



Letter to the Editor

The Out of Africa hypothesis and the ancestry of recent humans: Cherchez la femme (et l'homme)



Úlfur Árnason

Department of Brain Surgery, Faculty of Medicine, University of Lund, Sweden

ARTICLE INFO

Article history:

Received 29 December 2015

Received in revised form 3 March 2016

Accepted 14 March 2016

Available online 17 March 2016

Keywords:

Human evolution

Out of Africa hypothesis

Neanderthals

Denisovans

Palaeontology

Palaeogenomics

Biogeography

LCA, last common ancestor

Askur/Embla hypothesis

ABSTRACT

The Out of Africa hypothesis (OOAH) has been a mainstay in the discussion of human evolution since its presentation in the 1980's. However, recent advances in palaeontology and molecular genetics have made it possible to examine the hypothesis in a manner that was inconceivable at the time of its proposal. The palaeontological progress relates to early *Homo* finds in the Caucasus, Denisova finds in the Altai Mountains and Neanderthal finds in a wide range of localities from the Altai Mountains, the Caucasus, the Levant, Asia Minor, southern and Central Europe and the Iberian Peninsula. The Eurasian location of these finds and recognition of the principle of Last common ancestor (LCA) lend no support to OOAH. The same conclusion is drawn from genomic findings, which (a) have revealed the presence of Denisovan and Neanderthal nuclear DNA, primarily in the genomes of recent Eurasians and (b) have shown genomic introgression from early modern humans into Neanderthals in the Altai Mountains. Similarly, archaeological finds in Sulawesi and the discovery of $\approx 100,000$ years old human teeth in southern China constitute strong independent challenges to OOAH. The genomic and palaeogenomic results and the new palaeontological and archaeological discoveries suggest (a) that the ancestors of modern humans had their origin in a Eurasian (largely Asian) biogeographic region which may also have extended into NE Africa, and (b) that the founders of basal African lineages became separated, geographically and genetically, in the westernmost part of this region and spread from there to different parts of the African continent.

© 2016 Elsevier B.V. All rights reserved.

1. Introduction

"... They came across two logs and created people out of them. ... The man was called Ask (Icelandic: Askur), the woman Embla, and from them were produced the mankind ..." (Sturluson, ≈ 1220).

OOAH posits a dispersal of the ancestors of recent humans from Africa. Cann et al. (1987) provided the essential molecular basis of the hypothesis in a study that included a phylogenetic tree based on restriction maps of human mitochondrial DNA molecules (mtDNAs). The basal split of the tree was between a branch that contained exclusively African individuals and a branch that split between an African branch and a branch that consisted of mtDNAs of different geographic origins. The interpretation of the finding was that the basal split among the ancestors of modern humans had taken place in Africa between a branch

that had remained intact in Africa and another African branch from which other human lineages had departed at different times to other parts of the world.

OOAH has become acknowledged in a great number of molecular and non-molecular studies of human evolution. The hypothesis has also been taken as rebutting the so-called multiregional hypothesis on the origin and evolution of modern humans advocated by M. H. Wolpoff and co-workers (e.g. Wolpoff et al. 2000). There is, however, a fundamental and hitherto disregarded circumstance connected to OOAH, namely the African placement superimposed on the root of the tree. That position may have appeared reasonable at the time of the initial studies due to the paucity of the non-African hominid palaeontological record. Even so it should have been apparent that the very implementation of this root had the automatic effect that the direction of any early human transfer could never be into Africa, only out of or within that continent. O'Regan et al. (2011) and Turner and O'Regan (2015) examined the palaeontological record related to the dispersal of large mammals between Africa and Eurasia during Pliocene–Pleistocene. Although the studies were inconclusive with respect to OOAH they showed that mammalian dispersal between Africa and Asia was by no means a one-way route.

The phylogenetic relationship of recent humans, Neanderthals and Denisovans as recovered in studies of complete mtDNAs is shown schematically in Fig. 1. The figure is a simplification of the tree presented

Abbreviations: A/C-60, the molecular calibration point implying the divergence between ruminant artiodactyls and cetaceans (whales) set at 60 million years before present; *Hs*, *H. sapiens*, the ancestor of *Hss* and *Hsn*; *Hss*, *H. sapiens sapiens*, modern humans; *Hsn*, *H. sapiens neanderthalensis*, Neanderthals + Denisovans; *Hsnd*, *d* for Denisovans; *Hsnn*, *n* for Neanderthals; LCA, last common ancestor; mtDNA, mitochondrial deoxyribonucleic acid; MYBP, million years before present; OOAH, Out of Africa hypothesis; YBP, years before present.

E-mail address: ulfur.arnason@gmail.com.

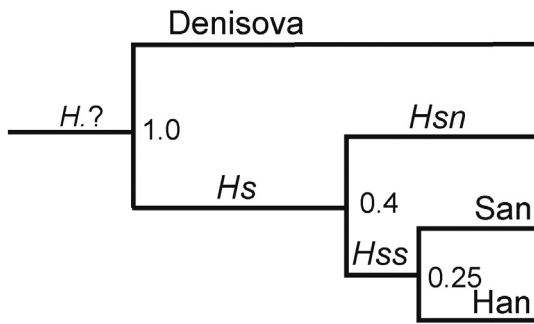


Fig. 1. Phylogenetic relationship among Denisovans, Neanderthals (*Hsn*, *Homo sapiens neanderthalensis*) and recent humans (*Hss*, *Homo sapiens sapiens*) as recovered in studies of mitochondrial DNA (mtDNA). Denisova is sister to a branch (*Hs*, *Homo sapiens*) that splits into Neanderthals and recent humans. Krause et al. (2010) estimated the divergence time between Denisova and *Hs* at ≈ 1 MYBP (million years before present) and that between Neanderthals and recent humans at 0.5–0.3 MYBP. The split between San and Han represents the deepest divergence within *Hss*. Molecular datings based on mtDNA place Denisova within the temporal realm of Eurasian *Homo erectus* and related taxa (e.g. Ferring et al., 2011; Lordkipanidze et al., 2013), but its mtDNA identity as to a defined taxon remains unknown. *H?* indicates an unspecified *Homo* outgroup.

by Krause et al. (2010) and those of Meyer et al. (2014) and Sawyer et al. (2015). The earliest bifurcation in the tree is between a branch that includes Denisovans and a branch that splits into *Homo sapiens sapiens* (*Hss*) and *Homo sapiens neanderthalensis* (*Hsn*). As a consequence the branch leading to *Hss/Hsn* is designated *Hs* for *H. sapiens*. In comparison, studies of nuclear DNA, Fig. 2, place Denisovans as the sister taxon of Neanderthals (Reich et al., 2010; Meyer et al., 2012; Sawyer et al., 2015). The effect of this discrepancy vis-à-vis the mtDNA tree is apparent in that *Hsnn* and *Hsnd* (*d* for Denisova) join on a common branch, *Hsn*, as the sister group of *Hss*. It should be noted that the length of the *Hs* branch leading to the split between *Hss* and *Hsn* remains unknown in the absence of a molecularly definable sister group of that branch.

Regarding the phylogenetic incongruity that may occur in analysis of nuclear and mitochondrial DNA it is noteworthy that as long as 25 years ago Pickford (1991) drew attention to this circumstance, with particular reference to OOA.

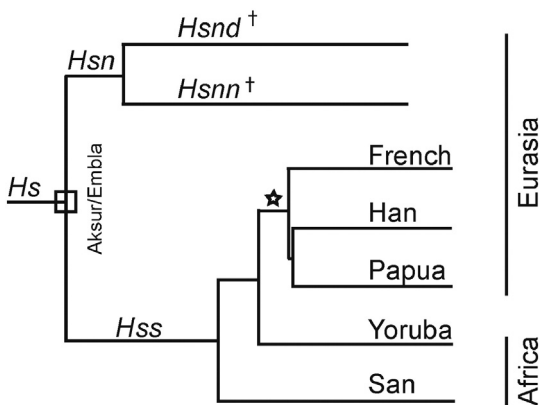


Fig. 2. Phylogenetic studies of nuclear DNA place Denisovans and Neanderthals as sister groups on a branch, *Hsn*, that is sister to recent humans, *Hss*. The relationship among recent humans is in accord with Reich et al. (2010). The star introduced in the tree indicates the deepest potential position for genomic transfers between Neanderthals/Denisovans (*Hsnn/Hsnd*) and the ancestors of recent humans (*Hss*). The position does not require, however, the presence of Neanderthal and/or Denisovan DNA in the genomes of all recent Eurasians. The location of the star implies, in conjunction with limited occurrence of Neanderthal/Denisovan DNA in African genomes, that the ancestors of San and Yoruba (both African) split from the Eurasian ancestors of recent humans prior to the genomic exchanges between the Eurasians and Neanderthals/Denisovans. With reference to Nordic mythology (Sturluson, ≈ 1220) the names Askur and Embla denote the biparental nature of the nuclear DNA of the last common ancestors of *Hsn* and *Hss*.

2. Discussion

The availability of sequences of ancient DNA, both mitochondrial and nuclear, from Neanderthals and Denisovans and progress in *Homo* palaeontology allow examination of OOA in a manner that could not have been envisaged in the 1980's. Thus, when OOA became accepted, the *Homo/Pan* calibration point was commonly placed at 4.5–5 MYBP. This age became significantly revised, however, with the description of *Orrorin tugenensis* (Senut et al., 2001) and *Sahelanthropus tchadensis* (Brunet et al., 2002), two fossils that in an instant required moving the *Pan/Homo* split to >7 MYBP.

The time of divergence between Artiodactyla (as represented by ruminants) and Cetacea (whales) set at 60 MYBP (Arnason and Gullberg, 1996; Ursing and Arnason, 1998) has become the primary molecular standard (A/C-60) for calculating evolutionary divergences among mammals in cases where the fossil record is inconclusive. A/C-60 was examined critically by van Tuinen and Hadly (2004) and shown to outperform other mammalian standards of this kind. Application of A/C-60 to the sequences of complete mtDNA molecules places the *Pan/Homo* divergence at ≥ 7.5 MYBP and the deepest divergences among recent humans at $\approx 1/30$ of this time, i.e. at $\geq 250,000$ YBP (Arnason et al., 2008). This dating is somewhat earlier than most other estimates of this divergence, a circumstance that may be related to differences in the applied approaches, not least the dating allocated to the divergence between *Pan* and *Homo*, which is still placed at ≈ 6.5 MYBP by some authors despite its conflict with established palaeontology. The 250,000 YBP estimate is consistent with the marked progressive Palaeolithic exploitation of small animals in the Levant $\geq 200,000$ YBP (Stiner et al., 1999) as a consequence of enduring human presence and faunal exploitation outside Africa. A much earlier and enduring presence of advanced *Homo* in the Levant (e.g. Acheulian Technocomplex) has also been documented archaeologically (Goren-Inbar et al., 2000; Goren-Inbar, 2011).

Based on analysis of the first complete Denisovan mtDNA, Krause et al. (2010) concluded that Denisova derived from a migration out of Africa ≈ 1 MYBP, followed by an exodus of early Neanderthals (also out of Africa) between 500,000 and 300,000 YBP and the ancestors of non-African modern humans $\approx 50,000$ YBP. The study did not clarify how finds in the Altai Mountains (Denisova Cave) could indicate migration out of Africa 1 MY earlier. Similarly, the exclusive location of Neanderthal fossils in Eurasia is problematic for the traditional OOA. Hublin (2009) referred to that crucial Neanderthal issue in the following manner: "... none have been documented in North Africa".

It should be borne in mind that Krause et al. (2010), at the time of the publication of their study, were incognizant of the phylogenetic discrepancy between the nuclear and mitochondrial DNA of Denisova mentioned above. They could therefore not examine the Neanderthal/Denisova relationship in a perspective that otherwise had made it difficult to reconcile OOA with the absence of Neanderthals in Africa. Martín-Torres et al. (2011) examined the study of Krause et al. (2010) from a palaeontological/archaeological point of view and expressed reservations regarding the latter's conclusions that Denisovans and Neanderthals derived from migrations out of Africa.

Groucutt et al. (2015) addressed OOA in a recent study by simulating different OOA scenarios. The authors maintained that current genetic, palaeontological and archaeological data indicated that *Hss* had originated in Africa and dispersed from that continent. The authors expressed, however, a particular qualification regarding this view, viz.: "Future fossil discoveries in Southern Asia have the potential to radically transform our understanding of that dispersal" (i.e. OOA). This reservation became actualized most recently at the palaeontological description of a collection of human teeth, with an age of 80,000–120,000 years, in Hunan Province, southern China (Liu et al., 2015) and soon thereafter by the demonstration of hominin presence in Sulawesi from $>200,000$ YBP until $\approx 100,000$ YBP (van den Bergh et al., 2016).

The basal mtDNA relationship of recent humans that Cann et al. (1987) obtained by midpoint-rooting has been recovered in virtually

Download English Version:

<https://daneshyari.com/en/article/2815012>

Download Persian Version:

<https://daneshyari.com/article/2815012>

[Daneshyari.com](https://daneshyari.com)