

Denisova Admixture and the First Modern Human Dispersals into Southeast Asia and Oceania

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It has recently been shown that ancestors of New Guineans and Bougainville Islanders have inherited a proportion of their ancestry from Denisovans, an archaic hominin group from Siberia. However, only a sparse sampling of populations from Southeast Asia and Oceania were analyzed. Here, we quantify Denisova admixture in 33 additional populations from Asia and Oceania. Aboriginal Australians, Near Oceanians, Polynesians, Fijians, east Indonesians, and Mamanwa (a “Negrito” group from the Philippines) have all inherited genetic material from Denisovans, but mainland East Asians, western Indonesians, Jehai (a Negrito group from Malaysia), and Onge (a Negrito group from the Andaman Islands) have not. These results indicate that Denisova gene flow occurred into the common ancestors of New Guineans, Australians, and Mamanwa but not into the ancestors of the Jehai and Onge and suggest that relatives of present-day East Asians were not in Southeast Asia when the Denisova gene flow occurred. Our finding that descendants of the earliest inhabitants of Southeast Asia do not all harbor Denisova admixture is inconsistent with a history in which the Denisova interbreeding occurred in mainland Asia and then spread over Southeast Asia, leading to all its earliest modern human inhabitants. Instead, the data can be most parsimoniously explained if the Denisova gene flow occurred in Southeast Asia itself. Thus, archaic Denisovans must have lived over an extraordinarily broad geographic and ecological range, from Siberia to tropical Asia.

Introduction

The history of the earliest arrival of modern humans in Southeast Asia and Oceania from Africa remains controversial. Archaeological evidence has been interpreted to support either a single wave of settlement¹ or, alternatively, multiple waves of settlement, the first leading to the initial peopling of Southeast Asia and Oceania via a southern route and subsequent dispersals leading to the peopling of all of East Asia.² Mitochondrial DNA studies have been interpreted as supporting a single wave of migration via a southern route,^{3–5} although other interpretations are possible,^{6,7} and single-locus studies are unlikely to resolve this issue.⁸ The largest genetic study of the region to date, based on 73 populations genotyped at 55,000 SNPs, concluded that the data were consistent with a single wave of settlement of Asia that moved from south to north and gave rise to all of the present-day inhabitants of the region.⁹ However, another study of genome-wide SNP data argued for two waves of settlement¹⁰ as did an analysis of diversity in the bacterium *Helicobacter pylori*.¹¹

The recent finding that Near Oceanians (New Guineans and Bougainville Islanders) have received 4%–6% of their genetic material from archaic Denisovans¹² in principle provides a powerful tool for understanding the earliest human migrations to the region and thus for resolving the question of the number of waves of settlement. The

Denisova genetic material in Southeast Asians should be easily recognizable because it is very divergent from modern human DNA. Thus, the presence or absence of Denisova genetic material in particular populations should provide an informative probe for the migration history of Southeast Asia and Oceania, in addition to being interesting in its own right. However, the populations previously analyzed for signatures of Denisova admixture¹² comprise a very thin sampling of Southeast Asia and Oceania. In particular, no groups from island Southeast Asia or Australia were surveyed. Here, we report an analysis of genome-wide data from an additional 33 populations from south Asia, Southeast Asia, and Oceania; analyze the data for signatures of Denisova admixture; and use the results to infer the history of human migration(s) to this part of the world.

Material and Methods

SNP Array Data

We analyzed data for modern humans genotyped on Affymetrix 6.0 SNP arrays. We began by assembling previously published data for YRI (Yoruba in Ibadan, Nigeria) West Africans, CHB (Han Chinese in Beijing, China) Han Chinese and CEU (Utah residents with Northern and Western European ancestry from the CEPH collection) European Americans from HapMap 3;¹³ Onge Andaman “Negritos”;¹⁴ and New Guinea highlanders, Fijians, one Bornean population, and Polynesians from seven islands.¹⁰

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