Earliest Evidence for Caries and Exploitation of Starchy Plant Foods in Pleistocene Hunter-Gatherers from Morocco

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Earliest evidence for caries and exploitation of starchy plant foods in Pleistocene hunter-gatherers from Morocco

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Dental caries is an infectious disease that causes tooth decay. The high prevalence of dental caries in recent humans is attributed to more frequent consumption of plant foods rich in fermentable carbohydrates in food-producing societies. The transition from hunting and gathering to food production is associated with a change in the composition of the oral microbiota and broadly coincides with the estimated timing of a demographic expansion in *Streptococcus mutans*, a causative agent of human dental caries. Here we present evidence linking a high prevalence of caries to reliance on highly cariogenic wild plant foods in Pleistocene hunter-gatherers from North Africa, predating other high caries populations and the first signs of food production by several thousand years. Archaeological deposits at Grotte des Pigeons in Morocco document extensive evidence for human occupation during the Middle Stone Age and Later Stone Age (Iberomaurusian), and incorporate numerous human burials representing the earliest known cemetery in the Maghreb. Macrobotanical remains from occupational deposits dated between 15,000 and 13,700 cal B.P. provide evidence for systematic harvesting and processing of edible wild plants, including acorns and pine nuts. Analysis of oral pathology reveals an exceptionally high prevalence of caries (51.2% of teeth in adult dentitions), comparable to modern industrialized populations with a diet high in refined sugars and processed cereals. We infer that increased reliance on wild plants rich in fermentable carbohydrates and changes in food processing caused an early shift toward a disease-associated oral microbiota in this population.

Dental caries involves progressive dissolution of the mineral component of dental tissues by organic acids produced during fermentation of food debris by bacteria in dental plaque. The development of carious lesions requires infection by disease-associated oral bacteria, as well as a suitable oral environment for their survival and proliferation (1). Examination of fossil and archeological human dentitions provides direct evidence for the prevalence of dental disease in the past. High caries rates are associated with sedentary food-producing societies that rely on foods rich in fermentable carbohydrates as staples (2–4). Frequencies of carious lesions in archaeological populations range from 2.2–48.1% of teeth for agricultural populations, but only 0–14.3% for hunter-gatherers (4). Analysis of bacterial DNA from ancient calculus deposits provides direct evidence of the disease environment, with recent research pointing toward a shift toward a more disease-associated oral microbiota following the onset of food production (5).

Grotte des Pigeons at Taforalt (Fig. 1) was a key location for ritual and economic activities during the Middle Stone Age and Later Stone Age (Iberomaurusian) (6, 7). Archaeological deposits document a marked intensification in the use of the cave during the Later Stone Age, with the rapid accumulation of thick ashy midden layers, known as the Grey Series, between 15,000 and 12,600 cal B.P. (8). The extreme dryness of the deposits has favored the preservation of organic material, including animal and human bone and charred plant remains. The Grey Series deposits incorporate numerous closely spaced burials of adults, children, and infants in a spatially demarcated area toward the rear of the cave (7, 9, 10). The large number of burials and exceptional preservation of charred macrobotanical remains in contemporaneous occupational deposits provides an opportunity to evaluate both oral health and the role of wild plants in the diet of a preagricultural population.

Methods

New excavations of the Iberomaurusian sequence at Taforalt began in 2003 (Fig. 1 and *SI Methods*). Trenches were located on the south side of the cave (Sector 8) and in a recess at the back of the cave (Sector 10). Human bone samples from Sector 10 were directly dated by accelerator mass spectrometry using ultrafiltration (11) and calibrated by OxCal 4.1. Oral pathology (12), tooth wear (13, 14), and tooth loss (15) were recorded in partial or complete jaws from 52 adults from the Iberomaurusian necropolis. Adults were classified as young ($n = 6$), middle ($n = 16$), old ($n = 3$), or undetermined ($n = 27$) using skeletal indicators (16). Macrobotanical remains were

Significance

We present early evidence linking a high prevalence of caries to a reliance on highly cariogenic wild plant foods in Pleistocene hunter-gatherers from North Africa. This evidence predates other high caries populations and the first signs of food production by several thousand years. We infer that increased reliance on wild plants rich in fermentable carbohydrates caused an early shift toward a disease-associated oral microbiota. Systematic harvesting and processing of wild food resources supported a more sedentary lifestyle during the Iberomaurusian than previously recognized. This research challenges commonly held assumptions that high rates of caries are indicative of agricultural societies.

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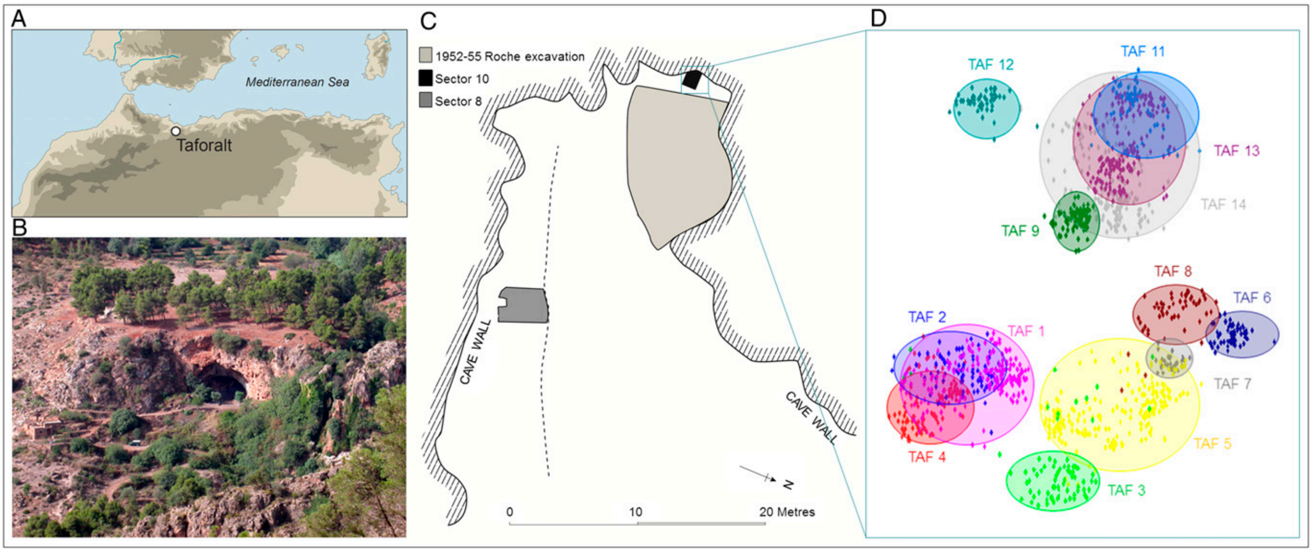

Fig. 1. Grotte des Pigeons at Taforalt. (*A*) Location of the site. (*B*) View of the cave. (*C*) Plan showing Sector 8 and Sector 10 and the hypothesized area of the Iberomaurusian necropolis excavated by Roche during 1954 and 1955. (*D*) Plot of *x-y* coordinates of skeletal elements assigned to 13 partially articulated skeletons excavated from Sector 10 from 2005 to 2013. The approximate location of the primary depositional context of each skeleton is circled and numbered in the same color.

collected from 100 soil samples (349.9 L) from four stratigraphic levels in Sector 8 (Fig. S1). The flot (light fraction) was passed through a column of sieves with a mesh size of 4, 2, 1, and 0.5 mm. Plant fossils were identified using a binocular microscope (8–80× magnification).

Results

The recently excavated Sector 10 (Fig. 1) and the burial deposits excavated by Roche in the 1950s form part of a contiguous and spatially demarcated collective burial area, with numerous closely spaced and intercutting burials. The distribution of articulated and disarticulated bones indicates intensive use and reuse of the area, with earlier burials disturbed or truncated by subsequent burials. Thirteen partially articulated skeletons have been recovered from Sector 10, together with disarticulated bones from additional individuals, including an adult skull (Fig. 1). Seven human bone samples from sector 10 yielded age estimations between 15,077 cal B.P. and 13,892 cal B.P. (Table S1), corresponding to the base of the Grey Series deposits in Sector 8. The skeletons excavated by Roche have not been directly dated, but were recovered from a greater depth of Grey Series deposits than those surviving in Sector 10. Burials situated toward the front of the cave and those higher within the deposits are likely to be progressively younger, and hence contemporary with higher levels in the Grey Series deposits recorded in Sector 8. Burials recovered during recent excavations are primary inhumations of complete bodies (7). The burials excavated in the 1950s include some bones or partial skeletons showing evidence of deliberate post mortem modification, including cut marks and extensive use of ochre (17, 18). This finding suggests a diversification in the treatment of bodies and skeletal parts during the period in which the cemetery was in use (7).

The Iberomaurusian occupants of Taforalt experienced impaired dental function from early adulthood because of a combination of poor oral health, heavy tooth wear, and cultural modification of the anterior dentition (Fig. 2, Table 1, and Table S2). Evulsion of the upper central incisors was recorded in more than 90.0% of adults from Taforalt (19). This intervention is characteristic of Iberomaurusian populations (20); it has a marked effect on dental and craniofacial architecture and limits the masticatory use of the anterior teeth (21). The prevalence of oral pathologies is exceptionally high (Table 1). More than half of surviving teeth (51.2%) exhibited carious lesions and only three of 52 adults showed no evidence of caries. Alveolar resorption affected 58.9% of observed teeth, resulting in exposure of the root surfaces. Root caries were present in 42.9% of individuals and 16.0% of carious teeth. The prevalence of root caries, caries forming at the mesial and distal contact points between teeth, and gross caries, often associated with a complete loss of structural integrity of the tooth, increased with age (Table 1).

Charred macrobotanical remains extracted from contemporaneous occupation layers in Sector 8 (Fig. S1) provide direct evidence of plant foods available and proxy dietary information. Twenty-two taxa were identified (Table 2 and Fig. S2). Acorns from the Holm oak (*Quercus ilex* L.) and pine nuts from the Maritime pine (*Pinus pinaster* Aiton) were the most abundant edible plants. Other edible plants include juniper (*Juniperus*

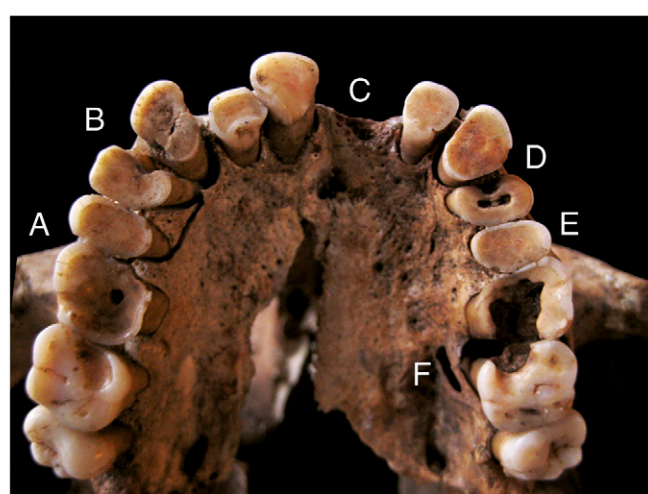

Fig. 2. Oral pathology on the maxilla of Taforalt XI C1: (*A*) heavy tooth wear, (*B*) contact caries, (*C*) evulsion, (*D*) attrition caries, (*E*) gross caries, (*F*) abscess.

Table 1. Number of observed sockets affected by postmortem and antemortem tooth loss and abscesses, and teeth affected by alveolar resorption and caries

	Young adult		Middle adult		Old adult		Undetermined age		Total	
Pathology	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%
Observable sockets	167		287		86		401		941	
Postmortem tooth loss*	25	15.0	36	12.5	9	10.5	104	25.9	174	18.5
Postmortem tooth loss*	10	6.0	23	8.0	22	25.6	40	10.0	95	10.1
Postcanine sockets	107		181		55		256		599	
Postcanine antemortem tooth loss	1	0.9	6	3.3	16	29.1	22	8.6	45	7.5
Abscesses*	2	1.2	9	3.1	17	19.8	23	5.7	51	5.4
Observed teeth	132		228		55		257		672	
Alveolar resorption†	75	56.8	155	68.0	28	50.9	138	53.7	396	58.9
Carious teeth†	44	33.3	125	54.8	29	52.7	146	56.8	344	51.2
Caries type‡										
Crown caries	40	90.9	123	98.4	29	100.0	140	54.5	332	96.5
Attrition caries	38	86.4	112	89.6	27	93.1	129	50.2	306	89.9
Molar fissure caries§	4	3.7	11	6.1	0	0.0	18	7.0	33	5.5
Buccal caries	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Lingual caries	0	0.0	1	0.8	0	0.0	0	0.0	1	0.3
Mesial caries	0	0.0	8	6.4	1	3.5	10	3.9	19	5.5
Distal caries	1	2.3	7	5.6	1	3.5	2	0.8	11	3.2
Pit caries	0	0.0	6	4.8	0	0.0	4	1.6	10	2.9
Rim caries	0	0.0	8	6.4	1	3.5	3	1.2	12	3.5
Gross caries	0	0.0	9	7.2	8	27.6	11	7.5	28	8.1
Root caries	4	9.1	13	10.4	4	13.7	34	13.2	55	16.0

*As percent of observed sockets.
†As percent of observed teeth.
‡As percent of carious teeth.
§As percent of postcanine carious teeth.

phoenicea L.), Terebinth pistachio (*Pistacia terebinthus* L.), wild pulses (*Lens* cf. *nigricans*, *Lathryus* sp., *Vicia* sp.), and wild oats (*Avena* sp.). These plants provide a broad range of nutrients and their representation reveals a preference for plant foods rich in carbohydrates and fats (Table S3). The majority of taxa ripen in autumn with a few ripening in spring or early summer, implying a human presence at the site from at least late spring to autumn. The abundance of acorns and pine nuts points to the deliberate selection of storable seeds with a high nutritional value that could be used as a staple food for most of the year.

Species identifications imply preferential exploitation of sweet Holm oak acorns, which have low tannin content and can be eaten without extensive processing (22). Acorn remains comprise mainly unpalatable parts that would have been discarded before consumption of the seed, such as bases of the acorn shell (abscission scar), shells (pericarp), and cup (cupule) fragments (Fig. 3). The rarity of charred seeds indicates that acorns were consumed raw or underwent an initial processing stage that did not involve the use of fire. The high number of cups points to systematic gathering and storage of unripe acorns, as cups detach naturally once the acorn is ripe. Ethnographic records describe the beating of trees to enable collection of green acorns, as ripe acorns are more prone to be eaten by ground-feeding competitors or infested by insects or fungi (22). Acorns could have been dried and stored, and subsequently peeled and pounded to produce flour or boiled and eaten whole (23).

Similarly to acorns, macrobotanical evidence of pine nuts in Sector 8 is composed primarily of food debris. Remains comprise relatively few seeds but a large number of seed scales, an inedible part of the cone that contains the seed. Pine nuts are typically gathered unripe and stored within their cones. When required, the cones are laid out in the sun or placed over a fire to open the scales and release the seeds for consumption (24). The nuts can be eaten unprocessed as a snack or pounded and boiled to make porridge (24). In *P. pinaster*, nuts are covered by a thin shell (approximately 0.1 mm) and there is no need to unshell the seed before eating.

Charred aerial root (rhizome) fragments of esparto (alfa) grass (*Stipa tenacissima* L.) are common throughout the Grey Series samples. Leaves from esparto grass are a traditional material for basketry and rhizome fragments are a common byproduct of this process. Charred rhizome fragments have been recorded at other prehistoric sites from the Iberian Peninsula and Morocco (25). The presence of these fragments implies that whole esparto plants were uprooted and carried to the site, where the leaves were used to produce basketry and unwanted rhizome fragments discarded into the fire. Baskets produced from esparto grass could have been used for collection, processing, storage, and cooking of seasonal foods, such as acorns.

Discussion

The late Iberomaurusian inhabitants of Taforalt were complex hunter-gatherers as demonstrated by the formation of rich cultural deposits, elaborate burials within a demarcated area, the potential use of grindstones in food preparation, and abundant evidence of systematic harvesting and processing of wild food resources, including acorns, pine nuts, and molluscs (26). The presence of rhizome fragments of esparto grass suggests that they were equipped with baskets and other plant fiber-made tools that could be used to collect, store, and process food plants. Taforalt was clearly a key location for ritual and economic activities but evidence for year-round use of the site is so far inconclusive. The more rapid formation of cultural deposits after 15,000 cal B.P. points toward an intensification of activity involving more prolonged occupation periods or a larger population or both. The cemetery includes complete primary burials, indicating that death occurred within the vicinity of the site (7), but there is some evidence for deliberate secondary deposition of

Table 2. Macro botanical remains from occupational levels in Sector 8

Plant remains	Common name	Yellow Series	Grey Series layers 28–29	24–27	0–23	Total
Avena sp., seed	Wild oat				13	13
cf. *Bromus* sp., seed	Brome		2		2	4
Cariophyllaceae, seed	Pink				1	1
Chenopodiaceae, seed	Goosefoot				1	1
Cistaceae, seed	Rock rose	1				1
Ephedra sp., bract	Ephedra	3	3			6
Fabaceae, seed	Wild pulse		1	2	3	6
Fumaria sp., seed	Fumitory		1		2	3
Galium sp., seed	Bedstraw	9	11		42	62
Juniperus phoenicea L., seed	Juniper		5		109	114
Lens cf. *nigricans* (M. Bieb.) Godr., seed	Wild lentil		1		2	3
Pinus pinaster Ait., seed	Maritime pine		2	2	20	24
Pinus pinaster Ait., seed scale	Maritime pine		28	31	232	291
Pistacia terebinthus L., seed	Terebinth pistachio				64	64
Poaceae, seed	Grass		9		2	11
Quercus ilex L., cupule	Holm oak				5	5
Quercus sp., cotyledon	Oak				14	14
Quercus sp., cupule	Oak		101	76	204	381
Quercus sp., abscission scar	Oak	1	3	2	73	79
Quercus sp., pericarp	Oak				16	16
Rosaceae, seed	Rose	1				1
Rosaceae-type, seed	Rose-type		1		1	2
Rosaceae-type, fruit	Rose-type				3	3
Rubiaceae, seed	Bedstraw				1	1
Sambucus nigra/ebulus L., seed	Elderberry				1	1
Small seeded legume, seed	Wild pulse	1	1		1	3
Stipa tenacissima L., rhizome	Alfa/ esparto		10	3	61	74
Tetraclinis articulata (Vahl) Masters, leaf	Arar				4	4
Vicia/ Lathyrus sp., seed	Wild pulse	1	3	4	15	23
Woody legume, seed	Woody legume				21	21
Indeterminate seed		3	7		17	27
Indeterminate fruit					3	3
Indeterminate nut					8	8
Total number plant remains		20	189	120	941	1270
Volume of sediment in liters		67.1	68.1	23.8	186.7	345.7
Item density per liter sediment		0.29	2.77	5.04	5.04	3.67

skeletal elements with post mortem modifications involving removal of soft tissues (12, 17). These elements may be selected parts of individuals who died elsewhere that were carried back for burial, suggesting that at least part of the community traveled away from the site on a seasonal basis, or may simply reflect an elaboration of funerary behavior over time.

Macrobotanical evidence suggests that the site was occupied from at least late spring to autumn, but both pine nuts and acorns could have been stored, enabling occupation through the winter. The recovery of high quantities of cupules and seed scales indicates that both acorns and pine nuts were systematically collected. Acorns could have been stored unripe and unprocessed (with cupule and pericarp) and then shelled before cooking, whereas pine nuts were probably stored inside the cones. Reliance on edible acorns as a staple food could account for the high caries prevalence at Taforalt because frequent consumption of fermentable carbohydrates is a key factor in the initiation and progression of this disease (2). Exploitation of a variety of acorns as a source of carbohydrates is well documented in the ethnographic record, both historically and in recent times (27). In the Iberian Peninsula, the consumption of sweet acorns from the Holm Oak as a raw food or processed to make flour is attested archaeologically and historically (22). Storage of acorns can lead to an increase in sweetness (23). Processing and cooking of starchy foods, such as acorns, to improve digestibility causes increased food stickiness and reduced food clearance rates within the oral cavity, providing an ideal environment for acid-tolerant bacteria (28). Carbohydrates from other identified food plants, including wild pulses and wild oats, may have contributed to the high caries prevalence at Taforalt. Land snails were intensively collected and consumed during the Iberomaurusian (26), and although these are not known to be cariogenic, abrasive particles present within the snails may contribute to tooth wear (29) and, hence, influence the location of carious lesions.

The rarity of charred acorn seeds throughout the Grey Series implies that acorns were not directly exposed to fire during preparation. Huge quantities of burnt and heat-shattered rock are found throughout the Grey Series deposits and could be the result of deliberate heating of stones for cooking purposes. Heated stones can be used to boil fresh or dried acorns in water-filled vessels made from basketry or animal skin (23). Alternatively patties made from ground acorns could have been cooked directly on heated stones. The high rate of tooth wear observed at Taforalt and the predominance of attritional and root caries are consistent with use of grindstones in food preparation. Incorporation of abrasive particles from grindstones into ground

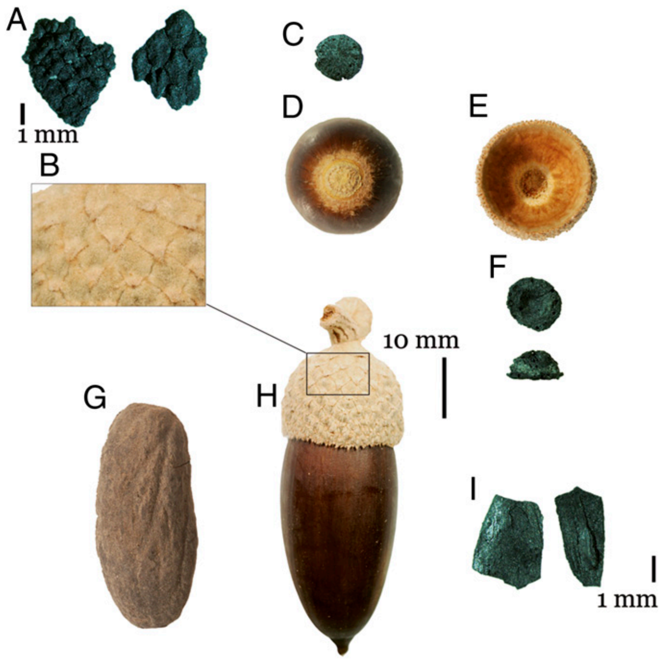

Fig. 3. Modern acorn (*Quercus ilex*) and archaeological specimens from Taforalt: (*A*) scales, archaeological; (*B*) scales, modern; (*C*) abscission scar, archaeological; (*D*) abscission scar, modern; (*E*) cupule, internal side, modern; (*F*) cupule, internal and lateral view, archaeological; (*G*) seed, archaeological; (*H*) acorn, modern; (*I*) Shell or pericarp, archaeological.

foods contributes to rapid attrition of the occlusal surface, leading to continuous tooth eruption to maintain functional dental occlusion and the initiation of caries on worn occlusal surfaces and exposed roots (2, 30). Ochre-stained stones (palettes and mortars) were recovered from recently excavated burial deposits, where they were placed within or directly above individual burials. Previous excavations have recovered grindstones in association with Iberomaurusian burials at Taforalt and Afalou (9, 31). The presence of these grindstones demonstrates knowledge of grinding or pounding activities that could have been used in the preparation of acorns, and their inclusion in funerary deposits suggests that they were accorded a high value.

Starch grains have been recovered on grindstones from Mid-Upper Paleolithic sites in Europe and the Levant, indicating that processing of plant foods was practiced from at least ∼30 ka (32, 33). Starch residues preserved in dental calculus provide direct evidence that Neanderthals consumed cooked carbohydrate-rich foods (34, 35). Despite this, Paleolithic modern humans and Neanderthals have a low prevalence of caries (36). Caries are present in semisedentary Natufian hunter-gatherers from the Levant populations whose diet included wild cereals prepared using grindstones, but at much lower prevalence than at Taforalt (37). The lower rates of caries in earlier and contemporaneous human groups may indicate a lesser reliance on foods rich in fermentable carbohydrates, but may also reflect a difference in bacterial virulence or changes in the pattern and likelihood of transmission between infected and uninfected individuals. Reconstruction of the demographic history of *Streptococcus mutans*, the main causative agent of human dental caries today, indicates an exponential population expansion within a time frame that broadly coincides with the earliest evidence for plant cultivation and domestication ∼10 ka (38). Nevertheless the estimated confidence interval for this expansion (95% confidence interval 3,268–14,344 y ago) does not preclude its onset before the origins of food production and the Taforalt population falls at the upper end of this interval.

The presence of carious lesions in 94% of adult dentitions implies that most, if not all, adults at Taforalt were infected by cariogenic oral bacteria. The colonization, survival, and proliferation of oral bacteria are influenced by a complex interaction of behavioral and environmental factors, as well as bacterial virulence (2, 39). The risk of transmission (colonization) is increased by frequent close contact between infected and noninfected individuals, sharing of food and utensils, and behaviors leading to higher salivary levels of cariogenic bacteria in source individuals, such as poor oral hygiene or frequent snacking on carbohydrate-rich foods (1). Correlates of a more sedentary lifestyle and changes in resource exploitation could have contributed to a high risk of both horizontal and vertical transmission of cariogenic bacteria. Potential risk factors include increased population density and shared childcare, resulting in close contact of uninfected infants with a larger number of potentially infected adults and children. Virulence factors, including adherence ability, acid tolerance, and acidogenicity influence the survival and proliferation of oral bacteria and, hence, the magnitude of pH reduction and the extent of enamel demineralization following fermentation of carbohydrates in the oral cavity (39). The Iberomaurusian occupants of Taforalt may have harbored particularly virulent bacterial strains that spread rapidly among the population, although the specific causal agent has not been identified.

Taforalt presents multidisciplinary evidence linking a high prevalence of caries to a reliance on highly cariogenic wild plant foods, predating other high caries populations and the first signs of food production by several thousand years. Systematic exploitation of wild plant resources may have developed within the context of a semiarid and highly seasonal environment during the latter part of the Iberomaurusian (40). Consumption of carbohydrates among modern hunter-gatherers is highest in groups inhabiting semiarid regions and tropical grasslands (41). Storage of plant foods rich in fat and carbohydrate is a traditional strategy for coping with seasonal food stress (42, 43). Regardless of its origins, this subsistence strategy had profound consequences on oral health. The combination of high caries prevalence, rapid tooth wear, and periodontal disease, together with deliberate removal of the upper central incisors—typically by early adulthood—would have severely compromised use of the dentition for mastication. Periodontal disease has been linked to serious health complications, such as respiratory and cardiovascular disease. Although there is uncertainty of the directionality between oral pathology and systemic health (44), the high prevalence of oral pathology recorded at Taforalt can be interpreted as an indication of overall poor health status with increased disease load and mortality.

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Supporting Information

Humphrey et al. 10.1073/pnas.1318176111

SI Methods

Site Description and Dating. The Iberomaurusian refers to a Later Stone Age industry characterized by microlithic backed bladelets and to the people who produced this industry, and is recorded at numerous sites from inland and coastal areas of the Maghreb (1). A key Iberomaurusian site is Grotte des Pigeons at Taforalt, which is located in the Beni-Snassen Mountains at an elevation of 720 m above sea level, near the border between Morocco and Algeria (34°48′38″ N, 2°24′30″ W). The enormous potential of the site came to light during excavations by Jean Roche (2). Roche described a number of stratigraphic layers containing Iberomaurusian, the upper ones being gray ashy (*couches cendreuses*) and the underlying ones clayey sand (*couches argilo-sableuses*) deposits (2). Excavations in 1954–1955 uncovered an extensive series of Iberomaurusian human burials in gray ashy deposits situated toward the back of the cave (2).

New work on the Iberomaurusian sequence at Taforalt was conducted between 2003 and 2013 (3, 4). Excavation trenches were located alongside the sections dug by Roche on the south side of the cave (Sector 8) (Fig. 1) and in a recess at the back of the cave (Sector 10) (Fig. 1). The Iberomaurusian sedimentary sequence for Sector 8 is 4.8 m deep and is shown in schematic form (Fig. S1). Within the sequence there is a major stratigraphic division between the Grey Series (Roche's ashy deposits) and an underlying Yellow Series (his clayey sands). The Grey Series are essentially anthropogenic sediments, originally more than 4 m thick and spread over an area in excess of 800 m^2. No human burials or other human remains were recovered in Sector 8.

The Iberomaurusian part of the Sector 8 sequence (Grey and upper Yellow Series) has been dated by radiocarbon accelerator mass spectrometry (AMS) using ultrafiltration (5), producing dates on bone and wood charcoal that span the period 20.5–12.6 ka (4). All of the dates lie within the range of the IntCal09 calibration curve (6, 7). The authors provide an earliest calibrated age for the Grey Series of 15,204–14,261 cal B.P. No clear stratigraphic subdivisions were discernible in Sector 10, which is made up of very loose ashy sediments. Burials in Sector 10 were situated within a recess at the back of the cave in an area of restricted height (Fig. 1). Seven human bone samples representing six individuals have been directly dated by AMS using ultrafiltration (Table S1). All samples had good collagen preservation (>2% collagen by weight), carbon content (41–47%), and CN ratio (3.1–3.2), but one sample, bone 4797 (OxA-16663), was very small (starting weight 100 mg) and consequently has a higher SE. The ages have been calibrated by OxCal 4.1 and occur within the same age range as the base of the Grey Series in Sector 8.

Dental and Skeletal Observations. The skeletal sample derives from the Iberomaurusian necropolis excavated by Roche in 1954 and 1955 (2) and recently excavated burials from Sector 10 (3). Preservation was variable, with some individuals represented by complete skeletons, and others only by fragmentary dental remains. In total, 52 individuals were represented by at least a fragment of the upper or lower jaw. All teeth and alveoli were observed in the sample, giving a total of 941 observable sockets.

Age Estimation. Where possible, age estimation was carried out using pubic symphysis morphology, auricular surface morphology, ectocranial suture closure, and sternal rib end changes (8). Based on these observations, the sample was divided into three age categories: young adult ($n = 6$), middle adult ($n = 16$), old adult ($n = 3$), and an undetermined category ($n = 27$).

Dento-Alveolar Parameters. A series of dento-alveolar parameters were recorded by I.D.G. The number of observations for each of these parameters depends on the presence and preservation of teeth and alveoli (tooth sockets). Observed sockets are defined as observable sockets minus sockets affected by postmortem tooth loss (PMTL). Observed teeth are the observable sockets minus sockets affected by postmortem and antemortem tooth loss (AMTL). All teeth were examined with good lighting and a magnification of 4× and 10×. The comprehensive data collection protocol of Hillson (9) was followed and each tooth site scored. For this study, data are summarized into broader categories.

Tooth Wear. Tooth wear was recorded using the Smith system (10) for incisors, canines, and premolars, and the Scott system for occlusal wear in molars (11). Left and right sides are not considered independently and the highest value was used if both sides were present. Tooth wear in upper and lower dentitions has been noted to vary (9), so upper and lower tooth wear rates are considered separately. Mean tooth wear for each observed tooth was calculated for all individuals in the sample. Tooth wear is reported for the whole sample and for subsamples of young adults, middle adults, and old adults (Table S2).

Tooth Loss. PMTL was defined as an empty socket showing no sign of alveolar remodeling (12). PMTL is reported as a proportion of observable sockets. AMTL was defined as an empty socket showing any sign of alveolar remodeling (12). Because of the high prevalence of evulsion of the upper central incisors in the Taforalt sample, we report AMTL as both total AMTL and postcanine AMTL. In both cases, AMTL is reported as a proportion of observed sockets.

Alveolar Bone Resorption (Root Exposure). Alveolar bone resorption was recorded as present if a distance of at least 2 mm was measured between the crest of the alveolar bone and the cemento-enamel junction on any surface of the tooth crown (mesial, distal, lingual, or buccal). Root exposure is reported as a proportion of observed teeth.

Abscesses. Abscesses were recorded by direct observation only and defined as a periapical cavity in the alveolar bone, with relatively smooth walls. Abscesses are reported as a proportion of observable sockets.

Caries Diagnosis. Caries were recorded using Hillson's categories (9). All tooth surfaces were observed for carious lesions. Caries were recorded for the following crown locations: (*i*) occlusal molar fissures, (*ii*) occlusal attrition caries in the dentine, (*iii*) buccal surface, (*iv*) lingual surface, (*v*) mesial surface, (*vi*) distal surface, (*vii*) pit caries, and (*viii*) rim chipping caries. Crown caries refer to the presence of caries on one of more of these locations. A carious lesion was considered present when there was clear penetration in the enamel (score 3 or above). Root surface caries describe lesions affecting any dentine surface below the enamel dentine junction. Gross caries was used when a lesion affected more than one location and its origin could no longer be determined (score 7 or 8). Caries prevalence is expressed as the proportion of carious teeth.

Macrobotanical Observations. Macrobotanical remains, excluding wood charcoals, were examined by J.M. in soil samples from a number of closely spaced columns in Sector 8 (Fig. S1). Samples collected in 2003 comprise three continuous sequences, each located slightly deeper into the cave than the one above. The 2003 samples are numbered (Fig. S1, from top) G88 to G96.3, G96.4 to G96.5 (G96.6 was not sampled), and G97 to G99. Sample G100 and the underlying samples from units Y1 to upper Y4 were collected in 2004–2005. These samples are in stratigraphic order but not in a continuous sequence and were located slightly toward the rear of the cave. Samples collected in 2009–2010 are from a continuous sequence from 10 to 475-cm depth and are numbered MMC 1–54 and MMC 80–130 (there was no actual gap between sample 54 and sample 80). These columns can be cross referenced to a central excavation column with Grey Series layers L1–L29 and Yellow Series layers Y1–Y4. The stratigraphic links between all these columns are shown schematically in Fig. S1; the real lateral distance between the G series (left-outermost) and MCC series (right-innermost) is ~5 m.

Macrobotanical remains were collected by floating each soil sample and then sieving the flot (light fraction) using a column of sieves with a mesh size of 4, 2, 1, and 0.5 mm. A total of 100 samples were analyzed, with a total volume of 349.9 L. The coarse stone fraction was removed from the soil samples on site and is excluded from volume measurements. Density of remains was high, averaging about 3.63 items per liter. In total, 1,273 macrobotanical items were collected. Density of macrobotanical remains is higher in the Grey Series samples than in samples from the Yellow Series, even though the Grey Series samples contain more fine stones than samples from the slower accumulating Yellow Series.

All plant remains are carbonized and very well preserved (Fig. S2). The plant fossils were identified using a binocular microscope (8–80× magnification) and the reference collections of the Department of Historical Sciences, University of Las Palmas de Gran Canaria (Spain) and the McDonald Institute for Archaeological Research, University of Cambridge. Identification to species level was attempted for key taxa. Identification of oak species based on seeds is difficult as there are several species growing in the region that produce edible acorns with a similar shape and size. Identification to species level was only possible if the scales in the cupules were well preserved. Scales in the remains from Taforalt are short, ovate, glabrescent, and apressed (Fig. 3), and these are diagnostic features of *Quercus ilex* (13). Although these data suggest that acorns from the Holm Oak were the focus of gathering, it is possible that other oak species present in the region were also exploited. In the case of pine cones, the scales have a prominent and pyramidal apophysis, a diagnostic feature that enabled identification as *Pinus pinaster* (13). Oak and pine remains occur throughout the Grey Series but only one fragment of oak and none of pine was identified in the Yellow Series samples. The number and range of plant species recorded in the Grey Series is similar in the soil samples collected in 2003–2005 and those collected in 2009–2010 (Table 2). Proportions of different taxa are similar throughout the Grey Series, suggesting that the plant assemblage is homogeneous. Information on ripening times and nutritional value of key plant taxa was assembled from published sources (Table S3).

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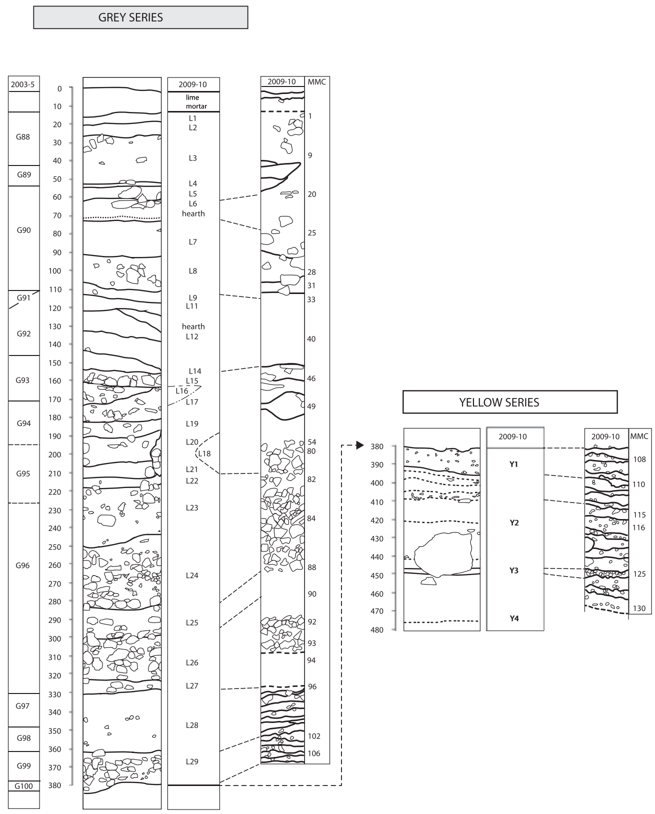

Fig. S1. Schematic section through the Iberomaurusian Grey and Yellow Series deposits in Sector 8, with the units sampled for macrobotanical analysis.

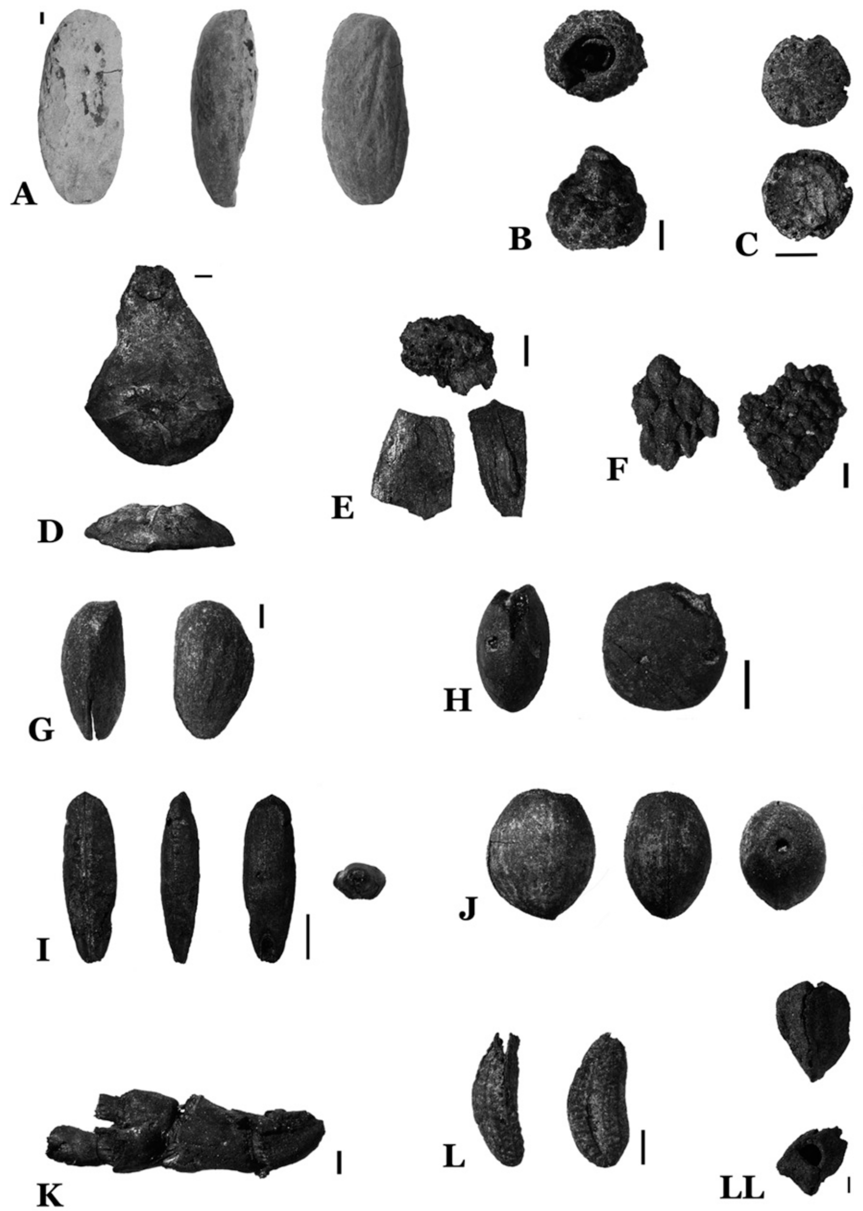

Fig. S2. Macrobotanical remains from Taforalt (scale, 1 mm): (*A*) *Quercus* sp., cotyledon; (*B*) *Quercus ilex*, immature cupule; (*C*) *Quercus* sp. abscission scar; (*D*) *Pinus pinaster*, seed scale; (*E*) *Quercus* sp. pericarp and pericarp still attached to the abscission scar; (*F*) *Quercus ilex*, scales of the cupule; (*G*) *Pinus pinaster*, seed; (*H*) *Lens* cf. *nigricans*, seed; (*I*) *Avena* sp., seed; (*J*) *Pistacia terebinthus*, seed; (*K*) *Stipa tenacissima*, rhizome fragment; (*L*) *Sambucus nigra/ebula*, seed; (*LL*) *Juniperus phoenicea*, seed.

Table S1. Radiocarbon determinations and calibrated ages (IntCal09) of human bone from Sector 10

Sample	Specimen	Layer	^{14}C determination	Calibrated (B.P.) 95.4%
OxA-16663	Infant humerus	Undisturbed primary burial	12470 ± 100	15077–14132
OxA-23660	Adult vertebra	Disturbed context	12380 ± 55	14930–14076
OxA-23778	Adolescent metatarsal	Undisturbed primary burial	12265 ± 50	14824–13920
OxA-23779	Infant humerus	Undisturbed primary burial	12255 ± 50	14805–13908
OxA-23780	Infant clavicle	Undisturbed primary burial	12355 ± 50	14890–14049
OxA-23781	Adult femur	Disturbed primary burial	12410 ± 50	14956–14120
OxA-23782	Adult femur (repeat)	Disturbed primary burial	12460 ± 55	15016–14163

Table S2. Mean tooth wear stages for upper and lower dentition

Upper or lower dentition	Age				Total
	Young adult	Middle adult	Old adult	Undetermined	
Upper					
M3	3	4	9	4	5
M2	5	6	5	6	6
M1	6	8	5	8	7
C	4	5	8	5	6
P4	4	6	8	5	6
P3	4	6	8	5	6
I2	4	5	8	5	5
I1	2	4		2	2
Lower					
M3	3	4	8	5	5
M2	4	6	9	6	6
M1	5	8	10	7	7
C	3	6	7	5	5
P4	3	6	7	5	5
P3	4	5	6	5	5
I2	3	5	4	5	4
I1	3	4	4	4	4

Table S3. Nutritional value and ripening season of the most abundant edible plants identified in Taforalt

Species	Common name	Nutritional value (g/100 g)			Ripening season
		Carbohydrates	Lipids	Protein	
Quercus ilex L. (1)	Acorn	53.0	10.5	3.0	Autumn
Pinus pinaster Aiton (1)*	Pine nut	5.0	51.1	33.2	Autumn
Juniperus phoenicea L. (2)	Juniper	18.0	4.0	5.0	Autumn
Pistacia terebinthus L. (2)	Terebinth pistachio	5.0	61.0	4.0	Autumn
Lens cf. *nigricans*, *Lathyrus* sp., *Vicia* sp. (3)†	Wild pulse	58.0	2.0	26.0	Summer
Avena sp. (4)	Wild oat	55.0	8.0	20.0	Summer
Sambucus nigra/*ebulus* (3)	Elderberry	55.0	1.0	7.0	Autumn
Triticum sp. (5)	Wheat	71.1	2.5	13.6	

Data for wheat provided as comparison.
*Data for *Pinus pinea* L.
†Data for *Lens culinaris* Medik.

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