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Dietary continuity and change at Panama Viejo from an interdisciplinary perspective, C. 600–1671

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ABSTRACT

The study of food consumption during the colonial period in Panama Viejo traditionally has been based on chronicles and archival documentation. The present analysis reassesses the historical information about diet in this colonial enclave based on microbotanical, isotopic and bioanthropological evidence obtained from the excavations within and outside the remains of the old city's Cathedral in two locations and four chronological periods to complement and contrast written sources. The ensuing data sets, once integrated, point to the consumption of native plants, particularly maize, among people of different ancestral origins from the settlement's earliest years, as well as the consumption of wheat – which could not be grown in the region – plantains and rice, whose cultivation was introduced successfully. Stable isotope evidence indicates a shift from dietary strategies based on maize, seafood and terrestrial animal meat in pre-Hispanic and early colonial times to diets featuring more C_3 plants, including rice, wheat, and plantains, as well beef and dairy products during the later colonial period. This gradual shift in dietary strategies appears among individuals of Indigenous American, African, European and mixed origins and ancestries, probably influenced by the nutritional and epidemiological stress registered in all of these populations.

1. Introduction

The attainment, processing, and consumption of food figures prominently in the history of population movements and adaptations to local conditions that increased voluntary and involuntary migrants' chances of survival. The classical visions of European flora and fauna invading the neotropics (Crosby 1986; Castillero 2010a, 2010b), are being nuanced by new perspectives that emphasize African and Indigenous American participation in the ecological adaptations developed (Earle 2012; Saldarriaga 2020, Aram and García Falcón 2021, Saldarriaga 2012). At the same time, archaeologists have unearthed new evidence that reveals the need to revisit historical sources (Hodgetts 2006, Chiavazza et al 2015, Aceituno and Martín 2017, Martín and Rodríguez 2006).

The present work follows a strategy for interdisciplinary analysis applied to the bioanthropological, microbotanical and multiple isotope evidence of strontium, oxygen (phosphate; PO_4^{3-}), nitrogen and carbon ($^{87}Sr/^{86}Sr$, $\delta^{18}Op$, $\delta^{15}N$, $\delta^{13}C$) recovered from individuals buried at Panama Viejo in four different temporal periods, and contrasted with extensive archival research. This study examines micro remains, mainly starch and phytoliths, extracted from the dental calculus of pre-Hispanic and colonial individuals buried in or outside Panama Viejo's Cathedrals, alongside bioanthropological and stable isotopic analyses of the same individuals' remains. The combination of such techniques in an area where high humidity and frequent floods impede the preservation of local documentation as well as the recovery of macro-remains by flotation, promise insights into individual lives that rarely or barely appear in the historical record.

In the case of Panamá Viejo, historian Alfredo Castillero Calvo has argued that European elites sought to maintain dietary habits that

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privileged wheat bread, whereas Indigenous Americans, Africans, and mixed Afro-descendants consumed mainly local products, particularly maize and yuca (manioc). Castillero has argued that Europeans modified the region's "agricultural paradigm" with the homogenization of crops, large-scale importation of cattle, and dependency on imported foodstuffs, leading to an important subsistence crisis in the mid-seventeenth century (Castillero 2010a, 2010b, 2016). Revising such arguments, a study published in 2017 pointed to European consumption of local products from nearly the time of the city's foundation as part of a "mixed" or "creole" agropecuary strategy with an important presence of local plant resources (Aceituno and Martín 2017). In particular, this work provided evidence of the grinding of maize (*Zea mays*), yuca (*Manihot esculenta*), beans (*Phaseolus vulgaris*), otoe (*Xanthosoma spp*.), and other plants that could not be identified, on artifacts recovered from colonial contexts. The present study goes a step further by examining starch particles preserved in the dental calculus of the colonial individuals themselves, and hence subject to complementary bioarchaeological and isotopic analyses. This evidence will be used to test the hypothesis that Panama Viejo's inhabitants consumed a growing diversity of local products as well as imported resources, when available.

2. Panama Viejo and its Population, 1519–1671

From its foundation on America's Pacific coast in 1519, Panama City (See Fig. 1) became a base for colonial expeditions into Central and South America (Aram 2008). Its settlement, like that of the corresponding Caribbean enclaves on the isthmus (Nombre de Dios and subsequently Portobello), responded to the possibilities of an unfamiliar geography, with the goal of facilitating transit between the Atlantic and Pacific Oceans, known as the Northern and Southern Seas (Castillero 2006). Over the following century, these cities articulated a principal axis for the Hispanic Empire's commercial routes, connecting and transforming societies and cultures by transporting persons and goods between Europe, Africa, America and Asia, in an irreversible process of early globalization (Martín and Aram 2020; Yun Casalilla 2019).

The foundation of Panama Viejo in 1519 took place on a site with previous Indigenous dwellings and burials dated 603–1430 CE (Capodiferro et al 2021). Alongside the area's natural port, in 1519 the Spaniards established a Main Square, with the requisite principal church, relocated in 1542 to an elevated, rocky terrain on the eastern side of the same Main Square, where its ruins remain visible today (Fig. 2) (Hernández, Martín and Aram, 2021). During the settlement's precarious early days, public meetings, in addition to baptisms, marriages, and burials, took place in its principal church. In 1522, Panama's governor announced the review of grants of 7484 adult natives associated with 29 indigenous chiefs to 103 settlers as well as others excluded from grants, who gathered in its principle church for Sunday mass (Meeting in the Church of Our Lady 1522, List of persons with encomiendas 1519). The governor also proclaimed ordinances to regulate the labor services associated with these grants, noting that on the mainland, unlike Hispaniola, every man required a woman to make his daily food, including balls of maize *(bollos), chicha* (from fermented corn), and *mazamorra* (corn porridge) (Ordinances 1521, Mena García 1989, 343). Whatever their origins, all of the new city's inhabitants depended upon maize. In the 1520′s and 30′s, many of Panama's early founders were drawn to the conquests of Nicaragua and Peru, which increased the numbers of clerics, merchants, Indigenous Americans, and Africans with diverse agricultural traditions and knowledge who passed through or labored in Panama Viejo (Cieza de León 1980).

The Cathedral provided a point of reference for all of these individuals, as well as a final resting place for many of those who died in Panama Viejo. According to the Cathedral Chapter's *maestreescuela,* in 1640 the diocese ministered to some seven thousand souls divided among 750 households in Panama City and its surroundings. Based on Cathedral records no longer preserved, the *maestreescuela* reported 13,158 baptisms from June 1638 through July 1640, and 8,910 burials from 1613 through 1638 (Requejo (1640) 1908: 20–21). To compensate for the loss of such historical records, additional information can be recovered from the human remains abandoned when the city relocated after 1671.

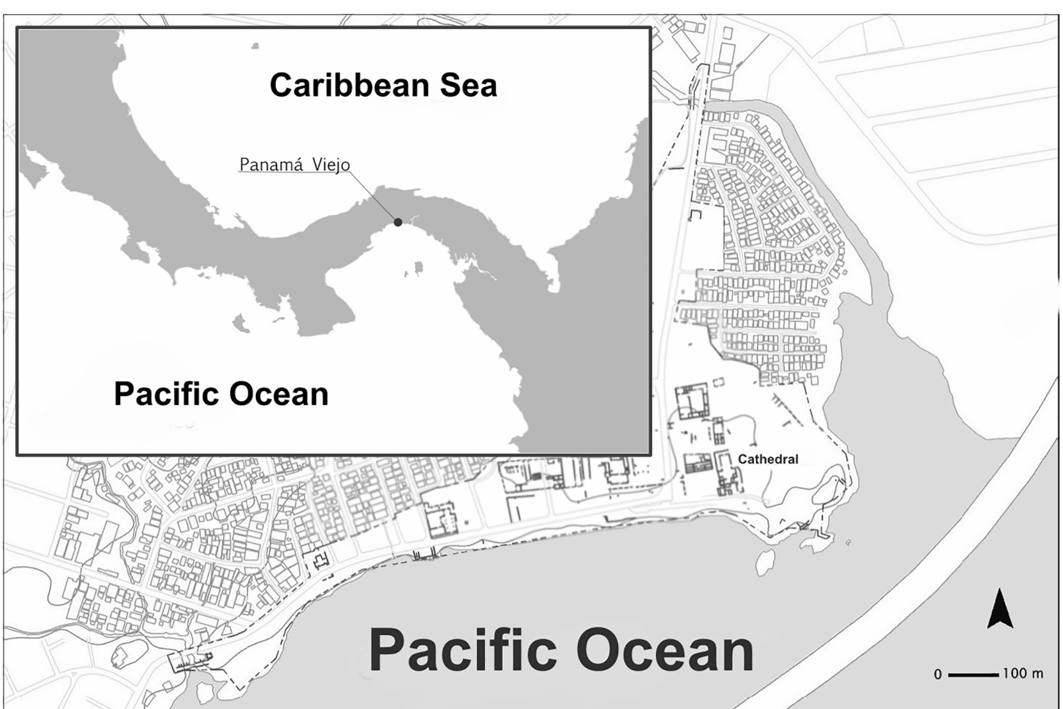

Fig. 1. Panama Viejo's location and group of historical monuments, declared World Heritage in 2003.

Fig. 2. View from the air of the ruins of Panama Viejo's Cathedral and Main Square, with the areas excavated in 2017 and 2018 marked. Photo by Juan G. Martín.

3. Archaeology, dating and sampling in Panama Viejo's Cathedrals and atrium

Excavations within the visible ruins of Panama Viejo's Cathedral (Brizuela 1998, Martín 2000a, Gómez 2005), in the Cathedral's atrium (Martín 2000b), and to the south of its Main Square (Martín 2004), made the site's funerary archaeology a formal part of its research project, which was able to identify characteristics of Catholic ritual in the funerary deposits and the reutilization of funerary space (Martín and Díaz 2000, Martín 2001). The human remains excavated in different sectors of the historical and monumental area through 2007 made it possible, moreover, to compare the settlement's paleopathological profile for the pre-Hispanic period and the colonial city (Martín, Rivera and Rojas 2009; Rojas, Rivera and Martín 2011).

In 2017 and 2018 additional excavation campaigns were undertaken in the framework of the interdisciplinary project, *ArtEmpire*, in order to respond to new questions about the impact of the Spanish conquest and colonization on a strategic "artery of empire" like the isthmus of Panama (Fig. 2). A total of 102 square meters were excavated, with the recovery of 175 individuals corresponding to the colonial period, 151 in the

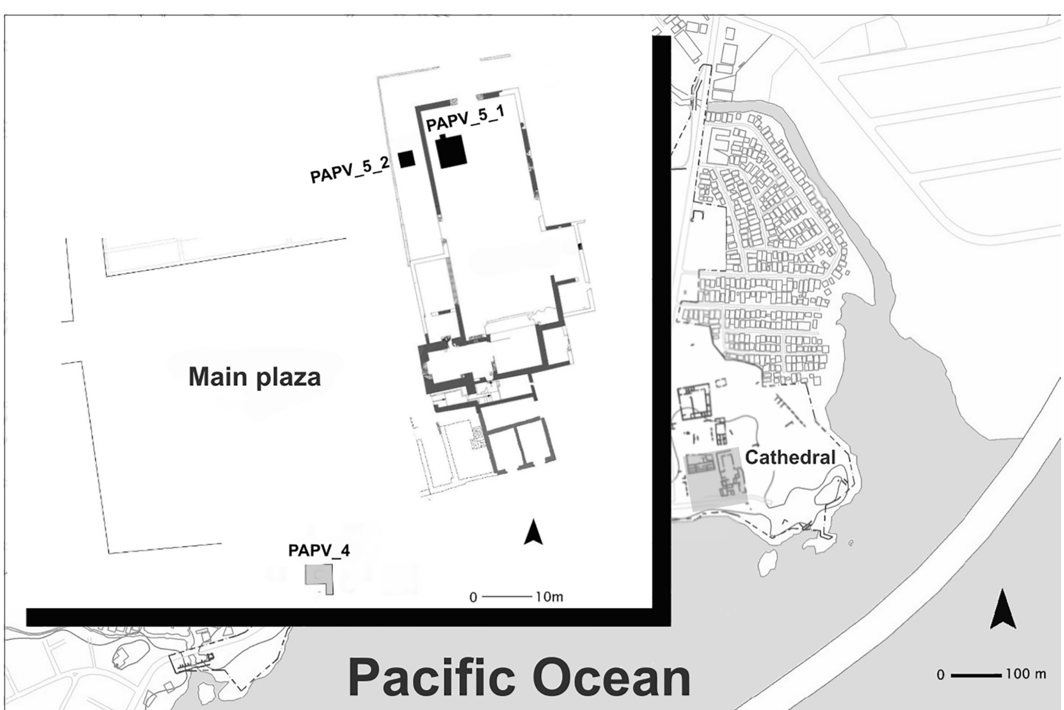

Fig. 3. Panama Viejo's ruins and the archaeological excavations undertaken in 2017 (PVCA 1 and PVCA 2) and 2018 (PVCA 4).

visible Cathedral's nave, 8 in its atrium, and 16 to the south of the main square, increasing the number of human remains that could be sampled to obtain new information about the populations' origins, demography, health, diet and social relations before and after the European invasion. To this end, different bioanthropological, paleopathological, microbotanical and isotopic analyses have been undertaken, while genetic analyses remain underway.

The analysis of the site's formation as well as the taphonomic details of the deposits excavated made it possible to establish a chronological sequence compatible with the historical information available. To the south of the Main Square, the data obtained made it possible to define an extensive and coherent area of interments oriented from west to east (with only one exception), which presumed the existence of an architectonic structure made of perishable materials, corresponding to Panama Viejo's main Catholic temple, 1519–1541, and, consequently, to the oldest colonial burials, associated with the excavation unit PVCA-4, with a total area of 36 square meters (Fig. 3). In 2003 and 2018, a total of 32 primary interments were excavated from this sector bordering the Main Plaza (Hernández, Martín and Aram 2021). In the following paragraphs, we refer to these burials as early colonial.

On the other hand, the stratigraphic information from the interior of the subsequent Cathedral, removed from the coastline after 1541, made it possible to define two periods of inhumation. The first, from 1542 through 1626 corresponded to the temple erected in wood (PVCA-1), which we label mid-colonial. A second phase identified, associated with the temple's reconstruction in limestone and mortar, included the insertion of stone bases for pillars (UE 1008 and 1013) in 1626, which configured the church's final period, through 1671, which we consider later colonial. One motive for renovations in 1626 entailed the stench produced by the decomposing bodies (Requejo 1908: 28) associated with the saturation of the middle burial layers (UE 1081), which confirms our inference regarding the primary interments on these levels (Fig. 4). Hence, burials below the stone bases or displaced by their insertion could be considered "mid-colonial", in contrast to the "later colonial" remains deposited after the stone bases. Only two layers of interments were rescued from the Cathedral's atrium, where the associated material culture indicated that these individuals also could be considered "mid" and "later colonial", and dated to the seventeenth century. In this way, the succession of colonial funerary deposits and relationships among elements within them made it possible to date burials with greater precision than offered by C14, which we used, nevertheless, to date the pre-Hispanic individuals sampled.

Fig. 4. Photogrammetry of UE 1081, where the intensive use of sacred space for inhumation can be observed as well as the limestone bases inserted for the temple's reconstruction in 1626.

The individuals recovered in 2017 and 2018 were subject to bioanthropological analysis in order to estimate their sex, age at death, height and possible ancestral filiations. They were then selected for sampling based on the presence of dental calculus (for microbotanical analysis); first and third permanent molars (for strontium and oxygen isotope analyses on phosphates) and a rib fragment (for carbon and nitrogen analyses), as well as the temporal petrous bone (for the extraction of ancient DNA). The samples extracted were also chosen to complement a previous round of sampling of pre-Hispanic and colonial individuals excavated before 2017, with attention to representation of all historical periods, both sexes, and different ancestral groups. Dental calculus was processed from a total of 41 individuals (7 pre-Hispanic and 34 colonial), and isotope analyses undertaken for 54 human individuals (23 pre-Hispanic and 37 colonial) as well as local faunal remains (pigs and cattle). As for the intersection of both data sets, isotopic analyses were performed on samples from the 7 pre-Hispanic and 18 of the colonial individuals with dental calculus examined. The present study focusses on this subsample of the total dataset, with reference to the larger samples analyzed, to evaluate dietary continuity and change at Panamá Viejo.

4. Analytical methods and materials

4.1. Bioanthropological analysis

Skeletal indicators of nutritional stress were analyzed in a total of 200 individuals, 44 associated with the pre-Hispanic period and 156 from the colonial period, from the Cathedral's excavations in 2017 and 2018, as well as some individuals excavated there previously (Martín 2000a, 2000b, 2002). The prevalence of porotic hyperostosis, cribra orbitalia and enamel hypoplasia was evaluated according to sex, age, ancestry, and chronological period. However, specific inclusion criteria were considered for the observation of each indicator (Waldron 2009). For example, the cribra orbitalia observations included individuals with the presence of at least one of the two orbital portions of the frontal bone (41 pre-Hispanic and 134 colonial individuals). For porotic hyperostosis, individuals with a representativeness greater than 25% of the cranial vault were analyzed, except for those in which the lesion was evident (42 pre-Hispanic and 147 colonial individuals). Finally, for the observation of enamel hypoplasia, individuals with permanent teeth and a representation of at least 25% of the structures were recorded, except those in which the injury was evident (41 pre-Hispanic and 101 colonial individuals). Sex in adults was estimated based on the dimorphic characteristics of the pelvis and crania (Phenice 1969, Acsadi and Nemeskeri 1970, Buikstra and Ubelaker 1994). With respect to age, changes in the pubic symphysis and the auricular surface of the ilium were registered (Brooks and Suchey, 1990; Buckberry and Chamberlain 2002; Lovejoy et al., 1985), and, secondarily, the closure of the cranial sutures (Acsadi and Nemeskeri, 1970; Meindl and Lovejoy, 1985). In the infantile and juvenile populations, the phases of dental development were registered to estimate age (Demirjian et al. 1973, Ubelaker 1989), followed by the processes of bone maturation and epiphyseal union (Schaefer et al. 2008, Scheuer and Black 2000). Estimations of the colonial individuals' ancestries took place with attention to the theoretical, methodological, and ethical challenges involved (Dunn et al. 2020). The methods applied involved algorithms of probabilistic prediction drawing upon craniometric observations (Navega et al., 2015), morphological characteristics of the facial skeleton (Hefner, 2009) and non-metric dental traits (Scott et al., 2018).

4.2. Microbotanical analysis in dental calculus

For the starch and phytolith analysis, dental calculus was removed with an odontological instrument sterilized after each sample extraction. Subsequently, a protocol for starch recovery based on the different densities of starch and heavy water was applied in the laboratory. The starch recovered was observed with a stereoscope microscope with 40X and 60X objectives (Piperno 2006a,b: 98–100). Finally, taxonomic identification took place through comparisons to modern as well as archaeological starches, as well as the consultation of specialized publications, with attention to the dimensions, shape and ornamental variables of the starch observed (Babot 2007; Dickau 2005; Dickau et al. 2007; ICSN 2011, Lentfer et al. 2002; Loy 1994; Pagan 2015; Piperno 1998; Piperno 2006a,b).

4.3. Carbon, nitrogen, strontium, and oxygen isotope analyses

This study applies multi-isotope analyses to teeth and bones in order to investigate possible origins and dietary habits of individuals whose remains were inhumed in Panama Viejo. We concentrate on the evaluation of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope compositions of bone collagen of individuals of local or regional origin, i.e. who likely grew up in Panamá Viejo or on the Panamanian isthmus according to the strontium ($^{87}Sr/^{86}Sr$) and oxygen ($\delta^{18}Op$) isotope record of their teeth. Nitrogen bound in collagen originates almost exclusively from dietary proteins, whereas carbohydrates and fats do not contain any nitrogen. Because collagen is a protein, most of its carbon also goes back to dietary proteins, with smaller contributions from carbohydrates and fats (Ambrose 1993; Clementz 2012; Fernandes et al. 2012). The method is well established to characterize the dietary habits of people and animals in the past, but also reflects agricultural practices (Ambrose et al. 1993; O'Brian 2015).

In the Panamanian context, carbon isotopes are especially informative of the proportions of C_3 and C_4 plants as well as marine sources in the human diet. C_3 plants with $\delta^{13}C$ values between −35 and −22 ‰ V-PDB comprise tropical fruit, root vegetables such as yuca (manioc), rice, as well as cereals including wheat, which had to be imported to Panamá. C_4 plants, with maize being the most important native crop in Central America, have higher $\delta^{13}C$ values of around −16 to −10 ‰ V-PDB (Cerling et al. 1997; O'Leary 1988), a range that overlaps with values found in marine fish and seafood (O'Brian 2015). Due to isotope fractionation, $\delta^{13}C$ values of bone collagen of herbivores are about 5 ‰ higher than the values of the plants at the base of the food web and increase by 0.8 to 1.3 ‰ (average c. 1 ‰) with every further trophic level (Bocherens and Drucker 2003; Drucker et al. 2005; Lee-Thorp et al. 2008). Isotope fractionation also causes nitrogen isotope values to increase along food chains by about 3 to 5 ‰ AIR (average 4 ‰; Hedges and Reynard 2007) or even up to 6 ‰ per trophic level (O'Connell et al. 2012). Nitrogen isotope compositions reflect the consumption of animal-derived or marine foodstuffs. Due to longer food chains in the sea, marine fish and seafood often exhibit higher $\delta^{15}N$ values than terrestrial organisms. Crop plants take up nitrogen directly from the soil, so that their $\delta^{15}N$ values reflect the isotopic composition of the nitrogen that is available from it. Therefore, the isotopic signal may vary spatially according to soil fertility and depend on anthropogenic influence due to manuring (Bogaard et al. 2013). The latter may obscure dietary information but is informative regarding land tenure and arable practices. Because of the diversity of factors that influence the isotope compositions, the interpretation of isotope data from human collagen requires comparative values from local animals.

Since the first carbon and nitrogen isotope analyses in L. Norr's dissertation (Norr 1991), paleodiet studies have only recently been resumed in Panamá. The isotope composition of collagen from deer bones from pre-Columbian contexts has confirmed the predominance of C_3 plants among natural sources of forage and suggests that indication for the consumption of C_4 plants, i.e. maize, reflects cultivation and anthropogenic contribution to the forage of wild game (Sugiyama et al. 2020). The study attests to remarkable variation in collagen preservation and provides $\delta^{13}C$ and $\delta^{15}N$ values of well-preserved collagen that constitute valuable comparative data, particularly from birds including parrots and waterfowl. Sharpe et al. (2021) offers a rich source of comparison data of human collagen from five pre-Hispanic contexts. The highly variable isotope compositions attest to the general importance of maize in the human diet and varying contributions of marine food.

The study presented here is the first to sample human collagen from a Spanish urban foundation in Panamá and aims to evaluate similarities and differences of average dietary compositions between the pre-Hispanic and the colonial populations at the same site and their possible changes over time. Because colonial cities accommodated some of the most diverse historical populations worldwide, we used strontium ($^{87}Sr/^{86}Sr$) and oxygen isotope compositions ($\delta^{18}Op$) to identify individuals who were likely local to Panamá Viejo or the wider hinterland of the Panamanian Isthmus. The analyses were performed on tooth enamel, the densest hard tissue of the human body. Because enamel is formed in childhood and not remodeled thereafter (Hillson 1996), the samples represent the isotope composition of elements that were taken up in the early years of human life. In order to trace possible residential moves in childhood and adolescence, we sampled two teeth from each individual, preferentially including a first molar, whose enamel mineralizes between birth and about three years and a third molar (wisdom tooth) whose enamel mineralizes from about seven years of life until adolescence (AlQahtani et al. 2010). If third molars were not available, second molars or premolars (mineralization between about three and seven year of life), were sampled instead. Strontium isotope ratios reflect the geological properties of the catchment from which humans obtained their food and drink during enamel formation (Bentley 2006; Capo et al. 1998). Strontium replaces the main element calcium and is biologically available from soils and water, whose isotope composition reflects the type and age of the source rock. Because isotope fractionation is very limited and corrected in the analytical process, $^{87}Sr/^{86}Sr$ ratios of biological tissues average the isotope composition of the food and drink that were ingested when the tissue was formed. Assuming geologically homogeneous dietary catchments and the consumption of locally produced foodstuffs, strontium isotope ratios can be used to identify non-locally born individuals and to exclude certain areas of origin.

On the Panamanian isthmus, the weathering products of Cretaceous to Tertiary volcanic rocks as recorded in $^{87}Sr/^{86}Sr$ ratios of river water and soils between 0.7034 and 0.7053 (Harmon et al. 2016) and seawater (0.7092; Peucker-Ehrenbrink and Fiske 2019) form the endmembers of the biologically available strontium. Strontium isotope analyses of bones, teeth and shells of faunal remains from archaeological contexts in Panama exhibited $^{87}Sr/^{86}Sr$ ratios of between 0.7043 and 0.7089 with a tendency of higher values near the coasts and on some of the islands and lower values further inland (Sharpe et al. 2021). For Panamá Viejo, the study reports a value of 0.7085 for a bone of an opossum.

Oxygen isotopes are an independent parameter for the identification of non-local individuals. Hydroxyapatite, the mineral fraction of teeth and bones, contains oxygen in the structural carbonate (CO_3^{2-}) and in the phosphate ion (PO_4^{3-}) that can be used for isotope analysis (Chenery et al. 2012). In this paper, we present the $\delta^{18}O$ values for the oxygen incorporated in the phosphate ion ($\delta^{18}Op$). The isotope composition of the oxygen bound in human enamel reflects this parameter in meteoric water, which is taken up via drinking water and food. The main reason for spatial variation is isotope fractionation due to temperature, elevation, and distance from the coast (Bowen and Wilkinson 2002). At Panama Viejo, where temperatures are fairly constant and average 27 °C year-round, seasonal differences of the amount of precipitation with higher values in the dry season and lower values in the rainy season and during heavy storms, have a strong effect (Higgins and MacFadden 2004; IAEA/WMO 2016; Benway and Mix 2004; Kern et al. 2016). On the Panamanian Isthmus, annual averages of $\delta^{18}O$ values of precipitation and surface waters exhibit a remarkable variation, with decreasing values away from the Caribbean Coast and in higher elevation (Lachniet and Patterson 2006; Lachniet et al. 2007; Benway and Mix 2004). Sharpe et al. (2021) reported the first oxygen isotope data of the structural carbonate of human enamel from Panama. However, because the present study works with data of the phosphate fraction, the datasets are not unrestrictedly comparable.

The isotopic data reported here are a subset from a larger project. These data include strontium and oxygen isotope data regarding 25 individuals (7 pre-Hispanic and 18 colonial) who were also tested for starch and phytolith preservation in dental calculus. In addition, we determined the strontium isotope composition of two cattle and four pig teeth from colonial contexts. Based on these data, we differentiated between probable local and non-local individuals. In order to enlarge the dataset of carbon and nitrogen isotope values of local individuals, we also report the data of the teeth of three colonial individuals, who were not tested for starch and phytolith preservation but had Sr and O isotope data within the local ranges.

Many people who died in Panama Viejo were first-generation non-locals born in Africa or Europe. These individuals may have lived in Panamá for several years or sickened and died in Panama City on their way to (or from) Peru. Therefore, the carbon and nitrogen isotope composition of their bone collagen may reflect a mixture of foodstuffs from several places and dietary traditions. In order to characterize local dietary practices at Panama Viejo, this paper presents and discusses the data of the seven individuals from pre-Hispanic and ten individuals from colonial contexts whose strontium and oxygen isotope values agree with the data ranges that are typical for the Panamanian Isthmus. Collagen was preferably extracted from ribs (n = 13). Furthermore, the sample set includes pieces of a femur and of the skulls of three pre-Hispanic individuals, for whom no ribs were preserved. Animal bones from six cattle, six pigs and one chicken served as comparative samples.

Collagen extraction followed the method laid out by Longin (1971) with modifications as described in Knipper et al. (2017a). Mechanically cleaned bone samples were demineralized in 0.5 N HCl, rinsed, reacted with 0.1 M NaOH, rinsed again, gelatinized, filtered with EZEE filter separators, frozen, and lyophilized. C and N contents and the stable isotopic compositions were determined in triplicates using a vario PYRO cube CNSOH elemental analyzer (Elementar) and an isoprime precisION isotope ratios mass spectrometer at the Curt Engelhorn Center for Archaeometry in Mannheim, Germany. The raw data were calibrated against the international standards USGS 40 and USGS 41 or 41a using the IonOS software for stable isotope analysis. Interspersed quality control standards had the following isotope compositions: $\delta^{13}C$: IAEA-CH-6: −10.34 ± 0.11 ‰, IAEA-CH-7: −32.24 ± 0.07 ‰, USGS 43: −21.24 ± 0.06 ‰ and $\delta^{15}N$: IAEA-N-1: 0.44 ± 0.09 ‰, IAEA-N-2: 20.42 ± 0.07 ‰, USGS 43: 8.39 ± 0.08 ‰, each standard n = 33.

Strontium isotope analysis also was carried out at the Curt Engelhorn Center for Archaeometry Mannheim and followed previously described methods (Knipper et al. 2014; Knipper et al. 2017b). Enamel samples were cut and mechanically cleaned, ground, pre-treated with 0.1 M acetic acid buffered with Li-acetate (pH 4.5) in an ultrasonic bath, rinsed, and ashed. Sr separation with Eichrome Sr-Spec resin was carried out under clean-room conditions. Sr concentrations were determined by Optical Emission Spectrometry (ICP-OES iCAP 7200) and the isotope ratios by High-Resolution Multi-Collector Mass-Spectrometry (HR-MC-ICP-MS Neptune Plus). Raw data were corrected according to the exponential mass fractionation law to $^{88}Sr/^{86}Sr = 8.375209$. Blank values were lower than 10 pg Sr during the whole clean lab procedure. The NBS 987 standards yielded $^{87}Sr/^{86}Sr$ ratios of 0.71031 ± 0.00005, 2 σ; n = 7 (after ion exchange chromatography) and 0.71027 ± 0.00004, 2 σ; n = 39 (without ion exchange chromatography). The Eimer & Amend (E & A) standards run along with the samples yielded $^{87}Sr/^{86}Sr$ ratios of 0.70805 ± 0.00007, 2 σ; n = 20, respectively.

Oxygen isotope compositions were determined for the oxygen bound to the phosphate fraction ($\delta^{18}O_p$) of aliquots of the enamel powder separated during Sr isotope analyses. Sample preparation followed Knipper et al. (2014; 2017b; 2018). The enamel was pretreated with 2.5 % NaOCl, rinsed three times with suprapure water and reacted overnight with 800 µl of 2 M HF. After vortexing and centrifuging, the solutions were transferred into new sample tubes and the CaF residues left behind. After adding a few drops of bromothymol blue as a pH indicator, the HF was neutralized with about 140 µl of 25 % NH_4OH solution. The addition of 800 µl of 2 M $AgNO_3$ solution caused the dissolved phosphate ions to precipitate immediately as yellow Ag_3PO_4 crystals, which were rinsed five times and dried over-night at 50 °C. Ag_3PO_4 was analysed in triplicates using a vario PYRO cube CNSOH elemental analyzer (Elementar) in pyrolysis mode and a precisION isotope ratios mass spectrometer (Isoprime) at the Curt Engelhorn Center for Archaeometry Mannheim. Raw data were corrected against IVA silver phosphate with $\delta^{18}O$ = 21.7 ‰ (certificate no: BN 180097). Ag_3PO_4 that was precipitated from NBS 120c prepared along with the samples gave $\delta^{18}O$ values of 22.10 ± 0.21 ‰ (1 SD). The IAEA 601 standard yielded an average value of 22.59 ± 0.57 ‰, the in-house standards of synthetic hydroxyapatite (HAP) gave 17.09 ± 0.17 ‰ and Roman pig bones from the site of Dangstetten (SUS-DAN) gave 14.37 ± 0.23 ‰; all standard n = 24. The $\delta^{18}O$ values of the standard substances are in agreement with published data by other research groups (Pellegrini et al. 2016; Sisma-Ventura et al. 2018).

5. Results

5.1. Starch grains and phytoliths

The processing of dental calculus led to the observation of phytoliths, vegetable fibers, microcarbons, calcium oxalates and pollen grains, as well as starch grains. Starches were identified in samples from 28 local and non-local individuals associated with each of the different temporal contexts: pre-Hispanic, roughly 600–1450 CE (7), early colonial, 1519–1541 (6), mid-colonial, 1542–1626 (5), and later colonial, 1627–1671 (6). In addition, 4 individuals recovered from the Cathedral's Atrium, c. 1600–1671, were sampled (see Table 1).

A total of 23 starches were recognized in the pre-Hispanic samples and 37 in dental calculus from colonial individuals, 20 of the later with probable European and/or African ancestry, according to the bioarchaeological analyses. The strontium and oxygen isotope data obtained for 18 of the 37 colonial individuals sampled for dental calculus (see below), indicate non-local (probably African or European) origins for 11 of these colonial individuals. The remaining seven individuals sampled for isotope analyses exhibited isotope data that agree with the respective ranges of the Panamanian Isthmus (Table 1).

Maize (*Zea mays*) proved the plant most frequently identified through starch grains analysis in the pre-Hispanic as well as the colonial populations. Maize starches (Fig. 5, e-g), characterized by a medium size (10–20 µm), appear polyhedral, angular, multifaceted, and in many cases (28) with a fissured *hilum*, one of their most conspicuous characteristics.

After maize, wheat constituted the second most representative plant consumed by Panama Viejo's colonial population. Starch recovery identified 13 particles of Triticeae, a branch of the Poaceae family, which includes the genera *Triticum* and *Hordeum,* corresponding to wheat and barley (Barkworth and Von Bothmer 2009). Since numerous historical sources describe the importation of wheat to Panama and none of them mentions barley, we attribute these starches to wheat flour. Significantly, wheat starches were associated with local and non-local individuals of probable European, African, and unidentified ancestries (Table 1, Fig. 5, a-d; Table 2, Fig. 7).

Three of the starches recovered were identified as yuca (*Manihot*

Table 1
Starches and phytoliths detected in dental calculus.

						Starches										
Context	UE	Chronology	Sex	Age	Ancestry	Maize	Bean	Plantain	Squash	Achira	Yucca	Arrowroot	Wheat	Pulses	Phytolith	Unidentified
PAPV_7	106	600-1450	F	35-55	Am	7										4
PAPV_8	110	600-1450	M	35-55	Am									1		
PAPV_8	112	600-1450	M	35-55	Am	1										
PAPV_8	118	600-1450	M	18-34	Am											1
PAPV_10	143	600-1450	U	18-34	Am	11					1					7
PAPV_10	146	600-1450	M	18-34	Am	2					1					1
PAPV_10	167	600-1450	M	35-55	Am	2								1		2
PAPV_4	20	1519-1541	M	18-34	E	2										
PAPV_4	27	1519-1541	F	18-34	Am	10				1		1				1
PAPV_4	4012	1519-1541	U	7-12	U								1		Pan	8
PAPV_4	4015	1519-1541	M	18-34	E/Am	1							1			
PAPV_4	4021	1519-1541	U	13-18	A/Am	3							1		Pan	15
PAPV_4	4022	1519-1541	F	18-34	Am							1	1			5
PAPV_5_1	1082	1542-1626	F	18-34	A/E										Chlo	2
PAPV_5_1	1086	1542-1626	M	18-34	Am/E								1		Pan	1
PAPV_5_1	1087	1542-1626	F	35-55	A	1	1				1				Rice	3
PAPV_5_1	1110	1542-1626	F	18-34	E/A											2
PAPV_5_1	1114	1542-1626	M	18-34	E/A				1							1
PAPV_5_1	1117	1542-1626	M	35-55	A								2			
PAPV_5_1	1129	1542-1626	F	18-34	E											
PAPV_5_1	1134	1542-1626	F	18-34	E								2			
PAPV_5_1	1135	1542-1626	M	18-34	E										Pan/Rice	1
PAPV_5_1	1180	1542-1626	F	18-34	A							2			Pan/Rice/Arun	
PAPV_5_1	53	1627-1671	F	35-55	U	3							1			3
PAPV_5_2	55	1627-1671	F	18-34	E	2							1			1
PAPV_5_1	1019	1627-1671	F	18-34	E			1								1
PAPV_5_1	1028	1627-1671	F	18-34	A/Am								1			
PAPV_5_1	1042	1627-1671	F	35-55	A	1	1								Pan	
PAPV_5_1	1047	1627-1671	F	18-34	A/E									1		1
PAPV_5_1	1049	1627-1671	F	35-55	A	1										
PAPV_5_1	1055	1627-1671	F	18-34	A/E		1									
PAPV_5_1	1066	1627-1671	F	18-34	A/Am											1
PAPV_5_1	1073	1627-1671	M	18-34	A				2							1
PAPV_5_1	1078	1627-1671	F	35-55	E/A	1										
PAPV_5_1	61	1600-1671	F	35-55	A	2									Palm	2
PAPV_5_1	62	1600-1671	F	18-34	E/A	2										
PAPV_5_2	2008	1600-1671	M	35-55	E/A								1			
PAPV_5_2	2009	1600-1671	F	18-34	A	1										1
PAPV_5_2	2012	1600-1671	U	18-34	E	1							1		Arun/Chlo	1
PAPV_5_2	2013	1600-1671	F	18-34	A	2										2
Total						56	3	1	3	1	3	4	14	3		66

Maize (*Zea mays*), Bean (*Phaseolus*), Yam (*Dioscorea* spp.), Squash (*Cucurbita* spp.), Achira (*Canna cf. Edulis*), Yuca (*Manihot esculenta*), arrowroot (*Maranta arundinace*), Wheat (*Triticeae*), Pulses (*Fabaceae*). UE. stratigraphic unit. Archaeological Contexts: PAPV_10-Morelos, PAPV_7-Visitor Center, PAPV_8- South Main Square, PAPV_3-Southeast Main Square, PAPV_5_1- Cathedral's nave, PAPV_5_2- Cathedral's atrium. Sex: F-Female, M-Male. Ancestry: Am-Amerindian, A-African, E-European, Am/E-Predominantly Amerindian with European traits, A/Am-Predominantly African with Amerindian traits, A/E-Predominantly African with European traits, E/Am-Predominantly European with Amerindian traits, E/A-Predominantly European with African traits, U-Unidentified

*Pan: Panicoideae; Arun: Arundinoideae; Chlo: Chloridoideae

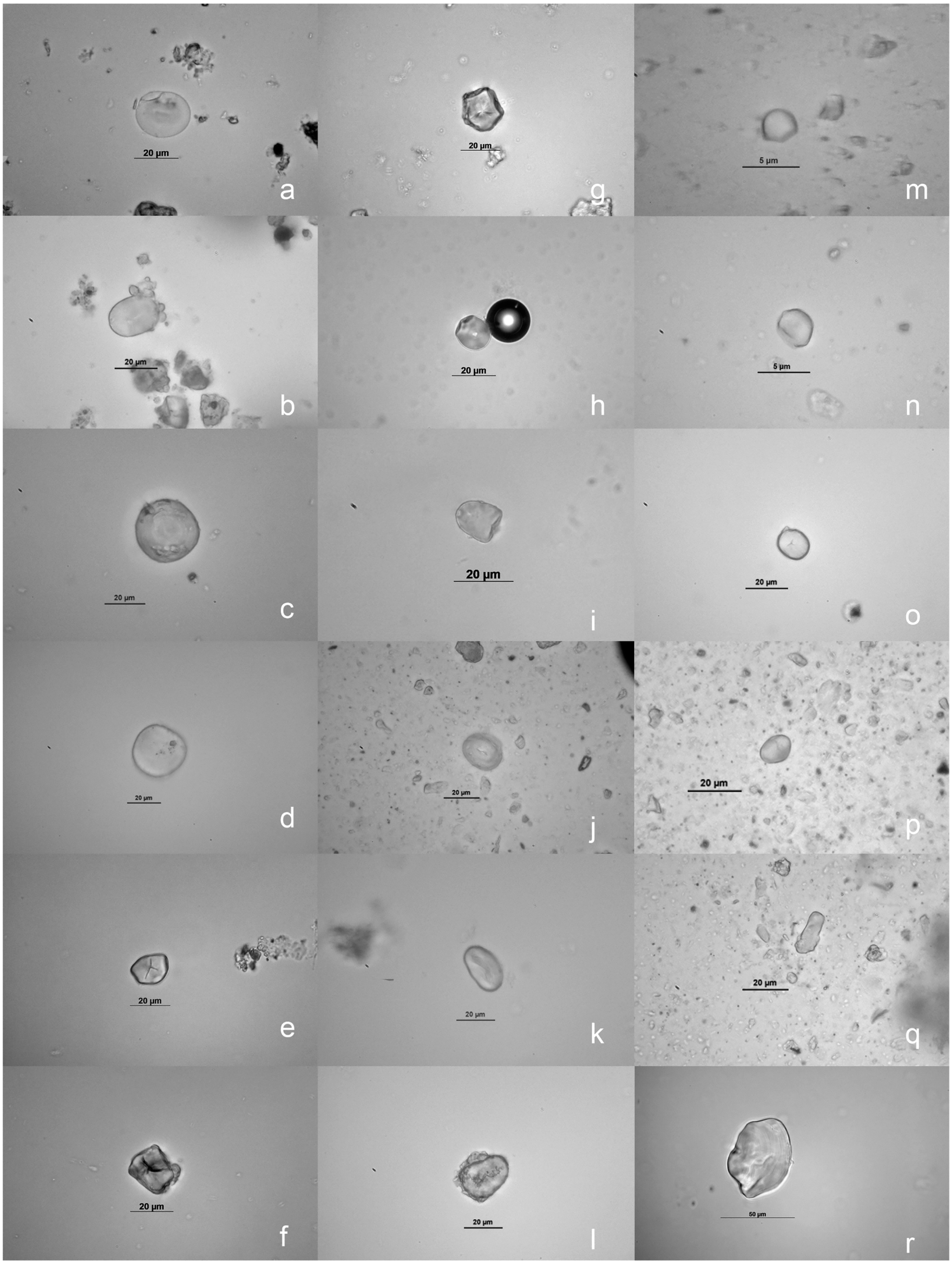

Fig. 5. Starches identified for wheat, maize, yuca (manioc), bean, squash, arrowroot, yam.

esculenta), with two of these corresponding to pre-Hispanic samples (Fig. 5 g) and the third from a mid-colonial individual of probable African ancestry (UE 1087) (Table 1, Fig. 5 c). Yuca starches are medium-sized (10–20 μm) in the shape of a bell, with a central *hilum* and a uni- or bi-faceted crown (Fig. 5, h-i).

The bean (*Phaseolus cf vulgaris*) has been identified in three oval-shaped and large (greater than20 μm) starch particles with visible *lamellae*, longitudinal fissures and the four-armed, blade-shaped cross of Malta that is a diagnostic feature of the *Phaseolus* genre (Fig. 5, j-l). These three microfossils are associated with mid and late-colonial individuals of probable African (UE 1042, 1087) and mixed Afro-European (UE 55) ancestry. Indeed, UE 1042′s Sr and O isotope compositions point to a non-local origin.

A starch particle diagnosed as achira (*Canna* cf. *Indica*) was also

Table 2
Oxygen and strontium isotope data of the human individuals investigated in this study. The teeth are numbered according to the FDI World Dental Federation notation.

Context	UE	Chronology	Sex	Age	Ancestry	Starches	Phytoliths	**Tooth 1**	**δ^{18}Op [‰ V-SMOW]**	**SD**	**^{87}Sr/^{86}Sr**	**2 SD**	**Tooth 2**	**δ^{18}Op [‰ V-SMOW]**	**SD**	**^{87}Sr/^{86}Sr**	**2 SD**	**Interpretation**
PAPV_7	106	800–1200	F	35–55	Am	Maize, Indet.		Tooth 17			0.70849	0.00003						local/regional
PAPV_8	110	800–1200	M	35–55	Am	Pulses		Tooth 16			0.70834	0.00001	Tooth 24			0.70846	0.00002	local/regional
PAPV_8	112	800–1200	M	35–55	Am	Maize		Tooth 36			0.70602	0.00003	Tooth 38			0.70608	0.00003	local/regional
PAPV_8	118	800–1200	M	18–34	Am	Indet.		Tooth 36			0.70734	0.00002	Tooth 18			0.70577	0.00002	local/regional
PAPV_10	143	800–1200	U	18–34	Am	Maize, Yucca, Indet.		Tooth 28			0.70536	0.00001						local/regional
PAPV_10	146	800–1200	M	18–34	Am	Maize, Yucca, Indet.		Tooth 38			0.70792	0.00003						local/regional
PAPV_10	167	800–1200	M	35–55	Am	Maize, Pulses, Indet		Tooth 28			0.70810	0.00002						local/regional
PAPV_4	20	1519–1541	M	18–34	E	Maize		Tooth 36	18.39	0.14	0.71402	0.00002	Tooth 38	17.04	0.11	0.71336	0.00001	non-local
PAPV_4	27	1519–1541	F	18–34	Am	Maize, Arrowroot, Indet		Tooth 26	18.73	0.19	0.71109	0.00002	Tooth 28	18.50	0.06	0.71042	0.00001	non-local
PAPV_4	4012	1519–1541	U	7–12	U	Wheat, Indet.	Maize	Tooth 16	17.10	0.13	0.70835	0.00003	Tooth 28	17.34	0.14	0.70747	0.00003	local/regional
PAPV_4	4015	1519–1541	M	18–34	E/Am	Maize, Wheat		Tooth 46	16.99	0.11	0.70472	0.00001	Tooth 38	17.56	0.10	0.70446	0.00002	local/regional
PAPV_4	4021	1519–1541	U	13–18	A/Am	Maize, Arrowroot, Indet	Maize	Tooth 46	16.97	0.03	0.70703	0.00003	Tooth 48	16.55	0.08	0.7068	0.00001	local/regional
PAPV_4	4022	1519–1541	F	18–34	Am	Arrowroot, Wheat, Indet.		Tooth 36	17.69	0.13	0.70703	0.00002	Tooth 38	17.16	0.11	0.70462	0.00002	local/regional
PAPV_5_1	1082	1542–1626	F	18–34	A/E	Indet.	Chloridoideae	Tooth 26	20.72	0.02	0.71582	0.00002	Tooth 28	19.72	0.15	0.71482	0.00003	non-local
PAPV_5_1	1086	1542–1626	M	18–34	Am/E	Wheat, Indet	Maize	Tooth 16	21.06	0.08	0.71248	0.00001	Tooth 28	21.04	0.13	0.71238	0.00004	non-local
PAPV_5_1	1135	1542–1626	M	18–34	E	Indet.	Maize, Rice	Tooth 36	20.24	0.20	0.72707	0.00003	Tooth 38	20.58	0.15	0.72681	0.00001	non-local
PAPV_5_1	1180	1542–1626	F	18–34	A	Arrowroot	Maize, Rice, Palm, Arundinoideae	Tooth 16	19.90	0.02	0.71914	0.00001	Tooth 28	20.04	0.12	0.72005	0.00002	non-local
PAPV_5 (Catedral 2017 - Nave PVCA-1)	1102	1600–1626	F	18–35	A/E	Not analyzed		Tooth 26	17.56	0.15	0.70512	0.00001	tooth 18	17.77	0.10	0.70647	0.00001	local/regional
PAPV_5_1	53	1627–1671	F	18–34	U	Wheat, Indet		Tooth 46	21.13	0.17	0.71083	0.00001	Tooth 48	21.66	0.08	0.71065	0.00002	non-local
PAPV_5_2	55	1627–1671	F	18–34	E	Wheat, Indet		Tooth 36	17.31	0.11	0.70709	0.00002	Tooth 38	17.72	0.13	0.70758	0.00001	local/regional
PAPV_5_1	1042	1627–1671	F	35–55	A	Maize, Bean		Tooth 26	18.45	0.10	0.70976	0.00001	Tooth 28	18.45	0.30	0.70968	0.00002	non-local
PAPV_5_1	1046	1627–1671	F	18–34	A/E	Maize	Maize	First molar	17.82	0.15	0.70892	0.00001	Tooth 17	18.24	0.17	0.70905	0.00001	local/regional
PAPV_5_1	1049	1627–1671	F	35–55	A	Maize		Tooth 16	17.93	0.08	0.70796	0.00001	Tooth 18	17.95	0.13	0.70778	0.00001	local/regional
PAPV_5_1	61	1600–1671	F	18–34	A	Maize, Indet.		Tooth 16	19.62	0.22	0.71261	0.00002	Tooth 38	19.69	0.05	0.71275	0.00001	non-local
PAPV_5_1	62	1600–1671	F	18–34	E/A	Maize		Tooth 16	19.00	0.12	0.71109	0.00003	Tooth 18	19.09	0.26	0.71113	0.00001	non-local
PAPV_5_2	2008	1600–1671	M	35–55	E/A	Wheat		Tooth 46	19.45	0.16	0.71218	0.00003	Tooth 38	20.15	0.18	0.71298	0.00001	non-local
PAPV_5 (Catedral 2000 - Nave-Oeste)	54	1626–1671	M	18–35	E	Not analyzed		Tooth 16	17.42	0.06	0.70713	0.00001	Tooth 17	17.18	0.16	0.70754	0.00001	local/regional
PAPV_5 (Catedral 2017 - Nave PVCA-1)	1044	1627–1671	mM	18–36	Am	Not analyzed		Tooth 26	17.78	0.04	0.70584	0.00002	Tooth 18			0.70685	0.00001	local/regional

recovered from an early colonial sample associated with a non-local female individual of probable indigenous ancestry (Table 1, UE 27). The achira starch granule is flat, with large dimensions (greater than30 μm), an excentric *hilum*, and visible *lamellae* (Fig. 5 r).

Starches associated with new taxons recovered from colonial samples also included: a) pumpkin or squash (*Cucurbita* cf *moschata*) (#3), b) plantain or banana (Musa spp) (#1); and c) arrowroot (#3, UE 4022, 1180) (*Maranta arundinacea*). Starch particles from squash are medium-sized (10–20 μm) and bell-shaped, with simple crowns. The three microfossils identified as squash entailed a medium, spherical granule, with a small depression on one edge, which is a trait found in present-day squash. The squash-like particles recovered proceeded from the dental calculus of one mid and one later colonial individual (UE 1073, 1114) identified, respectively, as having probable African and mixed Afro-European ancestry (Fig. 5 m-n). Another starch granule recovered of medium size, elongated with sub-rounded extreme sides (up and down) and an exocentric *hilum,* similar to the plantain starches (Fontes et al., 2017; Mesquita et al. 2016) was found associated with a later colonial female of probable European ancestry (UE 1019) (Fig. 5 q). Finally, arrowroot (*Maranta arundinacea*) was identified by its globular grain, exocentric and fissured *hilum*, and associated with an early colonial female of probable Indigenous ancestry (UE-4022) (Fig. 5 o-p), with local Sr and O isotope ratio.

As further evidence of plant consumption, we also recovered phytoliths from the dental calculus sampled. These included bi-lobed phytoliths associaded with *Panicoidae* (Fig. 6, a-b), a subfamily of the graminea to which maize belongs. These phytoliths were identified in the dental starch of six individuals from all of the colonial periods, two of them with probable African ancestry (UE 4012, 4021, 1180, 1135, 1086, 1046). Three phytoliths recovered, tentatively identified as rice (Oryza spp –Oryzeae-) are bulliform and larger than 10 μm, showing fish-scale-decorations and the scalloped lateral border common to bulliform rice phytoliths (Lautaro et al., 2017; Wang et al., 2019; Zhang et al., 2010) (Fig. 6 c-e). These three samples pertain to the colonial period, two of them being associated with individuals identified as having probable African ancestry, buried 1542–1626 (UE 1180 and 1087) and another with probable European ancestry, interred after 1627 (UE 1135). The Sr and O isotope values of the teeth of the individuals UE 1135 and 1180 are above the ranges that are typical on the Panamanian Isthmus and even the Iberian Peninsula, suggesting that these individuals may have grown up at different places on the African continent. This observation supports the argument that Europeans and Africans introduced African rice (*Oryza glaberrima*) to the region during the colonial period (Aram and García Falcon 2021). A palm phytolith (*Arecaceae*) was also recovered from the dental calculus of one of the same individuals (UE 1180), a non-local female with probable African ancestry buried in the second half of the sixteenth century. Finally, we recovered 3 *Arundinoideae* (UE 2012, 1180) and 2 *Chloridoideae* (UE 2012, 1082) phytoliths, although edible plants are associated with neither subfamily of graminea.

5.2. Strontium, oxygen, carbon and nitrogen isotope data

The strontium isotope ratios of the teeth of the seven pre-Hispanic individuals ranged from 0.70536 to 0.70849 (Table 2; Fig. 7). The difference between the isotope ratios of a first and a third molar was very small (<0.0002) in two cases and larger (0.00157) in one case, suggesting a possible residential move during childhood. Of the three other individuals, we sampled only one tooth.

The colonial individuals revealed much more heterogeneous $^{87}Sr/^{86}Sr$ ratios ranging from 0.70446 to 0.72707. Most pairs of early and late forming teeth exhibited very similar $^{87}Sr/^{86}Sr$ values (differences < 0.001). Exceptions were the individuals 1102, 1082 and 4022 with differences of greater than 0.001. The data ranges of the individuals from the earlier colonial phase (1519–1541; 0.70446–0.71402), the middle colonial phase (1542–1626; 0.70512–0.72707), and the later colonial phase (1627–1671; 0.70709–0.71298) overlapped widely. The individuals 1180 and 1135 stand out as their teeth contained strontium with remarkably more radiogenic $^{87}Sr/^{86}Sr$ ratios of above 0.72000. The enamel of the cattle and pig teeth exhibited $^{87}Sr/^{86}Sr$ ratios of between 0.70418 and 0.70816 without a clear distinction between both species (Table 3).

Oxygen isotope data, which are only available for the individuals of the colonial period, ranged from 16.55 to 21.66 ‰ V-SMOW (Table 2). In two cases, the earlier forming M1 had a more than 1 ‰ higher $\delta^{18}O$ value than the later forming M3, whereas the differences between samples from the same individuals were smaller in all other cases. Higher values in enamel of early forming teeth in the order of magnitude observed here likely reflect isotope fractionation of breast milk taken up in infancy (Knipper et al. 2018).

Regarding the differentiation between possibly locally and non-locally born individuals, we note that the $^{87}Sr/^{86}Sr$ ratios of all samples of the pre-Hispanic human teeth and the animal teeth revealed $^{87}Sr/^{86}Sr$ ratios of between 0.7092, the value of seawater, and the isotopic range of modern river water sampled from the Panamanian isthmus (Harmon et al. 2016). The data overlap with those of humans and animals from several sites on the Panamanian isthmus, including one value of a bone of an opossum from Panama Viejo itself (Sharpe et al. 2021). We acknowledge that some of the pre-Hispanic human teeth and the colonial animal teeth may represent strontium from the wider region instead of being confined to the site of Panama Viejo and its immediate surroundings. Sharpe et al. (2021) report evidence for residential mobility among the pre-Hispanic population on the Panamanian isthmus and Castillero (2010b, 111) maps the main regions for stock raising in 1609 along the Pacific coast between Panama Viejo and the Azuero Peninsula, as well as further to the west. Because the dietary catchment of the inhabitants of the colonial town extended well beyond its immediate surroundings, we cannot distinguish between isotopic data that potentially reflect the site of Panama Viejo itself and those from the Panamanian isthmus in general. We, therefore, consider all individuals with $^{87}Sr/^{86}Sr$ ratios below 0.7092 (the value of seawater) as possibly local, without differentiation between the site itself and its hinterlands. The comparatively similar $\delta^{18}O$ values (16.55 – 18.24‰) of all individuals with $^{87}Sr/^{86}Sr$ ratios below 0.7092 support their designation as local or regional (cf. grey area in Fig. 7).

We limited the evaluation of the carbon and nitrogen isotope data to the individuals with teeth whose Sr and O isotope compositions signify their probable local or regional origin. They include all seven pre-Hispanic individuals as well as ten samples from the colonial period, among which four represent the earlier, one the middle and five the later section (Table 4).

Most samples fulfilled the criteria for good collagen preservation with between 2.0 and 11.4 % of collagen, which comprised between 27.8 and 43.2 % carbon, 10.0 and 15.3 % nitrogen and had atomic C/N ratios of 3.2 to 3.5 (van Klinken 1999). The data from the pre-Hispanic individual 110 were excluded from evaluation, since his collagen exhibited an atomic C/N ratio of 3.7. The animal bones yielded between 2.8 and 14.3 % of collagen, 15.5 and 42.7 % of carbon and 5.5 and 15.3 % of nitrogen and had atomic C/N ratios of 3.2 to 3.5. Because their atomic C/N ratios were below 3.6, we included all samples in our evaluation.

Even though the strontium and oxygen isotope data attest to a local or regional origin of the individuals discussed here, the isotopic compositions of carbon and nitrogen in their bone collagen are highly variable (Table 4, Fig. 8). The pre-Hispanic individuals had $\delta^{13}C$ values of −10.9 to −8.2 ‰ (avg. −9.5 ± 1.0 ‰) and $\delta^{15}N$ values of 8.1 to 14.8 ‰ (avg. 11.8 ± 2.7 ‰; n = 6). The C and N isotope data of the samples of the earlier phase of the colonial period varied in about the same range with $\delta^{13}C$ values of −12.3 to −7.8 ‰ (avg. −9.9 ± 1.9 ‰) and $\delta^{15}N$ values of 7.7 to 13.3 ‰ (avg. 10.0 ± 2.7 ‰; n = 4). The five individuals of the later phase of the colonial period appeared to have slightly lower $\delta^{13}C$ values −13.2 to −9.2 ‰ (avg. −11.2 ± 1.4 ‰) and remarkably

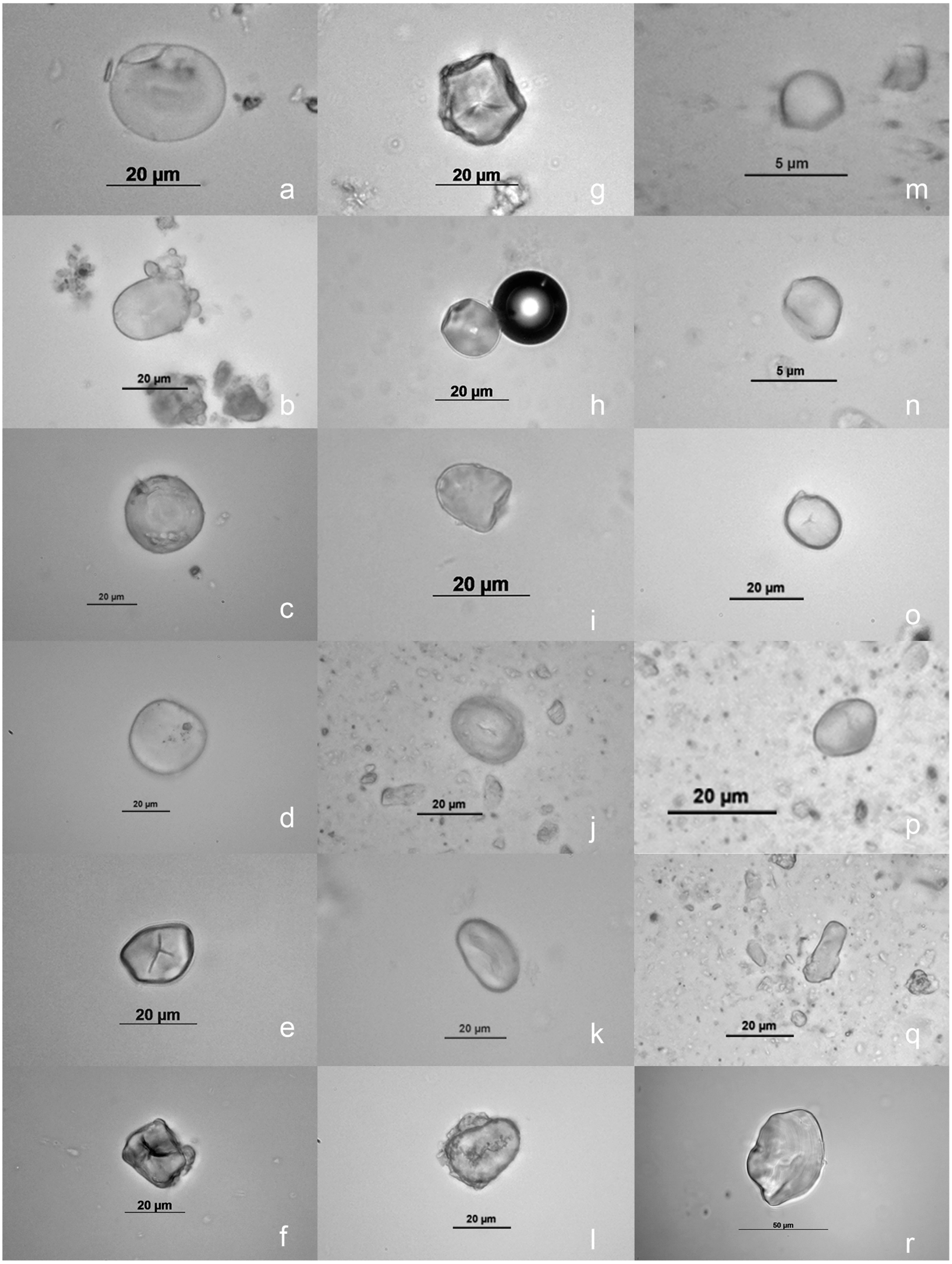

Fig. 6. Phytoliths identified for maize, rice and palm.

homogeneous δ^{15}N values with a similar average (10.5 to 11.1 ‰, avg. 10.73 ± 0.25). The only sample of the middle phase of the colonial period classified as local or regional based on its Sr and O ratios falls into the data cluster of the later colonial phase.

Among the animal samples, the cattle revealed higher and less variable δ^{13}C values (-12.5 to −6.9 ‰; avg. −9.1 ± 2.3 ‰) than the pigs (-18.5 to −7.8 ‰; avg. −13.4 ± 3.6 ‰), whereas the nitrogen isotope data of both species were similar with slightly less variation among the samples of the pigs (cattle: 4.0 to 7.8, avg. 5.8 ± 1.5 ‰; pigs: 4.7 to 7.1, avg. 5.9 ± 0.8 ‰). The collagen of the chicken revealed a higher δ^{15}N value (9.5 ‰) than the cattle and pigs and the second highest δ^{13}C value (-6.7 ‰) of all samples of this study (Table 5; Fig. 8).

The very wide range of δ^{13}C values of the animals attests to highly variable average forage. While some pigs were mainly fed C_3 plants that

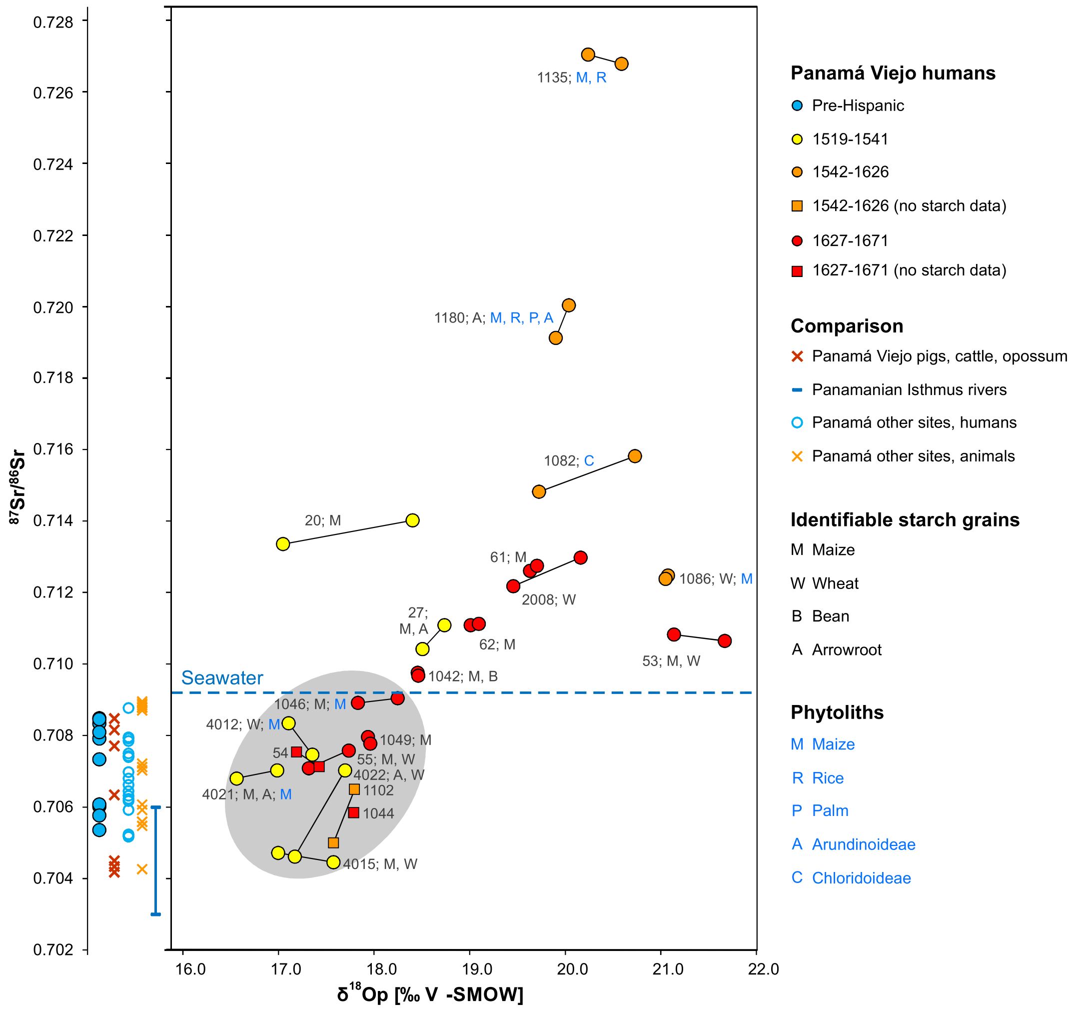

Fig. 7. Scatter plot of oxygen and strontium isotope data of the human teeth from the pre-Hispanic and colonial periods at Panama Viejo. Strontium isotope ratios are also plotted for pre-Hispanic human and colonial animal teeth from Panama Viejo (this study), human and animal teeth from different sites (Sharpe et al. 2021) as well as river water (total range between minimal and maximal values; Harmon et al. 2016) on the Panamanian isthmus. Lines connect data from the same individuals, letters are abbreviations for food crops identified by starch grains (black) and phytoliths (blue). The grey ellipse highlights the local ranges of the isotope compositions of the biologically available strontium and oxygen. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Strontium isotope ratios of domestic animal teeth from the colonial context of the Hospital San Juan de Dios in Panama Viejo.

Context	Species	Age	Tooth	$^{87}Sr/^{86}Sr$	2 SD
Hospital San Juan de Dios	Sus scrofa domesticus	Subadult-adult	Upper M3	0.70771	0.00002
Hospital San Juan de Dios	Sus scrofa domesticus	Adult	Upper M3	0.70450	0.00002
Hospital San Juan de Dios	Sus scrofa domesticus	Adult	Upper M3	0.70418	0.00002
Hospital San Juan de Dios	Sus scrofa domesticus	Infantile	Deciduous premolar	0.70816	0.00002
Hospital San Juan de Dios	Bos taurus	Infantile	Deciduous premolar	0.70434	0.00003
Hospital San Juan de Dios	Bos taurus	Infantile	Deciduous premolar	0.70634	0.00003

formed the natural vegetation at Panamá, others lived almost exclusively on C_4 plants, which indicates feeding of maize, a cultivated plant that did not belong to Panama's natural vegetation (Sugiyama et al. 2020). The average contribution of maize to the forage of cattle was even larger than observed for pigs, with four of six samples revealing an almost pure C_4 plant signal (cf. Szpak et al. 2016, Fig. 1).

The stable isotope data of the humans in general indicate that foodstuffs with high $\delta^{13}C$ values, such as maize, marine fish and seafood, or meat and dairy products of animals that fed on maize made up significant portions of their diet. In most pre-Hispanic and some early colonial samples, the contributions of C_3 plants to the carbon sourced from proteins is almost invisible. The $\delta^{13}C$ values generally become lower with the greater impact of plantains and rice as well as imported wheat in the seventeenth century. C_3 plants include squash, beans and tropical fruits that are native to Panamá, rice and plantains that flourished there and cereals that needed to be imported.

The data from the pre-Hispanic individuals attest to diets that were based on maize with highly variable contributions of marine fish and seafood. The values overlap with those of previously published pre-Hispanic human samples (Sharpe et al. 2021) and attest to – on average – even larger shares of maize and/or marine food sources

Table 4
Bone samples of human individuals of local or regional origin at Panama Viejo based on the oxygen and strontium isotope composition of their teeth along with information on collagen yields, nitrogen and carbon contents, as well as the isotope composition of both elements. The analytical data for UE 110 are crossed out as the atomic C/N ratio is just above the cutoff for well-preserved collagen.

Context	UE	Chronology	Sex	Age	Ancestry	Starches	Phytoliths	Skeletal element	Collagen yield [%]	**N [%]**	**C [%]**	**atomic C/N**	**$\delta^{15}N$ [‰ AIR]**	**$\delta^{15}N$ [‰ AIR] SD**	**$\delta^{13}C$ [‰ V-PDB]**	**$\delta^{13}C$ [‰ V-PDB] SD**
PAPV_7	106	800–1200	F	35–55	Am	Maize, Indet.		Rib	6.5	14.9	41.2	3.2	14.04	0.02	−9.24	0.07
PAPV_8	110	800–1200	M	35–55	Am	Pulses		Skull	~~1.3~~	~~12.6~~	~~40.4~~	~~3.7~~	~~9.47~~	~~0.08~~	~~−10.81~~	~~0.05~~
PAPV_8	112	800–1200	M	35–55	Am	Maize		Skull	4.2	14.3	43.2	3.5	8.11	0.03	−10.23	0.10
PAPV_8	118	800–1200	M	18–34	Am	Indet.		Skull	4.6	9.9	27.7	3.3	9.17	0.07	−8.45	0.12
PAPV_10	143	800–1200	U	18–34	Am	Maize, Yucca, Indet.		Femur	8.5	15.1	41.6	3.2	12.56	0.04	−8.21	0.01
PAPV_10	146	800–1200	M	18–34	Am	Maize, Yucca, Indet.		Rib	2.7	15.3	42.2	3.2	14.78	0.07	−10.91	0.07
PAPV_10	167	800–1200	M	35–55	Am	Maize, Pulses, Indet		Rib	3.8	15.2	41.8	3.2	12.12	0.02	−9.72	0.20
PAPV_4	4012	1519–1541	U	7–12	U	Wheat, Indet.	Maize	Rib	8.9	15.2	41.9	3.2	9.79	0.00	−10.26	0.02
PAPV_4	4015	1519–1541	M	18–34	E/Am	Maize, Wheat		Rib	4.2	15.3	42.2	3.2	7.73	0.03	−12.25	0.04
PAPV_4	4021	1519–1541	U	13–18	A/Am	Maize, Arrowroot, Indet	Maize	Rib	4.4	15.0	42.0	3.3	9.23	0.08	−7.78	0.05
PAPV_4	4022	1519–1541	F	18–34	Am	Arrowroot, Wheat, Indet.		Rib	2.7	14.7	41.2	3.3	13.34	0.01	−9.43	0.05
PAPV_5 (Catedral 2017 - Nave PVCA-1)	1102	1600–1626	F	18–35	A/E	Not analyzed		Rib	3.5	14.9	42.1	3.3	11.11	0.05	−12.66	0.02
PAPV_5_2	55	1627–1671	F	18–34	E	Wheat, Indet		Rib	5.7	13.6	41.4	3.5	10.63	0.03	−13.15	0.13
PAPV_5_1	1046	1627–1671	F	18–34	A/E	Maize	Maize	Rib	11.4	15.2	42.2	3.2	10.60	0.06	−10.97	0.03
PAPV_5_1	1049	1627–1671	F	35–55	A	Maize		Rib	1.9	12.5	36.4	3.4	11.14	0.07	−11.36	0.00
PAPV_5 (Catedral 2000 - Nave-Oeste)	54	1626–1671	M	18–35	E	Not analyzed		Rib	7.9	15.0	41.6	3.2	10.50	0.02	−11.29	0.03
PAPV_5 (Catedral 2017 - Nave PVCA-1)	1044	1627–1671	mM	18–36	Am	Not analyzed		Rib	10.8	15.1	42.1	3.3	10.75	0.05	−9.20	0.03

(Fig. 8). The similar data ranges of the human samples of the earlier colonial phase (1519–1541) imply a continuation of the consumption of highly variable food sources, ranging from diets based on a mix of C_3 and C_4 plants with little contribution of meat and seafood to a probable dominance of marine foodstuffs among the protein sources of the human diet. The data argue for a continuation of the use of very different food sources and against immediate standardization with the establishment of the colonial city.

On the other hand, dietary strategies appear to have changed by the later colonial period (1627–1671), in which average protein sources appear to have become more homogeneous. Still, the contribution of C_3 and C_4 plants varied – either consumed directly or taken up indirectly via meat and dairy products from animals, for which the data attest to a remarkable diversity of $\delta^{13}C$ values. The lower average of the $\delta^{13}C$ values of the human collagen, however, points to an increase of the importance of C_3 plants in the human diet, such as rice, wheat or pulses. Squash, yuca (manioc) and bananas (plantains) are also C_3 plants, but contain less protein and therefore have a limited influence on the stable isotope composition of the human collagen.

In light of the overall variation of the different data groups in this study, the $\delta^{15}N$ values of the humans of the later colonial samples appear very homogeneous. Moreover, the values are just above the average of the values to be expected for mammals that are one trophic level above the cattle and pigs sampled in this study. This observation suggests that meat contributed significantly to the protein fraction of the human diet. Especially both kinds of isotope ratios of the pigs are in good agreement with data expected for animals that are one trophic level below the humans. At first glance, this observation seems to be in contrast to the historical sources that attest to beef being the cheapest source of calories in the human diet (Castillero 2010a,b, 109–117). However, the average $\delta^{15}N$ values of the collagen of cattle and pigs are almost identical. The ranges of $\delta^{13}C$ values of cattle and pigs overlap and we do not know whether the distribution of values of cattle collagen observed among our samples is representative of the meat and dairy products that the humans in historical Panama actually consumed. Moreover, concluding that a single food source, such as pork, dominated the human diet would be too simplistic. The starch and phytolith data of the human calculus provide direct evidence of the consumption of plant food. Furthermore, the average $\delta^{15}N$ values of the animal bones sampled in this study are not high enough to explain the human nitrogen isotope data with only the predominance of herbivore meat in the average diet. Instead, these data support the inference of a mixed human diet that also included food sources with higher $\delta^{15}N$ values, such as marine fish and seafood or chicken. Such protein sources appear even more relevant if we consider that plant-based foodstuffs (with lower $\delta^{15}N$ values) were part of the human diet, as it is evidenced by the starch grains and phytoliths incorporated in the dental calculus of distinct individuals.

In many central European contexts, manuring of arable plots has been shown to raise the $\delta^{15}N$ values of the soil and the plants grown on them, so that the consumption of such crops becomes hard to distinguish from the meat of animals that foraged on unmanured plots (Bogaard et al. 2013; Knipper et al. 2020). In Panamá, the $\delta^{15}N$ values of the cattle and pigs are similar to those of deer (Sugiyama et al. 2020), which represent a non-anthropogenic environment. This observation is also valid for samples of domesticated animals whose high $\delta^{13}C$ values indicate feeding on maize and therefore in an anthropogenically influenced landscape. Unlike many European contexts, in which $\delta^{13}C$ values do not distinguish natural and anthropogenic C_3-vegetation and $\delta^{15}N$ values of domesticated herbivores should not be taken to infer the isotope composition of the plant component of the human diet (Bogaard et al. 2013; Hedges and Reynard 2007; Knipper et al. 2017a), in Panama, samples of cattle and pigs with high $\delta^{13}C$ values of around −8 ‰, likely reflect the $\delta^{15}N$ values of a maize-dominated diet. Even though we do not have direct evidence of the isotope composition of maize, the data from the colonial animals sampled indicate that manuring of arable plots did not raise the $\delta^{15}N$ values of maize to be high enough to explain the elevated $\delta^{15}N$ values of human collagen by anthropogenic influence on the arable plots, so that the consumption of such crops likely caused an increase of human $\delta^{15}N$ values.

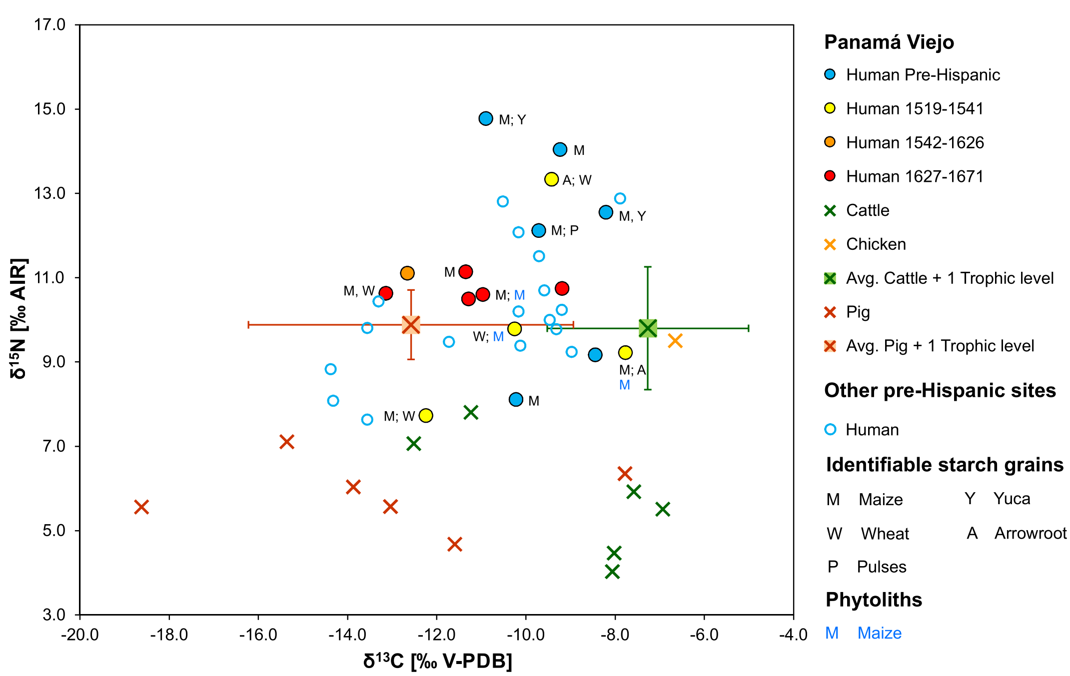

Fig. 8. Scatter plot of carbon and nitrogen isotope compositions of human and animal bone collagen investigated in this study. The larger crosses and error bars indicate the average ± 1 standard deviation of the isotope data to be expected for human individuals that are one trophic level above the pigs (red) and cattle (green). Comparative values from other pre-Hispanic sites on the Panamanian isthmus are taken from Sharpe et al. (2021). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 5

Bone samples of domestic animals from colonial contexts at Panama Viejo along with information on collagen yields, nitrogen and carbon contents as well as the isotope compositions of both elements.

Context	Species	Skeletal element	Collagen yield [%]	N [%]	C [%]	atomic C/N	δ^{15}N [‰ AIR]	δ^{15}N [‰ AIR] SD	δ^{13}C [‰ VPDB]	**δ^{13}C [‰ VPDB] SD**
Basurero de Casas Oeste	Bos taurus	Metatarsal	5.9	9.4	26.1	3.2	4.03	0.03	−8.07	0.14
Basurero de Casas Oeste	Bos taurus	Femur	7.2	9.0	24.9	3.2	5.92	0.02	−7.58	0.14
Basurero de Casas Oeste	Bos taurus	Radius	6.5	6.6	18.5	3.3	7.81	0.02	−11.23	0.24
Basurero de Casas Oeste	Bos taurus	Rib	6.1	5.5	15.5	3.3	4.47	0.02	−8.02	0.36
Basurero de Casas Oeste	Bos taurus	Radius	5.8	14.5	40.9	3.3	7.07	0.01	−12.52	0.09
Basurero de Casas Oeste	Bos taurus	Tibia	4.5	9.4	26.5	3.3	5.51	0.03	−6.93	0.08
Plaza Major	Sus scrofa domesticus	Metapodial	2.8	6.3	18.5	3.5	7.11	0.06	−15.36	0.31
Casas Oeste	Sus scrofa domesticus	Radius	14.3	14.6	40.3	3.2	5.57	0.04	−13.04	0.03
Casas Oeste	Sus scrofa domesticus	Rib	8.4	13.1	36.5	3.3	6.35	0.04	−7.78	0.12
Basurero de Casas Oeste	Sus scrofa domesticus	Metapodial	5.8	15.3	42.1	3.2	6.03	0.03	−13.88	0.07
Metales	Sus scrofa domesticus	Humerus	6.1	10.5	29.3	3.3	5.56	0.02	−18.62	0.07
Basurero de Casas Oeste	Sus scrofa domesticus	Tibia	8.2	10.4	28.6	3.2	4.68	0.02	−11.60	0.02
Basurero de Casas Oeste	Gallus gallus domesticus	Femur	13.5	15.3	42.7	3.3	9.51	0.03	−6.65	0.10

5.3. Nutritional stress and deficiencies

The consumption of a variety of plant foods at Panamá Viejo, which came to include plantains, rice and imported wheat, as well as significant quantities of animal meat by the seventeenth century, did not preclude signs of nutritional stress in the populations examined. Paleopathologists evaluate nutritional deficiencies and their effects on the lives of past populations to the extent to which bones manifest metabolic disorders that can be interpreted alongside the environmental and sociocultural factors that influenced this type of lesions (Meyer 2016: 862). Nevertheless, bone's monotonous response can complicate precise diagnoses based on these signs (Huss-Ashmore 1982, Meyer 2016). Cribra orbitalia, porotic hyperostosis, and dental enamel hypoplasia form part of a group of non-specific indicators of nutritional stress, which are generally associated with chronic episodes of morbidity, including periods of malnutrition, the effects of infectious, metabolic, or parasitic diseases, and exposure to unhealthy conditions, among other factors (Fornaciari y Giuffra 2009, Walker et al. 2009, Larsen 2015, Godde and Hens 2021, McFadden and Oxenham 2020, Pagán et al. 2005) (Fig. 9).

Table 6 presents the results of statistical significance set at $p \leq 0.05$ using the Chi squared test. Contingency tables were used with frequencies<5 and Fischerś exact test frequencies were calculated for the prevalence of signs of nutritional stress, according to chronological period, sex, age, and, additionally, population filiation (https://artempire.cica.es/archeo/list). With respect to the pre-Hispanic and colonial periods, significant differences are not detected in the incidence of porous lesions, but do emerge with respect to dental enamel hypoplasia ($\square^2$*: 3.994; gl: 1; p: 0.0457*), which became less frequent after 1500. A comparison between the individuals buried to the south of the Main Square with those interred in the Cathedral after 1542 also reveals significant differences in terms of dental enamel hypoplasia ($\square^2$*: 7.0018; gl: 1; p: 0.0081*) and porotic hyperostosis (*p: 0.0045*), although such differences do not appear between the pre-Hispanic and early colonial periods, suggesting continuity in the stress factors that provoked dental enamel hypoplasia and porotic hyperostosis, during at least the first decades after Panama Viejo's foundation.

Comparisons of the data with respect to sex within and among the chronological periods identified do not reveal significant differences by sex in any indicators of nutritional stress. Nor do comparisons during the colonial periods reveal significant differences with respect to age. On the other hand, a difference is observed between children (0–12 years) and other individuals within the pre-Hispanic population, revealing more cases of enamel hypoplasia in individuals over 12 years old (Table 6). Moreover, a difference in the prevalence of nutritional stress indicators is also observed upon comparing young adults (18–34 years) during the pre-Hispanic and colonial periods ($\square^2$*: 6.1176; gl: 1; p: 0.0134*), with more cases in the pre-Hispanic population. However, although a significant increase in the incidence of enamel hypoplasia is also observed in the infantile population before and after the city's foundation (*p: 0.0175*), this could also reflect the fact that the pre-Hispanic children's bodies sampled did not register evidence of stressful events associated with dental hypoplasia, while the children sampled in the colonial period present a prevalence of 66,67%. Nonetheless, the sample size of the colonial child population should be expanded to corroborate this hypothesis. Furthermore, these skeletal collections could respond to heterogeneous frailty and selective mortality, postulates of the osteological paradox that can have an important impact on paleopathological interpretations from a population perspective (Wood et al 1992). In this sense, the prevalence of nutritional stress indicators observed in the sample tend to decrease with age, suggesting that the child and youth populations were the most susceptible, followed by young adults (18–34 years). However, it is likely that the sample analyzed presents an underrepresentation of the child and youth populations, due to the conditions of preservation of the skeletal remains. At the same time, these individuals probably were not representative of the living population in the same age range, of course influencing in the estimation of the prevalence of stress indicators for this sector of the population.

Finally, when comparing the information obtained regarding nutritional stress indicators according to probable predominant ancestral filiation, the statistical tests show no significant difference in the proportion of African, Native American, and European groups showing such stress (Table 6). However, the prevalence of the stress indicators analyzed appear slightly higher among individuals of probable European ancestry, although roughly homogenous among the three overarching continental groups assigned for heuristic purposes: cribra orbitalia was detected in 10% of individuals with probable African ancestors, in 11.11% of those of probable Native American parentage and, 13.04% in individuals of likely European origins; porotic hyperostosis in 30% of individuals with probable African ancestry, 31.58% among those of with likely indigenous heritage, and 35.42% in individuals who probably had European parents; enamel hypoplasia appeared in 20.59% of individuals with prevalent African ancestry, among 20% of those whose parents were probably Native Americans, and in 21.95% of individuals with dominant European phenotypes.

6. Discussion

To date the history of diet and nutrition or "gastronomy" in Panama has been based on historical documents produced and conserved by elites (Castillero 2010a,b). At the same time, archaeological and microbotanical studies have explained the processes of domestication of numerous cultigens on the isthmus, as well as the diffusion of others from a long-term perspective (Brücher 1989, Piperno et al. 2019, Piperno 2018, Dillehay et al. 2017, McMichael et al. 2017, Larson et al. 2014, Isendahl 2011, Pagán et al. 2005). Such pioneering work, whether focused on the last 500 years or the preceding 8000, has revealed the isthmus a privileged scenario for the study of social and dietary change. Despite these advances, archaeological and historical perspectives normally have developed in isolation from each other and without input from isotopic and paleopathological analyses.

Diverse lines of evidence and results come together in the present study to challenge a number of commonplace beliefs about the impact of the conquest and colonization inspired by the work of Crosby (1986) and reflected in that of Castillero (2010b, 2016), among others. Specifically, the evidence from Panama Viejo contradicts the idea of a sudden dietary shift and early homogenization of cultigens with the European invasion. At the same time, our findings undermine the idea of distinct and separate dietary regimens based on individuals' geographic origins or ancestries. Rather than rigid social or culinary hierarchies, our data documents cases of social (as well as geographical) mobility and dietary change.

The starch and isotopic data reflect no abrupt homogenization, but instead, a continuation and diversification of cultigens following the conquest and early colonization of the isthmus of Panama. Delta^{13}C in bone collagen suggests diets based on a mixture of C_4 and C_3 plant foods during the pre-Hispanic and colonial periods, with an increased consumption of C_3 foods (including wheat, rice, beans and plantains) by the seventeenth century (Fig. 8). Laborers involved in agriculture and food preparation – often Native Americans, Africans and their descendants, as well as individuals of mixed parentage – may have enjoyed greater access to certain plants (Criado de Castillo 1575, Ruíz de Campos 1630).

Combining the results of the starch and phytolith analyses as hard evidence for the consumption of specific plants and the stable isotope data as a reflection of the protein sources of the human diet did not reveal any clear correlations. Instead, evidence for starches of maize (a C_4 plant) and wheat, yuca (manioc), arrowroot or pulses (C_3 plants) appear throughout the whole spectrum of stable isotope compositions of the human collagen, including the individuals at both ends of either spectrum of isotope values (Fig. 8). Moreover, the dental calculus of individuals with the highest δ^{15}N values, which attest to a significant contribution of marine food to the human protein intake, also revealed starch evidence of different plant species and reflect the importance of plant foodstuffs in the diets of these pre-Hispanic and early colonial individuals. The combined data also advise against overly simplistic interpretations based on single lines of evidence. While starch data constitute qualitative evidence and may not be used to quantify different dietary components, the stable isotope data are biased against foodstuffs with low protein contents.

Although starch evidence of wheat consumption was found in all of the colonial periods, the wheat consumed in Panama needed to be imported, initially from Castile and subsequently from Peru (Criado de Castillo 1575). In light of the long distances involved and high humidity in Panama, wheat flour often reached the city damaged or spoiled before more could arrive ("Abecedario de las mercaderías que entran y salen del puerto de Panamá" 1575). A merchant who issued his last will and testament in Panama in 1593 listed 640 *fanegas* (27.678 kilos) of wheat flour from the valleys of Peru among his possessions (Olivares 1598). By the seventeenth-century, the Costa Rica highlands also produced wheat for export, some of which may have reached Panama (Sabaja 1992). Given the necessity and difficulties of transporting and preserving wheat, its contribution to the human diet in Panama clearly proved subordinate to that of maize. Overall, carbon originating from C_4 photosynthesis prevailed in all samples of human collagen, attesting to the importance of maize either being consumed directly or contributing

Fig. 9. Principal lesions associated with indicators of nutritional stress: a) Cribra orbitalia (UE 1019); b) Porotic hyperstosis (UE 1088); c) Dental hypoplasia (UE 1080), d) Dental hypoplasia (UE 1070).

Table 6
Chi squared ($\square^2$) and Fisher tests for lesions associated with cribra orbitalia, porotic hyperostosis, and dental hypoplasia.

	CRIBRA ORBITALIA															
	PRE-HISPANIC								COLONIAL							
	Female		Male		Indeterminate		Total		Female		Male		Indeterminate		Total	
Age	A/O	%	A/O	%	A/O	%	A/O	%	A/O	%	A/O	%	A/O	%	A/O	%
Infant 1 (0-6 years)	-	-	-	-	1/13	7,69	1/13	**7,69**	-	-	-	-	-	-	-	-
Infant 2 (7-12 years)	-	-	-	-	1/2	50,00	1/2	**50,00**	-	-	-	-	0/3	0,00	0/3	**0,00**
Juvenile (13-17 years)	-	-	0/2	0,00	-	-	0/2	**0,00**	1/2	50,00	0/1	0,00	-	-	1/3	**33,33**
Young Adult (18-34 years)	0/2	0,00	0/7	0,00	0/3	0,00	0/11	**0,00**	5/47	10,64	3/25	12,00	0/2	0,00	8/74	**10,81**
Middle Adult (35-55 years)	0/2	0,00	0/9	0,00	-	-	0/12	**0,00**	1/12	8,33	1/6	16,67	-	-	2/18	**11,11**
Adult (+18 years)	-	-	0/1	0,00	-	-	0/1	**0,00**	1/20	5,00	0/7	0,00	0/9	0,00	1/36	**2,78**
Total	0/4	**0,00**	0/19	**0,00**	2/18	**11,11**	2/41	**4,88**	8/81	**9,88**	4/39	**10,26**	0/14	**0,00**	12/134	**8,96**
	POROTIC HYPEROSTOSIS															
	PRE-HISPANIC								**COLONIAL**							
	Female		Male		Indeterminate		Total		Female		Male		Indeterminate		Total	
Age	A/O	%	A/O	%	A/O	%	A/O	%	A/O	%	A/O	%	A/O	%	A/O	%
Infant 1 (0-6 years)	-	-	-	-	1/13	7,69	1/13	**7,69**	-	-	-	-	-	-	-	-
Infant 2 (7-12 years)	-	-	-	-	2/3	66,67	2/3	**66,67**	-	-	-	-	1/3	33,33	1/3	**33,33**
Juvenile (13-17 years)	-	-	0/2	0,00	-	-	0/2	**0,00**	0/2	0,00	1/1	100,00	-	-	1/3	**33,33**
Young Adult (18-34 years)	0/2	0,00	3/7	42,86	0/3	0,00	3/12	**25**	17/51	33,33	9/26	34,62	1/3	33,33	27/80	**33,75**
Middle Adult (35-55 years)	0/2	0,00	2/9	22,22	-	-	2/11	**18,18**	1/12	8,33	3/6	50,00	1/1	100,00	5/19	**26,32**
Adult (+18 years)	-	-	0/1	0,00	-	-	0/1	**0,00**	6/21	28,57	4/8	50,00	0/13	0,00	10/42	**2,38**
Total	0/4	**0,00**	5/19	**26,32**	3/19	**15,79**	8/42	**19,05**	24/86	**27,91**	17/41	**41,46**	3/20	**15,00**	44/147	**29,93**
	DENTAL HYPOPLASIA															
	PRE-HISPANIC								**COLONIAL**							
	Female		Male		Indeterminate		Total		Female		Male		Indeterminate		Total	
Age	A/O	%	A/O	%	A/O	%	A/O	%	A/O	%	A/O	%	A/O	%	A/O	%
Infant 1 (0-6 years)	-	-	-	-	0/13	0,00	0/13	**0,00**	-	-	-	-	-	-	-	-
Infant 2 (7-12 years)	-	-	-	-	0/3	0,00	0/3	**0,00**	-	-	-	-	2/3	66,67	2/3	**66,67**
Juvenile (13-17 years)	-	-	2/2	100,00	-	-	2/2	**100,00**	1/2	50,00	0/1	0,00	1/1	100,00	2/4	**50,00**
Young Adult (18-34 years)	1/2	50,00	4/7	57,14	2/3	66,67	7/12	**58,33**	9/47	19,15	9/27	33,33	0/2	0,00	18/76	**23,68**
Middle Adult (35-55 years)	1/2	50,00	3/8	37,50	-	-	4/10	**40,00**	0/10	0,00	1/5	20,00	-	-	1/15	**6,67**
Adult (+18 years)	-	-	1/1	100,00	-	-	1/1	**100,00**	-	-	0/2	0,00	0/2	0,00	0/4	**0,00**
Total	2/4	**50,00**	10/18	**55,56**	2/19	**10,53**	14/41	**34,15**	10/59	**16,95**	10/35	**28,57**	3/8	**37,50**	23/102	**22,55**

Note: Pre-Hispanic individuals correspond to PAPV_10-Morelos, PAPV_7-Visitor Center, and PAPV_8- Main Square. The individuals of the colonial period correspond to PAPV_3- Southeast Main Square (1519–1540), and PAPV _5_1- Cathedral's nave and atrium (1541–1671). A/B-Affected Individuals/Observed Individuals. %-Prevalence of lesions.

to the meat and dairy products obtained from animals feeding on it. Even individuals whose calculus contained wheat starch exhibited $\delta^{13}C$ values in accordance with a predominance of maize over wheat.

The detection of wheat starch in the dental calculus of local and non-local individuals with probable African and indigenous American ancestries entails a crucial finding that contradicts the idea of a rigid differentiations among groups of consumers based on origins or ancestries. Another key cultigen, rice, which initially entered the isthmus in small quantities from Iberia, Senegambia, and Cape Verde, was successfully grown on the isthmus by 1583 and become one of its most important exports in the following decades. In light of this information from the written sources, it seems more plausible to interpret the lower average $\delta^{13}C$ values of the human collagen and therefore increasing contribution of C_3 plants to the human diet after 1542 as a reflection of an increased consumption of rice (and perhaps plantains as well), rather than of wheat or native central American C_3 cultigens. Nevertheless, wheat also contributed to the human diet during this earlier colonial phase, as evidenced by a starch grain of this plant species in one of the calculus samples. Significantly, rice phytoliths were identified in the dental calculus of individuals of probable African and European filiation buried in Panama Viejo's Cathedral between 1542 and 1626. Such dietary practices may also allude to processes of social mobility. Not only were people of diverse – Indigenous, African, European and mixed – backgrounds buried in the Cathedral, they also all consumed products that written sources labeled "Spanish," "Black," or "Indigenous". The identification of a starch grain corresponding to the banana or plantain associated with a woman of likely European origin, cribra orbitalia and enamel hypoplasia (UE 1019) appears particularly significant. The grinding required for starch to form probably entailed the consumption of cooked (and thus, harder) bananas, although historical sources record their fresh consumption as well. According to the summary of an account compiled in 1607, Panama's population survived on corn and especially plantains when wheat flour from Peru was lacking or spoiled ("Descripción" 1607, 142, 147). Writing 33 years later, the Cathedral's schoolmaster claimed that the area's abundant bananas "generally sustained the Blacks" and were also popular among Spaniards "not for sustenance, but, rather, pleasure" (Requejo 1640, 73). The microbotanical and paleopathological evidence suggests otherwise.

Far from the abandonment of pre-Hispanic cultigens, starch grains preserved in human dental calculus point to the continued consumption of arrowroot, beans, and other legumes at Panama Viejo through 1671. Starches from maize and wheat, as well as squash, although less common, were associated with local and non-local individuals of all estimated ancestries. The identification of bean starch in association with three individuals of likely African ancestry supports the idea that this pre-Hispanic cultigen also became known as "food for Blacks," as recorded in a later sixteenth-century price list ("Abecedario de las Mercaderías que entran y salen del Puerto de Panamá" 1575). Another food reportedly consumed by native Americans and Afro-descendants ("Descripción de Panamá y su provincia, sacada de la relación que por mandado del Consejo hizo y envió aquella Audiencia" 1607, 147), the palm, also left a phytolith in the dental calculus of a women identified as probably African and interred in the atrium (UE 61) (Fig. 7).

While microfossils reveal specific plants eaten by particular individuals, the spectrum of plants consumed at any time could be greater than those preserved and identified. This study's archaeobotanical component has focused on samples from dental calculus, which do not usually contain a great number of vegetable microfossils in comparison, for example, with samples extracted from instruments used to grind flour, where otoe (*Xanthosoma*) has also been detected (Aceituno and Martín 2017). Along these lines, we would have expected to find evidence of the continued consumption of yuca (manioc), alongside maize and beans, in the colonial period (Requejo y Salcedo, 76). Similarly, although bananas flourished in the region (Requejo y Salcedo, 76–77, *Descripción de* Panamá y su provincia, sacada de la relación que por mandado del Consejo hizo y envió aquella Audiencia*1607,* 147), we were only able to identify one starch grain corresponding to the plantain (*Musa paradisiaca*), domesticated in Asia (Donahue and Denham 2009). An important number of starches detected, especially in the pre-Hispanic periods, also remain unidentified.

In terms of the plant and animal food available, the impact of the spread of livestock, especially cattle, merits particular attention. The consumption of beef and milk products derived from cows, including cheese, mentioned frequently in surviving historical documentation, should mark an important shift between pre-Hispanic and colonial times. Indeed, while still being diverse among samples from 1519 to 1541, the nitrogen isotope data of the human collagen become very homogeneous over time and exhibit a range that agrees with large shares of animal-derived foodstuffs, even though probably supplemented by marine fish or seafood contributing nitrogen with even higher $\delta^{15}N$ values. The human samples dated between 1542 and 1671 appear to be slightly more than one trophic level above those of the pigs, whereas the $\delta^{13}C$ value of collagen of potential average beef and dairy consumers should be about 5 ‰ higher (Fig. 8). This observation may, however, not be taken as evidence for the preference of pork over beef. Instead, the isotope data always reflect a mixture of all food sources consumed. They, therefore, may also reflect the historically documented increasing importance of beef – including meat from cattle that were predominantly fed on maize forage with high $\delta^{13}C$ values – and the byproducts of rice, a C_3 plant with $\delta^{13}C$ values at the lower end of the spectrum.

Moreover, the periodic arrival of fleets from Spain or Peru entailed a strain on the animal as well as plant resources available to feed the population. During the famous fairs of Nombre de Dios and Portobello, followed by the *trans*-isthmian transport of peoples and goods, temporary residents competed with locals for foodstuffs, including beef. Furthermore, mules consumed large amounts of corn otherwise used to nourish humans during the famous *trans*-isthmian transport of silver from the mines of Peru. Hence Panama's privileged geo-political location may have complicated access to animal and vegetable nutrients for large sectors of the local populations during times of scarcity or high demand.

While the diversity of plant and animal foods detected in dental calculus and reflected in isotope analyses undoubtedly influenced human health, food shortages may have been another, particularly significant factor. Relatively high rates of enamel hypoplasia detected in the samples from pre-Hispanic individuals (34.15%) as well as the colonial populations from 1519 to 1541 and 1626–1671 (22.55%), would reinforce references in historical accounts to particularly serious moments of food shortage during the early settlement and after 1640 (Castillero 2010a,b). In both the pre-Hispanic and colonial periods, nutritional stress could have been related to episodes of food scarcity, but we must also consider that this multifactorial condition also responds to trauma, intestinal, infectious, systemic, or metabolic diseases.

For example, a comparative study of pre-Hispanic and colonial populations in Georgia and Florida contrasts the low proportion of enamel hypoplasia in pre-Hispanic groups with an increase after the seventeenth century, linked to the reduction of marine products and an increase in the consumption of corn (Larsen et al. 2007). Likewise, in the region of Tlatilco, Mexico, dental hypoplasia went from an average of 20% in the pre-Hispanic period to 40% for the colonial era, explained by the change of diet due to the low consumption of protein and the increase in carbohydrates (Meza Manzanilla 2003: 830). Also in Mexico, in sixteenth- and seventeenth-century Campeche the prevalence of enamel hypoplasia in the first generation of slaves born in Africa, was found to be much lower than that of individuals born in Campeche who, regardless of their population affiliations, faced the same conditions for the formation of hypoplasia (Cucina 2010: 121). In South America, the data tend to be much more variable. For example, rates of hypoplasia in southwestern Colombia change from an average of 3.3% to 17.97% from the pre-Hispanic to the colonial period, while in the Savannah of Bogotá the rate of hypoplasia also increased from 5% to 14% after contact (Rojas and Rivera 2019: 232–233). Meanwhile in Lambayeque, north coast of Peru, a different trend is observed where there is a prevalence 1.29 times higher in the pre-Hispanic population than in the colonial period (Klaus and Tam 2009). The significant decrease in the prevalence of dental hypoplasia from the pre-Hispanic to the colonial period at Panama Viejo may be related to differences in infant morbidity and mortality, as reported in Peru (Klaus and Tam 2009, Klaus 2020) and Florida (Stojanowski 2013), and would not necessarily reflect an improvement in living conditions. This interpretation finds support in the figures for the other stress indicators that increase considerably after contact, especially in cases of porotic hyperostosis.

In relation to diet, porotic hyperostosis and cribra orbitalia have been associated with ferropenic and megaloblastic anemia, the second of these being principally caused by deficits of vitamin B12 and B9, and commonly accompanied by other nutritional deficiencies (Angel 1966, McInvale 2015, Oxenham and Cavil 2010, Walker et al 2009). These vitamins and iron are mainly obtained through the consumption of animal protein (meat, fish, lactates, and eggs) and pulses. Nevertheless, the excessive consumption of foods like maize and wheat, due to their high levels of phytates and polyphenols, may impede the absorption of many nutrients, especially iron (Larysse et al. 2000, Larsen 2015). This effect intensifies as a result of cultural practices including the use of ashes or nixtamalization in the processing of corn (Zizumbo Villarreal y Colunga García-Marín, 2016).

Different bioarchaeological studies of American agrarian groups during the pre-Hispanic and contact periods have reported a higher prevalence of porotic hyperostosis and cribra orbitalia, from 40 to 90%, with interpretations that emphasize the preferential consumption of maize and effects of phytates in inhibiting certain nutrients (Larsen 2015: 35). However, this situation cannot be generalized, since cases have also been reported in which parasites and gastrointestinal infections represent an additional risk for the absorption of vitamins and minerals in the diet (Ubelaker 1992, Walker et al. 2009). In this respect, parasites including *Plasmodium falciparum* were introduced when African and European populations reached the Americas, although recent genetic studies of the parasite suggest that strains of *Plasmodium vivax,* which originated in Australasia, could have reached the Americas at roughly the same time as its first humans (Rodrigues et al. 2018). Furthermore, we should consider the parasites' proclivity for standing water in relation to the proverbial "unhealthy" climate described in Nombre de Dios and Panama (Ocaña 1599). With respect to Panama, Shafroth (1953: 8) and Castillero (2010a: 201-5) have pointed to continual problems in the supply of fresh water, since it had to be hauled from outside the city, whose wells produced salt water, which would hardly favor the population's health. The collection of water and planting of rice in swampy areas entailed additional risks, since such environments provided reservoirs for parasites and mosquitos, the principal vectors of parasites pertaining to the genre *Plasmodium*, which could generate the inadequate absorption of nutrients that could lead to lesions such as cribra orbitalia and porotic hyperostosis (Smith-Guzmán 2015).

On the other hand, an increase in the prevalence of porotic lesions and dental hypoplasia in comparison with the pre-Hispanic period has been reported in other studies as a result of multiple stresses in other osteological series from the colonial period. These studies include different Spanish missions in Florida (Larsen et al. 2007, Larsen 2015, Stojanowski 2013), San Pedro de Mórrope, Peru (Klaus and Tam 2009), Mendoza, Argentina (Mansegosa et al. 2018), Campeche, Mexico (Cucina 2010) and Ecuador (Ubelaker and Newson 2002). Their authors have considered interpretations related to ancestry (Rodríguez Pérez 2010, Cucina 2010), the high consumption of maize and frequency of intestinal illness (Ubelaker y Newson 2002), parasitism (Godde and Hens 2021), as well as poor diet (Larsen et al. 2007). Among such explanations, our findings corroborate the probable impact of intestinal and parasitic infection.

To summarize, the historical and paleopathological data from pre-Hispanic and colonial Panama reveal a prevalence of bone and dental lesions that can be related to periods of nutritional stress, and explained by different factors including conditions that increased the chances of parasitic and infectious illness. In contrast to studies in other areas, the present research found the incidence of cribra orbitalia and porotic hyperostosis in Panama to be more frequent among the colonial than the pre-Hispanic populations sampled, and the opposite regarding enamel hypoplasia, which appeared more common among the pre-Hispanic individuals sampled. Nor did we detect significant differences during the colonial period in the incidence of these lesions in relation to sex or probable ancestry. In fact, the most frequent stress indicator, porotic hyperostosis, appeared more common among individuals with probable European ancestry (35%) than among other groups. In this regard, episodic increases in the population on the isthmus in colonial times, related to expeditions and the fleets' arrivals, would make demands on local production, and simultaneously import goods, affecting all peoples who reached or inhabited Panama Viejo. Parasitic intestinal ailments, which also inhibited the absorption of nutrients, would have exacerbated the ensuing nutritional deficiencies. In this case, conjunctural factors related to Panama City's role as a node connecting land and maritime transport routes figure into the equation. Moreover, the reliance on commerce may have led to a relative neglect of regional agriculture and fishing, which could have provided some protection against food shortages.

Like other early colonial populations (Ubelaker and Newson 2002, Larsen et al. 2007, Klaus and Tam 2009, Stojanowski 2013, Rojas et al. 2011, Cucina 2010, Rodríguez Pérez 2010, Larsen 2015, Mansegosa et al. 2018), the inhabitants of Panama Viejo confronted difficult living conditions influenced by multiple factors. These included environmental, infectious, parasitic, and nutritional stress, which, when prolonged over time, generated chronic illness.

7. Conclusions

Excavations undertaken in the funerary contexts of Panama Viejo's Cathedral and to the south of its Main Square in 2017 and 2018 were able to increase the number of individuals previously recovered from the same locations and other contiguous sites, where pre-Hispanic occupation had been identified (see details about this occupation in Mendizábal et al. 2021). As a result, samples could be compared from the pre-Hispanic (c. 600–1450) and colonial (1519–1542, 1543–1626, 1627–1671) periods. The identification of these specific contexts facilitated a broader study, crossing paleopathological data with the results of the microbotanical analysis of dental calculus, which has proven a valuable source of information regarding the plants specific individuals consumed in the past.

The microbotanical evidence presented indicates that Panama Viejo's early European settlers consumed local products, especially maize, but also squash and yuca (manioc), whose archaeobotanical register goes back to the mid-Holocene (Dickau et al. 2007). Although wheat was not grown in Panama, it was consumed there by individuals with probable European as well as non-European parentage, signaling social interaction among individuals of different ancestries and a lack of social differentiation based on diet. Alongside the consumption of wheat among individuals of different probable ancestries, the presence of rice phytoliths in the dental calculus of individuals with probable African and European ancestries constitutes an important finding.

Strontium and oxygen isotope compositions of tooth enamel differentiated individuals who likely grew up on the Panamanian isthmus from first-generation migrants. Carbon and nitrogen isotope data of the local individuals attest to maize (a C_4 plant) being a fundamental staple crop among the pre-Hispanic as well as the colonial populations. In addition, people of the pre-Hispanic and early colonial period (1519–1541) consumed highly variable shares of marine foodstuffs and terrestrial meat (Martín and Rodríguez 2006). In agreement with the evidence from the starches and phytoliths, there is no indication for an abrupt change or standardization of dietary habits at the beginning of the colonial period. Dietary practices, however, appear to have homogenized in later colonial times (1627–1671), particularly regarding sources of protein. The data indicate agreement with historical records that report the significance of meat, especially beef, in the provision of the colonial city, supplemented by seafood and fish as well as plant-based foodstuffs. Among the latter, C_3 crops, including rice, wheat and plantains, increased their average contributions to the human diet at Panama Viejo after 1542.

Ancestry determined health no more than diet at Panama Viejo. The detection of porotic hyperostosis, cribra orbitalia and dental enamel hypoplasia in similar percentages in groupings of all probable ancestries indicates that, regardless of their families' origins, Panama Viejo's inhabitants faced episodic difficulties accessing resources, including meat, as well as situations that favored ailments caused by parasites. In other words, the pathologies identified would have been produced by nutritional deficiencies as well as environmental factors, as found in other bioanthropological studies (Fornaciari y Giuffra 2009: 246, Rivera and Mirazón Lahr 2017). The etiology of the lesions associated with stress indicators observed in Panama Viejo's population during the sixteenth and seventeenth centuries responds to multiple factors that produced difficult living conditions. The variety of plant and animal foods that reached Panama Viejo did not prevent their periodic scarcity. Indeed, the most important foods on the isthmus – corn, wheat, rice, and beef – underwent huge fluctuations in supply and demand during the colonial period.

Finally, the lines of evidence presented here, including historical data, challenge a number of commonplace "historical" ideas. Rather than a swift biological conquest and ecological transformation of the isthmus, archaeobotanic, isotopic and historical findings point to African and European efforts to appropriate and to complement, but not to displace, Indigenous foods. Whatever ancestry, the people of Panama

Viejo sought and developed possibilities for dietary continuity in the consumption of foods that, for individuals from other regions, entailed dietary change. In the vortex of the ensuing micro and macrobiotic exchanges, illness, scarcity, hardship, and hunger may have catalyzed dietary and, indeed, cultural, adaptations.

CRediT authorship contribution statement

Juan Guillermo Martín: Conceptualization, Methodology, Writing – original draft. **Francisco Javier Aceituno:** . **Javier Rivera-Sandoval:** . **Corina Knipper:** . **Iosvany Hernández:** Data curation. **Bethany Aram:** Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data Availability

The data reported are openly available at artempire.cica.es.

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Further reading

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