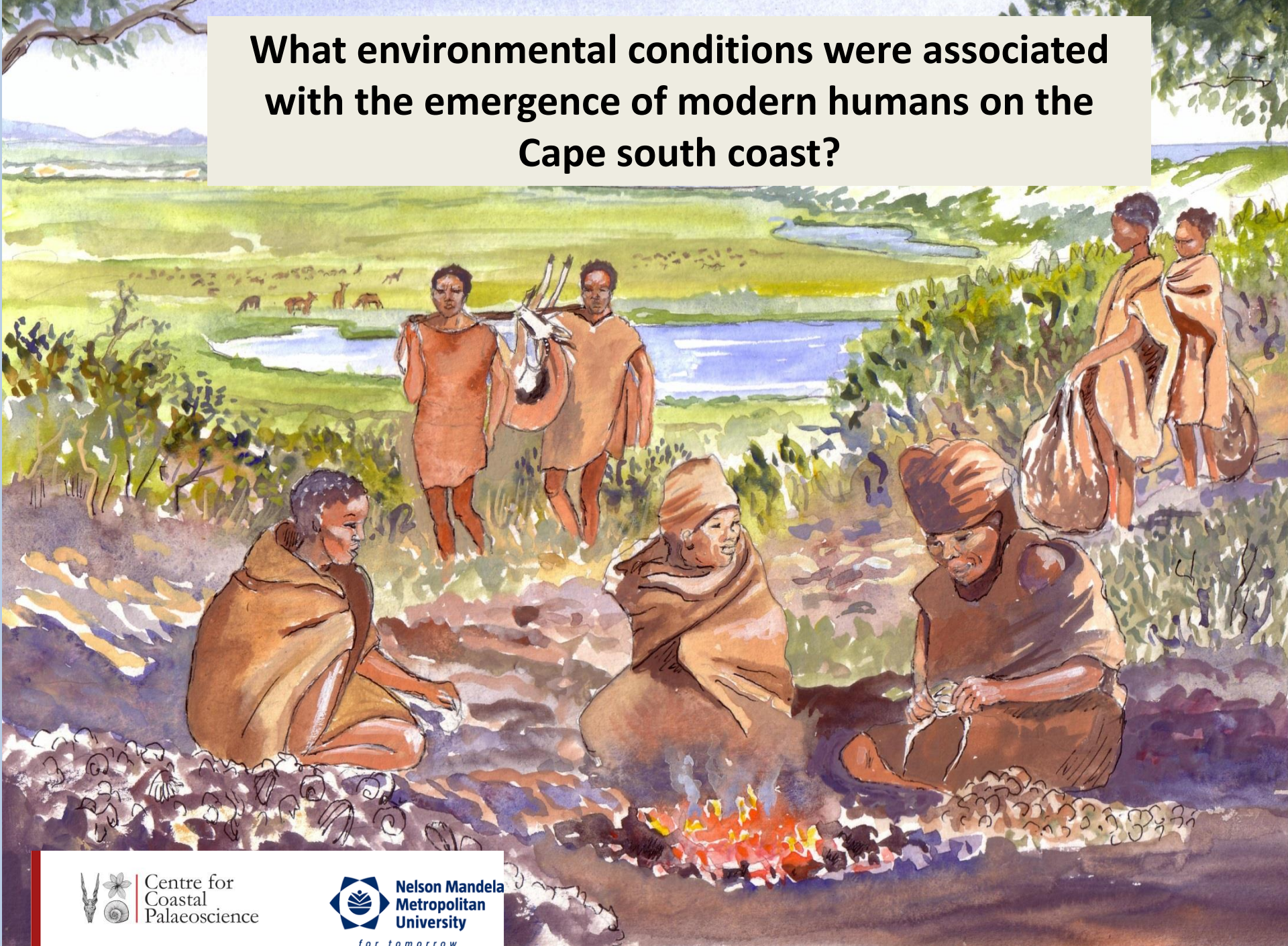


# What environmental conditions were associated with the emergence of modern humans on the Cape south coast?





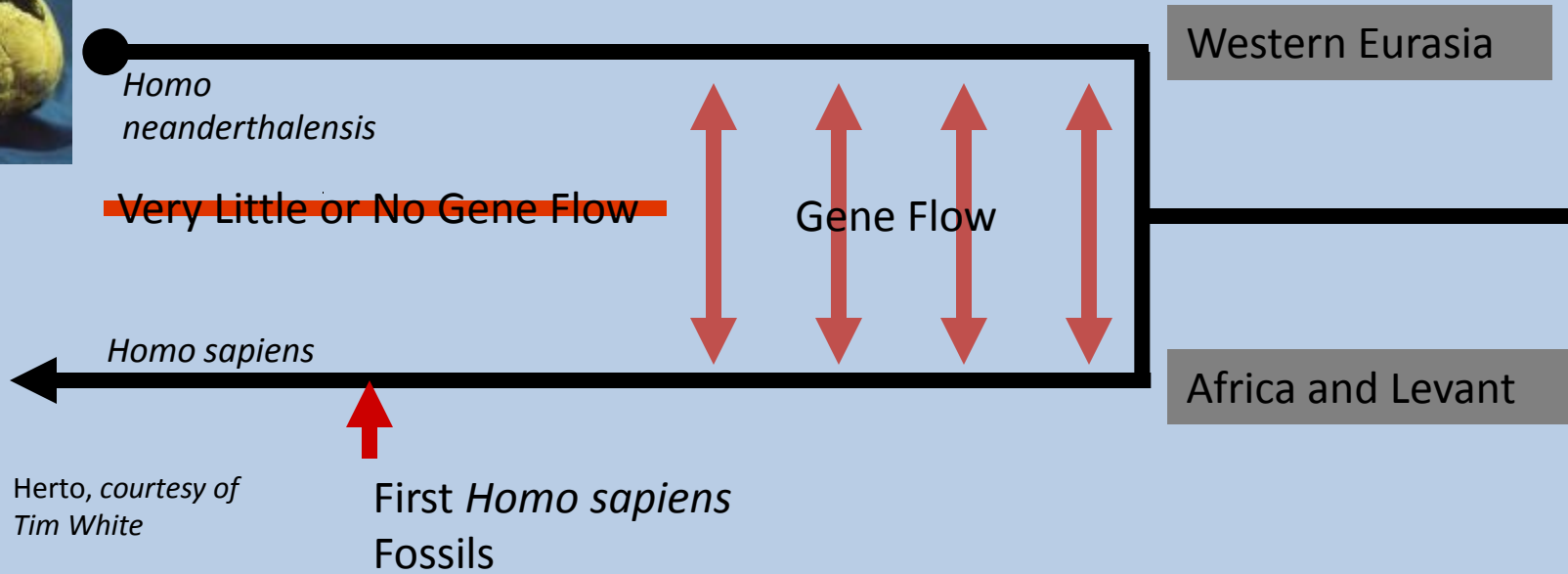
La Chapelle, courtesy of Yoel Rak



Bodo, courtesy of Tim White

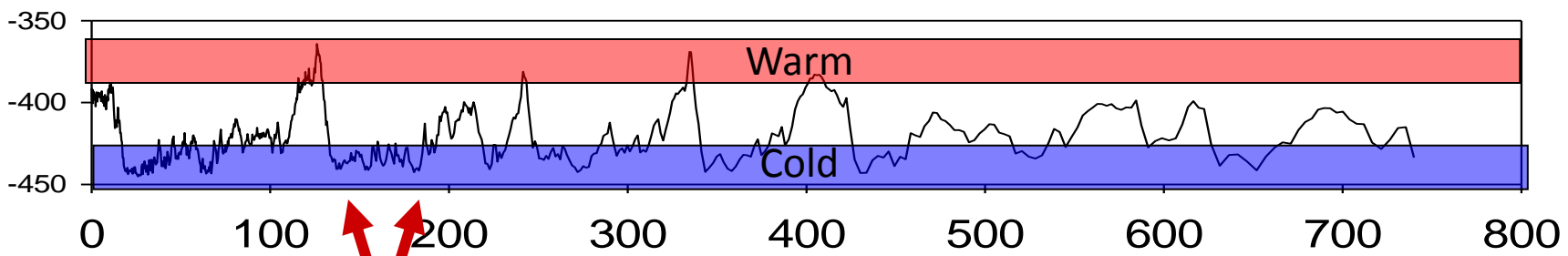


Herto, courtesy of Tim White



delta D EPICA

Ice Core



Long Cold Glacial Stage

## First Ancient Mitochondrial Human Genome from a Prepastoralist Southern African

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<sup>6</sup>Central Clinical School, The University of Sydney, Camperdown, New South Wales, Australia

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<sup>8</sup>Medical Faculty, University of New South Wales, Australia

<sup>†</sup>These authors contributed equally to

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Accepted: September 3, 2014

Data deposition: Assembled and

**Modern humans emerged in Southern Africa 108–157 000 years ago from an effective population size of ca. 9 000 individuals**

### Abstract

The oldest contemporary human mitochondrial lineages arose in Africa. The earliest divergent extant maternal offshoot, namely haplogroup L0d, is represented by click-speaking forager peoples of southern Africa. Broadly defined as Khoesan, contemporary Khoesan are today largely restricted to the semidesert regions of Namibia and Botswana, whereas archeological, historical, and genetic evidence promotes a once broader southerly dispersal of click-speaking peoples including southward migrating pastoralists and indigenous marine-foragers. No genetic data have been recovered from the indigenous peoples that once sustained life along the southern coastal waters of Africa prepastoral arrival. In this study we generate a complete mitochondrial genome from a 2,330-year-old male skeleton, confirmed through osteological and archeological analysis as practicing a marine-based forager existence. The ancient mtDNA represents a new L0d2c lineage (L0d2c1c) that is today, unlike its Khoe-language based sister-clades (L0d2c1a and L0d2c1b) most closely related to contemporary indigenous San-speakers (specifically Ju). Providing the first genomic evidence that prepastoral Southern African marine foragers carried the earliest diverged maternal modern human lineages, this study emphasizes the significance of Southern African archeological remains in defining early modern human origins.

**Key words:** ancient DNA, mitochondrial genome, Khoesan, southern Africa, marine foragers, archeological skeletons.

Southern Africa has arguably the richest and oldest fossil record of anatomically modern human existence outside of east Africa (Mitchell 2002; Brown et al. 2009, 2012; Marean 2010). The first genetic evidence for the significant role southern Africa has played in modern human evolution was provided using patterns of DNA variation in the maternally derived mitochondrial DNA (mtDNA) of contemporary populations (Chen et al. 1995; Ingman et al. 2000; Lombard et al. 2013). Concurring with archeological estimations (McDougall et al. 2005), mtDNA-derived molecular genetic age

estimations place modern human emergence around 200 ka (Behar et al. 2008). Sequencing of complete mtDNAs from contemporary populations has dramatically improved the resolution of the global human maternal phylogenetic tree. The first emerging major haplogroup L0d is estimated to have split from the remaining L0-lineages around 150 ka (Behar et al. 2008; Soares et al. 2009). Today this earliest diverging extant maternal lineage is largely restricted to Southern African populations, in particular the click-speaking forager or Khoesan peoples (Gonder et al. 2007; Tishkoff et al. 2007; Behar et al.

## Bayesian inference of ancient human demography from individual genome sequences

Ilan Gronau<sup>1</sup>, Melissa J Hubisz<sup>1</sup>, Brad Gulko<sup>2</sup>, Charles G Danko<sup>1</sup> & Adam Siepel<sup>1</sup>

Whole-genome sequences provide a rich source of information

We attempted to investigate these issues using recently released humans<sup>13–17</sup>. Although far have emphasized the ry of new genetic variants tions, these data are also on. We examined the p-b individuals from six different individuals is a member of ations of southern Africa

and integrating over possible phasings of diploid genotypes. We also describe a custom pipeline for genotype inference to mitigate biases from heterogeneous sequencing technologies and coverage levels. Our analysis indicates that the San population of southern Africa diverged from other human populations approximately 108–157 thousand years ago, that Eurasians diverged from an ancestral African population 38–64 thousand years ago, and that the effective population size of the ancestors of all modern humans was ~9,000.

During the past several decades, investigators from various disciplines have produced a broad outline of the events that gave rise to major human population groups drawing from genetic, anthropological and archaeological evidence<sup>1</sup>. The general picture that has emerged is that anatomically modern humans arose roughly 200 thousand years ago (kya) in eastern or southern Africa, that a small tribe began to expand throughout Africa ~100 kya, that a major migration out of Africa occurred ~40–60 kya and that the descendants of these migrants subsequently populated Europe, Asia and the remaining inhabitable regions of the world, possibly with some introgression from archaic hominids<sup>2,3</sup>. This outline is supported by analyses of mitochondrial and Y-chromosomal data<sup>4,5</sup>, autosomal microsatellite markers<sup>6,7</sup>, sequences for selected autosomal loci<sup>8–11</sup> and genome-wide genotyping data<sup>12</sup>. Nevertheless, much remains unknown about early human demography. Indeed, current estimates of key parameters such as the date of the migration out of Africa often vary by factors of two or three.

Known collectively as the San<sup>12</sup>. Along with other indigenous groups from central and southern Africa<sup>13,14</sup>, the San population shows the highest known levels of genetic divergence from other human populations and therefore should be highly informative about ancient human demography. For reasons of statistical power, our demographic analysis focused on the timing of early divergence events between major population groups, in particular between the San population and other groups (the 'San divergence'; Fig. 1) and between the Eurasians and other African groups (the 'African-Eurasian divergence').

In analyzing these data, we used a Bayesian statistical approach, based on coalescent theory, that was originally developed for individuals belonging to closely related but distinct species such as human, chimpanzee and gorilla<sup>20,21</sup>. This approach (as implemented in the computer program MCMCcoal) derives information about ancestral population sizes and population divergence times from the patterns of variation in the geneses at many neutrally evolving loci given a

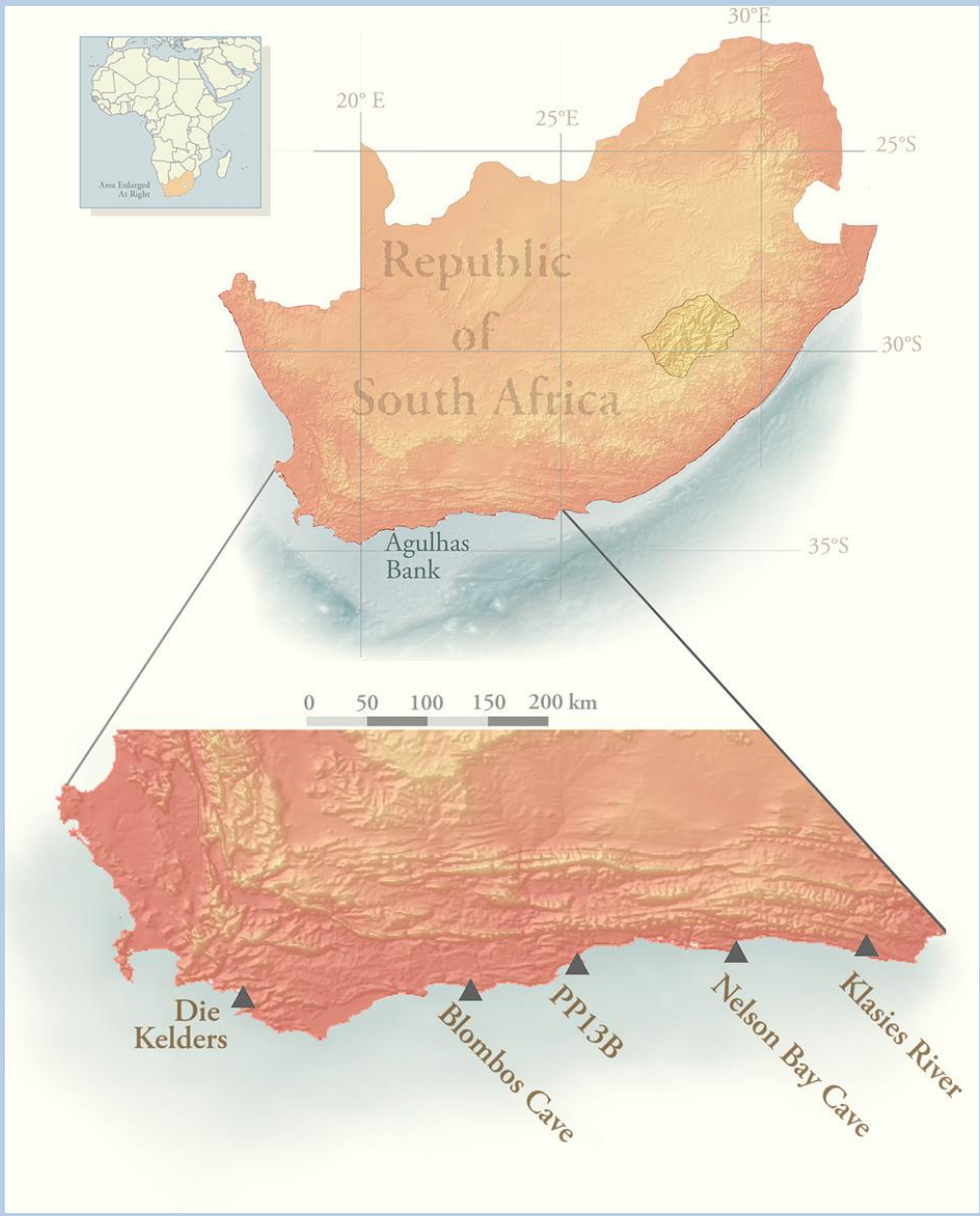
**Table 1 Individual genomes analyzed here**

Genome <sup>a</sup>	Population	Technology <sup>b</sup>	Reads <sup>c</sup>	Redundancy <sup>d</sup>	Coverage <sup>e</sup>	Depth <sup>f</sup>	HQCF <sup>g</sup>	Reference
Venter	European	Sanger	800 bp PE	7.5	0.912	8.4	0.577	13
NA18507	Yoruban	Illumina	35 bp PE	40.6	0.900	41.1	0.672	14
YH	Han Chinese	Illumina	35 bp PE	36.0	0.896	25.4	0.671	15
SJK	Korean	Illumina	36,75 bp	29.0	0.903	19.7	0.672	16
ABT	Bantu	SOLID	49 bp	>30.0	0.874	21.4	0.641	17
KB1	San	Illumina <sup>h</sup>	76 bp	23.1	0.901	23.6	0.621	17

<sup>a</sup>Genome identifiers are summaries of sequenced individuals (Venter). Identifiers for Control DNA samples (NA18507) or abbreviations introduced in published papers (YH, SJK, ABT and KB1). <sup>b</sup>Sequencing technology: Sanger; Sanger capillary sequencing; Illumina; Illumina Genome Analyzer; SOLiD; SOLiD system by Applied Biosystems. <sup>c</sup>Average read length in bp and whether or not paired-end (PE) reads were used. <sup>d</sup>Sequencing redundancy, or fold coverage, as reported in the previously published paper (see refs. column for the paper used). <sup>e</sup>Fraction of the genome covered by uniquely aligned reads according to the pipeline used here. <sup>f</sup>Average number of uniquely aligned reads at positions having at least one uniquely aligned read excluding duplicate reads. <sup>g</sup>Fraction of the genome covered by aligned reads that passed data quality filters. <sup>h</sup>KB1 was sequenced using both the 454 and Illumina methods, but the current analysis used the more abundant Illumina data.

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# LETTERS

## Early human use of marine resources and pigment in South Africa during the Middle Pleistocene

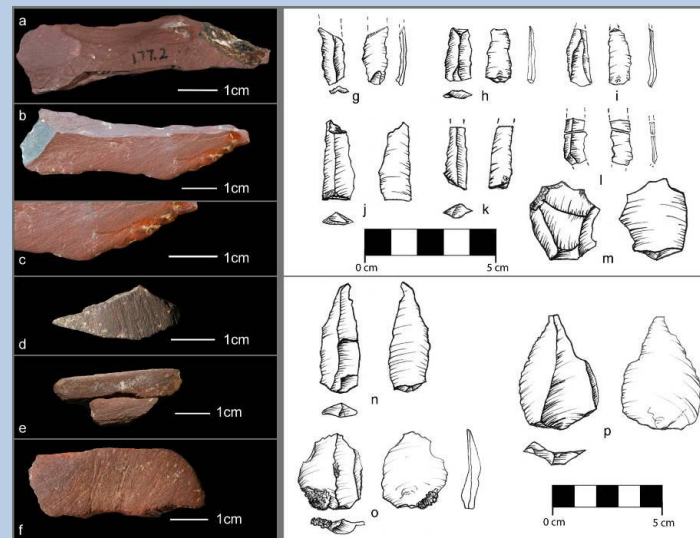
Curtis W. Marean<sup>1</sup>, Miryam Bar-Matthews<sup>3</sup>, Jocelyn Bernatchez<sup>2</sup>, Erich Fisher<sup>4</sup>, Paul Goldberg<sup>5</sup>, Andy I. R. Herries<sup>6</sup>, Zenobia Jacobs<sup>7</sup>, Antonieta Jerardino<sup>8</sup>, Panagiotis Karkanas<sup>9</sup>, Tom Minichillo<sup>10</sup>, Peter J. Nilssen<sup>11</sup>, Erin Thompson<sup>1</sup>, Ian Watts<sup>12</sup> & Hope M. Williams<sup>2</sup>



Brown mussel  
(*Perna Perna*)



Alikreukal  
(*Turbo sarmaticus*)



Ochre pigment and stone tools

**165 000 years ago**

# Fire As an Engineering Tool of Early Modern Humans

Kyle S. Brown,<sup>1,2</sup> Curtis W. Marean,<sup>2</sup> Andy I. R. Herries,<sup>3,4</sup> Zenobia Jacobs,<sup>5</sup> Chantal Tribolo,<sup>6</sup> David Braun,<sup>1</sup> David L. Roberts,<sup>7</sup> Michael C. Meyer,<sup>5</sup> Jocelyn Bernatchez<sup>2</sup>

[www.sciencemag.org](http://www.sciencemag.org) SCIENCE VOL 325 14 AUGUST 2009



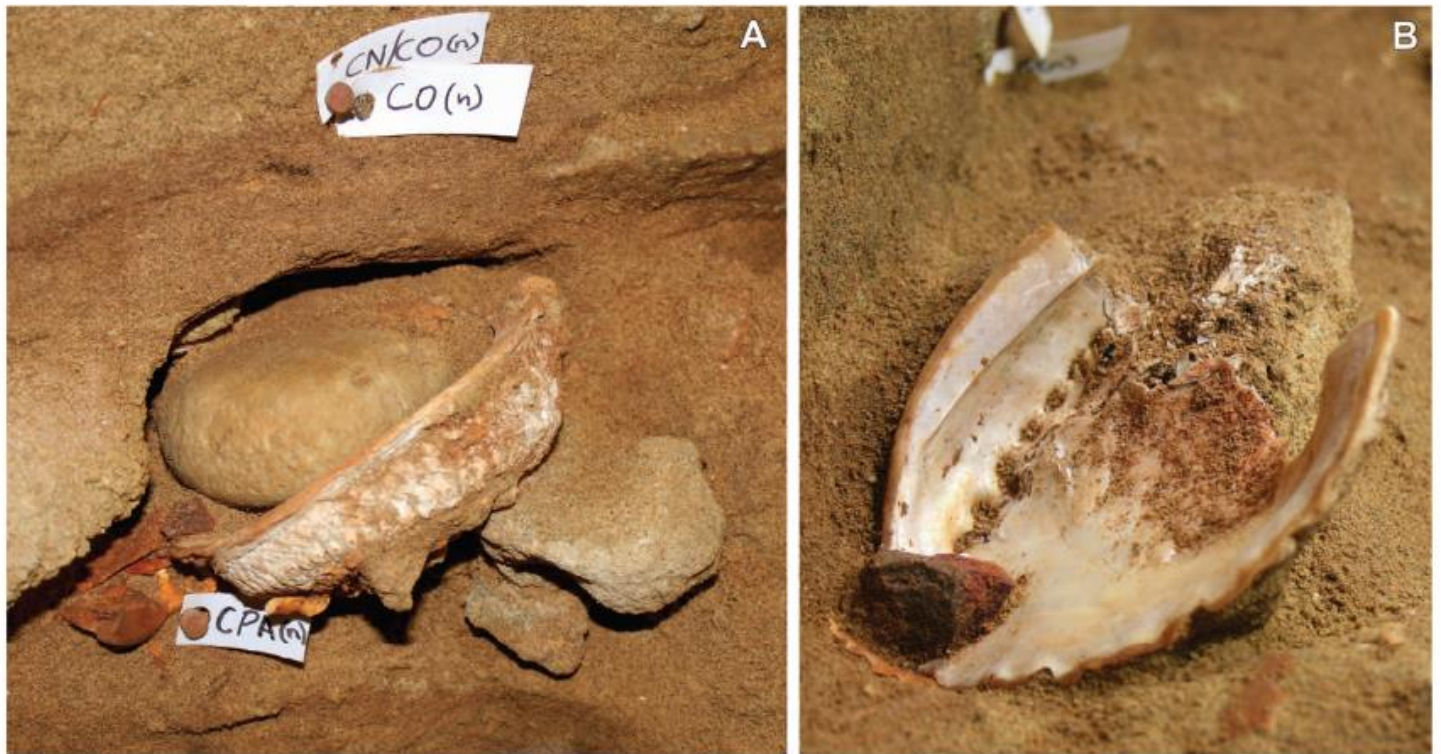
162,000 years Ago

# A 100,000-Year-Old Ochre-Processing Workshop at Blombos Cave, South Africa

Christopher S. Henshilwood,<sup>1,2\*</sup> Francesco d'Errico,<sup>3,1</sup> Karen L. van Niekerk,<sup>1</sup> Yvan Coquinot,<sup>4</sup> Zenobia Jacobs,<sup>5</sup> Stein-Erik Lauritzen,<sup>6</sup> Michel Menu,<sup>4</sup> Renata García-Moreno<sup>3</sup>

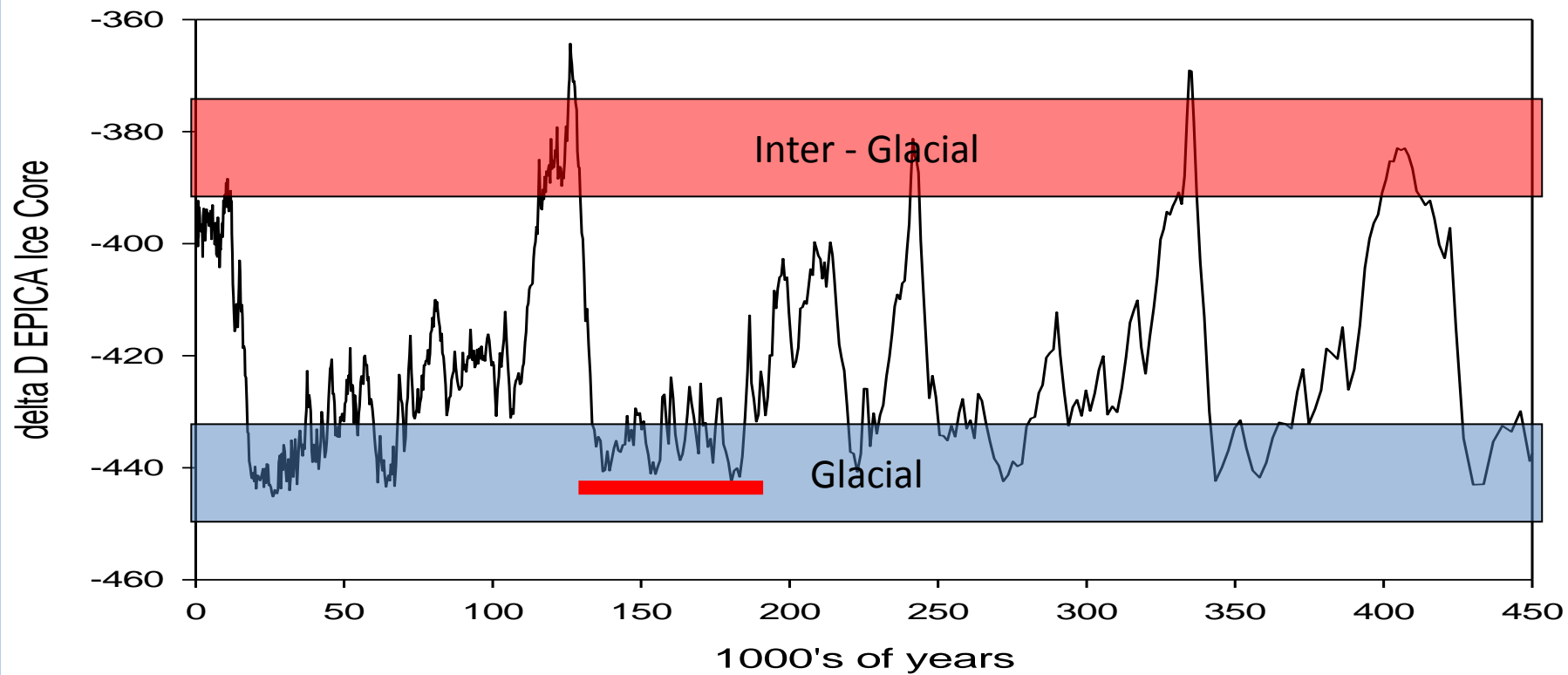
www.sciencemag.org SCIENCE VOL 334 14 OCTOBER 2011

## Ochre and the Sea Come Together

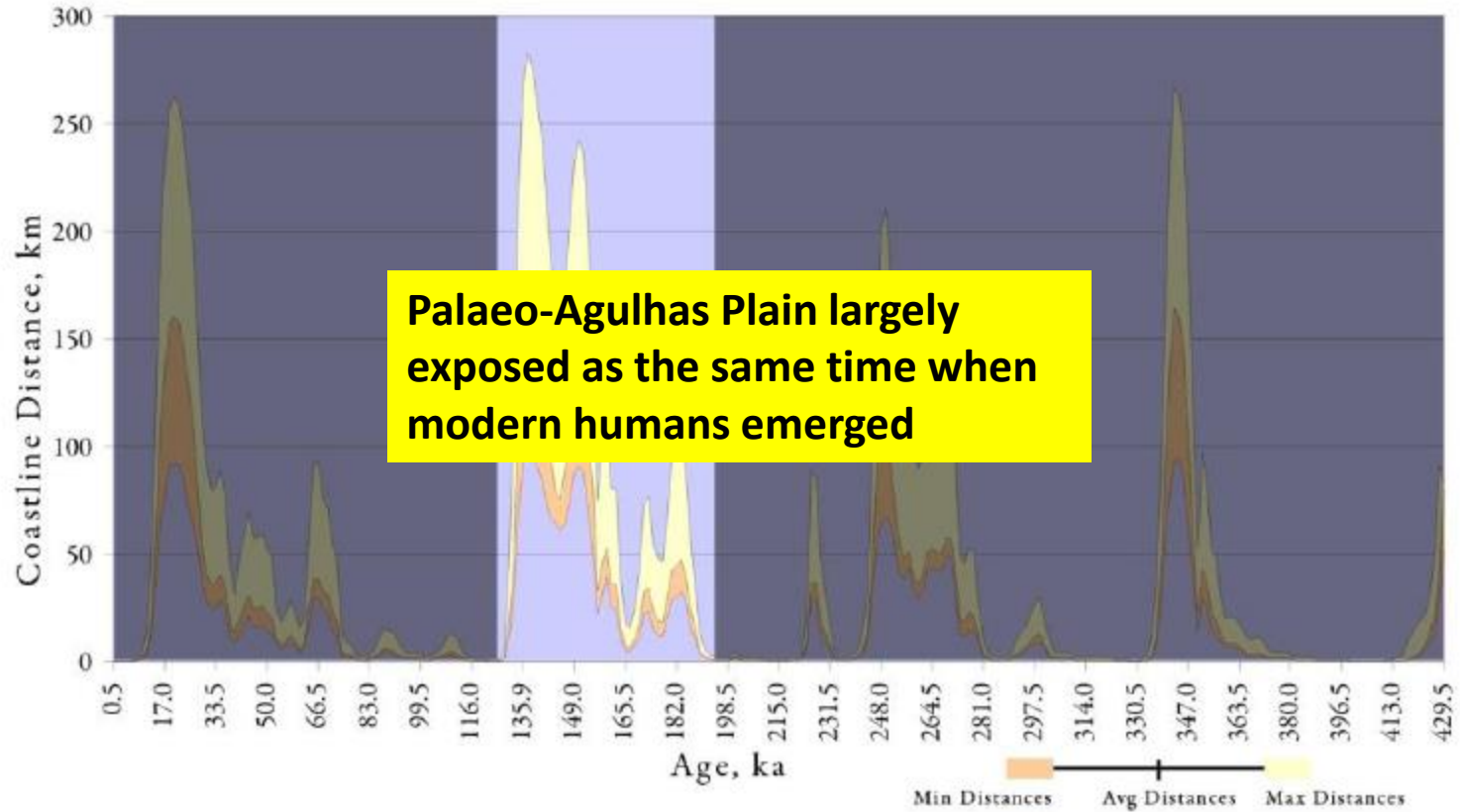


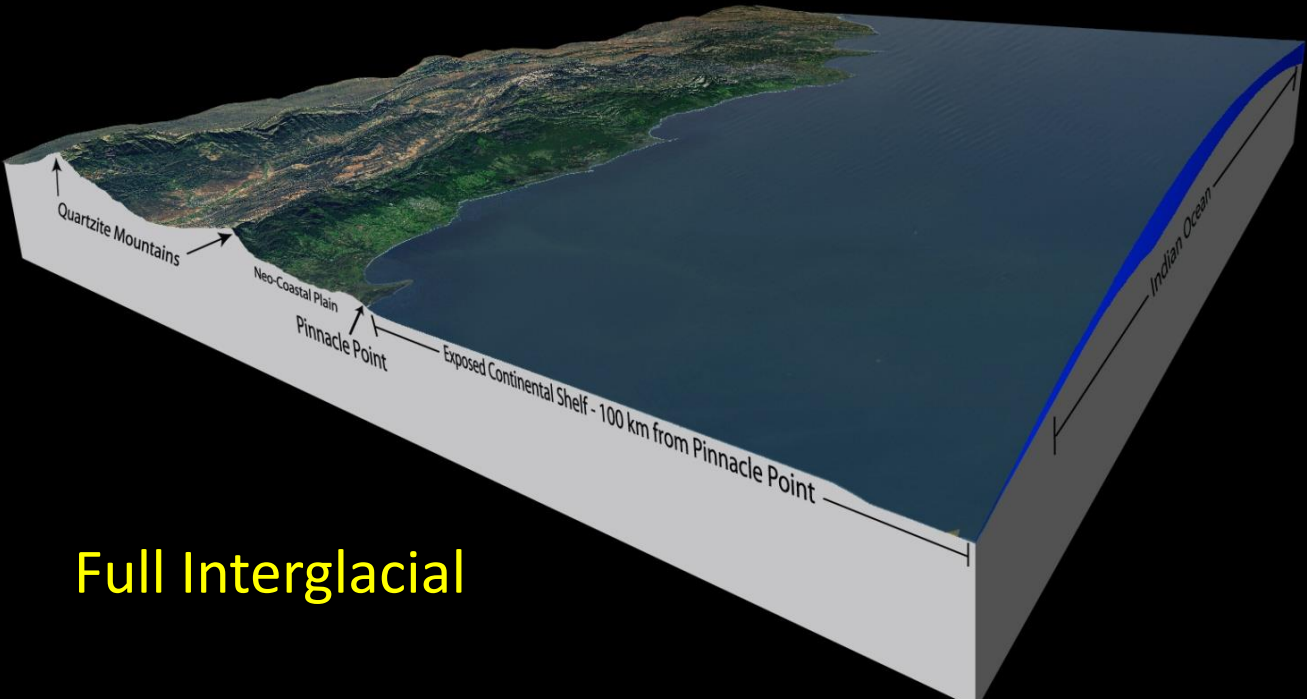
**Fig. 1.** Ochre-processing toolkits in situ showing Tk1 (A) and Tk2 (B). [Images: G. Moëll Pedersen]



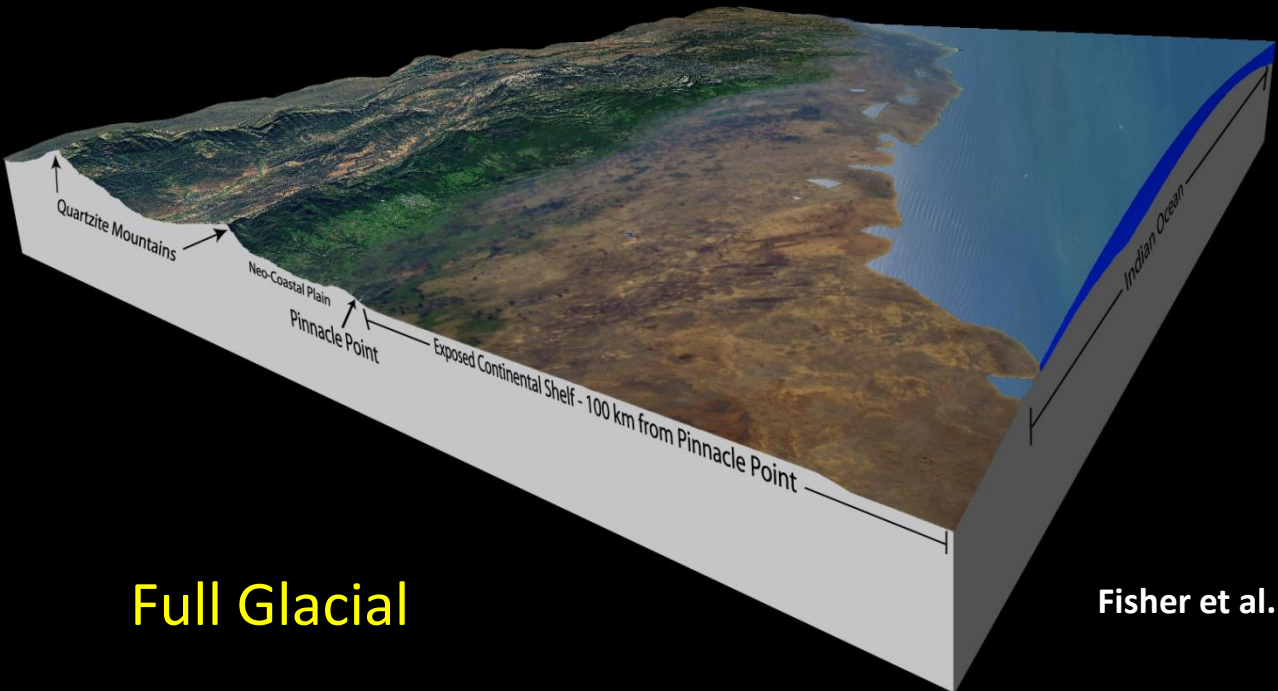


# MIS6

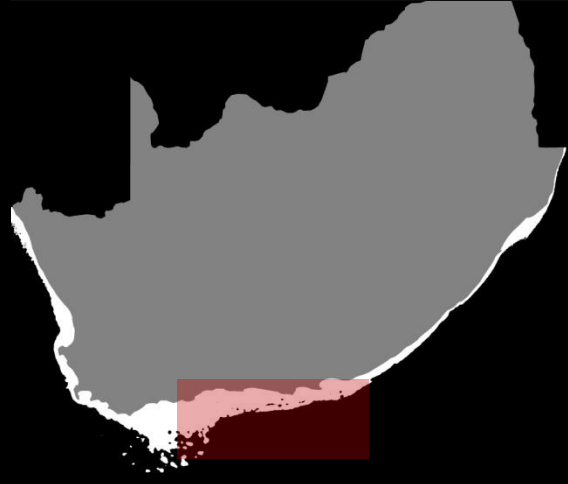




Full Interglacial

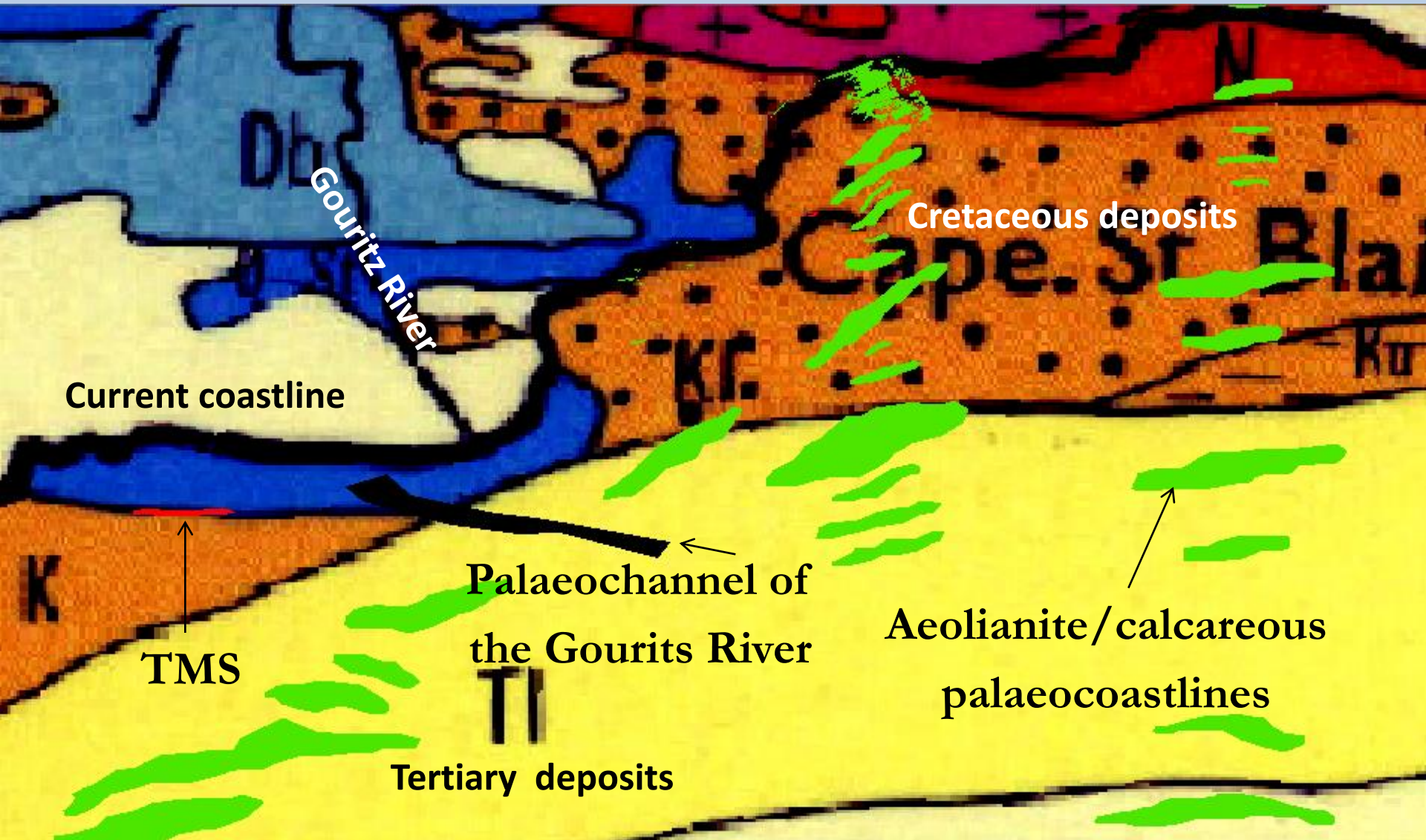


Full Glacial

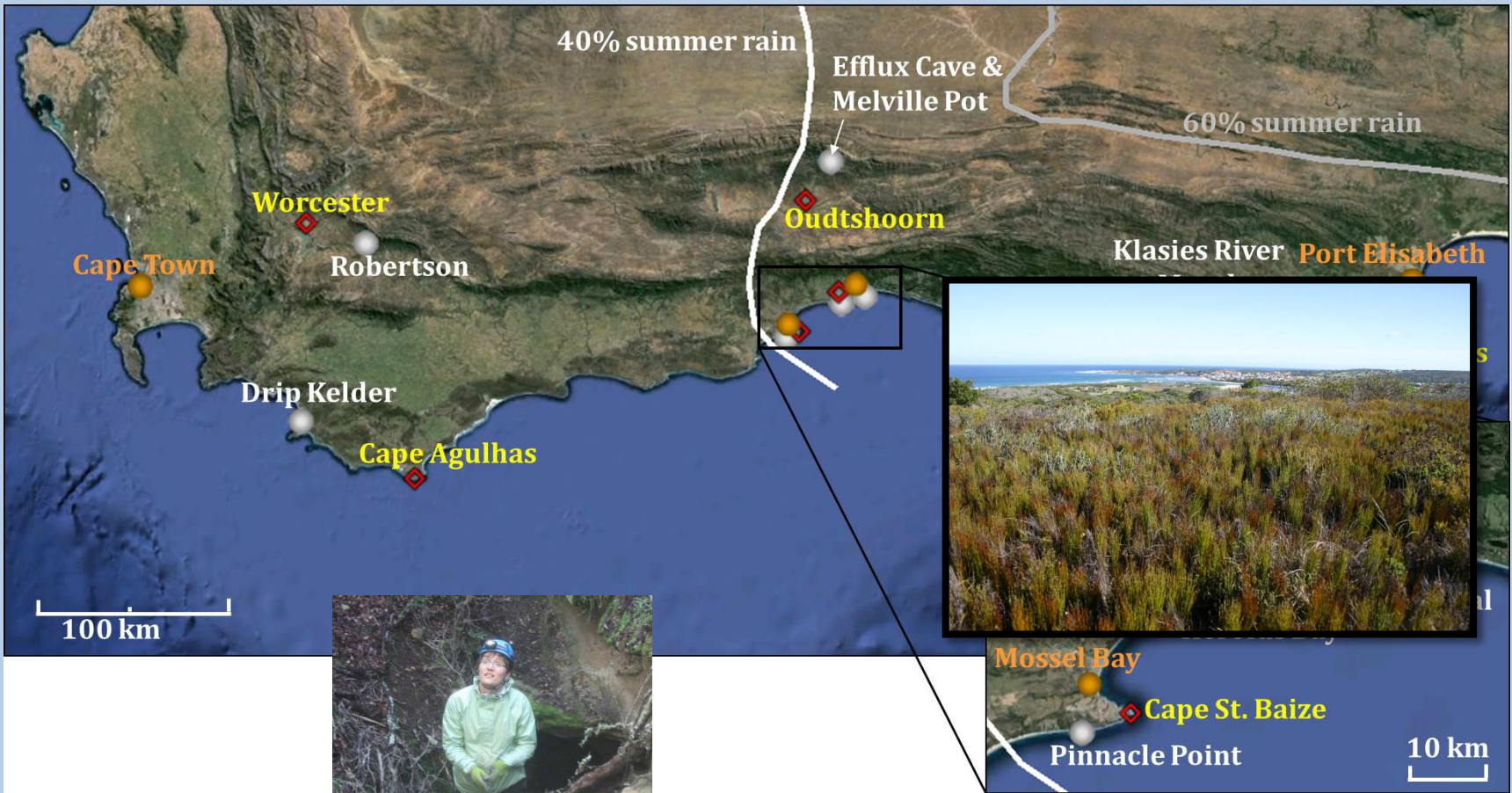






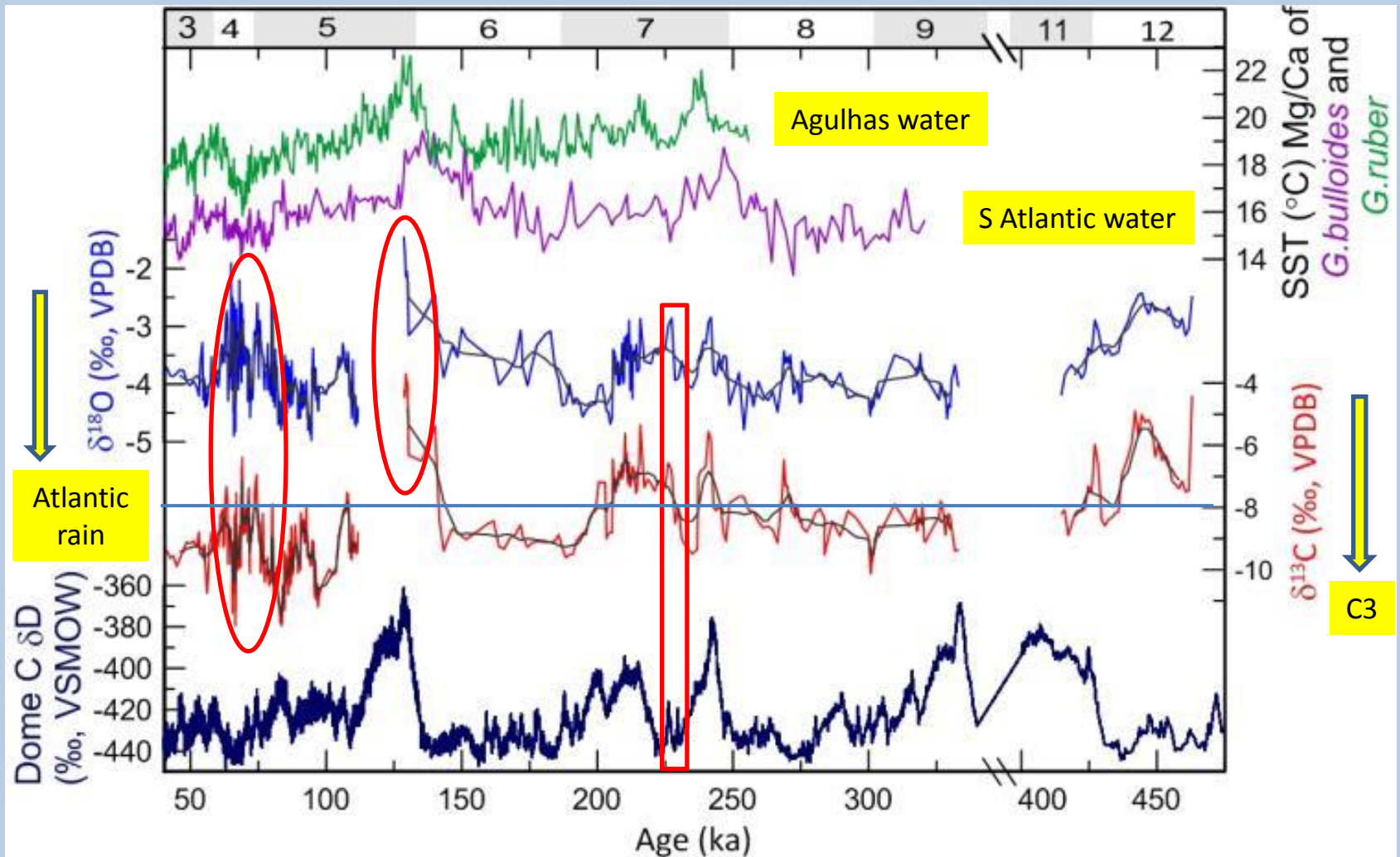




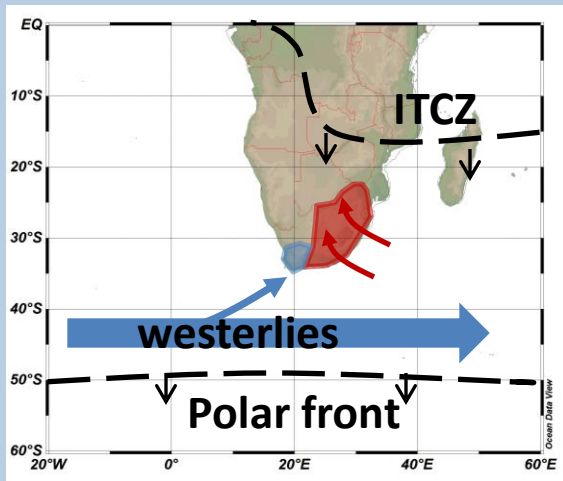


Kerstin Braun

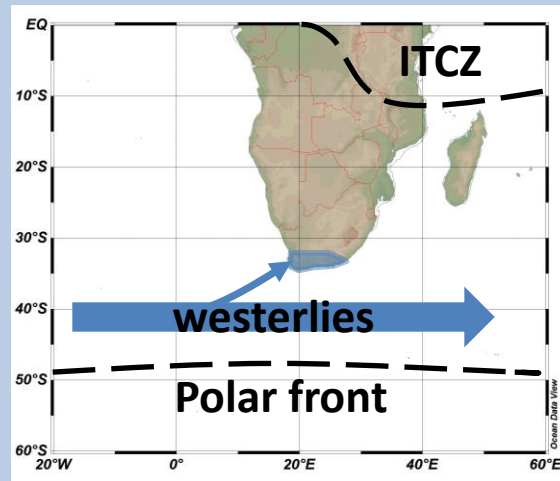




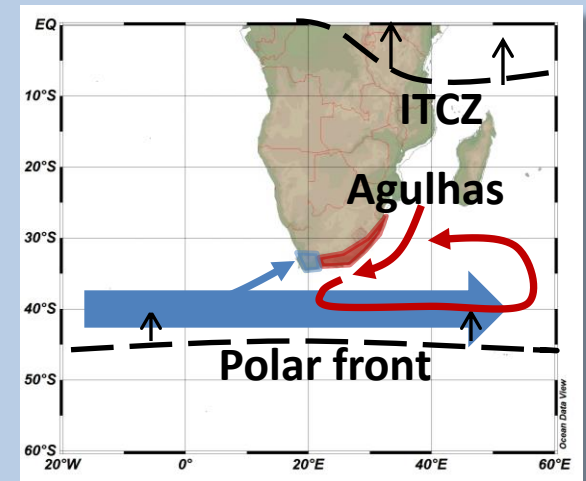
## Peak Interglacial



## Late Interglacial



## Glacial



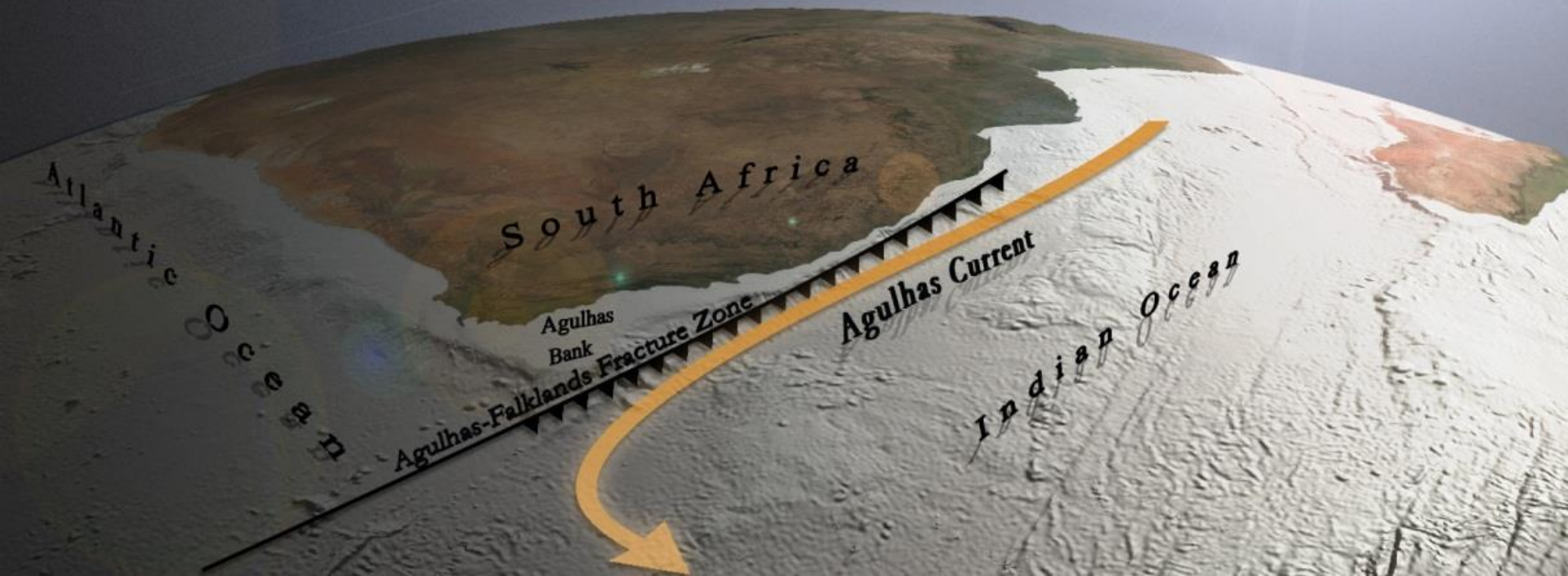
● Winter rain

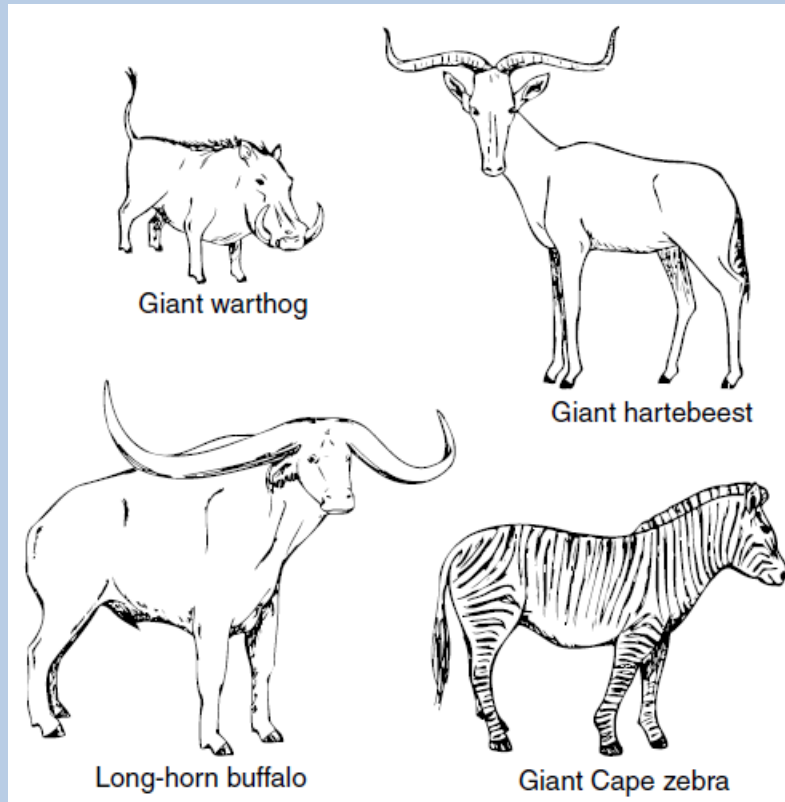
● Summer rain

- Polar front and ITCZ in southern positions
- **Atlantic/Winter rain from westerlies; Indian/Summer rain from easterly trades**
- Polar front in a southern position; ITCZ in northern positions
- **Westerlies continue to bring winter rain from Atlantic; Indian Ocean/summer rain is decreased**
- Polar front and ITCZ in northern positions
- **Strong westerlies bring Atlantic/winter rain and increase heat transport from the tropics to the south via the Agulhas Current**

# A persistently warm Agulhas Current provides a glacial refuge for humans

Durgadoo et al. 2013 *J. Phys. Oceanogr.*  
Simon et al. 2013 *Earth Planet. Sci. Lett.*





Giant warthog

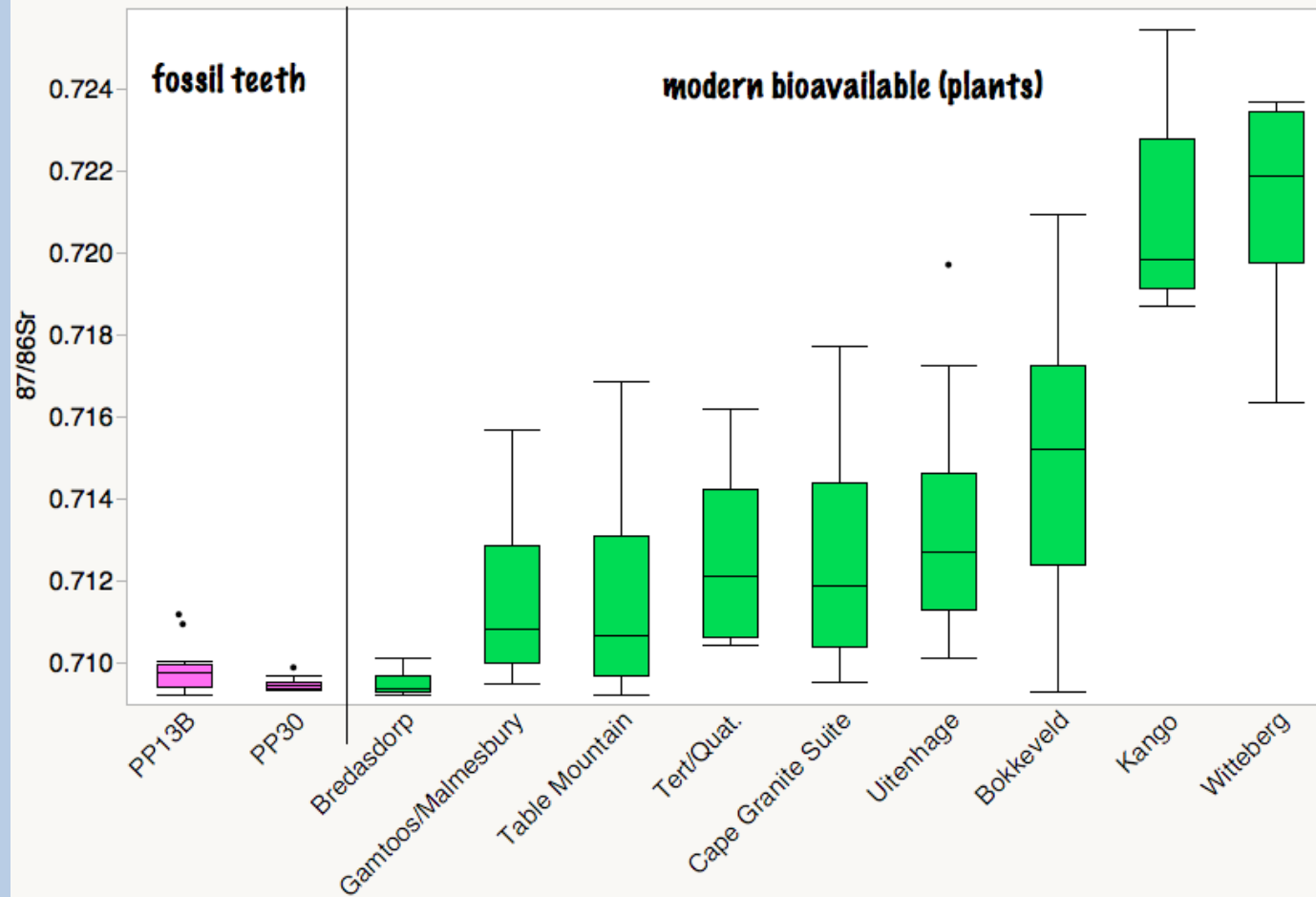
Giant hartebeest

Long-horn buffalo

Giant Cape zebra

## Richard Klein





Copeland et al. (2016) *Quaternary Science Reviews* 141 65e84

## WAS AGRICULTURE IMPOSSIBLE DURING THE PLEISTOCENE BUT MANDATORY DURING THE HOLOCENE? A CLIMATE CHANGE HYPOTHESIS

Peter J. Richerson, Robert Boyd, and Robert L. Bettinger

*Several independent trajectories of subsistence intensification, often leading to agriculture, began during the Holocene. No plant-rich intensifications are known from the Pleistocene, even from the late Pleistocene when human populations were otherwise quite sophisticated. Recent data from ice and ocean-core climate proxies show that last glacial climates were extremely hostile to agriculture—dry, low in atmospheric CO<sub>2</sub>, and extremely variable on quite short time scales. We hypothesize that agriculture was impossible under last-glacial conditions. The quite abrupt final amelioration of the climate was followed immediately by the beginnings of plant-intensive resource-use strategies in some areas, although the turn to plants was much later elsewhere. Almost all trajectories of subsistence intensification in the Holocene are progressive, and eventually agriculture became the dominant strategy in all but marginal environments. We hypothesize that, in the Holocene, agriculture was, in the long run, compulsory. We use a mathematical analysis to argue that the rate-limiting process for intensification trajectories must generally be the rate of innovation of subsistence technology or subsistence-related social organization. At the observed rates of innovation, population growth will always be rapid enough to sustain a high level of population pressure. Several processes appear to retard rates of cultural evolution below the maxima we observe in the most favorable cases.*

*Varias trayectorias independientes de la intensificación del sustento, muchas de las cuales condujeron a la agricultura, empezaron durante el Holoceno. No conocemos ninguna intensificación que usara muchos recursos vegetales durante el Pleistoceno, inclusive el Pleistoceno último, cuando las poblaciones humanas fueron muy sofisticadas en otros ámbitos. Datos recientes de cilindros de hielo sacados de Groenlandia, y de sedimentos oceánicos, muestran que la última glaciación fué extremadamente hostil a la agricultura, ya que fué—seca, baja en CO<sub>2</sub>, y extremadamente variable en el corto plazo. Proponemos que la agricultura fué imposible en estas condiciones de la última glaciación. La súbita mejora del clima al final de la glaciación fué seguida inmediatamente por la iniciación de usos mas intensivos de los recursos vegetales en algunos lugares, aunque mucho mas tarde en otras partes. Casi todo las trayectorias de intensificación en el Holoceno eran ocurrieron sin retroceso. Finalmente, la agricultura se convirtió en el modo principal de sustento en todas partes, excepto por zonas muy frías o muy secas. En el Holoceno, hacemos el hipótesis que la agricultura se vuelve, a final de cuentas, obligatoria. Usamos un análisis matemático para formular el hipótesis que los procesos limitante de la tasa de intensificación debe generalmente ser la tasa de la innovación tecnológica en las estrategias de sustento, o la tasa de innovación en las formas de organización social en relación al sustento. Con las tasas de innovación que se observan, el crecimiento de la población siempre es suficientemente rápido como para crear alto nivel de presión poblacional. Al parecer, varios procesos normalmente retardan la velocidad de la evolución cultural abajo de las tasas máximas que observamos en el modelo.*

**E**volutionary thinkers have long been fascinated by the origin of agriculture. Darwin (1874) declined to speculate on agricultural origins, but twentieth-century scholars were bolder. The Soviet agronomist Nikolai Vavilov, the American geographer Carl O. Sauer, and the British archaeologist

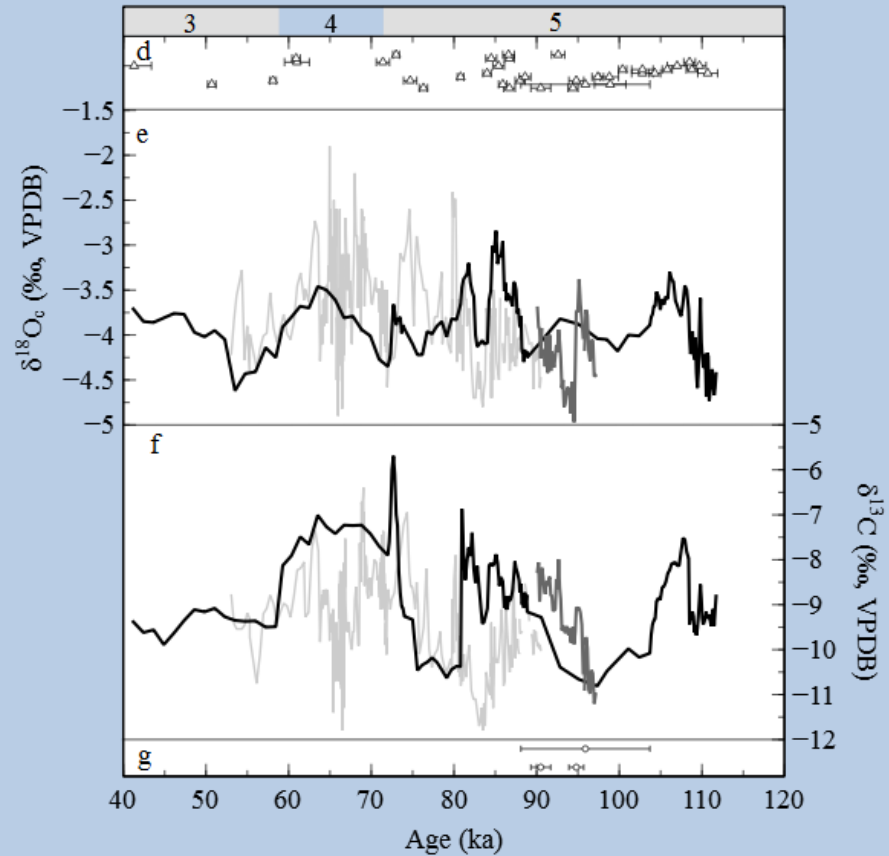
V. Gordon Childe wrote influential books and papers on the origin of agriculture in the 1920s and 1930s (see Flannery 1973 and MacNeish 1991:4–19 for the intellectual history of the origin of agriculture question). These explorations were necessarily speculative and vague, but stimulated interest in the question.

**Peter J. Richerson** ■ Department of Environmental Science and Policy, University of California–Davis, Davis, CA 95616, pjrigherson@ucdavis.edu

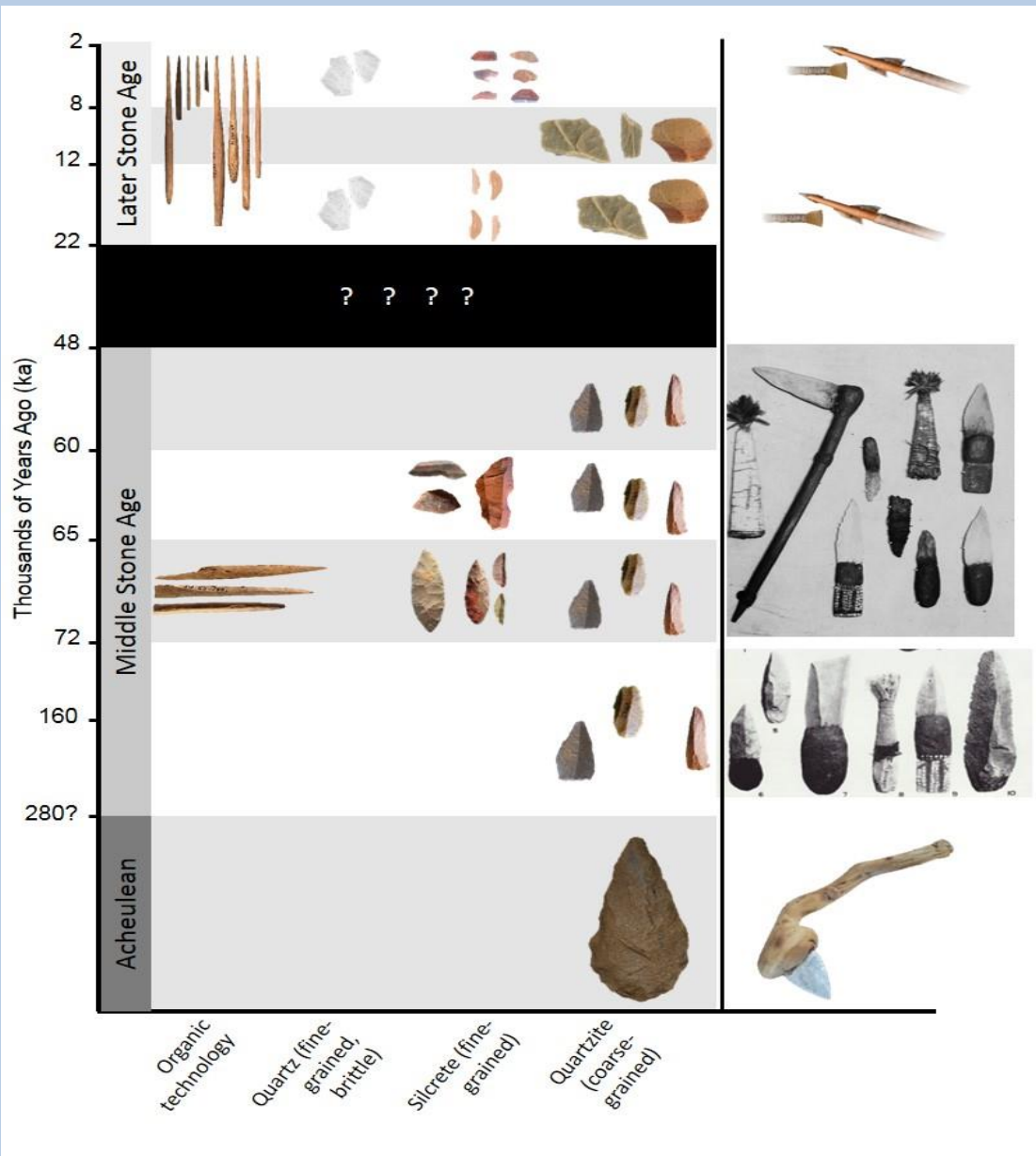
**Robert Boyd** ■ Department of Anthropology, University of California–Los Angeles, Los Angeles, CA 90095, rboyd@anthro.ucla.edu

**Robert L. Bettinger** ■ Department of Anthropology, University of California–Davis, Davis, CA 95616, rlbettinger@ucdavis.edu

American Antiquity, 66(3), 2001, pp. 387–411  
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Braun et al (subm) *Quaternary Science Reviews*



Marean et al. 2014. In: *Fynbos: ecology, evolution and conservation of a megadiverse region*. Oxford Univ Press

# Conclusions

**Glacial emergence of modern humans on the Cape south coast**

**Palaeo-Agulhas was exposed to varying degrees**

**Influence of a warm Agulhas Current**

**Region supported C4 grass dominated biomes under certain circumstances**

**Fauna suggestive of grasslands**

**Rapid changes in sea level may have disrupted cultural evolution**