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**Nutritional contribution of plant foods to human diet in evolution**  
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# CHAPTER 5

CONCLUSION



To conclude what, in three chapters, 100+ pages, and three peer reviewed publications, I have extensively researched, experimented, analyzed, and documented, merits a bit of backtracking to reestablish the original question. To quote myself in December 2011, I proposed, “a study of the tuber plant foods consumed by the Hadza hunter-gatherers of Tanzania, Africa, to assess their nutrient content and value as staple plant resources in the Hadza diet.” My desired final contributions were optimistically summarized as such, “The outcome of this study will enable us to paint a more complete picture of the nutritional landscape of human food resources in the East African savannah,” with the assumption that this deals only with food resources available to human foragers and not farmers. If I were to assess the actual outcome (unobjectively), then I have accomplished a portion of my original research goals, but with ample room for future investigations. To complete the picture of the digestibility of the Hadza tubers using *in-vitro* modeling, I have already conducted trials to simulate colonic fermentation of Hadza tubers by Hadza microbiota using the TNO *in-vitro* model of the large intestine (TIM-2). This work endeavors to answer whether Hadza microbiota do in fact work to provide the host with more metabolites for a secondary means of caloric or otherwise essential nutrient acquisition, to compensate for the overwhelming amount of indigestible material in Hadza tubers. The preliminary results so far suggest that microbial contribution to Hadza nutrition is not attributable to the quantity of metabolic products produced, but rather, the composition and timing of microbial substrate production may instead confer special health promoting attributes for the Hadza. The analysis for this forthcoming paper is underway and I anticipate publication within the year (2016).

This research had three components: 1. test the role of cooking on starch gelatinization, specifically in tubers; 2. assess the digestibility of wild East African tubers for a human consumer, informed and modeled after the diet ecology of Hadza hunter-gatherers, and quantify the relative proportion of nutrition accessible to small-intestine absorption; and 3. look at the role, specialization, and impact of the gut microbiota of the Hadza in facilitating nutrient acquisition and caloric buffering for a people still practicing a non-agrarian hunter-gatherer subsistence. The first two research phases were explored by proxy, and the third was approached directly, but using the technology, methods, and comparative references of an emerging field that is still in development. This means that more, and more precise, answers are still out there. However, I have succeeded in contributing information and evidence to support the significance of plant foods to human foragers in the tropical East African savannah-mosaic environment, which is the putative evolutionary landscape of our species. I constructed the premise for the importance, from an evolutionary perspective, of plant foods in the human diet in the introduction to this thesis, and it follows that in all the intervening text I have found that indeed African hunter-gatherers regularly eat essentially raw starchy plant foods, which are difficult to digest. However, with minimal control of fire and a highly adapted gut microbiota, these plant foods become easily consumable resources that are rapidly and readily metabolized by gut bacteria into secondary, but nutritious, host-specific metabolites. In addition, the tubers consumed by Hadza are rich in critical minerals necessary for brain development such as calcium, magnesium, iron,

potassium, and iodine, as well as potentially B12 vitamins that support nervous system function. Therefore, I suspect that wild tubers are an important in-land food resource that may somewhat supplant the presumed need for marine or aquatic resources by a large-brained hominin, or at least greatly ameliorate the stress of nourishing a metabolically demanding and nutritionally vulnerable organ.

While answering many initial questions about the importance of plant foods and their suitability as a staple resource throughout human evolution, there remains many unexplored areas on the topic of human digestive physiology, especially in relation to evolutionarily emergent biocultural and technological buffering systems. My broader academic goals are to help improve our understanding of hominin evolution by exploring physiological versus behavioral or technological responses to different environmental pressures as they relate to diet ecology. The dispersal of early hominins, and later archaic humans, across the globe is profoundly demonstrative of a bio-cultural marriage that has steered us on a unique evolutionary course towards co-dependence on the combined effects of our technology and our genetic heritage. While a lot of well-informed hypothesis exist about how and when early hominins became finicky omnivores with an increasingly unspecialized, yet diminishing, gut, only a few studies have set out to empirically test specific elements regarding how this could be accomplished given certain ecological and anatomical restraints. Gene polymorphisms along the human lineage that differentiate us from great apes, or even archaic humans, are powerful informants to help narrow our search for selectively advantaged phenotypes, and how, either by relaxing or increasing pressure, these came about. This in turn can lead to compelling inferences about the environment, diet, and human behavior circumscribing selective processes, which necessarily fills gaps in our knowledge where archaeological evidence is unobtainable.

The first step in framing possible future inquiries is to realize the bottlenecks that constrain our understanding of, and the actions surrounding, human evolution. From the results of my first roasting trial experiment, I concluded that probably the most significant hindrance to plant food consumption relates to comminution. In other words, humans must be able to physically reduce the particle size of their food through chewing or external processes to successfully consume and digest the food. When starch-based tuberous foods are subjected to brief thermal treatment, their parenchymateous tissues are significantly softened, while most of the interior starch remains ungelatinized, and for Hadza consumers, this is enough to make the tuber perfectly palatable. Therefore, the oral phase of digestion is one such bottleneck, and concomittant aspects of mastication include the activity of salivary amylase. Curiously, the salivary amylase gene has experienced positive selection for copy number variability among modern humans, indicating some functional significance of the alpha amylase enzyme. Whether the functional relevance under selection occurs during oral digestion or through initiation of downstream pancreatic enzyme activity and blood-glucose regulation is relatively unknown, and I intend to explore this topic in a project committed to ascertaining the physiological relevance of salivary amylase. Similarly, the functional significance and specialization of the human gut microbiome to the human host is poorly characterized, especially in non-Westernized populations.

It makes intuitive sense that the microbial population is cultivated over one's lifetime. However, recent evidence suggests that early life experiences are critical events that effectively establish a long-term scaffold for the adult microbial configuration, and that this may be somewhat immutable. Furthermore microbial communities that are identical in composition, can vary widely in functional coding and expression, leaving ample room for individual specialization or response to diet and disease. From my work with the Hadza, we know that human foragers harbor very different microbial communities from those found amongst Western human populations. Therefore, we can presume that aspects of forager life possibly require different functional configurations of the microbiota as well, which are likely tied to the activities and nutritional needs of the individual host. Specialized microbial activities that relate to diet may have allowed early humans to exploit a wider variety of resources than what we currently anticipate given our understanding of the size and absorptive limitations of the stomach and small intestine. Using both *in-vitro* and *in-silico* methods, I intend to pursue work in reconstructing rare microbial community functions and genes that may have enabled a human forager to acquire essential nutrients from the gut microbiota.

Whether human hunter-gatherers can successfully occupy and thrive in a savannah mosaic environments is self-evident. Rather it is *how* they have thrived in these environments, and still do, that captures our attention, awe and wonder. In the case of the Hadza, there is a clear and necessary dependence on local flora, particularly fibrous non-toxic tubers, and interesting concomitant adaptations. These adaptations seem to take the form of more plastic ontogenic (gut microbiome) and technological (brief roasting) developments rather than through strict inheritance of nuclear genetic traits. The implications of these findings is that humans, by virtue of their intellect and physiological non-specialization, are highly adaptable and innovative, making us the unsurprising victors in global colonization. Yet our herbivorous legacy is not so far behind us that it is surpassed in importance by our recently acquired intensive carnivorous history. Tropical modern human hunter-gatherers, as a proxy for pre-agricultural humans, beautifully exemplify the essential relationship between humans and plants. While heavily reliant on plant foods, they demonstrate the capacity for a materially and technologically minimalist existence, and yet preserve and cultivate the full spectrum of intelligence, curiosity, creativity, and sociality that are defining characteristics of our species.