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The populations of the Near East and nearby regions: evolution of diet and health status from the Neolithization to the Early Bronze Age

Françoise Le Mort, Anne-Marie Tillier

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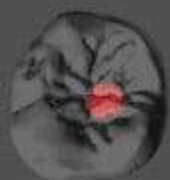
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Coordonné par/coordinated by F. LE MOIT et A.-M. TILLIER

*The populations of the Near East and nearby regions: evolution of diet and health status
from the Neolithization to the Early Bronze Age*

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*Les populations du Proche-Orient et des régions voisines :
évolution du régime alimentaire et de l'état de santé de la néolithisation au Bronze ancien*

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ALIMENTATION, SANTÉ, BIEN-ÊTRE : N'IDÉALISONS PAS LE NÉOLITHIQUE !

FOOD, HEALTH, WELL-BEING: LET'S NOT IDEALIZE THE NEOLITHIC!

J. GUILAINE

La transition néolithique a toujours été l'objet de jugements très contrastés. Pour certains, cette mutation socio-économique s'inscrit dans une trajectoire de progrès, telle qu'on la concevait au XIX^e siècle : la maison pérenne au confort toujours plus amélioré, le village vu comme une fédération de familles solidaires, le territoire exploité par l'agriculture et l'élevage, espace proche aux ressources multipliables à l'envi, la sécurité alimentaire et la possibilité de nourrir un plus grand nombre de bouches. Autant de gains sous-tendus par des avancées techniques toujours plus sophistiquées : le puits, la maîtrise de l'eau, les outils de déforestation et du travail de la terre, le champ et le pré, le fléau et le *tribulum*, l'exploitation minière, l'attelage des animaux, le joug et l'araire, les véhicules à roues, la comptabilité et les scellements, etc.

D'autres s'interrogent sur la réalité de ces « bienfaits », surtout lorsqu'ils sont envisagés dans une perspective historique longue. Le Néolithique est alors perçu comme une prise de distance avec la nature, l'engrenage de la croissance, la première mise à mal de l'environnement (et parfois comme la matrice de l'« anthropocène »), l'artificialisation du milieu végétal et animal, les atteintes à la biodiversité, une forme de banalisation linguistique et la disparition de certaines langues autochtones, l'apparition des inégalités sociales voire des guerres, les germes de tendances vers la domination des masses, l'explosion de maladies jusque-là latentes mais soudain libérées par la promiscuité humaine et animale, etc. Autant de dérives que l'on peut globalement mettre sur le dos de cette transition sans trop s'interroger sur les facteurs de ces perturbations : les choix politico-économiques de l'Homme lui-même. Et ces « pessimistes » de regretter la « société

The Neolithic transition has always been the subject of very contrasting judgments. For some, this socio-economic transformation is part of a trajectory of progress, as it was conceived in the 19th century: the permanent house with ever-improving comfort, the village seen as a federation of families in solidarity, the territory exploited by agriculture and livestock, a nearby space with infinitely multiplying resources, food security and the possibility of feeding a greater number of mouths. So many gains underpinned by ever more sophisticated technical advances: the well, waterbending, the tools for deforestation and for tilling the land, the field and the meadow, the flail and the tribulum, mining, the harnessing of animals, the yoke and the plough, wheeled vehicles, accounting and sealing, etc.

Others question the reality of these “benefits”, especially when they are considered in a long historical perspective. The Neolithic is then perceived as a distancing from nature, the spiral of growth, the first damage to the environment (and sometimes as the matrix of the “Anthropocene”), the artificialization of the plant and animal environment, the damage to biodiversity, a form of linguistic trivialization and the disappearance of certain indigenous languages, the appearance of social inequalities and even wars, the seeds of tendencies towards the domination of the masses, the explosion of diseases which had been latent until then but which were suddenly released by human and animal promiscuity, etc. So many drifts that we can globally put on the back of this transition without questioning too much the factors of these disturbances: the politico-economic choices of Man himself. And these “pessimists” regret the previous “affluent society”,

d'abondance » antérieure, ce supposé « âge d'or » paléolithique dont certains anthropologues ont loué les avantages.

Mais le Néolithique fut-il d'abord bénéfique à la santé et au bien-être des individus ? Question rarement posée. C'est pourquoi Françoise Le Mort et Anne-Marie Tillier ont judicieusement lancé une enquête de caractère alimentaire et sanitaire pour juger en quoi ce changement de genre de vie aurait eu des retombées profitables chez les sujets ayant, au fil des générations, vécu ce tournant capital de l'évolution. Elles ont pris comme cadre géographique le Proche-Orient et ses marges, c'est-à-dire le plus ancien foyer de la planète au sein duquel s'est opérée la transformation des chasseurs en fermiers. Dans le temps, leur enquête a été conduite sur un déroulé de temps long, meilleure approche possible dans la mesure où la néolithisation, loin d'être un processus rapide, s'est en fait étirée sur plusieurs millénaires depuis les premières tentatives natoufiennes de sédentarisation jusqu'aux communautés pleinement agro-pastorales ayant, au-delà des longues phases pré-céramiques, intégré définitivement la poterie à leur équipement domestique. Parfois même, l'investigation débute très tôt, au cœur des millénaires paléolithiques, autre façon de vérifier si des gains sanitaires sont vraiment à porter au crédit de la vie agricole.

De cette minutieuse expertise, les résultats peuvent laisser dubitatif sur les bénéfices de la transition. Il ne s'agit pas pour autant de faire un choix idéologique entre deux modèles socio-économiques mais de mesurer de façon critique et sans *a priori* l'état sanitaire des populations à divers moments de l'histoire humaine, libre au lecteur de se forger ensuite un jugement.

Passons en revue le contenu du dossier. Prenons d'abord un point de repère chronologique très à l'amont, celui de Qafzeh (Basse-Galilée), site dont A.-M. Tillier a analysé la série de 28 sujets laquelle peut donner la « photographie » d'une population anatomiquement moderne, autour de 100000 BC, c'est-à-dire à son stade ancien. Le bilan de cet échantillon de chasseurs-cueilleurs nomades met en évidence des anomalies de croissance, diverses pathologies buccales et osseuses, des lésions traumatiques imputables aux conditions de vie, des caries déjà très présentes, permettant à l'auteur de se demander si tous ces désagréments physiques ne seraient pas pour partie à mettre au compte d'une certaine dérive endogamique.

À partir d'un lot de 558 individus levantins issus de 24 sites et répartis sur une longue durée (13000/6000 BC), A. Stutz, F. Bocquentin, B. Chamel et M. Anton font de leur côté le constat que les stress biologiques enregistrés dès la petite enfance ont eu des conséquences délétères ayant entraîné une mortalité précoce dès l'enfance, l'adolescence et les premiers temps de l'âge adulte. Ces auteurs parviennent ainsi à la

this supposed Paleolithic “golden age” whose advantages some anthropologists have praised.

But was the Neolithic primarily beneficial to the health and well-being of individuals? This question is rarely asked. This is why Françoise Le Mort and Anne-Marie Tillier have wisely launched a food and health survey to judge in what way this change in lifestyle would have had beneficial effects on the subjects who, over the generations, lived through this crucial turning point in evolution. They have taken as their geographical framework the Near East and its margins, that is to say the oldest focus of the planet in which the transformation from hunters to farmers has taken place. In time, their investigation has been conducted over a long period of time, the best possible approach insofar as Neolithization, far from being a rapid process, was in fact stretched over several millennia from the first Natufian attempts at sedentarization to the fully agro-pastoral communities having, beyond the long pre-ceramic phases, definitively integrated pottery into their domestic equipment. Sometimes, the investigation even begins very early, in the heart of the Paleolithic millennia, another way of verifying if sanitary gains are really to be credited to agricultural life.

From this meticulous expertise, the results may leave one doubtful about the benefits of the transition. It is not a question of making an ideological choice between two socio-economic models, but of critically measuring the health status of populations at various moments in human history, without preconceived ideas; the reader is free to make up his or her own mind afterwards.

Let us review the contents of the dossier. Let us first take a chronological reference point far upstream, that of Qafzeh (Lower Galilee), a site where A.-M. Tillier analyzed the series of 28 subjects, which can give a “photograph” of an anatomically modern population, around 100,000 BC, i.e., at its early stage. The assessment of this sample of nomadic hunter-gatherers highlights growth anomalies, various oral and bone pathologies, traumatic lesions attributable to the living conditions, and caries already very present enabling the author to wonder if all these physical inconveniences would not be partly due to a certain endogamic drift.

From a sample of 558 Levantine individuals from 24 sites and spread over a long period of time (13,000/6,000 BC), A. Stutz, F. Bocquentin, B. Chamel and M. Anton have found that biological stresses recorded from early childhood had deleterious consequences leading to early mortality in childhood, adolescence and early adulthood. These authors thus reach the conclusion of a deterioration of the “average well-being” from the moment when the agricultural

conclusion d'une détérioration du « bien-être moyen » à partir du moment où les communautés agricoles se sont renforcées, le tout aboutissant à un impact négatif lors des phases terminales du processus (PPNC et début du PN, aux VII^e et VI^e millénaires BC), constat qui semble trouver confirmation dans la mauvaise santé des Anatoliens de Çatalhöyük. La transition néolithique, dans toute sa complexité interactive, montre une tendance statistique vers une augmentation de la mortalité et de la fécondité, impliquant la nécessité de mieux déterminer les imbrications entre fertilité, mortalité, conditions culturelles et processus migratoires.

Les changements induits par la stabilisation de l'habitat, la vie en communautés plus ou moins importantes, les transformations économiques et sociales, les stress démographiques supposés, les modifications du régime alimentaire : autant de facteurs aux conséquences biologiques. Le bilan que dressent, au Levant Sud, I. Hershovitz, R. Sarig et H. May, à partir d'une large enquête comparative allant des chasseurs natoufiens au Chalcolithique, voire au-delà (périodes romano-byzantine et ottomane) n'a rien de réjouissant. Si les néolithiques semblent moins vulnérables aux crises d'otites que les Natoufiens et les Chalcolithiques, en revanche, d'un point de vue plus général, les nouvelles conditions de vie s'accompagnent d'une certaine détérioration sanitaire : squelettes et mandibules se réduisent en taille et en robustesse au cours de l'Holocène, maladies dentaires, fractures osseuses, lombalgies, obésité et autres problèmes comme les maladies infectieuses sont en progression. À ce constat, les auteurs ajoutent une perte de l'espérance de vie chez les femmes...

Précisément, l'examen des pathologies dentaires s'avère être un bon repère pour évaluer les effets de l'alimentation chez les communautés d'agriculteurs. À partir de sept sites syriens de la séquence néolithique (PPNA, PPNB, Néolithique céramique) proposant un corpus de 4 307 dents attribuables à 312 individus, B. Chamel analyse en quoi la mastication peut engendrer caries, abcès, pertes de dents et maladies parodontales. Elle observe que ces diverses affections ne sont pas solidaires et ne vont pas systématiquement en augmentant avec le temps. Un pic de lésions, correspondant au PPNB moyen-récent (VIII^e millénaire) pourrait être dû à la fixation définitive de l'économie agro-pastorale, embryonnaire jusque-là, et à la morphologie désormais uniforme des céréales consommées. Par la suite, l'usage de la céramique dans la cuisson des aliments a pu entraîner l'adhérence aux dents de résidus, situation favorable au développement de bactéries.

Autre fléau : la tuberculose, dont le moment d'apparition chez les humains fait l'objet de débats. Lorsque le Néolithique est désormais bien établi au Proche-Orient, lors des VIII^e et

communities were strengthened, all leading to a negative impact during the terminal phases of the process (PPNC and beginning of the PN, in the 7th and 6th millennia BC), a finding that seems to be confirmed in the poor health of the Anatolians of Çatalhöyük. The Neolithic transition, in all its interactive complexity, shows a statistical trend towards an increase in mortality and fertility, implying the need to better determine the interrelationships between fertility, mortality, cultural conditions and migratory processes.

The changes induced by the stabilization of the habitat, the life in more or less important communities, the economic and social transformations, the supposed demographic stresses, the modifications of the diet: so many factors with biological consequences. The assessment that I. Hershovitz, R. Sarig and H. May have drawn up for the Southern Levant, based on a broad comparative survey ranging from the Natufian hunters to the Chalcolithic, and even beyond (the Roman-Byzantine and Ottoman periods), is not at all pleasing. If the Neolithics seem to be less vulnerable to ear infections than the Natufians and the Chalcolithics, on the other hand, from a more general point of view, the new living conditions are accompanied by a certain sanitary deterioration: skeletons and mandibles reduce in size and robustness during the Holocene, dental diseases, bone fractures, lumbago, obesity and other problems such as infectious diseases are on the increase. To this observation, the authors add a loss of life expectancy in women...

Specifically, the examination of dental pathologies proves to be a good indicator for assessing the effects of diet in farming communities. From seven Syrian sites of the Neolithic sequence (PPNA, PPNB, Pottery Neolithic) proposing a corpus of 4,307 teeth attributable to 312 individuals, B. Chamel analyzes how mastication can generate caries, abscesses, tooth loss and periodontal diseases. She observed that these various affections are not interdependent and do not systematically increase with time. A peak of lesions, corresponding to the Middle-Late PPNB (8th millennium) could be due to the definitive establishment of the agro-pastoral economy, embryonic until then, and to the henceforth uniform morphology of the cereals consumed. Subsequently, the use of ceramics in cooking food may have favored the adherence of residues to the teeth, a situation favorable to the development of bacteria.

Another scourge: tuberculosis, whose time of appearance in humans is the subject of debate. When the Neolithic is now well established in the Near East, during the eighth and seventh millennia, the presence of the disease is certain, as shown by various cases recognized from settlements in Syria, Israel and Jordan, but evidence concerning the ninth

VII^e millénaires, la présence de la maladie est certaine comme l'ont montré divers cas reconnus à partir d'établissements de Syrie, d'Israël et de Jordanie mais les indices concernant le IX^e millénaire sont très rares. Or, étudiant ici un sujet immature de Tell Aswad, décédé vers 2-3 ans, J. Oussama Baker, B. Chamel et O. Dutour mettent en évidence un nouveau cas probable de tuberculose au IX^e millénaire (PPNB ancien) c'est-à-dire au cœur des siècles au cours desquels se déroulent les processus mêmes de néolithisation et de domestication.

Sur un thème voisin, F. Le Mort et H. Duday évoquent le cas d'un homme adulte de la culture acéramique de Khirokitia (Chypre : VII^e millénaire), atteint de maladie hyperostotique (DISH), excroissances osseuses entraînant la fusion de vertèbres, associée à une arthrose vertébrale. Considérant que le DISH peut être lié à une alimentation trop riche, les auteurs s'interrogent sur le possible statut élevé de l'individu, posant la question d'éventuels dénivelés sociaux au sein de la population de Khirokitia, alors que des divergences de régime alimentaire n'ont pu y être observées à ce jour.

Les dents sont décidément très sollicitées dans ce dossier car elles sont manifestement porteuses de précieuses informations. Les chasseurs-cueilleurs les utilisaient beaucoup lors de leurs diverses activités quotidiennes. Au cours du Néolithique anatolien, on a continué de « travailler avec les dents » mais de telles pratiques se sont atténuées. Pour autant, une divergence semble dès lors s'opérer en fonction du genre et des travaux artisanaux exercés. Y. Selim Erdal a ainsi analysé 8 800 dents permanentes appartenant à 682 individus répartis chronologiquement de la fin de l'Épipaléolithique (vers 10000 BC) à la fin du Bronze ancien (vers 2200 BC). Encore largement attestées au PPNA, phase transitionnelle, les abrasions diminuent significativement dès le PPNB mais essentiellement chez les hommes. En revanche, certaines activités artisanales liées au travail féminin, et notamment tout ce qui concerne les confections à partir de fibres végétales et animales (tissus, paniers, fils, cordages), contribuent à maintenir chez les épouses des processus d'usure de leur dentition.

E. Herrscher et ses collègues ont, pour leur part, porté leur attention à une culture du Bronze ancien de la sphère caucasienne, le Kuro-Araxe (3500-2500 BC), certes en marge de l'aire levantine mais dont les mouvements d'expansion vers l'Anatolie, l'Iran et le Levant ont pu introduire dans ces zones périphériques à son foyer des éléments extérieurs tant génétiques que culturels. Les auteurs ont constaté, au sein de cette entité, une forte homogénéité alimentaire, essentiellement fondée sur la consommation d'orge et de viande d'herbivores, tradition peu modifiée au fil du temps. De ces pratiques codifiées, ils déduisent une politique entretenue de robuste

millennium are very rare. However, studying here an immature subject from Tell Aswad, who died around 2-3 years old, J. Oussama Baker, B. Chamel and O. Dutour highlight a new probable case of tuberculosis in the ninth millennium (early PPNB), i.e. in the heart of the centuries during which the very processes of neolithization and domestication took place.

On a similar theme, F. Le Mort and H. Duday evoke the case of an adult man from the Khirokitia aceramic culture (Cyprus: 7th millennium), suffering from diffuse idiopathic skeletal hyperostosis (DISH), bony outgrowths leading to the fusion of vertebrae, associated with vertebral arthrosis. Considering that DISH may be linked to an overly rich diet, the authors question the possible high status of the individual, which raises the question of possible social differences within the Khirokitia population, whereas divergences in diet have not been observed to date.

Teeth are definitely very much in demand in this dossier because they obviously carry precious information. The hunter-gatherers used them a lot during their various daily activities. During the Anatolian Neolithic period, people continued to "work with their teeth" but such practices became less common. However, a divergence seems to operate from then on according to the gender and the craft works exerted. Y. Selim Erdal thus analyzed 8,800 permanent teeth belonging to 682 individuals distributed chronologically from the end of the Epipaleolithic (around 10,000 BC) to the end of the Early Bronze Age (around 2,200 BC). Still widely attested in the PPNA, a transitional phase, abrasions decrease significantly from the PPNB onwards, but essentially among men. On the other hand, certain artisanal activities related to female work, and in particular everything related to the manufacture of products from plant and animal fibers (fabrics, baskets, threads, ropes), contributed to the maintenance of wear processes in the teeth of wives.

E. Herrscher and her colleagues have, for their part, focused their attention on an Early Bronze culture of the Caucasian sphere, the Kura-Araxes (3,500-2,500 BC), admittedly on the margins of the Levantine area, but whose expansion movements towards Anatolia, Iran and the Levant were able to introduce external elements, both genetic and cultural, into these areas peripheral to its hearth. The authors have noted, within this entity, a strong dietary homogeneity, essentially based on the consumption of barley and meat of herbivores, a tradition that has changed little over time. From these codified practices, they deduce a maintained policy of robust social coherence, thus not excluding any individual from the norm based on family ties and kinship structures.

cohérence sociale n'écartant ainsi aucun individu de la norme fondée sur des liens familiaux et des structures de parenté. Nourriture et pratiques culinaires semblent avoir été de puissants marqueurs culturels et identitaires.

En résumant quelques points essentiels de ce bouquet d'études sur la transition néolithique, le constat ne pousse pas à l'euphorie : stress biologiques de la petite enfance conduisant à des décès précoces, progression des fractures, des maladies infectieuses, des lésions dentaires augmentant avec la consommation des céréales puis de l'usage de la cuisson en pots, tuberculose attestée dès le PPNB ancien, travail des fibres confiés aux femmes les exposant à des détériorations de leur dentition. Si l'on ajoute à ce bilan une diminution de leur espérance de vie, on constate que les femmes paient un tribut certain à la « révolution agricole ».

Tout ceci ne donne guère du Néolithique une image positive sur le plan sanitaire. Tirons-en une conclusion lucide : la recherche permanente de meilleures conditions de vie se solde inévitablement par l'émergence de pathologies jusque-là ignorées ou demeurées latentes. Notre espèce doit donc intégrer qu'elle subira toujours des maladies imputables à son environnement physique et techno-culturel. Les éradications dues au progrès d'une médecine performante pourraient constituer une quête sans fin et toujours remise sur le tapis, une maladie chassant l'autre. Ainsi hier de la tuberculose, aujourd'hui des cancers et du Covid.

Food and culinary practices seem to have been powerful cultural and identity markers.

Summing up some of the main points of this collection of studies on the Neolithic transition, the findings do not lead to euphoria: biological stresses in early childhood leading to early death, progression of fractures, infectious diseases, dental lesions increasing with the consumption of cereals and then the use of cooking in pots, tuberculosis attested to as early as the Early PPNB, work with fibers entrusted to women and exposing them to deterioration of their dentition. If we add to this balance sheet a decrease in their life expectancy, we can see that women paid a certain tribute to the "agricultural revolution".

All this hardly gives a positive image of the Neolithic period in terms of health. Let us draw a lucid conclusion: the permanent search for better living conditions inevitably results in the emergence of pathologies that were previously ignored or remained latent. Our species must therefore integrate that it will always suffer from diseases attributable to its physical and techno-cultural environment. The eradications due to the progress of an efficient medicine could constitute a never-ending quest, one disease chasing the other. Thus yesterday tuberculosis, today cancers and Covid.

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ASPECTS OF HEALTH STATUS IN PRE-SEDENTISM POPULATIONS OF SOUTHWESTERN ASIA. EVIDENCE FROM QAFZEH SITE, LOWER GALILEE

A.-M. TILLIER

Abstract. *The Qafzeh site in Lower Galilee yielded a unique set of early modern Homo sapiens skeletal remains dated to ca. 100 ka BP and represents all age categories from perinatal to adulthood. Numerous and varied developmental abnormalities, dental and bone lesions, are reported that provide insights into life history among these Middle Palaeolithic nomadic hunter-gatherers from Southwestern Asia. Several pathological conditions affecting young subadults enable us to understand childhood mortality in past human populations. In addition, other skeletal variations provide information related to social care and funerary practices among the inhabitants at Qafzeh, ca. 100 ka BP.*

Résumé. *Le site de Qafzeh en Basse Galilée a livré un corpus unique de premiers Homo sapiens modernes datés d'environ 100 BP qui représentent toutes les classes d'âge depuis le stade périnatal jusqu'à l'âge adulte. Nombreuses et diverses anomalies du développement, lésions dentaires et osseuses ont été décrites et informent sur le déroulement de la vie au sein d'un groupe de chasseurs cueilleurs nomades du Paléolithique moyen en Asie du sud-ouest. Plusieurs pathologies affectant des jeunes individus permettent d'appréhender la mortalité des immatures au sein des populations du passé. De plus, quelques-unes d'entre elles informent sur le traitement social et les pratiques mortuaires de la part des occupants de Qafzeh, il y a environ 100 ka BP.*

Keywords. *Qafzeh, Middle Palaeolithic Homo sapiens, palaeopathology, growth disorders, caries, trauma*

Mots-clés. *Qafzeh, Homo sapiens du Paléolithique moyen, paléopathologie, troubles de la croissance, caries, trauma*

The Qafzeh site in Lower Galilee yielded an important collection of human remains (Vandermeersch 1966, 1969a, 1981, 1995; Vallois and Vandermeersch 1972; Tillier 1999; 2014a; Courtaud and Tillier 2005; Schuh et al. 2017; Coutinho Nogueira 2019) that are associated to a Middle Palaeolithic archaeological context. The collection of hominin fossils consists of virtually complete skeletons, partial skeletons, cranial and postcranial fragments and finally isolated teeth corresponding to at least 28 individuals. These individuals represent both subadults and adults that document a broad range of morphological variation, including both non-pathological

variations and pathological conditions. Given the elevated frequency of pathological bone alterations, the Qafzeh human sample holds a key position in the reconstruction of health status of Late Pleistocene hunter-gatherers in Southwestern Asia, prior to the emergence of sedentism. Here we present a summary of pathological features previously described in detail, with reference to these Qafzeh individuals, in the context of this special thematic issue devoted to Late Pleistocene Levantine populations that confronted new life-way conditions.

BRIEF ARCHAEOLOGICAL CONTEXT OF THE QAFZEH HOMININS

The Qafzeh site shows a spatial and temporal concentration of hominin remains that is intriguing. The human remains were unearthed on the terrace in Layers XVII to XXIII that contained a faunal assemblage indicating a prevalence of red deer (*Cervus elaphus*) and fallow deer (*Dama mesopotamica*), followed by a lower frequency of Bovids, Caprids and Equids (Rabinovitch and Tchernov 1995). Animal bones represent the sole information source in the reconstruction of subsistence strategies (Rabinovitch and Tchernov 1995; Vandermeersch and Bar-Yosef 2017), since site formation processes and continuous karstic activities produced some layer brecciation that did not allow for the preservation of plant remains. The lithic Mousterian assemblages published in detail (Hovers 2009) indicate evidence of a preference for Levallois production with less than 10% of retouch pieces, with side- scrapers being the common tool type. The site provides additional evidence for unique Middle Palaeolithic funerary practices, the presence of an engraved artifact, the use of ochre and marine shells associated with the area of the human remains and burials (Vandermeersch 1969a, 1969b, 1970; Tillier 1995; Hovers et al. 1997, 2003; Bar-Yosef et al. 2009; Vandermeersch and Bar-Yosef 2017).

The Qafzeh hominin sample was assigned to Oxygen Isotope Stage 5 by radiometric dates together with biostratigraphic evidence (Bar-Yosef and Vandermeersch 1981; Tchernov 1981; Schwarcz et al. 1988; Valladas et al. 1988). Thermoluminescence (TL) and Electron Spin Resonance/Linear Uptake (ASR/LU) set the range of the Mousterian sequence (layers XVII to XXII) from 92 ± 5 ka BP (TL dates), and 96 ± 13 to 115 ± 15 ka BP (ESR dates—early uptake and late uptake respectively).¹

The Qafzeh hominins document the early stage of anatomically modern human occupation in the Southern Levant (e.g. Howell 1959; Vandermeersch 1981; Tillier 1999). Within this group of remains, individuals who failed to attain reproductive adulthood were present in a high frequency and represent an important component in evaluating the social and overall conditions of health within the community. Several of the adult individuals offer insights into more ephemeral aspects of life conditions in Late Pleistocene hunter-gatherers. Growth-related disturbances as well as traumatic lesions and oral

pathologies have been previously described and discussed for each individual (table 1). This high incidence of skeletal and dental anomalies offers a unique opportunity to integrate relevant information on the health status to aspects of social behaviour in a group of nomadic foragers prior to Neolithization in Southern Levant.

GROWTH-RELATED DISORDERS

At ca. 100 ka BP, skeletal and dental anomalies have affected Qafzeh individuals in childhood to varying degrees (table 1). A few children showed severe skull pathological conditions that prevented normal growth, development and survival processes, and that might be associated with young-age mortality in those individuals (n = 3).

INFECTIOUS DISEASES

A determination of infectious diseases processes on human skeletal remains relies on the recognition of bone changes that are distinct from post-mortem taphonomic modifications. Two young individuals, Qafzeh 11 (ca. 13 years at death) and Qafzeh 12 (ca. 3 years old at death) display clear evidence of inflammatory disease of the middle ear. In the case of Qafzeh 11, alteration of auditory ossicles associated with inflammation of the left mastoid process support the previous diagnosis of otitis media, a common childhood disease of the middle ear (Arensburg and Nathan 1972; Tillier 1999; Quam and Rak 2008).

BENIGN BONE TUMORS

The analysis of micro-CT images of the Qafzeh 9 mandible reveals the presence of a benign tumor located near the mandibular angle of the left ramus that corresponds to a non-ossifying fibroma (Coutinho Nogueira et al. 2019: 106, fig. 4). This bone alteration can develop during growth, and affects both regions of the mandible and long bones. Since non-ossifying fibroma is asymptomatic, its frequency in recent populations is probably underestimated with only 20 cases reported in the literature since 1964.

Most of the skeleton of Qafzeh 10, ca. 6 years of age at the time of death (fig. 1), is preserved. The right femur presents a spherical cavity showing well-defined bony margins (fig. 2A-C)

1. Application of Gamma-ray non-destructive spectrometry to the adult Qafzeh 6 skull (Yokohama et al. 1997) reached similar results.

Table 1 – Dental anomalies, bone lesions and pathological conditions by individual within the Qafzeh hominin sample. For the stratigraphic provenance of the human remains, layer L from Neuville excavations is equivalent to layer XVII from Vandermeersch. Dental age of the children is based upon radiographic data: *ca.* (*circa*) indicates an estimated age using charts of dental development from recent human populations and not an individual's chronological age. PEIR=Pre-eruptive intracoronal resorption. Harris Lines and Linear enamel hypoplasia (LEH) are markers of physiological stress episodes during childhood.

| Specimen | Layer | Age | Oral health | Bone lesion | References |
|-----------|---------|------------------------------------|---|---|---|
| Qafzeh 3 | L | Adult skull remains | 3 carious lesions Dental calculus Periodontal disease | | Boydston et al.1988 Tillier et al. 2004 Trinkaus and Pinilla 2009 |
| Qafzeh 4 | L | ca. 7 years skull remains | 2 carious lesions | | Tillier et al. 2004 |
| Qafzeh 6 | L | Adult skull | Periodontal disease | Minor exocranial supraorbital injury | Tillier et al. 2004 |
| Qafzeh 7 | L | Adult skull remains | 2 carious lesions | | Tillier et al. 2004 |
| Qafzeh 8 | XVII | Adult partial skeleton | Periodontal disease | | Tillier et al. 2004 |
| Qafzeh 9 | XVII | 15-19 years preserved skeleton | 4 carious lesions PEIR on right M ₂ Mesio-occlusion of left I ² | Mandible with non-ossifying fibroma and osteochondritis dissecans Probably injuries on right calcaneus and toe | Tillier et al. 2004 Arensburg et al. 2006 Sarif and Tillier 2014 Coutinho Nogueira et al. 2019 |
| Qafzeh 10 | XVII | ca. 6 years preserved skeleton | Ectopic left I ² (germ) | Craniosynostosis and plagiocephaly, Right femur with chondroblastoma and Harris Lines | Tillier 1999, 2014b Tillier et al. 2004 Dutour and Tillier 2018 |
| Qafzeh 11 | XXII | ca.13 years partial skeleton | Left P ₂ mesio-buccally oriented | Cranio-encephalic trauma Ear lesion and otitis media | Arensburg and Nathan 1972 Tillier 1984, 1999, 2014b Coqueugnot et al. 2014 |
| Qafzeh 12 | XVII | ca.3 years partial skeleton | | Hydrocephalus Otitis media Upper limb hypodevelopment | Tillier 1999, 2014b Tillier et al. 2001 Quam and Rak 2008 |
| Qafzeh 13 | XVa | Perinatal partial skeleton | | Possible porotic hyperostosis ? | Tillier et al. 2004 |
| Qafzeh 15 | XVII | ca. 8-10 years partial skeleton | Left P ₂ agenesis Left M ₂ mesio-buccally oriented | | Tillier et al. 1998 Tillier 1999 |
| Qafzeh 25 | XVII | Adult partial skeleton | Left P ₂ disto-buccally and right M ₃ mesio-buccally oriented | | Schuh et al. 2017 |
| Qafzeh 26 | XVI | Adult isolated tooth | Multiple LEH on lower right C | | Tillier 2014a |
| Qafzeh 27 | XIX-XXI | Non-adult isolated tooth | Multiple LEH on upper right C | | Tillier 2014a |



Fig. 1 – Qafzeh 10 child skeleton in situ (cast M. Chech, photo M. Barazani).

on the disto-lateral surface indicating the location of an epiphyseal tumor. Previously attributed to an osteoid osteoma (Tillier et al. 2004), on further analysis this benign tumor is more likely a chondroblastoma (Dutour and Tillier 2018) that may have caused pain and the temporary restriction of movement (fig. 2B). Harris Lines (markers of physiological stress episode during long bone growth) are visible on the femur X-ray in the metaphyseal area (fig. 2C). Chondroblastoma has a low frequency in extant children (about 1% of bone tumors and 3% of benign tumors) and is not lethal, being more frequent in boys than in girls (e.g., Maroteaux 1982; Resnick et al. 2005).

DISORDERS OF SKULL GROWTH

Qafzeh 10 shows a single premature closure of the coronal suture (fig. 3A-B) that did not affect the intracranial volume, but this early fusion during cranial development (fig. 3C) caused plagiocephaly (Tillier 1999). The position of the coronal suture fusion, along a short distance of its right trajectory, raises questions concerning the aetiology of the synostosis. The presence of an external depressive surface adjacent and posterior to the synostosis is intriguing and suggests a probable link between the two bone alterations.

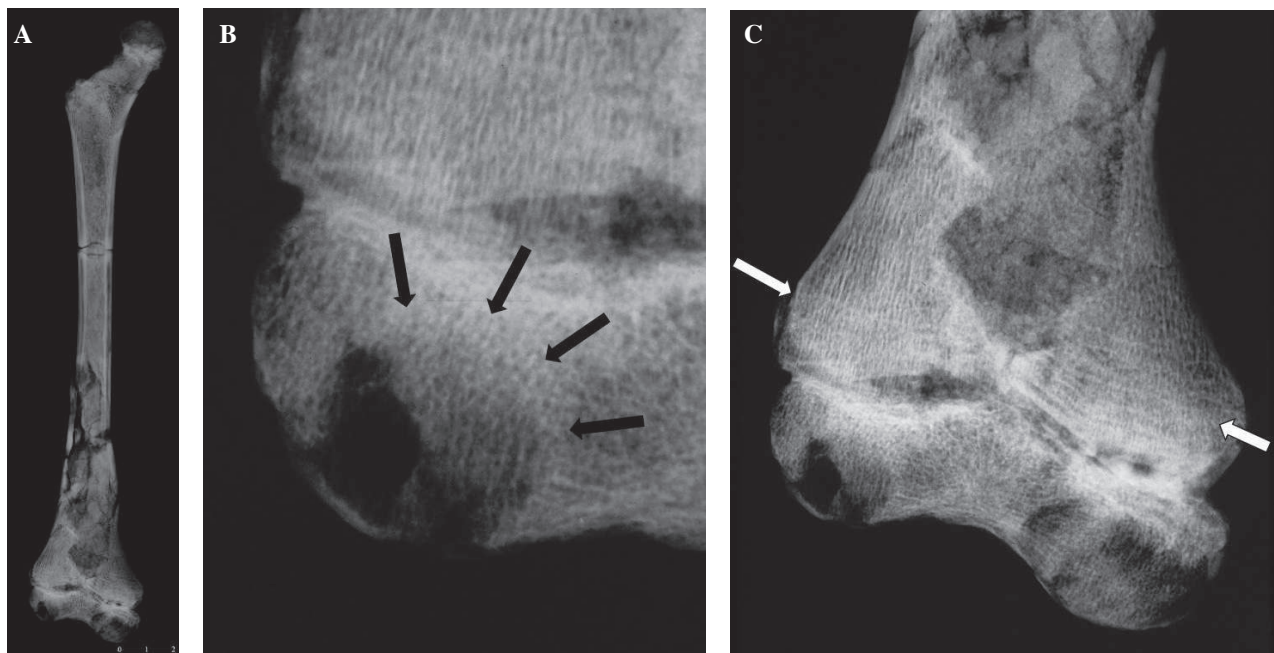


Fig. 2 – Radiographic views of the Qafzeh 10 right femur. **A.** A rounded osteolytic defect, with well-defined margins, can be seen on the disto-lateral part of the epiphysis; **B.** Magnification of the X-ray of the distal femur part showing the bone lacuna (10.3 × 7.8 mm) opening to the articular surface indicating presence of a pathological lesion (chondroblastoma); **C.** Location (arrows) of Harris Lines in the metaphyseal area.

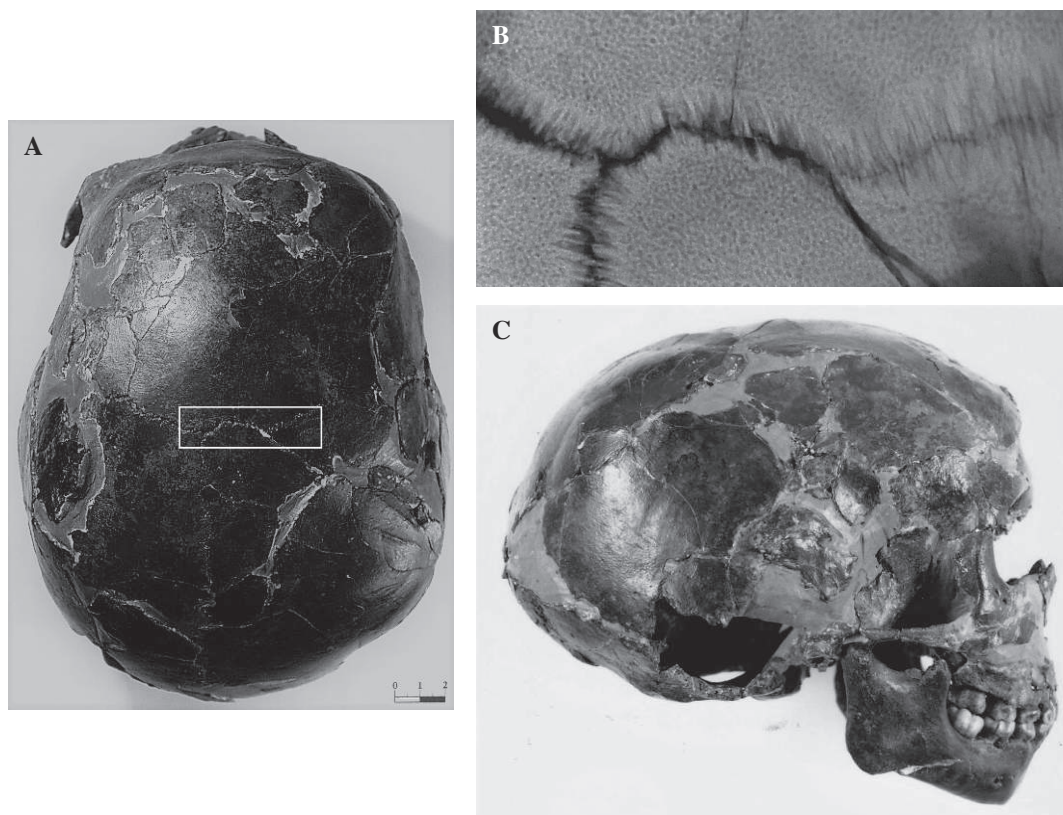


Fig. 3 – Skull of Qafzeh 10 child, ca. 6 years at death. **A.** Norma superior; **B.** Partial radiographic view with local premature closure of right coronal suture; **C.** Norma lateralis illustrating plagiocephaly.

The Qafzeh 12 skeletal remains manifest a serious developmental disorder that explains the young age at death of the child who clearly could not have survived without major medical intervention. The individual shows evidence of several cranial and related postcranial changes associated with hydrocephalus. Evidence of hydrocephalus in the cranium includes: a large anterior fontanelle (fig. 4), patent metopic suture, accentuated sagittal curvature of the frontal bone, increase in skull size, numerous lambdoid suture ossicles and asymmetry in the occipital region (Tillier et al. 2001: 167; fig. 2). The preserved postcranial bones displayed overall hypotrophy and shortness of the upper limb bones (Tillier et al. 2001: 169; fig. 3). Qafzeh 12, who died in early childhood, around 3 years (dental age), offers the earliest evidence of hydrocephalus among prehistoric populations. Hydrocephalus is not unusual in extant populations (2‰ of the children) while reported cases in the archaeological literature remain relatively scarce (Richards and Anton 1991).



Fig. 4 – Superior view of the frontoparietal region of Qafzeh 12 child skull (ca. 3 years old at death, dental age). Margins of the large (39 mm wide, 27 mm long) and asymmetric anterior fontanelle are characterized by long indentations.

BONE TRAUMATIC LESIONS

Bones may show breaks that occurred during life (ante-mortem, and referred to as fractures or trauma) or due to taphonomic processes after death (post-mortem; Waldron 2009). Pathological conditions in two Qafzeh skeletons originally were identified as ante-mortem (Dastugue 1981): a fracture of the calcaneus in Qafzeh 8 adult and the presence of a hallux valgus of the right foot of Qafzeh 9. However, a re-examination of these two individuals found evidence that the changes occurred post-mortem, not ante-mortem as originally described (H. Duday pers. communication; Arensburg et al. 2006²).

Cranial and postcranial ante-mortem trauma of varied severity exist on four other Qafzeh individuals. These result from either minor or major traumatic events.

MINOR TRAUMATIC INSULTS

The Qafzeh 6 adult skull shows a short straight indentation (depressed fracture) on the outer surface of the left supraorbital area. This minor insult appears to be a completely healed wound (Tillier et al. 2004). Qafzeh 9 presents minor traumatic lesions on the right calcaneus and third proximal foot phalanx (Arensburg et al. 2006) that might have produced temporary difficulties in prolonged standing and walking. The mandible of the same individual shows a small rounded defect located on the articular surface of the right condylar process. This defect studied through analysis of micro-CT images appears to be an osteochondritis dissecans (Coutinho Nogueira et al. 2019: 105; figs. 2, 3) which results from micro-recurrent trauma on the temporomandibular joint, due to malocclusion associated with a misalignment of the upper left lateral incisor (fig. 8).

SEVERE SKULL INJURIES

Two immature individuals, Qafzeh 10 and 11, experienced serious difficulties in childhood. On the Qafzeh 10 immature skull, a link between the depressed surface expanding behind the coronal suture and the premature closing of this suture on the right side (as mentioned above) cannot be excluded, in spite of post-mortem damage on these cranial remains (fig. 1).

Medical imaging techniques and especially updated 3D rendered images might enable us to better explore the right frontoparietal area, and determine if both cranial alterations are the consequence of a traumatic injury that the child suffered before his/her death at ca. 6 years.

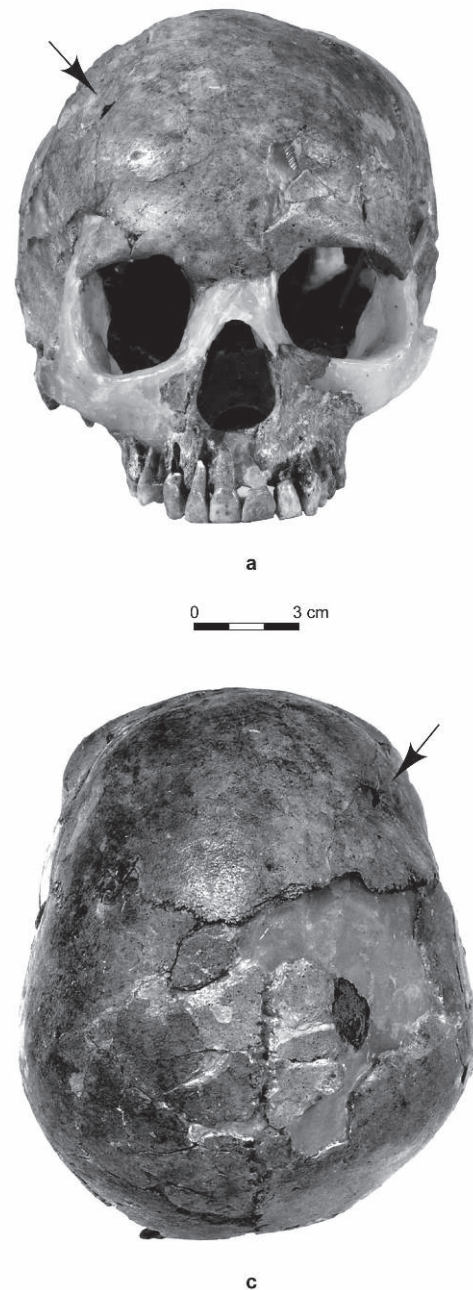


Fig. 5 – Qafzeh 11 skull in norma facialis and norma superior indicating location of the frontal trauma.

2. ARENSBURG B., DUDAY H. and TILLIER A.-M. 2006 – *Approche paléopathologique de la sépulture double de Qafzeh (Israël)*. Communication au Colloque du Groupement des Paléopathologistes de Langue Française, Lille, 25-26 mars 2006.

Qafzeh 11 suffered from severe injury on the right side of the skull (fig. 5) previously attributed to healed trauma (Dastugue 1981). The use of 3D rendered images and virtual reconstruction of the skull and endocranial cast enabled a re-evaluation of the impact of the skull lesion (fig. 6), and established both brain growth delay and neurological damage (Coqueugniot et al. 2014). Although Qafzeh 11 survived the injury for a few years (with motor and psychological disorders), one can reasonably speculate about the disabling conditions that this young individual had to face, which resulted in death at ca. 13 years of age (Tillier 1999; Coqueugniot et al. 2014). The nature of the trauma, accidental or deliberate, remains unknown, although evidence of special treatment of the deceased might exclude interpersonal violence.

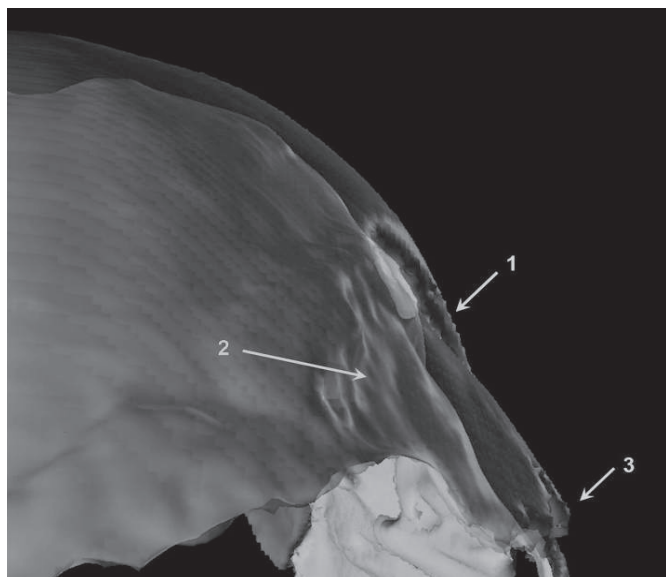


Fig. 6 – Close-up view of Qafzeh 11 skull 3D reconstruction showing in transparency the virtual endocranial cast in the trauma area (3D virtual reconstruction H. Coqueugniot 2014). **1.** Anterior part of the frontal bone depressed fracture penetrating the endocranial volume; **2.** Irregular shape of virtual endocranial surface indicating brain damage; **3.** Diastasis of the right coronal suture.

TOOTH ANOMALIES AND ORAL PATHOLOGICAL CONDITIONS

Analyses of dentition reveal developmental variants (hypodontia, tooth misalignment or rotation, carious lesions) and age-related changes that affected the oral health of Qafzeh individuals.

HYPODONTIA

Qafzeh 15, ca. 8-10 years at death, documents a case of dental agenesis (Tillier et al. 1998: 5; fig. 4). In present-day modern people, congenital absence of teeth in the permanent dentition can occur in the mandible and/or maxilla, and can be uni- or bi-lateral, affecting single or multiple teeth (Alt et al. 1998). Hypodontia or tooth agenesis is the most frequent hereditary dental anomaly, and the most usual missing teeth are the third molar and second premolar. In the case of Qafzeh 15, the left lower second premolar did not develop. It is possible that the right lower second premolar is anagenetic as well, but post-mortem mandible bone breakage in the region of this tooth precludes this assessment. Thus, the presence of a bilateral agenesis of the mandible second premolars remains an open question. The Qafzeh 15 maxillary dentition retains all its teeth.

TOOTH MALPOSITION AND ROTATION

There is no evidence of ante-mortem tooth loss on sufficiently preserved dental arches of Qafzeh hominins (vs. Tillier et al. 2004). At least five individuals (Qafzeh 9, 10, 11, 15 and 25; Tillier 1999; Sarig and Tillier 2014; Schuh et al. 2017) show anomalies of premolar or molar rotation (fig. 7) or position (table 1). Qafzeh 9 manifests a unique case of mesio-occlusion of the upper second left incisor (fig. 8), while the Qafzeh 10 child shows an ectopic germ of the same tooth. Tooth rotation is often considered to be genetically determined in extant populations (see references in Schuh et al. 2017: 57). Multiple incidents at Qafzeh (table 1) might address the question of broad familial relationships among members of the human group.

PERIODONTAL DISEASE AND DENTAL CALCULUS

Recession of the mandibular and maxillary alveolar margin and periodontal disease are common features in extant populations. At least three Qafzeh adults (Qafzeh 3, 6 and 8; Tillier et al. 2004) exhibit alveolar bone resorption. In addition, the preserved upper molars of Qafzeh 3 display evidence of mineralized plaque (dental calculus), together with cervical polished grooves resulting from the use of a tooth pick (Tillier et al. 2004: 138; fig. 1).



Fig. 7 – Superior view of Qafzeh 11 mandible showing the mesio-buccally orientation of left second premolar.

ENAMEL AND DENTINE HYPOPLASIAS

Linear Enamel Hypoplasia (LEH; a dental indicator of early life stress episodes) are identified on 2 isolated teeth (Qafzeh 26 and 27; Tillier 2014: 16, 19; figs. 2, 5). A low incidence of LEH may indicate either that stressful events occurred late in growth (i.e. after tooth crown completion) or that young immature individuals died before the body had time to respond

to the systematic cause (developmental disturbance, infection, trauma, nutritional deficiency etc.) responsible for the formation of such enamel defects. However, additional data brought from an application of micro-CT analysis allowing virtual reconstruction of permanent tooth germs might challenge this conclusion.

Exploration of micro-CT images of the Qafzeh 9 mandible indicates a defect on the second permanent molar crown; this defect below the dentin-enamel junction (fig. 9) corresponds to a pre-eruptive intra-coronal resorption (PEIR). The aetiology of this type of defect is still debated in extant populations due to its low frequency (Coutinho Nogueira et al. 2019). However, the usual consequence is a weakening of the dental structure and tooth defects such as caries.

CARIES RATE

A multi-factorial and complex aetiology for the occurrence of caries in modern people is currently accepted (Caselitz 1998). Yet most paleoanthropologists and archaeologists often considered caries dietary in origin, and changes in subsistence practices over time as the major category of cariogenic agents. Accordingly, low caries rates in Pre-Neolithic populations are routinely accepted.

Four Qafzeh individuals (table 1) show carious lesions on deciduous (Qafzeh 4) or permanent teeth (Qafzeh 3, 7 and 9). More than one defect is found in each individual (Tillier et al. 2004: 138; figs. 1, 10). The number of affected teeth (11 incisors and molars) is notable in association with four other cases

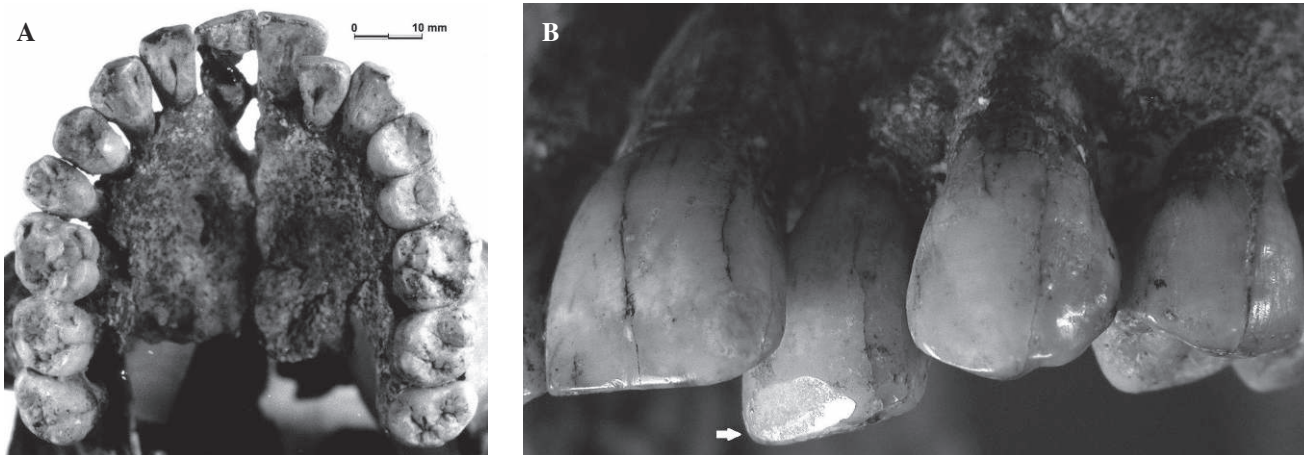


Fig. 8 – Qafzeh 9 palate. **A.** Superior view indicating the mesio-occlusion of left lateral incisor; **B.** Buccal magnified view of the tooth with the arrow pointing the wear facet impacted by malocclusion (photos A. Pinchasov and H. Duday).

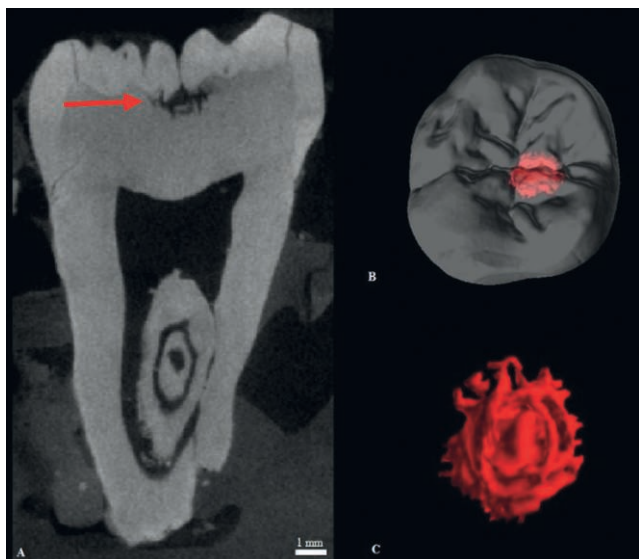


Fig. 9 – *A. Micro-CT slice of Qafzeh 9 lower right second molar with arrow pointing the dentine defect; B. 3D reconstruction of the tooth and pre-eruptive intracoronar resorption; C. 3D reconstruction of the defect (3D virtual reconstructions D. Coutinho Nogueira, 2019).*

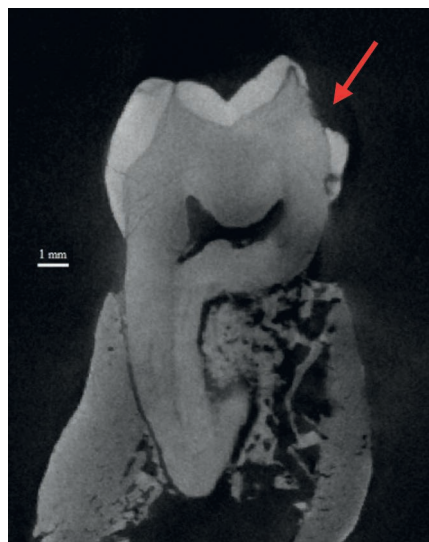


Fig. 10 – *Micro-CT slice of the lower left first molar of Qafzeh 9 with arrow pointing the carious lesion (3D virtual reconstructions D. Coutinho Nogueira).*

reported from other Middle Palaeolithic hominins in Southern Levant Amud 1, Skhul II, Kebara 27 and Hayonim 20 (Sognaes 1956; Tillier et al. 1995, 2004, 2014a, 2014b).

From a paleopathological perspective, comparative data from more recent individuals might produce a more synthetic work on caries rates in Southwestern Asia before the onset of food production. As yet there are very few, and often fragmentary, human remains from the early phases of the Upper Palaeolithic, according to either lithic assemblages or uncalibrated ¹⁴C BP dates, or both. These sites include Ksar Aqil in Lebanon (Ewing 1947; Bergman and Stringer 1989; Tillier and Tixier 1991), Hayonim, El Wad, Qafzeh and Manot Caves in Israel (McCown and Keith 1939; Arensburg et al. 1990; Vandermeersch et al. 2013; Sarig et al. 2019) but individuals from these sites do not include comparative data on caries. The human fossil record dated to late Upper Palaeolithic and early Epipaleolithic (23,000-14,500 BP) is unfortunately also sparse (Hershkovitz et al. 1995). Two carious lesions on the right upper third molar were recently reported from the Ohalo II H2 adult specimen dated to 19,000 BP (Willman and Lacy 2020).

Therefore, the data collected from the Qafzeh dental remains is the only comparative material that can be used for the Late Epipaleolithic (Natufians) and Neolithic populations of the Near East in the context of paleobiological research (Bocquentin 2003; Chamel 2014 and present volume: 83-96; Le Mort 2017). In the latter sample, the recorded dental caries rates document

inter-population variation among social groups who have experienced new dietary habits influenced by food production (table 2). Therefore, the frequency of carious lesions at Qafzeh deserves special attention in conjunction with the comparative data (table 2) assessed from the Natufians (Bocquentin 2003) or Neolithic inhabitants from Cyprus (Le Mort 2017).

Table 2 – *Diachronic variation in caries rates among Near Eastern past populations.*

| Populations | % affected teeth | References |
|---|------------------|---|
| Qafzeh 92 ± 5 ka BP (277 teeth) | 3.9% | Boydston et al. 1988; Tillier et al. 2004; Trinkaus and Pinilla 2009; Tillier 2014; Coutinho Nogueira et al. 2019 |
| Natufians 14-10th mill. BC (3,191 teeth) | 2.5% | Bocquentin 2003 |
| Cyprus 7th mill. BC (1,589 teeth) | 3.5% | Le Mort 2017 |
| Levant 8th mill. (962 teeth) | 10.4% | Chamel 2014, present volume: 83-96 |
| Levant 7-6th mill. BC (715 teeth) | 13.0% | Chamel 2014, present volume: 83-96 |

CONCLUDING REMARKS

The Qafzeh hominins are one of the richest Middle Palaeolithic samples ever recovered from Southwest Asian sites. This group of nomadic hunter-gatherers living in the Near East prior to sedentism and invention of agriculture display several growth anomalies, oral and bone pathological conditions, and traumatic lesions. Indeed, Qafzeh people occupy a key-position by the elevated number of recorded pathological conditions (minor and major), by comparison with the few pathological features described for other Mousterian inhabitants of the Mediterranean Levant, at Skhul (McCown and Keith 1939) and Kebara (Duday and Arensburg 1991).

Dental decay is observed on Qafzeh teeth, eleven show lesions that are mostly in the enamel, one (Qafzeh 9, see above) shows a carious lesion located at the dentine-enamel junction. The number of caries-affected individuals is substantial given the six dental cases reported for all Neanderthals in Europe (Arnaud et al. 2017). Finally, these findings point to a potential difference in immune response from dental disease between the two populations.

Several bone lesions and pathological cases (e.g. ossifying fibroma, osteochondritis dissecans, chondroblastoma, hydrocephalus, plagiocephaly) are for the first time identified in a Pre-Neolithic population. In three documented cases (Qafzeh 10, 11 and 12), relationships between the aforementioned bone lesions and the death of the individuals are strongly associated. Furthermore, few skeletal and dental variants are either exceptional in present-day modern people, or are known to have a strong genetic component (see above). This occurrence indicates probable isolation and/or an endogamic component of the Qafzeh inhabitants during the Middle Palaeolithic. Interestingly, in contrast with other Levantine sites, the radiometric dates seem to favour a relatively short Mousterian occupation span at Qafzeh (Valladas et al. 1988). With regard to the nature of human occupation, “the predominance of micromammals suggest a period when the site was used only occasionally for special activities” (Bar-Yosef 2000: 122). Indeed, the archaeological documentation from the Qafzeh site provides a wealth of information about behaviour patterns of Late Pleistocene nomadic hunter-gatherers, with the presence of deliberate burials (Vandermeersch 1969a, 1970; Tillier 1995, 2009) that shed light on the care taken for the deposition of the deceased.

The inhabitants might have used Qafzeh Cave as their burial ground, while their basecamp might have been located somewhere near the cave (Bar-Yosef 1989). In addition, the paleopathology survey in the Qafzeh skeletal remains provides

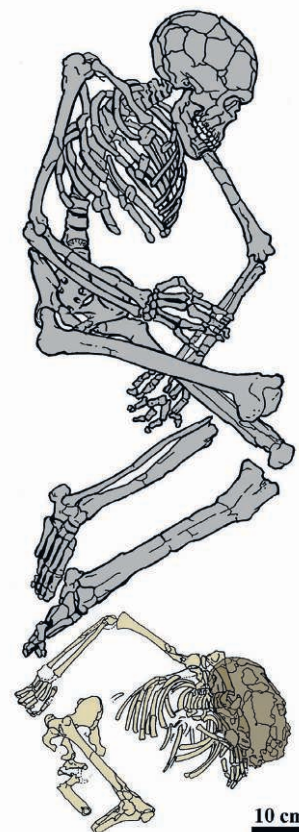


Fig. 11 – The double primary burial associating Qafzeh 9 and 10 (after a drawing by D. Visset in Tillier 1995). The two deceased were buried in a narrow pit (ca. 1.5 m long and 0.5 m large) and the corpses decomposed in a filled space.

insights into the social system and care of unhealthy individuals within the group. Unfortunately, in the case of Qafzeh 12, the hydrocephalous young child, questions concerning the taphonomic effects on the human remains are difficult to address since diagenetic processes certainly altered the skeletal remains to some degree. Interestingly, Qafzeh 9 and 10, both of whom exhibited tooth and bone lesions, were disposed together in a narrow, filled grave (fig. 11), documenting the earliest case of deliberate multiple burial in past populations. Due to the lack of successful aDNA, a familial relationship between these two deceased individuals can only be postulated by using phenotypic traits genetically driven (epigenetic dental and skeletal variants) that are present on both individuals (Tillier 1999). This excludes a maternal filiation since Qafzeh 9 whose age at death is estimated between 18.5 and 20.5 years is of male sex (Coutinho Nogueira et al.³). Finally, Qafzeh 11,

3. COUTINHO NOGUEIRA D., COQUEUGNIOT H. and TILLIER A.-M. n.d. – Qafzeh 9 early modern human from Southwestern Asia: a re-evaluation of age at death and sex estimation, submitted.

the injured subadult individual, was clearly subject to a unique ritual treatment at death (fig. 12): his/her hands were placed near the face during burial, with two fallow deer antlers intentionally placed in close contact. The hands location in conjunction with the uniqueness of the position of the animal bones, support the interpretation of a funerary offering.

In sum, the unusually high concentration of human remains at Qafzeh offers a unique opportunity to associate relevant health status information to aspects of social behaviour in a group of nomadic foragers prior to Neolithization in Southern Levant.

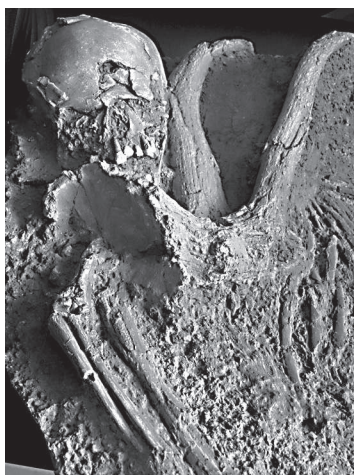


Fig. 12 – Partial view of Qafzeh 11 burial showing the deposit of the red deer antlers in close contact with the hands of the deceased (cast).

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THE EFFECTS OF EARLY CHILDHOOD STRESS ON MORTALITY UNDER NEOLITHIZATION IN THE LEVANT: NEW PERSPECTIVES ON HEALTH DISPARITIES IN THE TRANSITION TO AGRICULTURE

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Abstract. *This study investigates the causal relationships among early-life health conditions, mortality across the lifespan, and population growth during neolithization in the Levant. We analyze a comprehensive sample of 558 human skeletons, associated with mortuary features from 24 Levantine sites spanning the transition to agriculture, from the Early Natufian period to the Pre-Pottery Neolithic C (Southern Levant) and Pottery Neolithic periods (Northern Levant), mainly covering 13,000-6,000 BC. We find that early-life stress—as preserved in linear enamel hypoplasias (LEH) that we recorded in the study sample—not only increased dramatically in prevalence with the adoption of agriculture and village life. Early-life stress was also strongly associated with mortality in the juvenile, adolescent, and younger-adult life stages (ca. 5-29 years). This statistical link is independent of analysis of raw life-stage-at-death distributions, which may be heavily biased by ancient age or sex-skewed funerary recruitment practices. According to our results, biological well-being deteriorated with the adoption of agriculture and village life between ca. 9,000-6,000 BC. We find that the transition to agriculture raised risks for premature mortality across the Levant. We suggest that in the regional transition to agriculture, mortality and fertility rose together in a fragile dynamic, the balance of which may have shifted in the 7th millennium BC, as a rapid rise in early-life stress exposures reduced average well-being.*

Résumé. *Cette étude examine les relations de cause à effet entre l'état de santé des jeunes enfants, le taux de mortalité et la croissance de la population pendant la néolithisation du Levant. Nous analysons un échantillon de 558 individus découverts en contexte funéraire provenant de 24 sites qui couvrent la transition néolithique, du début du Natoufien au Néolithique précéramique C (Levant sud)/début du Néolithique céramique (Levant nord), soit entre 13000 et 6000 cal. BC. Nous constatons que le stress biologique en début de vie, identifié à travers les hypoplasies linéaires de l'émail dentaire (LEH) que nous avons enregistré sur l'ensemble du corpus, a augmenté de façon spectaculaire en termes de fréquence avec l'adoption de l'agriculture et de la vie villageoise. Nous constatons également que ces marqueurs de stress précoces sont fortement liés à la mortalité des enfants, des adolescents et des jeunes adultes (environ 5-29 ans). Cette corrélation statistique est indépendante de l'analyse des distributions par âge au décès, qui peut être fortement biaisée par le recrutement funéraire des défunts sur des critères liés à l'âge au décès et au sexe. Selon nos résultats, l'état de santé s'est détérioré avec l'adoption de l'agriculture et le développement de la vie communautaire entre 9000 et 6000 cal. BC. Nous constatons que la transition vers l'agriculture a entraîné une augmentation de la mortalité précoce dans tout le Levant. Nous suggérons que, lors de cette transition régionale vers l'agriculture, la mortalité et de la fertilité se sont développées en suivant une dynamique fragile, dont l'équilibre s'est rompu au VII^e millénaire av. J.-C. avec un développement fulgurant des stress biologiques en début de vie, et une réduction de l'état sanitaire général.*

Keywords. *Transition to agriculture, Levantine Epipaleolithic, Levantine Neolithic, Heterogeneity in frailty, Developmental origins of health and disease, Linear enamel hypoplasia, Paleodemography, Premature mortality*

Mots-clés. *Transition néolithique, Épipaléolithique levantin, Néolithique proche-oriental, variabilité de la fragilité, Origines Développementales de la Santé et des Maladies (DOHaD), hypoplasies linéaires de l'émail dentaire (LEH), Paléodémographie, mortalité précoce*

“Life is not so easy.”

Ofer Bar-Yosef

INTRODUCTION

The Natufian archaeological culture (ca. 13,000-10,000 BC) traces the last Near Eastern hunter-gatherer societies who lacked farming neighbors (Bar-Yosef and Valla 2013). The succeeding Neolithic periods (Pre-Pottery Neolithic A-C [PPNA-C], ca. 10,000-6,400 BC, and Early Pottery Neolithic [Early PN], ca. 7,000-6,000 BC; table 1), though, did not begin with an abrupt shift to cultivation, domestication, food storage, and village life. Rather, early PPN horticulturalist-forager-hunters had neighbors who only hunted and gathered (Bar-Yosef and Meadow 1995). By ca. 7,000 BC—roughly at the onset of the PPNC period in the southern Levant and the Early PN period in the northern Levant—the wider region remained a mosaic of farmer-herders, hunter-gatherers, farmer-hunters, and specialized pastoralists (Goring-Morris and Belfer-Cohen 2011; Asouti and Fuller 2013; Arranz-Otaegui et al. 2016; Ibáñez et al. 2018; Munro et al. 2018). As in other world regions that underwent early, gradual agricultural transitions (Smith 2001; Zeder and Smith 2009; Bar-Yosef 2012), the Near Eastern “neolithization” process was intricate. The development of domestication and agriculture also came to involve diversified and expanded food storage within the context of durable, multi-room house compounds. The long-term shift to agriculture thus shaped early village life (Kuijt 2008; Belfer-Cohen and Goring-Morris 2011, 2014). Yet, more broadly, Near Eastern communities developed domestication and commensal relationships with diverse plants and animals, while also ecologically altering the landscape at wider geographic scales (Asouti and Kabukcu 2014; Asouti et al. 2015). As human demographic systems changed, cultural worlds also transformed with their constituent, larger-scale, more complex social networks (Price and Bar-Yosef 2010). From its late Upper Paleolithic underpinnings (Snir et al. 2015), Near Eastern agriculture emerged through a complex mosaic of biocultural and environmental changes (Smith and Horwitz 2007; Kuijt 2008; Goring-Morris and Belfer-Cohen 2011; Asouti 2013; Asouti and Fuller 2013; Riehl et al. 2015; Bocquentin in press). This study focuses on how shifts in human health fit in the wider, systemically complex transition. We investigate the following questions: how did the prevalence of early-life stress—which we measure via observations of linear enamel hypoplasias (LEH) in teeth from

skeletons interred in Natufian and Neolithic sites—change with the development of Neolithic biocultural systems, and in turn, how did early-life health experiences affect regional patterns of survival and well-being at later life stages?

BACKGROUND

In substantial part, Near Eastern Neolithic research over the past two decades has highlighted the complicated biocultural and environmental interplay between local conditions and developments, on the one hand, and regional-scale connections—economic, ritual-religious, political, technological, and demographic—on the other (Asouti 2007; Goring-Morris and Belfer-Cohen 2011, 2014; Edwards 2016). Still, the long-standing, wider scholarly interest in the Near Eastern Neolithic period has found its focus on broad, hallmark biocultural evolutionary developments—not on the historical specificity of their origin. This is as much the case for understanding changes in economics, diet, health, demography, and variation in biological well-being, as it is for making sense of the community and cosmology-producing monuments, rituals and ritual offerings that constituted religious expression in early agricultural societies (Cauvin 2000; Guerrero et al. 2008; Pinhasi and Stock 2011; Bowles and Choi 2013; Winterhalder et al. 2015). In this article, we seek to reconcile these research trends, as we grapple with how neolithization’s complexity eventually gave rise to far-reaching transformations in human life and human conditions, as we investigate broad changes in health, demography and well-being.

This study relies on a comprehensive sample of 558 juvenile and adult skeletons from Natufian and Neolithic burial features (table 1), representing 24 archaeological sites across the Levant (fig. 1). Our focus is on life-stage-at-death-specific prevalence of LEH, which is a common, etiologically non-specific marker of physiological stress during dental crown formation (Goodman and Armelagos 1985; Goodman and Rose 1990; Lanphear 1990; Hillson and Bond 1997; Temple 2014, 2020). We investigate a question central to understanding the health of Natufian and early Neolithic people. How did community-level heterogeneity in exposure to early-life stress affect “downstream” mortality risks later in life? (Vaupel and Yashin 1985; Wood et al. 1992; Milner and Boldsen 2017) As domestication and agriculture became key components of Near Eastern biocultural systems, long-term changes in population variability in stress exposure would have had concomitant effects on heterogeneity in frailty. In turn, changes in the

Table 1 – Observed numbers of individuals (total MNI) and individuals with observable teeth whose crowns form between one and five years of age (LEH study) from the Levantine burial sample in this study.

| Period | Site | Region | Number of Individuals | |
|--|-------------------|--------|-----------------------|-----------|
| | | | Total MNI | LEH Study |
| Early Natufian 13,000-11,000 BC | Azraq 18 | South | 11 | 4 |
| | el-Wad | South | 66 | 60 |
| | Erq el-Ahmar | South | 3 | 3 |
| | Hayonim Cave | South | 21 | 19 |
| | Kebara | South | 77 | 17 |
| | Mallaha | South | 24 | 20 |
| | Raqefet | South | 31 | 23 |
| | Wadi Hammeh 27 | South | 5 | 5 |
| Late/Final Natufian 11,000-10,000 BC | el-Wad | South | 3 | 3 |
| | Hayonim Cave | South | 17 | 14 |
| | Mallaha | South | 70 | 51 |
| | Nahal Oren | South | 32 | 28 |
| | Shukbah | South | 4 | 4 |
| | Abu Hureyra | North | 1 | 0 |
| Pre-Pottery Neolithic A 10,000-9,000 BC | Sheikh Hassan | North | 8 | 6 |
| | Dja'de el-Mughara | North | 5 | 5 |
| | Tell Mureybet | North | 1 | 1 |
| | Tell Qaramel | North | 9 | 8 |
| Pre-Pottery Neolithic B 9,000-7,000 BC | Abu Ghosh | South | 5 | 3 |
| | Beisamun | South | 17 | 7 |
| | Motza | South | 18 | 8 |
| | Tel Roim West | South | 1 | 1 |
| | Abu Hureyra | North | 94 | 80 |
| | Dja'de el-Mughara | North | 63 | 47 |
| | Tell Aswad | North | 5 | 2 |
| | Tell Mureybet | North | 6 | 3 |
| Pre-Pottery Neolithic C 7,000-6,400 BC Early Pottery Neolithic 7,000-6,000 BC | Abu Ghosh | South | 4 | 1 |
| | Ashkelon | South | 26 | 5 |
| | Atlit Yam | South | 65 | 56 |
| | Beisamun | South | 19 | 6 |
| | Hagosherim | South | 3 | 2 |
| | Tel Roim West | South | 5 | 5 |
| | Abu Hureyra | North | 6 | 6 |
| | Tell Ain el-Kerkh | North | 56 | 46 |

distribution of frailty would have had cascading impacts on life-long health conditions, well-being and age-specific mortality risks (Cohen and Armelagos 1984; Bocquet-Appel 2002; Larsen 2006; Guerrero et al. 2008; Gage and DeWitte 2009; Goring-Morris and Belfer-Cohen 2011; Chamel 2014; Larsen et al. 2019). The analysis of statistical associations between early-life stress and life-stage-specific mortality can yield new insights into well-being and demography in the transition to agriculture.

Human biologists, economic historians, and bioarchaeologists, alike, have increasingly recognized the effects that early-life health experiences can have on later juvenile or adult health and survival outcomes. Theoretical modeling of life history

strategies (Vaupel and Yashin 1985; Wood 1994, 1998) contributed critically to the initial identification of the osteological paradox, where seemingly hidden heterogeneity in stress and frailty can have surprising, differential effects on the associations between skeletal health and age-specific mortality outcomes (Wood et al. 1992). In addition, clinical, economic-historical, and bioarchaeological studies of heterogeneity in frailty have generated extensive evidence for the “developmental origins of health and disease” (DOHaD) framework for understanding how early-life stress—including fetal exposures—can have lasting downstream effects on morbidity in the face of infections, malnutrition and cardiovascular disease (Barker et al. 1990; Barker 2004; Boldsen 2007; Armelagos

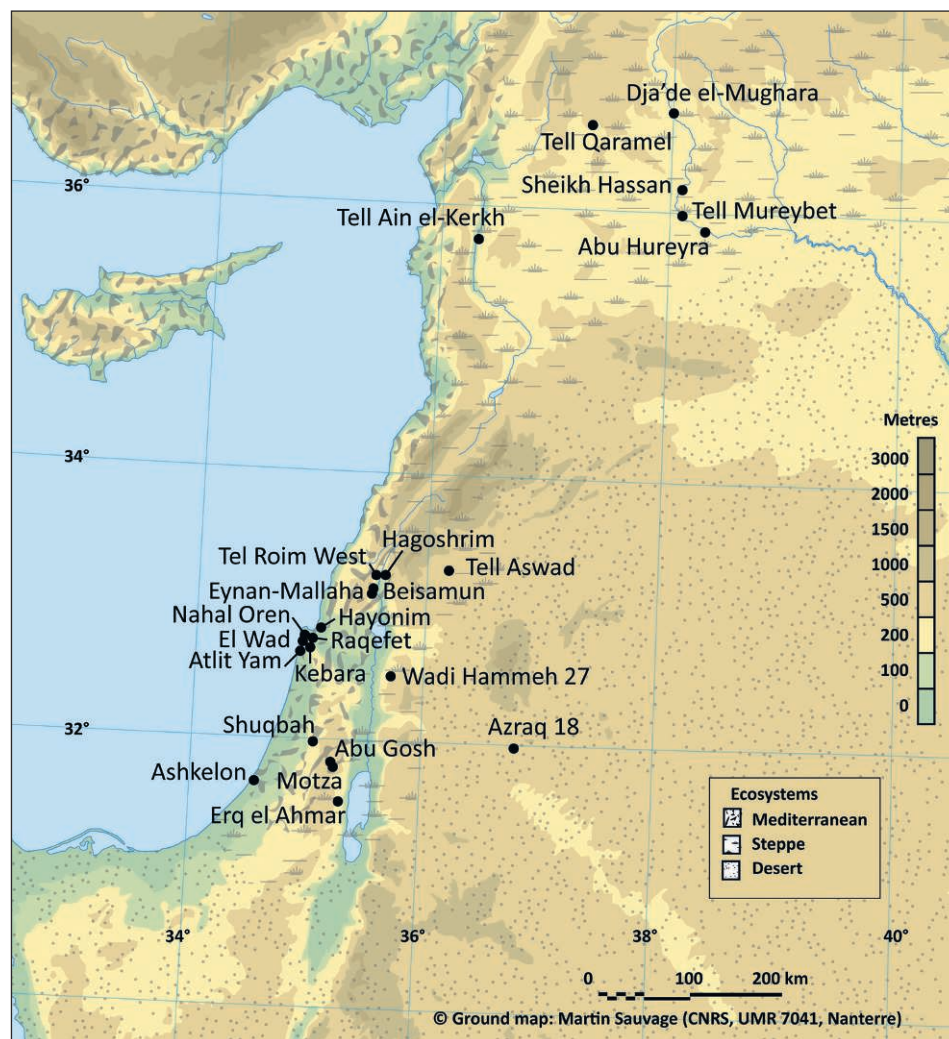


Fig. 1 – Natufian and Neolithic sites included in this study. See table 1 for details on time period/ archaeological culture.

et al. 2009; Bengtsson and Broström 2009, 2011; Gowland 2015; Yaussy 2016; Temple 2019). In general, the DOHaD model views prenatal and early-life stress—whether due to nutritional deficits, infection, or chronic-stress-related inflammation—as a particularly important cause of elevated frailty later in development and adulthood, ultimately influencing intergenerational patterns of inequality in health and heterogeneity in well-being (Barker et al. 1989; Barker et al. 1990; Barker 1995, 2004; Boginet et al. 2007; Armelagos et al. 2009; Gowland 2015; Wells and Johnstone 2017; Temple 2019). Measuring early-life stress and its potential impacts on later juvenile and adult mortality risk brings into focus such downstream life-history effects (Jones 2005), rendering visible population-level variability in frailty that would otherwise remain hidden (Vaupel and Yashin 1985; Wood et al. 1992; Wood 1994; Boldsen 2007; Milner and Boldsen 2017).

Building on foundational work on the associations between LEH and mortality in the prehistoric adoption of agriculture, we present a comprehensive effort to investigate the role of heterogeneity in frailty on changes in health and well-being in a long-term regional transition from hunting and gathering to agriculture (Goodman and Armelagos 1985; Armelagos et al. 2009). We emphasize that the DOHaD framework supports a major methodological advantage in bioarchaeology (Armelagos et al. 2009; Milner and Boldsen 2017; Temple 2019). Researchers have long recognized that direct paleodemographic analysis of archaeological age-at-death profiles entail profound theoretical difficulties. The reconstruction of life tables from age-at-death profiles typically requires uncertain assumptions about basic population rates (Bocquet-Appel and Masset 1977, 1982; Gage and DeWitte 2009). Methodological developments notwithstanding, age-at-death determinations themselves still have limited resolution and accuracy, at least for older adults (ca. ≥ 30 -40 years; Milner and Boldsen 2012; Lanteri et al. 2018; Cabec et al. 2019; Naji in press). The theoretically modelled statistical inferences about measurable age-at-death patterns in a target burial assemblage depend strongly on the reference populations used to build the statistical models (Masset 1990; Konigsberg and Frankenberg 1992, 1994). In particular, the reference population sample's age-specific variability in skeletal biology must be sufficiently comparable to that of the archaeological target population, so that inferences about skeletal aging patterns are accurate (Konigsberg and Frankenberg 2002; Usher 2002). Reference populations have been drawn from ethnographic studies, historical cemetery and anatomical collections, and diverse modern population records (Bocquet-Appel and Masset 1977; Gage and DeWitte 2009; Milner and Boldsen 2012). Moreover,

an observed archaeological age-at-death distribution can be affected by cosmologically structured or socio-politically driven funerary recruitment practices, which can bias archaeological representation with respect to age and biological sex (e.g., Masset and Sellier 1990). This is a fundamental concern that Bocquentin has discussed at length for the Levantine Natufian context (Bocquentin 2003, 2007, 2014). As we focus on studying early-life stress and its effect on survival to subsequent life-stages—from later juvenile growth periods to adulthood past 30 years—we emphasize that this “DOHaD-derived” approach can shed light on changes in health, well-being and mortality in the transition to agriculture, while circumventing the pitfalls of looking directly at life-stage-at-death profiles (Milner and Boldsen 2017).

In this study we thus investigate how LEH-formation may have shifted in its statistical associations with survival to particular life-stages in Levantine communities, from the Natufian time-frame (ca. 13,000-10,000 BC) to the PPNC/Early PN timeframe (ca. 7,000-6,400 BC). The DOHaD framework generates clear theoretical predictions about how changes in stress-exposure affect age-specific risks of suffering inflammation or other stress responses, leading to skeletal traces such as LEH. Moreover, the DOHaD model emphasizes that early-life episodes of inflammation critically disrupt prenatal, neonate, infant, or early juvenile growth and development. Those experiencing early-life inflammation will likely remain frailer, raising risks for mortality in subsequent life stages (fig. 2). Thus, physiological stress-response in infancy or early juvenile growth stages is expected to be a significant risk factor for premature mortality in later juvenile, adolescent, early adult, and mature adult life stages.

According to the DOHaD model, other things being equal, when a community faces a significant decline in health conditions, the hazards for inflammation in the face of early-life stress will increase, and in turn, heterogeneity in frailty will also increase. Many individuals suffering early-life inflammation will develop greater frailty, raising their morbidity in the face of subsequent stress episodes. Such a pattern has been empirically documented in LEH occurrence in Late/Final Jomon Period hunter-gatherers in Japan (Temple 2014 and 2020). Even in healthy preindustrial populations, LEH prevalence should be highest among the most frail, who may survive childhood, but who then embody higher mortality risks, already in their adolescent and young-adult years (ca. 10-30 years). If population-level health were to decline, average frailty would increase in the population, but there might be greater heterogeneity among individuals. The result would not only involve higher life-stage-at-death-specific LEH

rates across the board; we would also observe a “leftward”—that is, a younger—shift in the life-stage-at-death associated with the peak rate of early-life stress exposure. Figure 2 illustrates an idealized *ceteris paribus* scenario of age-at-death LEH prevalences for populations clearly differing in health conditions. In analyzing the statistical associations between LEH and life-stage-at-death in skeletal samples spanning the Levantine transition to agriculture, we take a first look at how the DOHaD framework may explain neolithization’s impact on well-being and mortality over long-term and regional scales.

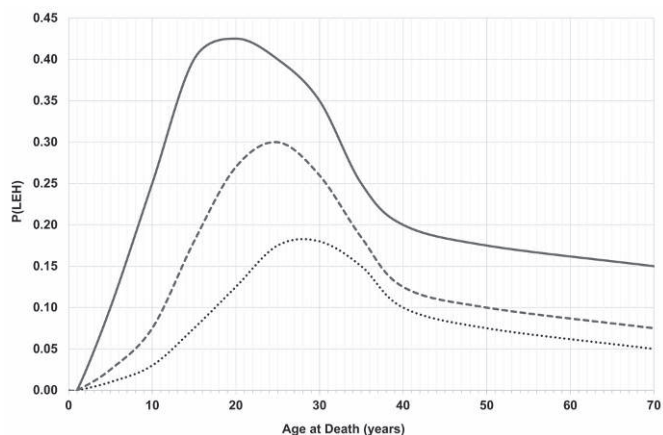


Fig. 2 – Theoretical distribution of linear enamel hypoplasia prevalence, $P(LEH_{1-5})$, for tooth crowns forming between ages of one and five years, across the span of mortality outcomes. The dotted line represents a relatively healthy preindustrial population, with LEH associated with lower rates of early-life inflammation, which are in turn most often linked to elevated mortality in early adulthood. The dashed line illustrates a relatively less healthy community—more frequently exposed to infection or nutritional stress—with higher rates of early childhood LEH, associated with a slightly reduced age at peak risk for early mortality. The solid line shows a substantially less healthy community, for which higher stress exposure (e.g., more frequent epidemics or nutritional stress) shift peak mortality associated with early childhood LEH formation downward, into the adolescent life stage.

MATERIALS AND METHODS

Our study draws on a comprehensive sample of 558 individuals recovered and documented as near-complete or partial skeletons with at least partial dentitions. The individuals come from mortuary features from 24 Natufian and Neolithic sites (table 1). FB, BC and MA have identified a total of 790 individuals (Bocquentin 2003, 2007; Lengyel et al. 2013; Chamel 2014;

Bocquentin and Garrard 2016; Bocquentin et al. *in press*), of which 549 meet the following joint criteria: they have associated or articulated permanent teeth whose crowns form prior to ca. 6 years; they could be aged to the broad categories 5-19 years (juvenile) or ≥ 20 years (adult); and they were archaeologically associated with a particular time period. These 549 individuals were used in finer-grained analyses of change through time in the association of LEH with life-stage-at-death. Nine additional individuals with observable permanent teeth are from stratified Natufian contexts, but they could not be assigned to Early versus Late/Final periods (Belfer-Cohen 1991; Bocquentin 2003). With these nine individuals included, we carried out analyses of change through time, from the entire pooled Natufian hunter-gatherer sample to subsequent Neolithic time periods. Thus, 558 individuals with at least one observable tooth were included in our analyses.

We studied LEH prevalence in permanent teeth from individuals aged ≥ 5 years, in order to evaluate how LEH forming in permanent tooth crowns in early childhood may associate with mortality in particular life stages later in childhood and adulthood. We focused on permanent incisors (I), canines (C), first premolars (P1) and first molars (M1), whose crowns form between 1 and roughly 5-6 years (Reid and Dean 2006; Reid et al. 2008). When LEH is present, these permanent teeth provide a record of early-childhood stress episodes that are expected to increase frailty later in the juvenile or adult life stages. With the study sample encompassing Levantine time periods from the Early Natufian (ca. 13,000-11,000 BC) to the PPNC/Early PN (combined northern and southern Levant, ca. 7,000-6,400 BC), we analyzed change over time in the associations between early-childhood biological well-being and mortality, across the transition from hunting and gathering to domestication, agriculture, expanded food storage, and village settlement.

DETERMINING LIFE-STAGE AT DEATH

We consider the following life-stages at death, examining individuals who survived early childhood (ca. > 5 years): younger juveniles (5-9 years at death), adolescents (10-19 years at death), younger adults (20-29 years at death), and older adults (> 30 years at death). Here, we favored methodological conservatism in order to reduce the risk of inaccurate age-at-death determinations.

Age at death for immature skeletons (\leq ca. 19 years) was determined according to visual and radiographic observation of tooth calcification, eruption, and wear. These subadult age

determinations were complemented by epiphyseal fusion data. Detailed methods are available in Bocquentin (Bocquentin 2003: 49-102). Those individuals aged 5-19 years were assigned to the broader “Juvenile” life-stage-at-death class. Where preservation permitted, we further subdivided them into younger juvenile (5-9 years) and adolescent (10-19 years) life-stage categories.

Among the skeletally mature individuals, life-stage at death was assigned to 20-29 year and ≥ 30 -year categories—again, where possible—mainly based on clavicular fusion and age indicators from the pubic symphysis and the auricular surface of the ilium (Webb and Suchey 1985; Schmitt 2005), complemented by a discriminant analysis function approach to dental occlusal wear (Bocquentin 2003). Further methodological details are presented in Bocquentin (Bocquentin 2003). Due to incomplete preservation for many individuals, the sample of more precisely aged adults with observable teeth was substantially restricted. Nonetheless, out of 375 skeletally mature, adult individuals with observable teeth, 177 could be aged more precisely into the younger and older adult life-stage-at-death categories.

IDENTIFYING LINEAR ENAMEL HYPOPLASIA (LEH) PRESENCE VERSUS ABSENCE ON THE PERMANENT TEETH

The study included all permanent incisors (I1 and I2), canines (C), first premolars (P1) and first molars (M1) associated with the 558 partial and near-complete individual skeletons from the Levantine Natufian and Neolithic contexts (tables 1, 2). Each tooth ($n = 5296$) was examined visually with an 8 \times magnification lens. A tooth was coded as LEH-present if at least one linear enamel hypoplasia was present. Some teeth exhibited multiple LEHs and some exhibited both LEH and enamel pitting. In reducing the coding to LEH presence versus absence, we aimed to consider as broadly as possible those dental traces of early-life stress that we hypothesize to associate with earlier mortality.

We emphasize that only a very small number of *coronal* LEHs were observed on the upper dentition, that is, for the teeth on which we focused: permanent incisors, canines, P1's, and M1's. For the respective superior and inferior teeth, the height of all single LEHs (measured as height in mm above the dentine-enamel junction) was always less than the height of the most worn tooth in the sample. In cases where multiple LEHs formed, the height of the last-forming LEH was always less than the height of the most worn tooth in the sample. Thus, it is

very unlikely that we have undercounted LEH presence on adult individuals with worn teeth.

STATISTICAL METHODOLOGY FOR ANALYZING ASSOCIATIONS BETWEEN LEH AND LIFE-STAGE-AT-DEATH

We carried out two successive statistical analyses of change in life-stage-at-death-specific LEH prevalence across the transition to agriculture. The first approach used the sample of 549 individuals, divided into juvenile (5-19 year) and adult (≥ 20 year) categories and separated into successive Early Natufian, Late/Final Natufian, PPNA, PPNB, and PPNC/Early PN periods. The time frames given for each period were based on published reviews of available radiocarbon dates (Goring-Morris and Belfer-Cohen 2011; Maher et al. 2011; Grosman 2013; Chamel 2014; Borrell et al. 2015; Edwards 2016). In table 1 we took a conservative approach in rounding beginning and end dates to the nearest half-millennium. The typologically Late Natufian sample from Raqefet Cave was assigned chronologically to the Early Natufian period, which spans the timeframe 13,000-11,000 BC (Barzilai et al. 2017). All other typologically Late or Final Natufian sites in our sample date to 11,000-10,000 BC (Grosman 2013). We recognized that the Natufian phenomenon is a Levantine archaeological culture. Yet, it is also largely definable as entirely coeval with the Late Epipaleolithic timeframe, consisting of an earlier and a later chronological horizon (Bar-Yosef and Belfer-Cohen 1989; Bar-Yosef 1998; Grosman 2013). There is limited chronological overlap between the Early and Late/Final Natufian archaeological cultures. Where ^{14}C measurements suggest penecontemporaneous Early and Late Natufian-associated occupations—in the western Galilee and Mt. Carmel area—the overlap lasts up to several centuries (Henry et al. 1981; Weinstein-Evron et al. 2012; Caracuta et al. 2016; Barzilai et al. 2017). As the Late Natufian-associated occupation of Raqefet Cave is unique within our Late/Final Natufian sample, predating 11,000 BC, we emphasized its chronological position. Our analysis focused on change over time, not on variability among temporally overlapping archaeological cultures. In a future publication we will consider the complex chronology of the Early-Late Natufian archaeological transition in the southern Levant. Here, we relied on recent results concerning the Early-Late/Final Natufian temporal framework (Weinstein-Evron et al. 2012; Grosman 2013; Caracuta et al. 2016; Nishiaki et al. 2017; Barzilai et al. 2017; Richter et al. 2017). In our study of long-term chronological change, the Natufian period overall

came into focus as a period with little clearly measurable overlap with the succeeding PPNA period (ca. 10,000-9,000 BC; Wicks et al. 2016). We further took into consideration the fact that the initial PN in the Northern Levant largely overlaps with the PPNC period in the Southern Levant. We combined these archaeological cultures into one temporal horizon, encompassing mainly ca. 7,000-6,000 BC (Chamel 2014; Edwards 2016; Borrell et al. 2019).

The aim of our first analysis was to consider gross differences in associations between early-life stress and mortality, here, distinguished as juvenile versus adult mortality, across the transition to agriculture. The study sample for this approach is summarized in table 2.

Table 2 – Tooth counts¹ and minimum number of individuals (MNI) in the analysis of LEH occurrence by more finely divided time-period and more broadly defined life-stage at death.

| Period | Life-Stage at Death | | Total |
|---------------------|---------------------|-------|-------|
| | Juvenile | Adult | |
| Early Natufian | 563 | 912 | 1,475 |
| <i>MNI</i> | 53 | 98 | 151 |
| Late/Final Natufian | 211 | 737 | 948 |
| <i>MNI</i> | 24 | 76 | 100 |
| PPNA | 23 | 165 | 188 |
| <i>MNI</i> | 3 | 17 | 20 |
| PPNB | 357 | 751 | 1,108 |
| <i>MNI</i> | 43 | 108 | 151 |
| PPNC/PN | 393 | 712 | 1,105 |
| <i>MNI</i> | 51 | 76 | 127 |

The second approach used a smaller subsample ($n = 347$), including only those individuals for whom juveniles could be divided into younger juvenile (5-9 years) and adolescent (10-19 years) categories. We further sampled those adults who could be divided into younger (20-29 years) and older (≥ 30 years) groups. The study sample for this approach included the additional nine Natufian individuals whose stratigraphic position could not be clearly linked to Early or Late Natufian components at el-Wad and Hayonim Caves. Here, the Natufian sample was pooled as a single terminal Pleistocene hunter-gatherer cross-sectional sample. The highly fragmentary PPNA sample included too few adult skeletons that could

be aged to the younger versus older categories. Thus, we excluded the PPNA period from the second analysis. Because our PPNA sample is only represented by sites in the Northern Levant—and because PPNA cultivation practices were highly variable, with domestication technologies barely developed or adopted (Willcox 2007, 2012; Asouti and Fuller 2012, 2013; Asouti et al. 2015; Arranz-Otaegui et al. 2016)—the second analysis could still focus on how early-life stress related to mortality across the more finely divided life history scheme, as we compared the association patterns before agriculture (all Natufian individuals, ca. 13,000-10,000 BC) with those after agricultural adoption (PPNB and PPNC/PN periods, respectively, encompassing ca. 9,000-6,000 BC). The second analysis sample is summarized in table 3.

Table 3 – Tooth counts² and minimum number of individuals (MNI) by broader time period and more detailed life-stage at death.

| Period | Life-Stage at Death | | | | Total |
|------------|---------------------|------------|---------------|-------------|-------|
| | Younger Juvenile | Adolescent | Younger Adult | Older Adult | |
| Natufian | 210 | 372 | 319 | 471 | 1,372 |
| <i>MNI</i> | 39 | 39 | 39 | 90 | 207 |
| PPNB | 543 | 441 | 331 | 701 | 2,016 |
| <i>MNI</i> | 22 | 21 | 14 | 17 | 74 |
| PPNC/PN | 216 | 177 | 63 | 133 | 589 |
| <i>MNI</i> | 35 | 16 | 5 | 10 | 66 |

Monte Carlo Simulation of Independence between LEH and Life-Stage-at-Death

In order to evaluate the statistical associations between LEH and mortality across age groups, we employed a nonparametric Monte Carlo simulation approach. The choice of statistical test was mainly driven by the highly variable preservation of dentitions among individuals. This was especially relevant for our statistical comparisons, because in general, different teeth exhibit significantly different liabilities to develop enamel hypoplasias (Goodman and Armelagos 1985; Goodman and Rose 1990; Lanphear 1990; Hillson et Bond 1997; Guatelli-Steinberg et al. 2004; Nelson 2018). As shown in figure 3, just over 20% of the total 5,296 teeth in the entire Levantine sample exhibit at least one LEH, but canines have a much higher LEH susceptibility than all other teeth, whereas M1's relatively rarely

1. Refers to the permanent teeth studied, with relatively early-forming crowns: incisors, canines, P1 and M1.

2. Refers to the permanent teeth studied, with relatively early-forming crowns: incisors, canines, P1 and M1.

form LEH. A G-test of independence (Sokal and Rohlf 1995) between LEH formation and tooth yields a remarkably high G-statistic of 497, with an associated p -value essentially at zero. The G-statistic equals $2 \times$ the sum of log-likelihood values for observed-relative-to-expected counts in each cell of the 10×2 contingency table; $p = 2.0 \times 10^{-101}$; $n = 5,296$ teeth; 10 upper and lower tooth types \times LEH presence versus absence yields d.f. = 9. The teeth that happen to be preserved in association with a particular individual skeleton thus strongly affect the likelihood that at least one LEH will be observed. In our resampling-with-replacement procedure (see below), we thus randomly shuffled the observed dentitions across individuals, holding life-stage at death and time period constant. This Monte Carlo approach controlled for variability in taphonomic post-mortem loss of teeth, simulating independence of LEH, life-stage at death, and time period. A key aspect of this scenario is that LEH risk is simulated as constant over time and with respect to life-stage at death. We sought to evaluate the null hypothesis that the observed chronological variation in association between LEH and life-stage at death could have occurred randomly. We included individuals with complete as well as partial dentitions—even those with just one associated tooth. This allowed us to maximize the available number of teeth observed (table 2, 3).

The Simulation Procedure: Repeated Random Resampling with Replacement

In each of our two analyses (see above), we employed a random-resampling-with-replacement procedure, repeated 100,000 times. For each randomly resampled case, we tabulated the LEH relative frequency (number of teeth observed with LEH present/all teeth observed) in each age group and time period. We then calculated the test statistic: the sum of the squared deviations from the expected relative frequency, which was estimated from the total number of teeth with LEH in the study sample. The repeated resampling procedure generated a simulated random distribution of summed squared deviations from the expected LEH frequency. From this simulated distribution, we estimated the probability that the observed sum of squared deviations could have occurred by chance. We also recorded the probabilities that observed relative frequencies for LEH prevalence within life stages and time periods—that is to say, the observed values in the respective life-stage-at-death \times time-period contingency tables in analyses 1 and 2—could have occurred by chance alone (Estabrook and Estabrook 1989; Estabrook 2011). Simulations for both statistical analyses described above were carried out with a custom macro in Excel VBA for Mac 2020.

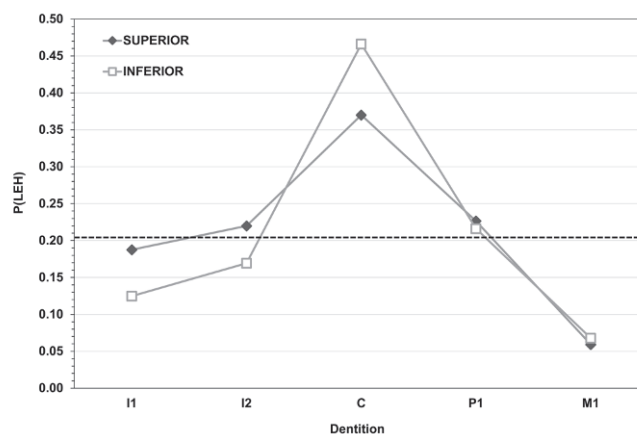


Fig. 3 – Relative frequency of linear enamel hypoplasia $P(\text{LEH})$ per tooth analyzed, separated into upper and lower dentitions. The dashed line marks the expected frequency of LEH on the 5,296 observed permanent teeth ($MNI = 558$), under the null hypothesis that all of the analyzed teeth have the same susceptibility to form LEH.

Procedures for ad hoc tests

Where Monte Carlo simulation results raised questions about particular ad hoc 2×2 comparisons between life-stages at death and time periods, we employed the G-test of independence, which Sokal and Rohlf (1996) recommend over the Chi-square test.

RESULTS

Charting the presence versus absence of LEH on juveniles and adults across five successive time periods, table 4 summarizes the results of the first analysis, based on the sample of 549 individuals from the southern and northern Levant. In the transition to agriculture there was a long-term increase in LEH risk associated with juvenile and adult mortality, alike. With the available observed dentitions, the null expectation of constant LEH risk in both life stages and all time periods yields an estimated prevalence of 0.21. For the two life-stages at death in this analysis, observed in each of five time periods—yielding the 2×5 table (table 4)—the sum of squared deviations of observed LEH prevalence from the expected, constant level is 0.14. The Monte Carlo simulation with 100,000 iterations of resampling with replacement yields $p = 0.03$ that the observed

sum of squared deviations could be as high or higher by chance alone. There is an overall non-random interaction effect among LEH risk, life-stage at death, and time period.

Table 4 – Relative frequencies of teeth with linear enamel hypoplasia (LEH).

| | P(LEH) ³ | |
|---|----------------------------------|----------------------------------|
| | Juvenile (5-19 Years) | Adult (≥ 20 years) |
| Early Natufian 13,000-11,000 BC | 0.16 | 0.16 p = 0.03 |
| Late/Final Natufian 11,000-10,000 BC | 0.09 p = 0.01 | 0.13 p = 0.004 |
| PPNA 10,000-9,000 BC | 0.35 | 0.11 |
| PPNB 9,000-7,000 BC | 0.27 | 0.15 p = 0.009 |
| PPNC/PN 7,000-6,000 BC | 0.46 p < 1 × 10 ⁻⁵ | 0.35 p < 1 × 10 ⁻⁵ |

This interaction effect is driven by the following significantly strong associations between higher or lower LEH risks, particular life-stage at death, and particular time period. First, Natufian hunter-gatherers interred in residential sites generally exhibit significantly low LEH risks, regardless of life-stage at death (table 4). Second, prior to the PPNC/PN time-frame—that is, before ca. 7,000 BC—adult mortality is associated with significantly low LEH prevalence, consistent with a key prediction of the DOHaD model. Reduced exposure to early-life stress is tied, in the maturation and aging process, to greater longevity. Third, LEH-risk shows a remarkable spike in association with juvenile and adult mortality, alike, in the PPNC/PN time period. Out of the 100,000 iterations of resampling with replacement, no randomized case yielded LEH risks as high as those observed for the PPNC/PN sample. Moreover, LEH prevalence is markedly higher for juvenile mortality than it is for adult mortality in the PPNC/PN period. This is consistent with one of the DOHaD model's fundamental predictions, that increased early-life exposure to stress raises frailty, with a

3. The LEH presence relative frequency in each cell is based on counts of LEH presence and absence on the permanent incisors, canines, P1s and M1s associated with individuals belonging to the set of individuals with that cell's life-stage at death and time period. The cells shaded in light grey exhibit statistically significantly low LEH risks, based on the Monte Carlo simulation with resampling with replacement. The dark grey cells exhibit statistically significant high LEH risks. The respective significant *p*-values are shown in the highlighted cells.

concomitant risk for earlier mortality (fig. 2). Among individuals dying in the juvenile life-stage, it was conspicuously more common to have experienced early childhood stress that led to LEH-formation. Figure 4 summarizes the results of this first analysis, illustrating the pattern of LEH risk with respect to the broad life-stage at death and the more finely detailed time-period.

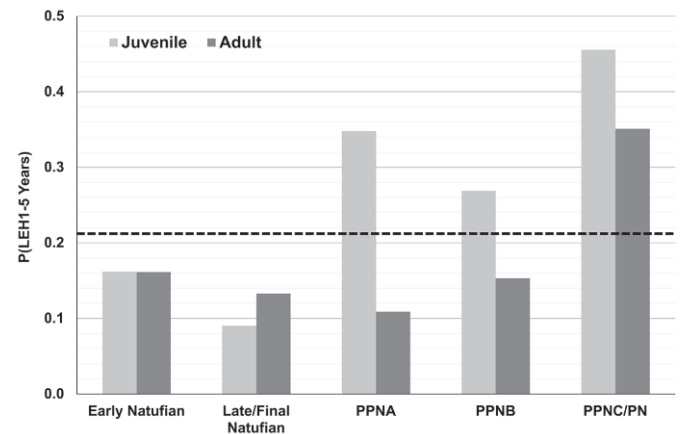


Fig. 4 – The relative frequency of linear enamel hypoplasias in teeth, the crowns of which form mainly between ages one and five years, $P(LEH_{1-5})$, according to time period and life-stage at death—broken down simply into 5-19 years at death (juvenile) and ≥ 20 years at death (adult). The dotted line marks the estimated expected risk of LEH formation on teeth, under the null hypothesis that in all time periods, survival to all life-stages is associated with the same constant LEH risk.

The second analysis involves the more restricted sample of better-preserved individuals, whose life-stage at death could be assigned to the categories younger juvenile (5-9 years), adolescent (10-19 years), younger adult (20-29 years), and older adult (≥ 30 years; $n = 347$). As noted above, this sample also includes nine additional hunter-gatherers who could be assigned to a pooled Natufian subsample. Table 5 and figure 5 summarize this analysis, clarifying long-term biocultural evolutionary change in how early-life stress impacted survival rates later in life. Prior to 10,000 BC—that is, well before the establishment of widespread cultivation, intensified storage, and larger village settlements—Natufian hunter-gatherers generally appear relatively healthy, exposed to early-life stress significantly less frequently than later PPNB, PPNC and PN farmers (compare fig. 2 and 5). As shown in figure 5, LEH is rarely associated with Natufian younger juvenile mortality, but LEH prevalence rises in association with younger adult mortality, before declining significantly among those surviving to at least

30 years. Overall Natufian LEH prevalence is relatively low: $P(\text{LEH}_{\text{Natufian}}) = 0.17$. In contrast, Neolithic agricultural populations—that is, PPNB, PPNC, and PN populations, ca. 9,000–6,000 BC—exhibit much higher LEH prevalence. Most strikingly, children born in PPNC/PN communities were exposed to early-life stress more frequently, regardless of how long they survived. The overall PPNC/PN frequency of LEH, $P(\text{LEH}_{\text{PPNC/PN}}) = 0.43$. However, this elevated rate of LEH-formation—and thus, the archaeologically visible rate of substantial early-life stress—appears mostly associated with mortality in the juvenile, adolescent, and younger-adult life stages. Those PPNC/PN individuals surviving to the “Older Adult” life-stage had somewhat lighter biological stress loads in early childhood, reflected in their life-stage-specific lower LEH frequencies (fig. 5). In the centuries after ca. 9,000 BP in the Levant, the peak LEH-mortality association shifts slightly, to an earlier life-stage—the adolescent stage. This result is strongly concordant with the predictions of the DOHaD model (fig. 2), suggesting that the long-term transition from Natufian hunting and gathering to Neolithic agriculture resulted in poorer early-life conditions, and that by the 7th millennium BC, this had led to increased mortality overall (cf. Paine and Boldsen 2002).⁴

Indeed, in the second analysis, the Monte Carlo simulation of constant LEH risk as a factor independent of life-stage survivorship and prehistoric time-period, reveals a statistically significant Natufian-Neolithic shift in association between LEH formation and life-stage at death. Among the cross-tabulated relative frequencies in each cell in the four life-stage-at-death \times three time-period table (table 5), the observed sum of squared deviations, 0.27, is very unlikely to have been at least as high by chance alone ($p = 0.001$). As detailed in table 5, Natufian juvenile and older-adult mortality exhibit statistically significantly low rates of LEH-association, while PPNC/PN juvenile, adolescent, and younger adult mortality is statistically significantly associated with high LEH-risk.

Table 5 – Linear Enamel Hypoplasia relative frequencies in the permanent dentition of the Natufian, PPNB, PPNC and early PN sample.

| Period | P(LEH) | | | |
|---------------------------|-------------------|--------------------------|---------------------------|--------------------------------|
| | Child (5-9 years) | Adolescent (10-19 years) | Young Adult (20-29 years) | Older Adult (≥ 30 years) |
| Natufian 13,000-11,000 BC | 0.08 0.0003 | 0.18 | 0.20 | 0.15 0.003 |
| PPNB 9,000-7,000 BC | 0.30 | 0.23 | 0.28 | 0.18 |
| PPNC/PN 7,000-6,000 BC | 0.39 0.0002 | 0.53 0.0001 | 0.52 0.02 | 0.33 |

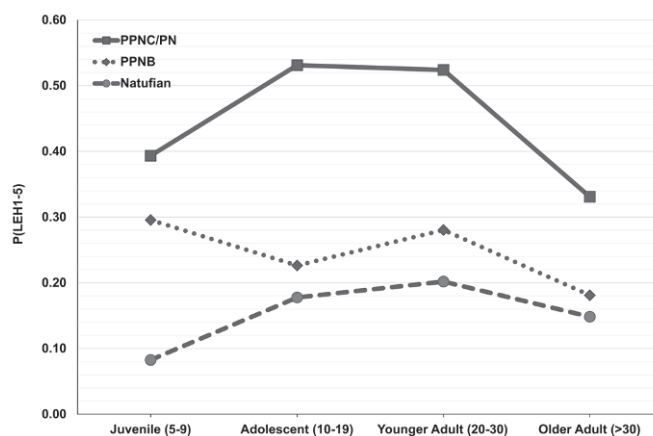


Fig. 5 – Prevalence of linear enamel hypoplasia in teeth, the crowns of which form mainly between one and five years, $P(\text{LEH}_{1-5})$, plotted by age at death—here, divided into the four life-stages shown. Compared are the pooled Natufian hunter-gatherer sample (ca. 13,000–10,000 BC), the early agricultural PPNB sample (ca. 9,000–7,000 BC), and the pooled PPNC/Pottery Neolithic (PN) sample (ca. 7,000–6,000 BC).

DISCUSSION

When Cohen and Armelagos (1984) presented their seminal edited volume of geographically focused syntheses, the *Paleopathology at the Origins of Agriculture* contributors discussed then available human osteological observations, sketching a robust, straightforward pattern. Agriculture

4. The LEH presence relative frequency in each cell is based on counts of LEH presence and absence on the permanent incisors, canines, P1s and M1s associated with individuals belonging to the set of individuals with that cell's life-stage at death and time period. The cells shaded in light grey exhibit statistically significantly low LEH risks, based on the Monte Carlo simulation with resampling with replacement. The dark grey cells exhibit statistically significant high LEH risks. The respective significant p -values are shown in the highlighted cells.

immediately brought with it multiple, increasingly prevalent sources of morbidity (Cohen and Armelagos 1984). Compared to earlier hunter-gatherer populations in the same region, the first-adopters of farming often exhibited archaeologically preserved skeletal lesions—markers of serious or recurrent stress and inflammation—regardless of life-stage at death (Larsen 1995; Pinhasi and Stock 2011). There are profound, still-debated paleodemographic challenges in interpreting archaeological life-stage-at-death distributions (Bocquet-Appel and Masset 1982; Sattenspiel and Harpending 1983; Paine and Harpending 1996; Bocquet-Appel 2002; Bocquet-Appel and Naji 2006; Bocquet-Appel and Bar-Yosef 2008; Gage and DeWitte 2009). It has remained difficult to establish that the agriculturally associated increase in morbidity actually led to increased mortality (Gage and DeWitte 2009).

More recently, Bogin and colleagues have stated, “Even under good conditions, the stages of human life history are replete with trade-offs for survival, productivity, and reproduction” (Bogin et al. 2007: 631). Disparities in early-life exposures to stress can drive very different investments in growth versus survival, generating population-scale heterogeneity in frailty. We suggest that our results—when considered in light of the DOHaD framework—constitute a new line of evidence, supporting the argument that, broadly across the Levant in the 7th millennium BC, rising rates of early-childhood stress were significantly tied to mortality later in childhood, adolescence, and younger adulthood. Our analysis has revealed strong statistical associations between early-childhood stress-exposure and life-stage at death. In light of the DOHaD framework, population-level heterogeneity in biological well-being (*sensu* Wood 1998) appears to have generally increased, from the Natufian to the PPNC/Early PN timeframes. Yet, average well-being likely began to deteriorate across the Levant, as domesticated plants and animals were extensively integrated into Neolithic economies, and as villages with more densely packed household structures were settled in the Late PPNB, ca. 7,500-7,000 BC. Our results most strongly suggest that the negative impact on biological well-being took hold across the Levant in the PPNC/Early PN, from ca. 7,000-6,000 BC (Kuijt 2008; Asouti and Fuller 2013; Arranz-Otaegui et al. 2016; Munro et al. 2018).

This main conclusion is consistent with previous and ongoing work. Our life-stage-at-death-specific LEH data for the Levant mirror the picture of relatively poor health among the 7th millennium BC people who inhabited the Pottery Neolithic village of Çatalhöyük in central Anatolia (Larsen et al. 2019). In the southern Levant, evidence for a decline in average health continues into the succeeding Chalcolithic

period (ca. 4,500-3,500 BC; Smith and Horwitz 2007). Bocquentin et al. (in press) have carried out an analysis of carious lesions and ante-mortem tooth loss in this study’s pan-Levantine sample. They observe an accelerating, long-term rise in the overall rates of caries formation, from the Early Natufian to the PPNC/PN time periods. They also see that ante-mortem tooth loss actually declined from the PPNB to the PPNC/PN periods. While dental caries formed more often in PPNC/PN individuals, the lesions tended to be smaller than those in the preceding Levantine PPNB sample. The trends they observe may more narrowly track the progressive addition of starch, as Neolithic diets became less variable. Bocquentin, Chamel, and Anton observe that overall somatic health can affect the individual’s susceptibility to carious lesions and other oral infections. They argue that there was likely an interplay between an overall decline in somatic health, in general, and oral health, in particular. This would account for the spike in population-level caries rates and stress that emerged by the 7th millennium BC across the Levant (Bocquentin et al. in press).

In this discussion we consider how the development and adoption of agriculture and settlement dynamics may have interacted with the demographic effects of increasingly prevalent early childhood stress, especially from the Late PPNB onward. We then address our finding of likely rising mortality in the PPNC/Early PN timeframe, viewed in light of Bocquet-Appel’s influential “Agricultural Demographic Transition” model.

DECLINING BIOLOGICAL WELL-BEING AND THE NEAR EASTERN TRANSITION TO AGRICULTURE

As we have emphasized above, recent research has highlighted that Near Eastern neolithization involved complex, long-term biocultural processes (Bocquentin in press; Kuijt 2008; Goring-Morris and Belfer-Cohen 2011; Asouti and Fuller 2013; Asouti 2013; Belfer-Cohen and Goring-Morris 2014; Chamel 2014; Asouti et al. 2015; Flohr et al. 2016; Ibáñez et al. 2018). In the southern Levant archaeobotanical evidence hints that—long prior to domestication—late Upper Paleolithic hunter-gatherers (ca. 21,000 BC) may have engaged in small-scale cultivation of wild-type wheat, barley, and oat plants (Snir et al. 2015). Because substantial carbonized seed assemblages are so rare in Pleistocene contexts, it is unclear whether this was a briefly adopted strategy to cope with Last Glacial Maximum environments, or whether it was the beginning of a very slow process of integrating horticulture into hunting, gathering and fishing economies. During the

subsequent Epipaleolithic (ca. 20,000-10,000 BC), a mosaic of hunting, trapping, gathering and fishing practices reflected, in part, variations in local ecology (Goring-Morris 2000; Munro 2004; Stutz et al. 2009; Grosman et al. 2016; Munro et al. 2016; Martin et al. 2016; Yeomans et al. 2017; Yeshurun and Bar-Oz 2018; Sharon et al. 2020). It is clear, though, that in zones of relatively high biomass productivity—with more rainfall and milder winter temperatures—Early and Late/Final Natufian populations, alike (ca. 13,000-10,000 BC), sustained strong hunting pressure on slower-growing or slower-reproducing game, from land tortoise (*Testudo graeca*) to diverse ungulate prey (Munro 2004; Stutz et al. 2009; Munro et al. 2016; Munro et al. 2018). This reflects a significant degree of long-term human population increase, from the Late Upper Paleolithic through the Natufian period—again, at least in more productive ecological zones, including southern Levantine Mediterranean vegetation zones and the wetland-dominated southern Rift Valley (Stiner 2005; Stutz et al. 2009; Munro et al. 2016; Stutz 2019). We face an important outstanding question. In the Natufian time-frame, key social and technological factors—including land-tenure, logistical mobility and investment in durable architecture—interacted with broad-spectrum resource exploitation and residential mobility between biomass-productivity zones. How did the feedbacks constituting such complex human systems influence pre-domestication cultivation (Weiss et al. 2006; Asouti 2013; Snir et al. 2015) and, eventually, the domestication of goat and sheep? (Munro et al. 2018) It is clear that Early Natufian foragers exploited a range of legumes that included the putative ancestor to domesticated fava beans (*Vicia faba*; Caracuta et al. 2016). Early Natufian food preparation technologies already involved winnowing, grinding, and sifting dried grains into flour, which was mixed in a dough with other wild starchy plant foods, baked as a bread (Arranz-Otaegui et al. 2018). Wild grain, legume, and grass seed collection and processing appears to have significantly increased in economic importance during the Late Natufian period across the Levant (Anderson 1999; Moore et al. 2000; Dubreuil 2004; Asouti and Fuller 2012, 2013), a pattern also seen in Younger Dryas settlements in southeastern Anatolia and in the hilly margins of lower Mesopotamia (Savard et al. 2006; Riehl et al. 2015; Rössner et al. 2018).

Subsequently, small-scale pre-domestication cultivation of locally available cereals and legumes clearly expanded during the PPNA period across the wider Near East (Willcox 2012; Asouti and Fuller 2013; Rössner et al. 2018). However, broad-spectrum cereal, legume, nut, fruit, grass-seed and wetland root foraging remained remarkably economically

important, from the final Epipaleolithic to the early Pre-Pottery Neolithic, ca. 11,000-9,000 BC (Hillman 2000; Savard et al. 2006; Willcox 2012; Asouti 2013; Riehl et al. 2015; Asouti et al. 2015). The association of iconographically rich monumental architecture with persistent broad-spectrum foraging in PPNA and early Pre-Pottery Neolithic B (EPPNB) southeastern Anatolia highlights how the collective investment in durable aggregation-site architecture, public storage, and ritualized gatherings—including communal feasting—were likely important in mediating mobility, social networks, and land tenure, in a flexible food economy that variably involved foraging, hunting, and small-scale pre-domestication cultivation (Dietrich et al. 2012). This pattern of negotiated, intense resource management, communal food processing, collective storage, feasting, and commemorative mortuary ritual appears to be a wider Near Eastern pattern in the PPNA (ca. 10,000-9,000 BC; Stordeur et al. 2000; Stordeur and Abbès 2002; Kuijt and Finlayson 2009; Finlayson et al. 2011; Goring-Morris and Belfer-Cohen 2011; Asouti and Fuller 2012; Asouti 2013).

Only later—from the MPPNB (ca. 8,000-7,500 BC) onward—do we see that fully domesticated cereals and legumes are consistently associated with Near Eastern archaeobotanical assemblages (Asouti and Fuller 2012, 2013; Arranz-Otaegui et al. 2016; Rössner et al. 2018). At roughly the same time, domesticated sheep and goat become important in archaeofaunal assemblages (Zeder 2012; Munro et al. 2018). By ca. 7,500 BC, agricultural production and animal herd management took on a significant economic and nutritional importance across the Levant, as PPNB economic systems began to structure anthropogenic vegetation regimes at a wider landscape scale, at least in Anatolia and the southern Levant (Asouti and Kabukcu 2014; Asouti et al. 2015). As we note above, it remains unclear how innovations in food economies, co-residence strategies, and social networks interacted with human demographic change. We emphasize that it is especially difficult to identify systemic feedbacks—that is, the complex causality—driving the adoption of domesticates, the emergence of agricultural production, the settlement of larger, more densely built Neolithic villages, and the incorporation of private household storage and food-processing equipment. It is clear, though, that LPPNB, PPNC and Early PN communities were materially constituted quite differently, when compared with preceding Epipaleolithic and initial Pre-Pottery Neolithic societies (Goring-Morris and Belfer-Cohen 2011; Asouti and Fuller 2013; Wright 2014).

As shown in figures 4 and 5, our PPNB skeletal sample captures a key trend. According to the DOHaD framework, long-term, population-level early-childhood health deteriorated

across the transition to agriculture. We suggest that this trend already had an impact on rising mortality in the PPNB timeframe, by ca. 9,000-7,000 BC. An *ad hoc* G-test of independence (Sokal and Rohlf 1995) between LEH formation and time period for Natufian versus PPNB juveniles (5-19 years) yields a G-statistic of 104, and with one degree of freedom, the one-tailed *p*-value is a very highly significant 1.8×10^{-24} . Early-childhood LEH formation is strongly associated with PPNB juvenile mortality, when compared with Natufian mortality. However, among the PPNB adults interred in the Levantine sites in our sample—and especially among those dying as older adults—the frequency of LEH is not significantly higher than that observed for Natufian older adults (G-statistic = 0.89, *p* = 0.35). Part of the complex causality we seek to elucidate, then, appears to involve an incipient deterioration in health, driven by early-life stress, that had already taken hold by PPNB times, during the 8th millennium BC.

Subsequently, during the 7th millennium BC (the PPNC/Early PN timeframe) in the Levant, early-life stress became ever more prevalent, apparently increasing frailty to an extent that raised mortality among older juveniles and adults. More specifically, high LEH frequencies are associated with death in the juvenile, adolescent, and younger adult life-stages, alike (table 4). More broadly, when compared with hunter-gatherers interred at least 3000 years prior—that is, among those interred in Natufian sites (ca. 13,000-10,000 BC)—we see that a higher proportion of PPNC/PN individuals experienced early-life stress, which constituted a significant predictor of death before the age of 30 (fig. 5). An *ad hoc* G-test of independence between LEH formation and time period, comparing those reaching the older-adult lifestage (≥ 30 years) during the Natufian versus PPNC/PN timeframes, yields a G-statistic of 23, with a highly significant *p*-value of 1.4×10^{-6} (one degree of freedom). At this time, even those surviving past 29 years had already suffered elevated rates of early-life stress. This has an important implication. With greater exposure to nutritional stress or infectious disease in early childhood, PPNC/PN populations were subject to wider heterogeneity in frailty—resulting in stronger mortality selection—between those dying before 30 and those surviving to at least 30 years.

Following Paine and Boldsen (Paine and Boldsen 2002), we suggest that the particularly strong PPNC/PN associations among high LEH prevalence and mortality in the younger-juvenile, adolescent, and younger-adult lifestages (table 5) are most parsimoniously, immediately explained by the emergence of higher endemic infection rates, combined with more frequent infectious disease outbreaks. Episodes of nutritional stress could have contributed to rising average frailty during

neolithization, but the statistical association between early-life stress and premature mortality among individuals ritually interred in PPNB and PPNC/PN Levantine village settlements could be entirely explained by more frequent exposure to food or waterborn gastrointestinal parasites, which could cause and further be transmitted by diarrhea. Still, Smith and Horwitz have emphasized that animal domestication in the PPNB would have led to increasing exposure to zoonotic pathogens (Horwitz and Smith 2000; Smith and Horwitz 2007). Goring-Morris and Belfer-Cohen raise the possibility that contagious disease outbreaks contributed to the abandonment or reorganization of several PPNC settlements in the later 7th millennium BC (Goring-Morris and Belfer-Cohen 2011). Our current sample is insufficient to evaluate this suggestion in detail, but community-level health would have tended to affect settlement history.

Although the strong observed association between LEH formation and premature mortality may have been immediately caused by repeated exposure to infectious disease outbreaks, we can identify wider biocultural, systemic factors favoring elevated human morbidity. As Prentiss and colleagues have recently suggested, community-level investment in sedentary settlement and food storage can catalyze positive-feedback cycles, accelerating human harvesting pressure on resources, creating greater vulnerability to more intense episodic food-resource shortfalls, raising infant mortality, and amplifying any existing heterogeneity in frailty (Prentiss et al. 2014; Prentiss et al. 2018; Prentiss et al. 2018). Puleston, Winterhalder and colleagues have presented complementary theoretical analyses, carefully validated by computerized simulations of a demographic model under conditions of limited productive land-area (Lee and Tuljapurkar 2008; Puleston and Tuljapurkar 2008; Lee et al. 2009; Puleston et al. 2014; Winterhalder et al. 2015; Puleston and Winterhalder 2019). They find that, under cultural systems of agricultural production and food storage, human demography can follow rapid expansion dynamics, quickly encountering Malthusian population constraints, largely without warning to the people constituting those populations (Puleston et al. 2014). Moreover, Puleston et al. infer that agricultural set-asides for next year's seed, while necessary for sustainable interannual farming yields, can dampen per capita calorie availability (Winterhalder et al. 2015), further driving pressures that would widen population-level heterogeneity in frailty.

We argue that our results confirm a fundamental aspect of neolithization in the Near East. The adoption of domestication technologies, the development of agricultural economies and land-resource management practices, and the settlement of

larger, more organizationally complex villages occurred despite long-term costs to community-level biological well-being (Larsen 2006; Larsen et al. 2019). However, this hallmark neolithization process—which extended from the late Upper Paleolithic through the PPNC/PN period—occurred via gradual, if geographically patchy, anthropogenic depression of wild ungulate populations (Munro et al. 2018), development of caprine domestication and herd management (Zeder 2012; Munro et al. 2018), landscape-scale transformation of vegetation regimes (Asouti and Kabukcu 2014; Asouti et al. 2015), expansion of small-scale agricultural fields (Asouti 2013; Asouti and Fuller 2013), and successive investment in settlements with durable, increasingly complex architecture, private storage and food-processing equipment (Goring-Morris and Belfer-Cohen 2008; Kuijt 2008; Wright 2014; Ibáñez et al. 2018).

Following Prentiss et al. (Prentiss et al. 2014; Prentiss et al. 2018; Prentiss et al. 2018), we would expect that sporadic, recurring food-resource shortfalls would have reduced biological well-being within communities, leading to settlement-reorganization and occasional abandonment. Yet, Neolithic landscapes underwent progressive, human-induced transformation, involving larger and marginally more densely distributed settlements. As cycles of settlement formation, abandonment, and new settlement unfolded, ecological refugia for hunting and gathering would have dwindled. This dynamic is arguably a continuation of a foraging-territory compression process that may have contributed to sedentary settlement among Late Epipaleolithic hunter-gatherers (Rosenberg 1998; Munro 2004; Yeshurun and Bar-Oz 2018). In the PPNB and PPNC timeframe (ca. 9,000-6,000 BC), reorganization of existing settlements or establishment of new ones would have depended on plant food storage and accessible agricultural fields. Food management technology and arable land would have initially offered relatively highly viable opportunities for increasing yields. Yet, as Winterhalder et al. have found, this would have quickly returned communities to strained, vulnerable Malthusian conditions, within only a few generations (Puleston et al. 2014; Winterhalder et al. 2015). Local biocultural systemic feedbacks among more frequent Neolithic food-insecurity episodes, susceptibility to infectious disease outbreaks, settlement abandonment/reorganization, and resettlement would have been intimately part of the Near Eastern transition to agriculture.

In this setting, wider social networks—and the cultural landscapes and repertoires that constituted social strategies and relationships, from close-kinship to regional scales—would have critically shaped the establishment and growth of those

new or reorganized settlements. From this perspective, rising average PPNC/PN mortality would not have simply been a byproduct of agricultural adoption. Rather, the long-term, archaeologically visible trend we interpret as poorer health and higher mortality would have been underlain by a more intricate biocultural dynamic, in which local communities more quickly and more often ended up subject to elevated heterogeneity in frailty and higher mortality.

THE PPNB/PPNC/PN INCREASE IN MORTALITY: REVISITING THE AGRICULTURAL DEMOGRAPHIC TRANSITION

Theoretical expectations in demography establish that differences in age-at-death distributions between mortality samples—from different sites or across time periods—are often more informative about shifts in fertility rates. Other things being equal, a burial sample with a relatively high proportion of juveniles (relative to all individuals) is expected to reflect higher fertility, rather than high early-life mortality (Bocquet-Appel and Masset 1977; Sattenspiel and Harpending 1983; Bocquet-Appel 2002, 2011; Bocquet-Appel and Bar-Yosef 2008). Still, Gage and DeWitte caution that the proportion of juveniles in an unbiased death assemblage could be variably influenced by the balance between fertility, mortality, and migration—that is, the local population growth rate (Gage and DeWitte 2009). The proportion of juveniles in an archaeological mortuary sample, in turn, is the result of a palimpsest of fluctuations in fertility, across social networks and settlements, over multiple generations. An archaeologically measured value of the proportion of juveniles does not necessarily—or even likely—correspond to a particular long-term average fertility rate. More cautiously stated, other things being equal, directional differences in the proportion of juveniles, observed among chronologically ordered mortuary samples, may only generally reflect corresponding directional changes in fertility rates.

In developing his widely influential “agricultural demographic transition” (ADT) framework, Bocquet-Appel compiled historical demographic records, observing a very high correlation between recorded fertility rates and the proportion of juvenile mortality (aged 5-19 years) among all deaths. He further employed a simulation methodology, conducting a sensitivity analysis of model preindustrial life tables. These results validated earlier theoretical analyses, along with the observed correlations between juvenile (5-19 years) mortality and fertility rates in the living population

(Bocquet-Appel 2002). Demonstrating that 5-19 year-olds become relatively more common in cemeteries post-dating the adoption of agriculture, Bocquet-Appel has situated his observations about agriculture and fertility in the context of a changing balance in metabolic load. He has argued that fertility would have rapidly risen in Neolithic biocultural systems. Mobility-related activity would have fallen with sedentism, and calorie-rich starchy diets would have helped reduce birth spacing. In his words, agricultural emergence would have fed a sustained Neolithic “baby boom” (Bocquet-Appel 2008: 35). In measuring the index ${}_5p_{15}$ (that is, the demographic notation for the proportion of deaths between 5-19 years among all deaths) in archaeological skeletal series, Bocquet-Appel and colleagues argue that they have identified an accurate paleoanthropological proxy for fertility rates (Bocquet-Appel 2002; Bandy 2005; Bocquet-Appel and Naji 2006; Bocquet-Appel 2008; Guerrero et al. 2008; Bocquet-Appel 2011). An empirical synthesis of ${}_5p_{15}$ changes in regional transitions may be interpreted as a decline in fertility in the centuries just prior to agricultural adoption, followed by a rapid rise in fertility, which possibly persists up to several millennia after agricultural economies gain a foothold. Archaeologists have largely taken as an article of faith that the “Neolithic demographic transition” scenario—as outlined by Bocquet-Appel in a series of articles and a key edited volume (Bocquet-Appel 2002, 2011; Bocquet-Appel and Naji 2006; Bocquet-Appel and Bar-Yosef 2008)—is reliably in evidence (Bocquet-Appel and Bar-Yosef 2008; Pinhasi and Stock 2011). We suggest that our results contribute to an updated evaluation of how the ADT model may fit the Levantine case.

As illustrated in figure 6, the average ${}_5p_{15}$ values per cross-sectional time period in our Levantine sample confirm previous results for a more restricted Levantine skeletal series (Guerrero et al. 2008). The pattern in figure 6 conforms with Bocquet-Appel’s expectations for how this paleodemographic index should directionally vary across the transition to agriculture.⁵ How do we consider the diachronic trend in the

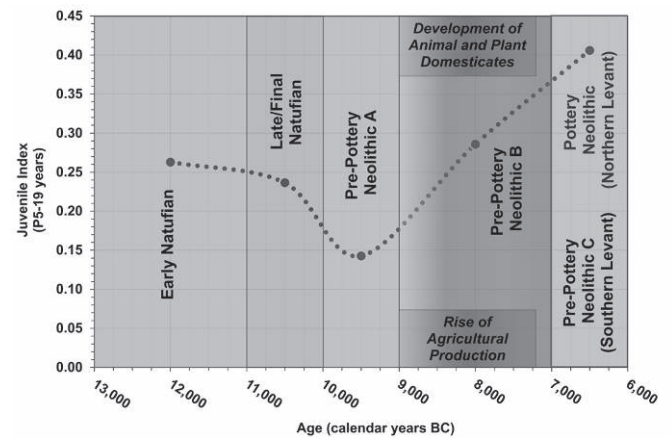


Fig. 6 – Proportion of juveniles 5-19 years in the total skeletal sample per time period. Note that the Juvenile Index is equivalent to Bocquet-Appel’s (2002) ${}_5p_{15}$ index.

proportion of juveniles (5-19 years) in Levantine burials? As emphasized above, we cannot easily rule out alternative explanations to the agricultural demographic transition scenario, including ones involving changing social biases in funerary recruitment. Still, in considering fit to the ADT model, the data—illustrated in figure 6—are tantalizing. Gage and DeWitte (Gage and DeWitte 2009: 652) suggest that Bocquet-Appel’s “death ratio” measures “pick up consistent, albeit weak, signals indicating a change in demographic regime during the transition to agriculture. It is even likely that this is due to changes in fertility, because ethnographic analogies suggest that the fertility of sedentary agriculturalists is higher than that of foragers...” (cf. Hewlett 1991; Bentley et al. 1993). A more recent, phylogenetic approach to analyzing variation in fertility rates between ethnographically documented agricultural and foraging societies confirms this general pattern. While hunter-gatherer and farming society fertility rates overlap, farmers and pastoralists tend to achieve statistically significantly higher completed fertility rates, typically involving one additional live birth per adult woman surviving to post-reproductive age (Sellen and Mace 1997). This agriculturally linked increase in fertility is significant but marginal. It is substantially smaller than that modeled by Bocquet-Appel (2008). Among the fundamental factors affecting fertility, sedentism would have already impacted maternal activity levels by the Early Natufian timeframe (Weissbrod et al. 2017; Yeshurun et Bar-Oz 2018; Liu et al. 2020), and the starch component of the diet probably already began to rise among Natufian hunter-gatherers (Dubreuil 2004; Arranz-Otaegui et al. 2018). Considered in long-term context, Natufian developments would have likely initiated a gradual decline in

5. In minor contrast with Guerrero et al.’s (2008) results, we observe a PPNA (ca. 10,000-9,000 BC) trough in the proportion of juveniles, across the cross-sectional time-period subsamples. Guerrero and colleagues illustrate a possible ${}_5p_{15}$ minimum already during the Late/Final Natufian period, ca. 11,000-10,000 BC. However, it is much better documented now that domestication, agricultural production, and sedentary village settlement only came to dominate during the PPNB timeframe (Belfer-Cohen and Goring-Morris 2008; Kuijt 2008; Goring-Morris and Belfer-Cohen 2011; Asouti and Fuller 2013; Arranz-Otaegui et al. 2016; Edwards 2016). Thus, the timing of the observed PPNA trough in figure 6 also fits Bocquet-Appel’s (2008) general model, involving a dip in ${}_5p_{15}$ values just prior to the PPNB agricultural transition (see also Bocquet-Appel 2002 and 2011; Bocquet-Appel and Naji 2006).

average birth spacing, with a concomitant slow rise in total fertility rates, from ca. 13,000-8,000 BC. As domestication and agriculture rapidly expanded in economic and dietary importance in the Middle and Late PPNB, ca. 8,000-7,000 BC, the increase in average fertility would likely have accelerated.

Common cautions about culturally biased funerary recruitment do apply for our results, however. Relative to actual deaths in the societies creating the archaeological record, those individuals buried in the on-site mortuary features that archaeologists excavate and study are not necessarily representative. Bocquentin's contextual analyses of changing burial practices in the Natufian periods (ca. 13,000-11,000 BC) document persistent gender-biased recruitment favoring males, while juveniles were not as likely to be interred in mortuary features in the Late Natufian period as in the Early Natufian period. This is despite the fact that infant and young juvenile burials do not show evidence of underrepresentation due to bone-density-dependent attrition (Bocquentin 2003, 2007). Given the rich variability in mortuary rituals in the Natufian and Neolithic periods across the entirety of the Levant (Kuijt 2000; Goring-Morris and Horwitz 2007; Maher et al. 2011; Nadel et al. 2013; Ortiz et al. 2013; Bocquentin 2014; Chamel 2014; Khawam 2014; Edwards et al. 2018; Benz et al. 2019; Richter et al. 2019; Chamel and Cocqueugniot 2020; Bocquentin in press), we confirm that the interpretation of long-term change in life-stage-at-death profiles themselves is especially challenging. Under conditions of heightened mortality, it could have been ritually efficacious for a community to handle the deaths of younger individuals by preferentially burying them within settlements. Across the Near East, mortuary ritual appears to have played a central role in how individuals, corporate groups, and whole communities negotiated complex co-residential, land tenure, and social network possibilities and dilemmas—especially as they faced changing variability in biological well-being. Thus, those who lived, died, and were ritually interred in Natufian and early Neolithic sites would have been part of a dialectic among culturally constituted and experienced worlds, social practice, and complex variations in environmental exposures and health outcomes. It remains difficult, quite simply, to tease out significant changes in fertility from our bioarchaeological observations.

We suggest that, if the time-period-specific values in the proportion of juveniles (5-19 years) “pick up consistent, albeit weak, signals” of change in fertility rates (Gage and DeWitte 2009), then according to the DOHaD model, our results track a rise in mortality that was closely, systemically tied to a PPNB-PPNC/Early PN increase in fertility. Bocquet-Appel and colleagues have emphasized that empirical

bioarchaeological observations confirm the metabolic load model's theoretical expectations; with higher population densities, earlier weaning ages, and lower dietary quality, agriculture would have brought an initial rise in fertility, followed by declining health and rising mortality (Bocquet-Appel and Naji 2006; Bocquet-Appel 2008, 2011; Bocquet-Appel et al. 2008). Bocquet-Appel has specifically proposed that, in the Near East—where the social organization and knowledge involved in agricultural production and management were developed and adopted over centuries or millennia—the joint increases in fertility and mortality would have occurred more slowly than in areas of secondary adoption (Bocquet-Appel 2011). Our results suggest that the demographic feedbacks between fertility and mortality were likely very closely, systemically coupled.

From this perspective, we observe that settlement sizes, household complexity, and site distributions are consistent with millennial-scale Neolithic population growth across the entirety of the Levant. Over this long time-frame, local and regional populations were hardly stationary. On the one hand, fluctuations in local populations were likely substantial. On the other hand, at a broad geographic scale, long-term average birth rates tended to be significantly—if only slightly—greater than death rates (Kuijt 2008; Flohr et al. 2016; Ibáñez et al. 2018). While stratigraphic evidence details how individual settlements underwent dynamic histories of growth, reorganization and abandonment, we note that recent analyses of a wide corpus of radiocarbon dates from Near Eastern Neolithic contexts have found no clear evidence for episodes of population explosion; nor have such summed calibrated date probability density distribution (SCDPD) analyses identified signals of population crashes, regional abandonments, or migrations (Borrell et al. 2015; Flohr et al. 2016). The contextual radiocarbon calibration evidence is consistent with a pattern of largely local population continuity, although dramatic changes in settlement, co-residence, mobility, monument construction, storage technologies, food management, and ritual practice unfolded in mosaic fashion across the Near East (Asouti 2013; Asouti and Fuller 2013; Flohr et al. 2016; Belfer-Cohen and Goring-Morris 2011). There is arguably a surprising degree of social and demographic resilience in the face of early Holocene climatic fluctuations (Flohr et al. 2016). There are, however, important exceptions. Borrell et al. identify a possible period of dispersed or falling population in the northern Fertile Crescent in the transition from the Early to Middle PPNB, ca. 8,000 BC (Borrell et al. 2015). More strikingly, the western Jordan region shows signs of major settlement decline over several centuries in the 7th millennium BC.

Long argued to be a total hiatus in Neolithic occupation (e.g., Perrot 1968), PPNC phases have recently been documented at several sites (Bocquentin et al. 2020; Vardi 2020).

The limited paleogenomic data from Epipaleolithic and Neolithic individuals in Anatolia, Syria, and the southern Levant are generally consistent with a resilient geographically structured population network that experienced genetic isolation by distance (Fix 1999; Lazaridis et al. 2016; Loosdrecht et al. 2018; Fregel et al. 2018). Although we have presented evidence consistent with increasingly frequent infectious disease outbreaks, there is no indication of an emergent south-western Asian pandemic that could have thoroughly shaped regional population turnover. As critically emphasized in the human population genetics literature, it is also theoretically challenging to quantify the actual long-term average rate of population growth under neolithization, which would have involved not only gradual demographic increase in the Near East, but also long-distance migration into neighboring areas, from north Africa to central Asia to Europe (Fix 1999). Local fertility and mortality rates would have fluctuated, primarily in response to immediate, contextual factors affecting food availability, workloads, and pathogen exposure. At the same time, regional social network connectivity—and the practices, material culture, and ideologies that mediated long-distance visits, exchange, and kinship alliances—would have had substantial impacts on demographic resilience.

It is plausible, then, that long-term trends in mobility and nutrition were sufficient to raise fertility, especially during periods when settlements were established or reorganized. In turn, population growth would have rapidly led to Malthusian constraints, raising mortality (Winterhalder et al. 2015; Puleston and Winterhalder 2019). In light of such inferred conditions, our results conform to the expectation of a time-averaged archaeological signal, in which mortality and fertility increased in tandem (figs. 4-6). High resolution stratigraphic data from individual Neolithic sites may elucidate the interplay—at centennial scale—among settlement, economic productivity, living conditions, fertility, and mortality.

CONCLUSION

This study has utilized Natufian and Neolithic human skeletal series from 24 separate sites, constituting the largest sample of mortuary features yet analyzed from communities spanning the emergence of agricultural food economies in the Levant. We aggregated skeletons interred in different sites,

from the southern and northern Levant, into chronologically cross-sectional samples, in order to maximize statistical power. This study's analytical methodology, based on theoretical considerations from the DOHaD model, yields robust results. We identify a highly significant average drop in regional, population-level biological well-being, involving an increase in mortality in the Neolithic transition to agriculture (figs. 4-5). Our results cannot yield a detailed quantification of life-stage-specific mortality rates. We can only demonstrate a statistically well-documented directional trend, involving rising mortality at least from the PPNB through the beginning of the PPNC/PN timeframe (ca. 7,000-6,000 BC). This agricultural-associated mortality increase occurred after a period of relatively good health and lower mortality during the Early and Late/Final Natufian periods (ca. 13,000-10,000 BC). Because the cemetery sample from the 9th millennium BC is so small, it remains statistically unclear whether PPNA populations (ca. 10,000-9,000 BC) already began to suffer more frequent early-life stress than their Natufian hunter-gatherer predecessors.

Based on our results, we encourage further contextual interdisciplinary inquiry, in order to resolve more finely the causes and interactions among fertility, mortality, migration, and prevailing biocultural conditions. In focusing on the developmental origins of health and disease (DOHaD), our analysis has highlighted how community heterogeneity in early-life environmental exposures likely played an important role in the Levantine transition to agriculture. Whether structured within settlements and their immediate resource catchments, or at a wider spatial scale, variation in stress exposure appears to have forced concomitant variation in health, shaping feedbacks among life-stage-specific survival chances and mortality risks, in turn, affecting the social alliances that mediated architectural construction, land-resource management, food economies, mobility, and co-residence that, together, underpinned early agricultural societies.

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TRENDS IN ANCIENT POPULATIONS' OSTEOBIOGRAPHY DURING THE HOLOCENE: THE LEVANTINE PERSPECTIVE

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Abstract. *The rapid changes in our surroundings during the Holocene challenge the human body. The current study, carried out on the terminal Pleistocene-Holocene populations of the Levant, presents several examples of how changes in the habitation and diet have affected the disease patterns and the gross morphology of long bones and mandibles. Our major findings were that the prehistoric Natufian (67%) and the protohistoric Chalcolithic (80%) populations exhibited a much higher rate of ear inflammation (otitis media) than all other populations: Neolithic, Roman/Byzantine, and Ottoman (50% ± 5%). A general continuous significant decrease in the relative femoral bone cortical area from the Natufian (77.8%) to present times (64.7%) was noticed (the Chalcolithic population was the exception). Mandibular shape has changed considerably, mainly between the pre-agricultural population (the Natufian) and the succeeding ones (i.e., the ramus became taller and narrower, the coronoid higher and pointed, the mandibular notch narrower and deeper, and the body more triangular). Possible behavioral, economic, and environmental factors associated with these changes are discussed.*

Résumé. *Les changements rapides de notre environnement au cours de l'Holocène mettent le corps humain au défi. L'étude actuelle, menée sur les populations du Pléistocène final et de l'Holocène du Levant, présente plusieurs exemples sur la manière dont les changements d'habitat et de régime alimentaire ont affecté les schémas pathologiques et la morphologie brute des os longs et des mandibules. Nos principales conclusions ont révélé que les populations préhistoriques du Natoufien (67 %) et celles protohistoriques du Chalcolithique (80 %) présentaient un taux d'inflammation de l'oreille (otite moyenne) beaucoup plus élevé que toutes les autres populations : néolithique, romaine/byzantine et ottomane (50 % ± 5 %). Une diminution générale continue et significative de la surface corticale relative de l'os fémoral entre le Natoufien (77,8 %) et l'époque actuelle (64,7 %) a pu être observée (la population chalcolithique étant l'exception). La forme de la mandibule a considérablement changé, principalement entre la population pré-agricole (le Natoufien) et les suivantes (c.-à-d., le ramus est devenu plus grand et plus étroit, le processus coronoïde plus haut et plus pointu, l'encoche mandibulaire plus étroite et plus profonde et le corps plus triangulaire). Les facteurs comportementaux, économiques et environnementaux possibles associés à ces changements sont discutés.*

Keywords. *Holocene populations, Levant, adaptation, diseases, physical stress, evolution, Neolithic, Natufian*

Mots-clés. *Populations holocènes, Levant, adaptation, maladies, stress physique, évolution, Néolithique, Natoufien*

For hundreds of thousands of years, our species has evolved, both anatomically and physiologically, into an efficient hunter-gatherer. When most of his “cousins” (e.g., Neanderthals, *H. Denisovans*, *H. Floresiensis*, and *H. Luzonensis*) disappeared, *Homo sapiens* continued to flourish and conquer new ecological niches, becoming undoubtedly the most successful representative of the genus *Homo*.

Until the beginning of the Natufian period (ca. 15,000 years ago), the selection forces that acted on humans to adapt them to life as hunter-gatherers had fluctuated very little. However, this situation changed dramatically during the Natufian period: the old life style, which was practiced for hundreds of thousands of years and involved hunting and gathering, was quickly replaced by a sedentary life style that largely relied on farming

(Bar-Yosef 1998; Belfer-Cohen and Goring-Morris 2011). Large communities were soon established, the demographic structure of the populations changed, a division of labor evolved, social stratification emerged, and cultures sometimes quickly changed (Hershkovitz and Gopher 2008; Belfer-Cohen and Goring-Morris 2011). From the Neolithic period onward, human populations underwent temporal and perhaps extreme changes in various aspects of their daily life (e.g., physical activity, diet, health, and demography; Hershkovitz and Gopher 1990, 2008; Eshed et al. 2004a, 2004b; May and Ruff 2016). Consequently, rapid fluctuations in selection pressure arose, requiring equivalent temporal changes in the population's fitness and its ability to adapt to changes. However, the population's biological adaptation could not occur at the same pace, leaving Holocene people seemingly trapped in the body of Upper Paleolithic hunter-gatherers. The social adaptation, however, was enforced through rules, prohibitions, and laws initiated by a newly evolved centralized political and economic system (Belfer-Cohen and Goring-Morris 2011).

Many studies have been published on the terminal Pleistocene-early Holocene populations of the Levant: the Natufian (13,000 BC-9,500 BC) and the Pre-Pottery Neolithic (9,500 BC-6,400 BC). During this period, one of the most dramatic events in human evolution occurred, namely, the "Agricultural Revolution". Changes in dental diseases as well as the attrition rates and patterns (Eshed et al. 2006), the prevalence of infectious diseases (Eshed et al. 2010) including the appearance of tuberculosis (Hershkovitz et al. 2008), physical loads (Eshed et al. 2004b; May and Ruff 2016), demography (Eshed et al. 2004a; Hershkovitz and Gopher 2008), physiognomy, and burial customs (Hershkovitz and Gopher 1990; Slon et al. 2014) have been reported. New ecological niches were conquered and people started to look for food not just on land, but also in the sea (Galili et al. 1993). For reasons not currently clear, the "golden age" of the Pre-Pottery Neolithic (PPN) culture in the Levant came to an end around 6,400 BC. The local populations started to flourish again in the Chalcolithic period (4,500 BC-3,900 BC), probably partially due to the introduction of new populations following migrations (probably from Anatolia) into the local population (Harney et al. 2018). This period became the prologue to some of the greatest achievements and milestones in human history including the "Secondary Products Revolution" (derivatives from animal sources such as wool, textiles, and dairy goods), metal production, the development of art and religion, and the emergence of specialized occupations and professions. The Chalcolithic period ended in Israel around 3,900 BC, with the rise of the Early Bronze civilization, marking the beginning of

urbanization, the appearance of kingdoms and empires, and most importantly, writings (Gilead 1988).

Studies of archeological populations that underwent changes in subsistence strategies from hunter-gathering to agriculture (Natufians vs. the Pre-Pottery Neolithic) have generally revealed a decline in health (Goodman et al. 1980, 1984; Angel 1984; Larsen 1995, 2006; Mummert et al. 2011). In the southern Levant, this was manifested by a decrease in the female life expectancy and an increase in the prevalence of infectious diseases and perhaps pandemics (Hershkovitz and Gopher 2008; Eshed et al. 2010).

The aims of the current paper were to follow the temporal changes in the biological and morphological features of Levantine populations during the Holocene, and to examine them in light of known data regarding their living conditions, subsistence strategies, and environmental conditions.

MATERIAL AND METHODS

Various skeletal remains (i.e., petrous, mandible, and femur) of different populations including Natufian hunter-gatherers, Pre-Pottery Neolithic early farmers, Chalcolithic farmers, Roman/Byzantine farmers, Ottoman farmers housed at the Anthropological collection, the Dan David Center for Human Evolution and Biohistory Research, Sackler Faculty of Medicine, Tel Aviv University as well as recent populations (approved by the ethics board of the Carmel Medical Center, number: 0066-11-CMC) were examined (table 1).

Table 1 – *Skeletal remains examined in the study, by population.*

| Population | Petrous | Femur | Mandible |
|-----------------------|---------|-------|----------|
| Natufian | 30 | 32 | 10 |
| Pre-Pottery Neolithic | 22 | 67 | 6 |
| Chalcolithic | 70 | 45 | 9 |
| Roman/Byzantine | 81 | 18 | 16 |
| Ottoman | 26 | 23 | - |
| Recent | - | - | 62 |

Estimating the presence of ear infection: The promontory of all petrous bones was examined using a flexible videoscope (PENTAX Medical VNL-CP, field 90°, depth of field 5-50 mm, distal end width 3mm, deflection 120°/120°, LED illumination) and an optical microscope (Nikon SMZ745T magnification range: ×6.7 to ×50). Interruptions in the integrity of the promontory bony surface were recorded as either manifesting or not

manifesting ear infection. These interruptions may appear either as bony bulges (appearing as isolated narrow bony crests or isolated bony spicules), or as zones of bone resorption (Folreanova et al. 2020).

Estimation of physical load: Mid-shaft cross-sectional images were obtained from the CT scans of the femora (Brilliance 64 [Philips Medical Systems, Cleveland, Ohio]: slice thickness 0.8-1 mm, 140 kV, 150 mA, rotation time 0.75 s, Pitch 0.39, and Matrix 512 × 512). The amount of the cortical bone was measured in relation to the total area of the cross section (i.e., %CA = cortical area/Total area × 100) via a dedicated software developed for this purpose (May and Ruff 2016).

Estimation of dietary quality: The relative size of the medullary cavity (medullary cavity diameter/total cross-sectional diameter) in long bones, mainly of the lower limbs can be used as indicator of food quality and the general health of a population (Garn et al. 1970; Ruff 1999; Heaney et al. 2000; Horocholyn and Brickley 2017). The medullary cavity diameters on the antero-posterior and medio-lateral axes were measured from the midshaft cross sections of the femur, obtained from CT. To control for body size, the AP and ML medullary cavity diameters were divided by the corresponding total diameter of the midshaft cross section.

Estimation of dietary habits: Shape analysis of hemimandibles was carried out on mandibles that either underwent a high-resolution computerized tomography (CT) scan (Brilliance 64, Philips Medical Systems, Cleveland, Ohio: slice thickness 0.5-0.8 mm, 100 kV, 150 mAs, rotation time 0.75 s., pitch 0.39, and Matrix 768 × 768), or were surface scanned via a Space Spider portable 3D scanner (Artec Europe, Luxembourg). For mandibles that were scanned via CT, a 3D surface mesh of the mandibles was reconstructed from CT stacks using Amira 6.3 software (www.fei.com). A semi-automated segmentation of CT stacks was carried out, based on gray level thresholds. Manual segmentation was performed where needed. For those mandibles scanned by the surface scanner, the image processing and alignment were carried out via Artec Studio 13 software (Artec Europe, Luxembourg). The 3D shape of the mandible was analyzed using the Procrustes-based geometric morphometrics method, which included 52 landmarks (16) and semilandmarks (36) representing eight curves (Sella Tunis et al. 2018). Landmarks were placed by the same researcher on the 3D surface mesh of the mandible using Evan Toolbox software 1.72 (www.evan-society.org). Semilandmark sliding was carried out based on the minimum bending energy technique (Gunz and Mitteroecker 2013).

CHANGES IN COMORBIDITY THROUGHOUT THE HOLOCENE: CHALLENGES AS WELL AS SPECULATIONS

In order to follow changes in disease prevalence over time, the disease must fulfil two a priori conditions, namely, it must leave distinct marks on the bones (many different diseases leave similar marks on the bones) and be common enough. Otitis media (OM), i.e., the inflammatory disease of the middle ear, fulfils these two basic requirements. Presently, acute otitis media affects about 11% of people each year (about 709 million cases), with half occurring in individuals below five years of age (Monasta et al. 2012). Chronic suppurative otitis media affects about 31 million, with 22.6% of these cases occurring annually in children under the age of five years (Monasta et al. 2012). The disease, regardless of type, may persist for months; this often leads to a remodeling of the osseous wall of the middle ear. The common cause of all forms of otitis media in children is dysfunction of the eustachian tube (Bluestone 2005).

Our laboratory developed a reliable method for identifying ear infection in skeletal material (Floreanova et al. 2020; fig. 1), in which remodeling of the promontory surface, a preserved structure in the middle ear, which under normal conditions, undergoes little remodeling if any, is used as an indicator of infection. Analysis of the middle ear of six populations that lived in the southern Levant during the terminal Pleistocene-Holocene revealed that two populations exhibited a higher prevalence of OM: the prehistoric Natufian (67%) and the protohistoric Chalcolithic (80%) populations. All other populations (Neolithic, Roman/Byzantine, and Ottoman) showed a prevalence of 50% ± 5% (Folreanova et al. 2020). Our results fall within the variation of the mediaeval pre-antibiotic period from different regions (Flohr and Schultz 2009, Krenz-Niedbała and Łukasik 2016).

What could explain the high prevalence of OM in these two populations that engaged in completely different lifestyles and dietary habits and that are more than 6,000 years apart? Why was morbidity so high in the Chalcolithic period? In our quest for possible answers, we examined several possibilities and present here what we think are the most likely ones.

The Natufians were the last hunter-gatherer population in Israel that used caves and terraces in front for habitation. Many of the large Natufian sites in Israel (e.g., Hayonim, Nahal Oren, and Rakefet) are actually cave-based camps. Since cave-dwellers are exposed to smoke, i.e., indoor pollution, to a much greater extent than people living in open areas, this may explain

the high prevalence of OM in this group. Indoor air pollution can cause upper respiratory infection as well as middle ear effusion because it irritates the mucus (Bruce et al. 2000). Many studies have shown that indoor air pollution (originating, for example, from smoking tobacco, cooking, and heating) places children at more risk for ear infections (Uhari et al. 1996; Ilicali et al. 1999; Bruce et al. 2000; Murphy 2006).

Although it is tempting to use this argument for the Chalcolithic population as well, since at least in the southern part of Israel the people during this period dwelled in artificial caves, the abundance of open sites suggests that a definitive causal explanation is more complex. Whatever the cause, considering the very high prevalence of this disease, it must have been distressing.

The Chalcolithic population, in contrast to their preceding populations, probably consumed dairy products (Gilead 1988;

Evershed et al. 2008). Interestingly, the association between cow's milk intake and recurrent ear infections in children has been documented in many studies (Juntti et al. 1999). Although there are rare cases of pathogens in milk directly causing ear infections, the link is thought to be due to milk allergies (Juntti et al. 1999). Ear infection is due to fluid building up in the respiratory passages, sinuses, and the eustachian tubes of the ears. Today, around 5% of children and adults seem to be either allergic or intolerant to milk (Ludman et al. 2013).

An additional possible factor for the increase in the prevalence of ear infections during the Chalcolithic period is the unique climatic conditions. In contrast to the preceding and succeeding periods, the weather was colder and wetter during the Levantine Chalcolithic period (Litt et al. 2012). Cold and wet weather is also considered a risk factor for ear infections (Šprem and Branica 1993).

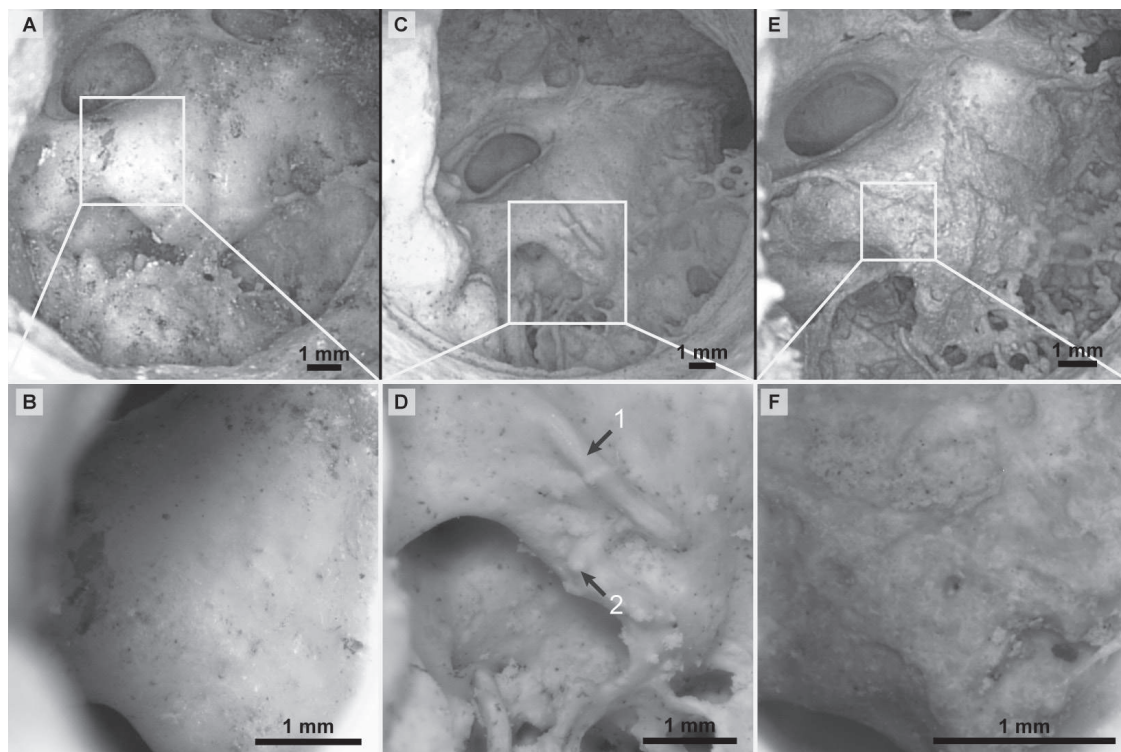


Fig. 1 – Ear infection diagnosis based on bone remodeling of the promontory surface (after Floreanova et al. 2020, modified bracket). **A, B**: No remodeling is evident; the surface is smooth when directly observed via a videoscope (PENTAX Medical VNL9-CP; A) and a light microscope (SMZ1270i, Nikon equipped with a digital camera DS-Fi3, Nikon; B); **C, D**: Isolated, bony overgrowths with clear margins appearing as a narrow bony crest (1) or a bony spicule (2) observed via videoscope (C) and a light microscope (D); **E, F**: Interruption of the integrity of the promontory bony surface observed via videoscope (E) and a light microscope (F).

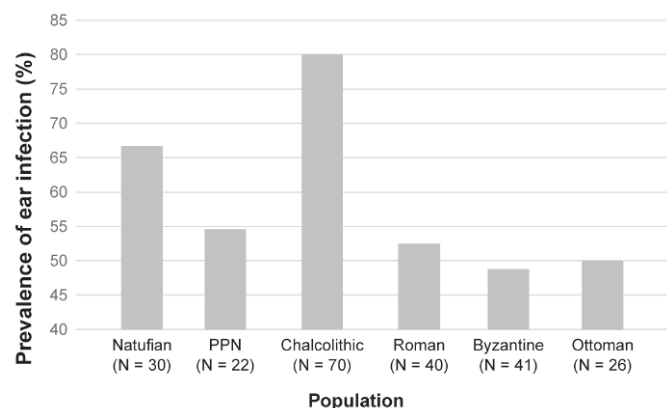


Fig. 2 – Prevalence of ear infections in various populations (adults only) during the terminal Pleistocene-Holocene Levant.

CHANGES IN THE PHYSICAL BURDEN OVER TIME

Throughout life, bone modeling and remodeling have dramatically changed bone strength, which can be enhanced through functional loading (Seeman 2008). Following the Mechanostat approach (Frost 2003), when all else is equal, individuals who are physically active should have stronger bones than their less active peers would. However, in order for loading to generate sufficient strain on the bone to elicit a response, the following should occur: the loading should be of sufficient magnitude; it should be distributed to the skeleton in abnormal directions, and it should be exerted at a regular frequency (Schoenau 2005). Since the skeletal response to loading is site specific (Sugiyama et al. 2010), some habitual activities can be detected (see, for example, Eshed et al. 2004b). However, determining which activity is more labor intensive is sometimes not straightforward or is even unsuccessful.

Since the majority of conventional weight-bearing exercises generate loading to the lower limbs, in the current study we examined changes in the relative cortical area (CA) of the femoral midshaft cross section during the Holocene. We preferred to present this parameter rather than other typically accepted cross-sectional geometry parameters because it includes information both on the strength of the bone as well as on its relative amount (Ruff et al. 2006). We noticed a general continuous significant decrease in %CA (cortical subperiosteal bone area/total cross-sectional area $\times 100$) from the Natufian period (77.8%) to present times (64.7%); however, the Chalcolithic population was an exception (fig. 3). For reasons

not presently known, the Chalcolithic population deviated from the general trend and exhibited a very high %CA, almost as high as the Natufian population (fig. 3).

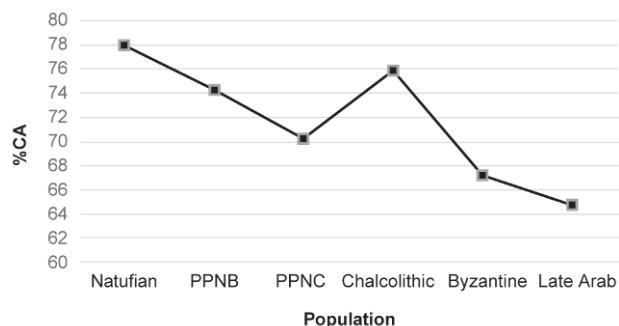


Fig. 3 – Changes in the relative subperiosteal cortical bone area ([cortical areatotal cross-sectional area at midshaft] $\times 100$) in southern Levant populations during the Holocene.

These results raised two intriguing questions: Is the general decrease in %CA due to an ongoing decrease in physical stress (mainly axial loading) over time? Why did the Chalcolithic population deviate so sharply from the general trend? As is well known, bone tissue is extremely dynamic, and continuously responds to diverse biochemical and physical stimuli, but to what stimuli?

As for the first question, the answer would be affirmative if we assume that the Natufians had walked long distances and had run (characteristics of hunting and foraging), i.e., both types of activities require greater resistance to axial loads (large cross-sectional areas). It has been shown that (a) low levels of physical activity contribute to reduced bone strength (Ryan and Shaw 2015), and (b) runners increase periosteal apposition (which augments bone strength through greater resistance against bending forces), compared with elite swimmers and non-athletic individuals (Hind et al. 2010, 2012). Periosteal apposition reduces bone fragility by adding more bone mass to the skeleton; it increases stiffness and strength by adding bone farther away from the central axis (Turner 2003). Ryan and Shaw (2015) have shown that the femoral head of mobile foragers possesses a significantly higher bone volume fraction and significantly thicker trabeculae compared with agriculturalists, who are more sedentary.

But what about the Chalcolithic population? Their lifestyle did not differ much from later populations. The only parameter common to both the Natufian and Chalcolithic populations examined in the current study was their residential environment (i.e., the geographic elevation), i.e., most of the Chalcolithic

sample studied here were from the Peqi'in Cave in the Upper Galilee and most of the Natufian material was either from the Upper Galilee or the Carmel mountain. It has already been shown that people who live at high elevations have a better bone status than those who live at low elevations due to the chronically greater daily activity caused by steep slopes in rural mountainous areas (Takeda et al. 2015).

CHANGES IN THE DIET QUALITY OVER TIME

Until the 1980s, the leading theory was that domestication of plants and animals resulted in improved nutritional status (i.e., the balance between the intake of nutrients by an organism and their expenditure in the processes of growth, reproduction, and health maintenance). However, Armelagos and Cohen (1984) revolutionized this line of thinking and claimed that the Neolithic transition brought about a decline in the food quality, which continued until the industrial revolution. Their arguments were mainly based on observations suggesting that the general health status of the population had declined, based on the tooth attrition rates and patterns, and the prevalence of various dental/oral diseases. The major drawback of the dental-based studies was that all of these markers can be used to gain insights on food consistency and preparation methods, but they often reveal very little about the quality of the diet.

One of the markers that can be used for such a purpose is the relative size of the medullary cavity (medullary cavity diameter/total cross-sectional diameter) in long bones, mainly of the lower limbs. In populations that are malnourished or exposed to high systemic stress, low bone mass is expected,

with an enlargement of the endosteal surface (Garn et al. 1970; Ruff 1999; Heaney et al. 2000; Horocholyn and Brickley 2017).

The availability of CT femoral diaphysis images of the Holocene Levantine populations allowed us to follow changes in the medullary cavity's relative size over time (changes in medullary cavity diameters along the antero-posterior and the medio-lateral axes of the femur in relation to the total cross-sectional diameters).

Our results clearly show a temporal increase during the terminal Pleistocene-Holocene Levant in the medullary cavity space, regarding the cortical bone thickness area (excluding the Chalcolithic population; fig. 4). The femora from the Chalcolithic period displayed a relatively small medullary cavity, similar to that of the Natufian femora. The overall increase in the relative medullary cavity size and consequently, a decrease in the relative cortical bone thickness imply a greater rate of endosteal resorption over time. This may indicate that nutritional factors, among other factors, may have been involved. Previous studies, based on skeletal and dental remains, suggested that in the Levant, nutrition deteriorated following the agricultural revolution (Smith and Peretz 1986; Hershkovitz and Gopher 2008). This may have been due to many factors, non-dietary (e.g., higher population density and reduced hygiene, and increased parasite load) and dietary factors (e.g., the transition to monotypic diets based on a few domesticated animals and plants bracket; Smith et al. 1984; Larsen 1995, 2003, 2006; Bar-Yosef 1998; Cordain et al. 2005; Lucock et al. 2014). Low intake of calcium and vitamin D, along with lower levels of dietary proteins as well as a decline in the health status, could have caused an imbalance in bone remodeling, leading to bone resorption and reduced cortical bone thickness (Garn et al. 1964; Garn 1970; Himes et al. 1975; Freudenheim et al. 1986; Owsley 1991; Hirota et al. 1992; Larsen 1995; Hannan et al. 2000).

What could have occurred in the Chalcolithic period to have caused the diet quality to improve so much? It is probably a combination of two factors: climate and the type of food consumed. Litt et al. (2012) suggested that the Levant underwent several climate change cycles throughout the Holocene, i.e., arid and warm weather in the early Holocene period (~10-6.5 ka cal. BP), wetter and colder weather in the mid Holocene (6.3-3.3 ka cal. BP), and drier and warmer weather in the late Holocene (~3.2 ka cal. BP to the present). Being an agrarian culture in nature, the Chalcolithic population greatly benefited from increased precipitation and consequently, a better, more diverse, and well-balanced diet. Their subsistence was based on farming crops—chiefly wheat, barley, and lentils—and on livestock: sheep, goats, and cattle. The livestock was also used

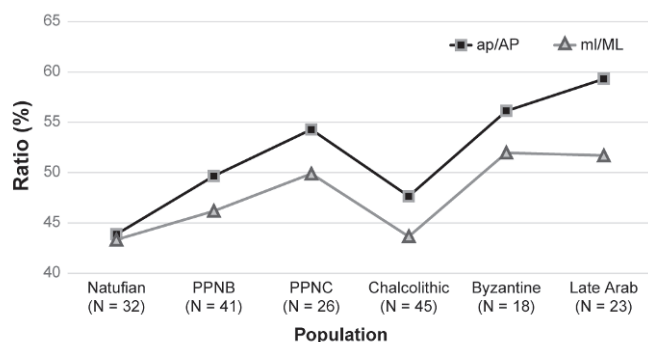


Fig. 4 – Relative medullary cavity breadth measured at the femoral mid-shaft cross section in samples from various periods during the terminal Pleistocene-Holocene Levant.

for producing wool and dairy products. People of the Chalcolithic period were also the first, in Israel, to grow cultivated fruit-bearing trees, such as date palms, olive trees, and pomegranates (Gilead 1988).

FOOD CONSISTENCY AND PREPARATION METHODS

The transition to food production was followed by changes in the food preparation techniques (e.g., grinding vs. pounding, and the introduction of cookware and other utensils; Gopher et al. 1992; Goren and Gopher 1995; Eshed et al. 2006). Changes in the cooking methods resulted in reduced stiffness of the food and therefore, in reduced mastication forces required for processing the food. Previous studies have shown that mandibular shape is associated with mastication loadings (Sella-Tunis et al. 2018). Accordingly, mandibles associated with high mastication loadings are associated with a wider, more trapezoidal-shaped ramus, a more massive coronoid (wide and low), and a rectangular body. In contrast, mandibles with lower mastication loadings are characterized by a tall and narrow ramus (more like a parallelogram), a pointed coronoid (narrow and tall), and a triangular body. We have demonstrated (Pokhojaev et al. 2019) that during the terminal Pleistocene-Holocene Levant mandibular shape had changed considerably, mainly between the pre-agricultural population (the Natufian) and the succeeding ones, and between the pre-industrial and the post-industrial populations. A tendency for a reduction in mandibular size was identified between the pre-agricultural population and the farmers. Changes in mandibular shape that correspond to mastication loadings are presented in figure 5.

Variance of mandibular shape, captured by 52 landmarks and semilandmarks, indicated that throughout the first PC (explaining 19.7% of variance), the mandibular shape changed from the pre-agricultural population (the Natufian) to the post-industrial population (the Modern), mainly regarding the mandibular body and ramus. The mandibular body became more triangular (a reduction in its posterior height, relative to its anterior one); the mandibular ramus became narrower, elongated, and posteriorly tilted; the coronoid process became narrower and elongated, extending beyond the condyle height, and the mandibular notch became narrower and deeper. The third PC (explaining about 11.1% of the variance) differentiated between the post-agricultural revolution populations (Neolithic, Chalcolithic, and Roman/Byzantine) and the post-industrial populations (the recent population) that exhibit mainly an increase in chin projection, a narrowing of the coronoid, and a lengthening of the condyle (fig. 6).

Although the impact of dietary changes on mandibular morphology was recognized in previous studies (Pinhasi et al. 2008; Cramon-Taubadel 2011; Galland et al. 2016; Katz et al. 2017), our study (Pokhojaev et al. 2019) is the only one that meticulously followed these changes in a series of Levantine populations. These changes in mandibular shape can be explained by the masticatory-functional hypothesis (Proffit et al. 2014; Sella Tunis et al. 2018); therefore, they can be reliably used as indicators of changes in dietary habits.

SUMMARY AND CONCLUSIONS

There is no doubt that Holocene populations experienced, in a relatively short time period, dramatic changes in

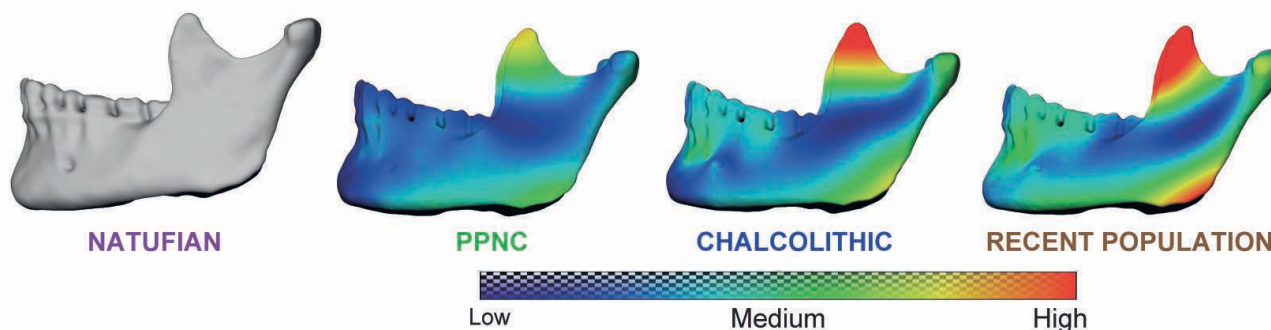


Fig. 5 – Patterns of mandibular shape transformation from Natufian hunter-gatherers to the present time. The magnitude of the shape transformation between the warped surfaces of the mean shape is presented via a color map (the lowest value is in blue and the highest is in red). Note that the coronoid process shape and the mandibular angle regions exhibit the highest change over time.

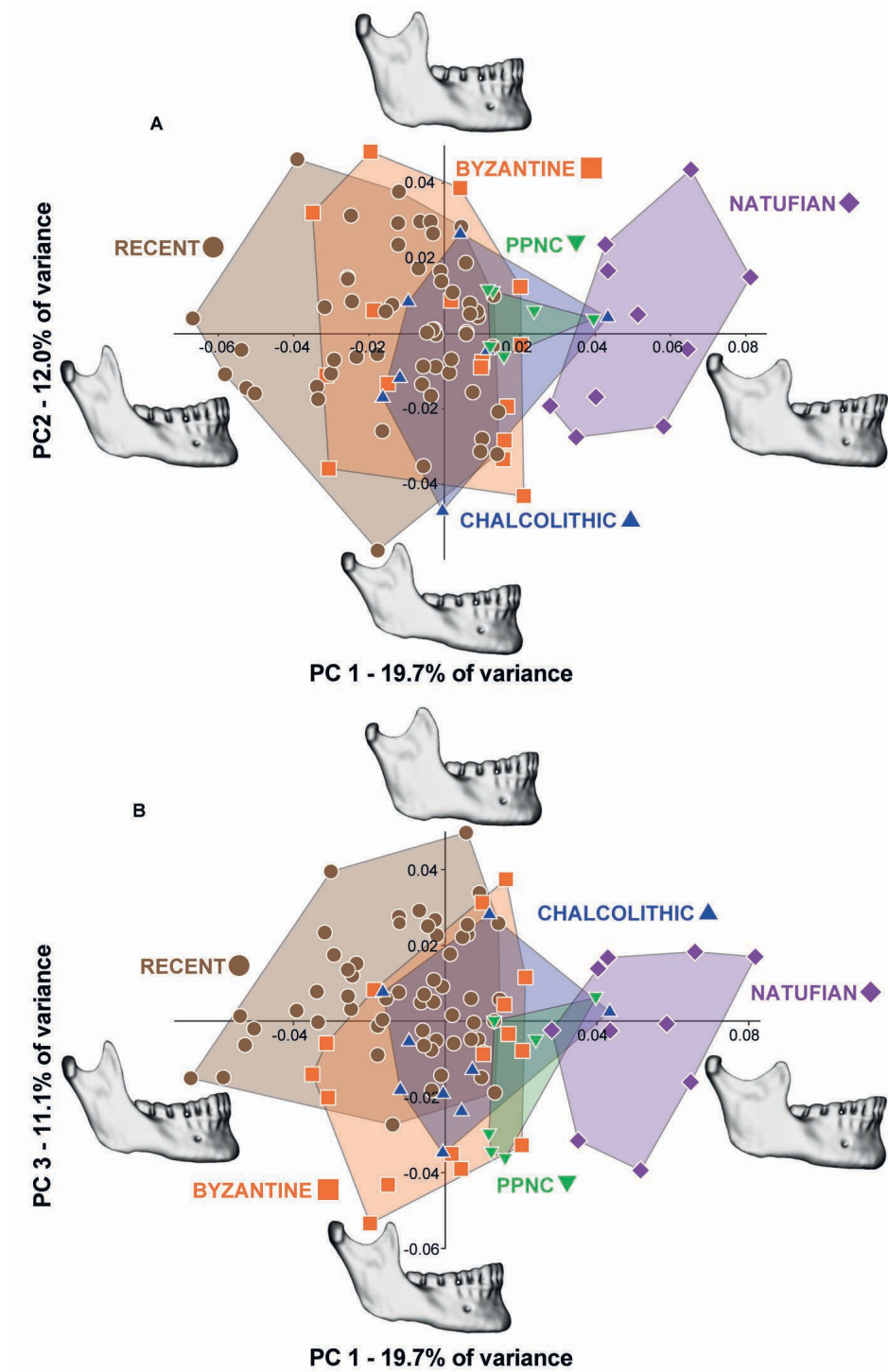


Fig. 6 – Principal component analysis of the hemimandibular shape by population (using a set of 52 landmarks). **Purple:** Natufian; **green:** PPNC; **blue:** Chalcolithic; **orange:** Roman/Byzantine; **brown:** recent population. **A:** The first two principal components (PCs) explain 31.7% of the variance; **B:** The first and third PCs explain 30.8% of the variance (figure modified from Pokhojaev et al. 2019).

almost all behavioral and cultural aspects. The transition from the Stone Age to the Apollo 13 landing on the moon took less than 12,000 years. It is still debated what triggered this dramatic change, but once humans abandoned their old life style of hunting and gathering, which was practiced for more than 2 my, and they adopted a food-producing behavior, the point of no return was crossed, and their lives changed forever. The abundance of well-dated skeletal remains from all periods, the relatively homogeneous (biologically and culturally) nature of the populations having their roots in the Natufians, the small geographical areas, and the similar environmental conditions, make the prehistoric populations of Israel ideal for testing the impact technological innovations had on human biology. Nonetheless, reconstructing trends overtime in body physique, life style, and health, and their possible causes must take into consideration, even when on a small scale, population dynamics (e.g., migration, population mixture). For example, we recently generated a genome-wide ancient DNA study from 22 individuals from Peqi'in Cave (Harney et al. 2018), a Chalcolithic site in northern Israel. Interestingly, we discovered that people from this site were part of a homogeneous population that can be modeled as deriving ~57% of their ancestry from groups related to individuals from the local Levant Neolithic, ~17% from groups related to individuals from the Iran Chalcolithic, and ~26% from groups related to Anatolian Neolithic individuals. It is therefore possible that population movements not only propelled cultural changes in the deep past, but also affected the biological characteristics of the local population. Our study of the skeleton and mandible of Levantine Holocene populations clearly shows a reduction in their size and general robusticity over time. With the changes in lifestyle, diet, and food preparation techniques, there was probably no longer a need to maintain a massive masticatory and locomotion system, which requires significant energy (De Paula and Rosen 2013). The dietary and physical changes experienced by Levantine Holocene populations had their toll, e.g., an increased incidence of dental

anomalies and dental diseases with time, an increased incidence of bone fractures (mainly hip fractures), low back pain, obesity, and many other physical and health hazards.

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DENTAL HEALTH STATUS CHANGES DURING THE NEOLITHISATION IN SYRIA: A DIACHRONIC PERSPECTIVE (9,820-6,000 CAL. BC)

B. CHAMEL

Abstract. *The Neolithisation of the Near-East is a key period in the history of humanity, when huge changes occurred in subsistence economy, triggered by agriculture and animal husbandry. Other changes in lifestyle were generated by sedentarization and by the invention of pottery as a container. The aim of this study is to see if these changes in Neolithic populations are reflected in oral health status, focusing on the most relevant markers. The 312 skeletons from seven Syrian sites (Tell Qaramel, Cheikh Hassan, Dja'de el-Mughara, Tell Aswad, Abu Hureyra, Tell Mureybet and Tell Ain el-Kerkh) were systematically examined for evidence of four pathological lesions—dental caries, abscesses, ante-mortem tooth loss and periodontal disease. Data were grouped by period to determine the impact of Neolithisation in a diachronic perspective. Results reveal that changes in oral health were not linear and that the adoption of agriculture and methods of food preparation were important factors influencing health status.*

Résumé. *La Néolithisation au Proche-Orient est une période phare de l'histoire de l'humanité : c'est en effet au cours de cette phase qu'interviennent de grands changements dans l'économie de subsistance, apportés par l'invention de l'agriculture et de l'élevage. D'autres changements dans le mode de vie sont également engendrés par la sédentarisation et, en dernier lieu, par l'invention de la céramique. L'objectif de cette étude est de voir si les bouleversements que connaissent les populations néolithiques s'observent dans l'état sanitaire bucco-dentaire, en se focalisant sur les marqueurs les plus pertinents. Les 312 individus, provenant de sept sites syriens (Tell Qaramel, Cheikh Hassan, Dja'de el-Mughara, Tell Aswad, Abu Hureyra, Tell Mureybet et Tell Ain el-Kerkh) ont donc été étudiés de façon systématique à la recherche de caries, d'abcès, de dents perdues ante-mortem et de maladie parodontale, et ces individus ont été regroupés par périodes afin de mesurer l'impact de la Néolithisation dans une étude diachronique. Ce travail a permis de mettre en évidence que les changements intervenus dans l'état de santé dentaire sont loin d'être linéaires ; il semblerait également que l'invention de l'agriculture et le mode de préparation des aliments aient joué un rôle important dans l'évolution de l'état de santé bucco-dentaire.*

Keywords. *Neolithic, Near-East, dental pathology, agriculture, pottery*

Mots-clés. *Néolithique, Proche-Orient, pathologie dentaire, agriculture, céramique*

NEOLITHISATION IN THE NEAR-EAST: CONTEXT AND MATERIAL

The end of the Paleolithic in the Near-East was marked with climate and environmental changes, followed by a major shift in subsistence patterns. The term “Neolithisation” groups together several processes that led to a significant advance in the long evolution of human societies. In the Near East, four major stages followed one another, occurring in different locations: sedentarization, agriculture, animal husbandry and the use of ceramics as containers. In the South Levant, from the Natufian around 12,000 cal. BC, hunter-gatherers sedentarized and settled in villages of round houses, often on the banks of rivers and in coastal regions. They still hunted, fished, and gathered plants and cereals (Bocquentin 2003; Belfer-Cohen and Goring-Morris 2020). Traces of this type of occupation have also been found on the banks of the Euphrates on the sites of Abu Hureyra and Tell Mureybet. The PPNA (9,500-8,700 cal. BC; Cauvin 1994) was composed of several cultures, in the North as well as the South. The architecture alternated between round houses and rectangular buildings when the first community buildings appeared (Stordeur et al. 2001). It is during this period that the first pre-domestic crops, such as wheat and barley, and perhaps also pulses—lentils and peas—appeared (Willcox 2000; Fuller et al. 2012). Later on, the Early PPNB (EPPNB; 8,700-8,200 cal. BC) can be found in the Northern Levant, on the banks of the Euphrates, in Anatolia and Cyprus (Asouti 2006; Guilaine 2017). Agricultural experiments continued and seeds with domestic morphology appeared. It was also during this period that the first signs of animal husbandry occurred (Helmer et al. 1998). The culture of the Middle PPNB (8,200-7,500 cal. BC; Cauvin 1994; Chambrade 2012) spread southwards, with more and more sites presenting a rectangular architecture. Agriculture and animal husbandry were now proven on most sites, although some still practiced hunting and gathering (Stordeur et al. 2010). The number of sites was at its highest in the Late PPNB (LPPNB; 7,500-7,000 cal. BC), with some very large settlements found in new areas; agriculture and animal husbandry were by then widespread, as well as trade between communities (Willcox 2000; Vigne 2005; Asouti 2006). Finally, the last major innovation attributed to Neolithisation was the invention of ceramics in the Pottery Neolithic (early 7th millennium).

The changes in diet that take place with new subsistence patterns are, in many parts of the world, linked to an increase in dental pathologies (Hillson 1979; Stock and Pinhasi 2011). It is indeed a fact that a raise in caries rates over time has been

observed worldwide and that past and present hunter-gatherers have a lower caries rate (average < 4%) than agriculturists (average > 7%; Turner 1979), despite the intragroup variations (Marklein et al. 2019). The increased consumption of carbohydrate-rich plants, such as cereals, makes teeth more susceptible to caries, abscesses and in the end, ante-mortem tooth loss (AMTL). Similarly, the use of ceramics as container, by changing the way food is cooked—giving the food a stickier consistency and facilitating the proliferation of bacteria (Molleson 1995)—may also have had an impact on the increase in dental pathologies.

The search for the impact that the adoption of agriculture and ceramics may have had on the state of health is in line with Smith’s early work (Smith 1970, 1991) and Cohen and Armelagos (1984). The first, on the Natufians, linked health status and food, and the second wondered about the links between infectious diseases and agriculture in different parts of the world. They both showed that the adoption of agriculture had an impact on the raise in the frequency of infectious pathologies and stress indicators. In contrast, the work of Eshed et al. (2006), based on Natufian populations of hunter-gatherers and agriculturists in the Southern Levant, have not shown any changes in the frequency of dental pathologies between the two periods.¹ But a wider study (Bocquentin et al, in press), undertaken by crossing data from Southern and Northern Levant, with a chronological field from Natufian to Pottery Neolithic, showed on the contrary a constant increase of carious disease.

The link between dental pathologies and diet must be tempered, however, because many other factors can be taken into consideration such as biological and physiological components specific to each individual (composition of saliva, dental morphology, dental hygiene...), age, sex, but also the presence of fluoride in the water, even the climatic factors (Reich et al. 1999; Lukacs 2008; Martinez-Mier and Zandona 2013; Marklein et al. 2019). Moreover, the consumption of carbohydrates does not date back to the adoption of agriculture, since cereals were already consumed in the form of harvested products (Tayles et al. 2000; Humphrey et al. 2014).

Human remains from seven Syrian sites were studied for infectious diseases, both on bones and teeth, and biological stress indicators (Chamel 2014). This paper will only present the data from the dental health status. Archaeological sites

1. Some researchers (Lukacs 2008: 909) linked this absence of changes in dental health with a gradual adoption of agriculture in core areas, in contrast to a more abrupt transition in peripheral areas leading to a brutal increase.

Table 1 – Comparison of the environment, archaeobotanical and archaeozoological data of the sites selected for the study.

| | Tell Qaramel | Cheikh Hassan | Dja'de el-Mughara | Tell Aswad | Abu Hureyra | Tell Mureybet | Tell Ain el-Kerkh |
|--------------------------|---|-------------------------------------|-------------------------|----------------------------|--------------------------------|--|--------------------------------------|
| Environment | steppic river valley | ripisylve steppic | river plain steppic | steppic forest | river plain steppic | river plain steppic ripisylve | lake valley steppic |
| Botanical remains | cereals pulses | no data | cerals + lens | cereals + peas, lens | cereals + peas | cereals ++ lens | cereals pulses |
| Faunal remains | aurochs + equids + gazelles - wild boar - | equids + gazelles + aurochs - birds | gazelles equids aurochs | gazelles - caprines + pigs | aurochs gazelles - caprines ++ | equids + gazelles - aurochs + caprines - | bovids caprines gazelles - cervids - |

were selected based on their availability and relevance, and with the aim of covering the entire Neolithic process, from 9,820 to 6,000 cal. BC. Four of them are in the Euphratic corridor (Dja'de el-Mughara, Cheikh Hassan, Tell Mureybet and Abu Hureyra), one in the Central Levant (Tell Aswad) and two in Northern Syria (Tell Qaramel and Tell Ain el-Kerkh, fig. 1). All the sites are in steppic environment, often near a watercourse, but each site is at the interface of at least two environments, creating a favourable terrain for hunting and gathering, but also for cultivation (table 1).

**Fig. 1** – Location of the studied sites in Syria (Chamel 2014).

The site of Cheikh Hassan was discovered and excavated in the 1970s, then a second time before it was covered by the waters of Lake Tabqa in 1994 (Cauvin 1980; Stordeur 1999). Initially located on the left bank of the Middle Euphrates, this tell, more than 12 m high, has yielded, among other things,

occupations from the end of the PPNA and the EPPNB (9,000-8,900 cal. BC; Stordeur and Ibanez 2008).

Tell Mureybet was located, before its submersion, on the left bank of the Euphrates, not far from Abu Hureyra and Cheikh Hassan (fig. 1). Three environments intersected: the river and its banks, the river plain, and the steppic plateau, encouraging the Natufians to settle here, not far from a primary flint site (Cauvin 1977; Stordeur and Ibanez 2008). Mureybet was occupied in a seemingly continuous manner for 2,000 years, from the final Natufian to the Middle PPNB. Human remains were discovered in phase III (Mureybetian), from PPNA (IIIA) to the transition from PPNA to PPNB (IIIB, about 8,900 cal. BC). Then the tell was occupied at a different location than previously from EPPNB, around 8,300 cal. BC (phase IVA) to Middle PPNB (phase IVB, 8,200 cal. BC; Evin and Stordeur 2008).

Further north, the site of Dja'de el-Mughara stands on a middle Quaternary terrace, above the left bank of the Euphrates river, and dominates the alluvial plain and the steppe hinterland of the Jezirah (Coqueugniot 1999; fig. 1). Dja'de was continuously occupied between the end of the PPNA to the end of the EPPNB, delivering three levels of the Pre-Pottery Neolithic (DJ1: 9,310-8,830 cal. BC; DJ2: 8,800-8,500 cal. BC; DJ3: 8,540-8,290 cal. BC),² each of them with human remains, with the largest number of individuals at DJ3 (Chamel 2014; Chamel and Coqueugniot 2020).

Abu Hureyra settled on one of the right lower terraces overhanging the Euphrates, at the interface of the alluvial plain and the arid steppe (fig. 1; Moore et al. 2000). The site was occupied in several phases, the first dating from the recent/

2. COQUEUGNIOT E. 2010 – *Dja'de el-Mughara*. Rapport Scientifique 2010, unpublished.

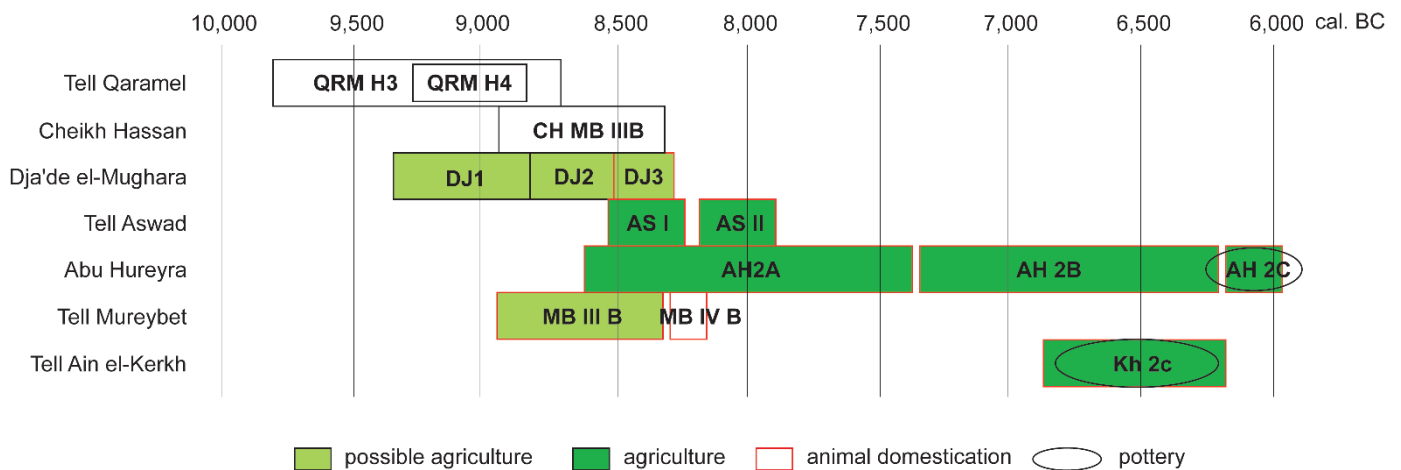


Fig. 2 – Chronological timeline presenting the types of subsistence economy of the sites studied.

final Natufian (AH 1: 11,500-9,650 cal. BC; Hillman 2000), after which the site was abandoned during the PPNA, then reoccupied at the Middle PPNB and the Pottery Neolithic after the tell was flattened by the new inhabitants (AH 2A: 8,650-7,350 cal. BC; 2B: 7,350-6,200 cal. BC; 2C: 6,200-6,000 cal. BC;³ Moore et al. 2000).

The site of Tell Aswad, in the Central Levant, is in the Damascus basin (fig. 1), on the edge of a lake that has now disappeared, with forest-steppe type vegetation (Contenson 1995). The site, excavated by Contenson and then by Stordeur, was occupied from the end of the EPPNB to the beginning of the LPPNB. If lithic industries prove that the different phases belonged to the PPNB dating by ¹⁴C remains inconclusive (Stordeur et al. 2010).

Tell Qaramel, excavated by a Syro-Polish team since 1999, is an 18.7 m high tell located in the valley of the Qoueiq River, in northern Syria (fig. 1; Mazurowski 2012). According to ¹⁴C and lithic industries, the site was occupied discontinuously between the Epipaleolithic and the end of the PPNA. Horizons H3 and H4, which represent the periods of the Middle and Late PPNB that yielded human remains are dated between 9,817-8,711 cal. BC for horizon H3, and 9,305-8,783 cal. BC for horizon H4 (Mazurowski et al. 2009).

Lastly, Tell el-Kerkh is located in the Rouj basin (fig. 1, northern Syria), in a plain on the banks of a lake that has now disappeared. The site encompasses three artificial tells,

Tell el-Kerkh 1, Tell el-Kerkh 2, and Tell Ain el-Kerkh (Tsuneki et al. 1997, 1998, 1999), and the human remains studied come from the latter. The occupation of Tell Ain el-Kerkh began in the LPPNB, between 8,500 and 8,300 cal. BC (Arimura 2007). After a hiatus, the site was reoccupied in the Late-Final PPNB, between 7,300 and 7,000 cal. BC. The main occupation took place during the Pottery Neolithic period (7,000-6,200 cal. BC; Iwasaki and Tsuneki 2003; Arimura 2007), and the human remains come from a “cemetery” of more than 200 individuals in a central area close to the dwellings (Hudson et al. 2003).

The archaeobotanical and archaeozoological data from the sites are summarized in table 1 and in figure 2, which also presents the modalities of the subsistence economy: presumed agriculture, confirmed agriculture, animal domestication and ceramics (Zeist 1970; Leroi-Gourhan 1974; Zeist and Bakker-Heeres 1982; Moulins 2000; Colledge 2001; Tanno and Willcox 2006, 2012; Willcox 2008; Willcox et al. 2008; Colledge and Conolly 2010; Douché and Pichon 2018). Sharing fairly similar environments, almost all the sites harvested or cultivated cereals: barley, emmer and einkorn wheat, and rye. Legumes such as peas, lentils and vetches were also consumed, although it is not known whether this was the result of harvesting or cultivation. As far as animals are concerned, cynegetic activities targeted aurochs, horses, deer and gazelles, depending on the environment. The domestication of aurochs was in progress in Dja'de during the DJ3 phase (Helmer et al. 2005; Edwards et al. 2007). Domestication of pigs, cattle, sheep and goats was effective in Tell Aswad, Tell Ain el-Kerkh and Abu Hureyra (Legge and Rowley-Conwy 2000; Helmer and Gourichon 2008, 2017), and of goats and cattle during the last period of Tell Mureybet (IVB; Gourichon 2004; Helmer et al.

3. The data given in the monograph by Moore et al. 2000 have not been calibrated with the current reference curves. The dates given here have been calibrated using the CalPal application to facilitate comparison between sites.

2005; Gourichon and Helmer 2008). Only the sites of Tell Qaramel and Cheikh Hassan show no evidence of plant cultivation nor animal domestication (Grezak 2012; Willcox and Herveux 2012).

Our corpus comprises 4,307 observable teeth belonging to a minimum of 312 individuals from the seven sites described above, and attributed to hunter-gatherers and agriculturists, from 9,820 to 6,000 cal. BC. We have subdivided the corpus into 4 chrono-cultural phases, the PPNA (MNI⁴ = 25, 9,820-8,780 cal. BC), the EPPNB (MNI = 83, 8,800-8,200 cal. BC), the Middle-Late PPNB (MLPPNB; MNI = 128, 8,650-6,200 cal. BC) and the Pottery Neolithic (PN, MNI = 76, 7,350-6,000 cal. BC; table 2). As the sample size of the PPNA is smaller than in other periods, it is less representative, and the results should be taken with caution.

Table 2 – Number of individuals and tooth studied by phase and by site. **QRM**: Tell Qaramel; **CH**: Cheikh Hassan; **DJ**: Dja'de el-Mughara; **Mb**: Tell Mureybet; **ASW**: Tell Aswad; **AH**: Abu Hureyra; **Kh**: Tell Ain el-Kerkh.

| Phases | Number of observable teeth | Number of observable individuals |
|-------------------|----------------------------|----------------------------------|
| PPNA | 409 | 25 |
| QRM | 125 | 10 |
| CH | 163 | 9 |
| DJ1 | 103 | 5 |
| Mb IIIB | 18 | 1 |
| EPPNB | 1,044 | 83 |
| DJ2-DJ3 | 1,013 | 81 |
| ASW IA | 31 | 2 |
| MLPPNB | 1,583 | 128 |
| ASW M-L | 71 | 6 |
| AH 2A-2B | 1,400 | 117 |
| Mb IVB | 112 | 5 |
| Pottery Neolithic | 1,271 | 76 |
| AH 2C | 90 | 6 |
| Kh | 1,181 | 70 |

METHODS

We collected all data with the same methodology, to make inter-site and diachronic comparisons. The teeth were observed macroscopically, and the observations gathered in a database constructed with Filemaker (Chamel 2014). Repeatability in the assessment of lesions, due to the study circumstances (thesis work, and collections stored in an unstable country), was very difficult to evaluate. Only a small segment of the Dja'de el-Mughara sample was revisited, with an agreement of 92%. Isolated teeth were excluded from the study to analyse the results not only per tooth, but also per individual, which could lead to observations related to age at death and sex (Hillson 2001).

In the populations observed, sex determination of individuals in the populations observed was very difficult, if not impossible, due to the poor conservation and representation of the remains. The methods used, when the coxal bones were sufficiently well preserved, are based on the visual method of Bruzek (2002) and the DSP of Murail et al. (2005). The estimation of age at death is based preferentially for immature individuals on dental remains, following the methods by Moorrees et al. (1963a, 1963b), and on degrees of bone maturation following the methods of Adalian (2002), Fazekas and Kosa (1978) and Scheuer and Black (2000). For adults, the method of Owing-Webb and Suchey (1985) on the degrees of fusion of the sternal end of the clavicle and the anterior crest of the ilium⁵ were preferred for the young adults, and the methods of Schmitt (2005, 2008) on the auricular surface of the ilium and the pubic symphysis for older individuals.

For this study, attention has been focused on four infectious dental pathologies, including caries, abscesses, ante-mortem tooth loss and periodontal disease (fig. 3). The etiology of these diseases, as seen above, can be partially explained by the introduction of agriculture, with a diet richer in carbohydrates, and the invention of cooking in pottery. However, multi developmental factors should also be considered, and the raw and estimated caries rate must be interpreted in relation to diet only in large samples over a long period of time.

Caries is an infectious condition that manifests itself as a progressive demineralisation of enamel and dentin, resulting in the formation of a cavity in the tooth (Hillson 2005). For their study, the recording system is adapted from the methodology developed by Hillson (2001, 2005), modified to suit the

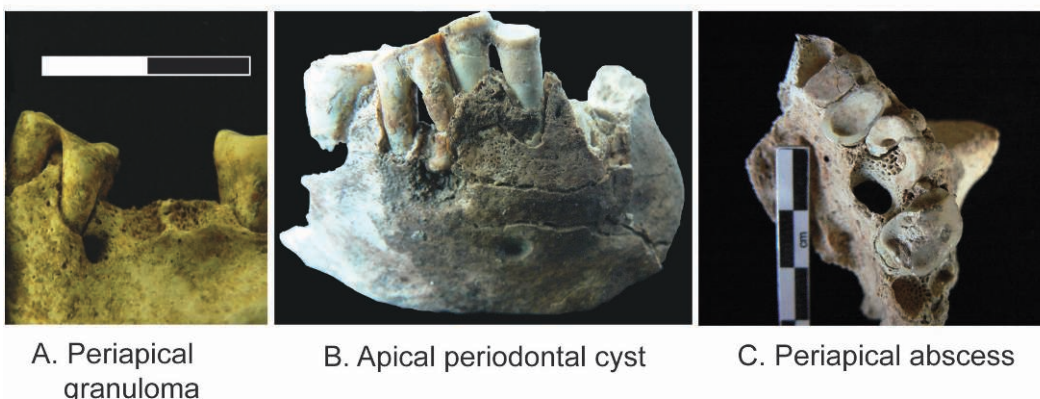
4. Minimal Number of Individuals.

5. The last bones to fuse in adults.

1. Caries



2. Abscesses



3. Ante-mortem tooth loss



4. Periodontal disease



Fig. 3 – Illustration of the pathologies presented in the text. **1. Caries:** **A.** Tell Ain el-Kerkh, ind. 712, stage 1; **B.** Tell Ain el-Kerkh, ind. 853 C-4, stage 2; **C.** Dja'de el-Mughara, ind. 283-A, stage 3; **D.** Tell Ain el-Kerkh, ind. 732 C-2, stage 4. **2. Abscesses:** **A.** Tell Qaramel, ind. 10-09, periapical granuloma; **B.** Dja'de el-Mughara, ind. DJ00-32, sep. 180 inf, apical periodontal cyst; **C.** Dja'de el-Mughara, ind. 283-B, periapical abscess. **3. Ante-mortem tooth loss,** Abu Hureyra, ind. 73-2952. **4. Periodontal disease,** Dja'de el-Mughara, ind. 245, stage 1.

archaeological context. We have therefore set up a rating into four stages: stage 1, brown spot on the tooth;⁶ stage 2, cavity in the enamel; stage 3, cavity in the enamel and the dentine; stage 4, very large cavity (Chamel 2014; fig. 3). As carious

lesions sometimes develop into abscesses,⁷ the damage to the alveolar bone was recorded as periapical granuloma, apical periodontal cyst and periapical abscess (fig. 3), depending on the type and size of lesion (Dias and Tayles 1997). Ante-mortem tooth loss, defined as the absence of the tooth and the remodeling of the corresponding tooth socket, was also considered (fig. 3). The raw frequencies are presented in the results section

6. The first clinical sign is usually a white spot but is too difficult to identify in archaeological human remains. The brown spot can be differentiated from diagenetic effects by the presence of a roughened enamel surface (Hillson 2005).

7. Abscesses are caused by an inflammatory reaction around the apex of the tooth, which may be acute or chronic, and manifest as a cavity in the alveolar bone.

Table 3 – MNI by age at death and sex for the sample. *QRM*: Tell Qaramel; *CH*: Cheikh Hassan; *DJ*: Dja'de el-Mughara; *Mb*: Tell Mureybet; *ASW*: Tell Aswad; *AH*: Abu Hureyra; *Kh*: Tell Ain el-Kerkh.

| Phases | Adults | | | Immatures | | | | | |
|------------------------------|--------|---|-------|-----------|-----|-----|-------|-------|-------|
| | M | F | Indet | 0-1 | 1-4 | 5-9 | 10-14 | 15-19 | Indet |
| PPNA (MNI = 25) | 1 | 0 | 17 | 0 | 0 | 3 | 1 | 3 | 0 |
| QRM (MNI = 10) | 1 | 0 | 7 | 0 | 0 | 0 | 0 | 2 | 0 |
| CH (MNI = 9) | 0 | 0 | 6 | 0 | 0 | 3 | 0 | 0 | 0 |
| DJ1 (MNI = 5) | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 1 | 0 |
| Mb IIIB (MNI = 1) | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| EPPNB (MNI = 83) | 1 | 2 | 39 | 4 | 12 | 15 | 4 | 6 | 0 |
| DJ2-DJ3 (MNI = 81) | 1 | 2 | 38 | 4 | 11 | 15 | 4 | 6 | 0 |
| ASW IA (MNI = 2) | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| MLPPNB (MNI = 128) | 3 | 2 | 77 | 7 | 9 | 15 | 7 | 6 | 2 |
| ASW M-L (MNI = 6) | 0 | 0 | 2 | 2 | 2 | 0 | 0 | 0 | 0 |
| AH 2A-2B (MNI = 117) | 3 | 2 | 72 | 5 | 5 | 15 | 7 | 6 | 2 |
| Mb IVB (MNI = 5) | 0 | 0 | 3 | 0 | 2 | 0 | 0 | 0 | 0 |
| Pottery Neolithic (MNI = 76) | 1 | 1 | 44 | 4 | 6 | 7 | 9 | 3 | 1 |
| AH 2C (MNI = 6) | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 |
| Kh (MNI = 70) | 1 | 1 | 41 | 4 | 6 | 7 | 6 | 3 | 1 |

for each condition, and a calibrated frequency for carious disease, including caries, abscesses and AMTL was performed, so as not to minimise the importance of this condition.

Periodontal disease is caused by the progressive destruction of the periodontal ligament which gradually leads to the destruction of the alveolar bone, and the exposure of the tooth root. This disease has also been recorded (fig. 3), although the study of the regression of alveolar bone is difficult in an archaeological environment, given the fragility of this bone. We chose four recording stages for bone loss when measurable, with stage 0 indicating no regression, stage 1 regression on less than one third of the root, stage 2 regression exposing half or more of the root, and stage 3 regression exposing almost all the root (Alexandersen 1967).

Comparing the frequencies of dental pathologies between the different periods required the use of statistical tests. Since

our variables were qualitative in nature, we used contingency tables, for which we calculated theoretical numbers. When these are greater than 5, the Chi² test is used; when at least one of the theoretical numbers is lower than 5, the exact Fisher test is used.

RESULTS

Table 3 presents the result of the MNI by age at death and by sex; as mentioned above, very little data on sex is provided, due to the poor preservation of bone remains. We will therefore not discuss this in the context of this study.

The results for the four selected pathologies are presented with charts for the raw frequencies per tooth/tooth sockets (fig. 4) and per individual (fig. 5).

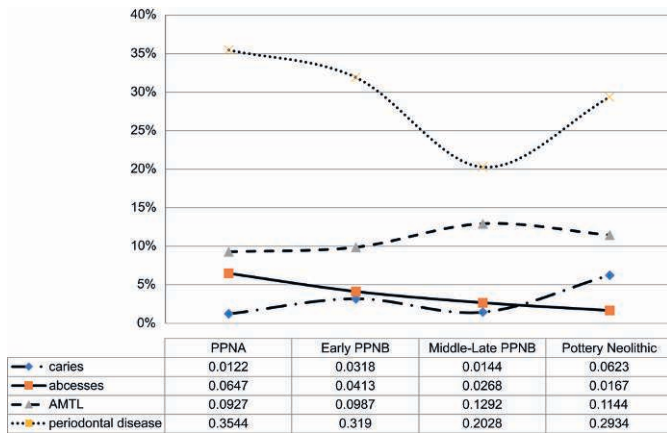


Fig. 4 – Variation of the frequencies of the oral health markers during the four phases of Neolithic (count per teeth and tooth sockets).

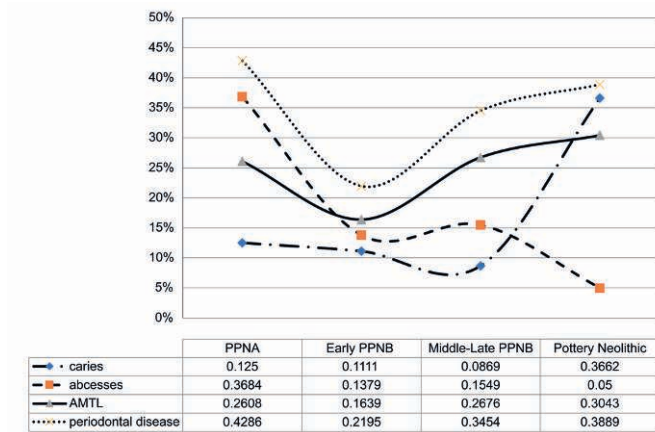


Fig. 5 – Variation of the frequencies of the oral health markers during the four phases of Neolithic (count per individuals).

Concerning the dental caries, the raw frequency per tooth increases from 1.22% to 3.18% (fig. 4) between the PPNA and the EPPNB, and then decreases to 1.44% in the MLPPNB. There is afterwards a much greater raise between this period and the latter, the PN, where the caries frequency per tooth reaches 6.23%. Statistically speaking, while the increase in caries frequency between the first two periods is not significant ($p = 0.0665$), the decrease recorded in the MLPPNB ($p = 0.0131$) and the new increase in the last period ($p = 0.0001$) are. For each period, the most affected teeth are the molars (Chamel 2014).

Looking at the types of lesions, our observations have shown that for the PPNA, only stages 1 and 2 are represented, with stage 1 at 75% and stage 2 at 25%. In the EPPNB, all four

stages are represented, with stage 1 still being the most present. While the frequency of caries decreases between the EPPNB and the MLPPNB (fig. 4), stage 3 is however better represented in the latter period. On the other hand, the PN shows, as in the PPNA, a higher rate of stage 1 caries than the others. The number of caries per tooth is also significant, because while teeth from PPNA have only one cavity, this is not the case from Early, Middle-Late PPNB and PN levels where there are teeth with two or three cavities.

Concerning the caries frequencies per individual (fig. 5), there is a progressive decrease between the PPNA and the MLPPNB, from 12.5% to 8.69%. This decrease is not statistically significant ($p = 0.5857$), the following increase in the PN, with 36.62% of individuals with carious lesions, is very significant ($p = 0.0001$). Immature individuals are not very much affected by this pathology: only one individual who died between the ages of 6 and 7 years in the EPPNB and 3 individuals (7-9 years, 10.5-15.5 years, and 14-15 years) in the PN have carious lesions. The amount of caries per individual will also increase between PPNA and PN, from an average of 1.3 caries per individual to 2.5 caries per individual.

Cysts, granulomas, and abscesses are relatively scarce for all periods combined: only 45 cases have been recorded in these populations. The frequencies per tooth sockets (fig. 4) decrease progressively from the PPNA (6.47%) to the PN (1.67%), and this decrease is very significant ($p = 0.0256$). The frequency of affected individuals (fig. 5) also decreases progressively from the first to the last period, with, however, a slight, not significant ($p = 0.7870$), increase between the Early and the MLPPNB. The curves per tooth socket and per individual for abscesses show the opposite of what happens with caries. Since abscesses are very often the consequence of caries, it is possible that the increase in caries over time is accompanied by a lower severity of lesions, as we have seen in the PN, where stage 1 caries are best represented. Thus, caries of lower severity generate fewer abscesses, which may explain the progressive decrease of the latter.

For AMTL (fig. 4), there is a steady increase between the PPNA and the MLPPNB, before a decrease in the last period, the PN. In terms of frequency per individual, there is a difference with the counting by tooth sockets. In fact, the frequency decreases from the PPNA to the EPPNB, and then increases in the MLPPNB up to the PN (fig. 5). However, none of these fluctuations are significant according to the statistical tests. The most affected teeth are the posterior teeth, in 78.1% of cases, mainly the M1, lower and posterior, the P2 and M2. No immature individual has lost any teeth, as this pathology is strongly correlated with age at death.

The calibrated frequency of carious disease (caries, abscesses and AMTL) is shown in table 4. A gradual decline in the estimated caries rate from the PPNA to the MLPPNB can be seen here, followed by a slight increase in the PN. The same trends for the raw frequencies per tooth are not found, except for this increase in the last period. As far as statistical tests are concerned, no increase nor decrease are significant.

Table 4 – Estimated frequencies of carious disease for the four phases (count per teeth and tooth sockets).

| Dental caries estimated number | | | |
|--------------------------------|-------|--------|-------------------|
| PPNA | EPPNB | MLPPNB | Pottery Neolithic |
| 9.36% | 8.27% | 7.45% | 8.9% |

The study of periodontal disease, which is not exempted of bias, could only be conducted on a small number of tooth sockets and individuals (figs. 4, 5). The frequencies per tooth sockets show a rate of more than 35% at the PPNA, which gradually decreases to the MLPPNB where it reaches 20.28%. It then rises to over 29% in the PN. According to statistical tests, these increases and decreases are highly significant. The frequency of periodontal disease per individual shows a slightly different pattern (fig. 5): the frequencies also decrease from the PPNA to the EPPNB, but then increase again in the MLPPNB. This then continues until the PN. The differences between periods, on the other hand, are not significant according to statistical tests. However, the high rate of periodontitis in the population does not really reflect the importance of this pathology; as very few individuals and tooth sockets are observable, the frequency may appear artificially high.

DISCUSSION

Before starting the discussion, it is worth mentioning the biases inherent in this type of study. Firstly, the small number of teeth and individuals studied for the PPNA minimises the significance of the increases and decreases in dental pathology between this period and the next, the EPPNB. Secondly, although environments are similar at many of the sites studied, as well as wildlife and archaeobotanical spectrum, the way in which food was prepared, about which we have little information, can play a very important role.

For all the pathologies observed, the study showed on the one hand that they do not progress at the same rate, and on the other hand that their frequency does not increase in a linear way from the PPNA to the PN, as might be expected.

Beyond the frequencies per tooth/tooth socket and per individual, the study of the different stages of lesion severity allows us to propose hypotheses about the health changes brought about by agriculture and ceramics. Figure 6 relates the data for abscesses, caries, and periodontal disease for the four periods. This graph shows a peak in lesion severity for the period of MLPPNB, visible on caries and periodontal disease. It is the period with the highest rate of stage 2 and 3 caries and stage 2 periodontal disease, followed by a lower level of lesion severity in the following PN period, returning to what can be observed in the EPPNB.

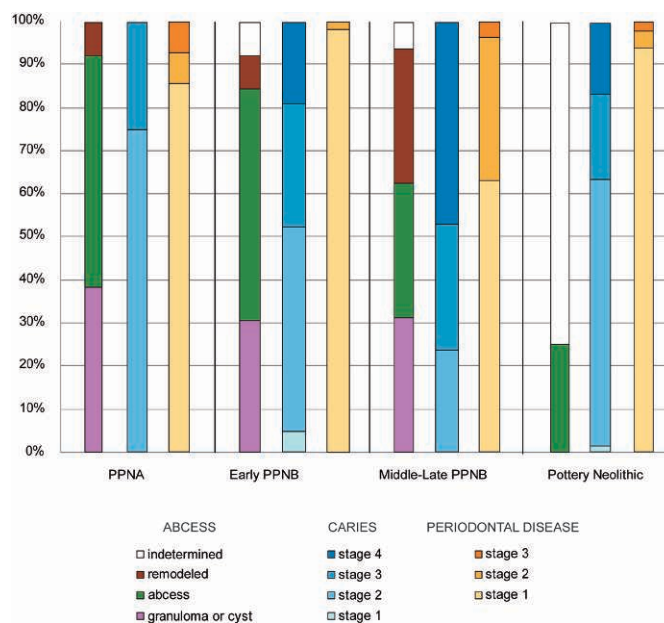


Fig. 6 – Type of abscess, stage of caries and stage of periodontal disease for the four phases of the Neolithic.

In our sample, we note that cultivated cereals are present from the EPPNB, even if the hypothesis of a proto agriculture from the PPNA has been proposed for some sites (fig. 2). The changes in all pathology frequencies (by teeth/tooth sockets) between the PPNA and the EPPNB are not significant. This may be due to the small sample size for the PPNA, but it is also possible that the switch to agriculture did not immediately have a strong impact on oral health status. Indeed, these were the early stages of plant domestication, and the harvesting of

cereals, plants and pulses continued, so there were no significant changes in diet here. For the frequencies by individuals, the decrease in almost all pathologies can be explained in our opinion by the bias induced by the PPNA sample.

In the following MLPPNB period, the increase in the frequencies of all pathologies, except abscesses, is to be related to the peak of lesion severity presented in figure 6. Agriculture is proven at each of the sites (fig. 2), and there is a real reduction in the variety of the diet, with a strong decrease in the spectrum of plants harvested in favour of cereals, with an increase in the carbohydrates present in the food. This is also the period in which animal husbandry begins, and it seems logical that there is a certain deterioration in sanitary conditions due to a new cohabitation between humans and animals (Mitchell 2003). A recent study offering a comparison between cultivated cereals (barley and emmer wheat) and their wild progenitors, suggests that there has been a shift towards larger seeds, with a higher glycemic load, while the relative contents of protein, fibers and minerals are lower (Hebelstrup 2017). This may explain the increase in caries frequency noted for the last period, the PN.

In the PN, the general increase in frequency can be explained by the change in diet, since all the sites studied for this period show domestication of plants and animals, and also by the introduction of a new type of food preparation by boiling cereal flour in a ceramic pot, thus making a porridge. This gives a slightly sticky consistency which tends to promote the development of bacterial colonies in the fissures and grooves of the molars and premolars (Larsen 1995). Thus, the invention of ceramics and the introduction of a new method of cooking cereals during this period may have played a role in the increase in the number of caries, a phenomenon which was already noted by T. Molleson at Abu Hureyra (1995).

The gradual decrease in the frequency of abscesses, both in terms of tooth sockets and individuals (figs. 4, 5) suggests, in our opinion, that the type of carious lesion has changed over time, and that caries which develop into abscesses have gradually been replaced by caries of lesser severity.

Comparisons with South Levant are difficult, as little data is available. The paper by Eshed et al. (2006), dealing with the transition from the Natufian to the Neolithic, shows that there were no differences between the two periods in the frequencies of caries per tooth (6.4%/6.7%) and abscesses (less than 1.5%), and only a very slight increase in the frequency of ante-mortem tooth loss (3.7%/4.5%). For periodontal disease, the frequency is higher among the Natufians (36.4%) than in the Neolithic populations (19%).

CONCLUSION

The study of dental pathologies for the four periods of Neolithisation gives us an idea of the influence of the shift in subsistence economy on the oral health status of populations. Despite the sample biases, it seems that the pattern here is less linear than it appears at first glance, and that all pathologies do not progress at the same rate. The peak in severity in most of the lesions in the MLPPNB, when agriculture was well established, can be explained by a drastic reduction of the variety of consumed plants. The increase in the frequency of pathologies during the last period, the Pottery Neolithic, is perhaps less due to a change in diet than to a new way of preparing food. In the future, the study of biological stress indicators such as porotic hyperostosis, *Cribra orbitalia* and linear hypoplasia of the dental enamel, still in progress, will undoubtedly provide new information to clarify our hypotheses.

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NEW PALEOPATHOLOGICAL EVIDENCE OF TUBERCULOSIS IN CHILD SKELETAL REMAINS FROM TELL ASWAD (8,730-8,290 CAL. BC, SOUTHERN SYRIA)

J. O. BAKER, B. CHAMEL AND O. DUTOUR

Abstract. *In palaeopathology, in addition to typical skeletal lesions, the study of secondary or minor lesions increases the level of detection of pathologies in human populations of the past. In this perspective, we examined skeletal remains from the Neolithic site of Tell Aswad, located in the central Levant (southern Syria) in order to detect lesions attributable to tuberculosis (TB) infection. Skeletal lesions, vertebral and endocranial, are observed on the skeletal remains of a child from the Early PPNB horizon. These endocranial lesions show the pattern of Serpens Endocrania Symmetrica (“SES”) that is attributed to leptomeningitis (chronic TB meningitis). On the anterior aspect of four thoracic vertebrae, a remodeling and enlargement of the vascular foramina were also observed, suggestive of TB infection. This new case represents another clue in favor of the early presence of human tuberculosis in the Levant dated to the Neolithic period, in the context of the adoption of agriculture and animal domestication.*

Résumé. *En paléopathologie, en plus des lésions osseuses typiques, l'étude des lésions secondaires ou mineures augmente le niveau de détection des pathologies dans les populations humaines du passé. Dans cette perspective, nous avons examiné les vestiges osseux du site néolithique de Tell Aswad, situé dans le Levant central (Syrie du Sud) afin de détecter des lésions attribuables à une infection tuberculeuse. Des lésions osseuses, vertébrales et endocrâniennes, ont été observées chez un jeune enfant daté du début de l'horizon PPNB. Ces lésions endocrâniennes présentent le schéma de Serpens Endocrania Symmetrica (SES) qui est attribué à la leptoméningite (méningite tuberculeuse chronique). Sur la face antérieure de quatre vertèbres thoraciques, un remodelage et un élargissement des foramens vasculaires ont également été observés, suggérant une infection tuberculeuse. Ce cas inédit constitue un nouvel indice en faveur de la présence au Levant de la tuberculose humaine dès le Néolithique dans le contexte de l'adoption de l'agriculture et de la domestication animale.*

Keywords. *Endocranial alterations, tuberculosis, Spinal TB, Syria, Neolithic, Early PPNB horizon*

Mots-clés. *Altérations endocrâniennes, tuberculose, tuberculose vertébrale, Syrie, Néolithique, PPNB Ancien*

INTRODUCTION

For a long time tuberculosis was considered as an infection originated from animals and transmitted to humans during the Neolithic, due to cattle domestication. This dogma was later

challenged by phylogenetic analyses of the *Mycobacterium tuberculosis* complex (Brosch et al. 2002). According to this new evolutionary model, tuberculosis existed as a human infection long before the Neolithic and animal domestication and was therefore more ancient than animal tuberculosis (Gutteriez et al. 2005). A more recent alternative model

proposes that animal tuberculosis is as old as human ancestry, but that the human TB pathogen postdated cattle domestication and did not emerge until 6,000 BP (Bos et al. 2014).

The Levant has provided the earliest evidence of human tuberculosis (TB): the sites of Dja'de el-Mughara, Tell Aswad, Abu Hureyra and Tell Ain el-Kerkh in Syria (Chamel 2014; Baker et al. 2015, 2017), Atlit Yam in Israel (Hershkovitz et al. 2008) and Ain Ghazal in Jordan (El-Najjar et al. 1996), are all dated from the Pre-Pottery Neolithic B and C periods, and correspond to pre- and early animal domestication phases. The skeletal remains of a young adult from the Early PPNB/Middle PPNB period of Tell Aswad (Syria) provided paleopathological evidence of Hypertrophic Pulmonary Osteopathy (HPO) attributed to TB, confirmed by lipid biomarkers analysis and paleoimaging study (Baker et al. 2015; Coqueugniot et al. 2015; Baker et al. 2017). The purpose of this paper is to investigate clues of tuberculosis among skeletons from the ancient phase of Tell Aswad, dating from the Early PPNB Horizon. The human remains from this period

were excavated by Henri de Contenson in the early 1970s (Contenson 1972, 1992, 1995), and were not studied in our previous analyses.

ARCHAEOLOGICAL CONTEXT

The site of Tell Aswad, located about 30 km from East-Southeast Damascus (fig. 1), was first excavated between 1971 and 1972 by Henri de Contenson. The study of lithic industry and the absolute dating by C-14 allowed archaeologists to define an ancient occupation divided into three chronological phases: phase IA, PPNA "Aswadian"; phase IB, Early PPNB; phase II, Middle PPNB (Contenson 1972).

Three decades later, new excavations were conducted from 2001 to 2007 by a Franco-Syrian archaeological mission co-directed by Danielle Stordeur and Bassam Jammous (Stordeur et al. 2010). This fieldwork led to a reinterpretation of

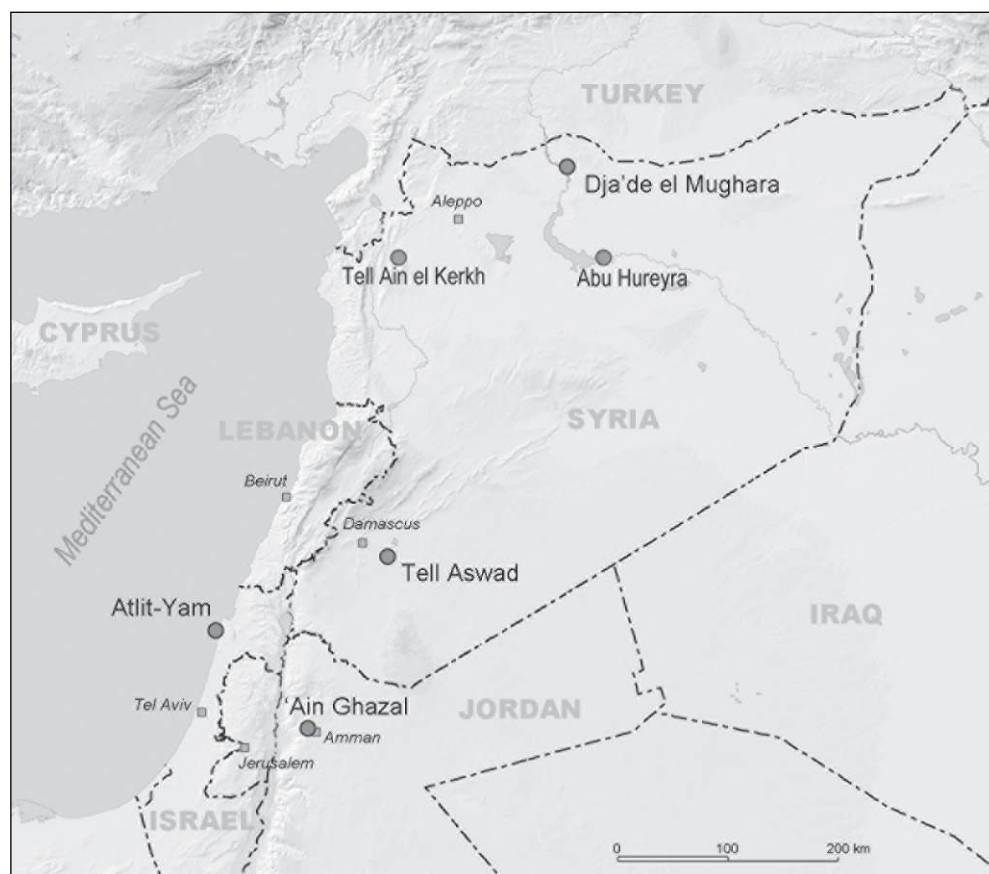


Fig. 1 – Location map showing Tell Aswad and other Neolithic sites of Middle East with evidence of TB.

the previous chronological frame defined by Henri de Contenson. The “Aswadian culture” was discarded and three PPNB phases were proposed: the first one (phase I or “Phase ancienne”, ca. 8,650-8,300 cal. BC) representing levels B12-B9, corresponds to the Early PPNB horizon. The following period (phase II or “Phase moyenne”, ca. 8,450-8,250 cal. BC) corresponding to levels B8-B1 is also dated from the Early PPNB horizon; finally, phase III or “Phase récente” is dated from the end of Early PPNB horizon and the Middle PPNB (ca. 8,300-7,800 cal. BC) and corresponds to occupation levels B0-B5 (Stordeur et al. 2010).

The chronological attributions made by Henri de Contenson were reviewed, following the AMS dates obtained from emmer wheat grains of *Triticum dicoccoides* from the 1972 excavations at Aswad (Willcox 2005; Stordeur et al. 2010), as well as the unpublished dates of Sánchez Priego and colleagues.¹ The phases are defined as follows:

- Phase IA (ca. 8,730-8,290 cal. BC): Early PPNB horizon, corresponding to phases I, II and III of the new chronology proposed by Danielle Stordeur and colleagues.
- Phase IB (ca. 8,550-7,950 cal. BC): Early PPNB horizon/Middle PPNB corresponding to phases I, II and III of the new chronology.
- Phase II (ca. 8,240-7,760 cal. BC): end of Early PPNB horizon/Middle PPNB corresponding to new phase III.

The study of the faunal assemblages indicated the presence of domesticated animals (goats, sheep and pigs) at the end of the Early PPNB horizon (Helmer and Gourichon 2008; Stordeur et al. 2010). Whereas cattle were mostly domesticated in the Middle PPNB, their domestic status is still not conclusive for the Early PPNB, due to the lack of data (Helmer and Gourichon 2008, 2017). The presence of *Triticum dicoccoides* remains (domestic form) attests to the domestication of plants from the earliest phases of the Tell’s occupation (Willcox 2000, 2005; Stordeur et al. 2010).

More than ninety burial deposits have been unearthed at Tell Aswad, both during ancient and recent excavations (Contenson 1972, 1992, 1995; Stordeur 2003; Stordeur et al. 2006, 2010; Stordeur and Khawam 2007; Chamel 2014; Khawam 2014; Khawam et al. 2016). Excavations carried out by Henri de Contenson uncovered two deposits: a double burial located in the Eastern survey and dated to the Early PPNB, and a collective burial in the Western survey, from the end of Early PPNB or Middle PPNB.

The Aswad East survey burial is a rectangular shaped pit that appears to have been dug into the virgin soil. It contains the skeleton of a mature or elderly individual, buried in a contracted position, lying on its right side. The upper limbs are flexed in front of the thorax, and the lower limbs are in a hypercontracted position against the rib cage. Skeletal remains of an immature individual were found against the right forearm of the adult individual, but it is not known if the skeleton was complete at the time of excavation (Contenson 1995). The type of deposition is primary: it would appear that we are dealing with an intentional double burial, possibly simultaneous, as the vertebrae and hand bones of the immature individual are located in front of the adult upper limbs, whereas the femur, on the other hand, is underneath the adult’s knee. It is therefore likely that the two individuals were buried together (Chamel 2014).

The Western survey burial is dated from the end of Early or Middle PPNB. All publications mention a “collective burial” comprising both primary and secondary deposits (Contenson 1992, 1995). The human remains were found about 1.5 m deep in pit 1, which had been dug into virgin soil. Following the original description, the skeleton of an adult individual was found at about 50 cm from the top of the pit in a contracted position and lying on its left side (Contenson 1972, 1995; Chamel 2014). As all the bones were in anatomical connection, the burial can be considered as primary. Henri de Contenson (1992, 1995) mentions the discovery of a child skeleton in anatomical connection at the same level of 2.90 m, but this was not precisely recorded, and other human remains are also described at the same level, consisting in four skulls, as well as infracranial skeletal bones of two adults and two immature individuals (Contenson 1972; Chamel 2014). This pattern suggests a secondary deposit.

In this pit, a child’s skeleton is also described as being “disarticulated” (Contenson 1992) and “scattered” (Contenson 1995). This might be either a disturbed primary deposit or a secondary deposit. Finally, Pit 1 also yielded an adult skull with a mandible at 2.55 m, which could result from a secondary deposit (Chamel 2014).

MATERIAL AND METHODS

This research was carried out at the Institut de Paléontologie Humaine (IPH) in Paris, France where the skeletal remains from the Neolithic site of Tell Aswad resulting from ancient excavations are currently stored. This osteoarcheological material was studied in the framework of the second author’s

1. J. Sánchez Priego, personal communication.

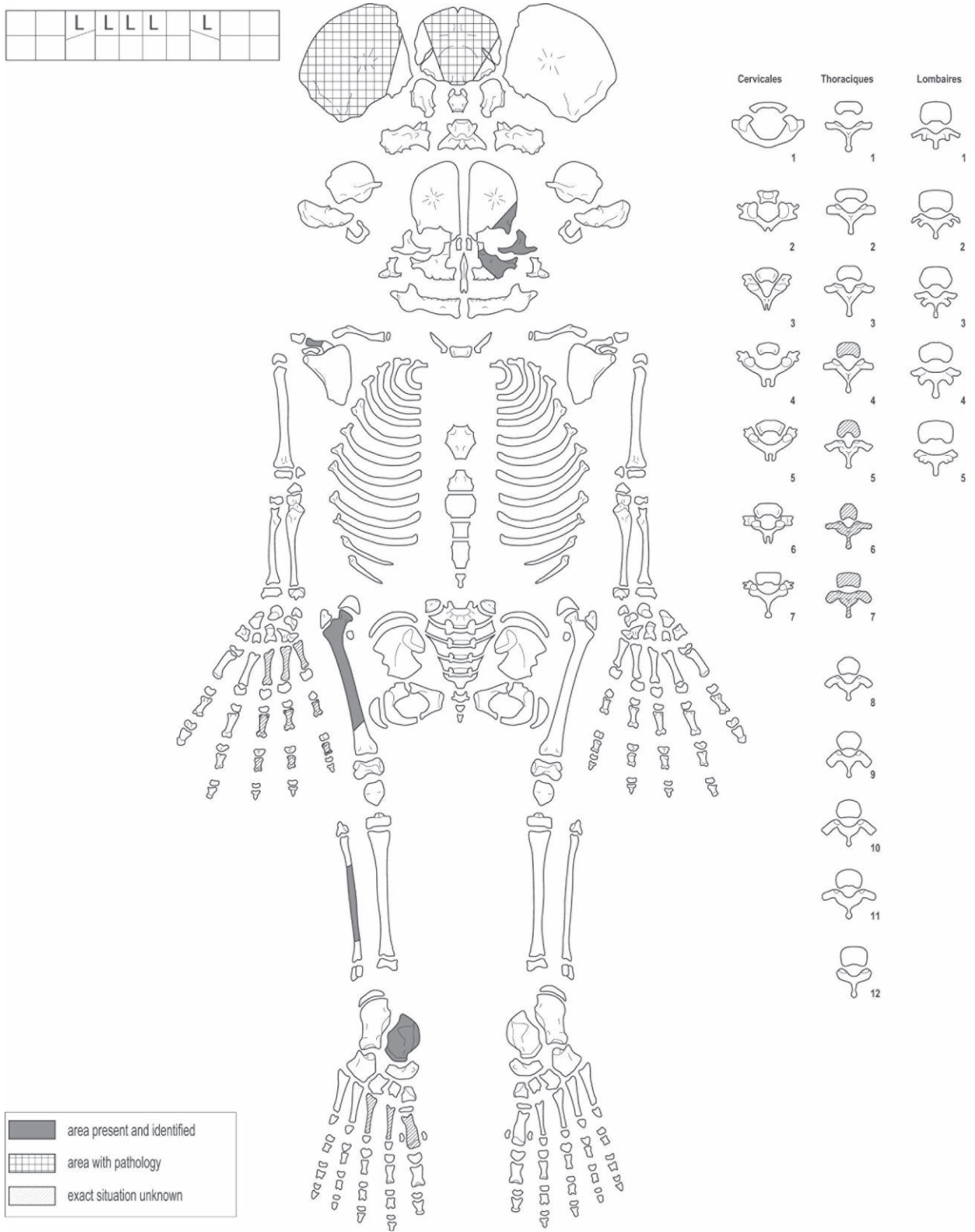


Fig. 2 – Osteological conservation of Aswad East immature (2-3 years old at death).

PhD (Chamel 2014). The material is comprised of the remains of ten individuals coming from two burials, resulting from the two archaeological surveys (West and East) performed by Henri de Contenson, and previously dated from the end of PPNB to Middle PPNB.

The collective burial of the West survey “Aswad Ouest” (level II, Layer III 3, 4-1,9 m) yielded a minimum number of 8 individuals (Chamel 2014; table 1), corresponding to the end of Early or Middle PPNB. The subject of the present work came from the East survey “Aswad Est” (level IA, Layer IA1 4,45-4,20 m) that provided the skeletal remains of two individuals, one adult and one immature, attributed to the Early PPNB.

Age-at-death estimation and observation of paleopathological alterations were carried out using the conventional methods of macroscopic and morphological examinations (Moorrees

Table 1 – Inventory of the human skeletal remains from the site of Tell Aswad studied in this paper. **HC**: Henri de Contenson; **DS**: Danielle Stordeur.

| Archeological survey/Burial | Phase HC | Phase DS | Period | Immature individuals | Adult individuals | MNI |
|-----------------------------|----------|----------|--|----------------------|-------------------|-----|
| Aswad East/ individual | IA | I & II | Early PPNB horizon (8,730-8,290 cal. BC) | 1 | 1 | 2 |
| Aswad West/ collective | II | III | End of Early PPNB horizon/ Middle PPNB (8,240-7,760 cal. BC) | 5 | 3 | 8 |

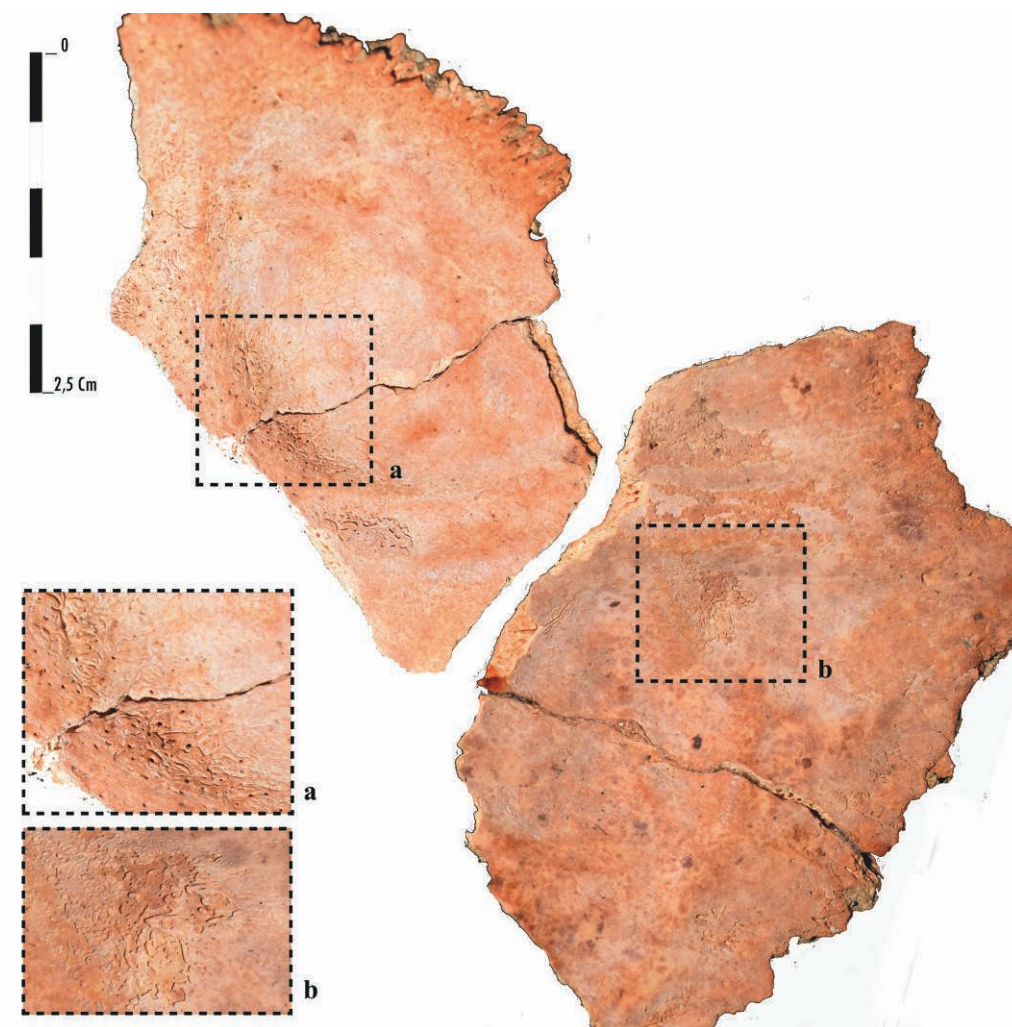


Fig. 3 – Two parts of occipital from the Aswad East immature show the characteristic changes of SES (Tell Aswad, end of Early PPNB horizon).

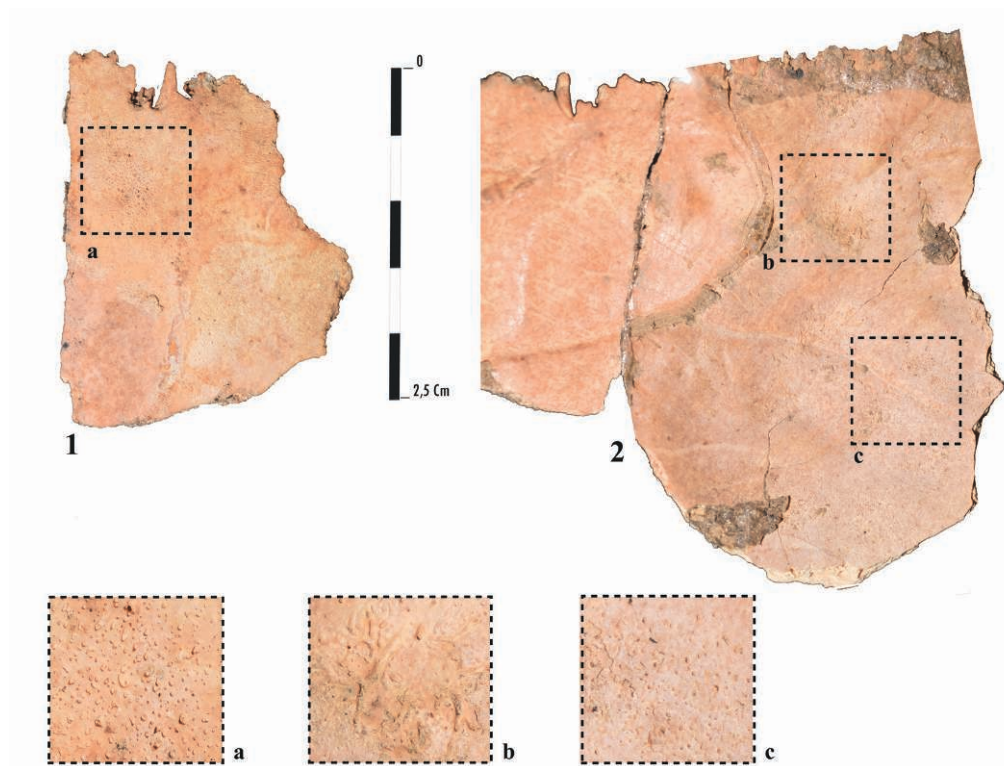


Fig. 4 – Elements of the right parietal from the same immature individual. **1.** Posterior view of the parietal exocranial surface showing porotic hyperostosis; **2.** The endocranial surface with SES-like pattern (*Serpens Endocrania Symmetrica*), micro-porosity and periosteal reaction.

et al. 1963a, 1963b; Steinbock 1976; Ubelaker 1978; Aufderheide and Rodriguez-Martin 1998; Baker 1999; Scheuer and Black 2000; Hershkovitz et al. 2002; Ortner 2003; Dutour 2008, 2011). Different skeletal expressions were considered for the paleopathological diagnosis of TB, according to our previous records (Baker 2014; Baker et al. 2015, 2017). Sex cannot be reliably determined due to the poorly preserved state of the coxal bone.

RESULTS

Ten skeletons from Tell Aswad were examined for paleopathological analyses. Two adults from the Eastern and Western surveys showed typical morphological lesions of *cribra orbitalia*, porotic hyperostosis and signs of vertebral osteoarthritis.

The paleopathological changes of interest in favor of TB were observed on the remains of the immature individual buried in the Eastern archaeological survey.

The age at death of this individual can be estimated around 2-3 years according to its dental maturation stages (Moorees et al. 1963a, 1963b; Ubelaker 1978). The skeleton is incomplete, mainly represented by skull fragments (frontal, occipital, parietal, and facial bones); four unfused thoracic vertebrae; fragmented right femur and fibula; incomplete metatarsal; right talus and six phalanges of right hand (fig. 2).

Endocranial lesions were observed on the occipital and on the right parietal bones. On the occipital, the new bone formation is located on the cerebral fossa, sagittal and transverse sulci, the cerebellar fossa and the internal occipital crest. The internal table, in those areas, is slightly discolored, presenting sinuous superficial changes, with labyrinth-like features characterized by convoluted superficial interconnected channels (fig. 3).

On the right parietal, two types of endocranial changes are observed: scattered lesions with labyrinth-like pattern are localized in the postero-superior portion, and micro-porosity



Fig. 5 – Isolated and unfused vertebrae of Aswad East immature showing hypervascularization of vertebral bodies.

associated with periosteal reaction on the surface of the postero-inferior area (fig. 4: 2). We also observe micro-porosities on the external face of the postero-superior portion, without any associated thickening of the diploe (fig. 4: 1).

The postcranial skeleton is poorly preserved; however, the few isolated thoracic vertebrae show signs of periosteal reaction and hypervascularization demarcated on the anterior part of the vertebral bodies, around an enlarged vascular foramen (fig. 5).

DISCUSSION

The morphological pattern observed on the skull has been described as *Serpens Endocrania Symmetrica* (SES) by Hershkovitz et al. (2002) and considered as resulting from a slowly developing and well remodeled endocranial periosteal

reaction most probably due to a chronic meningitis, attributable to TB leptomeningitis.

Several etiologies should be considered in the differential diagnosis of SES: metabolic disorders due to vitamin deficiencies (rickets, scurvy), marrow hyperplasia due to hematopoietic disorders (anemia) and subdural hematoma (mainly due to trauma; Mensforth et al. 1978; Roland et al. 1987; Hershkovitz et al. 2002). The SES pattern is very different from other bone changes, both in terms of morphology and location. According to Hershkovitz et al. (2002), it is due to changes in the primary and secondary anastomotic arteries crossing the dura mater, with the possibility that its typical sinuous pattern is related to increased blood flow linked to localized inflammation of the dura mater secondary to an infectious process.

When looking at the records of anatomical collections of individuals presenting endocranial changes, studies on the Hamann-Todd and Terry skeletal documented collections revealed a significant association with intrathoracic or respiratory infections, death by tuberculosis being at the top of the list (Hershkovitz et al. 2002; Pálfi 2012). Among the TB cases documented in the Coimbra Collection, endocranial lesions were observed on one individual with pulmonary TB. However, juvenile individuals who died from meningeal tuberculosis displayed only periosteal reaction on the long bones (Santos and Roberts 2001) corresponding to a so-called secondary syndrome (non hereditary), Hypertrophic Pulmonary Osteopathy (HPO). This syndrome may be associated with various pulmonary chronic diseases including cancer, sarcoidosis, sarcoidosis, fibrosis and tuberculosis (Kumari et al. 2018). However, HPO is mainly attributed to tuberculosis in paleopathology due to its frequency and association with other changes attributed to TB (Hershkovitz et al. 2002; Pálfi 2002; Maczel 2003; Pálfi et al. 2012; Masson et al. 2013).

Regarding external porosities on the cranial vault, they can be related to the so-called “porotic hyperostosis” (PH) or *hyperostosis spongiosa cranii* (HSC) or *cribra cranii* (CC) as cranial porosities can be observed without any thickening of the vault, that discard hyperostotic changes at the origin of these cranial porosities. This pattern is classically attributed to iron-deficiency anemia (Goodman et al. 1984; Stuart-Macadam 1987; Oxenham and Cavill 2010), but tuberculosis is also mentioned (Masson et al. 2015; Teschler-Nicola et al. 2015). A recent study (O’Donnell et al. 2020) suggested that porous cranial lesions should be considered as potential indicators of respiratory infections in bioarchaeological contexts. Even if tuberculosis was a major cause of pulmonary infections and fatal meningitis in the past, the paleopathological link between SES and PH/ HSC/CC is not yet evidenced (Hershkovitz et al. 2002).

Unlike cranial porosities, HPO is commonly associated with SES (Hershkovitz et al. 2002). In our case, no alterations in favor of HPO are found, whereas it should be noted that a case of HPO attributed to tuberculosis has been previously described in the same site (Baker 2014; Baker et al. 2015, 2017; Coqueugniot et al. 2015).

If the observed spinal changes may be of physiological nature and related to normal pattern of vertebral growth in children (anterior external vertebral venous plexuses or extra-spinal veins), they may also be due to tuberculosis. Indeed, the enlargement of foramina of the anterior aspect of vertebra associated with periosteal changes has been reported over a century ago by Ménard (1888) as being the expression of spinal TB distinct from classic Pott's disease, characterized by a hypervascularized aspect of bone tissue of the vertebrae's anterior surface (development of TB fongosities enlarging the orifices of the venous plexuses), involving five to twelve vertebrae in total. The vertebral changes were later described by Baker (1999) as lytic lesions with rounded walls called "smooth walled resorptive lesions" or "severe circumferential pitting" and attributed to an early stage of tuberculosis infection. Some cases were reported on immature individuals from skeletal collections, and attributed to TB (Pálfi et al. 2002, 2012). These lesions have been identified in osteoarchaeological samples and diagnosis of TB was supported by biomolecular analysis (Mays et al. 2002; Maczel 2003; Baker 1999; Baker et al. 2015, 2017; Coqueugniot et al. 2015).

Mariotti and colleagues (2015) studied the link of vertebral foramina observed on late adolescent and adults from the documented skeletal collection of Bologna with TB as cause of death. They found that cavities of various shapes (named foramina, other than vascular enlarged foramina) are present on one-fourth of adult individuals who died from pulmonary TB, that is almost five times more frequent than the frequency observed in the non-TB group. However, they studied mainly adults and their description and pictures do not match exactly the descriptions made by Ménard (1888) or Baker (1999).

Therefore, the associated skeletal changes we observed allow us to raise the issue of their tuberculosis origin.

CONCLUSION

We present here a new possible case of tubercular infection from the Early PPNB level of the Neolithic site of Tell Aswad. A young child (2-3 years old) from a burial in the Aswad East survey presents consistent associated changes: *Serpens Endocrania Symmetrica*, porotic hyperostosis, and vertebral changes (periosteal reaction and hypervascularization of the anterior aspect of vertebral bodies). Further studies (such as paleomicrobiological and paleoimaging analyses) will help in confirming this diagnosis. However, as the skeletal remains are part of a museum's collection, we were yet not allowed to perform any destructive sampling for paleomicrobiological investigation.

This study adds a new possible TB case, to the list of paleopathological cases of TB previously identified at Tell Aswad.

The paleopathological evidence from two Pre-Pottery Neolithic sites discovered in Syria, Dja'de el-Mughara and Tell Aswad (Baker 2014; Baker et al. 2015, 2017; Coqueugniot et al. 2015), demonstrated that tuberculosis already existed as a human infection at least as early as 10,000 years ago.

The number of paleopathological cases of TB dating from before or during the early phase of the Neolithization process in the Fertile Crescent (fig. 1), is now increasing. All these observations converge on the evolutionary model supporting the antiquity of human tuberculosis (Brosch et al. 2002; Gutierrez et al. 2005; Wirth et al. 2008; Comas et al. 2013).

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PROBABLE DIFFUSE IDIOPATHIC SKELETAL HYPEROSTOSIS (DISH) IN PRE-POTTERY NEOLITHIC CYPRUS: EVIDENCE FROM KHIROKITIA

F. LE MORT and H. DUDAY

Abstract. *The site of Khirokitia in Cyprus (7th-early 6th millennium BC) yielded one of the largest series of human remains for the Pre-Pottery Neolithic period in the Eastern Mediterranean and Near Eastern region (MNI = 243). The paleopathological study of this series allowed us to diagnose a probable case of diffuse idiopathic skeletal hyperostosis (DISH) affecting a male aged between 30 and 49 years, who also suffered from osteoarthritis. DISH has rarely been identified among prehistoric populations, especially in the Eastern Mediterranean and Near Eastern region; the case described here is currently the only one known for the Pre-Pottery Neolithic period. It provides new elements to our knowledge of the health status of the early Neolithic populations.*

Résumé. *Le site de Khirokitia à Chypre (VII^e-début VI^e millénaire avant J.-C.) a livré l'une des plus grandes séries de restes humains pour la période du Néolithique précéramique en Méditerranée orientale et au Proche-Orient (NMI = 243). L'étude paléopathologique de cette série a permis de diagnostiquer un cas probable de maladie hyperostotique (DISH) affectant un homme âgé de 30 à 49 ans qui souffrait également d'arthrose. La maladie hyperostotique a rarement été identifiée chez les populations préhistoriques, en particulier dans la région de la Méditerranée orientale et du Proche-Orient ; le cas décrit ici est actuellement le seul connu pour la période du Néolithique précéramique. Il apporte de nouveaux éléments à notre connaissance de l'état de santé des populations du début du Néolithique.*

Keywords. *Diffuse idiopathic skeletal hyperostosis (DISH), Neolithic, Cyprus, Khirokitia*

Mots-clés. *Maladie hyperostotique, Néolithique, Chypre, Khirokitia*

Ancient cases of diffuse idiopathic skeletal hyperostosis (DISH) have been reported as early as during the Middle Palaeolithic. Indeed, the pathological conditions observed on one of the Neandertal skeletons discovered at Shanidar in Iraq (Shanidar 1) support the diagnosis of DISH (Crubézy and Trinkaus 1992). The Kiiik Koba 1 Neandertal skeleton (Crimea) might also have been affected by DISH (Trinkaus et al. 2008). Cases are known in past populations from all around the world and from all periods as well as in various contemporary populations (Bloom 1984; Cassim et al. 1990; Kim et al. 2004; Westerweld et al. 2008; Mori et al. 2017; Sirasanagandla et al. 2018 inter alia) but the disease has rarely been recognized in

prehistoric populations (Faccia et al. 2016). Most of the known cases in past populations come from medieval and post-medieval European populations (Mays 2000; Kacki and Villotte 2006; Giuffra et al. 2010; Kacki et al. 2018; Tristaroli 2018 inter alia). DISH has also been reported, among other examples, in contexts as various as Meroitic Nubians from Sudan (Arriaza et al. 1993), royal mummies of ancient Egypt (Saleem and Hawass 2014), pre-Columbian North America (Ostendorf Smith et al. 2013), ancient northern Chile (Arriaza et al. 1993), ancient Chinese (Hukuda et al. 2000) and Korean (Kim et al. 2012) populations. As far as Near Eastern post-Paleolithic prehistory is concerned, data are very few; three

cases have been identified in the Natufian population, according to Bocquentin (2003, 88-89 and appendix IIE 13); they concern one adult male from Mallaha (Israel) and two adult individuals from Hayonim cave (Israel). Unfortunately, the description of the pathological changes observed on these individuals has not been published yet.

DISH is a systemic noninflammatory disorder characterized by ossification of spinal ligaments and possibly ossification of extra-spinal ligaments and tendons (Resnick and Niwayama 1976; Utsinger 1985; Crubézy and Crubézy-Ibanez 1993; Rogers and Waldron 2001; Kacki and Villotte 2006; Mader, Sarzi-Puttini et al. 2009; Waldron 2009, 2019; Pilai and Littlejohn 2014; Holgate and Steyn 2016). According to Mader et al. (2017), its average prevalence in today's population is approximately 10% of people over 50 years of age. Studies of DISH prevalence in Eastern Mediterranean and Middle Eastern populations are scarce; a prevalence of 10% has been observed among elderly subjects in a national tertiary care referral hospital in Oman (Sirasanagandla et al. 2018) and a prevalence of 17.9% in a Jerusalem hospital population (Bloom 1984). The aetiology of DISH remains uncertain; various causes have been suggested for this condition. Given its frequent association with other disorders such as obesity, diabetes or hyperinsulinemia, metabolic factors are often mentioned (Littlejohn and Smythe 1981; El Miedany et al. 2000; Denko and Malemud 2006; Mader and Lavi 2009; Mader, Novofestovki et al. 2009; Pillai and Littlejohn 2014 inter alia). According to several authors, mechanical factors or genetic predisposition may also be involved in the development of DISH (Pappone et al. 1996; Kim et al. 2004; Gorman 2005). A link with age has been established, most of the affected individuals being older than 40 years of age; males are more frequently suffering from DISH than females (Waldron 2009). As far as past populations are concerned, the condition is often considered to be linked to a particular way of life including rich diets that is frequently associated to a high social status (Rogers and Waldron 2001; Jankauskas 2003; Kacki and Villotte 2006 inter alia).

This paper reports on a new case dating back to the 7th millennium BC, discovered on the Pre-Pottery Neolithic site of Khirokitia in Cyprus (burial 641), which adds to the rare cases of DISH known in prehistoric populations.

MATERIAL AND METHODS

THE ARCHAEOLOGICAL CONTEXT

The site of Khirokitia, situated on a hill, at about 6 km directly from the present southern coast of the Cyprus island, was first excavated by Dikaïos between 1936 and 1946 (Dikaïos 1953). After a few soundings (Stanley Price and Christou 1973; Le Brun and Stanley Price 1977), the excavations directed by A. Le Brun were renewed in 1977 and completed in 2009. The occupation of the site, which illustrates the last phase of the Pre-Pottery Neolithic of Cyprus, took place in the 7th and early 6th millennium cal. BC. The settlement area could be evaluated at approximately 3 hectares of which only a part has been explored. The village consists of houses composed of several round-shape buildings. It is divided into two sectors, east and west. In the course of recent excavations, nine stratigraphic levels have been recognized in the east sector (A to H, J) which was occupied first and three (I to III) in the west sector; it also appeared that the boundaries of the village fluctuated during its occupation (Le Brun 1984, 1989a, 1994a, in press; Le Brun and Daune-Le Brun 2003, 2009; Daune-Le Brun and Le Brun 2016; Daune-Le Brun et al. 2017). The inhabitants of Khirokitia were engaged in farming, herding, hunting and gathering activities (Le Brun 1996; Davis 2003, in press; Pares and Tengberg 2017).

THE HUMAN REMAINS

Many burials were discovered at the site. These are primary burials. The bodies lie in a contracted position in burial pits that were dug into the floors of houses while those houses were occupied. There does not appear to be a preferred location for graves within the houses. The dead are buried in the same way, whatever their age is (Dikaïos 1953; Le Brun 1984, 1989a, 1989b, 1994a; Le Mort 1994, 2003). The study of the human remains from recent excavations and the reappraisal of the skeletons uncovered during the old excavations and in the course of the soundings allowed us to identify at least 243 individuals¹ including 135 juveniles and 108 adult individuals.

1. In a few cases, when bones from several burials uncovered during Dikaïos' excavations were mixed together, it was necessary to estimate the minimum number of individuals.

BURIAL 641

Structure 126 (East sector) was occupied from level B5 to level B2; it yielded three burials. One of them (infant burial 746) belongs to level B5; the two others were sealed by floor 541, the most recent in the structure, they include an infant burial (locus 624) and an adult burial (locus 641; Le Brun 1994b; Le Mort 1994). Burial 641 (fig. 1) contained the remains of an adult male aged between 30 and 49 years. The age at death was estimated according to the method developed by Schmitt (2005) and sex was determined using the method of Murail et al. (2005). The body, oriented south north, was resting in a contracted position in a pit 0.55 m deep; a quern (0.37 × 0.20 m), placed on the deceased before filling the pit, was covering the left hip bone, the sacrum, the inferior portion of the vertebral column and of the left hemithorax, as well as the left elbow.



Fig. 1 – Adult burial 641 in structure 126, level B.
Photo French Archaeological Mission at Khirokitia.

The preservation is rather good in regard to the relative completeness of the skeleton. On the other hand, most of the bones themselves are not in very good condition. The skull is almost complete. The majority of the ribs are present but fragmentary. The sternum is missing. The vertebrae are in a relative good condition compared to the other adult skeletons from the site. As far as the thoracic and lumbar vertebrae are concerned, the body is relatively well preserved, with the exception of the eighth thoracic vertebra (T8) and the fourth lumbar vertebra (L4), but the transverse processes as well as the spinous process are usually not complete. The sacrum appears very fragmentary. Regarding the hip bones, the areas of the iliac tuberosity

and of the auricular surface are partly fragmentary, as well as the ischium and the pubis. Most of the extremities of the long bones are fragmentary, as well as most of the tarsal bones (fig. 2). As is usually the case with prehistoric skeletal remains (human and animal) from Cyprus, the skeleton was covered with concretions. The bones were therefore cleaned with a dilute acetic acid solution in order to dissolve the concretions and to allow study of the skeleton, which gave quite good results.

DIAGNOSING DISH

After the first recognition of the disease by Forestier and Rotes-Quérol (1950), various diagnostic criteria, more or less restrictive, have been published (Kuperus et al. 2017; Holgate and Steyn 2016). They mainly focus on spinal changes although extra-spinal sites may also be concerned (Resnick and Niwayama 1976; Utsinger 1985; Crubézy and Crubézy-Ibanez 1993; Rogers and Waldron 2001; Kacki and Villotte 2006; Waldron 2009, 2019; Foster et al. 2018). Some authors have identified several DISH categories—definite, probable, possible—according to the observed criteria (e.g., Utsinger 1985; Crubézy and Crubézy-Ibanez 1993; Kacki and Villotte 2006; Foster et al. 2018). Diagnostic criteria for probable DISH include spinal and extra-spinal changes while diagnostic criteria for possible DISH involve spinal or extra-spinal changes (table 1). Currently, research is being conducted to better understand the pathogenesis of DISH by identifying the early stages of the disease (Mader et al. 2017; Kuperus et al. 2018, 2019; Castells Navarro and Buckberry 2020).

Skeleton from burial 641 was inspected for spinal and extra-spinal changes as far as the state of preservation of the bones allowed it² and the diagnostic was done according to the Utsinger criteria.

DESCRIPTION AND DIAGNOSIS OF PATHOLOGICAL CHANGES

CERVICAL VERTEBRAE

The first four cervical vertebrae (fig. 3) are fused together by concretions, as are the 5th and 6th cervical vertebrae (fig. 4).

2. At the time of the study, it was not possible to take X-rays.

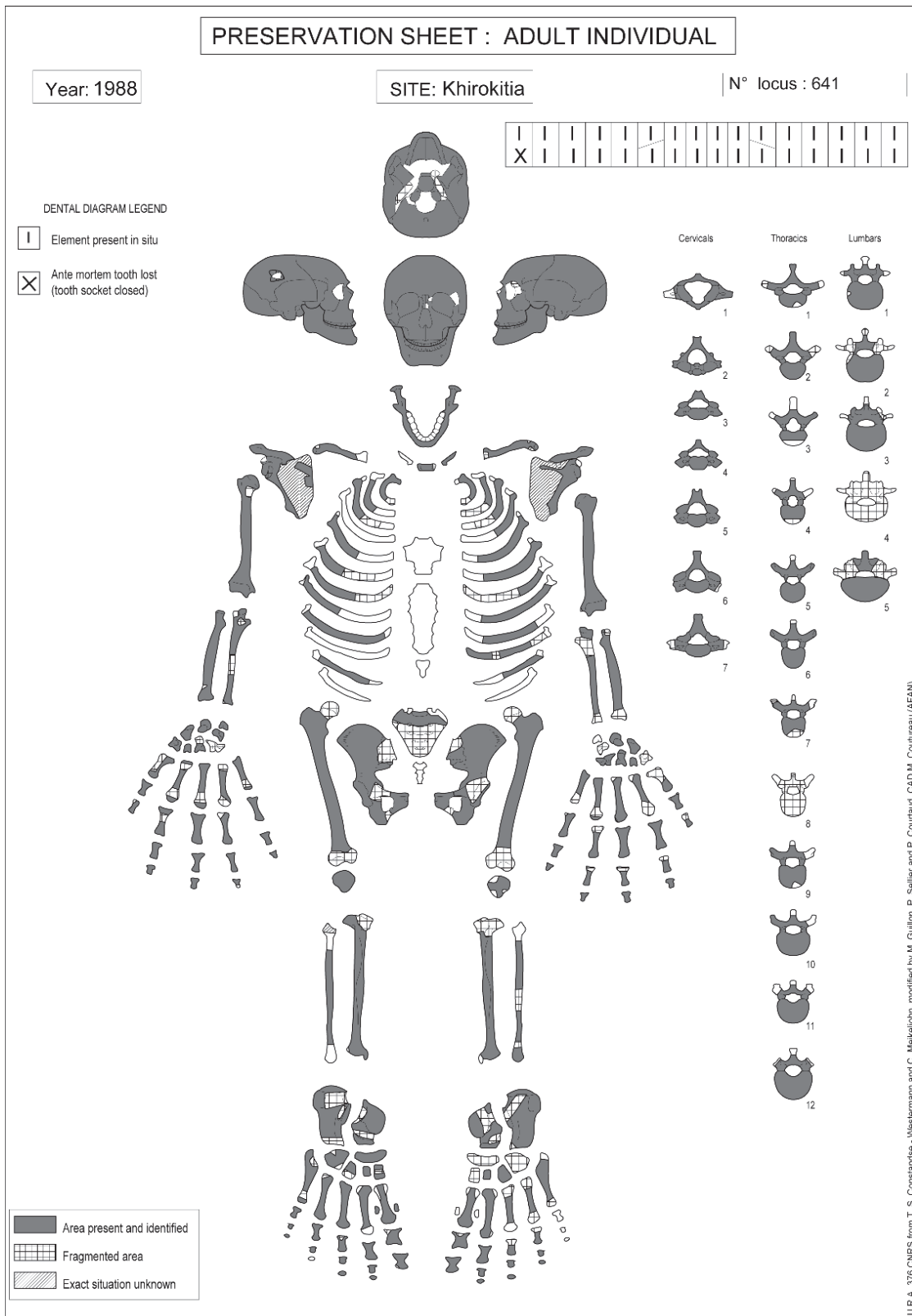


Fig. 2 – Preservation sheet of the adult individual from burial 641.

Table 1 – Diagnostic criteria for DISH categories—definite, probable, possible—in the literature. After Kacki et al. 2018, completed.

| | Definite DISH | Probable DISH | Possible DISH |
|--|--|--|--|
| Utsinger 1985 | <i>Spinal changes</i> Bridging of four continuous vertebral bodies in the thoracolumbar spine <i>Exclusion criteria</i> Signs of degenerative disc disease, apophyseal joint ankyloses | <i>Spinal changes</i> Bridging of two vertebral bodies <i>Extra-spinal changes</i> Bilateral patellar tufting, heel spurring, olecranon tufting | <i>Spinal changes</i> Two vertebrae joined Or <i>Extra-spinal changes</i> Symmetrical enthesophytes |
| Crubézy and Crubézy-Ibanez 1993 | <i>Spinal changes</i> Bridging of three vertebral bodies in the lower thoracic region or of four vertebral bodies at any level of the spine <i>Exclusion criteria</i> Sacroiliac joint erosion, sclerosis, or intraarticular osseous fusion | <i>Spinal changes</i> Bridging of two vertebral bodies <i>Extra-spinal changes</i> Symmetrical enthesopathies (posterior calcanei, olecranons, and upper patellae) | <i>Spinal changes</i> Bridging of two vertebral bodies Or <i>Extra-spinal changes</i> Symmetrical enthesopathies |
| Kacki and Villotte 2006 | <i>Spinal changes</i> Flowing ossification along the anterolateral aspect of four contiguous vertebral bodies in the thoracic spine, with or without ankyloses <i>Exclusion criteria</i> Intervertebral disc space narrowing, apophyseal joint ankyloses | <i>Spinal changes</i> Flowing ossification along the anterolateral aspect of two contiguous vertebral bodies in the thoracic spine, with or without ankyloses <i>Extra-spinal changes</i> Symmetrical enthesal changes (patellar tufting, heel spurring, olecranon tufting) | |
| Foster et al. 2018 | <i>Spinal changes</i> Flowing anterior longitudinal ligament ossification and ankylosis of at least four contiguous thoracic vertebrae <i>Extra-spinal changes</i> Bilateral enthesophytes at the olecranon, patella, tibial tuberosity or posterior calcaneus of at least moderate development | <i>Spinal changes</i> Evidence for ossification of the anterior longitudinal ligament or ankyloses of at least two vertebrae in the thoracic or lumbar spine <i>Extra-spinal changes</i> Bilateral enthesophytes at the olecranon, patella, tibial tuberosity or posterior calcaneus of at least moderate development | <i>Spinal changes</i> Evidence for anterior longitudinal ligament ossification, vertebral ankyloses Or <i>Extra-spinal changes</i> Bilateral enthesophytes at the olecranon, patella, tibial tuberosity or posterior calcaneus of at least moderate development |

The atlas shows a slight ossification of the atlanto-odontoid joint capsule on the right side. The anterior margin of the lower surface of the body of the 3rd cervical vertebra (C3) is slightly extroverted, scalloped and slightly protruding; the lesion is more severe on the right side. On the 4th cervical vertebra (C4), one finds the scalloped aspect of collar-like osteophytes which form the anterior and right lateral part of the margin of the upper surface of the body as well as the whole anterior margin of its lower surface; the right uncus is clearly flattened and everted, the left one being only very slightly everted. These lesions determine a noticeable narrowing of the intervertebral foramen, bilateral, but more pronounced on the right side (hourglass aspect). Similar lesions are found on the anterior and lateral margins of the upper and lower surfaces of the body of the 5th (C5) and 6th (C6) cervical vertebrae, the uncus being also everted. At the C4-C5 level, the narrowing of the vertebral foramen is more pronounced on the right side (as at the C3-C4 level), whereas at the C5-C6 level, a major narrowing is observed on the left side: at the level of the constriction, the transverse diameter of the foramen is hardly 1.8 mm. The posterior joints of all these vertebrae (C1 to C6) don't show any change.

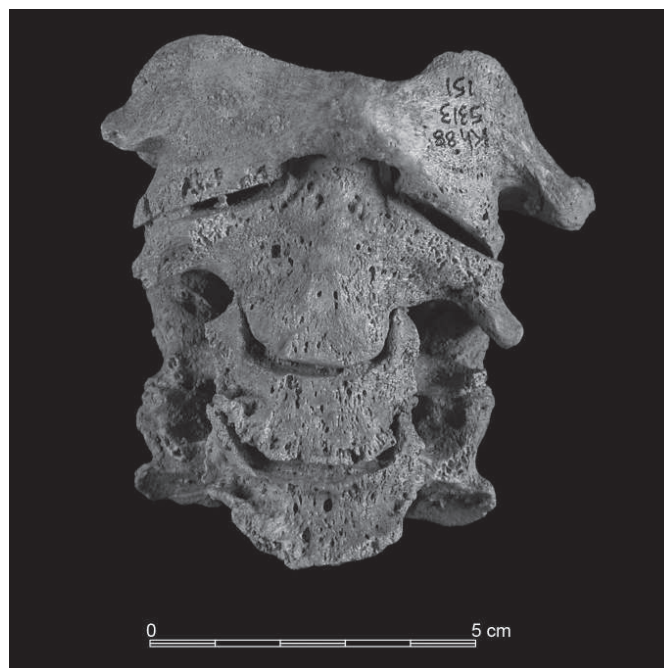


Fig. 3 – Anterior view of the first four cervical vertebrae showing evidence of osteoarthritis.

With regard to the 7th cervical vertebra (C7), the uncus are slightly flattened. The right inferior articular process is irregular, with numerous holes giving it a spongy appearance; its lower edge is everted backwards, thickened, and irregular bone appositions are observed on the posterior surface. The thickness of the process measured about 2 mm above the lower edge of the articular surface is about 2.7 mm on the left and 5.2 mm on the right.

Due to the blocks fused together by the concretion, only some of the upper and lower surfaces of the vertebral bodies can be observed. At the C4-C5 level, a few holes are visible in the posterior part of the surfaces. There are also a few holes at the C6-C7 level, associated with some more dense irregularities.

The pathological changes observed on the cervical vertebrae are strongly suggestive of spinal osteoarthritis, as defined by Waldron (2019).

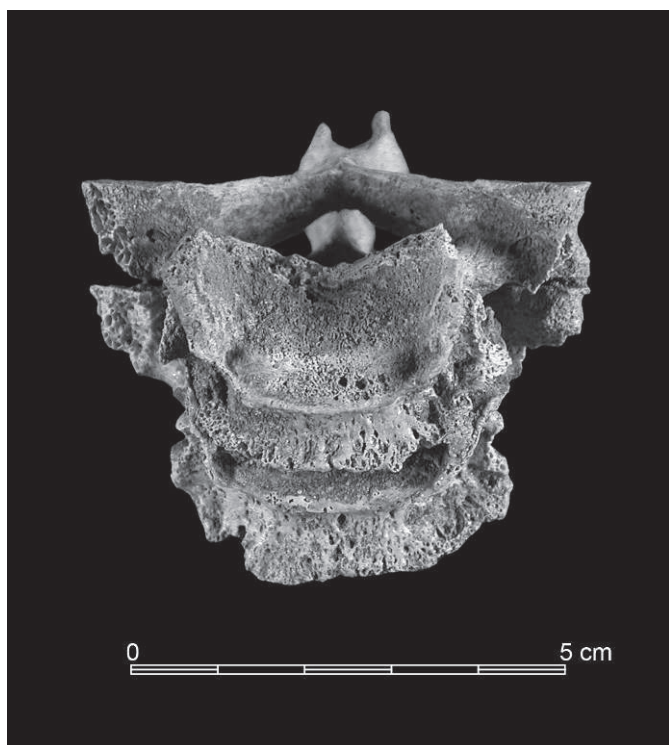


Fig. 4 – Anterosuperior view of the fifth and sixth cervical vertebrae showing evidence of osteoarthritis.

THORACIC VERTEBRAE

On the first thoracic vertebra (T1), the only significant anomaly concerns the right superior articular process in

relation to the anomalies observed on C7. Its lower limit is bordered by a ridge which determines the formation of a gutter in which the thickened articular process of C7 fits. The spinous processes of C7 and T1 are slightly deviated to the right; however, there is no asymmetry of the bodies which would lead to the suspicion of scoliosis. From the second thoracic vertebra (T2) onwards, the orientation of the spinous processes is normal. The second thoracic vertebra (T2) does not show any pathological change.

On the 3rd thoracic vertebra (T3), a very small spicule is visible at the superior-lateral end of the left transverse process (beginning of ossification of the intertransverse ligament). The lower surface of the 4th thoracic vertebra (T4) presents an expansion beyond the vertebral listel which mainly concerns the right lateral and anterior parts; this area is very irregular, vacuolated. On the 5th thoracic vertebra (T5), a small horizontal overflow can be seen in the anterolateral part of the upper surface of the body. The lower surface has a vacuolar appearance in its left half, particularly pronounced in the periphery of the listel in an enlarged and irregular area. The left costal facet for the 6th rib is also very enlarged with a vacuolar appearance.

On the 6th thoracic vertebra (T6), the left half of the upper surface of the body shows some holes immediately inside the listel; major irregularities of the listel are observed on the lower surface of the body. An almost circular cavity with a diameter of 8-9 mm which seems, at least in part, to be old, is present on the left. The vertebral arch is normal with only small spicules corresponding to minor enthesal changes of the yellow ligament.

With regard to the 7th thoracic vertebra (T7), minor enthesal changes of the yellow ligament are visible on the anteroinferior surface of the laminae. The right anterolateral side of the body presents a big syndesmophyte, which protrudes about 1 cm above the upper surface and 8.6 mm in front of and to the right of the original limit of the vertebral body (fig. 5). The left anterolateral part of the upper surface has been partly destroyed postmortem but the preserved part is normal. The lower surface of the body shows several non-taphonomic large holes in its posterior half as well as small excrescences predominating on the right margin.

The arch of the 8th thoracic vertebra (T8) also shows a minor enthesal change of the yellow ligament on the anteroinferior surface of the laminae. The upper surface of the body shows a few holes very likely to be of taphonomic origin and a right anterolateral scalloped excrescence (maximum development: 4.6 mm), made of spicules pointing forward or outwards and upwards. Small excrescences are also observed on the

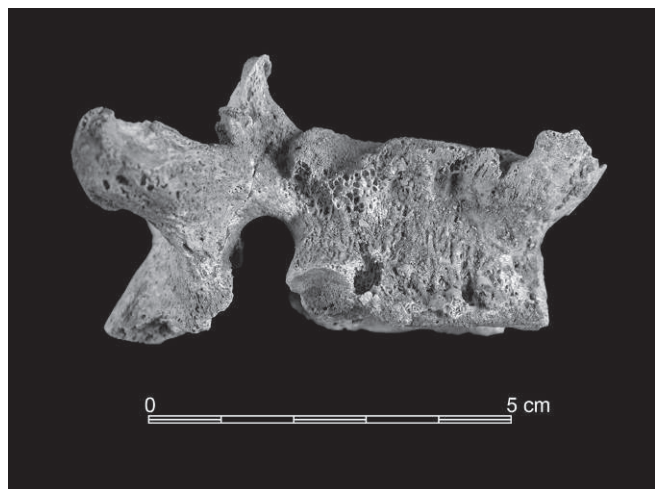


Fig. 5 – Right lateral view of the seventh thoracic vertebra exhibiting an ascending syndesmophyte.

preserved part of the margin of the lower surface of the body, especially on the right anterolateral side.

The 9th and 10th thoracic vertebrae (T9-T10) form a bi-vertebral block with fused syndesmophytes on the right anterolateral side (fig. 6a-b). The upper surface of the vertebral body of T9 has a vacuolar appearance in its posterior half. Between T9 and T10, the disc space is preserved and the posterior joints are free (fig. 6a). The changes exclusively concern the right half of the circumferential surface of the vertebral bodies. We also note excrescences, in the form of a collar with ascending spicules, on the right anterolateral side of the upper surface of the vertebral body of T9 and collar-like osteophytes on the right anterolateral side of the lower surface of the vertebral body of T10. On the anterior/lateral surface of the body of T10, one can observe enlarged vascular foramens as well as disorganized bone production.

On the 11th thoracic vertebra (T11), excrescences are present around the upper and lower surfaces of the body, more developed on the lower part of the right half of the body (fig. 7). The lower surface shows a very irregular spongy appearance immediately inside the listel. The 12th thoracic vertebra shows the same lesions but they are more extensive around the upper surface of the body. As on T10, enlarged vascular foramens and disorganized bone production are visible on the anterior/lateral surface of the bodies of T11 and T12.

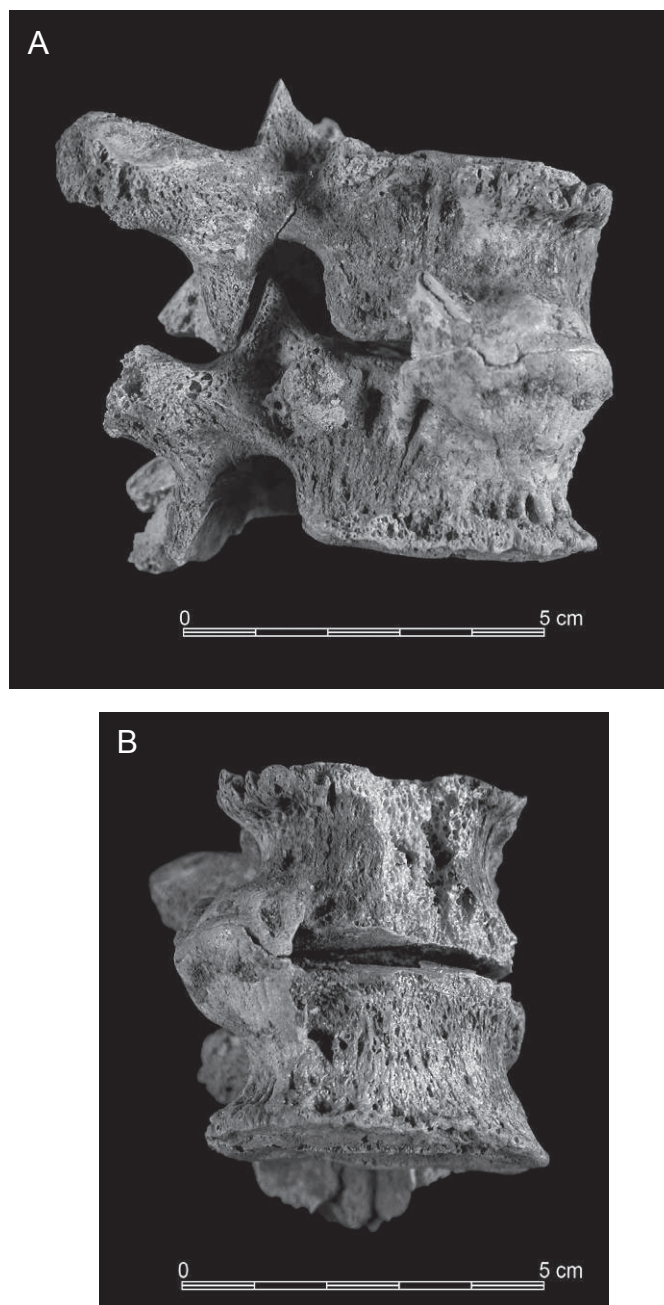


Fig. 6 – Right lateral view (A) and anterior view (B) of fused ninth and tenth thoracic vertebrae.

LUMBAR VERTEBRAE AND SACRUM

On the first lumbar vertebra (L1), we notice large vacuoles on the upper surface of the body, important loss of substance on the lower surface, excrescences along the anterior margin of the upper surface with a small ascending syndesmophyte on

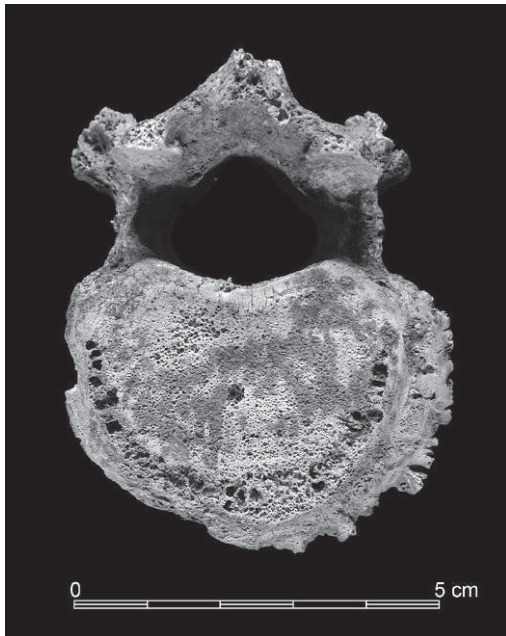


Fig. 7 – Inferior view of the eleventh thoracic vertebra showing excrescences more developed on the lower part of the right half of the body as well as a spongy appearance immediately inside the listel.

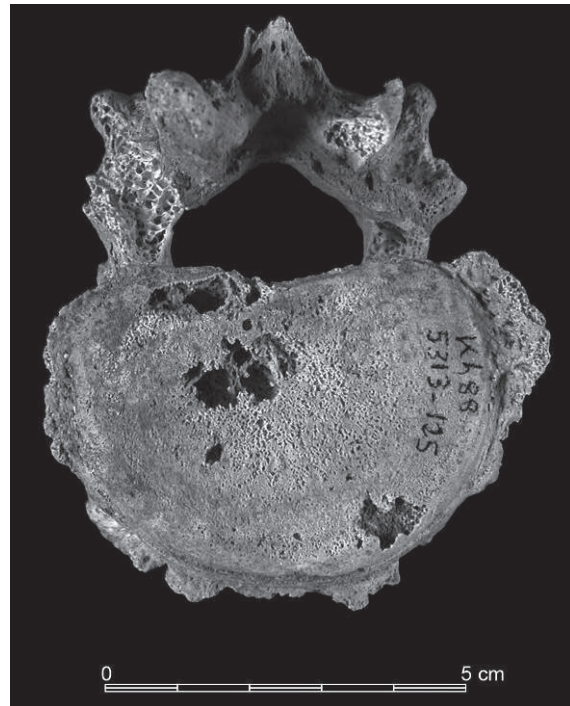


Fig. 8 – Inferior view of the first lumbar vertebra exhibiting collar-like osteophytes and a descending syndesmophyte on the right side.

the left, and collar of excrescences all around the lower surface more developed in the posterolateral right angle of the body (fig. 8). The left inferior articular process is enlarged with a pitted appearance partly masked by encrustation; all around, the bone has a spiky appearance with numerous neoformed spicules.

The upper surface of the body of the 2nd lumbar vertebra (L2) shows a huge, very deep hole (maximum anterior-posterior diameter: 5.6 mm, transverse diameter: 7 mm) suggestive of a Schmorl node and a large collar of osteophytes which protrudes 9.1 mm in the left anterolateral angle and 5.1 mm in the left posterolateral angle. The lower surface presents some irregularities and a slight collar of excrescences on the left lateral half. On the upper surface of the body of the 3rd lumbar vertebra (L3), there is a lacuna of uncertain origin on the left, vacuoles on the posterior margin and excrescences along the anterior margin with a small ascending syndesmophyte on the left anterolateral side. The lower part of the body exhibits another ascending syndesmophyte in the left anterolateral side connected to the previous one by a very dense bone column (fig. 9); the whole anterior margin of the lower surface is remodelled and everted upwards. The superior articular processes of L2 and L3 are normal but all around there are multiple ossified spicules which form irregular collars.

The 4th lumbar vertebra (L4) is very fragmentary and incomplete. The vertebral arch shows many irregularities. Peri-articular spicules can be seen especially above the left superior articular surface. In anterior and right anterolateral position with respect to the upper surface of the body, two enormous ascending syndesmophytes (maximum heights 28.8 and 30.2 mm respectively) protrude 23 and 22 mm above the upper surface (fig. 10a-b). The lower part of the body exhibits a descending syndesmophyte along the right margin of the lower surface.

The vertebral arch of the 5th lumbar vertebra (L5) is normal with however a few spicules around the right inferior articular surface. The upper surface of the body has been damaged post-mortem; there is an irregular area in the right posterolateral angle; a slight collar of excrescences develops in the right anterolateral part. The left anterolateral part of the lower surface of the body is depressed, irregular and vacuolated; on the periphery of the body, a collar of excrescences with a small descending syndesmophyte is observed on the lateral and left anterolateral side.

Furthermore, as on the lower thoracic vertebrae, enlargement of vascular foramen and disorganized bone production are observed on the anterior/lateral surface of the bodies of L1, L2, L3 and L4 (figs. 9, 10a).

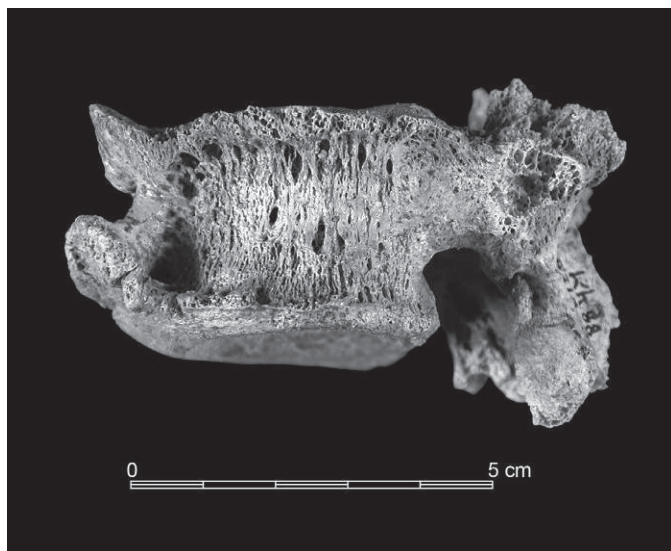


Fig. 9 – Left lateral view of the third lumbar vertebra showing two syndesmophytes connected by a dense bone column.

A small bony beak is observed at the upper part of the right superior articular process of the first sacral vertebra (S1). We also notice an irregularity of the upper surface of the body with, in the left anterolateral area, a small ascending syndesmophyte (fig. 11), responding perfectly to the lower syndesmophyte of the body of L5. The preserved portions of the auricular surfaces don't show any change.

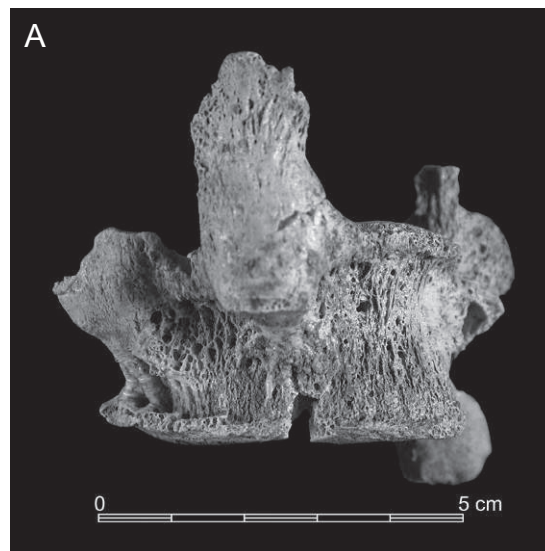


Fig. 10 – **A.** Anterior view of the fourth lumbar vertebra with two ascending syndesmophytes, one of them being broken. **B.** Fragment of syndesmophyte from the fourth lumbar vertebra.

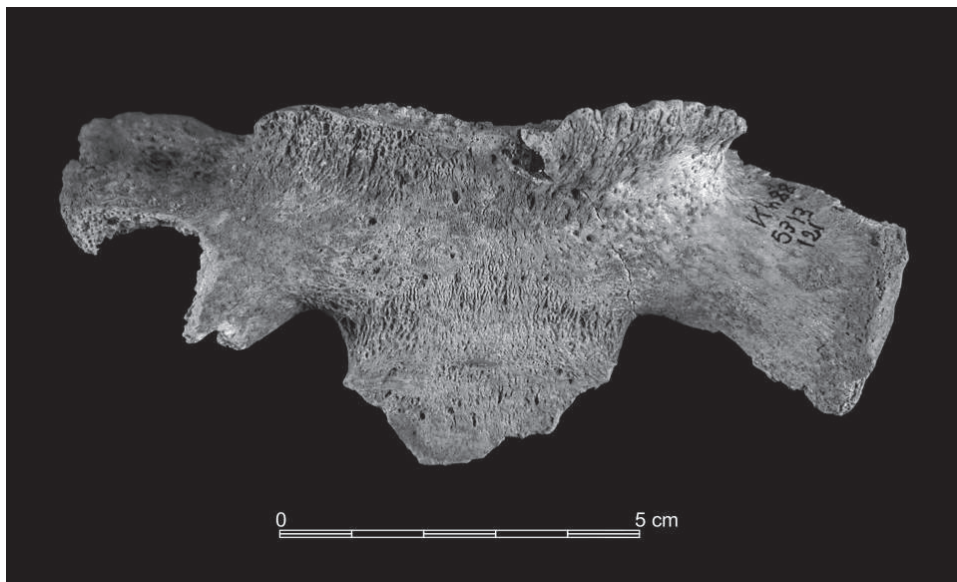


Fig. 11 – Anterior view of the upper part of the sacrum showing a slight syndesmophyte.

APPENDICULAR SKELETON

Due to the state of preservation of the skeleton, peripheral sites where enthesal changes are frequently observed in subjects affected by DISH, that is olecranon, upper patella and tibial tuberosity (e.g., Utsinger 1985; Crubézy and Crubézy-Ibanez 1993; Kacki and Villotte 2006; Mader et al. 2009; Foster et al. 2018), could not be observed. No change is visible on the hip bone and the proximal femur where DISH related changes often occur (Mader et al. 2009). Enthesophytes of moderate development are present on the two calcanei at the insertion of the Achilles tendon. Moreover, a bone spur 12 mm long, which could correspond to the ossification of a tract belonging to the supercostal muscle, is observed on the 11th left rib.

The only other extra-spinal pathological changes regard the metacarpals as well as the hand and foot phalanges. Osteophytes are observed at the metacarpophalangeal joint and at the interphalangeal joint of the right thumb, as well as at the second, third, fourth and fifth right distal interphalangeal joints. The left hand shows osteophytes at the fifth proximal interphalangeal joint and at the third, fourth and fifth distal interphalangeal joints. An osteophyte is also present on the right foot, at the second proximal interphalangeal joint.

DIFFERENTIAL DIAGNOSIS

The skeleton of the individual from burial 641 at Khirokitia show various pathological changes, most of them regarding the spine. All the changes exhibited by the cervical vertebrae are strongly suggestive of osteoarthritis, as are those observed at the metacarpophalangeal and interphalangeal joints (Waldron 2019).

The changes present on the thoracic and lumbar spine include bony outgrowths, osteolytic lesions at endplates, enlarged vascular foramen and disorganized bone production on the anterior/lateral surface of the vertebral body.

Diffuse idiopathic skeletal hyperostosis and ankylosing spondylitis both produce bone proliferation but the absence of change on the sacroiliac joint (Olivieri et al. 2009) allows us to rule out ankylosing spondylitis. The pathological changes observed on the thoracic and lumbar vertebrae consist mainly of ossification along the anterolateral aspect of vertebral bodies in the lower thoracic and lumbar regions. The right side is the only affected in the region of descending aorta (thoracic). The spinal outgrowths which are observed from T7 to S1 vary in size and there is a continuous new bone formation resulting in

the fusion of T9 and T10. This is suggestive of DISH. The association with symmetrical enthesal changes on the calcanei provides an additional criterion to support the diagnosis of probable DISH, according to the criteria proposed by Utsinger (1985; table 1). Furthermore, it has to be noticed that the bivertebral block does not show any narrowing of the intervertebral disc space and that posterior joints of the two vertebrae are not affected, reinforcing the probability that the individual was affected by the disease.

DISH and osteoarthritis are the result of different processes, but both conditions are usually age-related (Ortner 2003; Mader et al. 2009; Waldron 2009, 2019 *inter alia*) which may explain their simultaneous presence on the same individual.

The vacuoles observed on certain vertebral endplates cannot be linked to a possible spondylodiscitis as there is no vertebral collapse and, where their height can be assessed, the intervertebral discs seem to have retained their normal height (Aufderheide and Rodriguez-Martin 1998; Resnick and Niwayama 2002; Ortner 2003). They might be related to the limitation of mobility of the lower thoracic and lumbar spine (Munir et al. 2018; Zehra et al. 2019). The disorganized bone production associated with enlarged vascular foramens visible on the bodies of the lower thoracic and lumbar vertebrae might suggest an inflammatory process. However, an infectious origin due to tuberculosis is most likely to be excluded as there is no evidence of classical expression of vertebral tuberculosis (spondylodiscitis; Aufderheide and Rodriguez-Martin 1998; Resnick and Niwayama 2002; Ortner 2003).

According to the age and sex of the individual, the spinal changes might also be suggestive of fluorosis. Nevertheless, the lack of other bone changes such as increased density of bones or rib enlargement, and the absence of enamel defects (Petrone et al. 2013; Nelson et al. 2016, 2019; Walser et al. 2020) make it possible to exclude the hypothesis of fluorosis.

DISCUSSION

The individual from burial 641 at Khirokitia was most probably affected by DISH. It is the only one with this condition at the site and no other case is known from prehistoric Cyprus. Despite the presence of relatively extensive lesions in the thoracolumbar spine, it is likely that this subject presented only moderate disorders (stiffness, reduced mobility) related to DISH. The development of the bony outgrowths is indeed very insufficient to envisage a conflict with the viscera or vessels located in the vicinity of the spine. On the other hand, it is

likely that advanced degenerative damage to the cervical spine, with marked narrowing of several intervertebral foramina, was the cause of cervicobrachialgia.

As DISH could be linked to a particular way of life including rich diets that is frequently associated to a high social status (Rogers and Waldron 2001; Jankauskas 2003; Kacki and Villotte 2006 *inter alia*), the question of the social status of this individual has to be asked.

Regarding diet, the inhabitants of Khirokitia cultivated wheat, barley, pulses and flax and collected fruits from wild trees (pistachio, figs, olives and almonds). They raised sheep, goats and pigs; fallow deer was hunted (Le Brun 1996; Davis 2003, *in press*; Pares and Tengberg 2017). Preliminary isotopic analyses performed on a small set of samples suggest a diet significantly based on terrestrial resources, despite the proximity of the sea, as well as a low quantity of animal proteins or a high consumption of food resources with low $\delta^{15}\text{N}$ values as lentils (Lange-Badré and Le Mort 1998; E. Herrscher personal communication). A larger study is in progress; until now no difference in diet between individuals could be identified.

Mortuary practices are homogeneous on the site and the burial is not different from the others, whether by its location in a house, its type (primary pit burial under a floor), the position and orientation of the deceased or the grave goods. Its only possibly distinguishing feature is the location of the quern on the body. Querns were found in 18.5% of the adult burials and in two child burials. They were placed on the deceased, either on the head, the trunk or the pelvis before the pit is filled but the quern has been found on the pelvis in only three cases, including burial 641 (Dikaios 1953; Le Brun 1984, 1989a, 1989b; Le Mort 1994). The two other cases (burials VIII/II and XV[II]/III) were uncovered during Dikaios' excavations; unfortunately, only the skulls of the skeletons uncovered by Dikaios have been preserved, and there is no detailed description of the infracranial skeleton. In general, the significance of the querns in the graves is difficult to determine. They were found in different sectors and in different levels of the site and their presence does not seem to be linked to the age or sex of the deceased (Dikaios 1953; Le Brun 1984, 1989a-b, 1994; Le Mort 1994). Nevertheless, we cannot exclude that it is related to the social or health status of the individual, although if this cannot be proved.

Paleopathological comparison data are missing for the Pre-Pottery Neolithic of the Near East and very scarce for ancient Cyprus. According to the literature, there does not seem to be any other case prior to the Hellenistic period. DISH has been diagnosed by S. Fox (2005) on two adult individuals from one of the largest known collection of human remains

(MNI = 275) from the Cypriot Hellenistic and Roman periods, coming from the eastern necropolis of the ancient city of Nea Paphos.

CONCLUSION

The new case of probable DISH from the Pre-Pottery Neolithic site of Khirokitia in Cyprus described in this study is in addition to the scarce cases of DISH known from the prehistoric period. This study thus contributes to a better knowledge of the distribution of DISH in prehistoric populations. Although, according to the current state of knowledge, the oldest case was discovered in Iraq, it is the first time that a case dating to the Pre-Pottery Neolithic has been described in the Near East. Furthermore, this case comes from an island context, which makes it even more outstanding. The question arises as to whether the lack of described cases in other regions of the Pre-Pottery Neolithic Near East reflects a state of research or an actual absence of cases.

The fluctuating relationships of Cyprus with the neighbor mainland during the Neolithic period are only partly understood but it appears that connection between the island and the continent decreased during the 8th millennium, leading to the specificity of the late phase of the Pre-Pottery Neolithic in Cyprus (7th-early 6th millennium BC; Le Brun and Daune-Le Brun 2003). The numerous excavations carried out in the Near East have yielded an important anthropological documentation concerning the Neolithic period and bioarchaeological research is currently intensifying in the region. Nevertheless, certain approaches such as isotopic analysis of human remains or even deep palaeopathological studies are still rare for prehistoric periods. Future research in these domains should lead to a better understanding of the evolution of diet and health status of these populations during the Neolithization process. It would indeed be very interesting to be able to establish the prevalence of rheumatic diseases during the successive phases of the Neolithization process in the Near East and to analyze the influence of the island context.

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TOOTH AS A TOOL: ACTIVITY INDUCED DENTAL ABRASION IN PREHISTORIC ANATOLIA

Y. S. ERDAL

Abstract. *People use their teeth for habitual activities and occupational behaviors. The presence of aberrant abrasion decreased from a hunter-gatherer lifestyle toward more complex societies. In this study, dental remains of Neolithic, Chalcolithic, and Early Bronze Age people of Anatolia were analyzed to understand the effect of cultural changes on the human body. The results suggest that activity-induced dental abrasion in Anatolia decreased from Neolithic to Early Bronze Age. Moreover, gender differences have been observed in the use of teeth as an instrument. Agricultural lifeway has had an important effect on gender roles. Development of instruments, changes in technology, production of cordage, weaving, pottery and metallurgy together with labor differences, specialization and surplus product might have had an effect on the decrease of usage of teeth as a tool. Anatolia is one of the places where gender differences and changes in technology are well reflected on prehistoric human remains.*

Résumé. *Les hommes utilisent leurs dents pour effectuer des activités usuelles et pour certains gestes liés à leurs occupations. La présence d'abrasions aberrantes sur les dents a diminué lors de l'évolution d'un mode de vie de chasseur-cueilleur à celui de sociétés plus complexes. Dans cette étude, les restes dentaires de la population anatolienne du Néolithique, du Chalcolithique et de l'âge du Bronze ancien ont été analysés pour comprendre l'effet des changements culturels sur le corps humain. Les résultats suggèrent que l'abrasion dentaire provoquée par les gestes liés aux activités a diminué en Anatolie depuis le Néolithique jusqu'au début de l'âge du Bronze. De plus, on observe une différence entre les sexes dans les cas où les dents sont utilisées comme outil. Le mode de vie des agriculteurs a eu un effet important sur la répartition des rôles entre les sexes. Le développement d'outils, les changements technologiques, la production de cordages, le tissage, la poterie et la métallurgie ainsi que la diversification de la main d'œuvre, le développement de la spécialisation et la production de surplus pourraient avoir eu un effet sur la diminution de l'utilisation des dents comme outil. L'Anatolie est l'un des endroits où les différences entre les sexes et les changements technologiques se reflètent bien sur les restes humains préhistoriques.*

Keyword. *Paramasticatory wear, dental grooves, technological change, Anatolia, textile production, activity, Neolithic, Near East*
Mots-clés. *Usure dentaire, paramasticatoire, sillons dentaires, changement technologique, Anatolie, production textile, activités, Néolithique, Proche-Orient ancien*

Due to the plasticity of the human body, different types of human behavioral stresses may differently affect its morphology. Studies on human growth, adult stature, skeletal diseases, bone morphology, and dental diseases have shown that human bones are significantly affected by both cultural and environmental factors and that human skeletal and dental remains are among the most important elements for understanding changes in lifestyle in the past.

Archaeological studies and ethnographic research suggest that, besides feeding, when it is necessary people use their teeth for habitual activities and occupational behaviors (Cybulski 1974; Merbs 1983; Larsen 1985; Pfeiffer et al. 1989; Frayer 1991; Alt and Koçkapan 1993; Alt and Pichler 1998; Torres-Rouff 2003; Erdal 2008; Stojanowski et al. 2016; Tomczyk and Zalewska 2016). It is well known that teeth frequently lose their tissues due to close contact with non-food

materials during occupational activities. The most common mechanical and physiological loss of dental tissue is wear as a result of functional or parafunctional tooth-to-tooth contact (attrition), and friction or mechanical forces by tooth-food interaction and non-alimentary substances introduced into the mouth (abrasion; Mahoney and Kilpatrick 2003; Bartlett and Shah 2006; Erdal 2008; Tomczyk and Zalewska 2016; Watson and Haas 2017; Crane et al. 2020). Traces of these mechanical stresses can be macroscopically recognized if they are continuous and repeated. Occurrence and the type of traces depends on several factors such as continuity of usage, habits, cultural or individual preferences, occupation, size, shape, and hardness of the bitten objects, and the manner in which teeth have been used as a third hand. For this reason, Burnett and Irish (Burnett and Irish 2016) suggest that there is a great diversity in activity induced dental abrasion.

Occupation induced dental alterations are observed nearly worldwide and in all time periods. Abrasions resulting from non-alimentary purposes, as well as other activity induced dental alterations play an important role in the interpretation of habitual activities, behaviors, and the daily life of prehistoric people (Larsen 1985; Bocquentin et al. 2005; Erdal 2008).

They represent important data sources in the comprehension of complex social and economic processes such as the mode of production and intra- and inter-group differentiation (Barrett 1977; Schulz 1977; Merbs 1983; Larsen 1985; Lalueza et al. 1997; Lozano-Ruiz et al. 2004; Erdal 2008). It has been stated that in different areas of the world habitual and occupational dental abrasions change markedly from a hunter-gatherer lifestyle to an agricultural one and, more generally, with the adoption of a more complex *modus vivendi* (Lorkiewicz 2011).

Formerly described as the *Neolithic Revolution* by Gordon V. Childe, human populations living in the Near East experienced a long-term transition from a mobile to a sedentary lifestyle and from hunting-gathering-fishing to the domestication of crops and animals and to a fully agricultural lifeway, as well as being able to control production and distribution. One of the most important outcomes of this transition was the change in the processes of craft manufacturing and specialization (Özbek 2004; Eshed et al. 2006; Özdoğan 2014; Larsen 2015; Sagona and Zimansky 2015; Frangipane 2017, 2018a; Irvine et al. 2019; Larsen et al. 2019). Anatolia, together with the Zagros Mountains, northern Mesopotamia, and the Levant is one of the regions in which this transition first occurred.

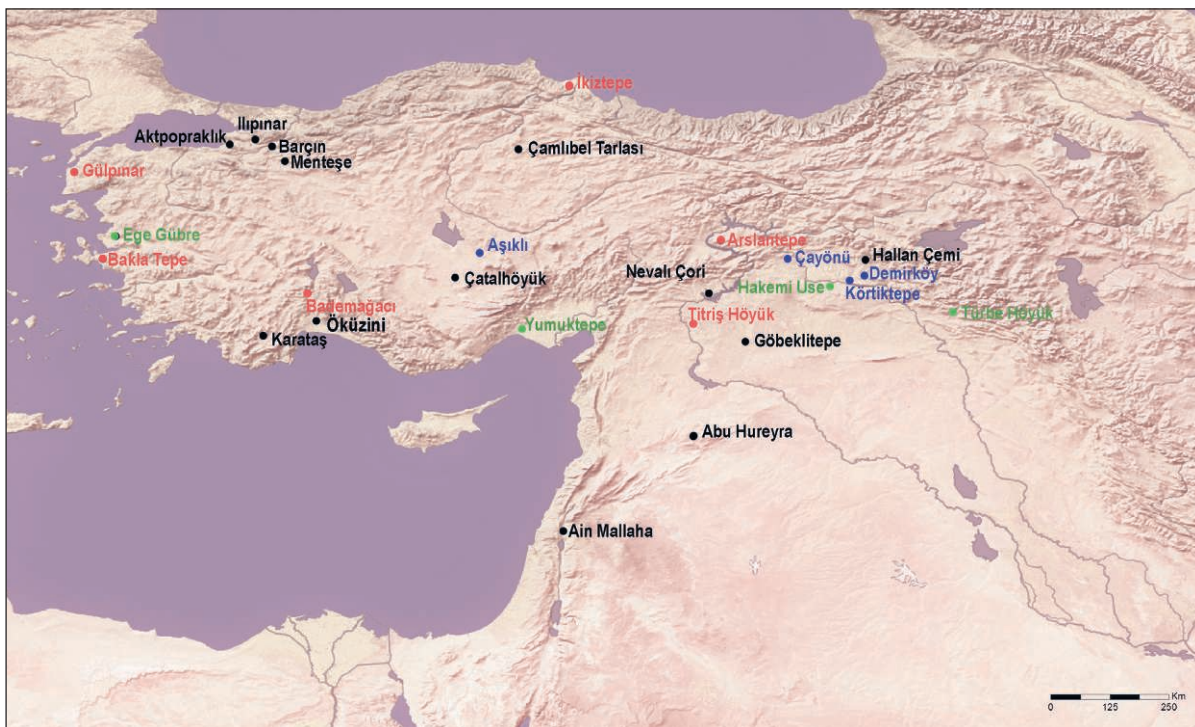


Fig. 1 – Map showing the location of settlements analyzed. **Blue:** Pre-Pottery Neolithic Settlements; **green:** Pottery Neolithic Settlements; **red:** Late Chalcolithic and Early Bronze Age Settlements; **black:** Other cited Settlements from Anatolia and Middle East.

Table 1 – Number of analyzed individuals and teeth from different prehistoric settlements of Anatolia. *PPN*: Prepottery Neolithic; *PN*: Pottery Neolithic; *C*: Chalcolithic; *LC*: Late Chalcolithic; *EBA*: Early Bronze Age.

| Settlement | Calibrated ¹⁴ C BC | Cultural Period | Number of Individual | Number of Teeth |
|--------------|-------------------------------|-------------------------------|----------------------|-----------------|
| Körtik Tepe | 10,450-9,350 | Late Epipaleolithic- PPNA | 246 | 1,987 |
| Demirköy | - | PPNA | 2 | 15 |
| Çayönü | 8,350-7,080 | PPNB | 24 | 264 |
| Aşıklı Höyük | 8,350-7,300 | EN/PPNB | 44 | 513 |
| Bademağacı | 6,400-6,220 | PN | 14 | 85 |
| Hakemi Use | 6,100-5,950 | PN Hassuna-Samarra culture | 78 | 761 |
| Türbe Höyük | - | PN Hassuna-Samarra culture | 5 | 35 |
| Ege Gübre | 6,200-6,000 | PN | 2 | 12 |
| Yumuktepe | 6,000-4,600 | PN-C | 10 | 180 |
| İkiztepe | 3,500-3,000 | LC-EBA | 137 | 3,318 |
| Arslantepe | 3,600-2,900 | LC-EBA | 20 | 331 |
| Bakla Tepe | 3,000-2,300 | EBA I-III | 46 | 712 |
| Titriş Höyük | 2,600-2,100 | EBA II-III | 54 | 538 |
| Total | | | 682 | 8,751 |

However, there are few studies into the effects of changes in the subsistence lifestyles of Anatolian populations on human remains (Koca et al. 2006; Koca Özer et al. 2011; Yılmaz and Pehlevan 2015). The main goal of this study is to investigate how the transition from a hunter-gatherer-fisher lifestyle to an agricultural one, and the development of intensive agriculture, as well as living in centralized and more complex societies, could affect Anatolian populations. The relation between changes in lifestyle and the specialization in craft manufacturing, such as rope production, weaving, basket production, mat processing, or habitual behaviors like using toothpicks are reflected on the dental remains. Hence, by analyzing Anatolian prehistoric material, an attempt is made to understand how gender differences and changes in the mode of production are reflected in the teeth.

MATERIAL AND METHODS

In this study, nearly 8,800 permanent teeth belonging to 682 individuals over the age of 15 from different archeological sites in Anatolia were analyzed with regard to activity induced dental abrasion (AIDA). Human remains are dated to a wide time span from the Late Epipaleolithic (ca. 10,500 BC) to the end of the Early Bronze Age (ca. 2,200 BC; table 1; fig. 1). Two skeletal samples belonging to the PPNA settlements of Körtik

Tepe and Demirköy, both located in Southeastern Anatolia, have been analyzed. People of these PPNA sites were hunter-gatherer-fishers, living in permanent settlements (Özkaya and Coşkun 2007; Özkaya 2009; Benz et al. 2015, 2017; Koruyucu et al. 2018). The PPNB¹ is represented by two sites: Çayönü and Aşıklı Höyük. Çayönü is located in the Diyarbakır region and Aşıklı Höyük in central Anatolia (Özbaşaran et al. 2018). A broad spectrum of hunting sources, including a variety of small prey, birds, and fish were present at both settlements (Özbek 2004; Erim-Özdoğan 2011; Stiner et al. 2018). Zooarchaeological and archaeobotanical studies suggest the domestication of animals and the cultivation of wild and domestic plants (Buitenhuis et al. 2018; Özbaşaran et al. 2018; Stiner et al. 2018). At Aşıklı, this suggestion is also supported by the discovery of domestic sheep remains in the earliest stratigraphic layers (Özbaşaran et al. 2018). Moreover, according to Erdal (Erdal 2018), labor differences with respect to gender existed at Aşıklı.

The Pottery Neolithic (PN) settlements are distributed all around Anatolia. Hakemi Use (Diyarbakır) and Türbe Höyük (Siirt) are located in southeastern Anatolia. Both sites are dated to the Hassuna-Samarra culture of northern Mesopotamia (6,100-5,950 BC; Tekin 2011, 2013; Erdal 2013; Kodaş et al. 2018). Studies on the human remains from Hakemi Use suggest

1. Chronologically, there is no PPNB period in Central Anatolia. Human remains from Çayönü and Aşıklı are almost contemporary to each other.

a gender difference for burial customs and pathological lesions related to daily life (Erdal 2013). Yumuktepe and Bademağacı are located in southern Anatolia; however, they are far away from each other. Bademağacı is located on the highlands of the Taurus Mountains and close to the modern district of Bucak, Burdur (Duru and Umurtak 2019; Erdal 2019a). Bademağacı also has individuals dated to the EBA II period. Yumuktepe is located on the lowlands on the shore of the Mediterranean, in the center of the modern city of Mersin (Erdal 2019b; Palumbi and Caneva 2019). Ege Gübre (İzmir) is in western Anatolia, on the shores of the Aegean Sea. Sub-floor burials in the PN settlements are few in number in the whole Near East. Moreover, there is almost no information on the extramural graveyards of these settlements. With the exception of Hakemi Use, all prehistoric settlements with a small number of human remains were investigated.

Gülpınar (Çanakkale) is a Middle Chalcolithic settlement in northwest Anatolia. Arslantepe and İkiztepe are LC-EBA settlements of eastern Anatolia and the central Black Sea region, respectively. Both settlements are famous for the presence of social stratification and a rich assemblage of metal objects made of arsenical copper alloy (Bilgi 1984, 1990; Frangipane 2017). Two other settlements, Titriş Höyük (Şanlıurfa) and Bakla Tepe (İzmir) are dated to the EBA and located in southeastern and western Anatolia, respectively. Both settlements contained skeletal remains dated to the EBA I and EBA II-III (Algaze and Matney 2011; Keskin 2011; Gündoğan et al. 2019). The economic systems of these two settlements were based on agriculture. However, Bakla Tepe has also revealed evidence of metallurgy. The LC and EBA settlements in Anatolia provide important information about the emergence of centralized control systems of production and distribution (Sagona and Zymanski 2015; Frangipane 2016, 2017, 2018a, 2018b), long distance trade and exchange networks, and hierarchical socio-economic systems (Massa 2015). Studies into the dietary habits suggested that there was a narrow range in cultivated crops and consumed food resources, with agricultural subsistence strategies focused on domesticated cereals and the exploitation of the ante-mortem products of domesticated animals (Irvine et al. 2019). Archaeological studies suggest that the EBA people were specialists in craft manufacture as well.

According to Waters-Rist and others (Waters-Rist et al. 2010), the representation and preservation of dental elements varies widely in archaeological populations, as observed in Anatolian prehistoric sites. For this reason, all teeth with an intact crown and neck were inspected for the presence of activity-induced abrasion. It is important to highlight that an

individual was accepted exclusively for study if each tooth type was represented in both the maxillary and mandibular quadrants.

Occlusal grooves (groove), notches, grooves on the neck (GON), and lingual surface attrition of the maxillary anterior teeth (LSAMAT) are accepted as types of AIDA. A groove is defined as being a narrow but long “U” or “V” shaped abrasion on the crown. These are channel-shaped abrasions with a narrow width compared to their length. Grooves are mainly directed mesio-distally or slightly distorted from this direction, but any direction can be observed. In some studies, grooving on the neck and crown, and notching have been interpreted together (Scott and Jolie 2008; Irish and Scott 2016; Stojanowski et al. 2016), even if they are caused by different occupational activities and habitual behaviors. Instead, the term notch is preferred if abrasion is very wide compared to its length. Notches are mostly unilateral, labio-lingually directed, and affect only the teeth involved in the grasping of an object. Notches are bigger than the grooves on both the crown and the neck (Blakely and Beck 1984; Pfeiffer et al. 1989; Alt and Pichler 1992). As described by Turner and others (Turner and Machado 1983; Irish and Turner 1987), LSAMAT is an oblique flattening of the lingual surface of the maxillary anterior teeth with no correspondence on the mandibular anterior teeth. The GON of a tooth, mostly on the interproximal area, but infrequently on the lingual or buccal surface, or even on the distal surface of the third molar with striations, are included in the AIDA types. It is important to differentiate AIDA from abfraction, which is a possible pathological loss of dental tissues caused by biomechanical loading forces (Sarode and Sarode 2013). The presence of polishing and longitudinal striation in the grooves is taken into consideration as diagnostic traits to distinguish AIDA from abfraction (Bonfiglioli et al. 2004; Scott and Jolie 2008).

All teeth were visually inspected using a low-strength (10×) magnifying glass under oblique light. In case of possible signs of AIDA, a low-power microscope (Leica MZ27) was additionally employed for a more detailed analysis. Digital sliding calipers and a microscope were used to measure the width and length of the dental grooves. Selected samples of different types of AIDAs were further analyzed by using a Scanning Electron Microscope (Zeiss Evo-50 EP). Sex was estimated by using morphological characteristics of both the pelvis and skull such as the subpubic angle, greater sciatic notch, pre and post auricular sulcus, shape of the pubic symphysis, supraorbital margin, development of the brow ridge, shape of the glabella, the nuchal crest, and theinion according to the

standards proposed by Buikstra and Ubelaker (Buikstra and Ubelaker 1994).

Since there is not enough skeletal and dental material from the Neolithic and Chalcolithic to adequately represent the individual sites and periods, groups belonging to the same period were combined for statistical analyses in order not only to provide a general representation of Anatolia, but also to understand changes over time and abrasion patterns between different cultural periods. AIDA and associated factors such as sex and chronological periods, have been tested using a Chi-squared Test, assuming $P < 0.05$ as the point of statistical significance. When more than 20% of cells had expected frequencies < 5 , a Fisher's exact test was performed. Statistical analysis was performed using IBM-SPSS statistics software (V. 21).

RESULTS

AIDA per individual

All prehistoric Anatolian populations show some degree of AIDA. The sample sizes of some sites such as Demirköy,

Bademağacı, Türbe Höyük, Ege Gübre, and Gülpınar are quite small. When these sites are excluded, AIDA is most frequently observed in the Körtik Tepe (42.6%), Yumuktepe (40%), Hakemi Use (37.2%), and Arslantepe (25%) sample populations (table 2). It is possible to state that Neolithic skeletal samples have more AIDA than the later populations. In fact, more than one third of the individuals have at least one AIDA during the Neolithic period. However, people from LC and EBA settlements have frequencies lower than 10%, except for Karataş (table 2). Table 2 and figure 2 show that some differences also exist between populations belonging to the same cultural period. For instance, a significant difference has been observed between the PPNB settlements of Aşıklı (15.9%) and Çayönü (29.2%; $P < 0.05$). Bademağacı (55.6%) and Hakemi Use (37.3%) have the highest frequencies of AIDA, and there are significant differences among the PN settlements ($P < 0.05$). Almost all of the individuals from Bademağacı (LN), Ege Gübre, Yumuktepe, Gülpınar, and Bademağacı (EBA) have AIDA. Differences between the sites are statistically significant (χ^2 : 1167.234, df: 13; P : 0.000).

On examination of the different chronological periods, it can be stated that the frequency of AIDA per mouth decreases over time (fig. 2). Since the sample size of some settlements, such as those of the PPNB and PN periods, is low in number,

Table 2 – Frequencies of AIDA in prehistoric populations of Anatolia (per individual). **O**: Observed; **I**: Inspected; **J**: Fisher's Exact Test applied; **§**: Karataş material published by Angel, 1970; **PPNA**: Pre-Pottery Neolithic Period A; **PPNB**: Pre-Pottery Neolithic Period B; **PN**: Pottery Neolithic period; **C**: Chalcolithic; **LC**: Late Chalcolithic; **EBA**: Early Bronze Age.

| Settlement | Cultural Horizon | Male | | Female | | Total | | χ^2 | P |
|--------------|------------------|-------|------|--------|------|---------|-------|----------|--------|
| | | O/I | % | O/I | % | O/I | % | | |
| Körtik Tepe | PPNA | 48/90 | 53.3 | 45/74 | 60.8 | 104/244 | 42.6 | 0.925 | 0.211 |
| Demirköy | PPNA | - | - | 1/2 | 50.0 | 1/2 | 50.0 | - | - |
| Çayönü | PPNB | 1/9 | 11.1 | 5/11 | 45.5 | 7/24 | 29.2 | 2.780 | 0.119¶ |
| Aşıklı Höyük | EN (PPNB) | 0/11 | 0.0 | 7/25 | 28.0 | 7/44 | 15.9 | 3.823 | 0.058¶ |
| Bademağacı | PN | 4/5 | 80.0 | 1/2 | 50.0 | 5/9 | 55.6 | 0.630 | 0.524¶ |
| Hakemi Use | PN | 7/19 | 36.8 | 13/35 | 37.1 | 29/78 | 37.2 | 0.000 | 0.610¶ |
| Türbe Höyük | PN | 0/3 | 0.0 | - | - | 1/5 | 20.0 | - | - |
| Ege Gübre | PN | - | - | 1/2 | 50.0 | 1/2 | 50.0 | - | - |
| Yumuktepe | PN | 1/2 | 50.0 | 3/8 | 37.5 | 4/10 | 40.0 | 0.104 | 0.667 |
| Gülpınar | C | 1/1 | 100 | 1/1 | 100 | 2/2 | 100.0 | - | - |
| İkiztepe | LC/EBA | 2/61 | 3.3 | 2/76 | 2.6 | 4/137 | 2.9 | 0.050 | 0.603¶ |
| Arslantepe | LC/EBA | 2/6 | 33.3 | 3/8 | 37.5 | 5/20 | 25.0 | 0.026 | 0.657¶ |
| Bakla Tepe | EBA | 0/16 | 0.0 | 4/21 | 19.1 | 4/37 | 10.8 | 3.417 | 0.091¶ |
| Bademağacı | EBA | 0/2 | 0.0 | 0/2 | 0.0 | 0/5 | 0.0 | - | - |
| Titriş Höyük | EBA | 3/23 | 13.0 | 2/18 | 11.1 | 3/51 | 5.9 | 1.240 | 0.538 |
| Karataş § | EBA | - | - | - | - | 13/77 | 16.9 | - | - |

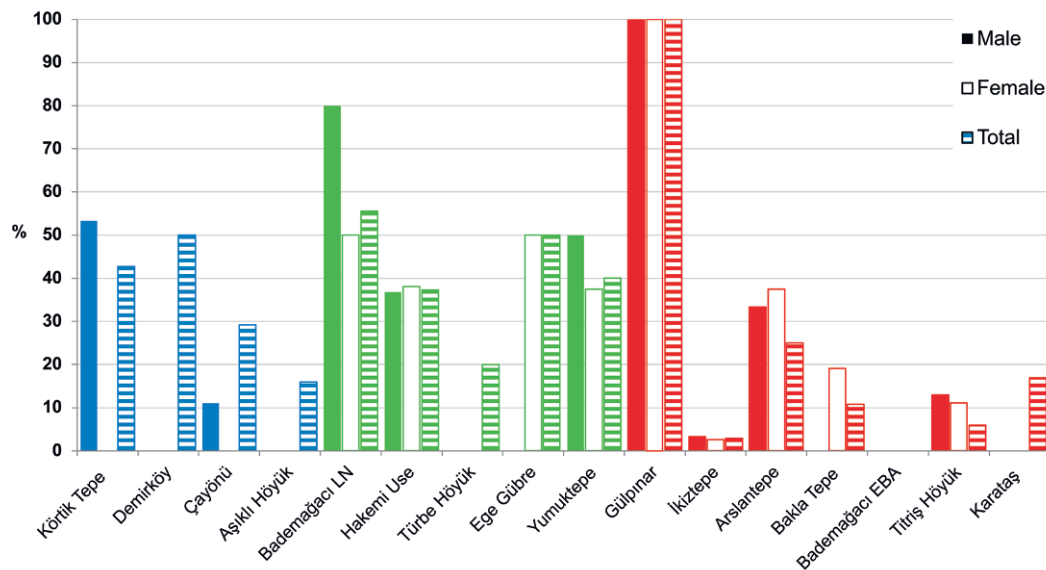


Fig. 2 – The Frequency of AIDA in the prehistoric settlements of Anatolia.

these settlements and chronological periods were combined in order to understand the changes in the frequency of teeth usage as a tool. As shown in table 3, the presence of at least one AIDA per individual decreases with time. This change does not appear gradual, but rather a significant shift seems to occur from the PPN to PN, and from the PN to LC-EBA periods (table 3). Differences between the time periods are also statistically significant (χ^2 : 99.737, df: 3; P: 0.000). Frequencies observed per mouth have revealed that females have higher AIDA frequencies compared to males, except for Bademağacı and Yumuktepe, (LN and EC periods—which only have a few individuals), and İkiztepe and Titiş (LC and EBA). However, differences between the sexes are not statistically significant (table 2). Furthermore, the combined data does not show any statistically significant differences between the sexes, except

for the PPNB period (table 3). The frequency of individuals with at least one paramasticatory abrasion in the mouth is 53.3% in males and 60.5% in females during the PPNA. These values, respectively, decrease to 39.3% and 36.6% in the PN, which suggests that the number of individuals with at least one unusual abrasion has a similar incidence. In other words, it can be said that the use of teeth in habitual and/or occupational activities was similar for both sexes at the same settlement and in the same chronological period (fig. 2). However, it is well known that some individuals present multiple teeth affected by aberrant wear and different types of AIDA at once. For this reason, it is more appropriate to analyze AIDA according to its type, tooth group, and the number of teeth affected by paramasticatory wear.

Table 3 – Frequencies of AIDA in different cultural horizons in Anatolia (per individual). **O**: Observed; **I**: Inspected; **f**: Fisher's Exact Test; *****: Statistically significant; **PPNA**: Pre-Pottery Neolithic Period A; **PPNB**: Pre-Pottery Neolithic Period B; **PN**: Pottery Neolithic period; **LC**: Late Chalcolithic; **EBA**: Early Bronze Age.

| Cultural Horizon | Male | | Female | | Total | | | |
|------------------|-------|------|--------|------|---------|------|----------|-------------------|
| | O/I | % | O/I | % | O/I | % | χ^2 | P |
| PPNA | 48/90 | 53.3 | 46/76 | 60.5 | 104/246 | 42.3 | 0.868 | 0.352 |
| PPNB | 1/20 | 5.0 | 12/36 | 33.3 | 14/68 | 20.6 | 5.790 | 0.016* \ddagger |
| PN | 11/28 | 39.3 | 15/41 | 36.6 | 32/86 | 37.2 | 0.052 | 0.820 |
| LC-EBA | 6/112 | 5.4 | 13/135 | 9.6 | 21/292 | 7.2 | 1.382 | 0.240 |

AIDA TYPE PER TOOTH GROUP

Table 4 shows that the distribution of AIDA on different tooth groups differs significantly between the populations. Similar to the distribution of AIDA per individual, the highest AIDA frequencies are observed in the Körtik Tepe sample population. At this site, occlusal grooves on the anterior teeth represent the most common AIDA type. Although other types of AIDA, such as notches (below 2%) and LSAMAT (4-5%), have also been observed on the anterior teeth, their frequency is low. However, at Körtik Tepe, GON on the posterior teeth are as common as occlusal grooves on the anterior teeth. In general, it can be stated that all AIDA types have been observed in both sexes of the early hunter-gatherer populations of Anatolia. Dental grooves on the crown are most commonly observed in the lateral incisors of females (26.4%) and males (18.6%),

followed by the central incisors (16.5%) and canines (14.4%) of females, and the central incisors of males (9.6%). Almost all types of AIDA at Körtik Tepe are more common in females (table 4). With the exception of notches and LSAMAT, these sex differences are statistically significant.

Among early agriculturalist populations, Çayönü and Aşıklı show a similar pattern. All types of AIDA were found in the populations of both sites. Nevertheless, it is possible to see that a decrease of AIDA occurs after the PPNA, especially in males. No, or few, males have AIDA at Çayönü, and no individual at Aşıklı. Conversely, females of both sites have grooves on their anterior teeth. At Çayönü, the frequency of grooves on the central and lateral incisors is 11% and 10%, respectively, in females. The differences between males and females are statistically significant for both settlements.

Table 4 – Frequencies of AIDA types in different tooth groups (per tooth). **N:** Number of teeth; **G:** Occlusal Groove; **No:** Notch; **L:** LSAMAT; **GON:** Grooves on the neck; **AH:** Aşıklı Höyük; **ARS:** Arslantepe; **BT:** Bakla Tepe; **ÇT:** Çayönü Tepesi; **HKM:** Hakemi Use; **IT:** İkiztepe; **KTK:** Körtik Tepe; **TH:** Titriş Höyük; **YP:** Yumuktepe; **PPNA:** Pre-Pottery Neolithic Period A; **PPNB:** Pre-Pottery Neolithic Period B; **PN:** Pottery Neolithic period; **LC:** Late Chalcolithic; **EBA:** Early Bronze Age.

| | | | I1 | | I2 | | C | | P1 | | P2 | | M1 | | M2 | | M3 | |
|------------------|---|-----|-----|------|-----|------|-----|------|-----|-----|-----|-----|-----|------|-----|------|-----|-----|
| | | | N | % | N | % | ON | % | N | % | N | % | N | % | N | % | N | % |
| KTK PPNA | ♂ | N | 156 | - | 134 | - | 189 | - | 189 | - | 189 | - | 157 | - | 208 | - | 155 | - |
| | | G | 15 | 9.6 | 25 | 18.7 | 5 | 2.7 | - | - | - | - | - | - | - | - | - | - |
| | | No | 2 | 1.3 | 1 | 0.7 | - | - | - | - | - | - | - | - | - | - | - | - |
| | | L | 4 | 2.6 | 1 | 0.7 | - | - | - | - | - | - | - | - | - | - | - | - |
| | | GON | 1 | 0.6 | 1 | 0.7 | 1 | 0.5 | 10 | 5.3 | 10 | 5.3 | 18 | 11.5 | 25 | 12.0 | 13 | 8.4 |
| | ♀ | N | 115 | - | 110 | - | 125 | - | 127 | - | 131 | - | 102 | - | 153 | - | 90 | - |
| | | G | 19 | 16.5 | 29 | 26.4 | 18 | 14.4 | - | - | - | - | - | - | - | - | - | - |
| | | No | 1 | 0.9 | 2 | 1.8 | 3 | 2.4 | - | - | - | - | - | - | - | - | - | - |
| | | L | 5 | 4.4 | 4 | 3.6 | 1 | 0.8 | - | - | - | - | - | - | - | - | - | - |
| | | GON | 1 | 0.9 | 1 | 0.9 | - | - | 4 | 3.2 | 4 | 3.1 | 18 | 17.7 | 14 | 9.2 | 7 | 7.8 |
| ÇT PPNB | ♂ | N | 9 | - | 13 | - | 11 | - | 12 | - | 12 | - | 16 | - | 15 | - | 11 | - |
| | | G | - | - | 1 | 7.7 | - | - | - | - | - | - | - | - | - | - | - | |
| | | No | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| | | L | - | - | 1 | 7.7 | - | - | - | - | - | - | - | - | - | - | - | |
| | | GON | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| | ♀ | N | 18 | - | 19 | - | 19 | - | 16 | - | 17 | - | 12 | - | 22 | - | 23 | - |
| | | G | 2 | 11.1 | 2 | 10.5 | 1 | 5.3 | - | - | - | - | - | - | - | - | - | |
| | | No | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| | | L | 2 | 11.1 | 1 | 5.3 | - | - | - | - | - | - | - | - | - | - | - | |
| | | GON | - | - | - | - | - | - | - | - | - | - | 1 | 8.3 | 1 | 4.5 | 1 | 4.3 |
| AH EN PPNB | ♂ | N | 19 | - | 20 | - | 23 | - | 20 | - | 18 | - | 15 | - | 19 | - | 15 | - |
| | | G | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| | | No | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| | | L | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| | | GON | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| | ♀ | N | 35 | - | 41 | - | 51 | - | 43 | - | 52 | - | 42 | - | 49 | - | 43 | - |
| | | G | 1 | 2.9 | 2 | 4.9 | 1 | 2.0 | - | - | - | - | - | - | - | - | - | |
| | | No | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| | | L | 3 | 8.6 | 4 | 9.8 | 1 | 2.0 | - | - | - | - | - | - | - | - | - | |
| | | GON | - | - | - | - | - | - | - | - | 3 | 5.8 | 2 | 4.8 | - | - | 1 | 2.3 |

| | | | I1 | | I2 | | C | | P1 | | P2 | | M1 | | M2 | | M3 | |
|------------------|----------------|--------------------------|-------------------------|------------------------------|-------------------------|----------------------------|-------------------------|-----------------------------|-------------------------|-------------------------|-------------------------|-------------------------|-------------------------|-------------------------|-------------------------|--------------------------|-------------------------|-------------------------|
| | | | N | % | N | % | ON | % | N | % | N | % | N | % | N | % | N | % |
| | | | | | | | | | | | | | | | | | | |
| HKM PN | +O | N G No L GON | 32 - 1 1 - | - - 3.1 3.1 - | 37 - 1 1 - | - - 2.7 2.7 - | 45 - - - - | - - - - - | 40 - - - 1 | - - - - 2.5 | 41 - - - 1 | - - - - 2.4 | 28 - - - - | - - - - - | 38 - - - - | - - - - - | 29 - - - - | - - - - - |
| | +O | N G No L GON | 37 7 1 1 - | - 18.9 2.7 2.7 - | 55 3 - 2 - | - 5.5 - 3.6 - | 60 3 1 1 - | - 5.0 1.7 1.7 - | 65 1 - - - | - 1.5 - - - | 55 - - - - | - - - - - | 64 - - - 1 | - - - - 1.6 | 68 - - - 2 | - - - - 2.9 | 49 - - - - | - - - - - |
| YTP PN | O ₃ | N G No L GON | 5 - - - - | - - - - - | 7 - - 2 - | - - - 28.6 - | 7 - - - - | - - - - - | 8 - - - - | - - - - - | 5 - - - - | - - - - - | 6 - - - - | - - - - - | 7 - - - - | - - - - - | 2 - - - - | - - - - - |
| | +O | N G No L GON | 20 - - 1 - | - - - 5.0 - | 23 - - 3 - | - - - 13.0 - | 28 - - - - | - - - - - | 22 - - - - | - - - - - | 25 - - - - | - - - - - | 26 - - - - | - - - - - | 22 - - - - | - - - - - | 17 - - - - | - - - - - |
| ARS LC EBA | O ₃ | N G No L GON | 9 1 - 1 - | - 11.1 - 11.1 - | 4 - - - - | - - - - - | 10 - - - - | - - - - - | 11 - - - - | - - - - - | 13 - - - - | - - - - - | 17 - - - - | - - - - - | 19 - - - - | - - - - - | 8 - - - - | - - - - - |
| | +O | N G No L GON | 16 - - 4 - | - - - 25.0 - | 15 2 - 1 - | - 13.3 6.7 - - | 19 1 1 - - | - 5.3 5.3 - - | 14 - - - - | - - - - - | 14 - - - - | - - - - - | 21 - - - 1 | - - - - 4.8 | 20 - - - 2 | - - - - 10.0 | 13 - - - - | - - - - - |
| IT LC EBA | O ₃ | N G No L GON | 151 - - 4 - | - - - 2.6 - | 168 - - 2 - | - - - 1.2 - | 209 - - 2 - | - - - 1.0 - | 210 - - - - | - - - - - | 216 - - - - | - - - - - | 222 - - - - | - - - - - | 209 - - - - | - - - - - | 165 - - - 1 | - - - 0.6 - |
| | +O | N G No L GON | 195 - 3 - - | - - 1.5 - - | 208 - - - - | - - - - - | 230 - - - - | - - - - - | 247 - - - - | - - - - - | 244 - - - - | - - - - - | 252 - - - - | - - - - - | 233 - - - - | - - - - - | 159 - - - - | - - - - - |
| BT EBA | O ₃ | N G No L GON | 32 - - 2 - | - - - 6.3 - | 39 - - 3 - | - - - 7.7 - | 43 - - 1 - | - - - 2.3 - | 36 - - - - | - - - - - | 38 - - - - | - - - - - | 27 - - - - | - - - - - | 34 - - - - | - - - - - | 20 - - - - | - - - - - |
| | +O | N G No L GON | 51 - - 8 - | - - - 15.7 - | 58 - 1 7 - | - - 1.7 12.1 - | 63 - - 8 - | - - - 12.7 - | 68 - - 1 - | - - - 1.5 - | 57 - - - - | - - - - - | 56 - - - - | - - - - - | 58 - - - - | - - - - - | 32 - - - - | - - - - - |

| TH | EBA | Sex | N | % | I1 | | I2 | | C | | P1 | | P2 | | M1 | | M2 | | M3 | |
|-----|-----|-----|----|----|-----|----|-----|----|-----|----|----|----|----|----|----|----|----|----|----|---|
| | | | | | N | % | N | % | ON | % | N | % | N | % | N | % | N | % | N | % |
| | | | | | | | | | | | | | | | | | | | | |
| TH | EBA | ♂ | N | 35 | - | 34 | - | 43 | - | 33 | - | 44 | - | 51 | - | 50 | - | 38 | - | |
| | | | G | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| | | | No | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| | | | L | 1 | 2.9 | 2 | 5.9 | - | - | - | - | - | - | - | - | - | - | - | - | |
| | EBA | ♀ | N | 15 | - | 22 | - | 31 | - | 32 | - | 36 | - | 36 | - | 30 | - | 18 | - | |
| | | | G | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | | |
| | | | No | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | | |
| | | | L | 1 | 6.7 | 1 | 4.5 | 1 | 3.2 | - | - | - | - | - | - | - | - | - | | |
| EBA | ♀ | N | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | | | |
| | | G | - | - | - | - | - | - | - | - | - | - | - | - | - | - | | | | |
| | | No | - | - | - | - | - | - | - | - | - | - | - | - | - | - | | | | |
| | | L | - | - | - | - | - | - | - | - | - | - | - | - | - | - | | | | |

At the PN site of Hakemi Use, although the frequency of AIDA is higher compared to PPNB and other PN settlements, almost all of the activity-induced dental grooves have been observed on the anterior dentition (table 4). However, it must be stated that this pattern was seen only in females. At Hakemi Use, only one male has a notch, another has LSAMAT, and another has two GON on his molars.

Few individuals of both sexes from the LN and C layers of Yumuktepe and Gülpınar have grooves and notches. Unfortunately, no, or few, human remains are available for these periods, both in Anatolia and beyond due to the decrease in sub-floor burials. Human remains from İkiştepe, Bakla Tepe, and Titriş Höyük have very few signs of AIDA (table 4). The frequencies of grooves on the anterior teeth of the Arslantepe females are comparable to those of the PN settlements. However, it must be remembered that the number of individuals, and especially of males, is small. Males from LC and EBA settlements only have LSAMAT, while few females have V, U, or semicircular shaped notches on the anterior dentition. Moreover, no interproximal grooves have been observed in the Late Chalcolithic and EBA populations.

TEMPORAL CHANGES OF AIDA

In order to understand diachronic changes of AIDA, differences in sample size have led us to combine populations of different cultural periods. The results suggest that AIDA frequency per tooth is very high in PPNA populations. Although all AIDA types have been observed in this period, occlusal grooves on the anterior teeth and GON of the posterior teeth are the most common types (table 5; fig. 3). In fact, although notches and LSAMAT have been observed in PPNA populations as well, their frequencies are lower. PPNB and PN populations present both types of grooves, however an important decrease occurs in the PPNB period. The PPNB and

PN settlements are characterized by a similar pattern, namely a decrease in the frequency of grooves, some notches and LSAMAT. With the transition to the LC-EBA period, AIDA frequencies decrease. There are observed some notches, very few GON, and almost no grooves. LSAMAT frequencies are similar to each other compared to other occupational and habitual abrasion types.

Based on these observations, it can be stated that AIDA frequency decreases in time and between different cultural periods. The most important changes have been recorded between the PPNA and PPNB periods, and later between LN and LC-EBA. Another important shift from the PPNA to EBA regards sex differences. In general, higher frequencies of AIDA have been observed in females. During the PPNA period, both males and females have similar frequencies and similar types of AIDA. It might be the result of the use of their dentition in similar occupational activities. During the PPNB and PN periods, a decrease of activity-related abrasions was seen in populations following an agricultural lifestyle. Moreover, during this cultural horizon, almost all activity-induced dental grooves have been observed in females. This may suggest an adverse effect at the beginning, and with the intensification, of agriculture on the increase of gender differences. In the LC and EBA, although AIDA has been observed in a few individuals, only females present notches and grooves on their dentition (fig. 4).

The number of teeth affected by AIDA per individual differ greatly over time. As seen in table 5, a common finding is of one AIDA per individual. Multiple AIDAs were only found on individuals of the PPNA period. The frequencies of multiple affected teeth decrease with time. Notches are mostly observed on one or two teeth according to the nature of the abrasion. However, in the case of LSAMAT, the involvement of multiple teeth has been observed in all chronological periods. No statistically significant differences exist between periods for LSAMAT (table 5). However, occlusal grooves and GON are

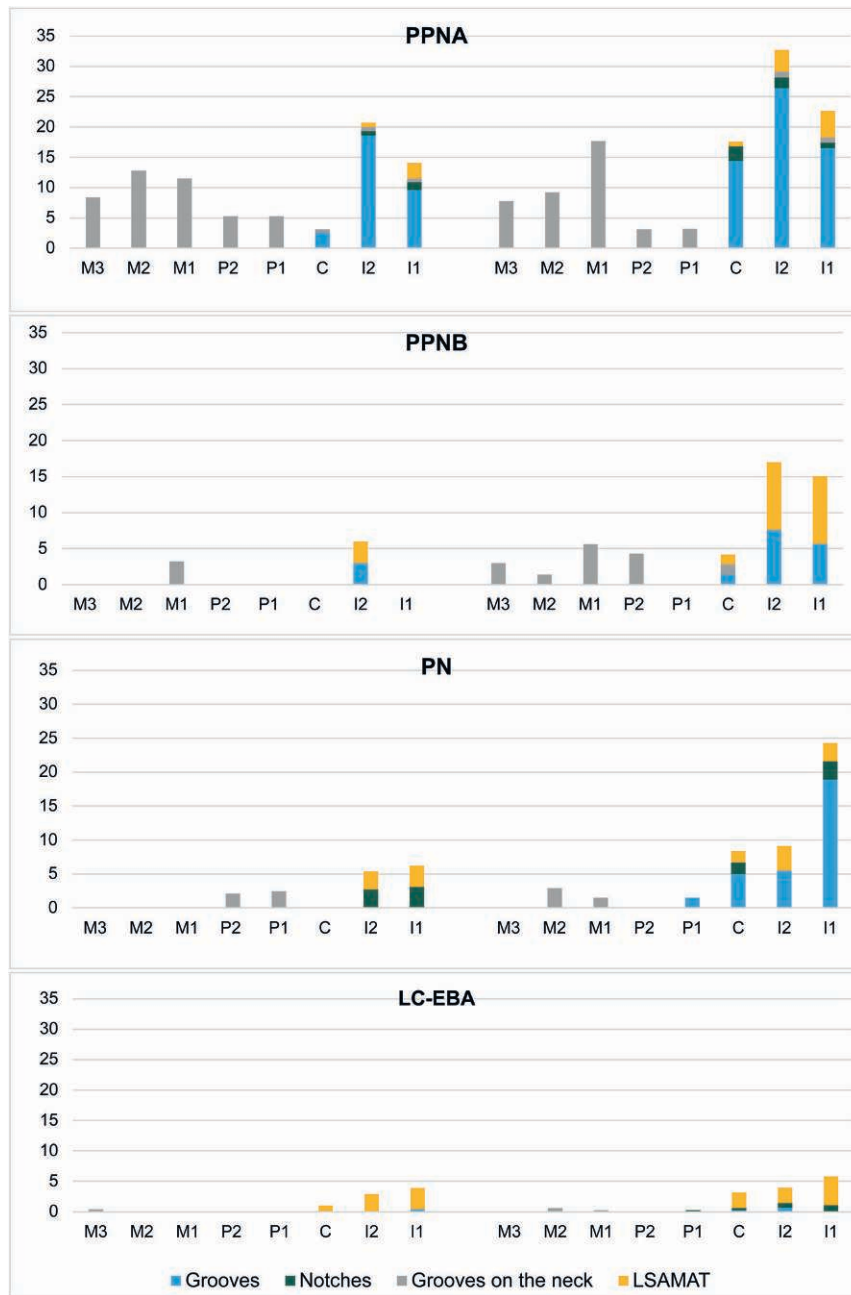


Fig. 3 – Types of AIDA in males and females in different cultural periods.

characterized by different patterns. The number of teeth with AIDA is very high among the PPNA sample populations. Occlusal grooves on one or more teeth have been observed only in PPNA individuals. A similar situation has also been observed for GON. A total of nine individuals have GONs on four teeth, in three individuals on five teeth, and in one

individual on 10 teeth. All multiple grooves and GON are observed in the PPNA period, except for one individual from the PN, and one from LC period. Diachronic differences in terms of GON and occlusal grooves are highly statistically significant (table 5).

Table 5 – Number of teeth in a mouth affected by different types of AIDA. **PPNA**: Pre-Pottery Neolithic Period A; **PPNB**: Pre-Pottery Neolithic Period B; **PN**: Pottery Neolithic period; **LC**: Late Chalcolithic; **EBA**: Early Bronze Age.

| Type of AIDA | Cultural Horizon | N | 1 | | 2 | | 3 | | 4 | | 5+ | | Statistics |
|------------------|------------------|-----|----|------|----|-----|---|-----|---|-----|----|-----|--|
| | | | n | % | n | % | n | % | n | % | n | % | |
| Occlusal Grooves | PPNA | 231 | 35 | 15.2 | 17 | 7.4 | 8 | 3.5 | 4 | 1.7 | 0 | - | χ^2 : 89.219* df: 12 p: 0.000 |
| | PPNB | 42 | 1 | 2.4 | 1 | 2.4 | 0 | - | 0 | - | 0 | - | |
| | PN | 70 | 4 | 5.7 | 2 | 2.9 | 0 | - | 1 | 1.4 | 0 | - | |
| | LC-EBA | 294 | 3 | 1.0 | 0 | - | 1 | 0.3 | 0 | - | 0 | - | |
| Notches | PPNA | 208 | 10 | 4.8 | 5 | 2.4 | 0 | - | 0 | - | 0 | - | χ^2 : 17.760* df: 6 p: 0.007 |
| | PPNB | 41 | 0 | - | 0 | - | 0 | - | 0 | - | 0 | - | |
| | PN | 70 | 3 | 4.3 | 4 | 5.7 | 0 | - | 0 | - | 0 | - | |
| | LC-EBA | 292 | 5 | 1.7 | 1 | 0.3 | 0 | - | 0 | - | 0 | - | |
| LSAMAT | PPNA | 164 | 3 | 1.8 | 4 | 2.4 | 1 | 0.6 | 1 | 0.6 | 0 | - | χ^2 : 16.990 df: 18 p: 0.524 |
| | PPNB | 39 | 0 | - | 0 | - | 1 | 2.6 | 1 | 2.6 | 0 | - | |
| | PN | 67 | 3 | 4.5 | 0 | - | 1 | 1.5 | 0 | - | 0 | - | |
| | LC-EBA | 293 | 5 | 1.7 | 4 | 1.4 | 0 | - | 1 | 0.3 | 2 | 0.6 | |
| GON | PPNA | 201 | 16 | 8.0 | 17 | 8.5 | 3 | 1.5 | 9 | 4.5 | 5 | 2.5 | χ^2 : 86.646* df: 21 p: 0.000 |
| | PPNB | 41 | 1 | 2.4 | 3 | 7.3 | 0 | - | 0 | - | 0 | - | |
| | PN | 69 | 2 | 2.9 | 2 | 2.9 | 0 | - | 0 | - | 0 | - | |
| | LC-EBA | 119 | 1 | 0.3 | 0 | 0 | 0 | - | 0 | - | 0 | - | |

DISCUSSION

This study has shown that abrasion types related to habitual activities and occupational behaviors differ widely from one cultural horizon to another. LSAMAT, notches, and grooves on the occlusal surface and on the neck have different etiologies and are the result of different types of dental usage. To interpret changes in daily activities, the different types of AIDA have been discussed separately and diachronically with respect to gender differences.

LSAMAT

It has been suggested that different types of activities such as eating and/or processing abrasive carbohydrate foods or fibrous tubers such as manioc, and sucking sugarcane result in LSAMAT (Turner and Machado 1983; Irish and Turner 1987, 1997; Watson and Haas 2017; Crane et al. 2020). Gripping abrasive materials between the maxillary anterior teeth and the tongue, as well as shredding or peeling some tough materials results in aberrant abrasions (Irish and Turner 1987). LSAMAT

is a frequent abrasion type in some regions of the New World and also in other parts of the world (i.e., Africa and Asia; Lukacs and Pastor 1990; Irish and Turner 1997; Porr and Alt 2006). Distribution of LSAMAT on the incisor and canines is similarly worldwide. In Anatolia, it is not typical for people to suck foods or peel vegetation using their mouths as much as prehistoric people of the Americas. Moreover, foods such as manioc did not grow in Anatolia and, thus, were not included among its main dietary sources. On the other hand, fibrous plants such as thistle, asparagus, and various plant shoots are sucked by traditional Anatolian people.

It is important to notice that the frequency of LSAMAT in Anatolia is low compared to other parts of the world, in which there is a close connection between LSAMAT and diet (Turner and Machado 1983; Irish and Turner 1987; Lukacs and Pastor 1990; Mickleburgh 2007). Even if food sources, dietary habits, and food preparation techniques changed from the Neolithic to the EBA (Irvine et al. 2019; Koruyucu 2019), the frequency of LSAMAT is similar in all analyzed cultural horizons. These data may suggest that LSAMAT was not resulted from dietary habits in Anatolia. In fact, the use of the anterior dentition as a third hand in some habitual activities (Irish and Turner 1987),

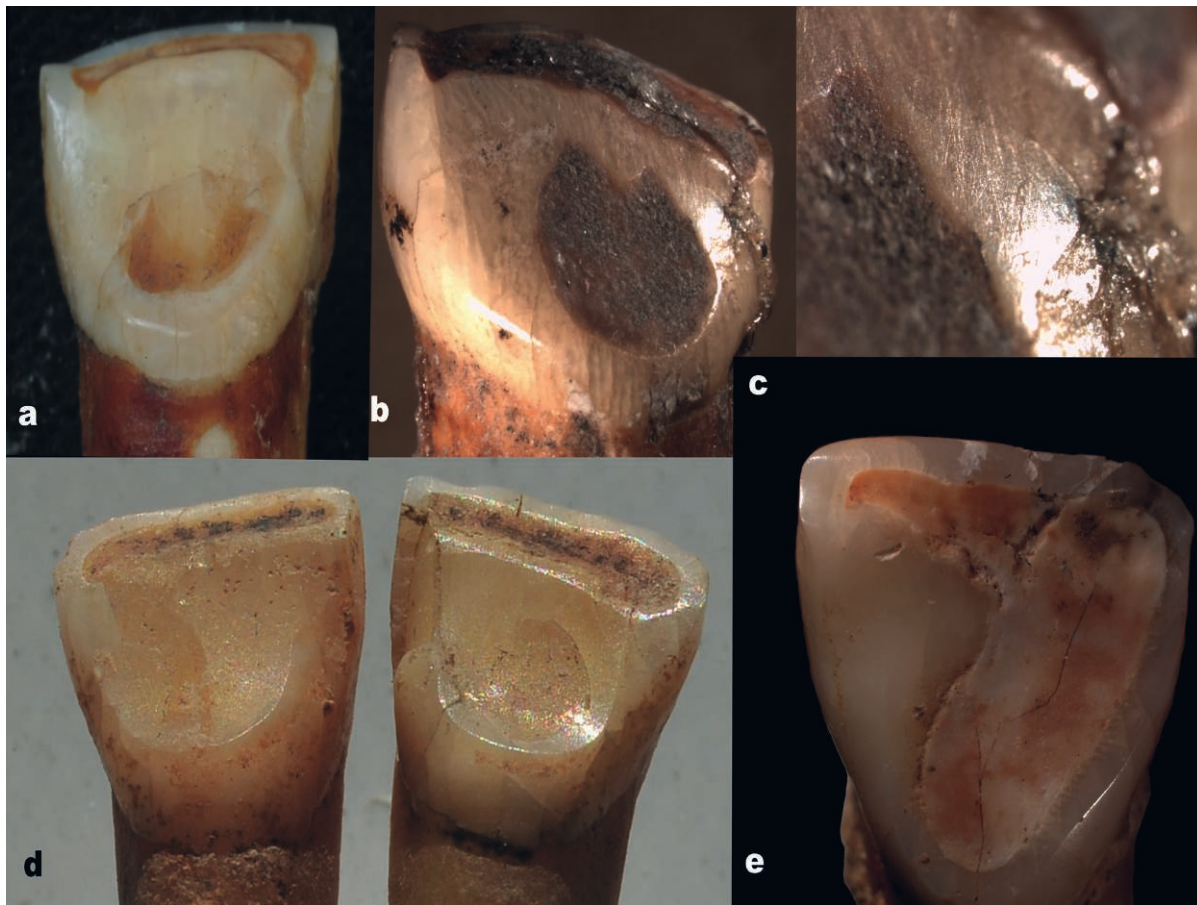


Fig. 4 – LSAMAT examples from different periods and settlements. **a:** A permanent incisor with a small groove developed on its distal corner; **b-c:** A deciduous incisor from Körtik Tepe and its close-up view; **d:** Central incisors from Arslantepe; **e:** Central incisors from Hakemi Use.

like leather processing (Pedersen and Jacobsen 1989), craft production, food processing (Lukacs and Pastor 1988), and the peeling of tough tubers (Mickleburgh 2007; Berbesque et al. 2012) represents other possible explanations for the causes of LSAMAT.

This type of aberrant wear has never been thoroughly investigated in Anatolian populations (fig. 4). This study in fact represents the first investigation that has considered this abrasion as well.² The presence of LSAMAT together with that of some dental grooves may suggest a multi-purpose use of teeth. Crane and colleagues (Crane et al. 2020) state that multiple etiologies of wear concurrently occur and interact in any given individual. This means that the development of the wear is affected differently and in multiple ways given that individuals

will be engaged in varied behaviors, and located in different time periods and regions. However, in Anatolia and beyond, no specific behavior seems to be directly connected with this type of aberrant wear. Though, the co-occurrence of occlusal grooves and LSAMAT may suggest a connection between these activities. Specific reasons behind this type of abrasion can only be understood by investigating both direct and indirect data such as subsistence activities, cultural patterns of the populations, and ethnographic data. Future, specifically detailed studies are required to understand the mechanism of LSAMAT in Anatolia.

NOTCHES

Based on contemporary research, it has been proposed that people with occupations such as tailor, carpenter, shoemaker,

2. Irvine et al. 2014 reported an unusual abrasion similar to LSAMAT on the labial surface of an incisor, possibly related to the pressing of leather or sinew during its preparation

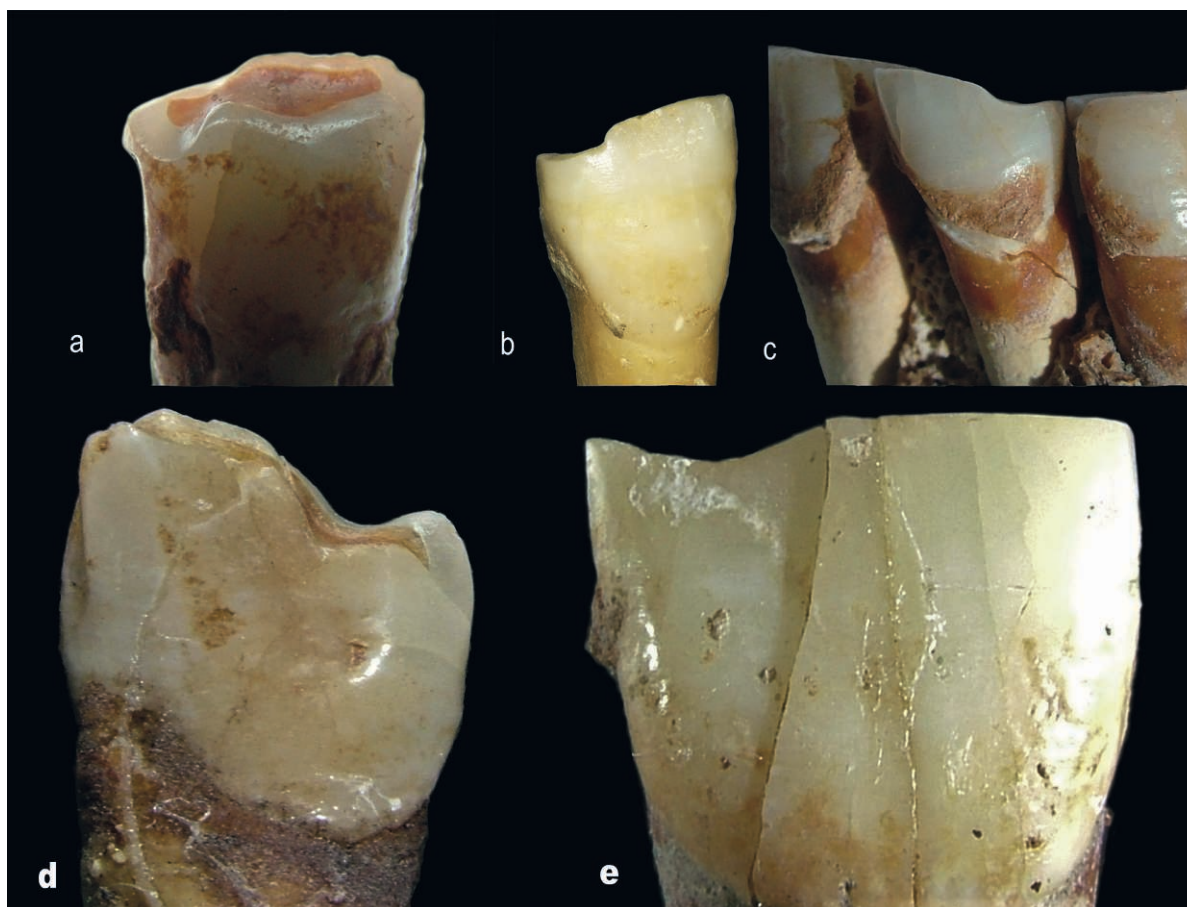


Fig. 5 – Labiolingually directed notches from different settlements. **a:** Lower canine from Körtik Tepe; **b:** Central incisor from Arslantepe; **c:** Lateral; **d-e:** Central incisors from Körtik Tepe.

and glass blower have dental notches. Behaviors such as pen biting and pipe smoking also result in the development of U- or V-shaped labio-lingually directed notches (fig. 5) on the related teeth (Pfeiffer et al. 1989; Ubelaker 1989; Hillson 1996; Anderson 2002; Walker and Henderson 2010). Moreover, holding nails (Turner and Anderson 2003) or tubes made of metal or reed (Angel 1968) are some of the behaviors proposed by bioarchaeologists that could result in dental notches. Gripping sinew, blood vessels, branches of trees, and the bark of plants such as willow or reed, might also cause notches on the teeth (Owsley and Bellande 1982; Merbs 1983; Blakely and Beck 1984; Pedersen and Jacobsen 1989; Alt and Pichler 1992; Turner and Anderson 2003). Furthermore, habitual eating behaviors like cracking seeds between the teeth are also responsible for notches (i.e., sunflower, pumpkin, and watermelon seeds; Alt and Pichler 1992; Bonfiglioli et al. 2004; Erdal 2008).

Similar to LSAMAT, notches are not a common type of abrasion in Anatolian prehistoric populations, with low frequencies of incidence (below 6%). Moreover, no PPNB individual has notches, and the number of teeth affected is also restricted by a maximum two teeth for all of the analyzed Anatolian sample population. Notches also have a low frequency of incidence in other parts of the world (Owsley and Bellande 1982; Merbs 1983; Blakely and Beck 1984; Alt and Pichler 1992; Turner and Anderson 2003). There are few publications that mention notches in Anatolia. Without any distinction from the occlusal grooves, Angel found that 16% of 77 EBA Karataş individuals had notches (Angel 1970). Özbek (Özbek 2000), in his publication on Öküzini, mentioned a notch on an isolated central incisor. Three teeth from LC Çamlıbel Tarlası have notches related to the working of fibers, yarn, and sinews, but the use of teeth also in lithic production and metallurgy cannot be ruled out (Irvine et al. 2014).

The size and shape of the notch seems to mostly be related to the biting or gripping of hard materials with the teeth. Notches on the anterior dentition of Anatolian prehistoric people might be related to the grasping of thicker objects when basket making, mat processing, bead and pendant production, preparing arrows, bows, and spears. It is also well known that these activities were very common during the Neolithic period. Almost all Neolithic and Chalcolithic sites have provided the remains of mats, as well as at many Near Eastern sites (Ryan 2011). Remnants of basket were found in some Anatolian sites such as Körtik Tepe, Çatalhöyük, Aşıklı, and Hakemi Use (Ryan 2011; Wendrich and Ryan 2012; Özbaşaran et al. 2018). Even though archaeological evidence of mat production and basket making using the anterior teeth like a pincher as part of the daily activities exists, they do not match with the habitual activities engaged by the majority of the population. Even if a small number of individuals was affected, the frequency of notches slightly decreased.

GROOVES ON THE NECK

GON are tunnel-shaped grooves that develop on the interproximal surfaces of the teeth, around the neck, but sometimes also on the root (fig. 6; Berryman et al. 1979; Frayer and Russel 1987; Brown and Molnar 1990; Lukacs and Pastor 1990; Frayer 1991). In many archaeological samples, GON are frequently observed on premolars, and especially on molars (Frayer and Russel 1987; Lukacs and Pastor 1990; Frayer 1991). One of the oldest examples was observed on an early *Homo* species (Ungar et al. 2001). However, despite its wide temporal and spatial distribution in populations, it is not overly common.

Some of the grooves on the neck related to abfraction are defined as erosion or corrosion of the dental hard tissue and generally related to gastroesophageal reflux. In fact, some diseases such as *anorexia nervosa* and *bulimia nervosa* may result in tissue loss, as well as the consumption of acidic foods and drinks (Mahoney and Kilpatrick 2003; Mulic et al. 2012). Similarly, in prehistoric populations, grooves on the neck have been interpreted as a result of saliva absorption or of vigorously swilling saliva or water in the mouth (Brothwell 1963; Pindborg 1970). Clinical studies suggest that the loss of dental hard tissue is the result of chemical processes mostly occurring in the crown rather than at the cemento-enamel junction. New studies have proposed a multifactorial etiology, namely a combination of occlusal stress, abrasion, and erosion proposed for abfraction. Nevertheless, this theoretical explanation has not yet been proved. Abfraction is frequently found on the

buccal surface, in few cases on the lingual, while no cases have been observed in the interproximal areas, as seen in archaeological populations (Sarode and Sarode 2013; González-Aragón Pineda et al. 2016). The frequencies of abrasion are not as high in Anatolian Neolithic settlements. The data presented here suggests that GON was not related to abfraction in Anatolian prehistoric samples.

SEM analyses on some of the reported interproximal grooves have displayed the presence of *striae* parallel to the longitudinal axis of the grooves (fig. 6; see also Waters et al. 2010). This may suggest a back and forth, or a unidirectional movement of materials across the surface of the tooth (Frayer and Russel 1987; Lukacs and Pastor 1990; Frayer 1991; Alt and Pichler 1992; Alt and Koçkapan 1993; Torres-Rouff 2003; Waters et al. 2010; Lorkewicz 2011). In fact, the use of a toothpick, likely a thin and pointed object of a hard material such as wood, bone or other hard substance repeatedly inserted between the teeth has been proposed as the most important cause of GON (Frayer and Russel 1987; Lukacs and Pastor 1990; Frayer 1991). Habitual activities like cleaning food remains from between and around the teeth can cause abrasions in the form of interproximal grooves in Anatolian Neolithic people (Ubelaker et al. 1969; Wallace 1974; Berryman et al. 1979; Lukacs and Pastor 1990; Bermudez de Castro et al. 1997).

However, statistical analyses demonstrate a close connection between the presence of grooves or notches on the anterior dentition and GON in Anatolian populations (Spearman's correlation: 0.825, P: 0.000). Ethnographic data from Australia and Pakistan has revealed that non-alimentary activities such as pulling fibers between the teeth and processing sinews or fibrous materials might result in GON (Schulz 1977; Blakely and Beck 1984; Brown and Molnar 1990; Lukacs and Pastor 1990). Even if there is no proof for the use of the teeth in yarn production, as suggested by Brown and Molnar, and also by Lukacs and Pastor (Brown and Molnar 1990; Lukacs and Pastor 1990), an implicit connection between different types of AIDA exists. Their frequency in Anatolia is high in the PPNA and PPNB settlements, and *in primis* in Körtik Tepe. Furthermore, grooves on the anterior teeth, and interproximal grooves have similar patterns of incidence, with both tending to decrease simultaneously. Each individual with occlusal grooves does not necessarily have GON, but conversely the presence of GON is frequently accompanied by occlusal grooves. Hence, the co-occurrence of these two types of grooves may suggest their implicit connection. Indeed, this concurrence has been observed not only in Anatolia but also in other settlements worldwide (Bocquentin et al. 2005;

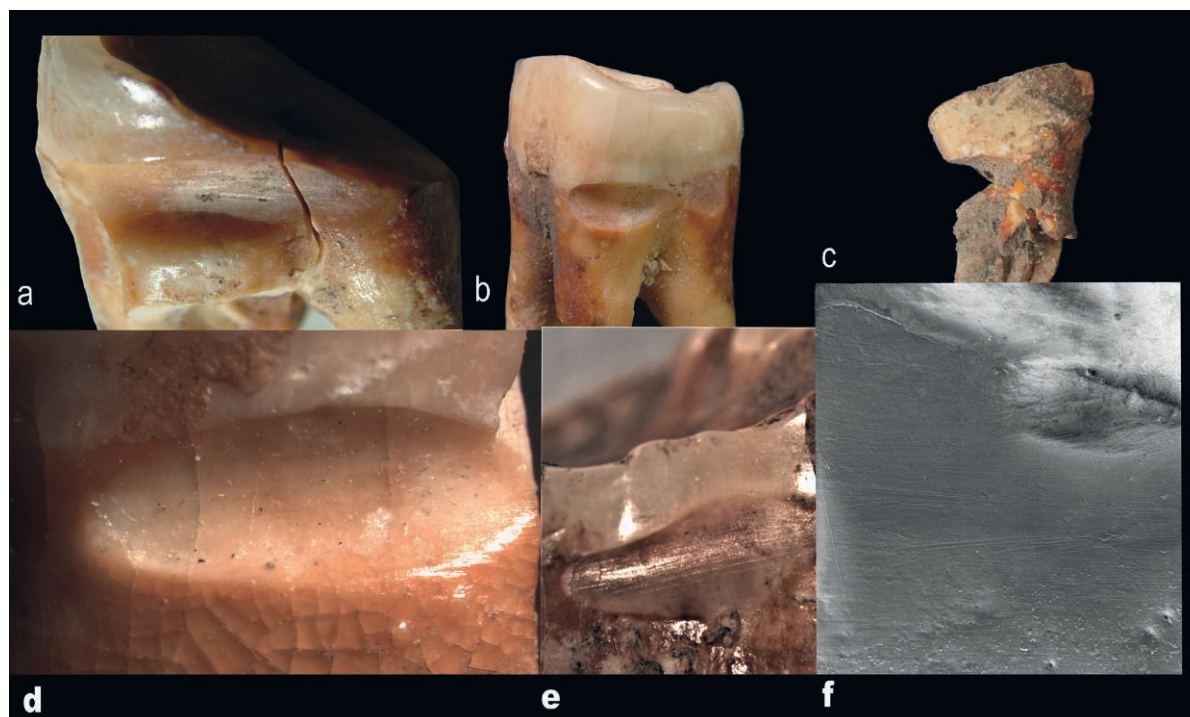


Fig. 6 – *a-e*: Deep grooves on the neck from Körtik Tepe; *a, c*: Almost half of the crown was cut by a groove related to a habitual activity; *e-f*: A close up view of a GON and a SEM image showing striae parallel to the long axis of the groove.

Waters-Rist et al. 2010; Lorkiewicz 2011; Watson and Haas 2017). As well known, the non-alimentary usage of teeth accelerates their abrasion, especially of those individuals involved in daily activities. Severe abrasions result in enlarged interdental spaces that require habitual probing by toothpicks with the purpose of cleaning stuck food. These enlarged spaces are in turn more suitable for the insertion of fibrous materials involved in production activities.

OCCLUSAL GROOVES

Narrow, shallow, and long grooves on the cutting surface of one or more anterior teeth have been considered in this group (Erdal 2008). It is generally accepted that dental grooves are related to different types of occupation such as spinner, carpet or rug maker, wicker, tailor, carpenter, fisherman, etc. Occlusal grooves on the anterior dentition are interpreted as the result of different types of manufacturing processes such as the production of cords and yarns from plant and animal fibers, the processing of sinew and small intestines, and stripping branches of the plants' fibers (Schulz 1977; Larsen 1985; Pedersen and Jacobsen 1989; Erdal 2008; Lorkiewicz 2011).

Teeth have also been used when weaving mats, rugs, carpets, and clothing, making baskets, nets and traps, and the working of leather (Cybulski 1974; Schulz 1977; Larsen 1985; Molleson 1994; Larsen et al. 1998; Minozzi et al. 2003; Bocquentin et al. 2005; Lorkiewicz 2011). The use of teeth in the production of a huge number of products made from different materials have been observed in different times and parts of the world and represented by different types of grooves (fig. 7). Thus, due to the wide variety of occupations that might have caused this type of abrasion, it is not possible to identify a specific causative behavior in such a broad time and space (Buikstra and Ubelaker 1994). However, archaeological, ethnographic and historical data may provide significant evidence (Turner and Anderson 2003; Erdal 2008; Stojanowski et al. 2014).

Yarn, cord, and end products from plant and animal fibers

The production, and the use, of threads or cords is known worldwide from the Upper Paleolithic period. The production and handling of strings from vegetable fibers and/or animal tissues in Anatolia is also quite old (fig. 8). The earliest known



Fig. 8 – Signs of mat, loose and fine woven fabrics. **a:** Reed phytoliths found on the back side of a skeleton from Hakemi Use; **b:** Red and black dyes on human bones resembling the weave of a fabric; **c:** Traces of phytoliths on the femur of an infant from Körük Tepe; **d:** An extremely rare case of fabrics from Körük Tepe; **e:** An extremely rare case of fabrics from Aşıklı Höyük.

mats and fabrics. Similar perforated stones were found at Hasankeyf and Demirköy. It can be stated that some of the grooves or notches observed on teeth dated to the Neolithic period may be related to the manufacture of the above-described objects. According to Alpaslan-Roodenberg (Alpaslan-Roodenberg 2001, 2008), grooves on teeth are probably related to weaving and baskets making, as part of domestic production. The discovery of needles and *spatulae* in the Late Neolithic layers prove the presence of weaving activities as well (Tekin 2013). At İkitztepe, yarn and textile production played an important role. Many of the burnt buildings excavated at İkitztepe contained hundreds of loom weights that suggest the existence of yarn and textile production from at least the Late Chalcolithic period. Differences in the types and sizes of spindle whorls may also suggest possible changes in the techniques of yarn production and other manufactured goods from

the Late Neolithic period onward (Barber 1991; Harlow et al. 2015). Progressive changes in the applied techniques led to a decrease of the necessity to employ teeth in craft production. This decrease probably reached its peak with the advent of metallurgy.

Fishing: A Probable Explanation

It seems that gathering and hunting were more important subsistence activities than fishing during the Neolithic period in Anatolia. As explained above, together with the production of baskets, mats, sacks and bags required in a hunter-gatherer lifestyle, it is very likely that teeth were used as a third hand in activities related to the production of arrows, bows, spears, harpoons, maces, and sickles. Nevertheless, fishing appears to be less known among the prehistoric populations of Anatolia.

Schultz (Schultz 1977) documented the presence of occlusal grooves in all adults of a prehistoric population of fishers in California. He noted that although a wide variety of activities might have produced the grooves, the preparation of plant fiber cordages for fishing nets was the most probable. Waters-Rist (Waters-Rist et al. 2010) stated that, unlike the populations living near the Baikal Lake, settlements located on the riversides commonly used their teeth for the production of nets and, more in general, for fishing activities. Similar observations have also been reported in Lorkiewicz's study (Lorkiewicz 2011). Many researches have emphasized the correlation between fishing activities and dental grooves (Schultz 1977; Larsen 1985; Waters-Rist et al. 2010; Coşkun et al. 2011). Thus, it can be concluded that along with weaving activities and the production of nets or baskets necessary for fishing, dental grooves can be the result of many other daily activities and tasks related to various productions.

Archaeological and bioarchaeological data support the hypothesis that the exploitation of aquatic/riverine sources was important at Körtik Tepe, Demirköy, Hasankeyf Höyük, Çayönü, and Aşıklı. More generally it can be said that riverine sources had a very important role in the broad spectrum of dietary patterns of Early Neolithic communities living on the banks of a river. Indeed, thousands of freshwater fish remains were found at Körtik Tepe, Hasankeyf Höyük, and also Aşıklı (Coşkun et al. 2011; Miyake et al. 2012; Itahashi et al. 2017). Moreover, fishhooks and harpoons were discovered at Körtik Tepe (Coşkun et al. 2011). Özbek (Özbek 2012), and Koruyucu et al. (Koruyucu et al. 2018) have highlighted the close relationship between auditory exostosis and regular exposure to cold water, fishing, and aquatic activities in the Early Neolithic populations of Anatolia. Stable isotope analysis of amino acids of human bone collagen conducted by Itahashi (Itahashi et al. 2017) on the samples of the Early Neolithic settlement of Hasankeyf, as well as zooarchaeological data, have confirmed the important role of freshwater fish consumption. Similar observations have been made for Körtik Tepe as well (Benz et al. 2016). These kinds of data suggest the significance of fishing during the Early Neolithic period in Anatolia and beyond (Coşkun et al. 2011).

Nevertheless, contrary to the aforementioned, archaeological data and stable isotope analysis of the Hakemi Use sample population have shown that fishing did not play an important role in daily life and in the nutritional dietary habits (Itahashi et al. 2019). In fact, stable isotope analysis has revealed that protein consumption (and thereby nitrogen values), especially from fish derived proteins, was significantly reduced. It is well known that radical changes occurred in dietary and subsistence

patterns during the Neolithic period. A broad spectrum of nutritional sources was replaced by a narrow dietary pattern based on domesticated cereals and animals (Irvine et al. 2019). Together with this new nutritional model, production-consumption relations seem to lose their importance in the settlements located near the sea (i.e. İkiztepe and Bakla Tepe) following the Late Neolithic. These revolutionary changes appear of great importance for better understanding the reduction in aberrant grooves. In fact, changes in the lifestyle and in the production-consumption systems had direct or indirect effects on the decrease in aberrant wear in Anatolia.

Temporal Changes

Dental grooves have been observed in many prehistoric populations such as the Natufian hunter-gatherers (Minozzi et al. 2003; Bocquentin et al. 2005; Eshed et al. 2006), at the Early Neolithic site of Abu Hureyra in the Near East (Molleson 1994), at Wandersleben in Thuringia (Alt and Pichler 1992), and among the Neolithic populations of Siberia (Waters-Rist et al. 2010) and Poland (Lorkiewicz 2011). They have also been reported in other prehistoric contexts worldwide, such as among the communities of California (Schulz 1977), in the Western Great Basin (Larsen 1985), in pre-contact British Columbia (Cybulski 1974), among the Cherokee Indians (Owsley and Bellande 1982), in the Caribbean (Larsen et al. 1998), and in Africa.⁴ Data shows that in many communities of the world, activity-induced dental abrasions reduce over time. Anatolia is one of the best geographical contexts that diachronically show this decrease together with the development of technology.

As mentioned before, the recent history of humanity represents a period in which rapid, but gradual cultural changes occur. These changes, such as the transition from seasonal mobility to permanent settlements, the domestication of plants and animals together with the exploitation of wild species, and a shift from a broad spectrum of food resources to a narrow range of domesticated food resources, pottery production, the introduction of terracotta and woven containers, the development of metallurgy, a fully accomplished whole range of artifacts, long distance trade and mobility, the formation of centralized administrative systems, organization of labor, surplus production, controlled production and reproduction, inequality, and warfare, can be considered as the most significant (Özdoğan 2014; Sagona and Zimansky 2015; Frangipane

4. Early Holocene hunter-gatherers from central Sahara, see Minozzi et al. 2003.

2017, 2018a; Irvine et al. 2019). The effects that these rapid and radical shifts have had on daily activities, dietary habits, and body composition have been widely investigated (Özbek 2004; Eshed et al. 2006; Larsen 2015; Irvine et al. 2019; Larsen et al. 2019). The decrease in AIDA frequency cannot be directly connected to one of these multiple socio-economic, cultural and political changes. Nevertheless, the effects of these radical changes may be directly observable in the form of technological and cultural development, for instance, in craft specialization and in more complex production processes, and in the social role of people. One of these changes can be observed in the roles of women and men in the production processes and the increase in division of labor based on gender.

Labor Differences by Gender

Occlusal grooves have been observed exclusively in males at several sites, two of which are the Western Great Basin (Larsen 1985) and Uan Muhuggiag, Libya (Minozzi et al. 2003). Another example is the Russian Late Neolithic-Bronze Age river site of Ust'-Ida I (Waters-Rist et al. 2010). As attested by many other studies, AIDAs have been observed in both sexes, but with higher frequencies in females (Angel 1968, 1970; Schulz 1977; Larsen et al. 1998; Bocquentin et al. 2005; Mickleburgh 2007; Waters-Rist et al. 2010). This study shows how gender differences existed in Epipaleolithic hunter-gatherer-fisher populations of Anatolia, and became more evident with the domestication of plants and animals in the early stages of agriculture. AIDA, and especially occlusal grooves, became a connotative trait of females in intensive agricultural communities. Similar results have been obtained for the Late Neolithic and Chalcolithic populations of Barçın, Meneteşe, and Aktopraklık (Alparslan-Roodenberg 2001, 2008). The present data suggest that males and females might have similarly used their teeth as tools in the early periods of sedentism, while gender differences seem to exist in the later PN and C periods, as no occlusal grooves have been observed in males.

It seems that teeth were not frequently used in such a way that resulted in the development of abrasion, in the form of grooves, in the LC and EBA Anatolian populations. Only some females have notches on their teeth. Ethnographic and archaeological data prove that gender differences in dental grooves exist worldwide and in different chronological periods (Cybulski 1974; Molleson 1994; Mickleburgh 2007; Erdal 2008; Waters-Rist et al. 2010). Anatolian settlements present important evidence of gender differences with regard to the previously mentioned occupations, especially for the Neolithic and

Chalcolithic people. It is clear that one of the most important results of this study is not only the decrease of AIDA frequencies with time, but also the increase in sex differences related to the use of teeth as a tool, and to habitual activities, the mode of production, gender, and social status. In ancient populations, production is a controversial subject matter in terms of both gender-based divisions of labor and social status. In this debate, the perception that domestic work done by women is trivial is notable. Some studies proposed a gender-based division of labor in the textile production (Asher-Greve 2008). Ethnographic studies support this approach as well. Also, this study encourages the hypothesis of a gender difference in the use of teeth as a tool in prehistoric Anatolia. Meskell (Meskell 2000) stated that the construction of women's and men's roles and identities is a relational process through which gender and sexual identities are constructed. Based on the data, and on that coming from skeletal materials, such as osteoarthritis, trauma, and burial customs (Erdal 2004; Erdal and Erdal 2012; Erdal 2015), it is possible to argue that gender differences were very weak among the first sedentary populations and increased over time in Anatolia. This differentiation supports a gender-based specialization in production. Craft specialization, which is an indicator of social complexity and of the development of hierarchical social organizations, was also an important factor in the consolidation of gender differences in Anatolia.

CONCLUSION

This study shows that the presence of AIDA in a mouth (observation per individual) cannot reflect the usage of teeth as a tool in detail. In fact, each tooth in a mouth has to be analyzed in terms of the type(s) of AIDA. Another important result achieved in this study is the detection of direct or indirect relations between occlusal grooves, GON, and (possibly) LSAMAT. These relations suggest a parallel decrease in the incidence of occlusal and interproximal grooves with the transition from a hunter-gatherer-fishing lifestyle to an agricultural one. The necessity to use teeth as a third hand in occupational activities and habitual behaviors weakened with the development of technology, craft specialization, and the increase of social complexity. This decrease is more evident in males. In fact, despite the decrease in the frequency of teeth used as a tool, it is important to highlight that women partially continued to employ their teeth during craft manufacturing, while men were not involved in such activities because their role in craft specialization and within society changed.

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DIETARY PRACTICES, CULTURAL AND SOCIAL IDENTITY IN THE EARLY BRONZE AGE SOUTHERN CAUCASUS: THE CASE OF THE KURA-ARAXES CULTURE

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Abstract. *Food and its interactions with the environmental, economic, social, and cultural spheres play an essential role in communities' cultural identity. This theory has been verified by an analysis of the Kura-Araxes (KA) culture, characterised by original cultural developments, which spread in the South Caucasus around the middle of the fourth millennium BC. This research aims to study the variability of dietary choices at the individual and population levels by analysing stable isotopes of carbon and nitrogen ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$). To monitor regional and diachronic changes in dietary patterns, we performed analysis on human, animal, and plant materials ($n = 144$) from eight KA highland and lowland sites in Georgia, Azerbaijan and Armenia compared with data ($n = 39$) from Post-KA sites already published (Herrscher et al. 2016, 2018b). Isotopic data show no significant differences with altitude. The KA diet is characterised by higher consumption of herbivore meat than pork and higher barley consumption than wheat. No relationship with age at death, sex, and burial traits were observed, suggesting "equal" access to food among community members. Human low isotope variability shows persistence over KA's entire duration (3,500-2,500 BC), while it is significantly different between KA and Post-KA subjects. The results confirm the homogeneity of KA communities' food practices that reinforces the theory of a "strong cultural identity" of the KA populations.*

Résumé. *L'alimentation et l'ensemble des interactions qu'elle entretient avec les sphères environnementale, économique, sociale et culturelle jouent un rôle important dans l'identité culturelle des communautés. Cette théorie a été vérifiée par une analyse de la culture Kuro-Araxe (KA), caractérisée par des développements culturels originaux, qui s'est répandue dans le Caucase du Sud vers le milieu du quatrième millénaire avant notre ère. Cette recherche vise à étudier la variabilité des choix alimentaires, aux niveaux individuel et populationnel, par l'analyse des isotopes stables du carbone et de l'azote ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$). Afin de suivre les changements régionaux et diachroniques des modes alimentaires, des analyses ont été réalisées sur des matériaux humains, animaux et végétaux ($n = 144$) provenant de sites d'altitudes différentes, huit en Géorgie, deux en Arménie et un en Azerbaïdjan et comparées à des données ($n = 39$) provenant de 4 sites Post KA de la région déjà publiées (Herrscher et al. 2016, 2018b) Les données isotopiques ne montrent aucun changement significatif avec l'altitude. L'alimentation KA se caractérise par une plus grande consommation de viande d'herbivore que de porc et une plus grande consommation d'orge que de blé. Aucune relation avec l'âge au décès, le sexe et les traits funéraires n'a été observée, ce qui suggère un accès « égal » à la nourriture entre les membres des communautés. La variabilité isotopique humaine montre une persistance sur toute la durée du KA (3500-2500 avant J.-C.), tandis qu'elle est significativement différente entre les sujets KA et Post KA. Les résultats convergent pour confirmer une homogénéité des pratiques alimentaires des communautés KA qui renforce la théorie d'une « forte identité culturelle » des communautés KA.*

Keywords. *Southern Caucasus, Early Bronze Age, Kura-Araxes, diet, bioarchaeology, carbon and nitrogen*

Mots-clés. *Caucase du Sud, début de l'âge du Bronze, Kuro-Araxe, régime alimentaire, bioarchéologie, carbone et azote*

INTRODUCTION

The differentiation of diets reflects the subsistence strategies resulting from the socio-economic systems' adaptation to the nutritional/edible resources available in specific environments. However, food cannot be considered exclusively as an ecofact (Parker Pearson 2003). Instead, food should preferably be evaluated as an interface between nature, society, and culture (Hastorf 2017: 17). The production, processing, preparation, and consumption of food are deeply entwined with economic and political "realities" (Twiss 2007: 2, 2012) and are thus actively operating in all societal processes (Hastorf 2017: 3). Food embodies significance as a means of reproduction and, at the same time, an expression of social and cultural realities. Also, food has the symbolic "power" to define cultural boundaries and different identity levels (Twiss 2007: 3-4, 2012; Hastorf 2017). The famous quote "Tell me what you eat, and I will tell you what you are," from the gastronome J. A. Brillat-Savarin, later echoed by the German philosopher Ludwig Feuerbach, emphasises the powerful symbolic role that dietary practices, as collective and ritualised performances, and food, as the nourishing material symbol that we incorporate daily, are actively participating in the construction and reproduction of both individual and collective identities, as well as in shaping group membership, differentiation, and exclusion (Twiss 2007: 1-2, 2012; Hastorf 2017: 3). With their well-codified material assemblage related to food preparation and consumption, the Kura-Araxes (hereafter KA) culture is an excellent case to test the hypothesis that cooking and food may unconsciously reveal the structure of a society (e.g., Levy-Strauss 1968) and potentially explain the structuring of a shared socio-cultural identity (Greenberg 2007: 266). This research aims to offer new insights to the discussions on KA life, socio-economic practices, and cultural identity using stable carbon and nitrogen isotope ratios analysis of human and faunal skeletal as well as botanical remains in the geographical context of the southern Caucasus.

The Caucasus, located between the Black Sea to the west and the Caspian Sea to the east, links Europe to Asia through the Great Caucasus mountain. This region is characterised by a mosaic of environments due to a strong climatic west-east gradient (humid subtropical to semi-arid continental) combined with an effect of the altitudinal gradient (sea level at over 5,000 m). In the middle part of the Kura River, the climate favors temperate grasslands, while eastward, in the Kura and Araxes valleys, the open steppes of the lowlands have a drier climate (Decaix 2012). In the middle Araxes River and

adjacent uplands, the climate leaves more wooded and humid vegetation. Paleoenvironmental data agree on a clear improvement of the climate between the Neolithic and the Bronze and Iron Ages, with different types of environment in different areas. The plain around the Kura and Araxes valleys appears to have retained its steppe character over time with the presence of Chenopodiaceae, Amaranthaceae, and Poaceae (Messenger et al. 2016, 2020). Several species of these steppe plants are C₄ plants that may have impacted the diet of the herds, leaving a C₄ footprint not necessarily due to millet consumption, which is only attested from the Middle Bronze Age in the South Caucasus (Herrscher et al. 2018a, 2018b; Martin et al. in press).

ON THE KURA-ARAXES CULTURAL TRADITION

CHRONOLOGICAL CONTEXT

The Kura-Araxes (ca. 3,500-2,500 BC) is one of the most durable and extensive cultural traditions in the Ancient Near East. Emerging and developing in the South Caucasus as early as the mid-4th millennium, the KA culture broke its pristine geographic boundaries and spread across wider areas towards the end of the fourth millennium. By the second quarter of the 3rd millennium BC, various elements of the Kura-Araxes repertoire are found throughout Anatolia, the South Caucasus, the Iranian plateau and the Levant (e.g., Sagona 1984, 2018; Palumbi 2008, 2016; Greenberg and Goren 2009; Chataigner and Palumbi 2014). This "expansion" has resulted from and involved complex dynamics and processes of cultural transmission in which human mobility and migration played a part (Greenberg and Goren 2009; Paz 2009; Batiuk 2013; Greenberg and Palumbi 2014; Rothman 2015). While the KA cultural phenomenon is highly distinctive, its expressions are not always uniform, and appear to represent multiple communities that shared many, but not all, material elements and traditions (Paz 2009; Palumbi and Chataigner 2014; Sagona 2018). Around the mid-third millennium, the KA communities disappear and their cultural traditions rapidly dissolve. The dynamics and factors behind this process are puzzling, but the changes that followed were sharp and radical in all terms. The conservatism of the Kura-Araxes ceramics gives way to new ceramic horizons (Martqopi and Bedeni). The stability of the Kura-Araxes villages is replaced by evanescent and flimsy traces of what appear short-lived and temporary occupations.

In the frame of the generalised adoption of a new mobile lifestyle, the, often very imposing, funerary mounds (kurgans) become new and more permanent landmarks of the landscape. Wooden wagons, as well as impressive concentrations of metals and golden jewelry contained in some of these kurgans (Makharadze et al. 2016) hint at the emergence of élites and hierarchised communities as well as at the new role that production, circulation and accumulation of metals played in constructing vertical inequalities among the so-called “Early-Kurgans” societies.

DAILY LIFE: SETTLEMENT PATTERNS AND AGRO-PASTORAL STRATEGIES

The KA communities were the first to live permanently in the mountains and highlands of the South Caucasus. It is still unclear if the process of sedentarisation in the mountains was the result of warmer and more stable climatic conditions (Connor and Kvavadze 2014) and/or to the adoption of new subsistence strategies. Both lowland and highland communities lived in small villages composed of small domestic units (with the exception of some small, and possibly communal, shrines). In spite of the large regional variability of architectural plans and building materials, the KA houses featured a recurrent set of principles related to the activities carried out in their interiors. Not only did KA houses host subsistence and production activities, but the spatial and symbolic centrality of the fire-places, trefoil-shaped hearths and anthropomorphic and zoomorphic andirons suggests that these fire-installations, were also the symbolic foci of ritual practices, beyond being the centre of cooking activities (Sagona 1998; Smith 2015). As to the “ingredients” that could have been consumed in the KA houses, archaeobotanical and archaeozoological data provide useful data to reconstruct diets and subsistence strategies. While in the past a strong pastoral and mobile connotation was suggested, both archaeobotanical and faunal data show that the KA communities were leading a settled type of lifestyle founded on an integrated agro-pastoral economy (Longford 2015; Sagona 2018; Decaix et al. 2019). The former data show that in comparison to the more diversified Chalcolithic and Neolithic agriculture recording a higher frequency of pulses (Hovsepian 2015; Longford 2015), the KA groups mainly practised cereal-focused agriculture, with barley and wheat representing the most cultivated crops (Hovsepian 2015; Longford 2015; Messenger et al. 2015; Decaix et al. 2019). While barley often predominated in the upland settlements, wheat

also played an important role at some sites (Longford 2015; Decaix et al. 2019) and it has been suggested that this wheat-barley changing ratio could have been a strategy of the KA farmers aimed at minimising risks of crop failure (Hovsepian 2015; Sagona 2018). Conversely to agriculture, the KA animal husbandry strategies were more diversified and did not show a uniform regional trend (Decaix et al. 2019). In general, caprines were the most common reared species (with sheep usually outnumbering goats); however, a higher incidence of, and preference for, cattle can be observed at some sites, while pigs were rare and mainly reared in the plains (Badalyan et al. 2008; Badalyan et al. 2014; Sagona 2018; Decaix et al. 2019; Samei et al. 2019). These data point to an absence of specialised husbandry strategies among the KA communities which, by means of diversification of the reared species seem to aim at herd security management and risk minimisation strategies (Samei et al. 2019). Similar strategies were also deduced from kill-off patterns focused at once on the maintenance of herd security and on the exploitation of meat rather than on specific secondary products (Piro 2008; Badalyan et al. 2014; Samei et al. 2019).

A NEW CERAMIC TRADITION FOR NEW FOOD-WAYS?

Ceramics are among the most “diagnostic” components of the KA culture (fig. 1A). In comparison to the Chalcolithic pottery, the “new” KA ceramics embodied a radically different *chaîne opératoire* and morphological repertoires (Sagona 2014). A significant investment in terms of time and labour for an accurate burnishing and polishing of the surfaces conferred a very distinctive shiny appearance to the Kura-Araxes ceramic containers thus enhancing their aesthetic impact (Iserlis 2009; Iserlis et al. 2015). Simultaneously, the contrastive red-black pattern between the exterior (black) and interior (red) surfaces which became an aesthetic “hallmark” of the KA ceramics, might have strengthened, as proposed by Greenberg (2007), symbolic connections between colour codes and vessels functions. All this could have aimed at “structuring the cultural attitudes to food and cooking” (Greenberg 2007) which reinforced the KA cultural identity throughout the large geographical area (Iran, East Anatolia and the Levant) involved in the expanse of this tradition. As a whole, the new aesthetics may stress a new role and meaning that the KA ceramics acquired in the frame of food-related practices. As to the latter, the KA containers also featured a very original morphological



Fig. 1 – **A.** Kura-Araxes ceramics of the second half of the fourth millennium (Phase KA I). *a.* Karnut; *b.*, *e.* Elar; *c.* Mentesh Tepe (after Lyonnet and Guliyev 2012; *b.*, *c.*, *e.* at the same scale); *d.* Gegharot (photo © R. Badalyan). **B.** Individual #669 excavated in the KA collective burial at Gegharot (T2E.662; photo © R. Badalyan).

repertoire. Tall-necked jars with ovoid bodies, large S-shaped bowls and circular lids are among the most common shapes to appear from the earliest stages of the KA tradition and represented a very distinctive and quite standard cooking-assemblage. The latter was significantly different from those of the Chalcolithic period and points to the emergence of new (and possibly different) practices related to the preparation, cooking and consumption of food. On this note, T. Wilkinson has suggested that the appearance of lids and the frequent occurrence of jars in the KA repertoires point to a shift in the alimentary practices, possibly more focused on boiling, stewing or steaming of foods than they were in the Chalcolithic period (Wilkinson 2014). Notwithstanding the diachronic regionalisation of the repertoires and decorative styles, a series of aesthetic, morphological and functional traits remained basically stable throughout the whole duration of this tradition (Badalyan 2014). Did this conservatism mirror a precise set of codified food-related functions that the KA vessels performed over time?

FUNERARY TRADITIONS

The funerary contexts, from which all the anthropological materials analysed in this paper derive, provide insightful data on both cultural variability and on the organisational principles of the KA society. Different types of structures, such as pit

burials, stone-cists, stone constructed, horse-shoe shaped, kurgans and catacomb tombs express highly diversified funerary traditions (Sagona 2004; Poulmarc'h et al. 2014). Similarly, the presence of both single and multiple inhumations (sometimes in the same cemetery), as well as primary and secondary burials (sometimes in the same tomb) testify to very diversified practices and choices related to both funerary recruitment and treatment of the bodies (fig. 1B; Poulmarc'h et al. 2014). In spite of this high variability two main “structuring” concepts were observed. First, there is a narrow range of not abundant grave-goods, usually including ceramic vessels, spindle-whorls, lithic tools and metal artefacts. The latter is usually limited to few body ornaments (double-spiral headed pins and hair-spirals are among the most common ones) but large concentrations of metals in the same tomb are usually very rare. As already pointed out (Palumbi 2007, 2008; Smith 2015), the restricted variability and the small quantities of the grave goods communicate a strong sense of repetitiveness and standardisation of the funerary practices that, altogether with the lack of concentrations of prestige items, emphasise a highly prescriptive and egalitarian funerary ideology.

Second, though single burials were a common practice, multiple burials are also found, possibly enlightening on another important concept structuring the social organisation of these communities. The number of people buried in the same funerary structure is highly variable, ranging from a few to several dozens of individuals as in the case of the kurgans in

Western Azerbaijan (Poulmarc'h et al. 2014; Laneri et al. 2020). Moreover, these multiple tombs hosted people of both sexes and of different classes of age (Poulmarc'h 2014; Erdal et al. 2019) thus highlighting an inclusive funerary ideology pointing probably to a kinship-based organisation.¹

In conclusion, the KA cultural package includes red-black and monochrome burnished ceramics produced through a unique traditional *chaîne opératoire*, typical houses with central hearths and decorated andirons, burials, symbolic artefacts, and specific forms of metal. Recent archaeobotanical and archaeozoological research also highlighted distinctive farming and animal husbandry practices (e.g., Berger 2013, 2018; Hovespyan 2015; Longford 2015; Samei et al. 2019) that established a mixed agro-pastoral based economy (Sagona 2018: 273-279; Decaix et al. 2019) of the KA groups that mostly appear as sedentary communities. Lack of evidence for socio-economic differentiation in the various components of the KA repertoire suggests an egalitarian model for Kura-Araxes populations (Palumbi 2008; Poulmarc'h 2014; Sagona 2018).

Within this archaeological framework, the goal of this archaeometric study is to explore the evolution of KA dietary habits through time, at various scales. What were their dietary preferences, were they similar for all members of a community, and how were they related to their environment considering the various ecological niches of the southern Caucasus? To disentangle these issues, this research explores the isotopic variability of human dietary choices at the individual and populational levels using data from a sample of sites spanning the KA and Post-KA periods and located across the highland and lowland of the southern Caucasus in Georgia (8 sites), Armenia (three sites), and Azerbaijan (one site).

PALAEODIETARY RECONSTRUCTION IN THE SOUTHERN CAUCASUS: AN ISOTOPIC APPROACH

Stable carbon and nitrogen isotope ratios measured on collagen are one of the most suitable proxies to accurately identify dietary characteristics and provide metabolic information on the nature of dietary proteins (terrestrial, marine) and their trophic levels (plants, meat) corresponding to the last diets (10-15 years) of the individual's life (Katzenberg 2008).

This isotopic analysis documents food items' dietary contribution with high trophic levels, such as animal proteins (domestic and wild animals, meat/milk) and freshwater fish, in the southern Caucasus. Consumer tissues are systematically enriched in heavy isotopes in comparison to diet. Isotopic fractionation between two consecutive (prey-predator) trophic levels is between 0 and 1‰ for carbon, between 3 and 5‰ for nitrogen (Bocherens and Drucker 2003; Hedges and Reynard 2007).

C₃-plants and terrestrial organisms are depleted in the heavier stable carbon isotope (¹³C) compared to C₄-plants and marine organisms (Smith and Epstein 1971; Schoeninger and DeNiro 1984; Fischer et al. 2007). Considering the location of archaeological sites far from the Black and Caspian seas and their position mostly above 1,100 m of altitude, marine resource consumption is not of significant interest. Conversely, the detection of C₄-plant consumers in contrast to wheat or barley consumers (C₃-plants) can be of interest since wild C₄-plants are documented across the southern Caucasus (Decaix 2012). Following a predictable stepwise enrichment in ¹⁵N between each successive trophic level (3-5‰; Bocherens and Drucker 2003), nitrogen stable isotope ratios are expected to be lower for plant protein consumers than for animal protein consumers, and for aquatic protein consumers (O'Connell et al. 1999). Marine protein consumption can be recognised thanks to the positive correlation between carbon and isotope values (Valentin et al. 2014). Nevertheless, it is harder to identify freshwater fish consumption because of their wide isotopic variability (Dufour et al. 1999; Katzenberg and Weber 1999). The possible detection of legume consumers from perceptible low δ¹⁵N collagen values can also be of great interest in the southern Caucasus as it was hypothesised for the Neolithic Mentesh Tepe population (Herrscher et al. 2018a).

Even though most of the mechanisms involved in isotope transfers along the food chains are understood, it is also well-demonstrated they rely on complex physiological processes involving numerous factors such as the environment, climate, or anthropic pressure. Altering plants' carbon and isotope ratios at the base of the food chain can consequently modify isotope ratios at the tissue consumer level (Heaton 1999; Schwarcz et al. 1999; van Klinken et al. 2000; Bogaard et al. 2007). Besides, isotope ratios recorded at bone tissue level may also be affected by particular physiological, pathological, or chronic conditions, such as osteomyelitis, fractures, metabolic disorders, as well as transitory states, like pregnancy or anorexia (Katzenberg and Lovell 1999; Fuller et al. 2004; Mekota et al. 2006). Thus, to reliably interpret human isotope ratios, controlling for local environmental and anthropic

1. Systematic aDNA analyses on Kura-Araxes collective tombs need to verify this assumption.

factors, as well as biological variables, is required (Herrscher and Le Bras-Goude 2010). Consequently, one of the first step to improve palaeodietary reconstruction is to provide a detailed description of local isotopic variability, including animal and plant dietary resources, in conjunction with anthropological criteria, such as age at death, sex, and pathologies. However, even in a detailed isotopic context, it is important to keep in mind that several combinations of food resources (mixtures) may lead up to similar isotopic records in consumer tissues, so the proposed reconstructions should always be considered with caution.

MATERIALS: ARCHAEOLOGICAL CONTEXT, SAMPLE PREPARATION AND ISOTOPIC MEASUREMENTS

ARCHAEOLOGICAL SAMPLING STRATEGY

To increase the isotopic reference base of archaeological food resources in Georgia and explore isotopic variability between highland and lowland KA communities, new analyses were performed on faunal remains recently excavated at Natsargora site near the Kura valley at 770 m asl, in the Shida-Kartli province (Puturidze and Rova 2012; Rova et al. 2017; n = 9) and at Sviana-Rostianebi site located in the south foothills at 1,550 m asl of the Great Caucasus in Dusheti area

(Ramishvili et al. 2004; Gogochuri 2010; n = 13). In addition, analyses were also conducted on the bioarchaeological material excavated from Kvatskhelebi (humans, fauna and cereals, n = 42), located on the Kura river at 635 m asl, in Georgia in Shida Kartli (Javakhishvili and Glonti 1962; Sagona 1984; Palumbi 2008). These new data were compared to isotopic sets of data already published for highland communities, located between 1,200 and 1,600 m asl in Georgia, respectively from the site of Kiketi in Kvemo-Kartli, nearby Tbilisi and the sites of Chobareti and Tiselis Seri in the southern part of the territory overlooking the Turkish border (Messenger et al. 2015; Herrscher et al. in press; n = 59; fig. 2).

For synchronic comparisons across the southern Caucasus, additional previously published data from Mentesh Tepe in the Middle Kura valley in Azerbaijan were also considered (Herrscher et al. 2018b) and new data from two KA sites located in Armenia, Kalavan-1 (n = 5) north of Lake Sevan and Gegharot (n = 3) in the Tsaghkahovit plain. In total, the research presented here is based on 144 KA isotopic samples from the three South Causasian countries, with a total of 34 human, 85 animal and 25 botanical remains. For diachronic comparisons across the southern Caucasus, 39 isotopic samples either already published (Ananauri, Chinchriani in Georgia; Herrscher et al. 2016; Mentesh Tepe in Azerbaijan; Herrscher et al. 2018b) or unpublished (Aknashen in the Ararat plain; n = 1) corresponding to the Post KA period (the so-called “Early Kurgans” cultures) were also considered (fig. 2; table 1).

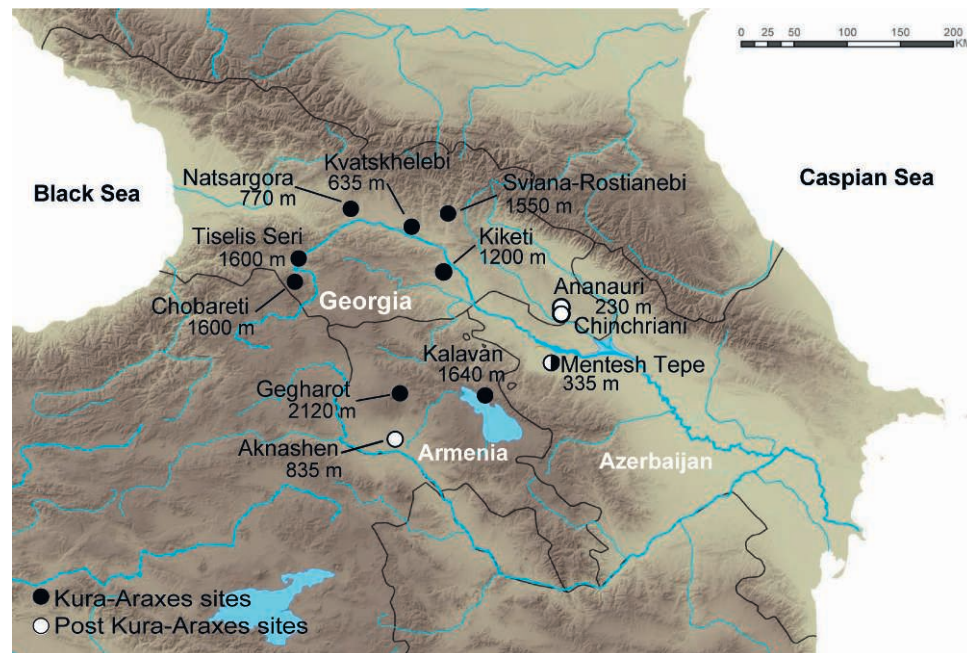


Fig. 2 – Location of Kura-Araxes and Post Kura-Araxes archaeological sites across the Southern Caucasus.

THE ARCHAEOLOGICAL SITES INCLUDED IN THE STUDY

Natsargora: located in the Kashuri district in Shida Kartli, 7 km from the Kura river, at 770 m asl. Excavations were first conducted by a Georgian team between 1984 and 1992 and later by a Georgian-Italian team in 2011-2012 (Puturidze and Rova 2012; Rova et al. 2017). The site consists of a small mound and the most recent excavations suggest a KA settlement that was abandoned and then a re-occupation of the site during the Early Kurgan period. Based on archaeological data and radiocarbon dates, the settlement is dated to the KA II (Rova 2014). Although 26 Early Bronze Age pit burials were excavated by the Georgian expedition (Puturidze et al. 2012), bone samples were not available for any of them. In contrast, a sampling of 10 animal bone remains from the KA settlement was done thanks to the 2011 Georgian-Italian excavation (Rova et al. 2017). According to archaeological data, all bones are dated from the KA period and the sample consists of three cattle, three sheep or goats and three suids as well as one *Cervus* sp. specimen (tables 2, 3).

Sviana-Rostianebe: is a settlement located in the territory of Dusheti municipality, near to the area of Mtiuleti Aragvi

river-head in the Khada gorge on the left bank of Khadis Tskali. The site is near the village of Sviana-Rostianebe at the altitude of 1,554-1,561 m asl and was discovered in 1988 during the construction of a gas pipeline. Ceramics are typologically compatible with those of the late stages of the KA culture (Ramishvili et al. 2004), as confirmed by one radiocarbon date on an animal bone (table 2). The sampling of animal bone remains was conducted at Dusheti Museum by a specialist to ensure the selection of different individuals. It consists of thirteen remains of domestic animals including four cattle, two sheep or goat, four goats and three wild animals, that is two *Capra caucasica* and one *Cervus* sp. (tables 2, 3).

Kvatskhelebi: located in the Shida Kartli region in Georgia, it is one of the best-preserved and thoroughly excavated Kura-Araxes sites. Excavations at the site were conducted between 1954-1964 as part of the Urbnisi Archaeological Project, and directed by A. Javakhishvili and L. Glonti, but only partly published (Javakhishvili and Glonti 1962; Sagona 1984; Palumbi 2008). The new Kvatskhelebi Research and Publication Project, headed by Sarit Paz, in collaboration with Mindia Jalabadze, has been working since 2014 to study and publish the material from the old excavations, with the aid of a research grant from the White-Levy Foundation (Paz

Table 1 – Description of samples used in this isotopic study according to sites, territories, and chronological attribution.
*: New isotopic data are published in this study for one barley seed.

| | Kura Araxes | | | | Post Kura Araxes/Early Kurgan | | | | Total | Isotopic references |
|--------------------|-------------|-----------|-----------|------------|-------------------------------|----------|----------|------------|------------|--|
| | Humans | Animals | Plants | Total KA | Humans | Animals | Plants | Total P-KA | | |
| Georgia | | | | | | | | | | |
| Chobareti | 10 | 21 | 8* | 39 | | | | | 39 | Messenger, Herrscher et al. 2015 |
| Tiselis Seri | 6 | | | 6 | | | | | 6 | Herrscher et al. in press, In: Marro Stoëllner |
| Kiketi | 7 | 7 | | 14 | | | | | 14 | Herrscher et al. in press, In: Marro Stoëllner |
| Kvatskhelebi | 3 | 30 | 9 | 42 | | | | | 42 | This study |
| Natsargora | | 9 | | 9 | | | | | 9 | This study |
| Sviana-Rostianebe | | 13 | | 13 | | | | | 13 | This study |
| Ananauri | | | | | 20 | 5 | | 25 | 25 | Herrscher et al. 2016 |
| Chinchriani | | | | | | 3 | | 3 | 3 | Herrscher et al. 2016 |
| Armenia | | | | | | | | | | |
| Kalavan1 | 4 | 1 | | 5 | | | | | 5 | This study |
| Gegharot | 3 | | | 3 | | | | | 3 | This study |
| Aknashen | | | | | 1 | | | 1 | 1 | This study |
| Azerbaijan | | | | | | | | | | |
| Mentesh Tepe | 1 | 4 | 8 | 13 | 4 | | 6 | 10 | 23 | Herrscher et al. 2018 |
| Grand total | 34 | 85 | 25 | 144 | 25 | 8 | 6 | 39 | 183 | |

Table 2 – AMS radiocarbon dates from KA and Post-KA human and animal individuals.
 *: ^{14}C dates were run on a different collagen samples than those used for isotopic analysis (this study).

| Sites | #Lab code | ^{14}C -Lab Code | Burial | Nature | ^{14}C dates results | Calibrated dates cal. BC (95.4% probability) | | Bibliography |
|-------------------------------|-----------|---------------------------|-------------------|-------------------|-------------------------------|--|-------|----------------------------|
| | | | | | Cal. BP | Min. | Max. | |
| Kura-Araxes sites | | | | | | | | |
| Kiketi | CG01 | Poz-60845 | Burial 6, Skull 1 | human | 4,195 ± 35 | 2,895 | 2,666 | Herrscher et al. in press |
| | CG04 | Poz-56572 | Burial 5, | human | 4,120 ± 35 | 3,325 | 2,920 | Herrscher et al. in press |
| | CG07 | Poz-60846 | Burial 4, Skull 3 | human | 4,330 ± 30 | 3,019 | 2,894 | Herrscher et al. in press |
| | GKF02 | Poz-60847 | Burial 4 | Ovis sp. | 4,315 ± 30 | 3,013 | 2,888 | Herrscher et al. in press |
| | GKF06 | Poz-60848 | -- | Bos sp. | 4,300 ± 30 | 3,011 | 2,880 | Herrscher et al. in press |
| Chobareti | CH0H05 | Poz-56370 | Burial 5 | human | 4,460 ± 30 | 3,346 | 2,944 | Messenger et al. 2015 |
| | CH0H08 | Poz-56371 | Burial 9 | human | 4,380 ± 40 | 3,264 | 2,902 | Messenger et al. 2015 |
| Sviana-Rostianebi | SVIA F07 | Poz-43670 | | <i>Bos taurus</i> | 4,195 ± 35 | 2,895 | 2,666 | This study |
| Post-Kura-Araxes sites | | | | | | | | |
| Ananauri | ANA H02 | Sac-43658 | Kurgan 3 | human | 3,970 ± 30 | 2,574 | 2,350 | Herrscher et al. 2016 |
| | ANAH03 | Sac- 43659 | Kurgan 3 | human | 3,965 ± 30 | 2,573 | 2,348 | Herrscher et al. 2016 |
| | ANAH04 | Sac-43660 | Kurgan 3 | human | 4,020 ± 30 | 2,620 | 2,471 | Herrscher et al. 2016 |
| | ANAH08 | Sac-43661 | Kurgan 3 | human | 3,980 ± 35 | 2,580 | 2,349 | Herrscher et al. 2016 |
| | ANAH10 | Sac-43663 | Kurgan 3 | human | 3,945 ± 30 | 2,567 | 2,341 | Herrscher et al. 2016 |
| | ANAH100 | Sac-43664 | Kurgan 3 | human | 4,010 ± 30 | 2,617 | 2,480 | Herrscher et al. 2016 |
| | ANAH101 | Sac-43665 | Kurgan 3 | human | 3,935 ± 35 | 2,565 | 2,298 | Herrscher et al. 2016 |
| Aknashen | (CAR 06)* | Ly-6992 | TR7 UF 5 F2 | human | 3,860 ± 35 | 2,464 | 2,203 | Poulmarc'h et al. in press |
| | (CAR 06)* | UGAMS-6460 | TR7 UF 5 F2 | human | 3,830 ± 30 | 2,351 | 2,198 | Poulmarc'h et al. in press |
| Kalavan-1 | (CAR 05)* | Lyon-9705 | UF 8 | human | 4,020 ± 35 | 2,620 | 2,471 | Poulmarc'h et al. 2016 |
| | (CAR 08)* | Poz-2234 | UF 9 | human | 3,990 ± 35 | 2,619 | 2,410 | Poulmarc'h et al. 2016 |
| Mentesh Tepe | CAZ 103 | Poz-63143 | ST54 1 | human | 3,920 ± 30 | 2,480 | 2,299 | Herrscher et al. 2018 |
| | CAZ 104 | Poz-63144 | ST54 2 | human | 3,970 ± 30 | 2,575 | 2,350 | Herrscher et al. 2018 |
| | AZH400 | Poz-82220 | ST 54 3 | human | 3,935 ± 35 | 2,558 | 2,295 | Herrscher et al. 2018 |
| | AZH228 | Poz-68643 | ST 54 Ind 5 | human | 3,785 ± 30 | 2,300 | 2,133 | Herrscher et al. 2018 |

forthcoming²). The site is located on the north bank of the Kura river, on a flat extension (ca. 635 m asl) rising over 30 m above the river. Several phases of the small village (ca. 3,500 m²) were discovered, among which Stratum C1 was destroyed by conflagration, and yielded remains of 25 structures with hundreds of complete vessels *in situ* in mostly domestic contexts. Several graves from a slightly earlier phase (C3-2) were excavated at the edge of the settlement. The site is dated to the KA II period, with new calibrated dates at ca. 2,900-2,800 BC. Due to the good preservation, Kvatskhelebi provides a unique contribution to the isotopic study, with material from both funerary and domestic contexts, including human, faunal and botanical remains. The latter two allow us to describe the

local environment isotopically. The sampled material included human skeletal remains of three individuals from Tomb #3 and Tomb #2 (Stratum C3-2). Thirty animal bones from Strata C and B were sampled, including domestic and wild herbivore, carnivores as well as suids. Finally, ten botanical samples of barley and wheat grains from Strata C1 and C3 were analysed (table 4).

Gegharot: is located near Aragats mountains at 2,124 m asl, in the Tsaghkahovit plain. It was excavated by Ruben Badalyan and Adam Smith from 2002 to 2018, in the frame of the Archaeology and Geography of ancient Transcaucasian societies (ArAGATS) project. The Early Bronze Age village, established on a hill, has been occupied during two phases of the KA horizon. The early phase (ca. 3,500/3,350-2,900 BC) yielded a collective funerary deposit including two to three adult individuals and one child buried in a square constructed

2. PAZ S. forthcoming – *Kvatskhelebi. An Early Bronze Age Village in the Shida Kartli Region, Georgia*. Leuven: Peeters (Ancient Near Eastern Studies, Supplement Series).

Table 3 – Elemental and stable isotope data of animals from KA Natsargora (NATS) and Sviana-Rotianebi (SVIA) sites in Georgia. *: Samples radiocarbon dated.

| #Lab code | Archaeol. Data | Species | Skeletal Element | Yld (mg/g) | %C | %N | C/N | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) |
|-----------|--------------------|-------------------------|------------------|------------|------|------|-----|---------------------------|---------------------------|
| NATS F10 | 2011- NTS 0077-E2 | <i>Bos</i> sp. | phalanx | 180.9 | 40.5 | 14.7 | 3.2 | -19.0 | 5.3 |
| NATS F11 | 2011- NTS 0077-E2 | <i>Bos</i> sp. | skull | 127.0 | 40.6 | 14.8 | 3.2 | -18.7 | 5.8 |
| NATS F12 | 2011 - NTS 0048 E8 | <i>Bos</i> sp. | radius | 2.9 | - | - | - | - | - |
| NATS F13 | 2011- NTS 0077-E2 | <i>Cervus</i> sp. | teeth | 154.0 | 40.9 | 14.8 | 3.2 | -20.3 | 8.9 |
| NATS F14 | 2011- NTS 0077-E2 | <i>Ovis/Capra</i> | teeth | 141.4 | 38.1 | 13.7 | 3.2 | -20.2 | 8.7 |
| NATS F15 | 2011- NTS 0077-E2 | <i>Ovis/Capra</i> | scapula | 124.1 | 40.5 | 14.8 | 3.2 | -20.3 | 4.8 |
| NATS F16 | 2011 - NTS 0048 E8 | <i>Bos</i> sp. | long bones | 36.1 | 37.2 | 13.3 | 3.2 | -19.7 | 7.8 |
| NATS F17 | 2011- NTS 0077-E2 | <i>Sus</i> sp. | phalanx | 173.7 | 41.7 | 15.1 | 3.2 | -20.3 | 5.3 |
| NATS F18 | 2011- NTS 0077-E2 | <i>Sus</i> sp. | maxilla | 131.6 | 41.3 | 14.8 | 3.2 | -15.8 | 8.2 |
| NATS F19 | 2011 - NTS 0048 E8 | <i>Sus</i> sp. | phalanx | 179.5 | 41.5 | 15.0 | 3.2 | -20.4 | 5.3 |
| SVIA F07* | -- | <i>Bos taurus</i> | skull | 68.3 | 39.2 | 14.3 | 3.2 | -18.1 | 6.4 |
| SVIA F08 | -- | <i>Bos</i> sp. | mandibula | 89.7 | 38.7 | 13.8 | 3.3 | -20.1 | 6.1 |
| SVIA F09 | 355-10 | <i>Bos</i> sp. | maxilla | 51.5 | 35.8 | 12.6 | 3.3 | -19.6 | 5.8 |
| SVIA F10 | bag 21 | <i>Bos</i> sp. | molar | 46.2 | 37.8 | 13.5 | 3.3 | -20.2 | 5.9 |
| SVIA F01 | -- | <i>Ovis/Capra</i> | calcaneum | 119.9 | 40.6 | 14.6 | 3.2 | -19.8 | 4.0 |
| SVIA F02 | bag 21 | <i>Ovis/Capra</i> | calcaneum | 134.8 | 39.6 | 14.0 | 3.3 | -20.0 | 4.3 |
| SVIA F03 | 493-10 | <i>Capra hircus</i> | corn | 115.4 | 38.8 | 13.9 | 3.2 | -19.0 | 4.0 |
| SVIA F04 | 363-10 | <i>Capra hircus</i> | corn | 137.4 | 41.1 | 14.7 | 3.2 | -19.9 | 4.5 |
| SVIA F05 | 361-10 | <i>Capra hircus</i> | corn | 109.6 | 40.3 | 14.4 | 3.2 | -19.7 | 4.2 |
| SVIA F06 | -- | <i>Capra hircus</i> | corn | 107.9 | 40.3 | 14.4 | 3.3 | -19.4 | 4.3 |
| SVIA F12 | bag 21 | <i>Capra caucasicus</i> | skull | 108.6 | 38.1 | 13.6 | 3.3 | -19.6 | 4.5 |
| SVIA F13 | -- | <i>Capra caucasicus</i> | corn | 117.5 | 39.5 | 14.0 | 3.3 | -19.6 | 4.0 |
| SVIA F11 | bag 21 | <i>Cervus</i> sp. | maxilla | 67.6 | 39.1 | 13.9 | 3.3 | -19.3 | 3.3 |

tomb (fig. 1C; Badalyan et al. 2008; Poulmarc'h 2014; Poulmarc'h et al. in press). The isotopic analyses from Gegharot were carried out on three human remains of the collective tomb (tables 2, 5).

Kalavan-1: is an open-air site situated 1,640 m asl on the south-west-facing slopes of the Aregunyats Range north of Lake Sevan. Archaeological and geological investigations were conducted between 2005 and 2009 as part of a collaborative Armenian and French project “Mission Caucas” (French Ministry for Foreign Affairs, dir. C. Chataigner; Montoya et al. 2013). The excavation revealed two main levels of occupation dated to the Terminal Palaeolithic, overlaid by a KA burial ground. Due to the steep topography above Kalavan-1, only a limited exposure of the archaeological remains could be made. Five burial pits were uncovered, four of which contained single primary burials; the 5th held the remains of at least three

individuals. Six consistent ^{14}C dates on human skeletal material bracket the use of the burial site between ca. 2,850 and 2,490 cal. BC (Poulmarc'h et al. 2016). The isotopic analyses from Kalavan-1 were carried out on four human bones from four single burials (tables 2, 5).

Aknashen-Khatunarkh: is located in the Ararat Plain, at 838 m asl m. The settlement mound was excavated by Ruben Badalyan and Armine Harutyunyan from 2004 to 2019, in the frame of the “Mission Caucas”. Neolithic and Chalcolithic levels were uncovered, as well as many burials ranging from the 6th millennium to the contemporary period. One of the burials (TR7 UF5 F2), cut into the Neolithic levels, is dated to the second half of the 3rd millennium, that is from the Post KA period (Badalyan et al. 2010). This subadult was sampled for isotopic analyses (tables 2, 5).

Table 4 – Elemental and stable isotope data of humans from KA Kvatskhelebi site (KVAT) in Georgia. VS: variable shape.

| #Lab code | Archaeol. Data | Age | Sex | Skeletal Element | Burial type | Funerary type | Yld (mg/g) | %C | %N | C/N | δ ¹³ C (‰) | δ ¹⁵ N (‰) |
|-----------|----------------|-------|-----|------------------|-------------|---------------|------------|------|------|-----|-----------------------|-----------------------|
| KVAT H01 | C3; Burial 2 | Adult | M | coxal | VS | Double | 101.8 | 40.2 | 15.0 | 3.1 | -18.2 | 10.6 |
| KVAT H02 | C3; Burial 2 | Adult | F | coxal | VS | Double | 183.3 | 39.4 | 14.7 | 3.1 | -18.9 | 10.4 |
| KVAT H03 | C3; Burial 3 | Adult | I | humerus | VS | Single | 27.2 | 35.4 | 13.0 | 3.2 | -18.8 | 9.8 |

Table 4 (suite) – Elemental and stable isotope data of animals from KA Kvatskhelebi site (KVAT) in Georgia.

| #Lab code | Archaeol. Data | #Collection | Species | Skeletal Element | Yld (mg/g) | %C | %N | C/N | δ ¹³ C (‰) | δ ¹⁵ N (‰) |
|-----------|-------------------|-------------|-------------------------|------------------|------------|------|------|-----|-----------------------|-----------------------|
| KVAT F01 | - | Burial 1 | <i>Bos taurus</i> | radius | 168.8 | 41.4 | 15.5 | 3.1 | -19.3 | 7.6 |
| KVAT F02 | C | Settlement | <i>Bos taurus</i> | skull | 25.6 | 34.7 | 12.6 | 3.2 | -18.0 | 5.8 |
| KVAT F03 | B | #15-55:531 | <i>Bos sp.</i> | maxilla | 60.5 | 40.0 | 14.9 | 3.1 | -18.9 | 6.5 |
| KVAT F04 | C2N1 | #15-55:214 | <i>Bos sp.</i> | scapula | 148.5 | 41.6 | 15.6 | 3.1 | -19.2 | 6.2 |
| KVAT F05 | C2 | #15-55:215 | <i>Bos sp.</i> | scapula | 120.5 | 41.4 | 15.2 | 3.2 | -19.4 | 5.7 |
| KVAT F06 | C2N1 | #15-55:219 | <i>Bos sp.</i> | scapula | 128.9 | 42.4 | 15.6 | 3.2 | -19.4 | 6.2 |
| KVAT F07 | B; Excavated area | #15-55:248 | <i>Bos sp.</i> | metacarpal | 84.7 | 41.5 | 15.5 | 3.1 | -19.9 | 7.4 |
| KVAT F08 | B; from squares | #15-55:260 | <i>Bos sp.</i> | calcaneus | 75.2 | 35.6 | 13.4 | 3.1 | -19.7 | 7.1 |
| KVAT F09 | B; from squares | #15-55:272 | <i>Bos sp.</i> | calcaneus R | 69.6 | 43.0 | 14.5 | 3.4 | -21.5 | 5.0 |
| KVAT F11 | B | #15-55:275 | <i>Bison</i> | calcaneus | 109.9 | 41.7 | 15.4 | 3.1 | -18.9 | 5.3 |
| KVAT F12 | C | | <i>Ovis aries</i> | skull | 71.8 | 35.3 | 12.9 | 3.2 | -19.7 | 6.1 |
| KVAT F13 | B; Trench 1 | #94 | Ovis/Capra | scapula | 139.6 | 41.0 | 15.2 | 3.1 | -18.3 | 6.9 |
| KVAT F14 | B; Trench 1 | #15-55:98 | Ovis/Capra | scapula | 124.5 | 41.2 | 15.3 | 3.1 | -19.4 | 4.5 |
| KVAT F15 | B1 | #561 | Ovis/Capra | mandibula | 113.2 | 41.6 | 15.3 | 3.1 | -18.5 | 6.7 |
| KVAT F16 | B1 | #570 | Ovis/Capra | mandibula | 93.1 | 41.0 | 15.3 | 3.1 | -19.2 | 6.2 |
| KVAT F17 | B1 | #575 | Ovis/Capra | mandibula | 58.2 | 40.9 | 15.2 | 3.1 | -16.4 | 5.8 |
| KVAT F18 | B1 | #586 | Ovis/Capra | maxilla | 117.2 | 41.1 | 15.2 | 3.1 | -18.8 | 5.8 |
| KVAT F19 | B; Trench 2 | #57 | <i>Capra sp.</i> | horn | 112.2 | 40.6 | 15.1 | 3.1 | -18.6 | 6.0 |
| KVAT F20 | B1 | #584 | <i>Capra sp.</i> | skull | 111.4 | 40.6 | 14.9 | 3.1 | -19.3 | 6.5 |
| KVAT F21 | C1N1 | #301 | <i>Sus scrofa</i> | femur | 30.6 | 32.6 | 12.0 | 3.1 | -16.1 | 5.4 |
| KVAT F22 | C1N2 | #355 | <i>Sus scrofa</i> | skull | 48.7 | 40.7 | 14.9 | 3.2 | -14.7 | 5.6 |
| KVAT F23 | C1N2 | #15-55:268 | <i>Canis familiaris</i> | skull | 27.4 | 39.4 | 14.7 | 3.1 | -18.3 | 10.0 |
| KVAT F24 | C1N1 | #306 | <i>Canis familiaris</i> | mandibula | 127.0 | 40.8 | 15.2 | 3.1 | -18.0 | 10.0 |
| KVAT F25 | C1N1 | #307 | <i>Canis familiaris</i> | mandibula | 170.1 | 42.1 | 15.8 | 3.1 | -17.9 | 8.2 |
| KVAT F26 | BN1 & N2 | #313 | <i>Equus sp.</i> | pubis | 156.1 | 42.2 | 15.7 | 3.1 | -20.3 | 4.5 |
| KVAT F27 | C1N6 | #218 | <i>Equus ferus</i> | scapula | 37.4 | 19.4 | 6.9 | 3.3 | -18.9 | 6.8 |
| KVAT F29 | B; Trench 1 | #60 | <i>Cervus elaphus</i> | antler | 116.2 | 41.6 | 15.4 | 3.1 | -20.2 | 3.1 |
| KVAT F30 | B; from squares | #314 | <i>Cervus elaphus</i> | antler | 143.3 | 40.8 | 15.2 | 3.1 | -20.8 | 3.8 |
| KVAT F31 | B | #316 | <i>Cervus elaphus</i> | antler | 10.3 | 35.7 | 12.8 | 3.2 | -21.1 | 3.6 |
| KVAT F32 | C; N1 | #435 | <i>Cervus elaphus</i> | metacarpal | 65.3 | 40.5 | 14.9 | 3.1 | -20.3 | 5.4 |

Table 4 (suite) – Elemental and stable isotope data of cereals from KA Kvatskhelebi site (KVAT) in Georgia.

| #Lab code | Archaeol. Data | #Sample | Species | Tissue | Yld (mg/g) | %C | %N | C/N | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) |
|-----------|----------------|----------|--------------------------|--------|------------|------|-----|------|---------------------------|---------------------------|
| KVAT P01 | C1N1 | Sample 1 | <i>Hordeum vulgare</i> | seed | 93.1 | 61.4 | 4.6 | 15.3 | -24.0 | 7.9 |
| KVAT P02 | C1N1 | Sample 1 | <i>Hordeum vulgare</i> | seed | 6.9 | - | - | - | - | - |
| KVAT P03 | C1N1 | Sample 1 | <i>Hordeum vulgare</i> | seed | 87.8 | 60.9 | 6.0 | 11.7 | -23.6 | 5.1 |
| KVAT P04 | C1N1 | Sample 1 | <i>Hordeum vulgare</i> | seed | 87.4 | 59.5 | 5.3 | 13.0 | -25.1 | 7.3 |
| KVAT P05 | C1N1 | Sample 1 | <i>Hordeum vulgare</i> | seed | 72.3 | 66.3 | 6.0 | 12.9 | -23.4 | 8.6 |
| KVAT P06 | C3N3 | Sample 8 | <i>Triticum aestivum</i> | seed | 67.6 | 60.1 | 4.1 | 17.0 | -21.8 | 5.4 |
| KVAT P07 | C3N3 | Sample 8 | <i>Triticum aestivum</i> | seed | 79.5 | 61.3 | 4.7 | 15.1 | -21.7 | 6.3 |
| KVAT P08 | C3N3 | Sample 8 | <i>Triticum aestivum</i> | seed | 35.1 | 60.6 | 4.8 | 14.6 | -21.5 | 4.4 |
| KVAT P09 | C3N3 | Sample 8 | <i>Triticum aestivum</i> | seed | 67.2 | 59.1 | 5.6 | 12.3 | -21.5 | 6.2 |
| KVAT P10 | C3N3 | Sample 8 | <i>Triticum aestivum</i> | seed | 67.0 | 60.8 | 4.3 | 16.4 | -22.4 | 6.1 |

METHODOLOGICAL ASPECTS

PROTOCOLS, ISOTOPIC MEASUREMENTS

The collagen extraction was performed at the Laboratoire méditerranéen de Préhistoire Europe-Afrique, Aix-Marseille University. Collagen extraction was performed according to the protocol of Longin (1971) modified by Bocherens et al. (1991). After cleaning the bone specimens (~ 250 mg) with distilled water, each sample was ground into a powder (> 700 μm for collagen and < 700 μm for apatite). One in-house lab standard of archaeological bovine bone powder is included in all batches to ensure the quality of the extraction procedure. The protocol calls for an acidic soak on stirrer (HCl 1M, 20') for demineralisation, following by a soak in a basic solution (NaOH 0.125M, < 18 hours) to remove humic contaminants. Then, collagen was solubilised in a weakly acidic solution (HCl pH = 2, 17 hours, 100 °C), and the purified "collagen" was lyophilised for 48 hours.

Pre-weighted bone collagen samples were analysed by a Europa Scientific elemental analyser connected to a Europa Scientific 20-20 (IRMS) at Iso-Analytical Limited (Cheshire, UK). Stable isotopes were measured relative to standards (V-PDB for carbon, AIR for nitrogen) and expressed in parts per mil (‰). The reference material for collagen is IA-R068 (soy protein, $\delta^{13}\text{C}_{\text{V-PDB}} = -25.22 \pm 0.02\text{‰}$, $\delta^{15}\text{N}_{\text{AIR}} = 0.99 \pm 0.07\text{‰}$), and for seed, IA-R001 (wheat flour, $\delta^{13}\text{C}_{\text{V-PDB}} = -26.43 \pm 0.02\text{‰}$, $\delta^{15}\text{N}_{\text{AIR}} = 2.55 \pm 0.02\text{‰}$). For collagen samples, measurements uncertainty was monitored using check samples with well characterised isotopic compositions: IA-R038 (L-alanine, $\delta^{13}\text{C}_{\text{V-PDB}} = 24.99 \pm 0.06\text{‰}$, $\delta^{15}\text{N}_{\text{AIR}} = -0.65 \pm 0.04\text{‰}$), IA-R069 (tuna protein, $\delta^{13}\text{C}_{\text{V-PDB}} = -18.88 \pm 0.05\text{‰}$, $\delta^{15}\text{N}_{\text{AIR}} =$

$11.60 \pm 0.09\text{‰}$) and a mixture of ammonium sulfate and IA-R046/IAEA-C7 (oxalic acid, $\delta^{13}\text{C}_{\text{V-PDB}} = -14.48 \pm 0.21\text{‰}$, $\delta^{15}\text{N}_{\text{AIR}} = 22.04 \pm 0.06\text{‰}$). Quality control check samples are calibrated and traceable to the international standards IAEA-CH-6 and IAEA-N-1.

For seeds measurements, measurements uncertainty was monitored using check samples with well characterised isotopic compositions: IA-R045/IA-R005 (mixture of ammonium sulfate and beet sugar, $\delta^{13}\text{C}_{\text{V-PDB}} = -26.03 \pm 0.11\text{‰}$, $\delta^{15}\text{N}_{\text{AIR}} = -4.71 \pm 0.07\text{‰}$), IA-R046/IA-R006 (mixture of ammonium sulfate and cane sugar, $\delta^{13}\text{C}_{\text{V-PDB}} = -11.64 \pm 0.03\text{‰}$, $\delta^{15}\text{N}_{\text{AIR}} = 22.04 \pm 0.06\text{‰}$). Quality control check samples are calibrated and traceable to the international standard IAEA-CH-6 and IAEA-N-1. Using calculation provided by Szpak et al. (2017) based on repeated measurements of calibration standards, check standards and sample replicates, precision ($u(R_w)$) was determined to be $\pm 0.19\text{‰}$ and $\pm 0.15\text{‰}$ respectively for collagen and seed $\delta^{13}\text{C}$, and $\pm 0.04\text{‰}$ for collagen $\delta^{15}\text{N}$ and $\pm 0.07\text{‰}$ for seed $\delta^{15}\text{N}$. The total analytical uncertainty is estimated, for collagen, to be $\pm 0.18\text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, and for seed, to be $\pm 0.19\text{‰}$ for $\delta^{13}\text{C}$ and $\pm 0.15\text{‰}$ for $\delta^{15}\text{N}$.

Collagen preservation was checked according to several criteria, such as the yield of extraction ($\geq 10 \text{ mg}\cdot\text{g}^{-1}$), the percentages of C and N ($\%C \geq 30 \%$ and $\%N \geq 11 \%$) and the atomic C/N ratio (between 2.9 and 3.6; DeNiro 1985; Ambrose 1990; van Klinken 1999).

STATISTICAL ANALYSIS

Statistical analyses were performed using the statistical program R (version 3.6.1) and RStudio (version 1.2.5033;

Table 5 – Elemental and stable isotope data of humans and animals from KA Armenian sites.
VS: variable shape; BPM: presence of a box in perishable material.

| #Lab | Site | Archaeo. data | Grave type | Funerary type | Age/ Species | Sex | Skeletal Element | Yld (mg/g) | %C | %N | C/N | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) |
|---------|-----------|---------------|------------|---------------|-------------------|-----|------------------|------------|------|------|-----|---------------------------|---------------------------|
| CAR 11 | Gegharot | Ind 669 | VS | Collective | Adult | M | hand phalanx | 197.3 | 41.7 | 15.1 | 3.2 | -18.7 | 9.4 |
| CAR 12 | Gegharot | Ind 670-1 | VS | Collective | Adult | M | metacarpal 2 | 152.6 | 43.1 | 15.5 | 3.2 | -18.9 | 10.8 |
| CAR 13 | Gegharot | Ind 670-2 | VS | Collective | Subadult | I | hand phalanx | 192.8 | 40.4 | 14.6 | 3.2 | -18.8 | 9.2 |
| CAR 03 | Kalavan-1 | 2006-UF1 | BPM | Single | Adult | F | radius | 121.9 | 40.5 | 15.1 | 3.1 | -19.3 | 9.7 |
| CAR 04 | Kalavan-1 | 2006-UF2 | BPM | Single | Adult | I | tibia | 65.8 | 39.2 | 14.4 | 3.2 | -18.8 | 9.6 |
| CAR 05 | Kalavan-1 | 2006-UF8 | Pit | Single | Subadult | I | tibia | 21.5 | 39.6 | 14.7 | 3.1 | -18.8 | 10.9 |
| CAR 08 | Kalavan-1 | 2006-UF9 | BPM | Single | Adult | I | hand phalanx | 60.1 | 41.2 | 14.9 | 3.2 | -19.1 | 9.6 |
| CAR F03 | Kalavan-1 | 2007 - UF5 | | | <i>Ovis/Capra</i> | | tarsal | 74.3 | 36.1 | 13.0 | 3.2 | -19.6 | 6.9 |
| CAR 06 | Aknashen | Tr7 UF5 F2 | Pit | Single | Subadult | I | tibia | 69.8 | 44.2 | 15.5 | 3.2 | -18.0 | 11.8 |

R Development Core Team 2005; R Core Team 2018). The non-parametric tests, Mann-Whitney-Wilcoxon and Kruskal-Wallis with FDR correction, were used to compare between series. The dependence of variables was tested using the Spearman rank correlation.

PRESERVATION OF NEW SAMPLES OF THIS STUDY

The new samples from Georgia and Armenia produced collagen with a yield above 10.3 mg.g⁻¹ for animals and 21.5 mg.g⁻¹ for humans (tables 3-5). Carbon and nitrogen percentage yields in the animal and human collagen samples range from 19.4 to 43.1 % for carbon and from 6.9 to 15.8 % for nitrogen. Atomic C:N ratios range between 3.1 and 3.2. Based on the classical criteria used to check the preservation of collagen samples (DeNiro 1985; Ambrose 1990; van Klinken 1999), one animal sample (KVAT_F27) exhibits percentage yields in carbon and nitrogen under the limit mentioned above, nevertheless its atomic C:N. ratio confirmed a non-altered collagen. The cereals (wheat and barley; table 3) from Kvatskhelebi exhibit carbon and nitrogen percentages ranging from 59.1 to 61.3 and 4.1 to 6.0, respectively. These values are in line with previous data recorded in southern Caucasus, as well as with the new barley data from Chobareti ($\delta^{13}\text{C}_{\text{V-PDB}} = -22.8\text{‰}$, $\delta^{15}\text{N}_{\text{AIR}} = 6.8\text{‰}$; %C = 61% and %N = 3.1%).

RESULTS AND DISCUSSION

DIVERSITY OF SOUTH CAUCASUS ENVIRONMENTS AND ISOTOPIC VARIABILITY OF DIETARY RESOURCES

All animal species from Georgian sites (Kiketi, Tiselis Seri, Natsargora, Sviana-Rostianebe, and Kvatskhelebi) exhibit $\delta^{13}\text{C}$ values from -21.5 to -12.3‰ (-18.9 ± 1.8‰, n = 85) and $\delta^{15}\text{N}$ values from 3.1 to 11.7‰ (5.9 ± 1.6‰, n = 85; tables 3, 4; Messenger et al. 2015, Herrscher et al. in press). Most animal $\delta^{13}\text{C}$ values (median -19.1‰ and -18.9‰ for lowland and highland respectively) agree with the presence of a C₃-environment consistent with the type of vegetation coverage in the South Caucasus. Several animals show $\delta^{13}\text{C}$ values above -15.8‰ much higher than all other animal carbon isotope values, suggesting the consumption of C₄-plants (figs. 3A-B). These animals are two *Bos Taurus* and two *Ovis/Capra* from Kiketi for highland sites, three *Sus* sp., and one *Ovis/Capra* from Natsargora and Kvatskhelebi for lowland sites. C₄ plants, such as Chenopodiaceae or Poaceae, are widespread in southern Caucasus and preferentially around the Kura Valley (Decaix 2012). This distribution could explain the values recorded for animals from Natsargora and Kvatskhelebi. These high carbon values, only observed for some specimens, could also support different herd management strategies related to a different human social group/family or the animal's age. For the Chobareti specimens, one hypothesis could be a different geographical origin linked either to human or animal mobility through market trade. On the other hand, the latter domestic animals' high isotopic values were discovered in association with human skeletons and were used as grave goods. These burial deposits raise a question regarding animals' status and

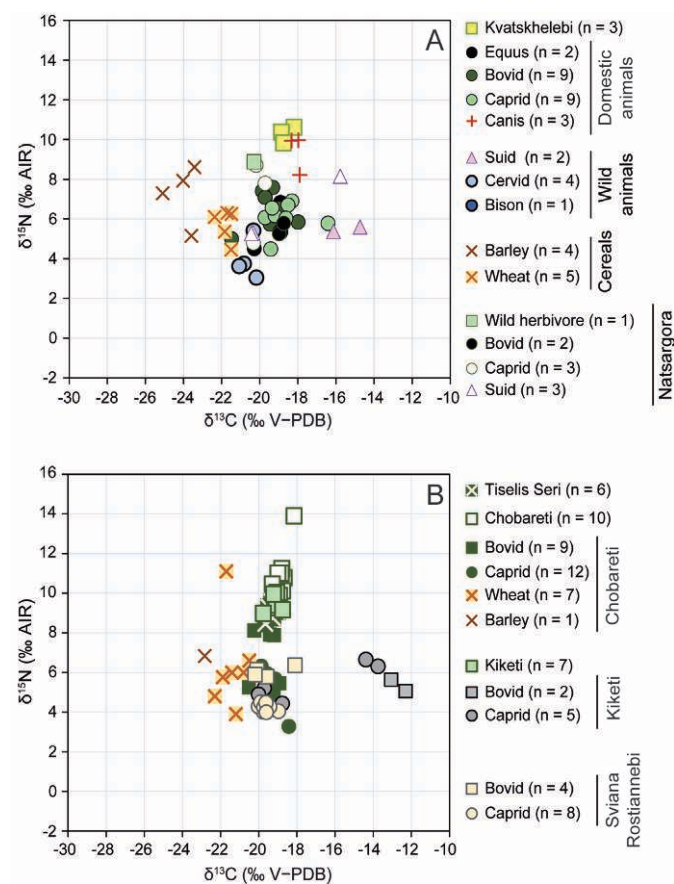


Fig. 3 – Human, animal and cereal carbon and nitrogen isotope ratios for Georgian archaeological sites. **A.** Sites below 770 m asl, Natsargora, and Kvatskhelebi sites (this study); **B.** Sites above 1,300 m asl, Sviana-Rostianebe (this study) and Kiketi, Tiselis Seri, Chobareti sites. After Messager et al. 2015; Herrscher et al. in press.

the use of animal remains (as “grave goods”) to establish an isotopic baseline of past dietary resources. Kruskal-Wallis tests performed between Georgian sites did not significantly differ in stable isotope ratios of carbon and nitrogen. However, a trend could be noted with the highest nitrogen values for carnivores compatible with their ethology (fig. 3) and the lowest isotopic values for carbon and nitrogen for Kvatskhelebi deer, consistent with the use of a more closed environment than domestic species. Mann-Whitney tests were conducted to identify the differences between animals more precisely, between archaeological sites according to the most represented species: cattle and sheep/goat. Only caprids from Sviana-Rostianebe showed significantly lower values compared to the other sites, while cattle showed similar carbon and nitrogen ratios for all sites. Concerning suids, despite the limited data available only for lowland sites (fig. 3A), $\delta^{15}\text{N}$ values, from 5.3 to 8.2‰,

are similar to those of herbivores, which could indicate a specific herding strategy with foraging based mainly on plants rather than on the usual human waste. Suid $\delta^{13}\text{C}$ values exhibit a wide dispersion from -20.4 to -14.7‰ defining two clusters, one with a median value around -20‰ and a second around -15‰. These suid specimens from settlement excavations would therefore be more representative of food resources actually consumed by humans. Thus, without rejecting a possible different geographical origin, a herding practice in a free pasture (wild environment with C_4 -plants) could explain the cluster with the highest $\delta^{13}\text{C}$ values. Outside Georgia, only two KA sheep/goat individuals from Kalavan and Mentesh Tepe are available, presenting similar isotopic values with the values of Georgian herbivores (table 5; fig. 6; Herrscher et al. 2018b).

At Kvatskhelebi and Chobareti, cereals $\delta^{13}\text{C}$ values are between -25.1 and -20.5‰ ($-22.8 \pm 0.8\text{‰}$, $n = 24$), and $\delta^{15}\text{N}$ values range between 3.3 and 8.1‰ ($6.5 \pm 1.5\text{‰}$, $n = 24$). For both sites, wheat values appear higher for $\delta^{13}\text{C}$ and lower for $\delta^{15}\text{N}$ compared to barley values. The same significant pattern is observed at Mentesh Tepe (figs. 4C, D). Mann-Whitney tests confirm a significant difference for both isotopic ratios between the two types of cereal when sites are pooled (p - $\delta^{13}\text{C}$ and p - $\delta^{15}\text{N} < 0.014$; figs. 4A, B).

Modification of $\delta^{13}\text{C}$ values with altitude is mentioned for different organisms with an increase of around 1.0-1.5‰ per 1,000 m (Heaton 1999; Hobson et al. 2003). No such strong effect has been reported for nitrogen stable isotope ratios (Ambrose 2000; Hobson et al. 2003). Other local environmental conditions, such as aridity, densification of vegetation cover, and soil composition, may have impacted plants’ stable isotope ratios and, consequently, those of consumers. For instance, aridity and the use of manure are known to increase plant nitrogen stable isotope ratios (Schwarcz et al. 1999; Bogaard et al. 2007), whereas forested cover can decrease both carbon and nitrogen stable isotope ratios (van der Merwe and Medina 1991; Rodière et al. 1996; Bonafini et al. 2013). Considering the distribution of these sites across the Caucasus, with the low altitude of Natsargora, Kvatskhelebi, and Mentesh Tepe below 800 m asl, in contrast to all the other sites above 1,200 m, we can ask if environmental factors might influence the isotope ratios recorded at different archaeological sites. To evaluate this hypothesis, we tested the correlation between isotopic data and altitude (fig. 5). Despite a wide dispersion of human and animal (grouped per species) isotopic values, results show no correlation over 0.38 between the two variables (figs. 5A,D). For cereals, wheat $\delta^{13}\text{C}$ values show an intermediate correlation of 0.64 (figs. 5E-F); however, the analysis is not robust enough to conclude a relationship between isotope

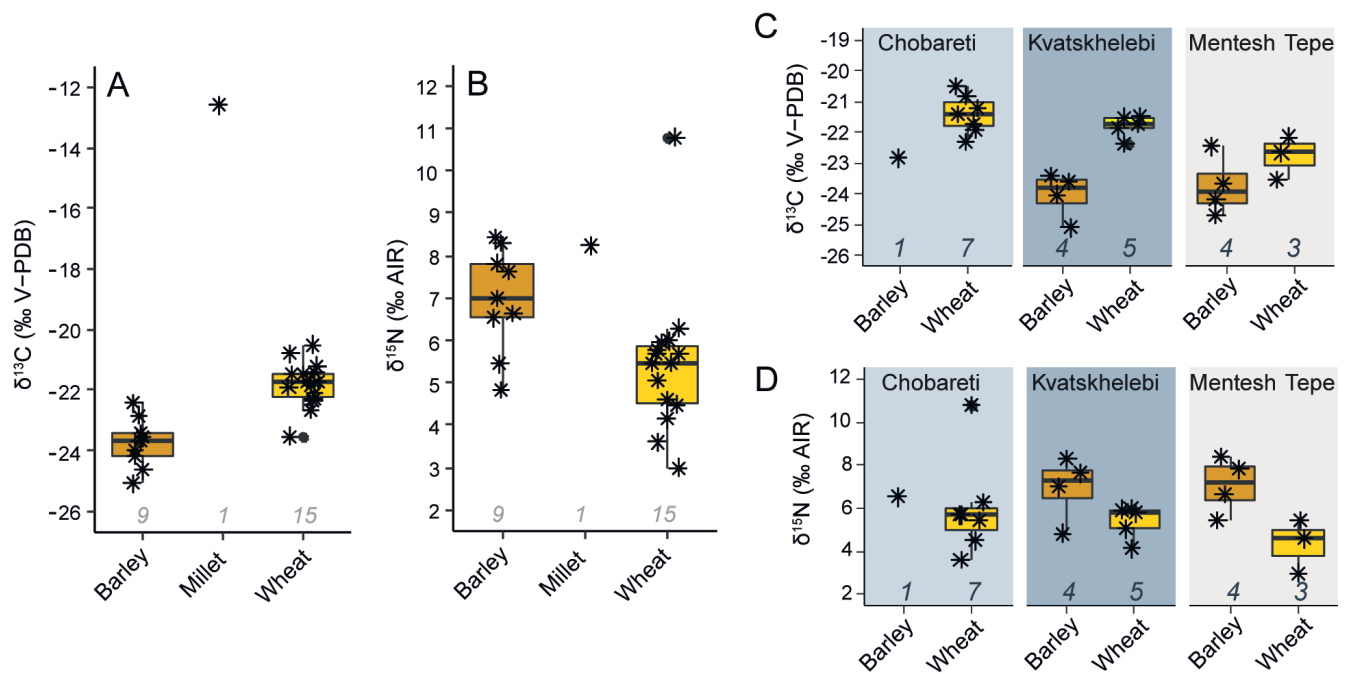


Fig. 4 – Carbon and nitrogen isotope ratios for cereals from Caucasian archaeological sites. Chobareti and Mentesh Tepe sites data from Messenger et al. 2015; Herrscher et al. 2018. Box-plot corresponds to median, Q1, Q3, with min, max, and outliers.

ratios and altitude. These results were unexpected since samples were numerically well represented and accounted for a significant altitudinal gradient from 335 m asl for Mentesh Tepe in Azerbaijan to 2,124 m asl for Gegharot in Armenia, and raises the question of geographical specificity. The diverse ecological niches (Messenger et al. 2020), combined with temperature and precipitation changes in the highlands during the 4th millennium BC (Connor and Kvavadze 2014), may have masked an altitudinal gradient effect on isotopic data. On the other hand, barley and wheat show consistent isotopic trends in all the sampled archaeological sites, regardless of their altitude (fig. 4), confirming their independence from the altitudinal gradient, which raises the question of a “universal” difference between both types of cereals that needs to be tested further in other geographical contexts and periods.

A warmer and more humid climate in the highland steppes during the 4th and 3rd millennium BC (Connor and Kavavadze 2014; Hovsepyan 2015) could echo our isotopic results with a uniform isotopic trend from the middle Kura valley to the Samtskhe-Javakheti highlands, as evidenced in the isotopic pattern of cereals. Our results suggest that climate change could provide a reasonable explanation for the stability of isotope ratios of animal and plant resources in relation to altitude in the South Caucasus. In addition, the results could also support the presence of similar traits in the daily life and

farming practices of KA communities throughout the South Caucasus, regardless of the various altitudes and ecological niches. The isotopic value recorded in bone tissue corresponds to an averaged signal from the last years of the individuals’ life; thus, the value’s lack of isotopic distinction between contrasting habitats does not strictly reject a seasonal, cyclical lifestyle between highland and lowland habitats.

As no consistent difference appears with geographical location and altitude, the isotopic variability of the resources was calculated by grouping the individual animal and plant data throughout the KA period and in the South Caucasus region to increase the statistical robustness. Thus, the isotopic baseline of KA food resources for the South Caucasus includes:

- Two plant resources (barley and wheat) to identify their relative contribution to the human diet with a higher enrichment in ^{15}N and lower enrichment in ^{13}C for barley consumers;
- “Herbivore meat” with typical $\delta^{13}\text{C}$ values of a C_3 -environment, combined with $\delta^{15}\text{N}$ ratios, may allow the identification of consumers of “cattle and sheep/goat meat” expected with higher values, and consumers of “wild herbivore meat/hunted meat” expected with lower values;
- The “suid meat” with higher carbon isotope values may identify pork meat consumers (fig. 6).

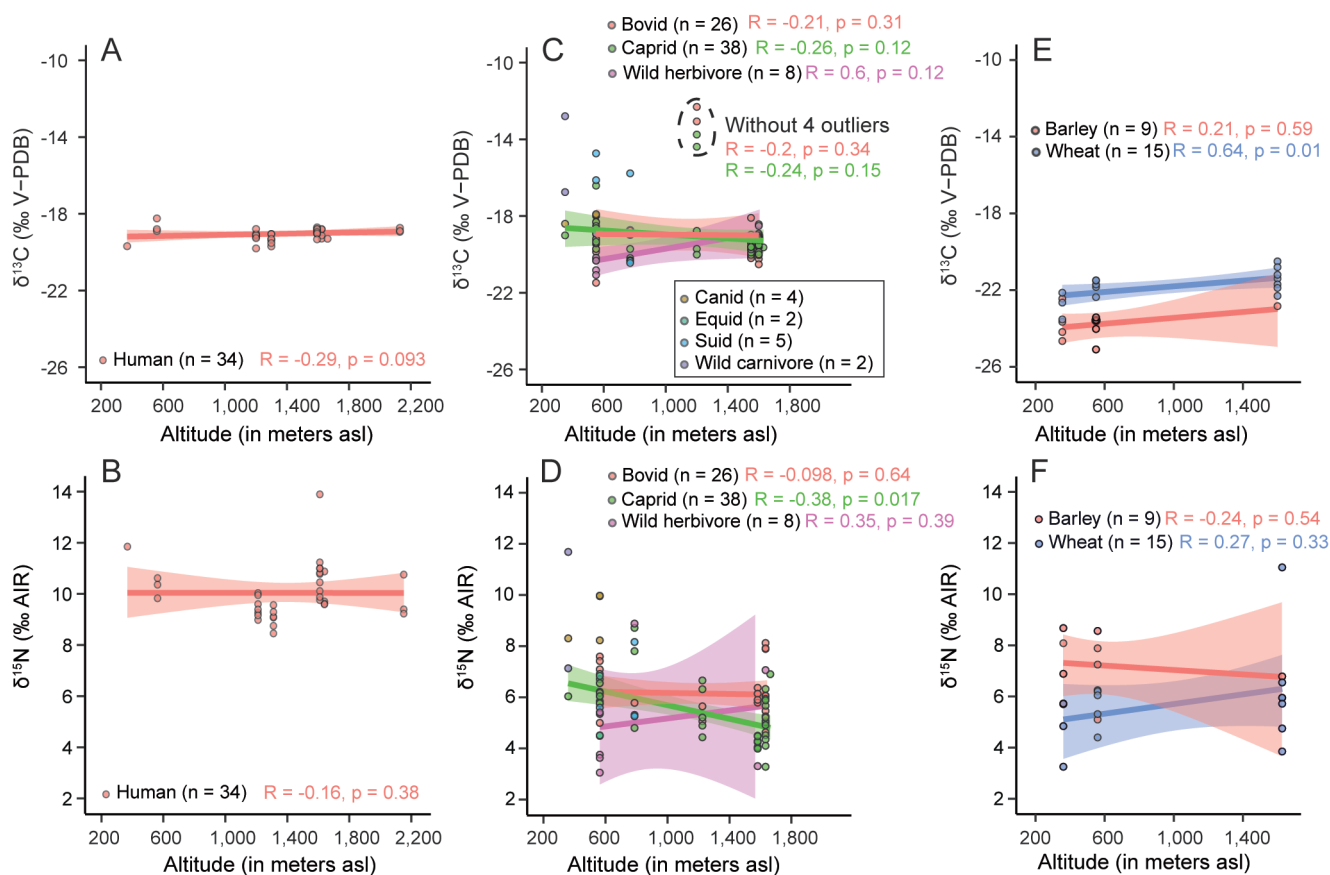


Fig. 5 – Carbon and nitrogen stable isotopic ratios according to the altitude of archaeological sites for Kura-Araxes humans (A, B), fauna (C, D) and cereals (E, F) across the southern Caucasus ($n = 144$).

KURA-ARAXES DIETARY PRACTICES IN THE SOUTHERN CAUCASUS

The maximum dispersion of human $\delta^{15}\text{N}$ values from Georgia was identified for highland individuals ranging from 8.5 to 13.9‰, as already discussed elsewhere (Messenger et al. 2015; Herrscher et al. in press; fig. 6). Even if an overlap exists between each series, the mean value increases significantly from Tiselis Seri and Kiketi to Chobareti without being explained by a significant difference in their dietary behaviour (Diff- $\delta^{15}\text{N} = 9.0/9.5$ to 10.9‰ p- $\delta^{15}\text{N} = 0.008$). Kvastkhelebi individuals are in the upper dispersion of human $\delta^{15}\text{N}$ values from Georgia, ranging from 9.8 to 10.5‰ , and overlap of Kiketi and Chobareti isotopic distribution (table 6; fig. 6). For carbon, a significant difference of 0.5‰ was observed only between humans of Tiselis Seri and Chobareti. Considering humans pooled into two groups (< 700 m asl and > 1,200 m asl), carbon isotope ratios exhibit a substantial overlap, with values ranging from -19.8 to -18.1‰ for the highland, and -18.9 to

-18.2‰ for the lowland sites, in agreement with a lack of significant isotopic difference between both altitude groups (p- $\delta^{13}\text{C} = 0.13$).

The 8‰ carbon isotopic range of food resources (animal and cereal) is much greater than the 2‰ human range, indicating a low range of human dietary choice in contrast to the wide isotopic range of food resources (fig. 6). Bearing in mind the theoretical isotopic fractionation (= enrichment factor in heavy isotope) expected between two consecutive trophic levels (food-consumer: $0\text{-}2\text{‰}$ for carbon, and $3\text{-}5\text{‰}$ for nitrogen; Bocherens and Drucker 2003), preferential consumption of herbivore meat (such as cattle, sheep or goat) associated with an insignificant consumption of suid meat, might be proposed to explain KA human isotope variability (fig. 6). In addition, the narrow range of human carbon values could also be explained by a significant consumption of cereals, in the form of bread and “porridge”, as a dietary staple. Therefore, the best candidate regarding the isotopic fractionation between food-consumers would be the barley. High-proportion

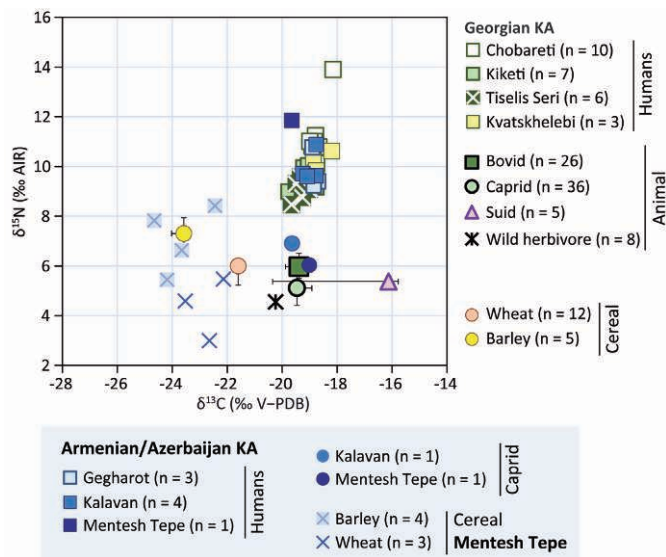


Fig. 6 – Human, animal and cereal carbon and nitrogen isotope ratios for Caucasian archaeological sites. Kiketi, Tiselis Seri, Chobareti and Mentesh Tepe sites data from Messenger et al. 2015; Herrscher et al. 2018, in press.

consumption of barley will induce much higher nitrogen values and lower consumer tissues' carbon values, fitting perfectly with the Kvatskhelebi and Chobareti isotopic data, whereas wheat consumption would have significantly increased the carbon values of consumer tissues.

At the broader regional scale of the southern Caucasus, the two Armenian and Azerbaijani caprid overlap the isotope variability of Georgian herbivores, as they do Armenian and Georgian human isotope data. The parsimonious interpretation to explain the comparable distribution between food-consumers would be similar dietary practices throughout the South Caucasus. As explained above, the subsistence strategies would reflect a selection of food products based on a preferential contribution of herbivore meat and barley grains to their diet. Pork consumption is still difficult to confirm due to the scarcity of isotope values for the Caucasian zone. For example, further analyses are needed to explain the two groups of suids formed by the five specimens in our study (fig. 3A). Are they related to different husbandry strategies based on a biological criterion? Or could this indicate a species identification problem with a mixture of domestic pig and wild boar, as observed in other Neolithic and Late Bronze Age Caucasian sites (Herrscher et al. 2014, 2015)? The low contribution of suid to the diet suggested by our isotopic results echoes the archaeological data, which suggests that the KA peoples' interest in pigs was low compared to cattle and sheep/goat. Moreover, Decaix et al. (2019) reported the sole presence of pigs at Natsargora based on

the comparison of eight KA sites' faunal assemblages, which raises the question of the animal's status in the KA economy. Furthermore, archaeological datasets reveal a low presence of wild animal remains in the KA sites, consistent with isotopic results not precise enough to identify the consumption of hunted resources by human consumers (Decaix et al. 2019).

Although evidence of fishing and fish consumption is scarce in the entire KA context, the geographical scale of this study with numerous waterways, freshwater resources could potentially be of great interest for protein intake in humans. Freshwater fish consumption could therefore be a possible explanation, especially for the KA individual from Mentesh Tepe, given the isotopic baseline established for this region and its highest nitrogen isotope value (fig. 6). The available modern isotope values of cyprinids from the Kura River (median values: $\delta^{13}\text{C} = -18\text{‰}$; $\delta^{15}\text{N} = 3,8\text{‰}$, $n = 2$) and the Khrami river around Tbilisi (median values: $\delta^{13}\text{C} = -22\text{‰}$; $\delta^{15}\text{N} = 10\text{‰}$, $n = 5$), relevant for the Kvatskhelebi series, located on the Kura riverbank, show no overlap with the expected human isotope values for this type of consumption, suggesting that fish was not a preferred food for these people. This interpretation would also agree with recent archaeological results on fish consumption at Tel Bet Yerah/Khirbet el-Kerak in Israel, where KA migrants settled ca. 2,850 BC (Lerneau et al. 2021). In the context of the highland and lowland series, a more specific local baseline would be needed to specifically document freshwater fish and discuss its contribution to KA communities' diet.

Despite no consolidated local isotope baseline being available for Armenia and Azerbaijan, comparison of the Georgian, Armenian, and Azerbaijani sites shows an apparent homogeneity of isotope data that would suggest a uniform KA model, implying similar dietary intake among KA communities. The diet of KA communities in the southern Caucasus seems to be characterised by a low range of dietary practices both within and between groups, which raises the question: could this apparent isotope homogeneity result from a decrease in the availability of food resources (climate/environmental factor), or from a reduced human choice/preference for specific domestic resources (cultural factor)? Since the South Caucasus is characterised by diverse climatic and geographic environments, with a high food isotopic variability in contrast with humans, and no observable spatial food trends, the most parsimonious interpretation would be to advocate for deliberate cultural choices.

To further test the isotopic homogeneity of this dietary model at the intra-population level and over time, investigating additional factors (e.g., biological, social), as well as the diachronic evolution of the variables, would help consolidate this hypothesis.

THE BIOLOGICAL AND TEMPORAL DIMENSION OF THE ISOTOPIC DATA

In order to identify the impact of demographic variables on dietary habits, age at death (adult/subadult) and sex (male/female) were determined for the human skeletons to evaluate the inter-individual isotope variability (Poulmarc'h 2014). The one-year-old child from Chobareti exhibits the highest nitrogen isotope values (13.9‰) consistent with breast milk consumption. Significantly higher carbon isotopic values were observed only for subadults in comparison to adults (fig. 3). Based on the coxal bone, the sex of seven individuals (four females and three males), out of 30 adults, could be diagnosed with the highest probability (Bruzek 2002; Murail et al. 2005). This small sample size prevented any significant statistical test by sex; however, a substantial overlap of data between sexes was observed for both carbon and nitrogen ratios (figs. 7A1, B1). Similarly, the analysis of funerary practices in Shida Kartli and Kvemo Kartli (Poulmarc'h 2014), among others, shows a high variability of funerary architecture (pit, ceramic vessel,

box in perishable material, variable shape in stone) and burial practices (single or collective). No isotopic clusters were identified in the KA communities based on these variables (figs. 7A3, B3). Furthermore, if we assume that the individuals buried in collective graves were linked together by some specific ties (such as kinship), the homogeneity of diets should apply to the members of the same social (possibly kinship-based) groups. According to our results, we can conclude that neither biological nor social factors influenced the homogeneity of the food practices among the KA communities. Conversely, the lack of diet distinctions could mirror the lack of social inequalities regarding access to food resources. Thus, the homogeneity of diets could be a consequence of the KA social organisation.

Based on the funerary practices, the social organisation does not seem structured according to individual status or hierarchical differences. Instead, groups appear to be structured on family and kinship ties which potentially reflects an egalitarian social model. There is also compelling evidence from settlements showing a household-based society with no

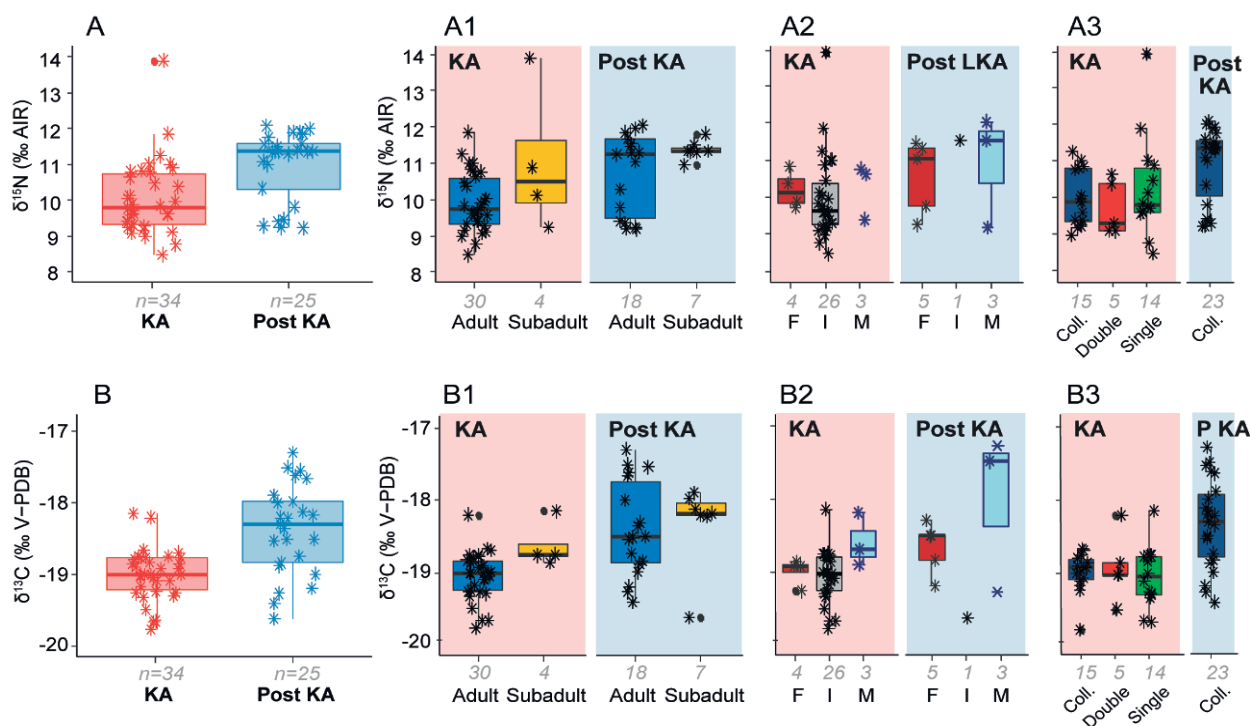


Fig. 7 – Human carbon and nitrogen isotope ratios for KA and Post-KA Caucasian archaeological sites according to several biological and funerary criteria. **A, B.** Isotopic distribution of pooled data. **A1, B1.** Isotopic distribution according to age groups. **A2, B2.** Isotopic distribution according to the sex. **A3, B3.** Isotopic distribution according to the type of burial. Coll. = collective, double, single; previously published data from Messenger et al. 2015; Herrscher et al. 2015, 2018, in press; Box-plot corresponds to the median, Q1, Q3, with min, max, and outliers.

socio-economic differentiation. The radiocarbon dates from seven KA sites with human remains examined in this paper cover the entire chronological span of the KA culture (from 3400 BC with Chobareti, then Gegharot 3,100-2,900 BC, Natsargora 3,100-2,850 BC, Kiketi 3,000-2,800 BC, Kvatskhelebi 2,900-2,700 BC, Tiselis Seri 2,800-2,600 BC, to 2,500 BC with Mentesh Tepe and Kalavan). The minimal isotopic difference measured between the individuals from these sites over the entire period suggests a diachronic persistence of dietary practices more focused on a preferential consumption of herbivores meat than pig meat, and barley rather than wheat, consistent with a previous archeozoological and archaeobotanical study (Decaix et al. 2019). Regarding the low dispersion of human isotopic data in contrast to animal and vegetal local baselines, we propose that a cultural homogeneity of KA subsistence strategies may have been the norm, with the persistence of a long-term “conservative” diet over one millennium. This diachronic stability/homogeneity of subsistence strategies and diets could correspond to an unchanging set of dietary practices and food-consumption patterns over time.

To explore the evolution of KA dietary homogeneity, comparative analyses were performed using published data on the post-KA/Early Kurgans period from Ananauri (Herrscher et al. 2016), Mentesh Tepe (Herrscher et al. 2018), and the subadult individual from Aknashen (Tr7 UF5 F2; Poulmarc'h 2014). In the data pooled by periods, the post-KA/Early Kurgans individuals exhibited higher carbon and nitrogen isotopic ratios than the KA individuals (p -values < 0.000; figs. 7A-B). In addition to different medians, the dispersion of data was also different, indicating a higher diversity of food resources consumed by post-KA/Early Kurgans individuals. Although there are no significant differences among age groups (figs. 7A1,B1), subadults are clustered and display low dispersion in the upper limit of adult variability for both carbon and nitrogen values. Finally, males show the highest dispersion of carbon and nitrogen values, which could be linked to greater human mobility of the post-KA/Early Kurgans individuals than observed among the KA people (figs. 7A2,B2). This isotopic dispersion is clearly visible in the Ananauri and Mentesh Tepe examples. For the Aknashen individual, the isotopic baseline is not documented enough to confirm this pattern. In summary, the KA isotopic characteristics described in this study seem to end during the following period with the emergence of the Martqopi and Bedeni cultures, thus clearly distinguishing KA communities' dietary specificities.

CONCLUSIONS

Contrary to the previous Neolithic (Herrscher et al. 2018) and the following post-KA/Early Kurgans (Herrscher et al. 2016) cultures, the dietary practices of the KA populations show a low dietary breadth, with preferential consumption of herbivores meat instead of pig meat, and extensive consumption of cereals (mainly barley). The low inter- and intra-group isotopic diversity has been interpreted as homogeneous dietary practices and a willingness to not discriminate between individuals within the group. This outcome would support normative dietary practices adopted by the KA communities that may reflect equal access to the same food resources regardless of biological, geographical, chronological, and social variables. Could these shared dietary traits have actively shaped the construction of the KA social and cultural identity?

Regarding the social sphere, the evidence for equal access to food corroborates the archaeological narrative suggesting no signs of socio-economic inequality in the funerary and residential contexts, as well as no political hierarchies. Thus, the KA communities appear to have been very cohesive and composed of undifferentiated, probably kin-based, social groups. Furthermore, the strong normative characterisation of the KA dietary habits is also reflected in food preparation and consumption practices and the associated material culture. Several authors have suggested (Sagona 2018) that some of the most conservative traits of the KA tradition are those expressed by a very distinctive “food-related” material culture such as pottery. Furthermore, the extensive geographical spread and diachronic persistence of the distinctive morpho-functional repertoires of the ceramic containers throughout the South Caucasus, coupled with the new aesthetics that could have enhanced the symbolic role of the containers, point to a strong link between ceramic traditions and daily practices of food processing and food consumption. Greenberg (2007) suggested that the KA ceramics' functions and colour codes seem to have been aimed at “structuring the cultural attitudes to food and cooking” and eventually at strengthening a kind of KA cultural identity through dietary practices. Moreover, the centrality of fire installations in the domestic space, yet another distinctive feature of the KA culture, may have played an active role in entwining practical and symbolic activities attached to cooking and food consumption.

The isotopic data presented in this research strengthens this argument by demonstrating a precise set of dietary traits and normative food-ways adopted by the KA communities. This innovative study complements the picture emerging from

archaeozoological and archaeobotanical results throughout the KA culture. The dietary habits outlined here could have acted as practical and symbolic means structuring and defining KA social and cultural identity. Food and related habits could have worked powerfully at the individual and collective levels, in the construction and persistence of a sense of group-membership across generations. Eventually, dietary practices actively shaped some of the most distinctive traits of the KA material culture. The continuity of traditional eating practices further supports this interpretation, in the scattered contexts of the KA sphere in Iran or Anatolia communities (Greenberg 2007; Greenberg and Goren 2009; Paz 2009; Longford 2015). Future isotopic studies ($\delta^{34}\text{S}$, $\delta^{18}\text{O}$, $^{87}\text{Sr}/^{86}\text{Sr}$) in these areas will hopefully provide further insights into the substantial existing evidence. The case of the Kura-Araxes communities is thus an exceptional example of the ways food and cultural identity are mutually constituted and tightly entangled. This study also demonstrates the fundamental benefits of food and dietary practices studies in archaeology for revealing society's operating principles.

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CONCLUSION

Il y a vingt-cinq ans, Bernard Vandermeersch éditait un numéro thématique de *Paléorient* consacré à l'anthropologie. Intitulé *Anthropology in the Middle East. Recent advances*¹, le volume tentait de faire le point sur le peuplement du Moyen-Orient au Pléistocène supérieur en impliquant des paléo-anthropologues des États-Unis, du Japon, de Grande-Bretagne, d'Israël et de France. Ce numéro proposait une perspective globale sur les aspects phylogénétiques et funéraires des populations préhistoriques et indiquait les orientations futures de la recherche en paléoanthropologie dans la région.

Ce nouveau numéro spécial de *Paléorient* consacré à l'anthropologie rassemble des contributions évoquant certains aspects des progrès réalisés dans l'étude de la biologie des populations du passé au Proche-Orient et dans les régions voisines (par ex. Méditerranée orientale, Caucase du Sud). Le volume opte donc pour une perspective géographique plus large et se place dans le contexte des populations pré- et protohistoriques, en se concentrant sur l'évolution du régime alimentaire et de l'état de santé, en relation avec les changements sociétaux majeurs apparus entre le début de la sédentarisation et l'âge du Bronze ancien.

Au cours des trente dernières années, de nombreuses fouilles menées dans la région ont livré de grandes quantités de restes humains. En dépit de cela, les populations anciennes « post-paléolithiques » étaient, jusqu'à récemment, mal connues en termes de pratiques mortuaires, de démographie, de nutrition et d'état de santé. Plusieurs raisons expliquent cette situation : une attention globalement moindre pour les découvertes « post-paléolithiques » qui n'étaient pas d'un intérêt primordial pour les chercheurs ; les conditions de conservation des collections ostéologiques qui étaient souvent dispersées dans différentes institutions ; la prévalence des études visant à établir uniquement l'identité biologique (âge, sexe) ; et enfin, le choix, heureusement de plus en plus rare, de réserver l'analyse anthropologique à une annexe de la monographie du site.

En 2010, le 7^e Congrès international sur l'archéologie du Proche-Orient ancien (ICAANE), qui s'est tenu à Londres, a été le premier à inclure un atelier spécifique consacré à l'étude des squelettes humains. Si un tel atelier a pu être organisé, cela

Twenty-five years ago, Bernard Vandermeersch edited a special thematic issue of Paléorient dedicated to anthropology. Entitled Anthropology in the Middle East. Recent advances,¹ the volume attempted to furnish state-of-the-art statements on Later Pleistocene peopling in the Middle East and involved paleoanthropologists from United States, Japan, Great Britain, Israel and France. It included a comprehensive perspective on the phylogenetic and funerary aspects of prehistoric populations and pointed towards future directions for paleoanthropological research.

This new special issue of Paléorient dedicated to anthropology intends to gather contributions that evince some aspects of the progress in studies of past human population biology in the Near East and the nearby regions (i.e., Eastern Mediterranean, South Caucasus). The volume therefore opts for a broader geographical perspective and places itself in the context of pre- and proto-historic populations, focusing on the evolution of diet and health status in relation to the major societal changes that appeared between the beginning of sedentarisation and the Early Bronze Age.

Over the last thirty years, numerous excavations conducted in the region produced large quantities of human skeletal remains. Despite this, "post-Paleolithic" ancient populations were, until recently, poorly understood in terms of mortuary practices, demography, nutrition and pathological conditions. There are several reasons for this situation: an overall less attention overall in "post-Paleolithic" finds that were not of primary interest to investigators; the conditions of conservation of osteological collections which were often dispersed among different institutes; the prevalence of studies designed for establishing only biological identity (age, sex); and finally, the choice, fortunately more and more rare, to reserve anthropological analysis for an appendix to the expected monograph of the site.

In 2010, the 7th International Congress on the Archaeology of the Ancient Near East (ICAANE) held in London was the first one to include a specific workshop dedicated to studies of human skeletons. If such a workshop could be held, it means that human remains were beginning to be considered as an

1. 1996 – Anthropology in the Middle East. Recent advances. *Paléorient* 21.1. [En ligne] https://www.persee.fr/issue/paleo_0153-9345_1995_num_21_2

signifie que les restes humains commençaient à être considérés comme faisant partie intégrante des découvertes archéologiques. Des avancées significatives ont été réalisées en ce qui concerne la reconstitution du mode de vie des populations anciennes du Proche-Orient ancien et des régions voisines, du Paléolithique aux périodes historiques. L'objectif du présent volume était donc de bénéficier des résultats obtenus par les auteurs dans différents contextes et de souligner en quoi les études de l'alimentation et de l'état de santé représentent une composante significative des recherches archéologiques et anthropologiques, en particulier pour les périodes marquées par de profonds changements dans les modes de vie, comme les débuts de l'agriculture.

Les articles de ce volume présentent des recherches récentes qui développent des études innovantes reposant sur l'analyse d'os et de dents humains. Outre les observations directes, ces études font appel à diverses techniques analytiques (microscopie électronique, imagerie médicale permettant d'accéder aux structures internes, reconstitution tridimensionnelle, analyse des isotopes stables). Elles fournissent des informations essentielles sur la structure, la morphologie, les maladies, les pratiques alimentaires, les activités et les habitudes culturelles des populations anciennes de la zone étudiée.

À travers une étude diachronique portant sur la période allant du Levant du début du Natoufien au début du Néolithique céramique (Nord)/fin du Néolithique précéramique (Sud), basée sur l'analyse de la fréquence des hypoplasies linéaires de l'émail dentaire sur un large échantillon d'individus, A. Stutz et ses collègues soulignent que la transition vers l'agriculture a conduit à une augmentation de la mortalité prématurée dans tout le Levant. Ils suggèrent que la mortalité et la fécondité se soient développées selon une dynamique fragile, dont l'équilibre s'est rompu au cours du VII^e millénaire av. J.-C., avec une augmentation spectaculaire du stress biologique au début de la vie et une péjoration de l'état de santé général.

Dans une étude chronologiquement plus large s'étendant jusqu'à la population ottomane du Levant, I. Hershkovitz et ses collègues exposent des exemples de la façon dont les changements dans l'habitat et dans le régime alimentaire ont affecté la morphologie des os longs, en particulier la proportion d'os cortical du fémur et la configuration de la mandibule. Ils rapportent également des variations dans le taux d'inflammation de l'oreille parmi les populations étudiées.

Les questions relatives à l'état de santé sont également abordées, selon diverses approches, dans les articles d'A.-M. Tillier (populations pré-sédentaires), B. Chamel, J.O. Baker et collaborateurs, F. Le Mort et H. Duday (populations néolithiques). A.-M. Tillier présente des anomalies de développement, nombreuses et variées, observées chez les

integral part of the archaeological findings. Significant advances have been made with regard to the reconstruction of lifestyle of past populations inhabiting the Ancient Near East and the nearby regions from the Paleolithic to the historical periods. Thereby the aim of this volume was to benefit from the experience gained by the contributors in different settings, and to stress that analyses of diet and health status represent a meaningful component of archaeological and anthropological research, especially for periods marked by profound changes in lifestyles, such as the beginnings of agriculture.

The articles in this volume present recent research developing innovative studies based on the analysis of human bones and teeth. In addition to direct observations, these studies use various analytical techniques (electron microscopy, medical imaging allowing access to internal structures, three-dimensional reconstruction, stable isotope analysis). They yield essential information about the structure, morphology, diseases, dietary practices, activities and cultural habits of past populations in the studied area.

Through a diachronic study regarding the period ranging from the beginning of the Natufian to the beginning of the Pottery Neolithic (North)/end of the Pre-Pottery Neolithic (South) in the Levant, based on the analysis of the frequency of linear enamel hypoplasias on a large sample of individuals, A. Stutz and colleagues point out that the transition to agriculture led to an increase of premature mortality throughout the Levant. They suggest that mortality and fertility developed in a fragile dynamic, the balance of which broke in the 7th millennium BC, with a dramatic increase in early life biological stress, and a reduction in general health status.

By means of a chronologically larger study extending to the Ottoman population of the Levant, I. Hershkovitz and colleagues present examples of how changes in the habitat and diet have affected the morphology of long bones, especially the relative femoral bone cortical area, and the mandibular shape. They also report variations in the rate of ear inflammation among the populations they studied.

Health status issues are also addressed, using various approaches, in articles by A.-M. Tillier (pre-sedentism populations), B. Chamel, J. O. Baker and colleagues, F. Le Mort and H. Duday (Neolithic populations). A.-M. Tillier reports on numerous and varied developmental abnormalities observed in the Middle Paleolithic hunter-gatherers from Qafzeh (Israel). J. O. Baker and colleagues present a new possible case of tubercular infection from the Early PPNB level of Tell Aswad (Syria), thus increasing the number of paleopathological cases of tuberculosis dating from the early phases of

chasseurs-cueilleurs du Paléolithique moyen de Qafzeh (Israël). J.O. Baker et ses collègues s'intéressent à un nouveau cas possible d'infection tuberculeuse provenant des niveaux PPNB ancien de Tell Aswad (Syrie), augmentant ainsi le nombre de cas paléopathologiques de tuberculose datant des premières phases du processus de néolithisation. F. Le Mort et H. Duday décrivent le plus ancien cas probable de maladie hyperostotique (DISH) connu à Chypre, fournissant ainsi de nouvelles données sur la distribution préhistorique d'une maladie qui a rarement été identifiée parmi les populations préhistoriques, en particulier dans la région de la Méditerranée orientale et du Proche-Orient.

Outre ces nouvelles informations relatives à l'ancienneté des maladies des os et des tissus mous au Levant et à Chypre, les études dentaires fournissent également de nouvelles données essentielles sur la santé bucco-dentaire (A.-M. Tillier, B. Chamel) ainsi que sur les activités et les habitudes culturelles (Y. Erdal) des populations anciennes du Proche-Orient.

Il est communément admis que la fréquence plus élevée des caries après le Paléolithique résulte à la fois de la diffusion de l'agriculture (lorsque la nourriture est devenue riche en hydrates de carbone) et de l'augmentation de la durée de vie. Au Levant Sud, l'incidence des caries dentaires chez les chasseurs-cueilleurs du Paléolithique moyen est maintenant bien connue (A.-M. Tillier). Le nombre d'observations reste cependant trop faible pour conclure que l'immunité contre les caries était plus faible chez les hominines du bassin méditerranéen oriental au Paléolithique moyen que chez les autres habitants pénécotemporains de l'Eurasie.

L'article de B. Chamel présente une analyse diachronique des changements de l'état de santé dentaire en Syrie, du PPNA au Néolithique céramique. Cette étude révèle qu'au cours du processus de néolithisation, les changements intervenus dans l'état de santé bucco-dentaire, en lien avec l'adoption de l'agriculture et de nouveaux modes de préparation des aliments, ont été moins linéaires qu'il n'y paraît à première vue.

L'utilisation des dents comme outils a été étudiée dans diverses régions du monde et pour diverses périodes, mais on ne savait presque rien sur cette pratique dans le Proche-Orient pré- et protohistorique. Le potentiel de l'analyse des modifications dentaires pour l'identification des activités des populations du Proche-Orient est bien illustré par la contribution d'Y. Erdal concernant l'abrasion dentaire induite par l'activité dans l'Anatolie préhistorique. Cette étude fournit quantité de nouvelles informations sur cette utilisation spécifique des dents, sur sa réduction du Néolithique au début de l'âge du Bronze probablement liée à des changements de mode de vie, ainsi que sur les différences de genre qu'elle fait apparaître.

the Neolithization process. F. Le Mort and H. Duday describe the oldest probable case of diffuse idiopathic skeletal hyperostosis (DISH) known in Cyprus, adding new data to the prehistoric distribution of a disease which has rarely been identified among prehistoric populations, especially in the Eastern Mediterranean and Near East region.

Besides this new information related to the antiquity of bone and soft tissue diseases collected in the Levant and Cyprus, dental studies also provide important and new data about the dental health status (A.-M. Tillier, B. Chamel) as well as the activities and cultural habits (Y. Erdal) of the ancient populations of the Near East.

There is a common agreement that a higher caries frequency in post-Paleolithic times is a consequence of both the spread of agriculture (when the food became rich in carbohydrates) and the increase in life span. In the southern Levant, evidence for incidence of dental caries relevant to Middle Paleolithic hunter-gatherers is now documented (A.-M. Tillier). Yet, the number of observations remains too small to conclude that caries immunity was lower among Middle Paleolithic hominins from the eastern Mediterranean Basin than among other Eurasian penecontemporary inhabitants.

The paper by B. Chamel presents a diachronic perspective of changes in dental health status in Syria from the PPNA to the Pottery Neolithic. This study reveals that changes in oral health were less linear during the Neolithization process as it appears at first glance and that the adoption of agriculture and methods of food preparation were important factors influencing dental health status.

The use of teeth as tools has been studied in various regions and for various periods all around the world but almost nothing was known on this topic for the pre- and protohistoric Near East. The potential of the analysis of tooth changes for the identification of activities of past Near Eastern populations is well illustrated by the contribution of Y. Erdal regarding activity induced dental abrasion in prehistoric Anatolia. This study provides a wealth of new information on this specific use of teeth, on its decrease from the Neolithic to the Early Bronze Age probably related to changes in lifestyle, as well as on the gender differences it reveals.

As far as the Near East and nearby regions are concerned, nutritional approaches such as stable isotope analysis are not numerous. They are now developing, leading to very promising results, as shown by the article by E. Herrscher and colleagues. Based on isotopic analysis of human, animal and cereal remains from archaeological sites dated to the Early Bronze Age (Kura-Araxes culture) in the South Caucasus, this study allows the authors to characterize the dietary habits of the

En ce qui concerne le Proche-Orient et les régions voisines, les approches nutritionnelles telles que l'analyse des isotopes stables ne sont pas nombreuses. Elles se développent aujourd'hui et donnent des résultats très prometteurs, comme le montre l'article d'E. Herrscher et collaborateurs. Fondée sur l'analyse isotopique de restes humains, animaux et de céréales provenant de sites archéologiques datés de l'âge du Bronze ancien (culture Kuro-Araxe) dans le Caucase du Sud, cette étude permet aux auteurs de caractériser les habitudes alimentaires des sociétés Kuro-Araxe, de mettre en évidence leur homogénéité et de montrer en quoi l'alimentation et ses interactions avec les sphères environnementales, économiques, sociales et culturelles jouent un rôle important dans l'identité culturelle des communautés.

En conclusion, la multiplication de nouvelles recherches dynamiques sur le terrain et en laboratoire a permis une série d'avancées importantes dans la connaissance des populations anciennes du Proche-Orient et des régions voisines. Les recherches dans les différents domaines de l'anthropologie biologique, qui utilisent des techniques analytiques plus ou moins récemment développées, et qui deviennent de plus en plus partie intégrante de l'étude de l'histoire des populations, améliorent progressivement notre connaissance des interactions entre les changements profonds des modes de vie (comme la néolithisation) et des pratiques alimentaires ainsi que de leur impact sur l'état de santé des populations de cette région.

Nous sommes profondément reconnaissantes à Jean Guilaine d'avoir accepté notre invitation à présenter ce numéro. Nous remercions également sincèrement les collègues qui ont accepté de contribuer à ce volume. Enfin, nous savons gré à tous les relecteurs du temps qu'ils ont consacré à faire bénéficier le volume de leur expertise, permettant ainsi de l'améliorer.

Kura-Araxes societies, to evidence their homogeneity and to show how food and its interactions with the environmental, economic, social and cultural spheres play an important role in the cultural identity of communities.

To conclude, the increase in new dynamic field and laboratory investigations has led to a series of important advances in the knowledge of past populations of the ancient Near East and nearby regions. Research in the various fields of biological anthropology, using more or less recently developed analytical techniques, and becoming more and more an integral part of the study of the history of human population inhabiting the region, is gradually enhancing our knowledge of the interactions between profound changes in lifestyles (such as Neolithization) and dietary practices as well as their impact on the health status of populations in this area.

We are deeply grateful to Jean Guilaine for accepting our invitation to introduce this issue. We also sincerely thank the colleagues who contributed to the volume for their willingness to take part in it. Finally we acknowledge all the reviewers who gave their time and expertise to make this volume better.

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