (horizontal) plane. Equal-area projections (bottom): open (solid) symbols show projection onto the upper (lower) hemisphere. AF, alternating-field level in mT; PLF, present local field; NRM, natural remanent magnetization. Samples were either drilled in the field as 2.5-cm cores, or collected as oriented blocks and drilled in the laboratory. Whenever possible, samples were oriented by both magnetic and solar compasses. Cores were trimmed to 2.2 cm length. Measurement of natural remanent magnetization was followed by alternating-field (AF) and thermal demagnetization, typically measured at the following steps: 5, 10, 15 and 20 mT; 150, 200 and 250 °C; and 30–80 mT with 10 mT intervals. Following the low AF steps, a few samples were thermally demagnetized to 580 or 665 °C; demagnetization was halted when either intensity dropped to zero or spurious magnetizations appeared.

tumbling into truly random orientations, the explosion-induced hyaloclastic breccia is likely to show some differential rotation but not completely random orientations among the clasts. Our breccia test is a statistical modification of the standard palaeomagnetic conglomerate test: instead of testing against a truly uniform distribution, we compare precision of the suite of clasts with the grouping from each of the *in situ* flows. If the precision of directions from a given magnetic component is significantly lower among the clasts than the *in situ* samples, then the test is positive and magnetization of that component probably occurred before brecciation. Alternatively, if the precision among the clasts is similar to precision from each other site, then that component post-dates the brecciation and is not reliable for estimating depositional palaeolatitudes

Sixteen clasts from the breccia at locality OVG show considerable scatter of characteristic remanent magnetization relative to the massive and pillowed andesite at the same and other localities (see Fig. 3b and Supplementary Information). Individual clasts carry reproducible directions (Fig. 3c), and the suite carries a well grouped PLF overprint similar to that found at other sites (Fig. 3d). Relative precision parameters are scaled against an *F*-ratio distribution, to determine the likelihood of indistinguishable precision[31]. Common precision between the distribution of each other site and that of the breccia suite can be rejected with >99% confidence for all flow-units, except for site OLL2 (~80%), whose coarse grain size may effect different bulk magnetic properties. The cluster of some of the clast directions towards the southwest may be due to minimal rotation of these clasts during explosive brecciation, or subsequent heating by later flows, or immediate hydrothermal alteration after brecciation. Notably, these samples are from the same proximity in outcrop, with anomalously low magnetic susceptibilities; this may indicate a chemical or mineralogical change due to immediate and localized hydrothermal alteration after emplacement of the breccia[10]. Considering the suite of clasts as a whole, however, their wide dispersion rules out any pervasive, secondary remagnetization at locality OVG, and the similarity of directions from *in situ* flows at OVG with other sites supports the interpretation that the characteristic remanent magnetization components were all obtained during deposition of the lavas.

This positive breccia test, in addition to a reversely directed site, implies that the high-coercivity, high-unblocking-temperature, characteristic remanent magnetization component from the *in situ*

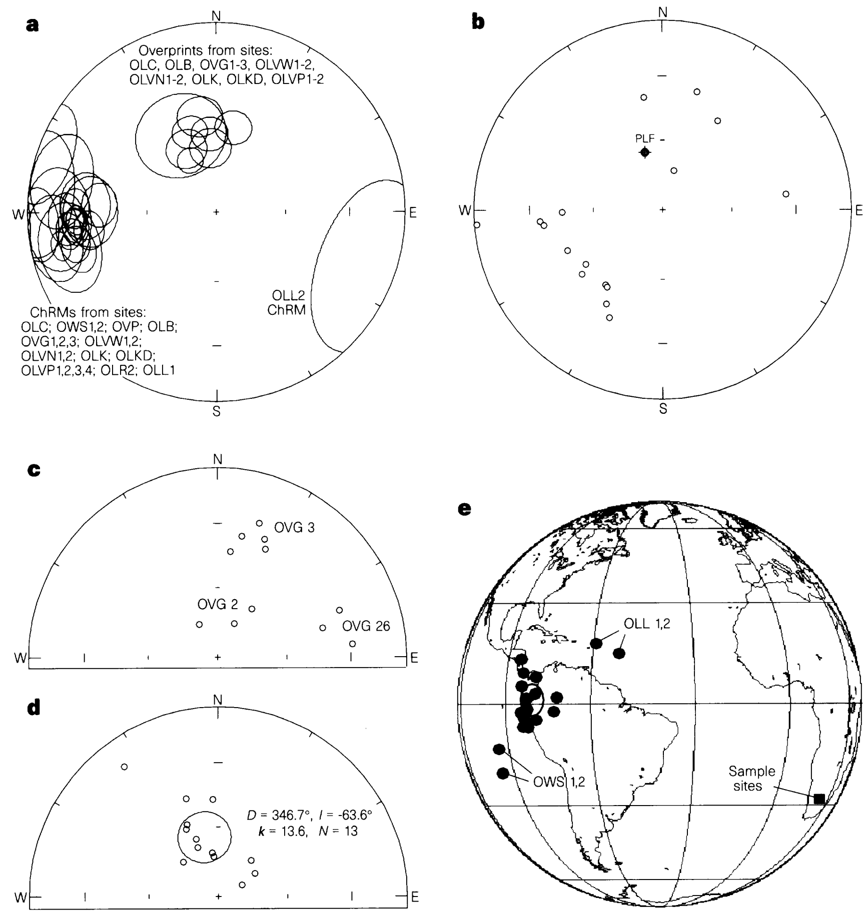

Figure 3 Summary of directional data. Large ellipses are 95% confidence intervals around Fisher mean directions from individual sites (**a–d**), or the mean palaeopole of virtual geomagnetic poles from all sites (**e**). **a–d**, Upper-hemisphere equal-area projections. **a**, Site means of characteristic remanent magnetizations (ChRMs) and overprints. Overprints are coincident with the present local field (PLF) at the sampling sites. **b**, Individual sample ChRMs from the hyaloclastic breccia best, each sample from a distinct clast. **c**, Reproducibility of discordant clast ChRMs. Internal consistency within each clast shows that the large dispersion in **b** is not spurious. **d**, Individual sample overprints from the breccia test. Good grouping about the present field direction at the sampling sites indicates the expected failure of the breccia test of the Recent overprint, and demonstrates that the wide dispersion in **b** is not caused by errors in sample orientation. *D*, declination; *I*, inclination; *k*, Fisher precision parameter; *N*, number of samples. **e**, Orthographic projection of virtual geomagnetic poles calculated from site-mean ChRMs (pole from site OLL2 inverted).

samples, is probably a thermal-remanent magnetization acquired by initial cooling of the lava flows. Within-flow scatter of directions is small, typically smaller than between-site scatter (see Supplementary Information), and the axially symmetric (Fisherian) distribution of virtual geomagnetic poles (Fig. 3e) supports the model that site-means are thermal-remanent magnetizations of geomagnetic secular variation about an axially geocentric dipole field. We find the tilt-corrected, normal-polarity palaeomagnetic pole at 0.5° N, 280.7° E, implying a depositional palaeolatitude of $11 \pm 5°$ for the Griqualand West region. On the seven-point 'Q' scale[32] of reliability, this pole rates a perfect seven.

The low palaeolatitude of the Makganyene diamictite compounds the enigma of Precambrian glaciations. Although glaciogenic deposits of generally Palaeoproterozoic age occur on many cratons, our study provides the first direct and reliable determination of any of these units. It is now documented that both of the broad intervals of Precambrian glaciation, near the beginning and end of the Proterozoic aeon, include glaciogenic sediments deposited in equatorial latitudes. This may indicate a global climate system fundamentally different (due, for example, to changes in Earth's orbital obliquity[33]) from that of the past 500 Myr, when glacial deposits were restricted largely to the polar regions. Alternatively, the low-latitude Precambrian glacial deposits could indicate severe, globally inclusive ice ages (a model called the "Snowball Earth"[34]). In that case, our planet's subsequent recoveries to more mild temperatures would indicate a remarkable resilience to extreme perturbations in climate. □

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Supplementary Information is available on *Nature's* World-Wide Web site (http://www.nature.com) or as paper copy from Mary Sheehan at the London editorial office of *Nature.*

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Table 1. Mean characteristic remanence directions and virtual geomagnetic poles for the Ongeluk Formation, Griqualand West region, South Africa.

Site/flow	South Lat.	East Long.	n/N	GDec	GInc	k	TDec	TInc	k	Plat(N)	Plong(E)
OWS1	27°07'	022°59'	5/7	239.6	-22.5	100	238.5	-26.9	99.1	-19.8	264.3
OWS2	27°07'	022°59'	6/6	246.2	-27.9	67.3	245.1	-32.4	70.0	-12.7	265.3
OVP	28°17.60'	023°19.68'	5/5	271.6	-26.0	89.8	271.6	-26.0	89.8	07.8	281.9
OLB	28°53.85'	022°48.52'	7/7	257.8	-16.9	118	257.8	-16.9	118	-06.4	279.2
OVG1	28°53.80'	022°49.26'	5/6	266.7	-26.2	54.9	267.5	-21.4	55.8	03.1	281.9
OVG2	28°53.80'	022°49.26'	6/6	265.8	-29.9	103	264.7	-25.4	103	01.9	278.5
OVG3	28°53.80'	022°49.26'	6/6	261.5	-18.8	17.9	260.9	-14.1	17.9	-04.4	282.1
Breccia	28°53.80'	022°49.26'	16/16	256.5	-62.5	3.4	255.5	-57.7	3.4	not used	
OLVW1	28°53.70'	022°50.20'	5/6	266.1	-05.8	34.5	266.1	-05.8	34.5	-02.0	288.4
OLVW2	28°53.55'	022°51.51'	6/7	270.0	-08.0	13.0	270.0	-08.0	13.0	02.0	289.3
OLVN1	28°53.55'	022°51.82'	6/6	259.8	-25.3	251	259.8	-25.3	251	-02.3	276.3
OLVN2	28°53.55'	022°51.82'	6/6	259.4	-21.9	159	259.4	-21.9	159	-03.6	277.8
OLK	28°53.60'	022°53.10'	6/6	261.3	-30.7	60.7	258.7	-24.3	59.4	-03.5	277.3
OLKD	28°53.66'	022°53.30'	8/8	264.2	-25.9	61.0	264.2	-25.9	61.0	01.6	278.2
OLVP1	28°53.62'	022°56.11'	4/4	267.4	-24.9	36.5	270.3	-33.4	36.5	09.0	277.0
OLVP2	28°53.62'	022°56.11'	4/4	269.8	-29.6	89.5	273.6	-37.8	89.8	13.0	275.7
OLVP3	28°53.68'	022°57.02'	6/6	266.8	-30.7	25.0	266.8	-30.7	25.0	05.2	276.9
OLVP4	28°53.68'	022°56.65'	6/6	261.5	-16.3	12.7	262.0	-22.1	12.7	-01.3	279.0
OLR2	28°53.59'	022°57.45'	6/6	256.6	-20.6	14.9	256.6	-20.6	14.9	-06.3	277.1
OLL1	28°53.61'	023°02.01'	6/6	289.0	-03.7	14.9	289.0	-03.7	14.9	17.5	300.8
OLL2	28°53.54'	023°02.77'	5/8	110.0	-11.1	6.0	110.0	-11.1	6.0	-14.6	128.0
Mean of 20 sites (OLL2 inverted):			114/122							00.5	280.7
										(K = 38.3, A_{95} = 5.3°)	

n, number of samples used; N, total number of samples; GDec, mean geographic (*in situ*) declination; GInc, mean geographic inclination; k, estimate of Fisher precision parameter; TDec, mean tilt-corrected declination; TInc, mean tilt-corrected inclination; Plat, pole latitude; Plong, pole longitude; K, precision parameter of site means; A_{95}, semi-radius of 95% cone of confidence.

Palaeoclimatology

An ice age in the tropics

Alan J. Kaufman

One of the enduring enigmas of Proterozoic Earth history (up until almost half a billion years ago) is the intimate association of glacial deposits with carbonates that appear to have formed in warm tropical seas. This palaeoclimatic paradox implies that, billions of years ago, Earth's surface thermostat was occasionally turned down low enough to allow glaciers to spread from the poles to very near the Equator, blanketing most of the planet in ice and snow. In contrast, the glaciers that scoured the Northern Hemisphere over the past few million years only reached as far south as the Ohio River valley in North America, and a line from near London to Kiev in Europe. The paradox might instead be explained by the formation of ancient carbonates in cold water at high latitudes, but support for at least one "Snowball Earth"[1] comes from a new palaeomagnetic study by Evans *et al.* on page 262 of this issue[2] — it suggests that glaciers covered most of southern Africa over two billion years ago, when that region sat roughly 11 degrees from the Equator.

Surface temperatures must have dropped considerably for glaciers to have existed in the tropics. The cause of the temperature drop was probably a decline in the atmospheric level of carbon dioxide, the greenhouse gas believed to be the main regulator of Earth's climate. The transfer of water from the oceans to a global network of Proterozoic glaciers would have lowered relative sea level, making the ocean more dense and salty; and the presence of thick, extensive sea ice might have caused the oceans to stagnate, by slowing down wind-driven circulation and blocking the sunlight that fuels biological photosynthesis and oxygen production. Covered with ice, the Earth would have reflected most of the Sun's warming rays back into space. Only a catastrophic event, like a huge volcanic eruption, a comet or asteroid impact, the sudden release of methane hydrates, or the overturn of a deep, stagnant ocean, could have pumped enough carbon dioxide back into the atmosphere to melt the planet's icy shell.

Some time after the Palaeoproterozoic ice age in Africa, molten rock erupted onto the surface to form the widespread Ongeluk Formation. Evans and colleagues make a strong case that this thick pile of volcanic rocks has remained largely unaltered, so that after two billion years certain iron-rich minerals still record the direction of Earth's magnetic field, like tiny compasses frozen in time. The angle of the preserved magnetic field is used to determine the latitude at which the rocks formed. The authors further suggest that there is no significant hiatus between these tropical lavas and the underlying glacial rocks. That is critical, because the age of this glaciation is not well known. A 20- to 40-million-year break between the ice age and the volcanic episode would have allowed the southern African continent enough time to travel from high to low latitudes. If, on the other hand, there is no time missing between the two units, the thick lavas may mean that the ice age was ended by the volcanic release of massive amounts of carbon dioxide to the atmosphere.

There are several other Palaeoproterozoic glacial deposits recognized worldwide, although the exact correlation of the ice ages that they mark is not well established. In Ontario and Wyoming, for example, there is evidence of three discrete Palaeoproterozoic glaciations (Fig. 1), but which, if any, of these matches the South African example is difficult to say. Immediately overlying the second of the North American glacial deposits is a layer of the enigmatic carbonates noted above, which are distinctive in both their fine-grained texture and chemistry, specifically in their carbon-isotope compositions[3,4]. Relative to most carbonates deposited in the oceans over the past 2,500 million years, these 'cap' carbonates atop both Palaeoproterozoic and Neoproterozoic glacial rocks have consistently low $\delta^{13}C$ (a measure of the ratio of ^{13}C to ^{12}C; see Fig. 2), suggesting that they were formed under very strange circumstances, by modern standards.

In the Neoproterozoic, where palaeomagnetic data also point to two low-latitude glaciations[5,6], strong positive-to-negative $\delta^{13}C$ excursions in carbonates bracket at least four discrete ice ages[7,8]; and the highly positive $\delta^{13}C$ values beneath Neoproterozoic glaciations match those in some Palaeoproterozoic carbonates[9]. At present, however, poor age constraints and stratigraphic uncertainties make it unclear whether these older biogeochemical event markers precede or post-date glaciation.

The remarkable positive-to-negative trends in $\delta^{13}C$ encompassing Proterozoic glaciations suggest that carbon cycling is at the heart of the palaeoclimatic paradox. These variations are consistent with the

Figure 1 **The smooth surface of a nearly two-billion-year-old glacial deposit in Ontario, Canada, polished and striated by modern continental glaciers. (Photo courtesy of P. F. Hoffman.)**

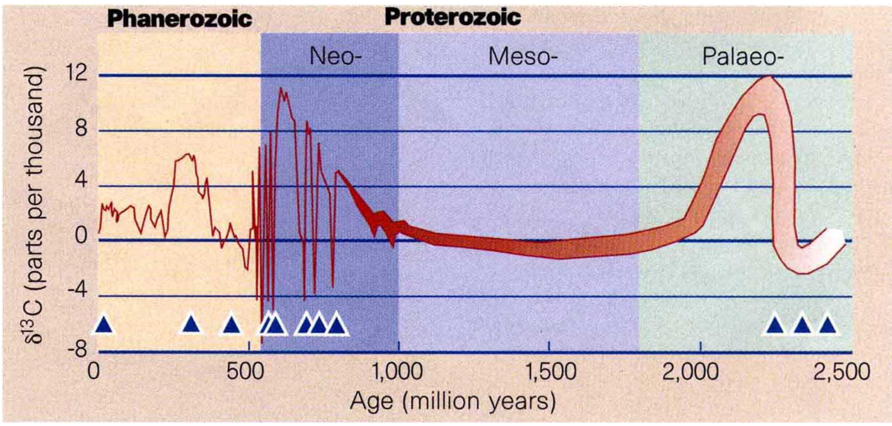

Figure 2 **Carbon-isotope variation in sea water over 2,500 million years, as determined by the analysis of marine carbonates. Strong positive-to-negative trends in the relative isotope ratio $\delta^{13}C$ bracket Neoproterozoic (and perhaps Palaeoproterozoic) glacial deposits (see triangles), and suggest that carbon cycling is at the heart of long-term global climatic change.**

hypothesis that high biological productivity (which effectively distils ^{12}C from sea water) in nutrient-rich Proterozoic oceans drove the $\delta^{13}C$ of surface water to positive extremes before the glaciation, helping the growth of continental ice sheets by removing carbon dioxide from the atmosphere[7,8]. The negative $\delta^{13}C$ values in the cap carbonates that follow these ancient glaciations might best be explained by the rapid mixing of shallow seas with deep oceans that are chemically and isotopically distinct[7,8,10,11]. Note that this process, which assumes that post-glacial Proterozoic oceans were somehow stirred more rapidly as the glaciers melted and surface temperatures warmed, is the opposite of how oceans are thought to have mixed after the most recent glaciations. If the ancient deep ocean was also a storehouse of carbonate alkalinity[10,11], degassing and the rapid precipitation of the cap carbonates during post-glacial mixing would have pumped enough carbon dioxide back into the atmosphere to ensure an end to the ice age.

The chilling possibility of Proterozoic glaciers in the tropics, inferred from palaeomagnetic data and from carbon-isotope evidence that is consistent with biological control of ice ages, highlights the many differences between recent and ancient Earth history. In particular, models that attribute the drawdown of atmospheric carbon dioxide — and the subsequent growth of continental glaciers — to increased chemical weathering of young mountains (over the past few million years, the Himalayas and Tibetan Plateau[12], for example) may be inappropriate for our understanding of long-term global climate change. □

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Dosage compensation

Remodelling chromatin with RNA

Huntington F. Willard and Helen K. Salz

One of the fundamental differences between males and females is the number of X chromosomes. Because some functions of the X chromosome require equal expression in the two sexes, several types of dosage-compensation system have evolved that have the effect of attenuating the possible phenotypic consequences of this difference in chromosome content. In the fruitfly *Drosophila*, transcription of most of the genes on the single male X chromosome is upregulated compared with expression from each of the two female Xs (Fig. 1). In nematodes, by contrast, genes on the two hermaphrodite X chromosomes are downregulated compared with genes on the single male X. And in mammals, most of the genes on one of the two female X chromosomes are not transcribed at all due to X-chromosome inactivation (reviewed in ref. 1). Although these three approaches to dosage compensation — hypertranscription, hypotranscription and transcriptional repression — are not obviously related mechanistically, studies including the papers by Herzing *et al.*[2] and Lee and Jaenisch[3] on pages 272 and 275 of this issue, and two reports in *Cell*[4,5], indicate a possible link: the complexes that are used to remodel chromatin structure on the X chromosome in each system show intriguing and unexpected parallels involving non-coding RNA molecules.

The mechanisms of dosage compensation are each reflected in changes in the structure of chromatin in the X chromosome. In the interphase nucleus of a female mammalian cell, the inactive X chromosome takes on a distinct heterochromatic form, which was recognized as the Barr body as early as 1949 (ref. 6). In *Drosophila*, the 'bloated' appearance of the single male X chromosome compared with the two female X chromosomes was first noted in the 1930s, and it was attributed by Dobzhansky[7] to the differential accumulation of "some products of gene activity" in the two sexes. Studies from Meyer and colleagues indicated that dosage compensation in nematodes is accomplished by the differential condensation of chromatin on the X chromosome in that organism as well[8,9].

In mammals, X-chromosome inactivation is under the control of a single *cis*-acting locus called the X-inactivation centre. Within this region, the most likely candidate identified to date is the non-coding *Xist* gene, which is expressed only from the inactive X chromosome, and has been implicated in the establishment of X inactivation on the basis of genetic and developmental data from humans and mice[10]. The RNA product of *Xist* associates closely with the inactive X chromosome in an RNA–Barr body complex. Now, Herzing *et al.*[2] and Lee and Jaenisch[3] have introduced ectopic copies of *Xist* into autosomes in murine embryonic stem cells, and they have recapitulated in these autosomes almost all of the molecular and chromosomal features that characterize X inactivation — namely, expression of *Xist* and localization of the *Xist* RNA in *cis*, gene inactivation, late DNA replication, and histone H4 hypoacetylation.

At least some of these effects can be seen with a cosmid containing the *Xist* gene alone[2], indicating that *Xist* probably is the X-inactivation centre and that it acts at the RNA level to remodel chromatin and to promulgate the X-inactivation signal along one of the female X chromosomes (Fig. 2). But significant questions remain. To what extent is the *Xist* RNA a required part of the chromatin-remodelling complex? Also, what other partners might be part of such a complex, and how does this suspected ribonucleoprotein–chromosome complex work in the context of the Barr body?

In flies, it is the genes on the male X chromosome that undergo chromosome-specific regulation. Four genes have been identified which are only required for hypertranscription of the male X chromosome, and they are named for their mutant phenotypes: *male-specific lethal-1*, *male-specific lethal-2*, *male-*

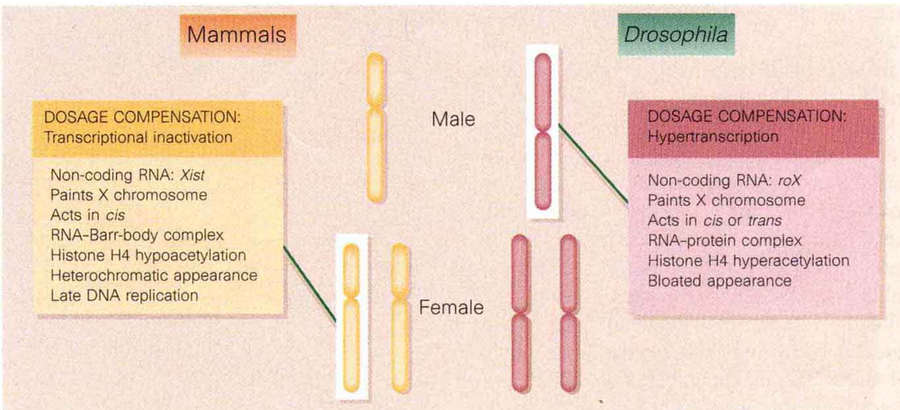

Figure 1 **Comparison of dosage-compensation mechanisms and consequences in mammals and *Drosophila*.**