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Testing modern human out-of-Africa dispersal models and implications for modern human origins

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ABSTRACT

The modern human expansion process out of Africa has important implications for understanding the genetic and phenotypic structure of extant populations. While intensely debated, the primary hypotheses focus on either a single dispersal or multiple dispersals out of the continent. Here, we use the human fossil record from Africa and the Levant, as well as an exceptionally large dataset of Holocene human crania sampled from Asia, to model ancestor–descendant relationships along hypothetical dispersal routes. We test the spatial and temporal predictions of competing out-of-Africa models by assessing the correlation of geographical distances between populations and measures of population differentiation derived from quantitative cranial phenotype data. Our results support a model in which extant Australo-Melanesians are descendants of an initial dispersal out of Africa by early anatomically modern humans, while all other populations are descendants of a later migration wave. Our results have implications for understanding the complexity of modern human origins and diversity.

1. Introduction

For most of the late twentieth century, discussion on human evolution and modern human origins, or anthropogeny (Varki et al., 2008), focused on validating or falsifying the polarizing models of either multiregional evolution or African origins and replacement of other hominins. Consensus on Africa as the primary birthplace for modern humans has emerged from palaeontological and genetic evidence, placing the common ancestral population between approximately 100 and 200 thousand years ago (~ka; White et al., 2003; McDougall et al., 2005; Fu et al., 2013b; Poznik et al., 2013; Scozzari et al., 2014). At the same time, hominin interbreeding has been proposed in order to explain the genetic affinities between extant and extinct hominin populations (Green et al., 2010; Reich et al., 2010, 2011; Hammer et al., 2011; Mendez et al., 2013; Prüfer et al., 2014; Sankararaman et al., 2014; The Sigma Type 2 Diabetes Consortium, 2014; Vernot and Akey, 2014). Similarly, a revival of the 'assimilation' hypothesis in human palaeontology (Smith et al., 1989, 2005) has encouraged continued assessment of taxonomically ambiguous fossils as descendants of hominin interbreeding events (Liu et al., 2010; Rogers Ackermann, 2010). As a result, the anthropogeny discussion has shifted toward assessing the degree, timing, and location of admixture between hominin populations (Sankararaman et al., 2012; Cooper and Stringer, 2013; Sankararaman et al., 2014). However, an alternative view is that genetic and phenotypic resemblance between extant and extinct populations is a consequence of deep population substructure in Africa, as well as drift following the out-of-Africa expansion (Mirazón Lahr and Foley, 1994; Mirazón Lahr, 1996; Green et al., 2010; Blum and Jakobsson, 2011; Ghirotto et al., 2011; Eriksson and Manica, 2012, 2014; Lowery et al., 2013; Reyes-Centeno et al., 2014). In this view, the context of the geographical and temporal niches occupied by recent hominins can explain, at least in part, the resemblance between Holocene populations and some Pleistocene

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hominins. This view suggests that genetic and phenotypic plesiomorphic traits in certain extant populations reflect differential diversity exported outside of Africa, particularly if the dispersal pattern out of the continent consists of multiple exits.

Given these competing views, understanding the spatial and temporal distribution of hominin populations in the Middle–Late Pleistocene is necessary for developing a coherent anthropogeny theory. Here, we review competing out-of-Africa dispersal hypotheses previously proposed from multidisciplinary evidence. We then design a test for assessing their spatio-temporal predictions using measures of cranial diversity between extant human populations and Pleistocene anatomically modern human (AMH) populations, or 'palaeo-demes' (Howell, 1999). Using a large craniometric dataset, we test the expected relationship of hypothetical ancestral palaeodemes from Africa and the Levant and descendant Holocene populations from Asia, as compared to hypothetical geographical routes of dispersal predicted under different out-of-Africa models.

1.1. The serial founder effect and eastward expansion hypothesis

Support for the origins of AMHs in Africa and their expansion out of that continent comes from the consistent observation that genetic (Eller, 1999; Harpending and Rogers, 2000; Prugnolle et al., 2005; Ramachandran et al., 2005; Liu et al., 2006; Li et al., 2008; Deshpande et al., 2009), linguistic (Atkinson, 2011), and cranial phenotypic (Manica et al., 2007; von Cramon-Taubadel and Lycett, 2008; Betti et al., 2009) diversity decreases with increasing distances from Sub-Saharan Africa. This pattern—referred to as a cascading bottleneck (Harpending and Rogers, 2000) or serial founder (Ramachandran et al., 2005) effect—is usually interpreted to represent a single dispersal event, with an iterative loss of diversity during modern human expansion caused by small bottlenecks and a loss in diversity following each successive founding process. Biological diversity decreases primarily along a latitudinal axis in Eurasia, consistent with a series of short, simple terrestrial migration routes, avoiding major geographic barriers (Liu et al., 2006; Ramachandran and Rosenberg, 2011). This eastward expansion (EE) scenario results in increasing rates of population differentiation and genetic linkage disequilibrium with increasing distances from Africa (Ramachandran et al., 2005; Jakobsson et al., 2008). The EE hypothesis is compatible with a scenario in which expanding AMHs admixed with other hominin populations, but where their genetic contributions would have had to be small (DeGiorgio et al., 2009).

1.2. The multiple dispersals and southern route hypothesis

An alternative hypothesis that is also consistent with decreasing diversity from Africa is a multiple dispersals (MD) scenario, whereby AMHs expanded out of the continent at different timescales and via distinct geographical routes (Mirazón Lahr and Foley, 1994; Mirazón Lahr, 1996). The MD hypothesis was derived primarily from comparative craniometric studies and associations with the available palaeoenvironmental record. It predicts that a first, opportunistic dispersal between 50 and 100 ka involved a rapid migration primarily along a coastal route, through the southern Arabian Peninsula, reaching Southeast Asia at roughly the same time that a second dispersal through the Levant prompted colonization of the rest of Eurasia between ~40 and 50 ka. Isolated populations throughout Southeast Asia are proposed to retain the signal of the initial 'southern route' dispersal, while others are palimpsests of the two dispersals. Hypothetical 'relic' populations include Australians, Melanesians, Papuans, Dravidian speakers of South Asia, and short-statured 'Negrito' populations of Southeast Asian islands, such as the Andaman Islanders of the Bay of Bengal and the Aeta/Agta of the Philippines. Following a biogeographical approach, the designation of 'relics' is in reference to the ecological context of populations that have become isolated as a result of occupying geographical refugia or exploiting specific ecological niches. The MD scenario predicts that these populations retain plesiomorphic traits because they diverged first from a structured ancestral African population, have remained isolated from subsequent population expansions, and consisted of smaller population sizes. A MD scenario has been questioned on the basis of autosomal genetic data (Wollstein et al., 2010; Reich et al., 2011) but has been supported by some recent genomic studies sampling proposed relic populations (Ghirotto et al., 2011; Rasmussen et al., 2011; Reyes-Centeno et al., 2014).

1.3. The multiple dispersals with isolation hypothesis

In an amendment to the MD hypothesis, the multiple dispersals with isolation (MDI) scenario suggests that Australians are the only isolated descendants of the southern route dispersal, while Papuans, Melanesians, and possibly the Aeta 'Negrito' from the Philippines retain a southern route genetic signal that is detectable but obscured due to admixture with members of the second dispersal (Rasmussen et al., 2011). An isolation scenario for Australo-Melanesians is consistent with uni-parental (mitochondrial and non-recombining Y-chromosome DNA) and genome-wide data, although gene flow from outside the region during historical times is still detectable at low levels in Northern Australia (Hudjashov et al., 2007; Pugach et al., 2013). The chronological separation between the dispersals is considered to be relatively short, with the first commencing between ~75 and 62 ka, as inferred from the divergence of Africans and Australians, and the second between ~38 and 25 ka, as inferred from the divergence of East Asians and Europeans. However, dates of divergence between Africans and Eurasians have been estimated as far back as ~140 ka (Gutenkunst et al., 2009), which is more in line with a southern route dispersal interpreted to have occurred as early as the late Middle Pleistocene or during the last interglacial, between ~131 and 114 ka (Stringer, 2000; Petraglia et al., 2010; Armitage et al., 2011; Boivin et al., 2013; Reyes-Centeno et al., 2014; Scozzari et al., 2014).

1.4. The single dispersal and beachcomber arc hypothesis

Given the discrepancies between the EE and MD/MDI hypotheses, a reconciling view is that of a single wave bifurcating outside of Africa, likely in southwest Asia (Mellars, 2006; Oppenheimer, 2012). This view is broadly similar to the EE hypothesis in that population divergence outside of Africa is largely due to the geographic barrier of the Himalaya mountain range, which obstructed migrations between northern and southern Asia. The EE scenario also acknowledges the importance of a coastal 'beachcomber arc' migration into Australia, along the Indian Ocean rim. Based primarily on uni-parental genetic evidence, this beachcomber single dispersal (BSD) hypothesis suggests a single out-of-Africa event at ~75 ka (Oppenheimer, 2012) or less than 65 ka (Mellars et al., 2013). Like the EE scenario, BSD considers a series of founding bottlenecks during this expansion. However, in contrast to the parsimonious latitudinal gene flow of EE, BSD implies substantial migration along a longitudinal axis. For example, in addition to a dispersal along the Indian Ocean rim, the 'beachcomber arc' also includes the eastern Pacific Ocean rim. Furthermore, it allows for migrations from southwest Asia back into Africa. Gene flow, therefore, is much more dynamic. The implication for biological diversity is that Eurasian populations differentiated in southwest Asia, and that extant North African and non-African