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Dental phenotypic shape variation supports a multiple dispersal model for anatomically modern humans in Southeast Asia

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ABSTRACT

The population history of anatomically modern humans (AMH) in Southeast Asia (SEA) is a highly debated topic. The impact of sea level variations related to the Last Glacial Maximum (LGM) and the Neolithic diffusion on past population dispersals are two key issues. We have investigated competing AMH dispersal hypotheses in SEA through the analysis of dental phenotype shape variation on the basis of very large archaeological samples employing two complementary approaches. We first explored the structure of between- and within-group shape variation of permanent human molar crowns. Second, we undertook a direct test of competing hypotheses through a modeling approach. Our results identify a significant LGM-mediated AMH expansion and a strong biological impact of the spread of Neolithic farmers into SEA during the Holocene. The present work thus favors a "multiple AMH dispersal" hypothesis for the population history of SEA, reconciling phenotypic and recent genomic data.

1. Introduction

Recent fossil and population genetic discoveries put Southeast Asia (SEA) at the forefront of the study of evolution and dispersal processes that shaped the biological history of anatomically modern humans (AMH) outside Africa (Reyes-Centeno et al., 2016; Stoneking, 2016). Current issues mainly revolve around the mode and timing of the earliest AMH arrival in the region (and their hypothetical biological interactions with pre-existing "archaic" humans), as well as the extent to which sea level variations related to the Last Glacial Maximum (LGM) and the Neolithic diffusion represented major factors in population expansions.

Based on the antiquity of several early AMH fossils (Détroit et al., 2004; Barker et al., 2007; Demeter et al., 2012, 2015) and the earliest evidence of human presence in Australia (Clarkson et al., 2015; O'Connell and Allen, 2015), the "consensus view" (Morley, 2017) considers that AMHs arrived in SEA ~50/60 ka. This view is challenged by fossil discoveries in southern China (Liu et al., 2010,

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2015; Bae et al., 2014) and Java (Storm et al., 2005), which suggest earlier arrivals, closer to the middle/late Pleistocene boundary. Aside from these chronological issues (Michel et al., 2016; Oxenham and Buckley, 2016), the mode of dispersal of the earliest AMH into eastern Asia and SEA is also debated. Most evidence indicates at least two late Pleistocene dispersals (Rasmussen et al., 2011; Reyes-Centeno et al., 2014; Oxenham and Buckley, 2016; Pagani et al., 2016; Stoneking, 2016), with an early migration wave along a southern coastal route (providing the earliest human evidence in SEA and Australia) and a subsequent later late Pleistocene expansion, probably following a more northern route (Oxenham and Buckley, 2016; Stoneking, 2016), that gave rise to "modern East Asians" (Rasmussen et al., 2011). While substantial admixture events are proposed between populations of these two dispersals (Rasmussen et al., 2011), "when, how and where the descendants of these northern and southern populations met" (Oxenham and Buckley, 2016:20) is unresolved. Other evidence suggests a single primary late Pleistocene AMH expansion from Africa into eastern Asia, in which successive population bottlenecks and drift played a major role (The HUGO Pan-Asian SNP Consortium et al., 2009; Mallick et al., 2016). Furthermore, the presence of pre-existing "archaic" hominin groups in the region during the early-/mid-late Pleistocene (Brown et al., 2004; Mijares et al., 2010; Détroit et al., 2013; Sutikna et al., 2016), as well as the detection of genetic material inherited from Denisovans among present day SEA populations (Reich et al., 2011), might signal unexpected patterns of biological interactions and coexistence during the period of early AMH diaspora(s) (Pääbo, 2015; Reyes-Centeno, 2016; Stoneking, 2016).

Early AMH dispersal routes throughout SEA (and into Australia) were obviously influenced by eustatic variations related to climate fluctuations (Voris, 2000; Balme, 2013). More contentious is the impact of the huge glacio-eustatic sea level variations into and out of the LGM on AMH migrations in the region. During the LGM sea level lowstand (19–26.5 ka; Clark et al., 2009), the sea level reached ~120 m (Lambeck et al., 2002), exposing the Sunda Shelf (Fig. 1), the most extensive continental shelf besides the polar regions (Hanebuth et al., 2000). During the LGM, this huge landmass, possibly partly covered by a "savanna corridor" (Bird et al., 2005; Boivin et al., 2013), connected mainland SEA (MSEA) to the western islands of Indonesia (e.g., Sumatra, Java, Borneo). The late Pleistocene/early Holocene post-glacial sea level rise (up to 16 m in 300 years—14 ka; Hanebuth et al., 2000) profoundly and rapidly impacted the landscape, reaching roughly the present day configuration ~7 ka BP (Pope and Terrell, 2008). Despite some claims that this period of drastic geographic and environmental change was probably a vector of human mobility (Solheim, 1984; Pope and Terrell, 2008; Barker and Richards, 2013), widely accepted hypotheses of population history in SEA do not assume significant AMH dispersals during the late Pleistocene and/or the early Holocene. This view, however, is challenged by several recent population genetic studies suggesting that major AMH dispersals occurred during the LGM (or during post-glacial sea level rise), shaping present day biological diversity in SEA significantly (Soares et al., 2008, 2016; Karafet et al., 2010; Jinam et al., 2012; Tumonggor et al., 2013; Brandão et al., 2016).

Preferred interpretations of the population history of SEA generally propose the Holocene Neolithic diffusion as the most important factor that shaped current biological and linguistic AMH diversity in SEA (Bellwood, 1997, 2011). However, the genetic impact of the diffusion of the Neolithic in the region is a strongly debated issue (Donohue and Denham, 2010; Bellwood, 2011; Barker and Richards, 2013) and the lack of Neolithic archaeological sites with clear chrono-stratigraphic contexts has for a long time hampered the debate. Osteological data from newly excavated sites such as Man Bac in Vietnam (Oxenham et al., 2011) and Ban Non Wat in Thailand (Higham and Kijngam, 2011) show that important morphological changes are apparent from the beginning of the Neolithic period (Matsumura and Oxenham, 2014). Proponents of a large scale expansion of Neolithic farmers interpret these mid/late Holocene morphological variations as the result of gene flow with populations arriving from the North (Matsumura and Hudson, 2005; Hanihara et al., 2012; Matsumura and Oxenham, 2014). For others, diachronic morphological changes are the result of "modernization" processes (Bulbeck, 1982) through in situ microevolution, without involving significant episodes of gene flow with northern populations (Turner, 1987, 1990; Hanihara, 1993; Pietrusewsky, 2006, 2010).

Hence, despite recent major discoveries and advances, the understanding of Pleistocene and Holocene population history of SEA remains controversial. The initial AMH diaspora (including possible episodes of hybridization with "archaic" humans), the critical environmental changes related to the LGM, and the spread of the Neolithic are alternatively presented as the major forces that shaped the biological history of AMH in the region and call for a direct evaluation of the main hypotheses concerning settlement.

1.1. *Competing hypotheses for the population history of SEA*

The "regional continuity" (RC) model recognizes the initial (~50–60 ka) Pleistocene AMH diaspora (Figs. 1 and 2) as the single major demographic expansion in the course of the population history of SEA, excluding the existence—or significant influence—of later hypothetical dispersal(s) from outside the region (Turner, 1987, 1990; Hanihara, 1993). Critical to the support of the RC hypothesis are the observations that cranial phenotype data (Pietrusewsky, 2006, 2010) and genetic affinities (The HUGO Pan-Asian SNP Consortium et al., 2009) between populations are broadly correlated to their geographic distances, a pattern consistent with a model of isolation-by-distance (Wright, 1943). The RC model thus implies a high level of genetic continuity from the late Pleistocene to present day SEA populations. In contrast with the RC model, the widely accepted "Two-Layer" (TL) hypothesis supports an additional broadly based late Holocene expansion related to the spread of Neolithic farmers from a southeastern Chinese homeland (Matsumura and Hudson, 2005; Matsumura and Oxenham, 2014; Figs. 1 and 2). Based on a multidisciplinary theoretical framework (Bellwood, 2011; incorporating archaeological, linguistic and biological data), this expansion of Neolithic farmers is correlated with the spread of Austronesian languages into island SEA (ISEA) and the Pacific via Taiwan, resulting today in one of the world's largest language families (Blust, 1999; Diamond, 2000; Gray et al., 2009). Under this model, extant "Negrito" populations—small bodied hunter-gatherer populations scattered in the Philippines, Malaysia, and Andaman Islands—are interpreted as "relic" descendants of the initial AMH late Pleistocene entry, assuming moderate to strong late Holocene admixture between Austronesians and Philippine "Negritos" (Lipson et al., 2014). The most parsimonious version of the TL hypothesis (TL_1) considers that the early Holocene source population (=southeastern Chinese homeland) of the Neolithic dispersal into SEA is descended from the initial AMH Late Pleistocene expansion, implying a population continuity from the pre-Neolithic to Neolithic cultural periods in China, as recently reported in northeast Asia (Siska et al., 2017). Nevertheless, this model is challenged by the accumulating genetic, paleoanthropological, and archaeological evidence pointing to at least two late Pleistocene AMH dispersals into Asia (Rasmussen et al., 2011; Reyes-Centeno et al., 2014; Malaspinas et al., 2016; Oxenham and Buckley, 2016; Pagani et al., 2016). The only way to accommodate the TL hypothesis (TL_2) with recent genetic evidence is to consider