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Plant microremains in dental calculus as a record of plant consumption: A test with Twe forager-horticulturalists

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ABSTRACT

Starch granules and phytoliths trapped in dental calculus preserve a record of plant consumption. Analysis of these microscopic plant remains has increased in popularity in recent years, providing information on diet that complements dental microwear and stable isotope studies. However, it is unclear how accurately these microremains reflect plant consumption. This study examines how well starch granules and phytoliths in dental calculus from a living population (the Twe) with a well-documented diet capture the range and intensity of plant consumption. We find that plant microremains are a poor predictor of plant consumption on an individual level, but may provide a good signal of plant consumption across a population, as well as evidence for plant processing in the mouth. This is the first study to test how well plant microremains in dental calculus reflect plant consumption in a population with a known diet. Results from this project have implications for interpreting plant microremain data from archaeological dental calculus samples.

1. Introduction

Starch granules and phytoliths in dental calculus are increasingly used as dietary markers in archaeological investigations. Direct signatures of ancient plant consumption are rare in archaeological contexts, but plant microremains in dental calculus have helped to elucidate diets in many contexts, ranging from the early consumption of domesticates in the Holocene (cf. Henry and Piperno, 2008; Mickleburgh and Pagan-Jimenez, 2012; Li et al., 2010; Piperno and Dillehay, 2008) to early hominin plant consumption (Henry et al., 2011, 2012; Henry, 2014; Salazar-García et al., 2013). Other direct measures of plant consumption such as carbon stable isotopes or tooth microwear analysis provide only general information on categories of plants consumed or the physical properties of those plants. Plant microremains like starches and phytoliths can be taxonomically distinct, and their presence in dental calculus sometimes reveals the consumption of specific plant families or genera.

Despite promising results in many time periods and geographic regions, we have yet to determine exactly what type of dietary signal plant microremains in dental calculus record. For example, some authors suggest that a high incidence of starches and phytoliths from certain plants indicates that those plants were consumed at high frequency (Henry and Piperno, 2008; Middleton and Rovner, 1994; Piperno and Dillehay, 2008). Others draw comparisons between individuals or groups based on the numbers of plants represented by microfossils (Dudgeon and Tromp, 2012; Henry et al., 2014; Mickleburgh and Pagan-Jimenez, 2012). While such comparisons are logically appealing, we do not yet understand the mechanism for preservation of microremains in dental calculus. It is recognized that calculus formation rates vary among individuals (Jin and Yip, 2002; White, 1997), and some researchers have acknowledged this as a potential source of variation in the preservation of microremains (Henry et al., 2014). However, the extent to which individual differences in calculus formation might create individual variation in the microremain record is unclear. Starches appear to be more plentiful than phytoliths in modern human dental calculus (Boyadjian et al., 2007; Fox et al., 1994, 1996; Henry and Piperno, 2008; Juan-Tresserras et al., 1997; Scott Cummings and Magennis, 1997), possibly because humans preferentially eat starchy foods, but we do not know what other biases may exist in the dental calculus record.

Here we present the first comparison of diet and plant microremains in dental calculus from a living population with a well-documented diet. We report on the relationship between plant consumption and plant microremains in dental calculus from Twe forager-horticulturalists in order to characterize the preservation of plant microremains in human dental calculus. Our analyses address the following questions: 1. Is diet consistently recorded across all individuals in the same population, given their similar diet? 2. Do plant microremains in Twe dental calculus reflect the range of plants consumed? 3. Is starch quantity in dental calculus proportional to dietary concentration? Initial results

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suggest that starches and phytoliths do record diet, but that the relationship between diet and microremains preserved in calculus is not as straightforward as previously assumed.

1.1. Background: plant microremains and dental calculus

Plant microremains are microscopic plant residues with taxonomically specific diagnostic features. Microremains include but are not limited to starch granules, phytoliths, diatoms, spores, and pollen granules. This paper discusses only starch granules and phytoliths. Starch granules are comprised of complex carbohydrates and are formed in plant tissues for energy storage. Starches are formed in specialized plant organelles called amyloplasts. Starch granule formation begins at a central point called the hilum, and continues with alternating layers of amylose and amylopectin. The alternation of amylose and amylopectin results in a semi-crystalline structure which gives starch some unique properties, such as a polarization cross under cross-polarized light (Barton and Fullagar, 2006; Field, 2006; Gott et al., 2006). Plants produce two types of starch, transient and reserve starches. Transient starches are formed for short-term energy storage in photosynthetic tissues like leaves, while reserve starch is formed for long-term energy storage in plant storage organs, fruits, and seeds (Gott et al., 2006; Henry, 2012; Sivak and Preiss, 1998). Transient starch morphologies are simple and of limited use in dental calculus studies (Shannon et al., 2009). Reserve starch morphologies may vary along taxonomic lines (Reichert, 1913; Torrence, 2006), but also within species and within individual plants. Surface features like the presence and placement of the hilum, striations called lamellae, cracks, and fissures, as well as the shape and symmetry of the polarization cross are used to distinguish between starches from different taxa (Torrence et al., 2004; Torrence and Barton, 2006).While starch can survive for thousands of years in certain conditions, heat and moisture cause starches to gelatinize, and acidic conditions and enzymatic activity also damage starches. Dental calculus provides a protective environment that facilitates starch survival (Henry, 2012).

Phytoliths are microscopic noncrystalline silica bodies that are formed in and between plant cells when soluble silica from the ground water precipitates into plant tissues (Henry, 2012; Pearsall, 2000; Piperno, 2006). Phytoliths provide structural support and defense against herbivory (Weiner, 2010). Many plants produce phytoliths, and phytolith production is largely under genetic control, such that phytolith-producing plants tend to occur in the same families, genera, and species, regardless of region of origin (Bamford et al., 2006). Environmental conditions including the soil temperature and water content, concentration of monosilicic acid in the soil, soil pH, and climate can also affect phytolith production (Madella et al., 2002; Piperno, 1988). Phytolith concentration is highest in leaves, husks, rinds, bark, and fruits (Piperno, 2006; Rovner, 1983). Phytolith morphologies are often taxonomically distinct, and may also reflect the specific plant tissue in which they form (Tsartsidou et al., 2007). Diagnostic features include size, shape, texture, and ornamentation (Madella et al., 2005; Piperno, 2006). Phytoliths are soluble in basic conditions (Rovner, 1983), but may persist for millions of years (see Prasad et al., 2005). The oldest phytoliths recovered from dental calculus date to at least 2 ma (Henry et al., 2012).

Dental calculus provides a protective environment where starches and phytoliths can survive for thousands of years (Henry et al., 2011). Dental calculus is mineralized plaque which forms both above and below the gingival margin. In this project we consider only supragingival calculus deposits, as calculus was recovered from living people. Supragingival calculus deposits form preferentially near the salivary glands in the mouth, on the lingual sides of mandibular incisors and the buccal sides of maxillary molars and premolars (Jin and Yip, 2002; Bergström, 1999). Supragingival calculus forms when plaque on tooth surfaces is bathed in calcium and phosphate rich saliva (Jin and Yip, 2002; Lieverse, 1999). The rate of mineralization varies among individuals according to age, oral hygiene, and possibly diet (Bergström, 1999; Lieverse, 1999). Smoking increases the rate of calculus formation (Bergström, 1999). Dental calculus is 80% inorganic, comprised of calcium phosphate in various phases, including hydroxyapatite, brushite, whitelockite, and octacalcium phosphate (Abraham et al., 2005; Lieverse, 1999). Older deposits tend to be richer in hydroxyapatite, while both young deposits and supragingival calculus are richer in brushite (Schroeder and Bambaur, 1966). The organic portion of calculus includes bacteria, DNA, lipids, proteins, pollen, phytoliths, and starch granules (Hillison, 1996; Lieverse, 1999; Warinner et al., 2014).

Due to individual variability in the amount and rate of calculus formation, we cannot assume a simple relationship between plant consumption and plant representation in dental calculus deposits. We know that starch granules are more common than phytoliths in human dental calculus (Boyadjian et al., 2007; Fox et al., 1994, 1996; Henry and Piperno, 2008; Juan-Tresserras et al., 1997; Scott Cummings and Magennis, 1997), but we do not know what factors bias starch preservation in dental calculus. For example, population-level or individual differences in salivary amylase copy number may correspond to differences in amylase activity (Perry et al., 2007). This in turn could affect the rate of starch digestion in the mouth, which combined with variable calculus formation rates complicates our understanding of starch incorporation. Below we assess how reliable Twe plant consumption is recorded in Twe dental calculus.

1.2. Background: the Twe

The Twe are a group of forager-horticulturalists who live in Northwestern Namibia and Southwestern Angola. Culturally they resemble the well-studied Himba pastoralists, but most Twe do not own animals and make a living by foraging and gardening (Vashro, 2014). The Twe live in an arid, mountainous environment with marked seasonality. During the rainy season, many Twe grow maize (*Zea mays* L.) which they dry and grind into a course meal, as well as pearl millet (*Pennisetum glaucum*L.), squash (*Cucurbita* sp.), melons (Cucurbitaceae, several species), and sugarcane (*Saccharum* sp.). The Twe also collect several wild foods during the rainy season, most notably *Berchemia discolor* (Klotzsch) Hemst. (bird plum) berries which are eaten in large quantities. Gardening is not possible during the dry season, and the Twe rely on dried maize meal and foraged foods including fruits from *Hyphaene petersiana* Klotzsch ex Mart. (makalani palm) and *Diospyros mespiliformis* L. (jackalberry), as well as various underground storage organs. Since the end of 2007 the Twe have received subsidies of maize meal from the Namibian government, as well as small herds of goats, which produce a limited amount of sour milk. Today the Twe are heavily reliant on the government maize meal subsidies, but still garden and regularly collect a wide range of wild plant foods.

The Twe are semi-mobile. Most people have a 'home' where they spend much of their time, but they also move to different compounds around the region and occasionally visit friends and families in distant locations where different foods may be available. This work focuses on Twe living at a government camp called Otjomoru in the Zebra Mountains and the nearby traditional settlement Okau, and Twe living at a government camp near Epupa Falls called Ohayuua. These camps are considered 'home' locations by many people due to the availability of government maize subsidies. The Twe do not have any access to dental care. Many people occasionally chew on a specific type of stick (called 'omundumise' in Herero), but no one uses toothbrushes, toothpaste, or dental floss, and there is no access to dental care and very limited access to medical care.

2. Methods

One of us (CL) stayed with the Twe in July–October 2012 (dry season) and April–May 2013 (late rainy season) in order to collect dental calculus samples, dietary information, and samples of plant