



Review

A phylogenetic view of the Out of Asia/Eurasia and Out of Africa hypotheses in the light of recent molecular and palaeontological finds



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ABSTRACT

The substantiality of the Out of Africa hypothesis was addressed in the light of recent genomic analysis of extant humans (*Homo sapiens sapiens*, *Hss*) and progress in Neanderthal palaeontology. The examination lent no support to the commonly assumed Out of Africa scenario but favoured instead a Eurasian divergence between Neanderthals and *Hss* (the Askur/Embla hypothesis) and an Out of Asia/Eurasia hypothesis according to which all other parts of the world were colonized by *Hss* migrations from Asia. The examination suggested furthermore that the ancestors of extant KhoeSan and Mbuti composed the first *Hss* dispersal(s) into Africa and that the ancestors of Yoruba made up a later wave into the same continent. The conclusions constitute a change in paradigm for the study of human evolution.

1. Introduction

The Out of Africa hypothesis (OOAH), which proclaims that modern humans (*Homo sapiens sapiens*, *Hss*) originated in Africa, is a common assumption in the discussion of the evolution and dispersal of *Hss*. Temporal estimates linked to the hypothesis have even been used to redefine the nature of palaeontological finds related to *Hss* evolution.

OOAH was examined recently on the basis of palaeontology and molecular data (Árnason, 2016). This study did not support OOA, proposing instead a scenario according to which *Hss* originated in an Asian/Eurasian biogeographic region from which Africa was later colonized. Here the Into Africa scenario is readdressed, primarily in the light of the age and location of Neanderthal (*Hsn*) fossils and newly presented genomic relationships within *Hss* that were not previously available.

The Out of Asia/Eurasia hypothesis (OOEH) presented here reverses the prevalent assumptions of *Hss* evolution and dispersal although the trees underlying OOEH and OOA are superficially the same despite the different messages that emerge when they are examined according to phylogenetic approaches.

It follows from the OOEH scenario that all other parts the world were colonized by *Hss* populations that had their roots in Asia.

2. The phylogenies behind OOEH and OOA

The phylogenetic *Hss* trees of nuclear DNA (nuDNA) and complete mitochondrial DNA (mtDNA) molecules are generally consistent with each other. Fig. 1 shows the main characteristics of the nuDNA tree of *Hs* (*Homo sapiens*). The nomenclature follows Árnason (2016). Regarding the depicted phylogeny it should be noted that analysis of complete mtDNAs of Neanderthals (Green et al., 2008) and Denisova (Krause et al., 2010) place Denisova as a sister-group to a branch that encompasses *Hss* and Neanderthals proper (*Hsnn*). The time of the divergence between *Hsn* and *Hss* is commonly placed in the range of 400,000–450,000 YBP (e.g. Krause et al., 2010; Meyer et al., 2012) relative to a *Pan/Homo* divergence set at 6–6.5 MYBP. In comparison estimates based on the common external calibration point A/C-60 place the *Pan/Homo* divergence at ≈ 7.5 MYBP (Árnason et al., 2008), resulting in an *Hsn/Hss* divergence at $\approx 500,000$ YBP. The estimated time of the deepest divergence among extant humans, that between KhoeSan/Mbuti and remaining humans, is about half that of the *Hsn/Hss* split, i.e. $\approx 250,000$ YBP.

An *Hsn/Hss* divergence $\approx 500,000$ YBP is upheld by palaeontological finds in Sima de los Huesos, Spain, which show that derived Neanderthal morphological features had developed as early as 430,000 YBP (Arsuaga et al., 2014, 2015; see also the *Hsn* nuDNA

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; *Hsnn*, *d* for Denisovans; *Hsmn*, *n* for Neanderthals; LCA, last common ancestor; mtDNA, mitochondrial deoxyribonucleic acid; nuDNA, nuclear DNA; MYBP, million years before present; OOA, Out of Africa hypothesis; OOEH, Out of Asia/Eurasia hypothesis; YBP, years before present

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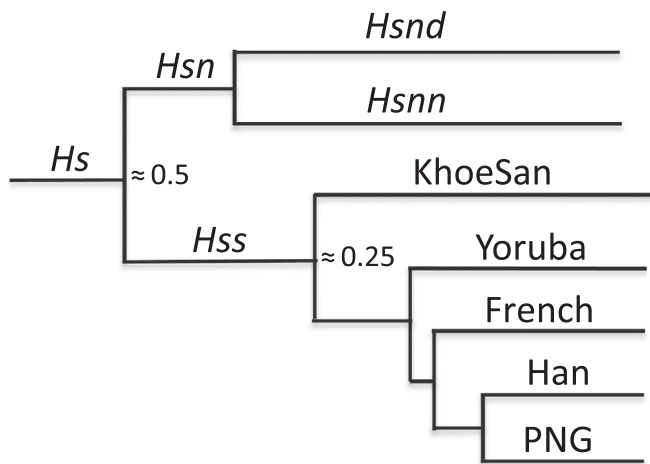


Fig. 1. A phylogenetic tree of *Homo sapiens* (*Hs*), based on nuclear DNA. The tree includes taxa that have particular significance for the evaluation of the Out of Africa and Out of Asia/Eurasia hypotheses (OOAH and OOEH). *Hs* encompasses the subspecies Neanderthals (*Homo sapiens neanderthalensis*, *Hsn*) and modern humans (*Homo sapiens sapiens*, *Hss*). Neanderthals proper (*Hsnn*) and Denisovans (*Hsnd*) constitute sister-groups within *Hsn*. KhoeSan and Yoruba represent African *Hss* populations, while French, Han (Chinese) and PNG (Papua-New Guinea) represent non-African taxa. The topology of the tree carries no information that allows distinction between OOAH and OOEH. Branch lengths are not in accord with a temporal scale. The ages of the divergences between *Hsn* and *Hss* (≈ 0.5 MYBP) and KhoeSan and its sister group (≈ 0.25 MYBP) have been marked.

results of Meyer et al., 2016). The temporal limits related to the site might be earlier still (Bischoff et al., 2007). The exclusive occurrence of Neanderthals in Europa and Asia and their absence from Africa restricts their origin to Eurasia (Árnason, 2016). As a consequence the origin of their sister-group, *Hss*, should be placed in the same continent, i.e. Eurasia (the Askur/Embla hypothesis, Árnason, 2016), in compliance with the LCA (last common ancestor) understanding that the LCA(s) of any two sister groups cannot be separated, neither in time nor space.

The Eurasian palaeontological record of *Hss* is sparse compared to that of *Hsn*. Therefore the results of Liu et al. (2015), who described the presence of humans with fully modern morphologies in southern China $\approx 90,000$ – $120,000$ YBP, were highly unexpected for the adherents of OOAH. The authors, Liu et al. (2015), expressed in two sentences the essence of their findings regarding *Hss* evolution: “The Daoxian sample is more derived than any other modern humans, resembling middle-to-late Late Pleistocene specimens and even contemporary humans. Our study shows that fully modern morphologies were present in China 30,000–70,000 years earlier than in the Levant and Europe”.

The Daoxian finds were inconsistent with OOAH, as that hypothesis prescribed that *Hss* finds of this age could not exist outside Africa. The location of the samples was also challenging as OOAH predicted that the *Hss* colonization of Eurasia should go eastward from Africa and not westward from easterly Asia as maintained by Liu et al. (2015). Kuhlwilms et al. (2016), in their comprehensive molecular study, concluded the following regarding these palaeontological circumstances: “The recent demonstration that modern humans may have been in

Table 1
Estimates of the ages of population divergences related to the OOEH scenario.

Population pairs	25%	50%	75%
Non-Africans/KhoeSan	82,000	131,000	173,000
Non-Africans/Mbuti	66,000	112,000	171,000
Non-Africans/Yoruba	45,000	63,000	123,000
Yoruba/KhoeSan	58,000	87,000	120,000
Yoruba/Mbuti	32,000	56,000	84,000

The estimates (Mallick et al., 2016) show the times at which 25%, 50% and 75% of the lineages in each pair of populations coalesced into a common ancestral population. In the context of the OOEH phylogeny shown in Fig. 2b the estimates are consistent with an early KhoeSan/Mbuti dispersal into Africa followed by a corresponding migration of the ancestors of Yoruba. The figures related to KhoeSan/Yoruba and Mbuti/Yoruba suggest genetic exchange (probably in Asia) between Yoruba and Mbuti at a scale that exceeded that between Yoruba and KhoeSan.

China as early as 120,000 years ago (Liu et al., 2015) also suggests that modern humans migrated early out of Africa. Thus, early modern humans may have had the opportunity to admix with archaic hominins before the migration of the modern human ancestors of present-day non-Africans.”

Pagani et al. (2016) in an extensive analysis of 483 human genomes (379 new) followed Kuhlwilms et al. (2016) regarding the inclusion of an *Hss* population that had left Africa and became extinct prior to the successful expansion of *Hss* into Eurasia. In accord with this understanding the authors concluded that $> 2\%$ of the genomes of recent Papuans could be traced to an early *Hss* exodus from Africa.

Also Mallick et al. (2016) adhered to OOAH in another comprehensive genomic analysis that was based on 142 extant *Hss* populations. The study included a series of pairwise comparisons related to basal *Hss* divergences. These results have particular significance for the examination of OOEH and OOAH, as they present an opportunity for a direct evaluation of the two hypotheses.

The study of Mallick et al. (2016) showed that the ancestral *Hss* population had begun to develop genetic substructures $> 200,000$ YBP, an age that is compatible with the commonly accepted estimates of the basal divergence of extant *Hss*. Furthermore, the analysis demonstrated that the basal divergence among extant *Hss* fell between non-Africans (as represented by a French genome) and Africans (as represented by KhoeSan and Mbuti). The authors presented also estimates of several *Hss* divergences that involved Yoruba, the African population that is commonly taken as constituting the founder of non-Africans. Regarding a potential connection between Papuans and an early OOAH dispersal Mallick et al. (2016) concluded that indigenous Australians, New Guineans and Andamanese had the same ancestry as other non-Africans.

Fig. 2 summarizes the phylogenies behind OOAH (2a) and OOEH (2b) with African taxa marked in red and Eurasian in blue. The trees are presented in an open-book display in order to facilitate the comparison between the two hypotheses. It can be seen that the topologies and taxon contents of the two trees are the same but their phylogenetic messages are diametrically opposed.

Fig. 2a is consistent with the acknowledged African split between *Hss* and *Hsn* and an early *Hsn* exodus into Eurasia. This divergence was

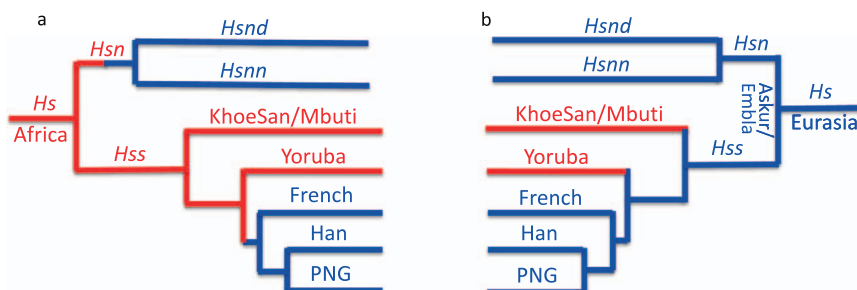


Fig. 2. The phylogenies behind OOAH and OOEH.

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