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ARTICLE

Late Holocene Maize Diversity and Cultural Remains from the Northern Neotropics: The Site of Cueva La Capilla, Venezuelan Andes

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Abstract
In the northern neotropics, given poor preservation of macro-fossils and funding/research biases, our understanding of ancient cultures' dynamics is limited. Here, we document the botanical and cultural remains at an early ceramic archaeological site, Cueva La Capilla, northeast of the Venezuelan Andes, which contains funerary remains linked to the Tocuyanoid ceramic tradition, as well as maize rachises. We employ a multidisciplinary approach to study the diversity of the maize remains—including radiocarbon dating and ancient DNA—and show that the maize rachises, here radiocarbon-dated to the terminal Tocuyanoid at AD 395–460, present diverse morphologies, suggesting the simultaneous use of different maize varieties. We also find evidence of plants pertaining to different environments, suggesting long-distance trade or heterogeneous cultivations. The DNA analysis of a masticated maize stem confirms human action, revealing new insights into the Tocuyanoid cultural development and resource management.

Resumen
En el neotrópico septentrional, la escasa conservación de los restos macroscópicos y los sesgos en la financiación e investigación han limitado nuestra comprensión de las dinámicas culturales antiguas. En este estudio documentamos restos botánicos y culturales de un yacimiento arqueológico cerámico temprano, la Cueva La Capilla, ubicada al noreste de los Andes venezolanos. El sitio contiene restos funerarios vinculados a la tradición cerámica tocuyanoide, así como raquis de maíz. Aplicamos un enfoque multidisciplinario para estudiar la diversidad del maíz —incluyendo datación por radiocarbono y análisis de ADN antiguo— y demostramos que los raquis de maíz, datados en la fase terminal tocuyanoide (395-460 dC), presentan una morfología diversa, lo que sugiere el uso simultáneo de distintas variedades de maíz o de diferentes etapas de domesticación. Asimismo, hallamos evidencia de plantas procedentes de distintos entornos, lo que apunta a un comercio a larga distancia o a prácticas agrícolas heterogéneas. El análisis genético de un tallo de maíz masticado confirma la intervención humana, aportando nuevas perspectivas sobre el desarrollo cultural tocuyanoide y la gestión de recursos.

Keywords: aDNA; radiocarbon dating; Tocuyanoid; Venezuela; *Zea mays*

Palabras clave: ADN antiguo; datación por radiocarbono; tocuyanoide; Venezuela; *Zea mays*

The northeastern Andes and the Llanos in northwest Venezuela represent a crossroad in human migrations and cultural exchanges between South America and the Caribbean. Here, one of the most long-standing ceramic traditions of western Venezuela, the Tocuyanoid—Macro-Tocuyanoid Tradition, as defined by Oliver (1989)—developed between Period II (1050 BC–AD 350) and Period III (AD 350–1150), as proposed by Cruxent and Rouse (1958), during a time that saw the rise of local developments and cultural stabilization (Navarrete 2008). Historically, the Tocuyanoid constituted part of what was called "the first painted horizon" of northwestern South America (Bischof 1969; Cruxent and Rouse 1958; Reichel-Dolmatoff 1965), together with the La Pitía and Lagunillas materials of the Maracaibo Lake Basin of northwestern Venezuela (Gallagher 1976; Wagner 1980; Wagner and Tarble de Ruíz 1975). The Tocuyanoid was also associated with the first stable agricultural traditions in the states of Falcon and Lara from 300 BC (Arvelo and Oliver 1999). Maize has been a staple food in the region, and the relationship with this plant and its domestication process has been a central topic in the literature on demographic and cultural changes (Navarrete 2008; Sanoja 1981).

Given the known distribution of the Tocuyanoid culture, it has been suggested that their economic orientation was broad-based, as they occupied a wide variety of environments in Venezuela (including the Andean area of Lara, the Yaracuy River Valley, the coastal area and the Middle Orinoco; Arvelo 1995; Arvelo and Oliver 1999; Oliver 1989; Sanoja and Vargas-Arenas 2007). Furthermore, analysis of the settlement pattern in the Quibor Valley has purportedly supported Sanoja and Vargas Arenas's (1974) hypothesis, according to which these groups organized themselves into predominantly egalitarian societies (Arvelo 1995).

Tocuyanoid funerary practices have been described as varied (Arvelo and Oliver 1999). There are reports of secondary burials in painted or unpainted urns (Arvelo et al. 1994) and of primary burials with offerings of necklaces and vessels (Nectario 1942; Sanoja and Vargas Arenas 1967). Archaeological surveys conducted in the northeast Lara Andes during the 1990s revealed a series of caves that contained archaeological evidence of a funerary context. One of these is named here Cueva La Capilla, located in the northeastern Andes of Venezuela, at Moran Municipality in the Lara State. The first excavations from 1996 yielded Tocuyanoid ceramics associated with botanical remains and other cultural artifacts made of perishable materials, which are here described systematically for the first time. The most prominent findings of Cueva La Capilla are represented by a group of maize cobs characterized by different morphologies and numbers of rows.

The domestication of maize is a complex process that touches on various morphological (and molecular) steps, from the wild form teosinte (*Zea mays* ssp. *parviglumis*) until the establishment of common maize (*Zea mays* ssp. *mays*) as a staple food across the Americas (Kistler et al. 2020). The first domestication process of teosinte in southern Mexico, approximately 9,000 years ago, resulted in a first lineage called "Pan-American," due to its wide distribution (Kistler et al. 2018; Piperno et al. 2009). Archaeological and molecular studies suggest that the earliest domesticated corn from Mesoamerica reached Panama around 7,500 years ago and South America around 6,500 years ago. These remains, found in various forms and states of preservation, appear along the coast of Peru, the Andes, and the lowlands of Bolivia, with dates ranging between 6,500 and 6,300 years ago (Grobman et al. 2012; Iriarte et al. 2020; Lombardo et al. 2020). Genetic and archaeological evidence suggests that the southeastern Amazon was likely a secondary center of partial corn domestication after the arrival of the Pan-American lineage (Kistler et al. 2020). South American and Mexican lineages of maize may have diverged independently, eventually giving rise to local varieties (Vallebueno-Estrada et al. 2023). Linguistic evidence confirms the local, independent development of lexicon for maize and its cultivation in Mesoamerica (Uto–Aztecan, Otomanguean, Mixe–Zoque, and Mayan language families) and in the Andes (Quechua and Aymara language families; Staller et al. 2006).

Teosinte and maize morphologies are very distinct. The teosinte ear has few kernels (5–12), which are fruitcase-enveloped and easily shatter into single-seed units at maturity. Maize has one or two multiple-ranked ears (the whole female inflorescences), each with hundreds of naked grains, not shattering at maturity (Chen et al. 2020). Early domesticated maize cobs from Mexico, dated to 6,250 years ago, are small and bear two rows of alternating seeds that did not disarticulate naturally but required human intervention in harvest and reproduction (Benz 2001; Piperno and Flannery 2001). A younger Mexican

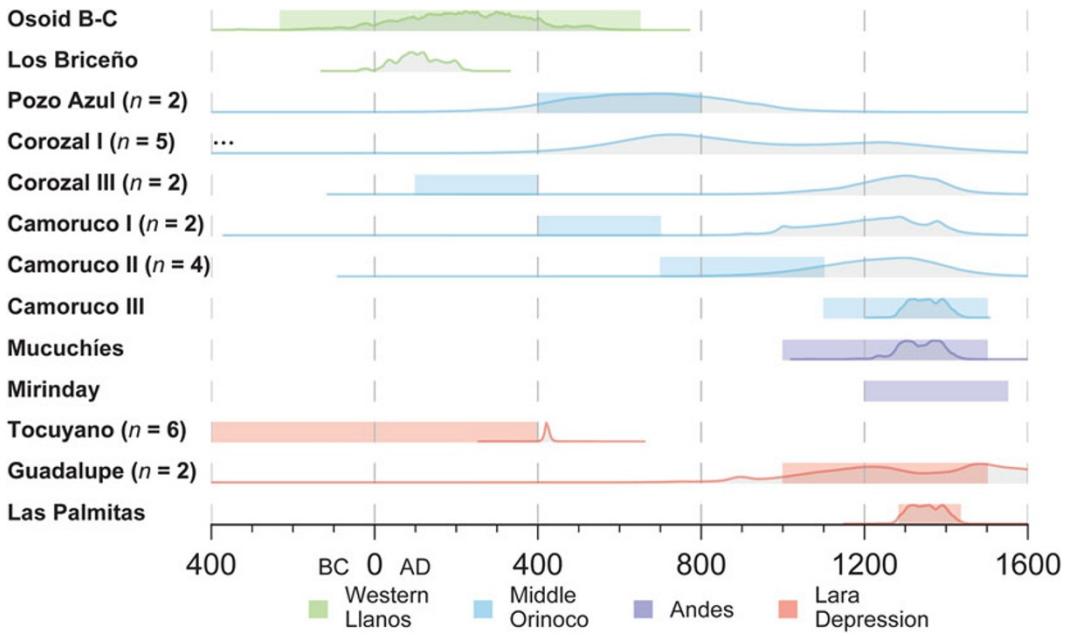

Figure 1. Chronology for archaeological phases linked to maize remains in Venezuela, according to region. Bars represent previously proposed relative chronologies, while the uni-/multi-modal distributions represent ^{14}C ages obtained directly on maize remains or on closely associated organic material (see Supplementary Table 1 and Supplementary Figure 1). For the latter, each distribution corresponds to either a single calibrated age or a summary produced using the KDE_Model function in OxCal (Bronk Ramsey 2017). For summarized distributions based on multiple ^{14}C ages, the sample size is noted as *n* = x. (Color online)

site dated to 5,300–4,950 years ago also showed small nondisarticulating cobs, associating them with human-mediated domestication (Benz and Iltis 1990). Different morphologies are therefore associated with early domestication stages, with selection first for rigid rachis that do not disarticulate and keep the seeds in the plant, and then for an increase in the size of the grains, ear, and number of kernels per row (Doebley 2004). Understanding the process of maize domestication in South America requires data from various geographic regions and time periods. Increased sampling has revealed further variation and patterns that were not apparent when sampling was limited to the Andes, as in the discovery of "primitive" forms of maize within the last millennium in lowland Eastern Brazil (Costa et al. 2024). Insights can be gained not only from macro-fossils but also from micro-fossils such as phytoliths and starch grains (Iriarte 2024). In Venezuela, there are several findings of maize in the archaeological record (Figure 1; Supplementary Table 1 and Supplementary Figure 1), with the earliest evidence being the La Betania site, possibly dating to between 96 BC and AD 542 (Wagner and Zucchi 1966; Zucchi 1967).

This study expands the geographic range of early maize for this country and the broader neotropics, supported by direct radiocarbon measurements. The goal of this study is to give a first and nonexhaustive morphological, chronological, and genetic description of some of the botanical remains in the site of Cueva La Capilla, with a focus on the maize remains. The maize remains from Cueva La Capilla are contextualized alongside other domesticated, endogenous and exogenous, plant species, offering new insights into the agricultural landscape of the region. Further evidence of the Tocuyanoid tradition is provided by a figurine and carved wooden artifacts, as well as skeletal, ceramic, and lithic remains—the latter three elements still under investigation. Additionally, in a key aspect of this study, we examine the presence of different maize rachis morphologies, situating these findings within the broader continental context of maize domestication (Bonavia 2013). This analysis is part of a multidisciplinary approach that includes radiocarbon dating, morphological material descriptions, and ancient DNA (aDNA) analysis of plant remains.

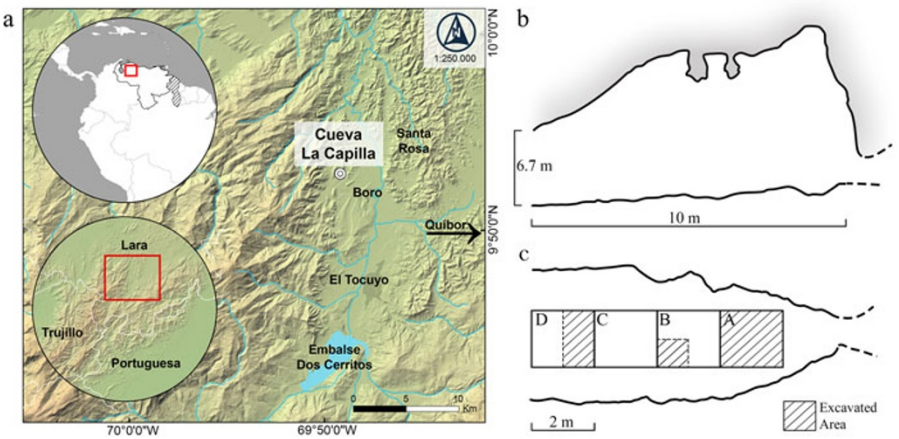

Figure 2. Location and site description for Cueva la Capilla, Lara State, Venezuela: (a) site location at different map scales; (b) profile of the site; (c) excavated area. (Color online)

Materials and Methods

Location, Excavation, and Description of Archaeological Remains

Cueva La Capilla is part of a sandstone outcropping located in Cerro Negro in the Lara Andes, west of the Quíbor Depression and near the town of Boro, Morán municipality (Figure 2a). The cavity has a depth of 8.57 m, a maximum height of 8 m, and a width of approximately 2.90 m (Figure 2b). The temperature inside ranges between 28ºC and 22ºC, with a low level of humidity that ensures an environment conducive to the conservation of organic remains.

At the extremity of the explored area, the cave leads to the opening of an unexplored chamber. The area adjacent to this opening exhibited significant disturbance. However, the accumulation of several centimeters of fine dust, ash, and guano over the remains (and the entire cave) ensures the integrity of the site. It can be inferred that this removal was due to the reiterative funerary activity in the cave; that is, its repeated use for primary burials and the processing of bodies for secondary burials (Gil 2002).

Three excavation areas were established within the cave (Figure 2c). The first was a 1 × 0.5 m grid located below the drip line (marked with D in the figure), the second was a 0.5 × 0.5 m excavation in the center of the cavity (B), and the third was a 1.0 × 1.0 m area at the bottom, where part of the mentioned disturbance was located (A). This third area was the only one containing archaeological material. The entirety of the collected material, without apparent order, was found at depths of 0 cm and 20 cm. At depths of 20–40 cm, within fine, compacted sands, only minor ash lenses without material remains were discovered. The precise stratigraphy of the site cannot be reconstructed due to the reported disturbance. Photographic documentation from the 1990s illustrates the context of the site, showing the presence of mixed human bone remains (Figure 3; Supplementary Figure 2).

The botanical remains (Supplementary Table 2; Figures 4–6) are curated at the Instituto Venezolano de Investigaciones Científicas (IVIC). Plant determinations were conducted by Stephen Szlatenyi Tillett, former director of the Herbario de la Facultad de Farmacia, Universidad Central de Venezuela.

The maize botanical remains consisted of 24 rachises and one piece of fiber. We classified the fragments according to their origin in the rachis (proximal, medial, distal) and measured the width and length of the rachis as well as the width of the alveoli. A Mitutoyo digital vernier was used for this purpose. The rachises were classified according to the number of grain rows observed.

Skeletal, ceramic, and lithic remains are preserved in the Museo Antropológico de Quíbor (MAQ) and were not further catalogued nor described. These include (1) lithic material: a grinding stone and a slab; (2) three ceramic fragments—one of these exhibited a black-on-white bichrome painting with a curvilinear motif, which is diagnostic of the Tocuyanoid Tradition (400 BC–AD 400; Oliver 1989); (3) disarticulated, fragmented, and unoriented human bones, attributable to multiple individuals,

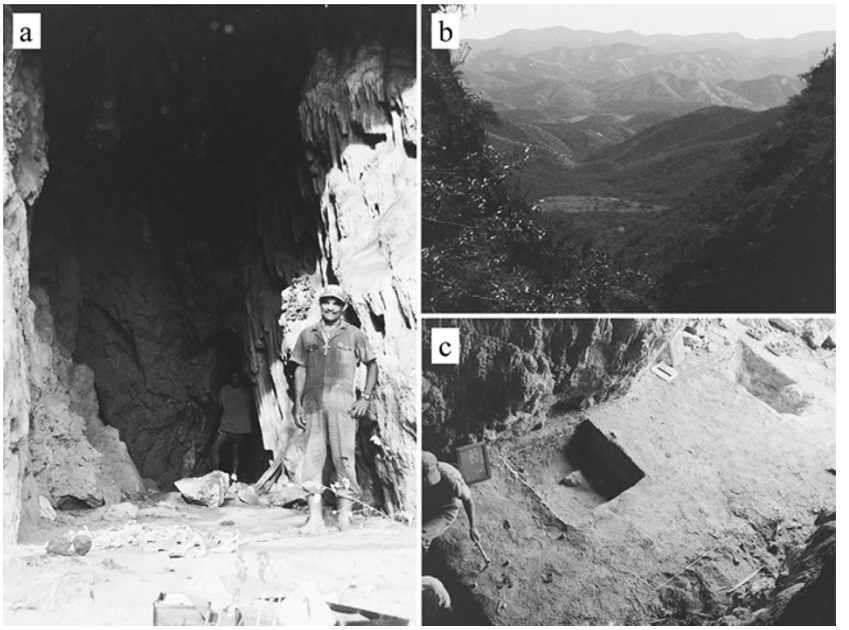

Figure 3. Original photos from the first excavation at the La Capilla site, Lara, northeast of the Venezuelan Andes: (a) entrance to the cave; (b) view of the Andes from the entrance of the cave; (c) excavation grid with a 1 m2 test pit within the excavation area.

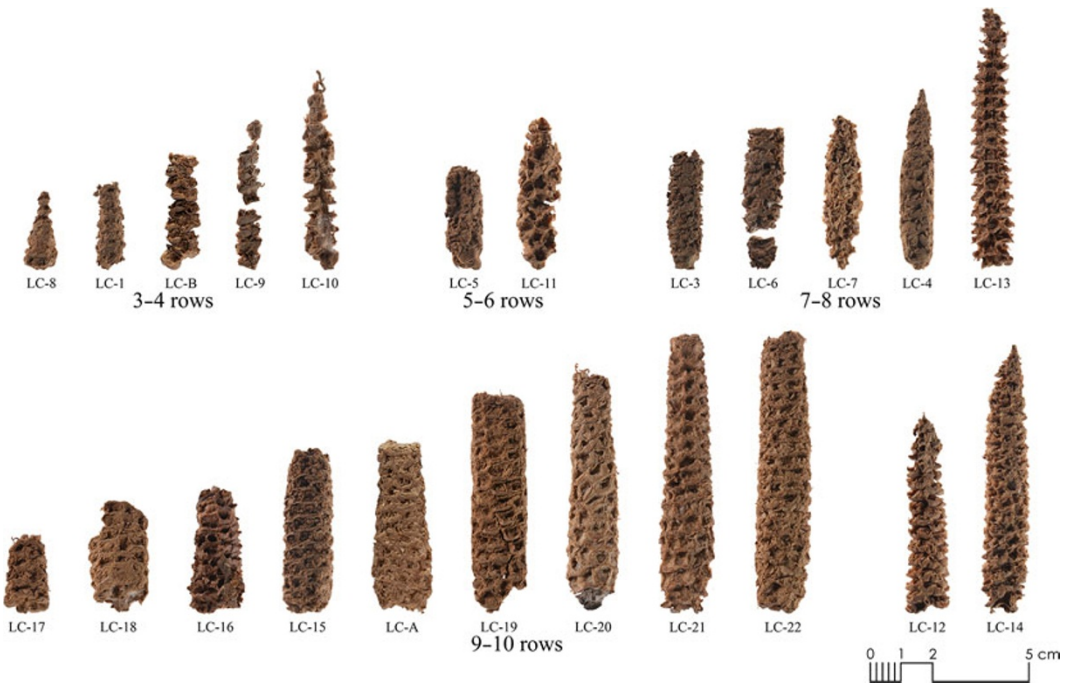

Figure 4. Maize rachis samples from the La Capilla site, sorted by number of rows. Sample LC-2 was excluded from the figure since its number of rows could not be quantified. (Color online)

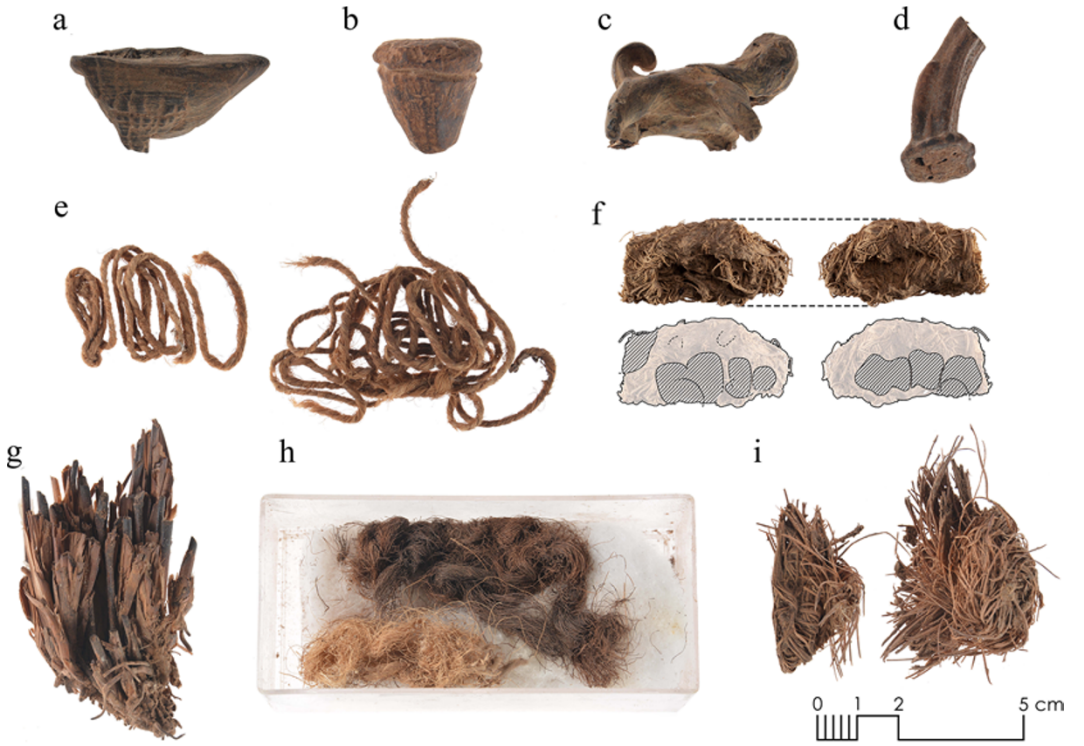

Figure 5. Carved wood and elaborated fibers from the La Capilla site: (a) fragment of carved wood with incised grid pattern; (b) carved stopper; (c) figurine, probably representing a dog; (d) pumpkin cut stem (*Curcubita* sp.) ; (e) strings of nonidentified fiber; (f) maize fibers with mastication marks, with a drawing of the human tooth prints (also named sample LC-C in the aDNA and radiocarbon dating analysis); (g) torch or incense with tied base (Gramineae); (h) braided corn silk; (i) tied nonidentified fibers. (Color online)

which exhibited evidence of cutting at the epiphyses and were presumably encased in fiber material. The wooden slats discovered beneath the remains, consistent with burial practices previously documented in the Lara region (Gil 2002), were found alongside evidence of cutting and dismemberment, a phenomenon also reported at other Tocuyanoid sites (Martín 1976).

Radiocarbon Dating

Seven maize remains were processed for radiocarbon dating at the ORAU using the "VV" pretreatment method (Brock et al. 2010; Table 1). These include different morphologies of maize cob and a piece of supposedly maize fiber with human bite marks. Briefly, the protocol involves a sequence of acid, base, and acid rinses for decontamination. Calibration and Bayesian chronological modeling were done using the IntCal20 curve (Reimer et al. 2020) and OxCal 4.4 (Bronk Ramsey 2009). For the latter, a uniform, single phase was used. Summarization of chronometric data (e.g., Figure 1; Supplementary Figure 1) was done using the KDE_Model function in OxCal (Bronk Ramsey 2017). Calibrated and modeled outputs are reported at the 95.4% highest probability density, with estimates rounded to five years. All OxCal code—needed for reproducibility—is noted in Supplementary Text 1.

DNA Extraction and Bioinformatic Methods

A preliminary genetic analysis was conducted on three specimens of the seven that were also radiocarbon-dated: LC-A (large maize cob), LC-B (small maize cob), and LC-C (pieces of maize fiber with human bite marks). Molecular work was carried out at the Università di Firenze in dedicated ancient DNA clean room facilities, applying strict criteria to prevent contamination during all experimental

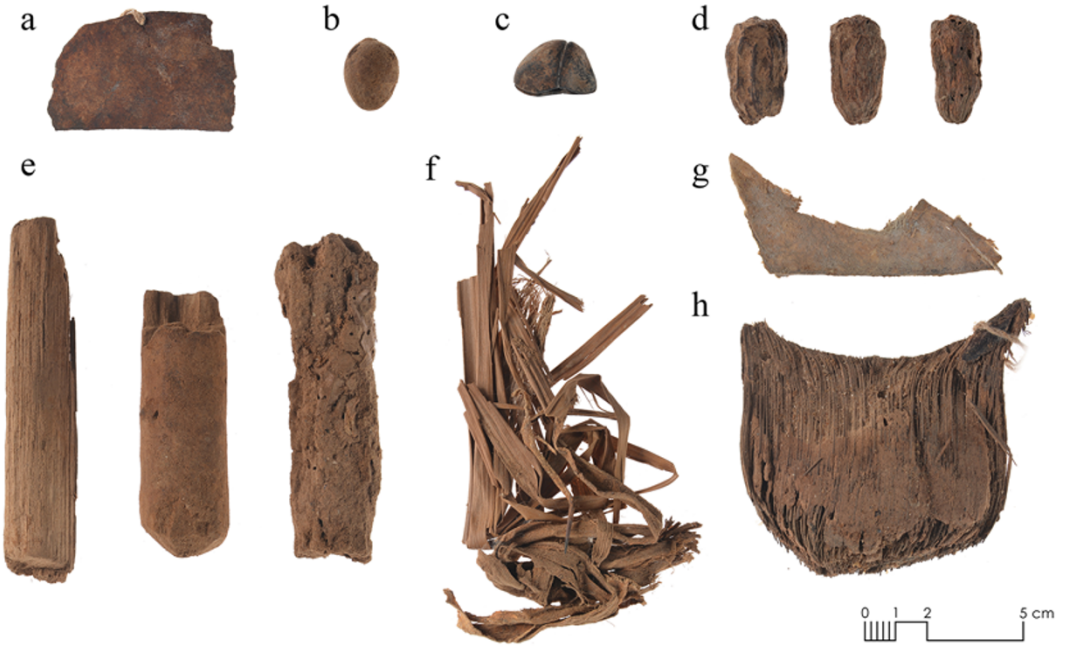

Figure 6. Other organic material from the La Capilla site: (a) fragment of totuma (*Crescentia cujete*); (b) nonidentified hollow seed; (c) cascabel seed (*Thevetia peruviana*); (d) jobo seeds (*Spondias* sp.); (e) fragments of wooden slats; (f) unidentified Gramineae; (g) leather; (h) palm tree bark. (Color online)

Table 1. Chronometric Information for the La Capilla Maize Samples.

Sample	P Code	%C	$\delta^{13}C$ (‰)	Laboratory No.	Date (Years Ago)	±	Date AD (95.4% CI)
LM-LC-A	W	39.9	−8.6	OxA−44116	1644	17	381–533
LM-LC-B	W	43.4	−9.2	OxA−44117	1596	17	424–538
LM-LC-C	W	42.8	−10.9	OxA−44118	388	16	1450–1619
LM-LC−14	W	40.1	−8.7	OxA−44452	1632	19	405–536
LM-LC−10	W	38.6	−9.0	OxA−44453	1649	19	365–533
LM-LC−4	W	37.5	−10.5	OxA−44454	1641	18	381–535
LM-LC−1	W	36.5	−10.1	OxA−44470	1619	16	413–536

Notes: P code: pretreatment method used (see Methods); %C: percentage of carbon in the combusted sample. $\delta^{13}C$ values are expressed in per mille (‰) relative to Vienna Pee Dee Belemnite. Calibration was done using the OxCal 4.4 software and the IntCal20 calibration curve.

procedures. Moreover, blank controls were processed along with the samples during DNA extraction and library preparation to monitor for contamination in the reagents. For a minimally invasive sampling, we took apical parts of specimens LC-A and LC-B, and a solid piece of fibers from specimen LC-C, avoiding the part with the human bite. A scalpel was used to slice each sample into small pieces subsequently pulverized with mortar and pestle. Two samplings were performed for specimen LC-A, the second one with an extra step of UV lights for 10 minutes after pulverization. Approximately 50 mg of powder per sample were used for DNA extraction following a protocol for ancient plant remains as described in Wales and Kistler (2019), omitting the phenol step, as suggested for maize cobs. The extracted DNA was converted into four double-stranded Illumina libraries with double indexes, using established protocols with minor modifications (Meyer and Kircher 2010). Libraries were not UDG treated to keep all the deamination patterns useful to verify the authenticity of the ancient DNA. Quantified libraries were pooled and shotgun sequenced on Illumina NovaSeq 6000 with 2×100+8+8 run parameters. A total of 128,366,534 of raw reads were screened for downstream analysis.

We applied a competitive map approach to classify sequencing reads, inspired by Kjær and others (2022). Specifically, after a preprocessing step in which we removed adaptors with *EAGER* (Peltzer et al. 2016), we mapped reads using Bowtie 2 (Langmead and Salzberg 2012). These were then parsed with SAMtools (Li et al. 2009) and reads shorter than 35bp were filtered out. Ancient DNA Damage profiles were analyzed using DamageProfiler (Neukamm et al. 2021). For competitive mappings including more than two reference genomes, the mapped reads were then assigned to the different taxa using metaDMG (Kjær et al. 2022; Michelsen and Fernandez-Guerra 2022), based on the NCBI taxonomy (Schoch et al. 2020). All genomes present in the NCBI by July 1, 2024, were used as references.

To remove taxonomic assignments to putatively contaminated assemblies in the NCBI we applied a strict filtering scheme in which we removed taxonomic assignments with signatures of false associations, specifically those to unplaced scaffolds for which no additional evidence of a true assignment was found. We filtered out reads associated to *Brassica oleracea* var. *oleracea*, a species for which we found 126, 155, 1,052, and 1,317 reads in LC-A, LC-A_UV, LC-B, and LC-C, respectively, mapped to this genome. Remarkably, while over 90% of the reference genome sits in assembled chromosomes, all reads mapped to five unplaced scaffolds, and zero to the assembled chromosomes. None of the reads mapped to genomes of the same species, except for the specific cultivar *oleracea*. We interpret these reads as possibly deriving from microbial organisms which were assembled in the BOL *Brassica oleracea* var. *oleracea* reference genome.

To estimate the affinity of our samples to known maize lineages, we extracted reads that in our pipeline matched the maize reference unambiguously using all plant species. We then mapped these reads to the B73 NAM reference genome, so that we could compare our samples with a dataset of 1,515 lines of accessions and 46 million high-confidence genetics variants of the genus *Zea*, including the domesticated maize as well as wild progenitors (Grzybowski et al. 2023). We restricted our analyses to LC-A, LC-B, and LC-A_UV, as LC-C did not produce enough authenticated reads. For all samples, due to the low coverage and the impossibility to call reliably estimates, we extracted pseudohaploid calls using bcftools mpileup (Li and Durbin (2009)) and only considered variable sites in modern populations, limiting the effect of ancient DNA errors, which are expected to mostly introduce new variants not shared with existing populations.

Results

Description of Maize and Other Excavated Remains

The maize remains at the La Capilla cave comprise a series of rachises and a fiber with human bite marks. The 24 rachises include samples ranging from three to 10 rows (Figure 4). Their maximal length, proximal, medial, and distal width, and number of rows are presented in Supplementary Table 2. Among the remains, there is also a residue of thick corn trunk fiber with human teeth marks that appears chewed (Figure 5f).

Other organic remains at the site consist of three carved wooden objects, including one zoomorphic figurine (probably representing a dog) and one possible stopper (Figure 5); seeds of at least three species: three seeds of *Spondias monbin* (Anacardiaceae, the same family as that of the cashew), one seed of *Theretia peruviana* (Apocynaceae, dogbane family), a fragment of a totuma (*Crescentia cujete*), and one unidentified hollow seed; burned palm remains; a peduncle of a *Cucurbita* cf. *moshata* (pumpkin); traces of a wooden structure; two braids made of corn silk (*Stigma maydis*); one bark of a palm tree; two cords of unidentified fiber; and a fragment of unidentified leather (Figure 6).

Other remains were reported from the excavation: a funeral bundle with human bone remains (Supplementary Figure 2), as well as ceramic and lithic remains. These were not further cataloged and described and are therefore not included in the present study (see Materials and Methods).

Radiocarbon Dating of the Maize Samples

Samples successfully radiocarbon-dated are noted in Table 1. Sample LM-LC-C (showing human bite marks; OxA-44118; AD 1450–1619) dated considerably younger than the rest of the La Capilla maize measurements. Given that processing standards do not show contamination by young/modern carbon,

Table 2. Mapped DNA Reads for the Four Libraries Obtained from Three Maize Specimens.

	Total Mapped Reads	% Reads Mapped to Maize Total	% Deaminated Reads Mapped to Maize (PMDtools)	% Deaminated Reads Mapped to Human (PMDtools)
LC-A	100	12.0	25.00	3.4
LC-A_UV	139	13.7	26.30	2.5
LC-B	1,914	8.4	36.25	3.6
LC-C	5,314	4.6	35.20	13.6

the discrepancy is likely due to sampling issues or disturbances at the site. When sample C is excluded, a single-phase Bayesian chronological model estimates the date of the cultural event at AD 395–460 (using the "Date" function in OxCal), with a likely duration of up to 85 years (using the "Interval" function in OxCal).

Ancient DNA Analysis: Mapping of Reads to the Maize and Human Genome

We extracted DNA and produced four Illumina libraries (LC-A, LC-A_UV, LC-B, and LC-C) from three maize specimens, following standard procedures in dedicated clean room facilities for ancient DNA analysis (see Methods). Sample LC-A was subjected to a second round of UV treatments, and two libraries were prepared from the same sample. After shotgun sequencing, we first aimed to identify reads that could be mapped to the maize genome and estimate human contamination. To this end, we mapped the reads to a merged genome reference composed of the human genome reference *hg19* and the maize reference genome. The total number of unique reads mapped corresponds to 100 for LC-A, 139 for LC-A_UV, 1,914 for LC-B, and 5,314 for LC-C. For all the libraries, we found reads mapping to maize—though human DNA was relatively high for all libraries, with the highest proportions of reads mapping to maize in LC-A and LC-A_UV (12–14%) and the lowest in the LC-C fibers (4.6%; Table 2). After filtering deaminated reads, we found that a larger proportion of deaminated reads mapped to maize, contrary to the human reads, supporting the hypothesis that human DNA was due to contamination. We suggest caution, however, in interpreting these patterns, as differences in divergence between the human and maize DNA in our samples compared to their available reference genomes might affect the relative proportions of reads. Interestingly, LC-C, which had the highest proportion of human DNA, also had the highest proportion of human deaminated reads, potentially consistent with part of the human DNA being ancient. Damage profiles for reads mapped in maize and humans are shown in Supplementary Figures 3 and 4. In Supplementary Figure 3, we notice how the small number of reads for LC-A and LC-A_UV mapped in maize (12 and 20, respectively) prevented the construction of clean DNA damage profiles, while these were noticeable for LC-B and LC-C. Deamination patterns for humans were more apparent, though less pronounced at the peaks, due to the larger amount of reads (Supplementary Figure 4). Remarkably, human-mapped reads in LC-C appeared noticeably more deaminated than LC-B. The limited availability of authenticated ancient reads prevented the recovery of sufficient nucleotide variants for population genetic comparisons.

Classification of the Reads to Plant Taxa

Second, to verify the uniqueness of the maize classification of the samples, we compared our DNA libraries to the entire NCBI collection of plant genomes. To this end, we first downloaded all plant, protist, and plastid sequences from NCBI, including intermediate taxonomic clades and kingdoms, and used the pipeline described above to map our reads against this dataset. We also added the human *hg19* genome reference to this dataset. To avoid spurious classification and false positives, we discarded taxa for which less than 2% of the mapped reads were classified. To further curb the effect of contamination in the NCBI dataset, for genomes for which chromosome-level assemblies were present, we discarded classified taxa for which >99% of the reads were mapped to the unplaced scaffolds versus actual chromosomes. An example of a plausible contaminant identified through this process is shown in Materials and Methods. The classification is available in Supplementary Table 3, where we report all the reads that

map to species and their corresponding upstream clades. We observed that a large proportion of reads can be assigned to plant genomes, though not specifically to maize. Maize, in addition to humans, was always the second most abundant species for all libraries except LC-C, where an insufficient amount of plant reads forbid a clear classification. Only one other plant species in addition to maize was reported through our screening: a small amount of DNA attributable to *Herrania umbratica* (wild cocoa), a plant native to Colombia, was found in LC-A_UV. This genetic screening provides information on the botanical diversity at the site at a species level, even though further population genetic comparisons were not possible. The preservation at the site is suboptimal, and aDNA studies such as this one necessarily operate on scarce, highly fragmented DNA.

Mapping Variants against Modern Maize Accessions

For samples LC-A, LC-A_UV, and LC-B we could retrieve respectively 24, 15, and 97 informative sites at which our reads overlapped variable biallelic single nucleotide variants in the dataset of Grzybowski and others (2023). We estimate per nucleotide divergence to be about 1% from the reference genome, including sequencing errors and ancient DNA damage, therefore placing our maize specimens within the variance of available maize accessions. We calculated the proportion of mismatches between each of our samples and the 1,515 accessions as the number of informative sites at which a mismatch was observed over the total number of variable sites (Supplementary Figure 4). Samples LC-A and LC-A_UV showed zero mismatch for a substantial number of accessions, specifically 548 for LC-A and 476 for LC-A_UV. This prevents specific inferences for these samples, as the large number of identical accessions matching the limited number of informative sites makes it impossible to identify preferentially related lineages. Remarkably, LC_B returns a more informative distribution, with only 19 lineages showing zero mismatches and an average proportion of mismatches of about 7%. The lineages with zero mismatches mostly belong to the SS group in Grzybowski and others (2023), which includes temperate North American stiff stalk accessions. LC_B has also a small proportion of mismatches with South American accessions, a slightly higher proportion of mismatches with Tropical accessions, and the highest proportion of mismatches with the wild relatives present in the comparative accession database, confirming that the sample is not closely related to wild progenitor types.

Discussion

The excavated evidence indicates a ceremonial site associated with the precontact Tocuyanoid tradition (Oliver 1989), based on style similarities with its type-site, El Tocuyo, in the Lara State (Cruxent and Rouse 1958). The Cueva La Capilla findings offer unprecedented insight into the agricultural, cultural, and funerary practices related to this tradition. The radiocarbon dates obtained (AD 395–460) link the site to the terminal period of the Tocuyanoid tradition, which was previously set at around AD 400 (Oliver 1989). A revision of the ceramic traditions and their chronologies, however, already suggested a possible extension to the temporal span of the Tocuyanoid (Vargas 2024).

The site included a funeral bundle with human skeletons (see Materials and Methods). The finding is remarkable, since only secondary burials in urns (which include only long bones) and direct burials with votive paraphernalia were known for the Tocuyanoid (Arvelo and Oliver 1999). We interpret this context as the evidence of a defleshing stage and preparation of the bones that preceded a secondary burial, which is an activity practiced until recent times by indigenous communities in Venezuela (Finol and Fernández 1999; Reverol 2018; Scaramelli and Tarble 2000). The contents of the bundle—including a seed of *Thevetia peruviana* (commonly used as a rattle), a totuma container (*Crescentia cujete*), and a stopper and Gramineae (likely used as incense)—were probably intended as offerings or artifact fragments for funerary ceremonies. The presence of other plant remains, including evidence of authenticated aDNA traces from *Herrania umbratica*, a plant associated with tropical environments, indicates a greater plant diversity than previously identified in the northwestern Venezuelan archaeological record, suggesting long-distance trade or cultivation of exogenous plants and anthropogenic vegetation landscapes different from those of today.

The further use or specific purpose of the plant remains found within the funerary context cannot be determined, as many of these plants are widely and diversely used by indigenous communities and

contemporary Venezuelan society. For instance, *Crescentia cujete* is commonly used as a container in Barí societies (Lizarralde 1997), for serving food and storing curare by Barí (Perera 1991), in childbirth rituals by the Ye'kuana (Duarte Herrera and Amodio 2006), and in ceremonies intended to ward off evil in Kariña (Delascio 1989). *Thevetia peruviana* is used to make rattles among various Amazonian peoples (Alcantara Rodriguez 2023) and for medicinal purposes (Chauhan et al. 2023). Likewise, *Spondias mombin* is known for its edible fruit and medicinal properties in Warao (Wilbert and Haiek 1991). Notably, some indigenous groups are able to distinguish different varieties within the same species, categorizing them as distinct folk genera (Lizarralde 1997), an ethnobotanical nuance that complicates archaeological interpretation.

The most notable element in Cueva La Capilla is the set of 24 maize rachises. This element, in a funerary context, might represent a deliberate offering such as those documented in the indigenous ceremony of Las Turas, which are still celebrated in the states of Lara and Falcon in Venezuela. In this practice, corn offerings are made to celebrate the harvests (Herrera Pacheco and Contreras Espinoza 2016) and also occur in caves (Sociedad Venezolana de Espeleología 2000).

The contextual record of dated archaeological maize samples of great morphological diversity indicates a genetic diversity of forms, including smaller types with ancestral features together with forms twice as long. A row number less than eight in a cob is considered a "primitive" trait (Costa et al. 2024), while modern domesticated maize has 18–20 rows. Small cob types with a reduced number of rows were retrieved after the domestication process was already advanced (Benz 2001; Piperno and Flannery 2001). Persistence of ancestral morphology was also found in Peruaçu Valley, southeastern Amazonia in Brazil, dating to between AD 940 and 1380 (Costa et al. 2024). Significant phenotypic differences and genetic distance between archaeological maize and landraces were found in the Atacama Desert of Chile (Vidal et al. 2019). Our report agrees with previous studies that suggest the sustained morphological and genetic diversity of the maize population, long after its domestication (Kistler et al. 2018, 2020). The joint occurrence of different maize morphotypes at AD 395–460, some of which could be considered "primitive" and "derived" in the domestication series, is a unique case in South America.

The morphological differences observed between the maize samples (Figure 4) is notable. The rachis with the highest number of rows exhibited less variation in alveolar width, ranging from 0.3 to 0.4 cm (see Supplementary Table 2). This greater uniformity, in contrast to the rachis with fewer rows, can be interpreted as a more derived domesticated type oriented toward increasing grain production. However, fragmentation and the limited number of available elements prevented additional statistical tests or a clear morphological classification. The presence of different contemporaneous morphologies does not yet have an explanation, but it is consistent with a nonlinear domestication process, to the circulation and exchange of seeds, to differentiated functions and uses of maize varieties, to a heterogeneous agricultural landscape, and even to a transitional moment in crop development. Taken together and considering the rest of the plant remains recovered at the site, these scenarios contradict the narrative of the simple, linear dynamics of maize domestication and merit future research.

These findings prompt a deeper exploration of the social and environmental conditions that enabled ancient Venezuelan societies to sustain and cultivate such diversity in a domesticated crop central to their culture. The small number of unambiguously mapped reads does not allow any phylogenetic analysis for the maize samples. Further genetic analysis is necessary to better understand the diversity of these maize specimens and locate their origin within different suggested sources of domestication and spread such as present-day Mexico, the Andes, and a Mesoamerica lowland group that contributed to the Caribbean via a putative route through Venezuela (Bedoya et al. 2017).

The discovery of a chewed residue composed of thick corn trunk fibers suggests a deliberate plant management practice aimed at extending availability and enhancing the consumption of vegetable proteins. This practice has been described in ethnographic reports from Mesoamerica (Mangelsdorf et al. 1967). Groups of Maya origin in Chiapas (Mexico) consume the young trunk of the maize during the summer, while the ears are not consumed until a later phase, after the rainy season, when they have matured and the proteins have migrated from the trunk to the fruits. The human bite marks

here interpreted as mastication marks on the maize stem are direct evidence of a similar practice in Cueva La Capilla (Figure 5). Ancient DNA analysis reveals a percentage of deaminated reads mapping to maize comparable to that found in the other specimens (Table 2). However, due to the limited number of retrieved reads and the stringent screening criteria applied, this match cannot be confirmed with certainty through further analysis of the whole plant reference database (Supplementary Table 3). Nevertheless, this sample exhibits a significantly high proportion of authentic ancient reads mapping to the human reference, consistent with the mastication of fibers by a human.

The compilation of reports of archaeological maize in Venezuela presented in our work is, to our knowledge, exhaustive. However, future research may additionally draw information on the impressions of rachis applied to the bases of ceramic vessels—a known and relatively common but rarely documented feature in the precontact pottery of western Venezuela (Oliver 1989:443).

In conclusion, Cueva La Capilla is a radiocarbon-dated site with a diverse set of maize unique for this region of the continent. Our findings highlight the importance of protecting these caves as valuable sites for expanding our understanding of how ancient communities utilized these environments. We note a total lack of faunal remains that contrasts sharply with the relative abundance of botanical ones. This could be the result of specific activities carried out at the site, selective preservation conditions, or, more speculatively, could indicate that the inhabitants had a diet rich in plants. Additional archaeological information is required to investigate the composition of ancient dietary practices in the broader region.

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Author Contributions. AJ conducted the first excavations at the site of Cueva La Capilla. AJ, CB and MRSV conceived and supervised the study. DV analyzed the material. LBV performed radiocarbon dating and Bayesian chronological modeling. CB coordinated the genetic analysis. ML and AM performed aDNA extraction and sequencing. FM performed bioinformatic analysis. MRSV wrote the first draft of the manuscript; MSV, DV, CB and AJ finalized the manuscript with inputs from all coauthors.

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Data Availability Statement. Ancient DNA raw reads have been deposited in the European Nucleotide Archive (ENA) at EMBL-EBI under project accession PRJEB85740, accession numbers ERR16008941–ERR16008944.

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Supplementary Table 1. Previous Findings of Maize in the Archaeological Record of Venezuela and Associated Radiocarbon Dates.

Supplementary Table 2. Features and Measurements of the Maize Rachis from the La Capilla Site.

Supplementary Table 3. Ancient DNA Reads Assigned to Species and Nodes.

Supplementary Figure 1. Calibrated and modeled radiocarbon data for archaeological phases linked to maize remains in Venezuela. The plot includes the KDE_Model function, as noted in the main text, which was used to summarize sets of radiocarbon ages according to region. Outputs of this analysis are included in Figure 1, with the OxCal code included below.

Supplementary Figure 2. Original photos from the first excavation at the La Capilla site: (a) assemblage of human skeletal remains from multiple individuals, including long and short bones, pelvic fragments, ribs, and vertebrae; (b) excavation pit with human remains, including a scapula, one lumbar and one thoracic vertebra, a proximal hand phalanx, and a possible clavicle fragment, still in place in the excavation context.

Supplementary Figure 3. Ancient DNA damage error profiles for the reads mapped to the maize genome reference, for each of the four libraries.

Supplementary Figure 4. Ancient DNA damage error profiles for the reads mapped to the human genome reference, for each of the four libraries.

Supplementary Figure 5. Analysis of genetic variants against a reference panel of 1515 accessions of genus *Zea*.

Supplementary Text 1. OxCal Code and Supplementary References.

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