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Reconstructing Middle Horizon Camelid Diets and Foddering Practices: Microbotanical and Isotope Analyses of Dental Remains from Quilcapampa, Peru

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Abstract

This study uses isotope and microbotanical data from the analysis of teeth and dental calculus to investigate camelid diet and foddering practices at Quilcapampa (AD 835–900). By providing taxonomically specific evidence of foods consumed, botanical data from dental calculus complement the more general impressions of photosynthetic pathways obtained through isotopic analysis. Results suggest that the camelid diet incorporated maize (*Zea mays*), algarrobo (*Prosopis* sp.), potato *chuño* (*Solanum* sp.), and other resources. The life-history profile of one camelid (Individual 3) reveals dietary change from mainly C₃ plants to more C₄ plant contributions as the animal aged. This pattern is supported by carbonate isotope results indicating that this individual spent its youth in the mid-valley ecozone before becoming more mobile later in life. As this life-history example shows, isotopic and microbotanical analyses are complementary approaches, clarifying a pattern of seasonal transhumance that linked the lives of humans and animals along the Middle Horizon (AD 600–1000) caravan networks that crisscrossed the central Andes.

Resumen

Este estudio emplea datos isotópicos y microbotánicos obtenidos del análisis en dientes y cálculo dental para investigar la dieta y prácticas de alimentación de los camélidos en Quilcapampa La Antigua (835-900 dC). Los datos taxonómicos específicos de los alimentos consumidos, sumado a los datos botánicos del cálculo dental complementan las impresiones más generales de las vías fotosintéticas obtenidas mediante el análisis isotópico. Los resultados sugieren que la dieta de los camélidos incorporó maíz (*Zea mays*), algarrobo (*Prosopis* sp.), papa chuño (*Solanum* sp.) y otros recursos. El perfil de la historia de vida de un camélido (Individuo 3) revela cambios en la dieta, principalmente desde plantas C₃ a mayor consumo de plantas C₄ a medida que el animal envejecía. Este patrón está respaldado por los resultados de isótopos de carbono que indican que este individuo pasó su juventud en la ecozona del valle medio, antes que su vida se tornara más móvil. Este ejemplo de historia de vida muestra que los análisis isotópicos y microbotánicos son enfoques complementarios y revelan un patrón de trashumancia estacional que unió la vida de humanos y animales a través de las redes de caravanas que atravesaban los Andes centrales durante el Horizonte Medio (600-1000 dC).

Keywords: mobility; animal management; starch; stable isotopes; Middle Horizon; Andes

Palabras clave: movilidad; manejo de animales; almidón; isótopos estables; Horizonte Medio; Andes

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Camelid management was a cornerstone of interregional interaction and societal sustainability in the ancient central Andes. Small-scale agropastoral practices—the cultivation of crops and management of livestock—predominated in pre-Wari eras, during which locally oriented animal husbandry often limited intergroup exchange and long-distance trade (Bonavia 1996). Widening interactions associated with the emergence of the Wari Empire in the Middle Horizon (AD 600–1000) brought about significant changes in the relationships between humans and camelids. This article explores some of these seasonal pastoral management decisions in southern Peru using an innovative combination of stable isotope analysis of dentition and microbotanical analysis of dental calculus (see also Cagnato et al. 2021). When contextualized within a broader set of zooarchaeological and paleoethnobotanical data, complementary analyses of stable isotope and microbotanical data provide a more robust picture of camelid diets and management practices.

Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope studies have shaped our knowledge of the timing and amount of C_4 plant consumption, as well as the use of fertilizer in agriculture (e.g., Bogaard et al. 2007; Santana-Sagredo et al. 2021; Szpak et al. 2012). Isotopic analyses of stable oxygen ($\delta^{18}\text{O}$) and radiogenic strontium ($^{87}\text{Sr}/^{86}\text{Sr}$) have shed light on migration and pastoral transhumance practices (e.g., Hakenbeck et al. 2017; Knudson 2009; Knudson et al. 2014). However, isotopic approaches without context are limited by a lack of dietary resolution. For example, $\delta^{13}\text{C}$ values can speak to the relative amount of C_3 and C_4 plant consumption but cannot identify the genus/species of the plant(s) consumed (DeNiro and Epstein 1978; van der Merwe 1982).

Microbotanical analysis offers promise in addressing the limitations of isotopic analysis. Seminal starch granule and phytolith studies of South American contexts (e.g., Dickau et al. 2012; Duncan et al. 2009; Pagán-Jiménez et al. 2016; Zarrillo et al. 2008) demonstrate that microbotanical techniques complement macrobotanical analysis by producing direct evidence of food consumption from analyzing residues such as dental calculus. Dental calculus is a mineralized plaque biofilm that forms through the calcification of plaque deposits on the surface of teeth (Hillson 2005; Wright et al. 2021). Calculus deposits are located near salivary glands, where saliva provides the mineral components of calculus (Hillson 2005:289) and the enzymes (α -amylase) that break down carbohydrates (e.g., starch; Scannapieco 1993).

Calculus is common in domestic animals because their softer diets require less mastication, but wild animals can also produce thin, darkly stained patches that are presumably calculus (Hillson 2005:289–290). Microbotanical analysis of dental calculus is a burgeoning area of research into archaeological evidence of human plant consumption (Hart 2014; Henry and Piperno 2008; Liu et al. 2015; Madella et al. 2014; Mickleburgh and Pagán-Jiménez 2012; Piperno and Dillehay 2008). Yet the use of dental calculus to elucidate animal subsistence strategies has been underexplored (but see Asevedo et al. 2012; Middleton and Rovner 1994; Weber and Price 2016)—particularly in herbivores—and rarely paired with stable isotope results (cf. Asevedo et al. 2012).

This article combines microbotanical analysis of dental calculus ($n = 9$) and isotopic analysis ($n = 10$) to study camelids from the site of Quilcapampa (AD 835–900) in the Sihuas Valley of Peru. This dual approach is particularly useful for studying periods with limited architectural evidence of camelid management, such as the Middle Horizon. Our synthesis of both datasets reveals that distinct life-history stages were marked by shifts in camelid dietary composition and mobility strategies.

Background

Agropastoralism remains an important part of the political economy throughout much of the Andes (Bonavia 1996; Capriles 2014; deFrance 2016; Moore 2016; Szpak et al. 2014, 2015; Takigami et al. 2020; Wheeler et al. 1995). Of the four camelid species native to the region, two are wild—vicuñas (*Lama vicugna*) and guanacos (*Lama guanicoe*)—and two are domesticated: llamas (*Lama glama*) and alpacas (*Vicugna pacos*). Andean people commonly use camelids for food, as pack animals, and for economic products such as fibers that can be woven into textiles. Domesticated camelids require grazing, and family units often manage herds by foddering with agricultural fields on a rotational basis (Bonavia 1996; Browman 1974:191, 1990; Caro 1985; Dantas et al. 2014; Flores Ochoa 1968; Kuznar 2016).

Domesticated camelids can travel long distances, with the llama serving as a pack animal. Central Andean verticality contributes to notable variation in plant growing conditions and native fauna. Lower plateaus, such as the *yungas* (2,300–500 m asl), offer arid to temperate growing conditions, whereas only frost-resistant crops can grow on the snowy higher plateaus (e.g., *puna*: 4,800–3,500 m asl; Gomez Molina and Little 1981; Vining 2016). Yet the *yungas* experiences greater seasonal variation in wild vegetation than the highlands. Camelid caravans can connect resource zones into “vertical archipelagos” (Murra 1960; Vining 2016; Vining and Williams 2020). They can also connect coastal river valleys along “horizontal archipelagos” (Shimada and Shimada 1985).

Foods eaten by domesticated camelids vary because camelids can stay local or travel across eco-zones. Maize is commonly incorporated into direct camelid foddering and grazing strategies today (Popenoe et al. 1989). However, Cadwallader and colleagues (2012) argue that maize, a C₄ crop, may only represent one-third of the Andean dietary carbon isotope signal in the archaeological record based on their study of $\delta^{13}\text{C}$ values of nearly 90 wild plants from the Peruvian south coast. A mixed diet makes sense ethnographically because amaranth (*Amaranthus caudatus*) or *kiwicha*, also a C₄ crop, and field stubble are commonly grazed (Brack Egg 1999; Candia and Dealmaso 1995; Gross et al. 1989). Saltgrass (*Distichlis spicata*), matted grama (*Bouteloua simplex*), and *muhly* (*Muhlenbergia* sp.) are other C₄ wild coastal plant taxa available to herds (Candia and Dealmaso 1995; Dufour et al. 2014; Panarello and Fernández 2002; Shimada and Shimada 1985; Thornton et al. 2011; Vining 2016). Important C₃ plant contributions to the contemporary herd diet include (1) cultivated potato (*Solanum* spp.) and quinoa (*Chenopodium quinoa*), (2) fruits of algarrobo trees (*Prosopis* spp.), and (3) wild grasses such as *ichu* (*Stipa ichu*) found in the altiplano at 3,500 m asl (Cadwallader et al. 2012; Samec et al. 2017; Vining 2016).

Decreasing human mobility and the increased corralling of newborn animals and large camelids suggest that camelid herding and management practices appear by about 4600–3000 BP (Mengoni Goñalons and Yacobaccio 2006). Izeta and colleagues’ (2009) study of $\delta^{13}\text{C}$ values in southern Argentinian camelids reveals higher $\delta^{13}\text{C}$ values over time, suggesting the increased consumption of C₄ plants. In conjunction with cultivated terraces and corrals, the evidence suggests people began feeding agricultural refuse to camelids during the first millennium AD (211).

Dietary isotope signals can be complicated by transhumance. Andean foddering practices are particularly difficult to interpret because of interactions across the “vertical archipelago” (Knudson 2009; Knudson et al. 2014; Scaffidi and Knudson 2020). Herd management practices and foddering sources can be especially hard to disentangle during periods of heightened long-distance interaction like the Middle Horizon (AD 600–1000; Isbell 2009). Stable oxygen ($\delta^{18}\text{O}$) and radiogenic strontium ($^{87}\text{Sr}/^{86}\text{Sr}$) isotopes can aid in differentiating between foddering and seasonal migrations by adding detail regarding altitudinal history (Hakenbeck et al. 2017; Thornton et al. 2011).

The difficulties of understanding Middle Horizon agropastoralism are exemplified in Quilcapampa, a Wari settlement in the *yungas* zone where communities could access both coastal and highland resources. Understanding which resource zones were used by Wari people can contribute to our broader understanding of Andean trade, mobility, and identity practices during this period. To reconstruct animal management strategies at the site, we summarize extant knowledge of the local environment and agropastoral practices before interpreting the results of isotope and microbotanical analyses of camelid teeth.

The *Yungas*, Quilcapampa, and Camelid Foddering

Quilcapampa was a 2 ha Wari outpost located about 80 km from the Pacific Ocean near the northern edge of southern Peru’s Pacific Piedmont, where the coastal plain meets the Andean foothills (Figures 1 and 2; Supplemental Text 1; Jennings et al. 2018, 2021). Llama (*L. glama*) and alpaca-sized (*V. pacos*) individuals were present at the site, with osteological analysis suggesting that the animals were used for meat, transport, and fiber (Alaica et al. 2021). At 800 m asl, Quilcapampa was situated in the mid-altitude *yungas* zone (2,300–500 m asl). With only 50–200 mm of rainfall each year, the hyperarid region offered limited camelid fodder. Cacti (*Haageocereus* sp., *Neoraimondia* sp., *Opuntia* sp.) were present on the valley slopes and *quebradas*, although river sedges (Cyperaceae),

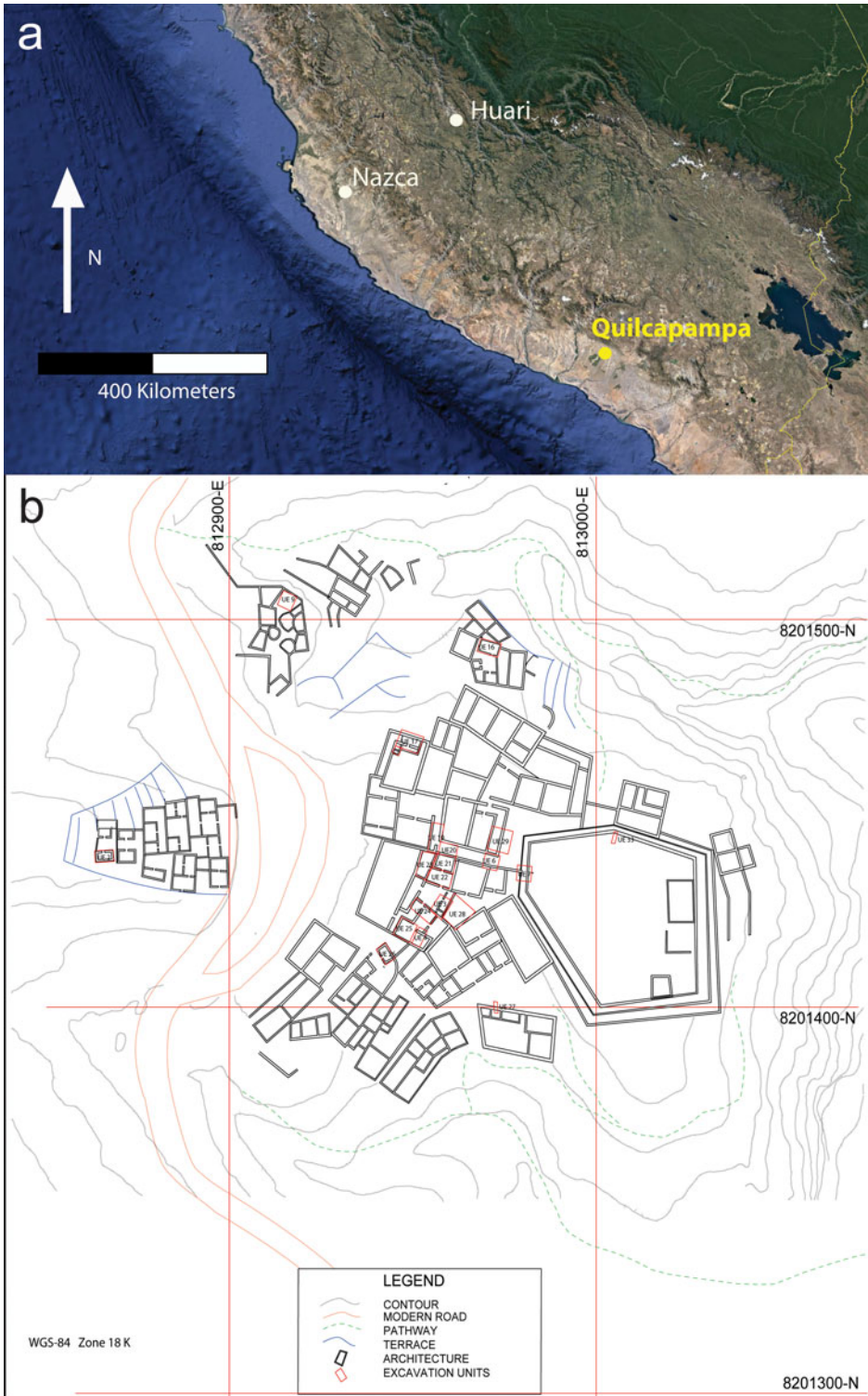


Figure 1. (a) Location of Quilcapampa and other sites mentioned in the text (Landsat imagery courtesy of NASA Goddard Space Flight Center and US Geological Survey); (b) plan of Quilcapampa showing the raised plaza, core compounds immediately to the west, and a surrounding outlying area. (Color online)



Figure 2. Aerial view of Quilcapampa showing the contrast between fertile river bottoms and arid upland areas. Photograph courtesy of Stephen Berquist. (Color online)

algarrobo (*Prosopis* spp.), and grasses/shrubs (e.g., *Atriplex* sp., *Baccharis* sp., *Bidens* sp., *Eragrostis* sp.) were restricted to the river bottoms (Biber 2019; Moneresinos-Tubée and Mondragón 2014). Cultivated fodder included maize, pacay (*Inga feuillei*), and lúcuma (*Pouteria lucuma*). Quinoa and potato, both highland-associated foods, were also available for consumption at Quilcapampa (Supplemental Table 1).

Isotopic and Dental Calculus Analysis

To better understand camelid foddering strategies at Quilcapampa, our study combines stable isotope analysis of camelid teeth with microbotanical analysis of starch granules/phytoliths from the corresponding dental calculus. We selected 10 teeth (NISP = 10) representing four individuals (MNI = 4) identified through macroscopic observation of diagnostic features (Gifford-Gonzalez 2018; Pacheco Torres et al. 1979; Reitz and Wing 2008; Wheeler 1982). Dental eruption and occlusal wear indicate that these individuals range from nine months to three years in age (Figure 3; De Nigris 2004; Hillson 2005; Wheeler 1982). Calculus was recovered from nine of the 10 teeth. After we collected the calculus, these teeth were analyzed for stable and radiogenic isotopes.

Stable and Radiogenic Isotope Analyses

Stable and radiogenic isotope analyses can be conducted on animal bone, enamel, dentin, and fiber. These tissues have different rates of formation and remodeling. Cranial and postcranial bone, for example, remodels every few years, whereas dental enamel is formed in utero or during the first years of life and does not remodel (Wheeler 1982). Two types of tissues were subject to analysis: dentine collagen ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopes) and enamel carbonate ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$, and $^{87}\text{Sr}/^{86}\text{Sr}$ isotopes).

The arid, warmer environment of the coast is ideal for C_4 vegetation, enriching $\delta^{13}\text{C}$ values of foddered and grazing herds. Because wild grasses (C_3 plants) are commonly used as livestock fodder in the



Figure 3. Camelid dentition and wear patterns: (a) Individual 1; (b) Individual 2; (c) Individual 3; and (d) Individual 4. (Color online)

highlands (Samec et al. 2017), carbon isotopic compositions tend to be lower than at the coast (Bryant and Farfan 1984; Reiner and Bryant 1986; Szpak et al. 2013; Vining 2016). Estimating the contribution of C_3 and C_4 to diet in collagen samples is possible by using the estimated mean preindustrial $\delta^{13}C$ values of pure- C_3 and pure- C_4 feeders (Dufour et al. 2014:Figure 5).

$\delta^{15}N$ isotopic compositions of vegetation vary based on aridity, input from marine ecosystems, and the fertilization of agricultural fields using bird guano (DeNiro and Epstein 1981; Santana-Sagredo et al. 2021; Szpak et al. 2012). On the coast, herds have access to wild vegetation from arid contexts and seaweed (or *yuyo*). Greater quantities of these sources contribute to increasing $\delta^{15}N$, which reaches values as high as 10.0‰.

Elevation, season, humidity, and temperature affect $\delta^{18}O$ from water sources. Lower $\delta^{18}O$ values are more common in high-altitude locations (La Paz Bolivia: -13.3‰ to -10.8‰) than on the coast (or *chala*, 500–1 m asl) or the mid-valley (or *yungas*, 2,300–500 m asl: -3.3‰ to -5.7‰ ; Knudson 2009). Positive $\delta^{18}O$ values are related to consuming water from evaporated sources, which was recorded in camelids from the central coast (Tomczyk et al. 2019).

Radiogenic strontium ($^{87}Sr/^{86}Sr$) values vary broadly by lithology and crustal age, which correlate with elevation in the Andes; the coast has lower ratios (0.705–0.708) than the highlands (0.707–0.711; Knudson et al. 2014; Thornton et al. 2011; Scaffidi and Knudson 2020). In Arequipa, strontium baseline analysis conducted on local plants ($n = 8$) revealed a range of $^{87}Sr/^{86}Sr = 0.70797 \pm 0.00115$ (1σ ; Knudson et al. 2014). To establish the local strontium baseline for Quilcapampa, we use two standard deviations (2σ) in values, resulting in a reference range from 0.70567 to 0.71027.

Stable and radiogenic isotope analysis of 10 dental specimens from Quilcapampa was conducted in the Archaeological Chemistry Laboratory (ACL) and Metals, Environmental and Terrestrial Analytical Laboratory (METAL) at Arizona State University (ASU). In the ACL, samples were photographed and mechanically cleaned with a Dremel Minimite-750 cordless drill equipped with a rotary burr. This process removed adhering organic matter or contaminants and the outermost layer of enamel most susceptible to diagenetic contamination (Budd et al. 2000; Montgomery et al. 2000; Waldron 1981, 1983; Waldron et al. 1979). The outer surfaces of the roots were also abraded to remove cementum. Each tooth was sampled for both dentine and enamel. Enamel powder was sampled using a Dremel burr first along the column of the tooth crown; then the dentine was sampled with a

Dremel saw to extract a thin slice running the length of the crown to the root. Sample preparation methods for dental collagen, hydroxyapatite carbonate, and enamel samples are described in Supplemental Text 2.

Starch and Phytolith Analysis

Formation Processes and Micro-Taphonomy. Starch and phytolith recovery from dental calculus are limited by diagenetic factors related to formation processes and micro-taphonomy. The frequency of starch granules found archaeologically is greatly reduced by the immediate breakdown of starch and conversion to sugars by salivary α -amylase, an essential part of the dental calculus formation process (Scannapieco et al. 1993). The chemical breakdown of starch by saliva during the approximately 15 s that camelids retain their cud (Fowler 2010) may also be exacerbated by any preexisting damage to the starch caused by food preparation or cooking techniques; *chuíño blanco* starches, for example, would be more susceptible to destruction than unaltered potato starch because they are typically swollen beyond normal dimensions, resulting in damage to their margins and internal morphology (Melton et al. 2020). The physical breakdown of starches can also be induced by mastication, which is repeated by camelids about 25–35 times per bolus (Fowler 2010). Starchy diets may create more opportunities for deposition in calculus and survival to archaeological identification; however, counts of recovered starches cannot be directly related to exploitation intensity (Leonard et al. 2015). Phytoliths are typically present in nonedible plant parts (e.g., maize cobs, husks), but because these parts are not chewed or consumed by all animals, there is a bias against the recovery of phytoliths as opposed to starch. Thus, archaeological calculus typically reveals small numbers of starches and phytoliths, identifying specific foods consumed while not excluding unidentified taxa from dietary reconstructions.

Laboratory Procedures. Camelid dental calculus samples from Quilcapampa were collected using sterile dental picks cleaned with methanol. Starch granules and phytoliths were extracted from nine samples of calculus in the Integrative Subsistence Laboratory at the University of California, Santa Barbara (UCSB-ISL). Modern contamination was controlled through standard approaches (Crowther et al. 2014; Henry and Piperno 2008). Each tube was subject to extraction and slide mounting according to UCSB-ISL standard laboratory procedures (Supplemental Text 3) based on published protocols on the isolation of microbotanical remains from dental calculus (Henry and Piperno 2008; Mickleburgh and Pagán-Jiménez 2012).

Initially, it was unclear whether macrobotanical desiccated potatoes found at the site could be identified as *chuíño*. To assess whether these potatoes could be a possible source for any *chuíño* starch granules found in camelid dental calculus, we selected for microbotanical analysis one desiccated potato (*Solanum tuberosum*), with a brown appearance and a white interior, from the macrobotanical assemblage. Supplemental Text 4 discusses procedures for starch collection from the desiccated potato.

We used a Brunel SP-400 Metallurgical Microscope ($\times 50$ – $\times 600$), equipped with transmitted/incident illumination systems and polarization filters, in microbotanical identification. Slides were scanned for starch granules under transmitted nonpolarized/polarized light at $100\times$ magnification, followed by removal of the polarization filter and a separate scan for phytoliths at $200\times$ magnification. All microbotanicals were photographed at $400\times$ under nonpolarized transmitted light, with starch granules also photographed under polarized light to record the presence/appearance of extinction crosses (typically visible in undamaged and mildly damaged starch granules) and the degree of birefringence (which can be decreased or nonexistent due to damage).

Starch granules and phytoliths were identified with reference to micrographs of modern plants native to the study region (Capparelli et al. 2015; Giovanetti et al. 2008; Musaubach and Berón 2017; Pagán-Jiménez 2015) and the UCSB-ISL paleoethnobotanical comparative collection. Interpretations of damage patterns were based on the results of modern experimental studies (Babot 2003; Henry et al. 2009) and recent research on the impacts of *chuíño* production practices on starch morphology and metrics (Melton et al. 2020). Taxonomic identification was not always possible: some plant specimens were too severely damaged or lacked diagnostic features altogether. As a result, these specimens were classified as “unidentified.”

Results

Stable Isotope Analyses

Stable and radiogenic isotope analyses of 10 dental specimens from Quilcapampa were successful for all samples, except the dentine collagen from ACL-10424 (Individual 1); the carbon to nitrogen ratio of this dentine sample was outside the range for acceptable preservation (2.9–3.6; DeNiro and Epstein 1978, 1981; Figures 3–6; Table 1). Each dental specimen was sampled along the tooth column. Isotopic compositions for each tissue relate to four individual animals.

Individual 1 is represented by a first molar (M1; ACL-10424) yielding $\delta^{13}\text{C}_{\text{carb}} = -12.0\text{‰}$, $\delta^{18}\text{O}_{\text{VPDP}} = -4.3\text{‰}$, and $^{87}\text{Sr}/^{86}\text{Sr} = 0.70609$ (Figures 4 and 5). The isotopic composition indicates that this individual had a diet of <20% C_4 plants (Figure 6a; Dufour et al. 2014). This animal consumed high amounts of C_3 plants and resided in the *yungas* and lower *quechua* ecozones (2,300–500 m asl; Knudson 2009). This association suggests that its mother made frequent sojourns to higher-altitude regions during the formation of its first molar.

Individual 2 is represented by a deciduous fourth premolar (dP4) and M1 yielding average $\delta^{13}\text{C}_{\text{coll}} = -17.2\text{‰}$, $\delta^{15}\text{N}_{\text{coll}} = 9.55$, $\delta^{13}\text{C}_{\text{carb}} = -10.5\text{‰}$, $\delta^{18}\text{O}_{\text{VPDP}} = 2.1\text{‰}$, and $^{87}\text{Sr}/^{86}\text{Sr} = 0.708925$ (Figure 6a–b). The collagen and carbonate isotope signatures indicate that this individual had a diet of ~30% C_4 plants (Figures 5 and 6; Dufour et al. 2014). Individual 4 is represented by a second molar (M2) yielding $\delta^{13}\text{C}_{\text{coll}} = -18.4\text{‰}$, $\delta^{15}\text{N}_{\text{coll}} = 7.5$, $\delta^{13}\text{C}_{\text{carb}} = -9.3\text{‰}$, $\delta^{18}\text{O}_{\text{VPDP}} = 1.8\text{‰}$, and $^{87}\text{Sr}/^{86}\text{Sr} = 0.70775$. The collagen and carbonate isotopic composition indicates that this individual had a diet of 20%–40% C_4 plants. The isotopic compositions of teeth from Individuals 2 and 4 indicate a higher contribution of C_4 plants than for Individual 1, which suggests access to greater crop diversity and even mobility between the coast and highlands.

Individual 3 is represented by a deciduous third premolar (dP3), dP4, permanent P4, M1, M2, and third molar (M3) yielding average $\delta^{13}\text{C}_{\text{coll}} = -18.1\text{‰}$, $\delta^{15}\text{N}_{\text{coll}} = 7.3$, $\delta^{13}\text{C}_{\text{carb}} = -9.5\text{‰}$, $\delta^{18}\text{O}_{\text{VPDP}} = -2.8\text{‰}$, and $^{87}\text{Sr}/^{86}\text{Sr} = 0.70729$. The collagen and carbonate results indicate that this individual had a diet of 20%–30% C_4 plants. The average isotopic compositions for early-forming teeth (dP3, dP4, M1, and M2) differ from late-forming teeth (P4 and M3). Comparing the contribution of different foddering sources, early-forming teeth reflect a diet of 20%–30% C_4 plants, whereas late-forming teeth reflect a diet of 30%–40% C_4 plants. Earlier in this animal's life it consumed more C_3 plants, indicated by lower carbon isotopic

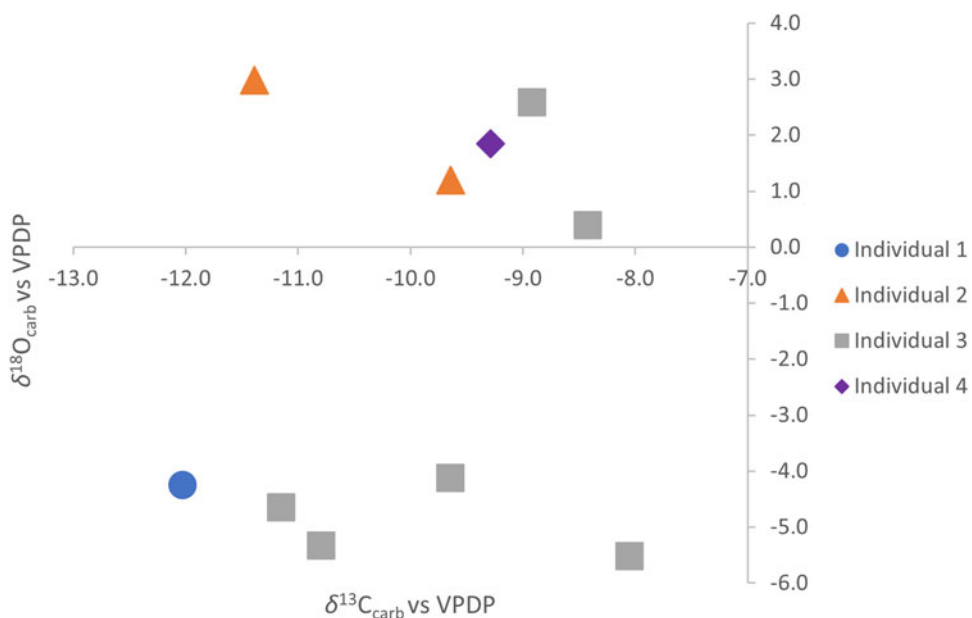


Figure 4. Scatterplot of stable carbon and oxygen isotopes from enamel carbonate for Individuals 1–4.

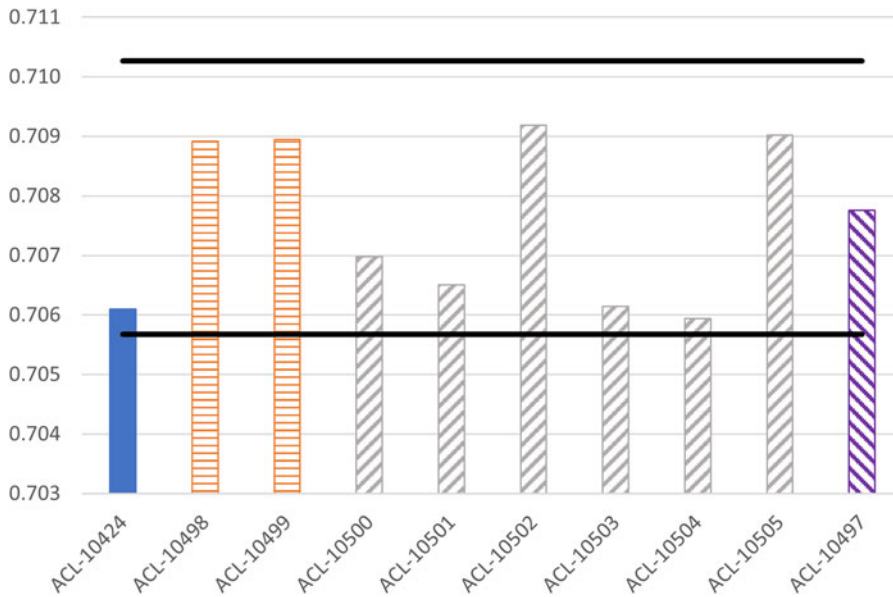


Figure 5. Bar graph indicating variation of strontium values: Individual 1 (blue, solid), Individual 2 (orange, horizontal lines), Individual 3 (gray, left-diagonal lines), and Individual 4 (purple, right-diagonal lines), with the local baseline range demarcated. (Color online)

composition and water sources with lower oxygen isotopic composition. Individual 3's diet changed through time, with a higher contribution of C_4 plants later in life.

The 10 dental specimens analyzed for stable and radiogenic isotopes indicate mixed C_3 and C_4 plant consumption and mobility between the coast and highlands. Isotope analyses of teeth formed in utero are important for understanding the mobility of pregnant female animals. Life-history findings from our multitooth analysis are elaborated by the results of our microbotanical analysis of dental calculus.

Microbotanical Analysis of Camelid Dental Calculus

Four starch granules and one phytolith were recovered from calculus on camelid teeth from three individuals (Table 2). Individual 1 is represented by one sample (ACL-10424) yielding a starch granule consistent with maize (Figure 7a–b) in terms both of its size and morphological presentation. This angular and irregular granule has an extinction cross obscured in the lower-left corner of the starch in Figure 7b, likely due to damage. The cause of this damage is unclear because of its mild presentation.

Individual 2 is represented by one sample (ACL-10498) yielding an unidentified phytolith (see Figure 7i). This phytolith does not clearly match any taxonomically diagnostic criteria and thus remains unidentified. Unfortunately, except for the phytolith finding that broadly suggests dental contact with some form of hardy plant remains (e.g., leaf, stalk, or cob), microbotanical results do not provide any additional insights into the diet of this individual.

Individual 3 is represented by two samples (ACL-10500, 10501) yielding one algarrobo granule and two potato starch granules (see Figure 7c–h). Algarrobo fruits are a foraging source today for both humans and camelids, particularly in the *yungas* where the trees are abundant (Román Godines 2013; Rostworowski 1981:61). The connection between algarrobo and camelids also extends into the past: dung from the site of Cerro Sapamé (Late Intermediate to Late Horizon period) provides direct evidence of algarrobo as fodder (Shimada and Shimada 1985). Although algarrobo seeds are absent from Quilcapampa's macrobotanical assemblage (Biwer and Melton 2021), starches have been recovered from artifacts associated with feasting at other sites (e.g., Buena Vista; see Duncan et al. 2009).

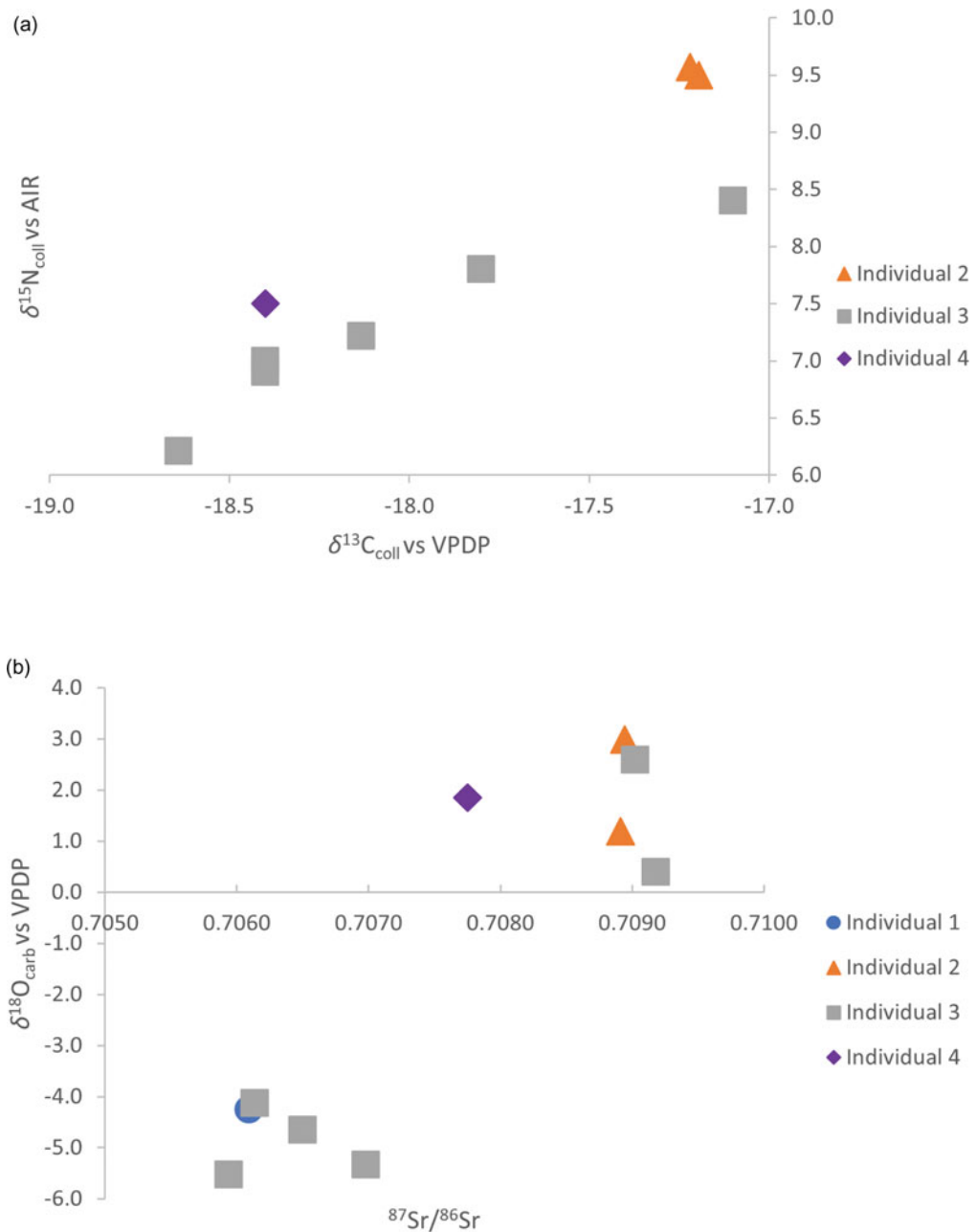


Figure 6. (a) Scatterplot of stable carbon and nitrogen isotopes from dentin collagen for Individuals 2–4; higher carbon isotopes are related to greater contributions from C_4 plants; (b) scatterplot of stable oxygen and radiogenic strontium isotopes from enamel for Individuals 1–4.

Thus, we cannot rule out the possibility that algarrobo fruits may have been obtained by camelids through provisioning and trash raiding, in addition to free grazing.

The potato granule found in the ACL-10500 sample has a size, shape, and hilum location that fit expectations for *chuño*, but its internal structure is clearly damaged as signified by its faded appearance (see Figure 7c–d). Its extinction cross is obscured on the left side due to damage. This starch fit expectations for *chuño negro* based on the softened appearance of its border, bubbled internal presentation,

Table 1. Stable and Radiogenic Isotope Values for Individuals 1–4.

ACL #	Side	Location	Tooth	Individual	Artifact	Age	%C	%N	$\delta^{13}\text{C}_{\text{coll}}$	$\delta^{15}\text{N}_{\text{coll}}$	C/N	$^{87}\text{Sr}/^{86}\text{Sr}$	$\delta^{13}\text{C}_{\text{carb}}$	$\delta^{18}\text{O}_{\text{carb}}$
ACL-10424	Left	Upper	M1	Individual 1	1028.1	2 years	12.5	3.7	−18.3	8.8	4.0	0.70609	−12.0	−4.3
ACL-10497	Right	Upper	M2	Individual 4	1828.57	1 year, 5 months	39.6	15.4	−18.4	7.5	3.0	0.70775	−9.3	1.8
ACL-10498	Left	Lower	dP4	Individual 2	1886.36	6–9 months	41.1	16.1	−17.2	9.6	3.0	0.70891	−9.6	1.2
ACL-10499	Left	Lower	M1	Individual 2	1886.36	6–9 months	39.3	15.5	−17.2	9.5	3.0	0.70894	−11.4	3.0
ACL-10500	Right	Upper	dP3	Individual 3	1886.19	3 years, 9 months	23.2	8.0	−18.4	7.0	3.4	0.70698	−10.8	−5.3
ACL-10501	Right	Upper	dP4	Individual 3	1886.19	3 years, 9 months	37.7	14.6	−18.6	6.2	3.0	0.70650	−11.1	−4.6
ACL-10502	Right	Upper	P4	Individual 3	1886.19	3 years, 9 months	30.8	11.6	−17.8	7.8	3.1	0.70918	−8.4	0.4
ACL-10503	Right	Upper	M1	Individual 3	1886.19	3 years, 9 months	36.0	13.9	−18.4	6.9	3.0	0.70614	−9.6	−4.1
ACL-10504	Right	Upper	M2	Individual 3	1886.19	3 years, 9 months	39.0	15.5	−18.1	7.2	2.9	0.70594	−8.0	−5.5
ACL-10505	Right	Upper	M3	Individual 3	1886.19	3 years, 9 months	40.0	15.9	−17.1	8.4	2.9	0.70902	−8.9	2.6

Table 2. Morphological Attributes of Starch Granules and Phytoliths in Dental Calculus of Quilcapampa Camelids.

Sample No.	Individual	Size (Length × Width)	Starch/ Phytolith	Common Name	Scientific Name	Hilum	Shape/ Morphotype	Lamellae	Extinction Cross	Fissure	Surface Topography	Border	Margin
ACL-10424	1	18.5 × 15 μm	Starch	Maize (consistent with)	<i>Zea mays</i>	Visible; centric; closed	Angular; irregular	Not visible	Centric; visible; obscured in bottom half, possibly due to damage (type uncertain)	Y-shaped; present	Bumpy; possible pressure facet	Visible; single	Angular (with some undulation on top side)
ACL-10498	2	45.5 × 39 μm	Phytolith	Unidentified phytolith	—	—	Spheroid echinate	—	—	—	Bumpy surface	—	—
ACL-10500	3	26.5 × 25.6 μm	Starch	Potato	<i>Solanum tuberosum</i>	Open; visible; eccentric	Slightly ovate (possibly due to damage)	Not visible	Eccentric; visible; slightly obscured on left side (likely due to damage)	N/A	Holes throughout; relatively flattened appearance (but slightly raised laterally)	Low visibility; possibly not intact in upper left corner	Undulating; irregular
ACL-10501	3	16.5 × 22.2 μm	Starch	Potato	<i>Solanum tuberosum</i>	Visible; open	Slightly ovate	Not visible	Centric; visible; extremely obscured on right side due to damage	N/A	Fractured appearance; particularly along border; uneven internal texture	Low visibility; not intact along upper and lower sides	Undulating
ACL-10501	3	27 × 35 μm	Starch	Algarrobo	<i>Prosopis</i> sp.	Centric; open; visible	Angular (roughly hexagonal); irregular	Not visible	Centric; visible; obscured in bottom-right quadrant	X-shaped (barely)	N/A	Mostly intact; damaged along right side	Irregular; undulating on top-right corner

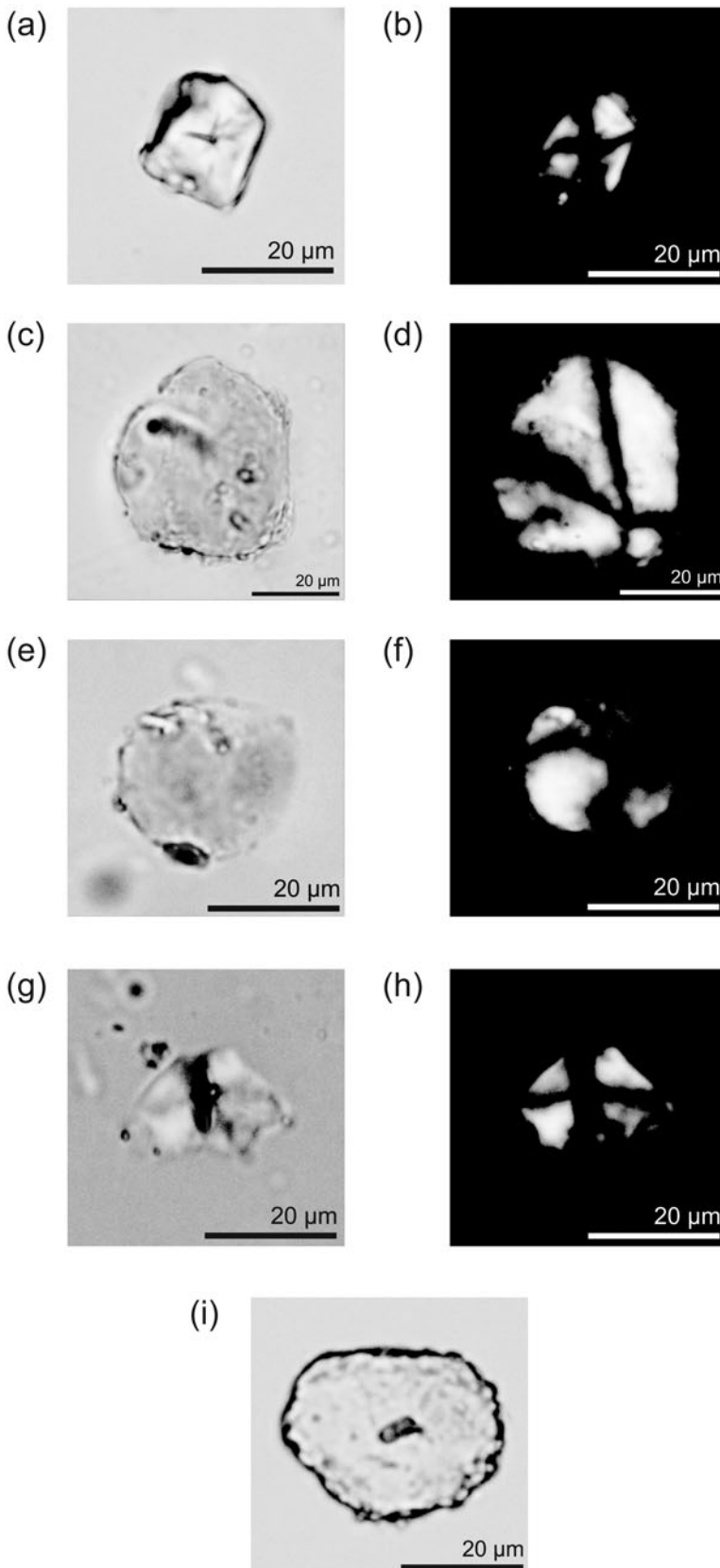


Figure 7. Starches and phytolith recovered from dental calculus of Individuals 1–3: (a) maize-like starch granule, ACL-10424, non-polarized light; (b) maize-like starch granule, ACL-10424, polarized light; (c) potato starch granule, ACL-10500, nonpolarized light; (d) potato starch granule, ACL-10500, polarized light; (e) potato starch granule, ACL-10501, nonpolarized light; (f) potato starch granule, ACL-10501, polarized light; (g) algarrobo starch granule, ACL-10501, nonpolarized light; (h) algarrobo starch granule, ACL-10501, polarized light; and (i) unidentified phytolith, ACL-10498, nonpolarized light. Scale bar in each micrograph is 20 μm in length.

and appropriate length-to-width ratio (Melton et al. 2020). ACL-10501 also yielded one potato starch granule. Damage is indicated by missing areas along the upper portion of the border (see Figure 7e) that obscure the upper-right quadrant of the extinction cross (see Figure 7f). Based on the broken nature of the border, the damage was likely caused by grinding activities. Grinding damage is expected for dental calculus, particularly from camelids, because of the mastication involved in food consumption. There is also a possibility the granule was exposed to boiling or baking based on its uneven internal texture (Henry et al. 2009), which could have occurred before consumption. To gain more guidance on the human use of *chuño* at Quilcapampa, we looked to starches from the desiccated potato sampled for starch analysis.

Starch granules from the archaeological potato (Figure 8) are generally irregularly ovate in shape, with some projections that result in a triangular or trapezoidal appearance (see Figure 8a). Transverse and longitudinal fissures are common, with hila openings devoid of fissures being abundant but less common. Cracks occur around the perimeters of some starches (see Figure 8e) representing damage and are seen most frequently in starches exposed to physical damage (Henry et al. 2009); for micrographs of unaltered starches from modern Andean potato varieties, see Cruz and coworkers (2016) and Rumold (2010). In her study of modern *chuño* starches, Babot (2003) found granules with fragmentation around the perimeter and in other locations. Physical damage to *chuño* starches is most likely the result of trampling that is part of both *chuño negro* and *chuño blanco* production processes. Several granules exhibited a faded, more transparent appearance that is characteristic of *chuño* starches; the borders of these starches are faint, and they demonstrate occasional vacuoles and missing areas under polarized light (see Figure 8b). Extinction crosses are visible in most but not all starches because starches with a faded appearance do not exhibit birefringence: this is a diagnostic characteristic of these starches. Extinction cross arms are bent or widened in some starches, particularly near the hilum (see Figure 8d). One arm per starch is occasionally bent (a defining characteristic of *chuño negro* starches; see Melton et al. 2020); however, the bend angle is not always like that observed in modern *chuño negro* examples. Our observations of this specimen help support the availability of *chuño* to camelids in a *yungas* context while also providing a morphological record that can be compared with archaeological starches from other sites.

Discussion

The abundance of macrobotanical potato (likely *chuño negro*) and maize remains at Quilcapampa supports our suggestion that *chuño* and maize were consumed by camelids living at this site. The absence of algarrobo in the macrobotanical record associated with anthropogenic refuse deposits suggests that it may have been largely used as camelid fodder. Because algarrobo trees are located closer to the Sihuas River, the introduction of algarrobo pods into camelid diets may have occurred during periodic grazing along the river's edge. Moreover, morphological characteristics of the desiccated potato recovered at Quilcapampa are consistent with expectations for *chuño*, which was also identified in microbotanical residues on ceramic and groundstone artifacts at the site (Biwer and Melton 2021, 2022). Situating our microbotanical results alongside the site's stable and radiogenic isotope findings, other botanical and faunal datasets, and environmental conditions allows us to consider how camelids may have gained access to the identified resources.

During the Middle Horizon, camelids around Quilcapampa had few grazing opportunities because of the high aridity and limited availability of weedy plants during dry seasons. Although llamas and alpacas in the highlands could graze on various wild grasses, camelids living in the *yungas* of Peru's southern coast likely relied almost exclusively on what grew in the heavily cultivated river valley bottoms. To sustain their animals, herders depended in part on staple foods and evaporated water sources for hydration. Stable isotope analysis demonstrates variation among the diets of different camelids at Quilcapampa, with some individuals having a greater contribution of C₄ plants than others. All radiogenic strontium isotopic compositions are within the local range (see Figure 5; Knudson et al. 2014), but Individual 3 displays an important difference between its early- and late-forming teeth. The early-forming teeth have characteristic signatures for the *yungas* ecozone, whereas the later-forming teeth have a higher strontium isotopic composition. Oxygen signatures support this pattern: the early-forming teeth fall within the *yungas* ecozone, and late-forming teeth have isotopic compositions

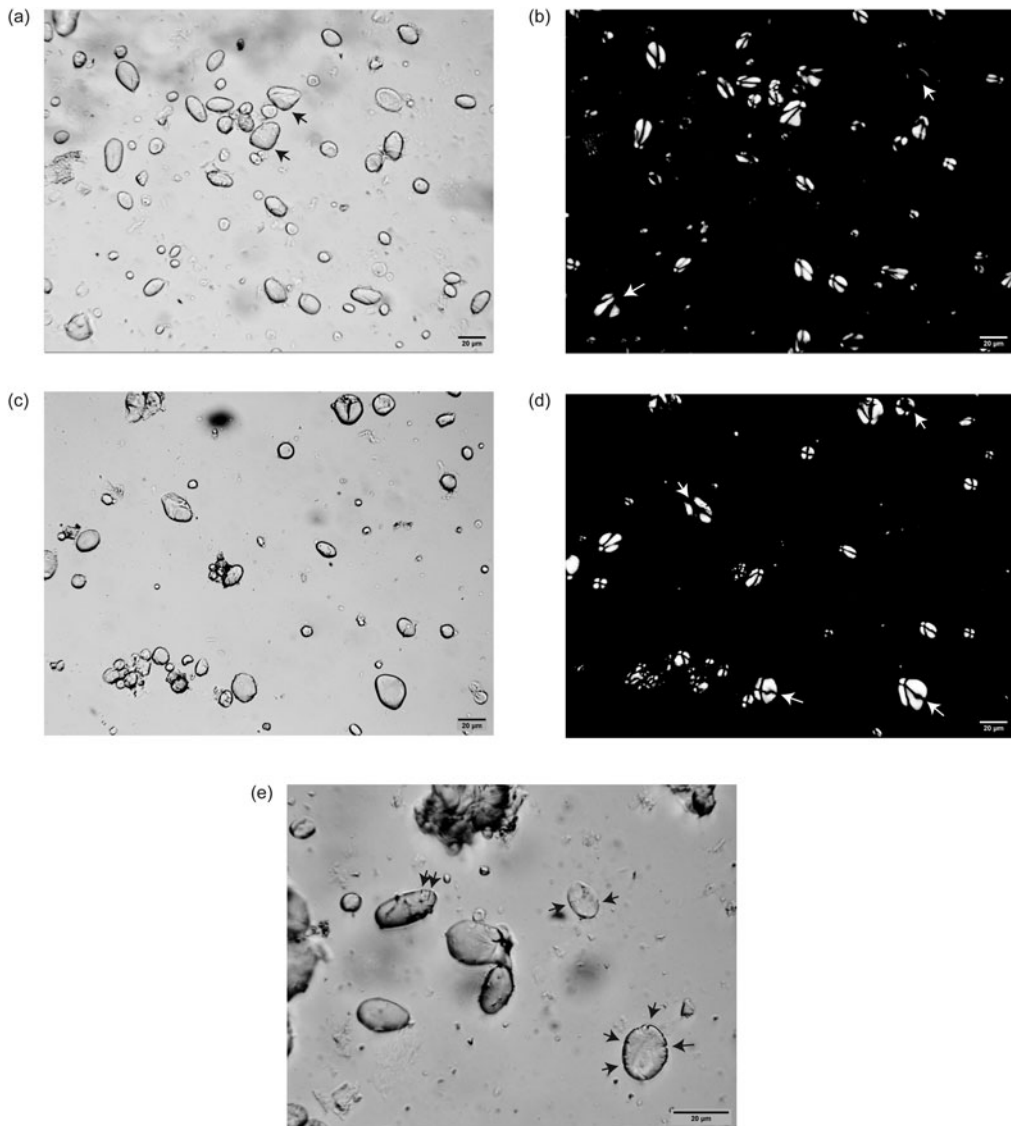


Figure 8. Starch granules in desiccated potato from the Quilcapampa macrobotanical assemblage: (a, c) nonpolarized lighting at 200 \times magnification; (b, d) polarized lighting at 200 \times magnification; (e) nonpolarized lighting at 400 \times magnification. Scale bar in each micrograph is 20 μ m in length. Arrows indicate features referenced in text.

that indicate the consumption of water from evaporated sources. This finding aligns with the greater mobility that older camelids typically experience when they join caravan herds. Thus, our results from Individual 3 highlight a possible life history of early rearing in more coastal or *yungas* environments and later life sojourns to the highlands and coast (a seasonal rotation of foddering camelids on maize stubble was noted by Dantas and colleagues [2014]).

Our understanding of local management strategies is deepened by pairing isotopic and botanical data. Although no starch granules/phytoliths from wild grasses were identified, *ichu* thatch and seeds were found in a few excavation units, suggesting that seasonal grasses and sedges could have been provisioned as C_3 fodder from the valley bottom or highland sources (Bruno and Hastorf 2016). Microbotanical analysis provides direct evidence for algarrobo fruits as a C_3 source, either provisioned by humans or consumed during visits to the evaporated water sources that these trees tend to inhabit in otherwise arid landscapes (Beresford-Jones et al. 2009).

Human-processed C_3 cultigens were also incorporated into camelid diets. Microbotanical results from dental calculus revealed starch granules of potato, likely *chuño negro*. *Chuño* was an imported resource at Quilcapampa, indicating connections to the highlands and perhaps the Wari heartland. Lightweight, edible for years, and nutrient-rich, *chuño* could have been directly given to herds as fodder, consumed by camelids rummaging through middens, or both. Desiccated *chuño* potatoes are prevalent in the core area of Quilcapampa, indicating that they likely served as an everyday staple.

Microbotanical analyses also supplement stable isotope findings by indicating that maize contributed to C_4 plant inputs. Maize was widely processed at Quilcapampa and was thus available to camelids in many ways. Our findings align well with the isotopic evidence for maize foddering at Conchopata, a contemporaneous Wari site in the Ayacucho Basin. Finucane and colleagues (2006) found higher carbon isotopic compositions among Conchopata's camelids, which suggests the active pasturing of herds on maize fields. A similar scenario could have unfolded in Quilcapampa, where the *yungas* zone provided fertile lands for maize agriculture, although direct foddering and camelid rummaging in middens represent additional possibilities.

Quilcapampa's location is ideal for maize agriculture, and the maize consumed by the camelids was likely grown nearby. However, dental calculus represents accumulated dietary behaviors (like stable isotopes), and the deposition of *chuño*, algarrobo, and maize-like starch could be from a single meal or from long-term habitual practices in a seasonal round. Isotope results suggest that Quilcapampa camelids varied in diet and grazing locales over the course of their lives. Individual 3, for example, was reared largely on C_3 plants as a juvenile but had greater input (~30%–40%) from C_4 sources later in life (see Figure 6a). Strontium isotope results demonstrate that this animal spent its early years in a lower radiogenic region compared to its later development. This shifting pattern suggests that Individual 3 spent its juvenescence grazing in fertile coastal pastures, followed by a switch to a more arid locale like Quilcapampa, where grasses were less available and agricultural C_4 staples were necessary to supplement input from local grazing resources. The nitrogen isotopic composition of teeth supports this switch: higher isotopic composition among late-forming teeth indicates that Individual 3's later life may have been spent in arid environments. Additionally, *chuño* can only be produced at altitudes above about 3,800 m asl (de Haan et al. 2010), thus serving as an indicator of relations with the highlands that were almost certainly supported by llama caravans.

Middle Horizon caravan trails bisect the northern edge of the Pacific Piedmont (Bikoulis et al. 2018). Quilcapampa, like other Pacific Piedmont sites of the era (Nigra et al. 2017), was oriented around these trails: both petroglyph evidence and faunal remains at the site reveal the important role that camelids played in maintaining Wari contacts between the highlands, coast, and intervalley regions of the *yungas* (Alaica et al. 2021; Berquist et al. 2021). Ceramic, lithic, botanical, and textile evidence suggest that Quilcapampa's residents maintained interregional interactions throughout the site's short occupation. It is important to juxtapose these long-distance connections with local animal management in the *yungas*. Camelids were central to Quilcapampa's socially charged feasting regime that tied the core area's residents to those living elsewhere in the valley (Alaica et al. 2021). Balancing the use of camelids as a source of meat, transport, and fiber required careful decision-making. Herders needed to calibrate the male:female and adult:subadult ratios of their animals and provide them with adequate fodder and water, whether at home or on the move.

Conclusions

Integrating stable isotope data on camelid teeth with microbotanical data of dental calculus adds specificity to ancient camelid foddering techniques, providing greater resolution of the diets and subsistence sources of animals managed by humans. Stable and radiogenic isotope analyses across the life histories of four animals from Quilcapampa revealed both C_3 and C_4 plant input and vertical mobility but were limited in their ability to identify specific resources that contributed to isotopic signatures. Microbotanical analysis of dental calculus from these same camelids identified C_3 (algarrobo and potato) and C_4 (maize) resources and showed that potatoes were likely processed by humans into *chuño* (likely *chuño negro*) before consumption by camelids. No starch granules or phytoliths of

wild grasses were found in the calculus, but their absence does not eliminate the possibility that these resources may have been used for grazing when available.

Situating these results in the context of Quilcapampa's environmental surroundings and excavated subsistence assemblage suggests that camelid foddering in the *jungas* largely took place within the narrow confines of an arid and heavily domesticated landscape. Camelids ate a combination of local fodder and cultivated staples obtained from nearby fields or long-distance exchange, all of which were either actively or unintentionally supplied to the animals. Limited grazing opportunities meant that feeding camelids at Quilcapampa, as at other *jungas* settlements, was fundamentally different from many highland or coastal locales where native grasses were more plentiful. Our research suggests that these *jungas* settlements would have served critical roles as vital caravan nodes where camelids were provisioned, ensuring their sustenance in traversing terrain with sparse natural fodder. Newcomers to a region, like those who founded Quilcapampa, therefore needed regular access to local fields, fertile algarrobo groves, and evaporated water sources but also used imported highland foods to help sustain their herds. Although much work remains in unraveling seasonal migration, trade, and inter/cross-regional interactions during the Middle Horizon, we hope that this case study encourages future research combining different methodological approaches to understand mobility more fully in the ancient Andes.

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Data Availability Statement. All microbotanical and stable isotope data are reported in the body, figures, tables, and supplemental files of this manuscript. Macrobotanical data are available through the Digital Archaeological Conservancy (tDAR), and remains are curated in the University of California, Santa Barbara Integrated Subsistence Laboratory. There are no remaining microbotanical or stable isotope samples in curation.

Competing Interests. The authors declare none.

Supplemental Material. For supplemental material accompanying this article, visit <https://doi.org/10.1017/laq.2022.80>.

Supplemental Table 1. Macrobotanical Remains Identified at Quilcapampa.

Supplemental Text 1. Extended Descriptions of the Quilcapampa Site Related to Faunal and Macrobotanical Findings.

Supplemental Text 2. Stable and Radiogenic Isotope Sample Preparation Procedures.

Supplemental Text 3. Microbotanical Sample Extraction and Slide Mounting Procedures.

Supplemental Text 4. Procedures for Sampling Desiccated Potato Remains for Starch Analysis.

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