



## Did a discrete event 200,000–100,000 years ago produce modern humans?

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### ARTICLE INFO

#### Article history:

Received 20 January 2012

Accepted 25 April 2012

Available online 2 June 2012

#### Keywords:

Africa

Anatomical modernity

Quantitative genetics

Modern human origins

Molecular genetics

### ABSTRACT

Scenarios for modern human origins are often predicated on the assumption that modern humans arose 200,000–100,000 years ago in Africa. This assumption implies that something ‘special’ happened at this point in time in Africa, such as the speciation that produced *Homo sapiens*, a severe bottleneck in human population size, or a combination of the two. The common thread is that after the divergence of the modern human and Neandertal evolutionary lineages ~400,000 years ago, there was another discrete event near in time to the Middle–Late Pleistocene boundary that produced modern humans. Alternatively, modern human origins could have been a lengthy process that lasted from the divergence of the modern human and Neandertal evolutionary lineages to the expansion of modern humans out of Africa, and nothing out of the ordinary happened 200,000–100,000 years ago in Africa.

Three pieces of biological (fossil morphology and DNA sequences) evidence are typically cited in support of discrete event models. First, living human mitochondrial DNA haplotypes coalesce ~200,000 years ago. Second, fossil specimens that are usually classified as ‘anatomically modern’ seem to appear shortly afterward in the African fossil record. Third, it is argued that these anatomically modern fossils are morphologically quite different from the fossils that preceded them.

Here I use theory from population and quantitative genetics to show that lengthy process models are also consistent with current biological evidence. That this class of models is a viable option has implications for how modern human origins is conceptualized.

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### Introduction

Scenarios for modern human origins are often predicated on the assumption that modern humans arose 200,000–100,000 years ago in Africa (e.g., Lahr and Foley, 1998; Mellars, 2006; Tattersall, 2009; Mearns, 2010). In fact, the out-of-Africa (recent African origin or African replacement) model, some variant of which is the most widely accepted model for modern human origins,<sup>1</sup> is regularly characterized as having as one of its tenets that modern humans arose in Africa 200,000–100,000 years ago (e.g., Aiello, 1993; Stringer, 2002; Relethford, 2008). This assumption implies that something ‘special’ happened 200,000–100,000 years ago in

Africa. This could be the speciation that produced *Homo sapiens*, in which case ‘modern human’ and ‘*H. sapiens*’ would be synonyms, a severe bottleneck in human population size, or a combination of the two. These occurrences could have been related to each other in a variety of ways. For instance, the speciation that gave rise to *H. sapiens* could have been triggered by a bottleneck in human population size. The common thread is that after the divergence of the modern human and Neandertal evolutionary lineages ~400,000 years ago, there was another discrete event near in time to the Middle–Late Pleistocene boundary that produced modern humans. I will refer to this class of models for modern human origins as *discrete event* models.

Alternatively, modern human origins could have been a lengthy process that lasted from the divergence of the modern human and Neandertal evolutionary lineages to the expansion of modern humans out of Africa, and nothing out of the ordinary happened 200,000–100,000 years ago in Africa (e.g., Bräuer, 2008). As with discrete event explanations, multiple specific models for modern human origins could be considered *lengthy process* models. Perhaps the simplest explanation of this form would not include any bottlenecks in human population size in Africa before modern humans expanded out. In other words, human population size in

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<sup>1</sup> Any model that includes admixture between expanding modern humans and non-modern Eurasians could be considered a multiregional model (Relethford, 2001; Wolpoff, 2002). While this definition is precise, the term ‘multiregional’ then encompasses quite different models, such as those with persistent, long-term gene flow among geographic regions and those with only a short period of admixture between expanding and indigenous groups. Consequently, I prefer to use ‘out-of-Africa’ to refer to any model that emphasizes recent range expansions of modern humans from Africa, even if there was limited admixture.

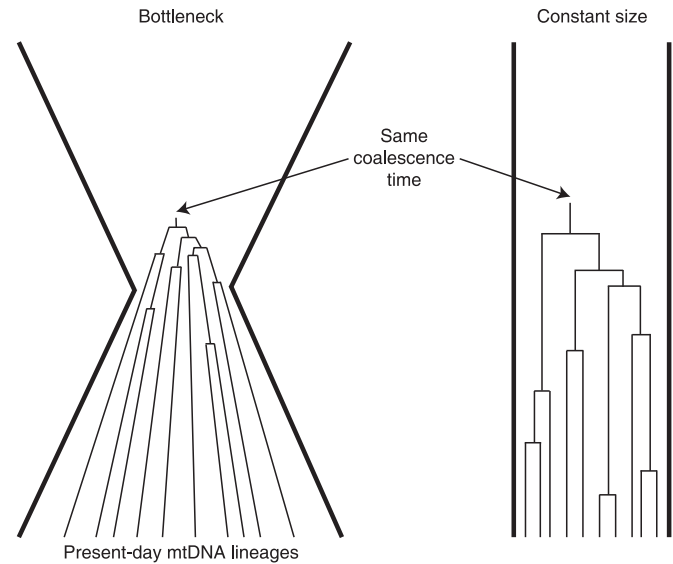
Africa remained roughly constant over the time period from ~400,000 years ago, when the modern human and Neandertal evolutionary lineages diverged, to 60,000–50,000 years ago, when modern humans expanded out of Africa. Models that do include bottlenecks could be classified as lengthy process models as long as the bottlenecks occurred throughout the time period in question with no change in their severity or frequency 200,000–100,000 years ago.

Discrete event and lengthy process models, as I have defined them here, are concerned with what happened in Africa before modern humans expanded out, so they are both compatible with admixture between expanding modern humans and non-modern Eurasians, as has been suggested based on comparisons of Neandertal (Green et al., 2010) and Denisovan (Reich et al., 2010) ancient DNA sequences with those of extant humans. Additionally, although it is important to investigate possible links between the biological (fossil morphology and DNA sequences) and cultural (archaeological or behavioral) evidence for modern human origins, in what follows, I will concentrate on the biological evidence. Variation in fossil morphology is determined, at least in part, by variation in alleles at particular genetic loci, so it should be possible to interpret both kinds of biological evidence with similar models from quantitative evolutionary theory. While quantitative theory for cultural evolution exists (reviewed in Henrich and McElreath, 2007; McElreath and Henrich, 2007), the models are quite different from those for biological evolution. The dynamics of biological and cultural evolution differ for various reasons, including the possibility of cultural transmission between any set of individuals, rather than just from parents to offspring, and throughout an individual's lifetime, rather than only at conception. There is also no clear consensus about whether biological and behavioral modernity should match up. For example, these two kinds of modernity might have appeared at different times (e.g., Klein, 2008) or in multiple species (e.g., d'Errico, 2003). These complications could lead to a situation where the biological evidence supports a discrete event model whereas the cultural evidence supports a lengthy process model, or the other way around, but both conclusions are correct.

Three pieces of biological evidence are usually cited in support of discrete event models. First, living human mitochondrial DNA (mtDNA) haplotypes coalesce ~200,000 years ago (Cann et al., 1987; Ingman et al., 2000; Kivisild et al., 2006; Behar et al., 2008). This coalescence time would support discrete event models if it were the signature of a severe bottleneck in human population size, the origin of *H. sapiens*, or both. Second, fossil specimens usually classified as 'anatomically modern' seem to appear shortly afterward in the African record (Deacon, 1995; White et al., 2003; McDougall et al., 2005). Third, it is argued that these anatomically modern fossils are morphologically quite different from the fossils that preceded them (e.g., Lieberman et al., 2002; Tattersall, 2009). In other words, there is evidence for punctuated morphological change in Africa 200,000–100,000 years ago. My purpose is to evaluate whether lengthy process models are consistent with current biological evidence. In particular, can the three pieces of biological evidence that are usually said to support discrete event models be explained by lengthy process models?

### mtDNA coalescence, demography, and speciation

If there was a severe bottleneck 200,000 years ago, the reduction in population size could cause mtDNA lineages to coalesce rapidly around this time, and the coalescence time would represent an actual demographic event. However, the same coalescence time could be produced in a constant-sized population with an effective

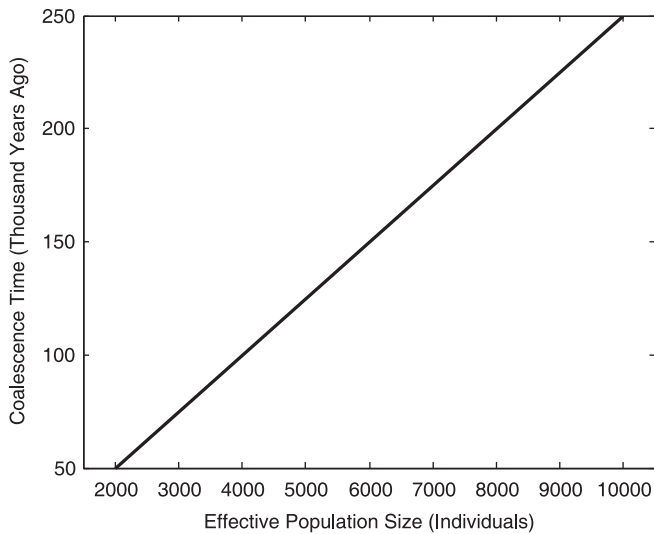


**Figure 1.** Schematic illustration of how the same coalescence time could be produced with or without a bottleneck. The thick lines show changes in human population size going back in time. The thin lines show the coalescence of present-day human mtDNA lineages. Modified from Weaver and Roseman (2008).

population size equal to the harmonic mean effective population size<sup>2</sup> of the severely bottlenecked population (Fig. 1). In the case of the constant-sized population, the mtDNA coalescence time would not reflect a demographic event at all. Alternatively, there could have been bottlenecks throughout the period from 400,000 years ago to when modern humans expanded out of Africa, and nothing out of the ordinary happened at 200,000 years ago in Africa. The key point is that only in some of these cases would the coalescence time correspond with an actual demographic event. For similar reasons, there is no reason to expect that the coalescence time for human mtDNA will correspond with the date of the speciation that produced *H. sapiens*.

To further illustrate this point, let us consider a specific example. Imagine that for the past 400,000 years the human population has been constant in size. In this case, according to population genetics theory (Hartl and Clark, 2007), there will be a linear relationship between the expected coalescence time of present-day mtDNA sequences and effective population size (Fig. 2). For this example, by definition, no demographic events have occurred in the past 400,000 years – the population has been constant in size – but the expected coalescence time could vary widely, depending on the effective size of the human population. Additionally, the observed coalescence time could be quite different from the expected time for a given effective population size, because the coalescence process is stochastic (Hartl and Clark, 2007). The bottom line is that the coalescence time for human mtDNA, by itself, tells us nothing about whether or not the human population experienced a bottleneck.

<sup>2</sup> Effective population size is a population genetics parameter that roughly corresponds to the number of breeding individuals in an idealized population that would have as much genetic drift as in the actual population. The harmonic mean effective population size is the reciprocal of the mean of the reciprocals of the effective population sizes for each of the generations under consideration. For example, the harmonic mean for three generations with effective population sizes of 1000, 100, and 1000 is 250. Genetic drift in this bottlenecked population will produce, on average, the same coalescence time as in a population with a constant effective population size of 250.



**Figure 2.** Expected linear relationship between mtDNA coalescence time and effective population size for a population that is constant in size. The male and female effective population sizes are assumed to be the same.

While summaries of human mtDNA variation other than the coalescence time, such as the shape of the distribution of pairwise sequence differences between individuals (Slatkin and Hudson, 1991; Rogers and Harpending, 1992), provide some information about ancient human demography, mtDNA can be considered a single genetic locus, and it is usually not possible to make robust inferences with data from only one locus. Fortunately, information about present-day human genetic variation is now available for numerous nuclear loci, and multiple researchers have fit demographic models to the patterns of variation. These studies have been extremely consistent in finding evidence for bottlenecks – technically, founder events – as modern humans migrated out of Africa (Marth et al., 2004; Voight et al., 2005; Fagundes et al., 2007; Keinan et al., 2007; Boyko et al., 2008). However, inferences about African demography have been more variable. The results of some studies are compatible with constant population size until a very recent expansion in size (Voight et al., 2005), others are consistent with older expansions (Marth et al., 2004; Boyko et al., 2008), and others with an ancient bottleneck followed by an expansion (Fagundes et al., 2007). Considering these studies together, the evidence for bottlenecks in Africa before modern humans expanded out is equivocal.

Recently, Li and Durbin (2011) used the complete diploid genome sequences from seven present-day humans to make the most robust and detailed inferences to date about ancient human demography. Unlike previous studies, such as the ones discussed above, which fit demographic models with just a few changes in effective population size, the effective population size of different human populations was estimated for any time in the past, producing an approximately continuous record of changes in size. While computationally intensive, the basic principles behind Li and Durbin (2011) method are quite straightforward. Because each individual has two copies of each autosomal chromosome, in addition to there being genetic variation among individuals, there is also genetic variation within any given individual, and the amount of variation at a particular locus in the genome is a function of the coalescence time for the individual's two chromosomal copies. Consequently, the diploid genome of a single individual can be used to produce a distribution of coalescence times for hundreds of thousands of independent loci. Because coalescence events tend

to occur during periods of low effective population size and they tend not to occur when effective size is high, it is possible to use the distribution of coalescence times across the genome to make inferences about how effective population size has changed. Using this approach, Li and Durbin (2011) found no evidence for a bottleneck in human population size 200,000–100,000 years ago. In fact, their results show that the lowest human effective population sizes in the last million years occurred roughly 700,000–500,000 years ago and 50,000–30,000 years ago. The latter decrease seems to have been longer lived and more severe in non-Africans, which is presumably a signature in non-Africans of their ancestors' migration out of Africa. The important point for models of modern human origins is that Li and Durbin (2011) detected no bottlenecks over the time period from the divergence of the modern human and Neandertal evolutionary lineages ~400,000 years ago to the modern humans expansion out of Africa. These results are consistent with lengthy process models and inconsistent with those discrete event models that depend on a bottleneck in human population size 200,000–100,000 years ago.

### Appearance of anatomical modernity

A model for morphological evolution is needed to make predictions about when anatomical modernity would be expected to appear in the fossil record if modern human origins were a lengthy process. Two main assumptions about morphological evolution underlie the specific lengthy process model that I investigate here (see the Appendix for mathematical details). First, the genetic basis of a metric trait is a large number of genetic loci that contribute equally and additively (i.e., no interactions among them) to the value of the measurement. This is the classical quantitative genetics model of heredity (Fisher, 1918; Falconer and Mackay, 1996), which has received empirical support recently from studies of human stature (Weedon et al., 2007; Aulchenko et al., 2009; Lango Allen et al., 2010). Second, mutation and genetic drift are the only evolutionary forces causing morphological divergence; in other words, the model assumes neutral evolution. The second assumption seems to be a useful starting point given the general consistency of present-day human and Neandertal cranial variation with neutral evolution. Natural selection has not left an obvious signature on most of the cranial differences between Neandertals and present-day humans and among present-day human groups (evidence reviewed by Roseman and Weaver, 2007; von Cramon-Taubadel and Weaver, 2009). Of course, the classical quantitative genetics model of heredity may approximate poorly the genetic basis of certain traits, and natural selection may sometimes have played a strong role in shaping patterns of variation. I mention evidence in support of these two assumptions simply to build a case that predictions about morphological evolution based on them will be realistic enough to be useful for evaluating lengthy process models for modern human origins.

In addition to a model for morphological evolution, a statistical definition of modernity for a morphological trait is needed. Most researchers decide whether or not a particular fossil specimen should be classified as anatomically modern for a particular metric trait by comparing the value of the fossil specimen to the mean and variation around the mean of a sample of present-day humans. Therefore, a definition that makes intuitive sense is that a metric trait will be considered modern if the value of its measurement is within one standard deviation of the present-day human mean (i.e., the value of the measurement is fairly typical for present-day humans). The purpose of this definition is not to operationalize it by selecting a particular present-day human sample and actually calculating the mean and the standard deviation; it is to capture mathematically what most researchers are already doing when

they argue that African fossils from 200,000 to 100,000 years ago are anatomically modern.

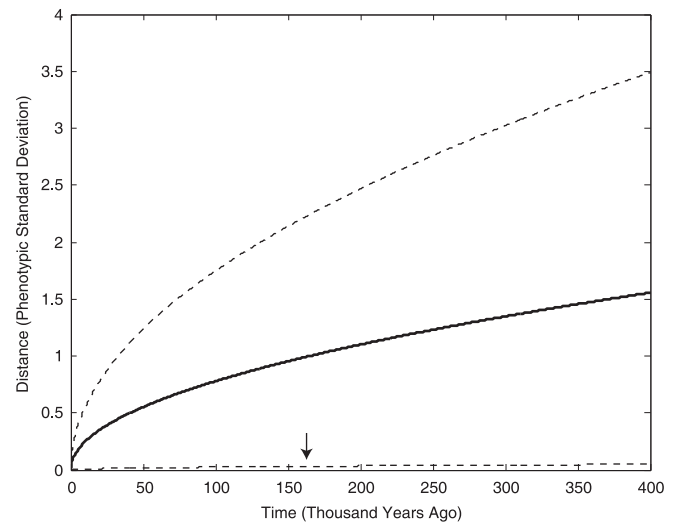
The model has three parameters whose values need to be specified: narrow-sense heritability, a parameter related to the amount of additive genetic variance introduced into the species by mutation per generation, and the generation length (Table 1). I used the heritability and the mutation parameter values that were previously estimated by Weaver and colleagues (2008) from patterns of DNA sequence and cranial variation in present-day human populations. I assumed a generation length of 25 years, which is fairly standard in studies of human genetic variation (e.g., Li and Durbin, 2011). These same parameter values also produce estimates for when the modern human and Neandertal evolutionary lineages diverged based on cranial measurements (Weaver et al., 2008) that are quite similar to divergence times estimated from ancient Neandertal and extant human DNA sequences (Noonan et al., 2006; Green et al., 2010).

Given the assumptions discussed above, if the origin of modern human was a lengthy process, the morphological distance between the present-day and past human means is expected to increase with time (Fig. 3). In other words, African fossils that document the evolution of modern humans will tend to appear less modern the older they are. Additionally, because neutral divergence is driven by mutation and genetic drift, both of which are stochastic, some traits will appear more modern than others (Fig. 3), resulting in a mix of modern and non-modern traits. Perhaps the most interesting result is that the past mean for any given trait is expected to be within one standard deviation of the present-day mean for this trait – statistically modern – about 165,000 years ago (Fig. 3). The predicted date of appearance of statistical modernity is fairly robust to changed assumptions about generation time. Increasing the generation length to 30 years or decreasing it to 20 years changes this date to 198,000 and 132,000 years ago, respectively. These results show that even if there was not a speciation event or a bottleneck (i.e., lengthy process models), looking back into the past, fossils would be expected to appear modern about 200,000–100,000 years ago.

### Fossil evidence for a punctuated event

For two of the pieces of biological evidence – mtDNA coalescence time and the timing of the appearance of anatomical modernity – that are typically cited in support of discrete event models, I have shown that lengthy process models make similar predictions to discrete event models, so these pieces of evidence cannot be used to distinguish between the two model classes. For the third piece of evidence – morphological change in Africa 200,000–100,000 years ago – discrete event and lengthy process models have different expectations. Discrete event models predict punctuated change at this time, whereas lengthy process models do not predict an increased rate of morphological evolution. However, at the moment, there is no consensus about whether the African fossil record provides evidence for punctuated morphological change near the time of the Middle–Late Pleistocene boundary.

Some researchers argue that African cranial remains that are 200,000–100,000 years old (including similarly aged fossils from just outside of Africa from the sites of Qafzeh and Skhul, Israel) are fundamentally different from those of older fossils (e.g., Lieberman



**Figure 3.** Morphological distances between the present-day and past human means for any given trait under the specific lengthy process model considered here (see text for details). The distances are given in units of phenotypic standard deviations. The solid line gives the expected distance and the dashed lines encompass a 95% confidence interval for the distance for any particular trait. The arrow along the x-axis indicates when the past mean is expected to be within one standard deviation of the present-day mean (about 165,000 years ago).

et al., 2002; Tattersall, 2009). Others characterize these same fossils as only ‘near modern’ in their anatomy (e.g., Klein, 2008) and maintain that the fossil record shows a gradual process of modernization with different modern features appearing in a mosaic fashion (e.g., Bräuer, 2008; Pearson, 2008). This disagreement stands in contrast to the situation for Europe for which the fossil record is typically interpreted as documenting the gradual and mosaic appearance of Neandertal cranial morphology (Hublin, 1998, 2009; Stringer, 2002), although some researchers do see evidence for punctuated change (Rosas et al., 2006). The main problem may be that the fossil record for cranial evolution during the Middle and Late Pleistocene is much poorer in Africa than the comparable record in Europe. There is also disagreement about how to interpret African postcranial remains from the Middle and Late Pleistocene, with some researchers recognizing punctuated morphological change (e.g., Tattersall, 2009) and others describing a gradual, mosaic pattern (e.g., Pearson, 2000). Given the lack of consensus, it seems difficult to make a definitive argument that lengthy process models are inconsistent with the African fossil record.

### Conclusions

Lengthy process models for modern human origins are consistent with current biological evidence. That this class of models is a viable option has implications for how modern human origins is conceptualized. Perhaps most importantly, if modern human origins was a lengthy process, then the two events that deserve the most attention when developing explanations for modern human origins are the divergence of the modern human and Neandertal evolutionary lineages and the expansion of modern humans out of Africa. Why did these events happen when they did? And why did nothing noteworthy occur in the time period between these two events? Lengthy process models shift the focus away from 200,000 to 100,000 years ago to earlier and later. Additionally, if modern human origins was a lengthy process, then the statement ‘modern humans originated’ followed by a discrete time, such as 100,000 years ago, does not make much sense, unless one is referring to the

**Table 1**  
Parameter values for the model for morphological evolution.

Heritability ( $h^2$ )	Mutation parameter ( $m$ )	Generation length
0.37	$1.2 \times 10^{-4}$	25 years

split ~400,000 years ago of the evolutionary lineages leading to Neandertals and modern humans. This is not to say that discrete event models are clearly incorrect or that it is well established that nothing significant for modern human origins happened 200,000–100,000 years ago in Africa. At the moment, both discrete event and lengthy process models appear to be compatible with the available evidence. My goal is simply to show that lengthy process models are consistent with current biological evidence and to heighten awareness of the implications of these models for understanding modern human origins.

## Acknowledgments

Versions of the ideas expressed in this article were presented at an EVAN symposium ‘Transitions from archaic to modern: quantitative approaches’ organized by K. Harvati and J.-J. Hublin, and an AAPA symposium ‘Muddles in the middle: current perspectives on Middle Pleistocene human evolution’ organized by S.E. Freidline and S.L. Wang. I would like to thank the participants of these two symposia, attendees of ‘Paleo Group’ at UC Davis, C.C. Roseman, T.E. Steele, and three anonymous reviewers for helpful comments; and the Max Planck Society and the University of California for funding.

## Appendix

This appendix describes the equations that were used to predict how far back in time to expect modern traits in the fossil record if modern human origins was a lengthy process. Let  $X_t$  be the measurement mean for a particular metric trait for fossil modern humans living  $t$  generations in the past, and  $X_0$  be the mean for present-day humans. Let  $V_m$  be the average amount of new additive genetic variance introduced into the species by mutation per zygote per generation. Assuming mutation drift equilibrium (balance between the amount of new additive genetic variance introduced into the species by mutation and the amount removed by genetic drift) and that natural selection does not contribute to morphological divergence, the squared difference between the present-day and past means is expected to be (Lynch and Hill, 1986; Turelli et al., 1988; Weaver et al., 2008):

$$(X_0 - X_t)^2 = 2V_m t. \quad (1)$$

Let  $m$  be a mutation parameter,  $h^2$  be the narrow-sense heritability for the measurement, and  $\sigma^2$  be the within species phenotypic variance. Then,  $V_m$  can be redefined as (Lynch, 1988; Weaver et al., 2008):

$$V_m = m(1 - h^2)\sigma^2. \quad (2)$$

Combining Eqs. (1) and (2) gives:

$$(X_0 - X_t)^2 = 2m(1 - h^2)\sigma^2 t. \quad (3)$$

Rearranging terms in Eq. (3) and taking the square root of both sides of the equation allows the expected morphological distance between the present-day and past means to be expressed in units of phenotypic standard deviations as:

$$\frac{|X_0 - X_t|}{\sigma} = \sqrt{2m(1 - h^2)t}, \quad (4)$$

where the vertical lines signify the absolute value and  $\sigma$  is the within species phenotypic standard deviation. Morphological divergence as modeled by the above equations is driven by mutation and genetic drift, both of which are stochastic, so the squared difference between the present-day and past means for any

particular trait can be thought of being sampled from a chi-square distribution with one degree of freedom (Lande, 1979; Turelli et al., 1988; Lynch, 1989) that is shifted so that the distribution mean is given by Eq. (3). Consequently, it is possible to construct a 95% confidence interval for the morphological distance in units of phenotypic standard deviations for any particular trait by multiplying Eq. (4) by the square root of the 0.975 and 0.025 cumulative density values for a chi-square distribution with one degree of freedom to give the upper and lower bounds, respectively, of the interval.

The definition that a trait will be considered modern if its measurement is within one standard deviation of the present-day human mean can be expressed mathematically as:

$$\frac{|X_0 - X_t|}{\sigma} = 1. \quad (5)$$

It is evident from Eq. (4) that the condition given by Eq. (5) is satisfied when:

$$t = \frac{1}{2m(1 - h^2)}. \quad (6)$$

The time given by Eq. (6) is counted in generations, so it needs to be multiplied by an estimate of the average generation length to give the time in years.

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