

MOSTLY OUT OF AFRICA, BUT WHAT DID THE OTHERS HAVE TO SAY?

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The Recent Out-of-Africa human evolutionary model seems to be generally accepted. This impression is very prevalent outside palaeoanthropological circles (including studies of language evolution), but proves to be unwarranted. This paper offers a short review of the main challenges facing ROA and concludes that alternative models based on the concept of metapopulation must be also considered. The implications of such a model for language evolution and diversity are briefly reviewed.

1. Introduction

As is very well known, the modern human origins debate is now definitely closed and the general consensus is that the Recent Out of Africa model (Stringer & Andrews, 1988) explains perfectly well the genetic, palaeoanthropological and archaeological patterns observed. So, a fairly recent (around 200,000 years ago) and localized (a single population in (East) Africa) origin of modern humans followed by global expansion and replacement explains everything... But, is it really so?

2. The evidence

The issue of modern human origins is very important, profoundly influencing the range of explanations for the emergence, maintenance and evolution of language and the interactions between population genetic and linguistic structures. The impression outside the palaeoanthropological circles, is that the Recent Out-of-Africa model (henceforth ROA) is true, perception usually reinforced through the popularization press. In fact, there *is* a debate going on and the matters are *very far* from being settled.

I have selected the most recent papers (post 01.2000 but also a few earlier very important ones), dealing with cases where the ROA model does not fit or fits equally well as the alternative models. The search was not exhaustive and the further selection for inclusion in the review was rather strict, but still, the count

is quite large for a “closed” debate. This is the list of the main such points:

The transition to modern *Homo sapiens* was not sudden: the appearance of modern humans is sometimes clad as a heroic myth (McBrearty & Brooks, 2000), as a sudden transition, as a revolution. But there wasn't any such revolution (McBrearty & Brooks, 2000), neither morphologically, nor behaviorally, instead a mosaic of independent transitions to skeletal and behavioral modernity took place in Africa.

The modern humans originated from a structured population: the X chromosome disprove a single panmictic population, favoring models which “incorporate admixture between divergent African branches of the genus *Homo*” (Garrigan *et al.*, 2005a; Harris & Hey, 1999; Harding & McVean, 2004).

Some genes have very deep, non-African branches: the *RRM2P4* pseudogene has a MRC of ~2 MYA in East Asia (Garrigan *et al.*, 2005b), suggesting introgression from archaic local humans. The *dystrophin* gene presents a haplotype predating the ROA expansion and virtually absent from Africa. It might have left Africa earlier and introgressed later (Ziętkiewicz *et al.*, 2003). A noncoding region of the X chromosome (Xq21.1-21.33) shows a variant possibly arisen in Eurasia > 140 KYA (Yu, Fu & Li, 2002). Templeton (2002), applying nested clade analysis, finds a pattern of interbreeding between expanding and local populations.

Regional morphological continuity: one of the oldest claims against ROA-type models (Weidenreich, 1947). Wolpoff *et al.*, (2001) analyzed transitional cranial forms in two peripheral regions (Australia and Czech Republic) and concluded that they have dual ancestry. Wu (2004) concludes evolutionary continuity in China between *sapiens* and *erectus*. Demeter, Manni & Coppens (2003) supports regional continuity in the Far East with a morphometric analysis of 45 fossil crania. The most ancient European modern (Romania) presents a “mosaic of archaic, early modern human and possibly Neanderthal morphological features” (Trinkaus *et al.*, 2003). The most well-known such case is the Abrigo do Lagar Velho infantile skeleton (Duarte *et al.*, 1999), showing a mixture of modern and Neanderthal morphological characters (Duarte *et al.*, 1999; Trinkaus & Zilhão, 2003), still accepted despite the critics. Given the burial context, the child was considered as a full community member.

There is also a series of arguments usually considered to support ROA, but which turn out not to be decisive:

Ancient Neanderthal *mtDNA* proves them a different species: the conclusion from extraction studies (Krings *et al.*, 1997; Lalueza-Fox *et al.*, 2005; Krings *et al.*, 2000; Ovchinnikov *et al.*, 2000) is that Neanderthal *mtDNA* is different from modern, seemingly supporting a replacement model. **But** Gutiérrez, Sánchez & Marín (2002) show ancient *mtDNA* is very sensitive to phylogenetic methods, diagenetic modifications have altered the sequences, and conclude that Neanderthal and modern *mtDNA* may overlap. Nordborg (1998) probabilistically proved that any single locus cannot resolve between replacement and admixture, being necessary to consider many loci in parallel (Wall (2000) suggests 50-100). *mtDNA* was extracted from a fossil modern gracile Australian *Homo sapiens* (Adcock *et al.*, 2001) and proved outside the modern pool. Later, the finds (LM3) were redated to 40 ± 2 KYA (Bowler *et al.*, 2003) and the methodology contested (Cooper *et al.*, 2001), without denying that *mtDNA* lineages can be decoupled from other parts of the genome (Relethford, 2001a).

Based on living primates, the hominid clade was speciose: contested by Hunt (2003), who argues that if appropriate models are considered (the great apes), the hominin lineage may be seen “as a single, phenotypically diverse, reticulately evolving species” (Hunt, 2003).

Neanderthal morphology separates them from moderns: Harvati, Frost & McNulty (2004) used 3D primate craniofacial models and concluded Neanderthals and moderns to be separate species, but Ahern, Hawks & Lee (2005) considered this approach not capable of distinguishing between same or different species. Morphological differences could be due to non-genetic factors (Bogin & Rios, 2003): rapid dramatic morphological changes in modern Mayans accompanies migration to the USA, cautioning against morphological differences in fossil humans as diagnostic for species.

Genetic structure of living populations shows greater diversity in Africa and an African origin of human genes: generally, Africa harbors the greatest genetic diversity of living humans and most gene trees coalesce there (Jobling *et al.*, 2004) but this pattern is not true at least for the X chromosome. The greater genetic diversity of Africa can be explained by a greater long-term population size (Relethford, 2001b), also accommodating the majority coalescence (Takahata, Lee & Satta, 2001).

Modern humans are genetically very uniform: not precluding geographical differentiation (Bamshad *et al.*, 2003) and is usually considered the effect of a major population bottleneck, either a speciation or a migration/founder effect (Jobling *et al.*, 2004) or both. But this can be interpreted as a metapopulation

evolutionary history (Relethford, 2001b; Templeton, 2002; Harding & McVean, 2004; Eswaran, 2002), accommodating the small effective population size (Rousset, 2003) with a large enough adult population. Yu *et al.* (2003) shows the chimpanzees genetic diversity to have been overestimated.

There are some other arguments, like the **relative abundance of hybrids in primates** (Jolly, 2002), suggesting ubiquitous admixture in humans or the **unexpected diversity of our genus**, highlighted by the recent discovery of *Homo floresiensis* (Brown *et al.*, 2004), also pointing to advanced cognitive and technological capacities of *Homo erectus*, allowing him to cross Wallace's line.

3. The suggested class of alternative models

The data presented above (and more not included) suggests that an alternative class of models should be considered, but choosing it demands awareness to the influence of certain non-scientific factors, like political/moral (Wolpoff & Caspari, 1997), personality clashes/ambitions (Jobling *et al.*, 2004) and favored source (genetic, archaeological, fossil).

Generally, a polarity is described between the ROA model and *multiregionalism* (Wolpoff & Caspari, 1997; Relethford, 2001b; Lewin, 1998; Jobling *et al.*, 2004), but, (Relethford, 2001b), there are *two* distinct dimensions: the *mode of transition* between archaic and modern humans and the *location and timing of this transition*. Our analysis suggests a recent African origin, a structured ancestral population (metapopulation), a mosaic/accretion of independent traits (morphological and behavioral/cultural) and is disfavoring a speciation event. It suggests a reticulate evolution, where constant gene flow between demes insures local adaptation and continuity while spreading globally the modern genetic-cultural complex. These seem to be satisfied by various models proposed (for example, Relethford, 2001b, Eswaran, 2002 and especially Templeton, 2002), but for our purposes, the following main points are relevant:

- no abrupt speciation event separating moderns from archaics;
- culturally, an accretionary evolution and not a sharp revolution;
- admixture between the migrating waves and locally adapted and differentiated archaics, insuring various degrees of regional continuity;
- metapopulation evolutionary model, whereby demes are constantly created, replaced and extinguished, maintaining genetic and cultural flows,

such that there is a global evolutionary accretion of genes and cultural traits without a “core” source population of the full package, Africa being demographically dominant.

4. Conclusions: implications for language evolution and diversity

Opposed to ROA, such a model can accommodate the language capacity as a mosaic of independent traits evolved in different demes. Language has a more or less specific genetic component, (Stromswold, 2001), confirmed by the *FOXP2* gene (Enard *et al.*, 2002) and seemingly supported by Williams syndrome (Bellugi, Korenberg & Klima, 2001). It is conceivable, for example, that the human-specific *FOXP2* mutations arose in different demes at different times and coalesced with the qualitatively different languages they allowed. The discovery (Mekel-Bobrov *et al.*, 2005; Evans *et al.*, 2005) of recent variants of two genes related to brain growth and development, with signatures of strong positive natural selection, not yet fixated and with marked population structures supports this mosaic evolutionary process.

There could exist minor inter-population genetic differences in linguistic capacity (because of regional continuity, founder effect or not yet fixated advantageous alleles), offering new perspectives on language evolution, given that the basic requirement is heritable variation. Such a model highlights the early evolution of the language capacity and languages as two inter-related phenomena in metapopulations, leading to the modern linguistic capacity, able to support an immense linguistic (almost neutral) variation.

Another possibility is that besides the accidental correlations between genes and languages (Cavalli-Sforza *et al.*, 1994), there might also exist a slight non-accidental correlation, whereby specific genetic configurations favor/are favored by specific linguistic features. A fictional example could be a population with a high incidence of articulatory incapacity to produce a trilled /r/, which in turn will select for languages realizing the phoneme /r/ as an approximant. Conversely, speakers with such a deficiency will not incur any fitness penalty when immersed into a community speaking the /r/-approximant language. This hypothetical example can be extended to more plausible cases, like the better control of rapid orofacial movements (supposedly) brought by the human-specific mutation(s) in *FOXP2*.

Acknowledgements

My work has been supported by an ORS Awards Grant 2003014001 and a CHSS Studentship, The University of Edinburgh.

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