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The cultural context of biological adaptation to high elevation Tibet

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ABSTRACT

Permanent, year-round occupation of high elevation, low oxygen environments is next to impossible for human populations adapted to low elevation, high oxygen environments. Sustained human habitation of high elevation environments is therefore a comparatively late development in global human history. Though we are beginning to understand the biological differences between contemporary highland and lowland populations, we do not understand how, or when, these differences evolved. This paper presents a hypothesis for the historical context of human adaptation to the Tibetan Plateau. Archaeological data suggest that Neolithic agricultural groups living on the northeast margins of the Plateau expanded to the altitudinal limits of their farming systems by 5200 cal BP, but also to the limits of human physiological capacity for high elevation (at ~2500 m above sea level). With the introduction of novel, exotic domesticates (namely barley, wheat, and sheep), Neolithic agriculturalists started to push these limits, and in roughly 1600 years (by 3600 cal BP) small groups of people were living at higher elevations and deeper into the Tibetan Plateau. This required and encouraged novel cultural solutions to high elevation settings, but also imposed heavy selective pressure on the physiological capacity for low oxygen environments. These new cultural capacities enabled people to move into a stronger environment of selection (above 2500 m above sea level) that favored the physiological capacities for life at high elevation, which in turn became more common across these populations. This hypothesis about bio-cultural evolution is testable with a combination of high-resolution archaeological evidence and high throughput sequencing of datable prehistoric human DNA.

1. Background

Sustained human occupation of high-elevation settings (>2500 masl)[1] requires biological and cultural adaptation to a range of environmental factors including reduced ambient oxygen pressure, strong ultraviolet radiation, limited plant and animal resources, time compressed biotic productivity and pronounced seasonality, and volatile, unpredictable patterns of temperature and precipitation (see Aldenderfer, 2006). The history of human life on the Tibetan Plateau, for example, must be understood in light of these factors and remains an active field of inquiry for archaeologists, paleogeographers, linguists and biologists alike (Aldenderfer and Zhang, 2004; Brantingham and Gao, 2006; Brantingham et al., 2003, 2007, 2013; Chen et al., 2015; d'Alpoim Guedes, 2015; d'Alpoim Guedes et al., 2013; Miehe et al., 2009, 2014; Peng et al., 2011; Qi et al., 2013; van Driem, 2005; Zhao et al., 2009 and all of the papers in this Special Issue).

An important question is whether or not the constraints of elevation on physiological performance mitigated against the human occupation of the Tibetan Plateau. If so, we want to know when, and ultimately how human physiology evolved to meet these constraints, and we want to understand why it took as long as it did. We know that people (of some kind) lived in the lower elevation areas adjacent to Tibet by at least 80,000 years ago,[2] and likely much earlier (Bettinger et al., 2010a; Morgan et al., 2011), yet the earliest archaeological evidence for people in Tibet dates somewhere from 20,000–15,000 years ago (Brantingham et al., 2013; Zhang and Li, 2002). Furthermore, sedentary (or at least semi-sedentary) low-level agriculturalists appear adjacent to the Plateau by roughly 7900 years ago, with full-blown sedentary farming in place by 6200 years ago (Barton, 2009; Barton et al., 2009b) whereas significant numbers of people do not live on the Plateau until after 4000 years ago (Chen et al., 2015; d'Alpoim Guedes, 2013, 2015). The timing of sustained, year-round occupation of the Tibetan Plateau is a subject of considerable debate, addressed by nearly every paper in this Special Issue. Through a combination of archaeological data like these, inference from the human genome, evidence for human impacts to high elevation ecosystems, and a theoretically informed approach to understanding the interactions among each of these things, we will ultimately identify population-level processes that made it possible for people to live high up on the Tibetan Plateau throughout the year.

Though I recognize that our understanding of the physiological processes that make year-round life possible and productive at high

[1] Here we follow Bigham and Lee (2014) in defining high elevation environments as anything above 2500 m above sea level (masl), at which point oxygen saturation of hemoglobin begins to fall in most humans (also see Niermeyer et al., 2001).

[2] All dates provided herein are calendar years before present (cal BP).

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elevation is rapidly improving (e.g. Simonson, 2015), that this suite of physiological attributes differs in different parts of the world (e.g. Beall, 2007), and that some of the molecular foundations for at least some of these adaptations may pre-date permanent life at high elevation (e.g. Huerta-Sanchez et al., 2014), I also suggest this is a fruitful opportunity for hypothesis building. Now that the archaeology of the Tibetan Plateau is improving rapidly, and our ability to sequence vast portions of the nuclear genome from ancient human remains reliably is an increasing reality (see Raghavan et al., 2014; Rasmussen et al., 2014, 2015), such hypotheses will help to stimulate further research. This is the spirit in which this Special Issue on the Peopling of Tibet was organized.

This essay provides a hypothesis about the context of physiological adaptation to high elevation environments, based on archaeological data surrounding the Tibetan Plateau. Here I aim to establish the cultural and historical environment of selection that might have made such adaptations common among groups of inter-connected people who eventually colonized the high plateau successfully and permanently.

2. Physiology at high elevation

Organisms unaccustomed to the declines in barometric pressure and absolute concentration of oxygen associated with increasing elevation experience a variety of physiological and reproductive challenges largely associated with hypoxia — generally, an inadequate supply of oxygen in the blood (Bigham and Lee, 2014; Niermeyer et al., 1995, 2001). In humans, chronic hypoxia has been linked to individual manifestations of heart disease, stroke, anemia, pulmonary hyptertension, low birthweight and infant mortality that carry population-level consequences (excellent recent reviews include: Beall, 2013; Bigham and Lee, 2014; Scheinfeldt and Tishkoff, 2013; Simonson, 2015). As with other organisms (see Storz et al., 2010, 2013), several human populations have developed geographically distinct, and genetically-based pulmonary, hematological and/or vascular adaptations to low-oxygen environments (Beall, 2007; Hornbein and Schoene, 2001; Scheinfeldt and Tishkoff, 2013; Simonson et al., 2012). Genome-wide analyses of contemporary Tibetan populations, for example, suggest that the genetic foundations for at least some of these adaptations were under strong directional selection, a likely testament to the fitness benefits associated with them (Beall et al., 2004, 2010; Bigham et al., 2010; Peng et al., 2011; Simonson et al., 2010; Wang et al., 2011; Xu et al., 2011; Yi et al., 2010). Exactly how these genetic changes produced fitness-enhancing adaptations is uncertain and is the subject of very active research, yet it seems increasingly likely that the physiological adaptations to hypoxia result from multiple gene interactions (Bigham and Lee, 2014). One thing revealed in the genetics of Tibetan populations is that there are numerous adaptations to explain, among them tolerances for different environmental and atmospheric contexts. Furthermore, a variety of genetic analyses suggest that natural selection for adaptations to high-elevation hypoxia is ongoing in contemporary Tibetan populations (Beall, 2007).

3. Tibetan origins

Efforts to understand the genesis of Tibetan people, heritage, culture, and identity, are diverse. Those tuned to the early history of Tibet focus on two distinct angles: 1) the molecular (e.g. Qi et al., 2013; Qian et al., 2000; Su et al., 2000; Torroni et al., 1994; Wang et al., 2011; Zhao et al., 2009) and linguistic (e.g. Sagart, 2005; van Driem, 2002, 2005) *ancestry* of people who currently identify as "Tibetan" (broadly construed); and 2) the *antiquity* of a human presence in a high-elevation geographic province called the Tibetan Plateau (Aldenderfer, 2006; Aldenderfer and Zhang, 2004; Brantingham and Gao, 2006; Brantingham et al., 2001, 2003, 2007, 2013; Huang, 1994; Tang and Hare, 1995; Tong, 1985; Zhang and Li, 2002). On their own, neither of these things tells us very much about the evolutionary process that makes contemporary highlanders biologically distinct (they are merely parts of the story). Yet this process of relatively recent biological adaptation provides important insights about the nature of evolution under selection, and expands our ability to track gene-culture co-evolution in more complex gene–environment interaction systems.

Molecular phylogeographies have been used to track the movements of people (namely those who today identify with Tibet) from geographic points of origin, as well as the genetic underpinnings of physiological adaptations to high elevation. Much of the debate is really about where (or from whom) the Tibetan people came and how long ago they went their separate ways. Recent reports differ on the strength of the historical relationships between contemporary Tibetans and people currently living in different parts of Asia; essentially, current interpretations of the molecular evidence for the history of these people are conflicted, contradictory, and uncertain (for an excellent summary see Rhode, 2016–in this issue). Our understanding of this molecular history will change dramatically, hopefully with greater clarity, in the coming years.

Furthermore (and unfortunately), the chronology for much of this story is only beginning to emerge, and estimates often conflict. Chronologies based on molecular coalescence estimates alone suggest that the divergence of contemporary Tibetan populations, the emergence of physiological adaptations to oxygen deprivation, and therefore persistent human occupation of the Tibetan Plateau, range from approximately 30,000 BP to little more than 3000 BP.

Some geneticists suggest that contemporary Tibetans may have first moved to the Plateau during the late Pleistocene (Qi et al., 2013; Zhao et al., 2009). Yet the bulk of the studies using molecular data suggest that contemporary Tibetans moved, in number, to the Plateau at some point during the Neolithic (Qi et al., 2013; Wang et al., 2011; Zhao et al., 2009). If true, both inferences seem reasonable: though small populations of people may have lived on the Tibetan Plateau during the late Pleistocene, they were later over-run by increasing numbers from somewhere else. But the dating remains equivocal. One has to wonder just how much of this molecular age estimation is informed by an archaeological record that can barely speak for itself with any confidence.

Recently, one hypoxia pathway gene (called *EPAS1*) present at relatively high frequency in modern Tibetan populations was identified in a fossil finger bone from Denisova Cave in the Siberian Altai (Huerta-Sanchez et al., 2014). If the context and dating of the element are correct, this finding suggests that at least one person on earth possessed at least some of the genetic underpinnings of at least one adaptation to hypoxia, approximately 50,000 years ago. This is of course interesting, and the authors suggest many contemporary Tibetan people possess this gene because of an ancestral pattern of introgression. However the antiquity of this gene says little about population-level adaptations, and does not confirm that the Denisovans were capable of life at high elevation. Furthermore, neither the antiquity of this hypoxia pathway gene nor the evidence for inter-specific introgression says anything about the environment of selection that made it common in modern Tibetans (or anyone else), or when this might have happened.

Though many geneticists acknowledge that coalescence-based age-estimates are problematic, the enormous variance in these estimates makes it impossible to track the process of adaptation to high-elevation environments in light of emerging cultural and environmental contexts of natural selection. Beyond the historical time-line of physiological adaptations, we also need to be able to explain how cultural behaviors (including adaptations to cold stress, and resource risk and uncertainty) evolved to meet the demands of higher elevations. The archaeology of the Tibetan Plateau and surrounding regions provides a baseline for addressing these issues.

4. Early human activity on the Tibetan Plateau

While there is some indication of ephemeral human activity on the central Tibetan Plateau during the Last Glacial Maximum, ca. 20,000 BP (Zhang and Li, 2002), the earliest firm evidence for human presence