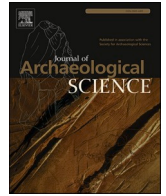




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## Human origins in Southern African palaeo-wetlands? Strong claims from weak evidence

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### ABSTRACT

Attempts to identify a 'homeland' for our species from genetic data are widespread in the academic literature. However, even when putting aside the question of whether a 'homeland' is a useful concept, there are a number of inferential pitfalls in attempting to identify the geographic origin of a species from contemporary patterns of genetic variation. These include making strong claims from weakly informative data, treating genetic lineages as representative of populations, assuming a high degree of regional population continuity over hundreds of thousands of years, and using circumstantial observations as corroborating evidence without considering alternative hypotheses on an equal footing, or formally evaluating any hypothesis. In this commentary we review the recent publication that claims to pinpoint the origins of 'modern humans' to a very specific region in Africa (Chan et al., 2019), demonstrate how it fell into these inferential pitfalls, and discuss how this can be avoided.

### 1. Introduction

A paper published by Chan and colleagues titled "Human origins in a

southern African palaeo-wetland and first migrations" reported 198 novel whole mitochondrial DNA (mtDNA) genomes and inferred that 'anatomically modern humans' originated in the

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Makgadikgadi–Okavango palaeo-wetland of southern Africa around 200 thousand years ago (Chan et al., 2019). This claim relies on weakly informative data. In addition to flawed logic and questionable assumptions, the authors surprisingly disregard recent data and debate on human origins in Africa (Scerri et al., 2018; Scerri et al., 2019; Henn et al., 2018; Schlebusch and Jakobsson, 2018). As a result, the emphatic and far-reaching conclusions of the paper are unjustified.

### 1.1. Weakly informative data

Chan et al. (2019) sampled 198 Southern African individuals, sequenced the full mtDNA genome and merged their data with ~1000 other published mtDNA genomes, mostly from southern Africa. They then proceeded by inferring the phylogenetic structure of the mtDNA genealogy, estimating the ages of various branches on that tree (with a particular focus on branches found in southern Africa), and considering their modern geographic distribution. Mitochondrial DNA can be useful for addressing certain population history questions (e.g. Karmin et al., 2015), and it is good to focus on under-sampled populations, but the phylogenetic tree at any single non-recombining locus (such as mtDNA) is one outcome of a strongly stochastic genealogical process that is only weakly constrained by population history. In practice, this means it contains useful but limited information about that population history. In particular, information content reduces rapidly as we look further back in time, no matter how many present-day samples are included. Near the time when all mtDNA lineages coalesce to their most recent common ancestor – the part of the tree where Chan and colleagues focus their analysis – mtDNA lineages represent only a small fraction of the thousands of ancestors that present-day humans have at that time, and therefore provides little or no information to distinguish between plausible models of human population history. If we consider another well-resolved single locus phylogenetic tree – that of the Y chromosome – a different phylogeographic structure is apparent (Mendez et al., 2013).

Modern population genetic approaches take advantage of hundreds of thousands of independent gene trees (obtained from whole-genome sequencing and genome-wide SNP genotyping), gaining several orders of magnitude in statistical power (Kelleher et al., 2019). While each tree is only weakly constrained by demographic history, by combining many trees with probabilistic approaches it is possible to quantify the likelihood of different demographic scenarios. However, in the absence of informative ancient DNA data from the periods in question, precise inferences on the location of origin of *Homo sapiens* still require strong and likely unjustified assumptions about human mobility in the intervening period, and so must be treated with caution. Genome-wide studies of contemporary and Holocene African populations indicate complex demography, including deep structure and varying migration rates over time (Schlebusch and Jakobsson, 2018; Tishkoff et al., 2009; Schlebusch et al., 2012; Schlebusch et al., 2017; Pickrell et al., 2012; Skoglund et al., 2017; Mazet et al., 2016; Bergström et al., 2020; Henn et al., 2011; Fan et al., 2019). However, despite the far greater information content, no genome-wide study has been able to justify such geographic and temporal precision for modern human origins as that of Chan and colleagues.

### 1.2. Lineages are not populations

While the methods used to estimate the mtDNA tree and its node dates are relatively uncontroversial, it is important to note that there is no natural level at which branches should be assigned haplogroup status, and no special meaning for the age of any arbitrarily defined haplogroup. Chan and colleagues cherry-pick lineages and treat them as representing real populations of prehistoric humans. Lineages in a gene tree correspond to lines of parent-offspring descent, and each node in the tree corresponds to the most recent common ancestor (MRCA) of two lineages. Such lineages demonstrably do not correspond to populations today, and there is little reason to assume that they did in the past.

Instead, multiple distinct lineages are usually shared across many different populations, and that degree of sharing is an outcome of random processes that are shaped by population demographic history. There is also little reason to assume that branch split dates in the mtDNA tree correspond directly to population-level splitting events. Instead, lineage split dates will usually predate a population split, often by a substantial margin which is itself shaped by the population size around the time of the split, and subsequent migration rates.

Chan and colleagues also applied Bayesian Skyline analysis to their arbitrarily selected lineages to infer ancestral population size change through time. This imposes a sampling bias that breaks a key assumption of Bayesian Skyline analysis (i.e. the data are from a lineage sample rather than from the model-assumed unstructured population sample), invalidating their reconstructions of population sizes through time (Heller et al., 2013). Chan et al. justify their use of this approach by citing two previous publications (Gandini et al., 2016; Soares et al., 2012). However, the latter of these publications (Gandini et al., 2016) simply cites the earlier one (Soares et al., 2012) on this issue, both publications merely state that Bayesian Skyline analysis “might nevertheless signal demographic processes” and neither provide any theoretical validation of this claim. Consequently, Chan et al. simply repeat this error without credible justification.

### 1.3. Populations are not static

A key issue with inferring geographic origins from contemporary genetic data is the extent to which population history is a ‘palimpsest’ of overlaid demographic processes (migration, population fission, fusion and size change, etc.) throughout the intervening period. Chan and colleagues’ claims rest on the implicit assumption that the locations of present-day individuals represent those of past populations. This assumption of static populations over a period of more than 100,000 years is problematic in the light of well described (by both archaeological and ancient DNA studies) long and short range migrations, population contractions, expansions and replacements – not only in Eurasia, the Americas and Oceania, but also in Africa (e.g. Schlebusch et al., 2017; Pickrell et al., 2012; Skoglund et al., 2017; Bergström et al., 2020). The assumption of static populations would need to be supported by archaeological, fossil, and ideally ancient DNA evidence; to date no such evidence has been presented for such a deep time period anywhere in Africa. On the contrary, studies of raw material transport demonstrate high levels of mobility among Pleistocene hunter-gatherers that are at odds with the notion of isolated populations over a period of more than 100,000 years (e.g. Scerri, 2017; Brooks et al., 2018). This issue remains regardless of whether single locus (e.g. mtDNA) data or more strongly informative multi-locus genomic data are considered.

### 1.4. Palaeoanthropology

Chan and colleagues conclude that ‘anatomically modern humans’ evolved in the Makgadikgadi–Okavango palaeo-wetland of southern Africa around 200,000 years ago. However, fossil hominin data from across Africa indicate the presence of morphology characteristic of *H. sapiens* more than 300 thousand years ago at the opposite end of the continent (Hublin et al., 2017). The evolution of *H. sapiens* morphology is characterised by a mosaic of different derived and primitive features across time and space, and these data do not indicate a single origin point (Scerri et al., 2018; Gunz et al., 2009; Stringer, 2016). Chan and colleagues use archaeological evidence for ‘modern human behaviour’ from southern Africa between 60 and 100 ka to corroborate their claims of human origins in that region more than 100 ka earlier (Henshilwood, 2012). However, evidence of complex culture is found in other African regions around this period (e.g. (Scerri, 2017; Brooks et al., 2018)). Together, current palaeoanthropological data do not support claims that one single area of Africa was the ‘homeland’ of contemporary *H. sapiens*.

## 1.5. Climate reconstructions

Using climate reconstructions to contextualise inferences based on genetic data is a commendable aim. However, while Chan and colleagues argue that wetlands were a stable habitat, they give no evidence that wetlands provide ecologies that are well-suited to ancient humans, and do not consider palaeo-wetlands elsewhere in Africa (Wrangham et al., 2009). Without addressing these issues, it is difficult to see how any type of climate reconstruction can provide a test of their origins model. Other ecologies, such as grasslands, savannahs and Mediterranean biomes were also inhabited by *H. sapiens* for long periods of time, and were therefore clearly suitable for long term *H. sapiens* occupation (Scerri et al., 2018; Hublin et al., 2017). An equally plausible alternative hypothesis (Potts, 1998) is that semi-desert conditions would be a suitable habitat for humans, because of their strong variations in climate on seasonal/annual timescales. The climate model that Chan and colleagues employ would not capture those features well. General overviews of African palaeoclimatic and palaeoanthropological data for the relevant time period exists (Blome et al., 2012). Relationships between climate and human demography are best explored through spatially explicit modelling (e.g. Eriksson and Manica, 2012) rather than *post-hoc* explanations which ignore other relevant data from across Africa.

## 2. Concluding remarks

Although admittedly common in human evolutionary studies, a particularly troubling aspect of Chan and colleagues' study is that the authors make no attempt to quantify how well their data can be explained either by simpler models of population history than the one they claim, or by equally complex but dramatically different models, such as those involving an origin of *H. sapiens* elsewhere in Africa, or indeed, in multiple locations throughout Africa.

One hundred years ago, in the first study using biomarkers, Hirschfeld and Hirschfeld (1919) typed different populations from around the world at a single genetic locus (ABO blood groups). While the study was revolutionary, the authors concluded that there were two ancestral human 'races', corresponding to the A and B blood groups, with two different geographical origins that subsequently mixed globally. Later developments in population genetics, genomics, archaeology and palaeoanthropology have revealed a very different and more complex picture. But the dangers of basing conclusions on limited data and problematic assumptions remain just as relevant today. Presentation of such studies, with predictably high-profile media and broader scientific community attention, and simple yet questionable results, does not serve the science of human origins, nor its broader dissemination.

### Author contributions

CMS, LL and MGT drafted and wrote the manuscript with contributions from other authors. All authors read and approved the manuscript.

### Declaration of competing interest

The authors declare no competing interests.

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