



A biogeographic perspective on early human colonization of the Tibetan Plateau



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ABSTRACT

Whence came the early human colonizers of the Tibetan Plateau? Recent genomic research of modern Tibetan gene pool diversity provides evidence of numerous different founding haplogroups among populations. Age estimates suggest that much of the Tibetan gene pool is the product of Holocene migration and admixture, but at least one distinct ancestral haplotype may pre-date the last glacial maximum. Key genes conferring high-altitude adaptation to Tibetan populations suggest that those populations diverged from Han Chinese ancestors between ~8–18 cal ka BP. Diverse Upper Paleolithic technological packages existed in different regions around the margins of the Plateau that could have been carried up by potential early colonizers. However, archeological evidence of early (pre-Neolithic) occupation on the Plateau itself is remarkably uniform, consisting of small short-term camps with a mixed lithic technology featuring simple flakes and shatter, microblades and microcores, larger blades or bladelets, discoidal tablet cores, and occasional bipolar pebble cores; well-dated sites are all post-glacial in age. A simple biogeographic model, the “up from the north” hypothesis, asserts that human groups best suited to colonizing the harsh alpine Plateau environments would have been those adapted to life typical of higher latitudes, and those advantaged northern-latitude colonizers routinely carried microlithic technology with them in hunting the same Palearctic steppe fauna found on the Plateau. The archeological record of early colonizers on the Plateau should therefore be dominated by the north Asian epi-Paleolithic technological package in which microblades were a key component. Complications to this simple model, and possible scenarios addressing the disparity between the evidence from historical genetics and the archeological record, are considered.

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1. Introduction

The Tibetan Plateau's rugged complexity has been widely appreciated and described by both its residents and its many visitors alike over the past two centuries. United by altitude, central Asia's big high heartland is complicated by topography, geology, climate, biology, subsistence economies, and inter-societal relations (cf. Madsen, 2016—in this issue). Surrounding the Plateau is even more environmental variety, its 7000-km long perimeter bounded by the world's tallest mountains, carved by some of its deepest river gorges, cloaked in thick subtropical forests, and subtended by broad arable valleys or vast sandy deserts.

In the late Pleistocene and into the Holocene, these circum-Plateau habitats were occupied by peoples who employed various Upper Paleolithic tool technologies. Different groups, taking different pathways from different sources, could have tried to make a go of it on the high Plateau, some with more success than others. A range of source areas have been posited for early Tibetan colonizers, ranging from the drylands north and northeast of the Plateau (Brantingham et al., 2003; Han et al., 2014; Madsen et al., 2006; Torroni et al., 1994), the Yellow River drainage and eastern plains in Gansu, Qinghai and Sichuan

(Kang et al., 2012; Shi et al., 2008; Su et al., 2000; Van Driem, 1998, 2002), the river canyons and Hengduan Mountains southeast of the Plateau in Yunnan and Sichuan (Li et al., 2015a; Wang et al., 2011), the Himalayan forelands of Nepal, Sikkim, and Bhutan south of the Plateau (Aldenderfer, 2003; Blench and Post, 2014), and the jagged Kashmir, Hindu Kush, and Pamir ranges to the west (Dambricourt Malassé and Gaillard, 2011; Su et al., 2000; Van Driem, 1998:80).

We might thus expect to see a rich archeological mosaic of early foraging technologies and strategies all along the Plateau's edges and in its interior (Aldenderfer, 2011:146). In this paper I review likely source areas of early Tibetan populations, primarily from an archeological and biogeographic perspective. What source areas and technologies of the early inhabitants of the Tibetan Plateau can be expected and discerned across the Plateau? Should a diversified set of Paleolithic toolkits be expected on the high Plateau? I find that technologies signaling early high Plateau occupation are not at all diversified and argue on biogeographic grounds that they shouldn't be. First, to set the stage I draw on recent results from population genomics.

2. Historical insights from Tibetan genetics

Studies of Tibetan DNA have undergone a productive explosion in the last two decades, yielding phylogeographies that posit both source

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areas of and age estimates for ancient migrations (Qi et al., 2013; Qin et al., 2010; Rowold et al., 2015; Torroni et al., 1994; Wang et al., 2011; Zhao et al., 2009). Taken together, these studies demonstrate substantial genetic diversity in Tibetan populations, a “complex tapestry” of multiple founding lineages from which to borrow (Stoneking and Delfin, 2010:R188). Within this variety, most lineages point overwhelmingly to sources in northern and eastern Asia. A recent large survey focusing mainly on the southern Tibetan Plateau (Qi et al., 2013) found ~20 y-chromosomal haplogroups (Table 1). Of these, just two main lineages account for nearly 90% of participants: D-M174 (primarily central Asia and western China) and O3 (found widely in east/southeast Asia). Likewise, of ~80 different founding mtDNA lineages obtained, nine make up >90% frequency, with predominantly eastern Asian distributions. These lineages show strong connections between Tibetans and north/northeast Asian groups (Shi et al., 2008; Su et al., 2000; Torroni et al., 1994; Wang et al., 2011), as well as evidence for migrations or admixture from the east/southeast (Kang et al., 2012; Li et al., 2015a; Wang et al., 2011). South and southwest Asian haplogroups are negligible in Plateau populations, pointing to a strong but directional genetic barrier along the Himalaya and Karakorum ranges (Cordaux et al., 2004; Gayden et al., 2007, 2009, 2013; Kraaijenbrink et al., 2014; Wang et al., 2012). A number of indigenous Tibetan lineages have been identified, reflecting in-situ genetic drift (Li et al., 2015a; Qin et al., 2010; Zhao et al., 2009). Drift or founders' effects likely account for the differences between Tibetan

haplogroup frequencies (Table 1) compared with those of major eastern Asian populations (Zheng et al., 2011).

Calculated ages of coalescence (time to the most recent common ancestor) and divergence (time since the split of related lineages) for various y-chromosome and mtDNA lineages range from ~4 kiloannum (ka) before present (BP) to as early as 60 ka BP; the oldest ages correspond to lineage roots, not Plateau occupation (Li et al., 2015a; Qi et al., 2013; Qin et al., 2010; Shi et al., 2008; Yi et al., 2010; Zhao et al., 2009). A very few Tibetan-prevalent lineages (e.g., M62b) may have coalesced before ~20 cal ka BP though not necessarily on the Plateau, as noted by Qin et al. (2010). The age estimates for these rare lineages have been widely used to argue for Plateau occupation before the last glacial maximum (LGM) by ur-Tibetans employing Upper Paleolithic technologies, who (it is argued) persisted on the Plateau through the worst of the LGM (Aldenderfer, 2011; Li et al., 2015a; Qi et al., 2013; Qin et al., 2010; Zhao et al., 2009). However, only two major East Asian lineages (B4 and D4) that occur on the Plateau expanded in population size before the LGM (Zheng et al., 2011); the great majority of Plateau lineages coalesced and expanded post-LGM (reflecting migrations of late Paleolithic or epi-Paleolithic groups) or in the Holocene (reflecting Neolithic, Bronze Age or later migration or admixture).

Alongside this phylogeographic information we have a wealth of new and exceedingly important studies on the genetic basis of Tibetan adaptations to high altitude. Extremely low oxygen pressures at high altitude select strongly for genetic mutations leading to hypoxia tolerance (Beall, 2007, 2014; Beall et al., 2004; Bigham et al., 2010; Petousi and Robbins, 2014; Simonson et al., 2010; Wuren et al., 2014; Xiang et al., 2013; Xu et al., 2011; Yi et al., 2010). Several areas of genetic modification related to hypoxia have been identified in Tibetan populations, most notably the genes *EPAS1* and *EGLN1* (among others). The estimated ages of those genetic modifications might indicate when populations carrying them became subject to strong positive selection by the acute rigors of living high.

The *EPAS1* gene has many associated genetic variations that affect gene expression and contribute to high-altitude adaptation (Beall et al., 2010; Lou et al., 2015; Peng et al., 2011a, 2011b; Wang et al., 2011; Xu et al., 2011; Yi et al., 2010). Peng et al. (2011b) estimated divergence times (relative to a Han Chinese reference population) for several strongly-selected single nucleotide polymorphisms (SNPs) and arrived at an average divergence time of ~18.25 cal ka BP. Lou et al. (2015) estimated that the age of selection for a large copy-number deletion mutation was ~12.8 cal ka BP. Model assumptions about mutation rates, population sizes, potential inbreeding rates, generation length, and selection forces make these estimates highly variable and often suspect, some varying by more than an order of magnitude. All such estimates would benefit from confirmation with solid archeological support (Brantingham et al., 2010; Aldenderfer, 2011).

Intriguingly, a recent study showed that part of the Tibetan *EPAS1* region is highly differentiated from other modern human haplotypes but is found in the archaic north Asian hominin Denisovan genome (Huerta-Sánchez et al., 2014). “The haplotype associated with altitude adaptation in Tibetans is likely a product of introgression from Denisovans or Denisovan-related populations,” note Huerta-Sánchez et al. (2014:196). Gene-flow from Denisovan-like populations, possibly from southeast Asian sources (Skoglund and Jakobsson, 2011), would have been given to modern humans before the Han and Tibetan populations diverged, and became subject to positive selection after the Plateau was colonized, an example of pre-adaptive introgression from archaic hominins (Lin et al., 2015; Vernot and Akey, 2014). Recent studies confirming the very ancient occupation of anatomically modern *Homo sapiens* in southern China (Dennell, 2015; Liu et al., 2010, 2015), and of evidence of persistent archaic traits in hominin skeletal material dating to the Pleistocene–Holocene transition from southwest Chinese sites such as Longlin and Zhiren caves, does indeed suggest a genetically “complex evolutionary history for East Asians” (Curnoe et al., 2012), including genetic admixture of archaic and modern populations (Curnoe

Table 1

Haplogroups Represented in 41 Tibetan Populations (from Qi et al., 2013). Underlined subhaplogroups are most common, >4% of grand total population.

Major haplogroup	Subhaplogroups	Main distribution
<i>Paternal lineages – Y-chromosome (STR variation) (n = 2354)</i>		
D (54.33%)	<u>D-M174: D3a-P47, D1a-N1, D3*-P99, D1*-M15, D*</u>	Tibet/Mongolia, central and Northeast Asia
O (33.47%)	<u>O3a3c1-M117, O3a3c*-M134, O3a*-M324</u>	Central, East, and Southeast Asia
N (5.30%)	<u>N1*-LLY22G</u>	North, Northeast Asia
R (2.4%)	<u>R1a*-M173, R1a1-M17, R1b*-M343, R1b1b1-M73</u>	Central Asia, western Eurasia
C (2.00%)	<u>C3*-M130/217, C3c-M48, C3e-P53.1</u>	Northeast Asia, Northwest China
Q (1.23%)	<u>Q-M242</u>	North, Central Asian
J (0.64%)	<u>J-M172</u>	Southwest Asian
K-M (0.42%)	<u>K-M9</u>	South Asia, Southwest China
T (0.13%)	<u>T-M272</u>	Southwest Asia, South India
E (0.08%)	<u>E-M40</u>	Southwest Asia
<i>Maternal lineages – Mitochondrial DNA (HVS-1 variations) (n = 6109)</i>		
M9a (22.48%)	<u>M9a, M9a1a, M9a1b, M9a1b1</u>	East and Southeast Asia
D (16.53%)	<u>D*, D4, D5, D5a2, D5a3, D6a</u>	Northeast, central Asia
A (14.63%)	<u>A10, A11, A11a, A4, A5, A7</u>	Southwest China, East Asia
F (11.44%)	<u>F1, F1a, F1b, F1c, F2, F2b</u>	East and Southeast Asia
G/M12 (8.22%)	<u>G, G1a, G2a, G2b, G3, G3a1, M12a1b</u>	Mongolia, Tibet, Japan, northeast Asia
C/M8/Z (7.71%)	<u>C, C4a, C5, M8, Z</u>	Siberia, northeast Asia
M13 (4.22%)	<u>M13a, M13a1, M13a2, M13b2</u>	Tibet, central Asia, southern Siberia
B (3.76%)	<u>B, B4, B4a, B4c, B4e, B5a, B5b</u>	Central, East, and Southeast Asia
M62 (2.35%)	<u>M62, M62a, M62b</u>	Tibet, Southwest China, South Asia
U (1.65%)	<u>U, U1, U2a, U2b, U2e, U4, U7, K</u>	Western, Central Eurasia, India
M10 (1.06%)	<u>M10a</u>	East, Southeast, and Central Asia
Other M (each >1%, total 4.29%)	<u>M11, M20, M25, M49, M5b2, M61, M70, M7b, M*</u>	East Asia
Other N (1.17%)	<u>N*, N10, N11a, W, N9a1, Y</u>	Central, East and Southeast Asia
Other R (0.78%)	<u>R0, H, R11, R2, R5</u>	Southwest, South Asia
JT (0.72%)	<u>J, T1a, T2</u>	Southwest, Central Asia

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