Title
The Precarious State of Subsistence: Reevaluating Dental Pathological Lesions Associated with Agricultural and Hunter-Gatherer Lifeways

Journal
Current Anthropology, 60(3)

ISSN
0011-3204

Authors
Marklein, Kathryn E
Torres-Rouff, Christina
King, Laura M
et al.

Publication Date
2019-06-01

DOI
10.1086/703376

Peer reviewed

The Precarious State of Subsistence

Reevaluating Dental Pathological Lesions Associated with Agricultural and Hunter-Gatherer Lifeways

by Kathryn E. Marklein, Christina Torres-Rouff, Laura M. King, and Mark Hubbe

Online enhancements: supplemental table and references.

Numerous bioarchaeological studies emphasize an increase in dental lesions associated with the transition to agricultural subsistence. Over the years, this diachronic trend has led to the conflation and oversimplification of specific dental indicators of oral health with broad subsistence strategies, emphasizing intergroup variation at the expense of intragroup variation. In order to explore such hidden variation, this metastudy uses published data from 185 archaeological sites to test the hypothesis that the prevalence of dental lesions (carious lesions, antemortem tooth loss, and periapical abscesses) among classified agricultural groups is higher than among hunter-gatherers. As a secondary hypothesis, this study also tests the association between climatic variables (temperature variation, altitude, and precipitation) and dental lesion prevalence. Our results show that, despite significant differences in the average prevalence of carious lesions between agricultural and hunter-gatherer populations, the variation in caries prevalence shows high overlap (>70%) between subsistence patterns. Additionally, differences in the prevalence of antemortem tooth loss and periapical abscesses between agricultural and hunter-gatherer populations are not significant, showing even larger overlaps in prevalence ranges. Complementing the lifestyle analyses, climatic factors (mean temperature, annual temperature, and precipitation) are significantly correlated with the prevalence of specific dental pathological lesions and not others. Our results emphasize the need to reevaluate certain dental conditions as direct indicators of broad subsistence patterns, calling attention to the complex multifactorial pathogenesis of dental lesions and the nonlinear relationship between oral indicators of health and subsistence lifeways.

> *It is often—but falsely—said that dental caries is a "disease of civilization." There is no human population that has completely escaped it.* (Grmek 1989:115)

The emergence, development, and transition to agricultural subsistence economies is one of the major transformations in human history, and as such has inspired decades of bioarchaeological research across temporal and geographical expanses (e.g., Bocquet-Appel and Bar-Yosef 2008; Cohen and Armelagos 1984; Lambert 2000; Pinhasi and Stock 2011). In much early research, the socioeconomic movement toward agricultural practices was regarded as an improvement in human quality of life (Childe 1950, 1957). Agriculture was considered the landmark of civilization, and the abandonment of nomadic, mobile lifestyles for more stable, sedentary regimes was often defined as a revolution in modern human history (Braidwood 1960; Morgan 1877). Direct shifts toward primary food production instead of food acquisition correlated with population expansion, which, arguably, predicated increased social complexity (Gehlsen 2009). Agricultural lifestyles eventually predominated over all other human subsistence lifeways. The dominant paradigm held that the adoption of agriculture augmented fertility rates, extended life expectancies, and established roots for later civilizations, thus casting hunter-gatherer societies to a lower position in a linear social trajectory of human societies. In short, agriculture was argued to have promoted quality and extent of life (Boserup 1965; Hayden 1981; contra Cohen 1977, 1989).

However, during the second half of the twentieth century, this paradigm began to be criticized from several angles. At

Kathryn E. Marklein is Visiting Assistant Professor in the Department of Anthropology of the University of Louisville (Lutz Hall Room 228, Louisville, Kentucky 40292, USA [kathryn.marklein@louisville.edu]). **Christina Torres-Rouff** is Associate Professor in the Department of Anthropology in the School of Social Sciences Humanities and Arts of the University of California, Merced, and a department member of the Instituto de Arqueología y Antropología of the Universidad Católica del Norte (San Pedro de Atacama, Chile). **Laura M. King** is a former student researcher at Colorado College. **Mark Hubbe** is Associate Professor in the Department of Anthropology of Ohio State University (4074 Smith Laboratory, 174 West 18th Avenue, Columbus, Ohio 43210, USA), and Adjunct Professor, Instituto de Investigaciones Arqueológicas y Museo, Universidad Católica del Norte, Chile. This paper was submitted 09 VI 16, accepted 08 VI 18, and electronically published 15 V 19.

 0011-3204/2019/6003-00XX$10.00. DOI: 10.1086/703376

the 1966 "Man the Hunter" symposium, which marked the first comprehensive overview of contemporary hunter-gatherer societies, cultural anthropologists ushered in a new perspective for hunter-gather studies, challenging the established view that hunter-gatherer groups led "short, brutish" existences (Lee and DeVore 1968).

Focusing on human skeletal remains, studies in paleopathology and bioarchaeology also approached the agricultural transition, seeking to characterize the consequences—detrimental or ameliorative—that agricultural subsistence had on modern human populations throughout history (Brothwell 1963; Cohen and Armelagos 1984; Cook and Buikstra 1979; Goodman, Armelagos, and Rose 1980; Hillson 1996; Larsen 1995, 1997, 2015). In 1984, the conference on "Paleopathology at the Origins of Agriculture" brought the first generation of bioarchaeologists together to discuss the skeletal and dental changes associated with the transition from hunter-gatherer to agricultural subsistence strategies. The monumental work that resulted from this symposium, a hallmark publication and promising application of the discipline, presented a comprehensive synthesis of human bioarchaeological data and approaches to this significant question in recent human history (Cohen and Armelagos 1984).

"Paleopathology at the Origins of Agriculture" collated more than 30 regional osteological studies and demonstrated a collective application of specific skeletal biomarkers to cross-population comparisons of agricultural transitions (Cohen and Armelagos 1984, 2013; Goodman et al. 1984). Overall, results suggested declines in physiological health associated with the advent of agriculture, as reflected in the general increase of pathological lesion prevalences. These results strongly countered the simplistic view that the adoption of food production by human societies led to improvements in all aspects of human life. Subsequent compilations and reviews of the effects of the agricultural transition on health (Cohen and Crane-Kramer 2007; Larsen 1997; Pinhasi and Stock 2011) have largely supported the symposium results, showing similar patterns in pathological lesions and physiological adaptations correlated with the implementation and intensification of agricultural practices.

At the time of the symposium, bioarchaeology as a discipline was asserting its efficacy in identifying and contextualizing patterns in disease, nutrition, and interpersonal interactions within skeletal series (Zuckerman and Armelagos 2011). Skeletal biologists and paleopathologists were codifying biological age, sex, and pathological lesion standards in order to promote dialogue and comparative studies between varying skeletal assemblages (Aufderheide and Rodríguez-Martín 1998; Bass 1987; Buikstra and Ubelaker 1994; Brickley and McKinley 2004; Ortner and Putschar 1985). While these standardized suites, especially pathological lesions, have been used effectively to assess adaptive responses to environmental and sociohistorical changes, bioarchaeological research nevertheless risked essentializing not only skeletal lesions and biomarkers but also the political systems, social statuses, and economic subsistence of the past populations arguably represented by these skeletal series.

Two serious risks of relevance here exist when essentializing past human lifeways: the first involves the disconnection of pathological lesions and etiological processes, conflating correlation with causation and establishing linear associations between lesions and behavior. While skeletal biologists have more accurate understandings of circumstances and conditions affecting changes in skeletal tissue now than they did 50 years ago (Gosman, Stout, and Larsen 2011; Martin et al. 1998), a great deal of information is still unknown about the causes and manifestations of specific skeletal and dental pathological and nonpathological lesions (Ortner 2003; Ortner and Putschar 1985). As a result, the etiology of certain pathological lesions has become generalized and is usually considered synonymous with exclusively nutritional, epidemiological, or environmental conditions (e.g., porotic hyperostosis and iron-deficiency anemia; caries and carbohydrate consumption; linear enamel hypoplasia and nutritional stress events).

The second risk for bioarchaeologists, and any researcher of past populations, is the typologization of human lifeways, that is, the simplification of complicated and nuanced subsistence strategies into discrete categories. Ancient skeletal populations, through archaeological context, may be classified broadly as hierarchical/egalitarian, simple/complex, or agricultural/hunter-gatherer. These labels enable cross-population comparisons and the testing of global biocultural hypotheses of past populations associated with major human lifestyle changes, such as agricultural transitions. However, while these may be valid analytical tools, such categories tend to create false dichotomies that do not easily incorporate overlaps and overlook the complex natures of regional population histories (Baadgsaard, Boutin, and Buikstra 2012; Buikstra and Beck 2006). Moreover, as only a few aspects of human life can be assessed through the analysis of skeletal remains, there has been a natural tendency to overemphasize those aspects as identifiers of past lifestyles, simplifying the relationship between individual biology and environment to a few typological categories that are assumed to represent human populations across the planet. As a result, past populations may be classified foremost according to their diet, and variation among groups may be de-emphasized to improve our ability to make broader comparisons. The simplification of the agricultural lifestyle to the nature of an acquired food type is an iconic example of this kind of bias.

Turner (1979), albeit acknowledging the diversity in mixed economies, presented a syllogistic relationship between subsistence lifestyles and dental indicators of diet in his seminal survey of dental caries among modern and archaeological hunter-gatherer and agricultural populations. Based on studies that dental pathological lesions, specifically dental caries, were well-established physical proxies for past human diets, notably, carbohydrate ingestion (Leverett 1982; Rowe 1975), Turner compared the prevalence of carious lesions between many agricultural and hunter-gatherer populations and showed a significantly higher prevalence among the former. The differences he observed led to the definition of caries cut values between dichotomously defined subsistence strategies: 0%–4% (average 1.72%) carious lesion prevalence suggested hunter-gatherer subsistence, while prevalences between 2.3% and 26.9% (average 8.56%) intimated agricultural subsistence. Following Turner's original publication, regional and continental overviews of the agricultural transition supported this increased trend in dental caries when considering broad subsistence strategies (Cohen and Armelagos 1984; Larsen 1995, 1997; Steckel and Rose 2002; Steckel et al. 2002). However, studies in dental pathological lesions among agriculturalists by bioarchaeologists researching the adoption of rice agriculture in South Asia (Domett 2001; Eshed, Gopher, and Hershkovitz 2006; Oxenham 2006; Oxenham, Cuong, and Thuy 2006; Tayles, Domett, and Halcrow 2000) demonstrated the effects of variability in agricultural cultigens, emphasizing that not all cultigens exhibit equal cariogenicity. While increased caries prevalence generally aligns with the adoption and intensification of maize agriculture (Cohen and Armelagos 1984; Larsen 1982, 1997), this pattern does not characterize the dental record among rice agriculturalists and does not reflect the variation within identical cultigens ascribed to different processing and preparation techniques or consumption practices (Cucina et al. 2011; Powell 1985). Tayles and colleagues (2000, 2009) highlighted that considerable diversity exists in the cariogenic quality between and within cultigens pre- and postprocessing, diversity that should not be overlooked but rather explained and expanded upon through archaeological context.

In addition to variation observed between agricultural populations, recent studies of hunter-gatherer groups in Europe (Lubell et al. 1994), Africa (Humphrey et al. 2014), and South America (Da-Gloria and Larsen 2014) have shown markedly high carious lesion percentages that fall within, and in some instances exceed, recorded prevalences of caries in agricultural populations. Humphrey and colleagues (2014), for example, described a high percentage of dental caries among all recovered teeth (51.2%) and individuals (94.2%) within a Pleistocene foraging population in Morocco, which directly contradicted Turner's expectations. Similarly, the early Holocene Lagoa Santa hunter-gatherers (central Brazil) exhibited higher frequencies of caries than other hunter-gatherer groups represented in the comparative Global History of Health Project worldwide database (Da-Gloria and Larsen 2014). In a study of contemporary Hadza subgroups—bush, intermediate, and village residents—Crittenden and colleagues (2017) observed significantly higher incidence of carious lesions among females residing in village environments rather than bush camps, results in line with previous bioarchaeological findings in agricultural transitions, but, inversely, higher occurrences of carious lesions among bush camp males than village males. Based on these findings, Crittenden et al. (2017) concluded that oral health cannot be a direct indicator of lifeways in transition but that the process and mechanism of cariogenesis are nuanced and circumstantial. These case studies, among others, have exposed a need to reevaluate the agricultural transition paradigm in place within bioarchaeological research, specifically that dental and oral-skeletal lesions provide reliable dietary proxies from which broader population subsistence information can be extrapolated (Rose et al. 1984).

Therefore, the purpose of this global metastudy is to explore potential factors behind the prevalences of oral pathological lesions across worldwide populations. Initially, we use the data gathered to test the variation in oral pathology prevalence that is due to subsistence patterns among populations. As an exercise to explore alternative sources of variation in dental marker prevalence, we also test the correlation between common climatic factors (temperature, humidity, among others) and dental markers. A few studies have looked at the clinal distribution of caries prevalence to infer potential confounding climatic variables (i.e., Frayer 1989; Meiklejohn and Zvelebil 1991; Lukacs and Pal 1993); however, they are restricted to specific regions of the planet. While we do not presume to explain the direct causal relationships between climate and oral health, in the cases where this association occurs, the comparison with climate variables offers an important comparative framework for the predictive power of subsistence in oral health. Although diet is usually heralded as the discriminatory variable affecting oral health deterioration, environmental factors inherently affect dietary decisions and have the potential to affect oral conditions and microbiomes directly or indirectly. If the ecological environment independently affects dental health, then all populations (regardless of subsistence) should exhibit significant correlations between latitude, temperature, and precipitation variables. Consequently, the secondary hypothesis is used to compare the relative explanatory power of the subsistence pattern to explain variation in the dental data, when contrasted with sources of variation not directly tied to subsistence.

The primary intention of this article is to contribute to a deeper discussion about processual bioarchaeological approaches (Temple and Goodman 2014), arguing for a reconsideration of the idiosyncratic processes and variables that eventuate in physiological biomarkers of stress among different populations. For this study, we focus on dental pathological lesions, as they have been adopted and incorporated into bioarchaeological research to infer past diets (see comprehensive review in Larsen 1997, 2015) and have been widely reported in the specialized literature. We question the causal, often dichotomized, relationship between subsistence lifeways and population dental lesion profiles and suggest further biocultural contextualization of caries, abscesses, and antemortem tooth loss (AMTL) to understand the associated processes contributing to dental pathogenesis and progression. Comprehensive etiological and contextual understanding of these conditions will ultimately lead to better informed and more reliable reconstructions of past lifeways based on dental biomarkers.

Dental indicators of oral health and life-style relationships. In bioarchaeology and dental anthropology, dental lesions—namely, caries, abscesses, and AMTL—have been operationalized as biological proxies for past diets (e.g., Larsen 2015, and references therein; Rose et al. 1984; Steckel and Rose 2002). These causal relationships between diet and dental lesions are derived from past and modern dental literature, which present studies linking dietary components to dental pathologies (e.g., Burt and Pai 2001; Gustafsson et al. 1953; Kidd and Joyston-Bechal 1997; Truhe 1996). Accepting similar etiologies and manifestations of dental disease in modern and ancient populations, anthropologists have built a suite of dental lesions considered indicative of subsistence and have applied these biomarkers to broader research questions in sociopolitical and ecological history. This brief overview introduces the three lesion types addressed within this study, their etiologies, and correlative variables contributing to their onset and development.

Carious lesions. Carious lesions are by far the most explored marker of oral health, due both to their preponderance and impact among modern societies and to their abundant presence in the prehistoric record. Carious lesions reflect the outcome of a process in which the enamel matrix demineralizes; when the plaque environment encasing a tooth reaches a high pH level, the body buffers these acidic solutions by donating ions from the surrounding teeth. If the tooth is unable to repair the enamel matrix before further cariogenic insults, carious lesions consequently develop (Soames and Southam 2005). Research confirms that the presence of the disease is contingent upon at least three major factors: existence of specific oral bacteria, occlusal surface exposure, and diet (Larsen 1997, 2015; Legler and Menaker 1980; Soames and Southam 2005), although different physiological factors due to hormonal fluctuations and saliva secretion and composition have also been shown to have a large role in dental caries development (Lukacs and Largaespada 2006). In particular, further research into sex differentials in caries prevalence has shown inherent biological sex differences, which promote higher risk of carious lesions among females. Specifically, frequent lifetime hormonal shifts for females associated with puberty, menses, and pregnancy contribute to significant alterations in the microbacterial and biochemical landscapes of the oral cavity, which in turn increase the predisposition for carious lesions (Lukacs 2017*a*). However, for the most part, bioarchaeological studies focus on dietary composition,[1] which is the factor they can identify or extrapolate from archaeological remains, historical records, or stable isotope ratios (Hillson 1996; Larsen 1997). As such, it is sometimes still assumed that past diets can be reconstructed from the prevalence and distribution of caries (e.g., Hubbe et al. 2012).

While several bacteria have been associated with caries development, *Streptococcus mutans*, in particular, strongly correlates with high caries incidence among modern populations (Gross et al. 2012; Thibodeau and O'Sullivan 1999). Recent studies in oral microflora show strong heritability, indicating that—regardless of diet—certain populations may be differently predisposed to carious lesions (Cole, Wirth, and Bowden 2013; Henne et al. 2016). Intra- and interpopulation biological differences may also present as variability in jaw architecture (Carlson and Van Gerven 1977; Lieberman et al. 2004), which can be associated with higher caries rates (e.g., dental crowding; Hixon, Maschka, and Fleming 1962; Stahl and Grabowski 2004; but see Helm and Petersen 1989 for a counterargument).

Concurrent with biological factors, cultural variables directly influence the dietary component of cariogenesis. Although populations may consume diets with high carbohydrate proportions, the molecular state of the carbohydrate during consumption determines its cariogenicity. Processed carbohydrates with more adherent textures pose a greater cariogenic risk than unprocessed complex carbohydrates (e.g., starch; Harris 1963). Navia (1994) confirmed the carious volatility of simple sugars in a global review of sugar consumption and *Streptococcus* and *Lactobacillus* bacteria, concluding that sucrose was the only sugar alcohol capable of "promoting the implantation and colonization" of caries-inducing oral bacteria (Navia 1994:724S). Simple sugars also affect the mouth's pH level, thereby stimulating a salivary response to reestablish oral homeostasis (Edgar et al. 1975; Edgar, Higham, and Manning 1994; Mandel 1989). While saliva mitigates oral acidity, overproduction or perpetual stimulation of saliva may lead to dental erosion (Ilie, van Loosdrecht, and Picioreanu 2012; Zero 1996). These findings have implications for possible eating behavior affecting caries prevalence. Hunter-gatherers, such as the Hadza and Ju/'hoansi, who consume foods continuously throughout the day (Lee 2013; Marlowe 2010), have been shown to exhibit elevated caries incidence (Berbesque, Marlowe, and Crittenden 2011). In this respect, it is not so much the dietary components themselves but rather eating habits that influence the dental lesion development. These modern analogies are salient when considering not only what resources past populations subsisted on but also how these foods were processed, stored, and consumed. It is exactly this heavy emphasis on the linear carbohydrate factors in caries development that has promoted the adoption of the syllogistic relationship between lifestyle, diet, and caries (e.g., Hubbe et al. 2012; Watson 2008).

Periapical abscesses. Periapical abscesses of the maxillary and mandibular bones develop when bacteria, generally exogenous *Staphylococcus*, *Prevotella*, or *Fusobacterium* species, are introduced into the root cavity via the dental pulp or an open lesion in the gums (Dymock et al. 1996; Robertson and Smith 2009). Unchecked by antibiotics, bacteria incite proximal inflammatory and suppurative responses from the local tissues and

1. Despite the focus on direct evidence of diet from archaeological contexts, it should also be acknowledged that demographic shifts (i.e., the Neolithic demographic transition) have been implicated as important factors contributing to agricultural and hunter-gatherer carious lesion differentials (Cucina and Tiesler 2003; Temple 2011*b*; Willis and Oxenham 2013). Increases in fertility with the adoption of agricultural practices may have factored into more carious lesions among agricultural females, who would have experienced more pregnancies and associative oral biome shifts, during their lifetimes.

ultimately abscesses (Gill and Scully 1990; Nair 2004). Skeletally, this oral infection generates an alveolar cyst, from which a sinus canal may develop to drain away pus (Waldron 2009).

Although differing bacteria (*Streptococcus* and *Staphylococcus* genera) are required for caries and abscesses, several authors (e.g., Costa 1980; Hillson 19962001; Lukacs 1992; Robertson and Smith 2009; Turner, Moore, and Shaw 1975) suggest that severe carious lesions, which penetrate the enamel and dentine layers, expose the vascular network in the pulp cavity to extraoral microbacteria. This lesion, therefore, provides a window through which exogenous bacteria can enter the bloodstream and subsequently affect tissues. As such, abscess prevalence in archaeological populations can also to be associated with a cariogenic diet (Beckett and Lovell 1994; Hubbe et al. 2012; Keenleyside 2008; Lukacs 1989, 1992).

Antemortem tooth loss. AMTL occurs when the surrounding bone and gingivae can no longer secure the tooth within the maxillary or mandibular arcade. As a result, the tooth is lost and alveolar resorption follows. Among modern populations, AMTL is associated with periodontal disease, periapical abscesses, and caries (Hillson 1996, 2014), although extensive dental attrition observed in past populations may also lead to pulp exposure and subsequent tooth loss (Lukacs and Pal 1993). These preconditions to AMTL compromise the structure of bone and mucosal tissue, eventuating in tooth loss. As with abscesses, AMTL is the outcome of many possible acute or traumatic conditions, working separately or concurrently (Lukacs 2007). However, the strong correlation observed between carious lesions and AMTL (Hubbe et al. 2012; Lukacs 1992, 1995) has resulted in its use as a complementary marker for broad diet composition in the past (e.g., Larsen 1997, and references therein). The relationship between AMTL and caries has been deemed so strong that some authors defend its quantification as an important component on the analysis of carious lesions, since the latter can be significantly underestimated when teeth lost due to caries pulp exposure in archaeological settings are not considered (Lukacs 1995, 1996).

Material and Methods

The present metastudy compiled information published from peer-reviewed anthropology articles as well as peer-reviewed volumes, monographs, and reports from 1975 to 2011 (table S1, available online). The scope of these references included, but was not limited to, the *American Journal of Physical Anthropology*, *International Journal of Osteoarchaeology*, *Current Anthropology*, and *The Backbone of History*. In total, 185 skeletal samples, representing 6,000 years of history across 60 countries, were included in this study (fig. 1). The complete list of series included, and their corresponding primary sources, can be found in table S1. We restricted our analysis to the methods most commonly reported in the literature, which increased the number of sites in the comparative samples, although we recognize that this decision oversimplifies the known sources of variance in oral health indicators and adds limitations/caveats to our comparisons, as detailed below. We collected data both on the percentage of teeth (caries) or alveoli (AMTL and abscesses)

Figure 1. Geographic distribution of archaeological sites included in the meta-analysis. A color version of this figure is available online.

affected and on the percentage of individuals affected for each marker. While these are general statistics that do not take into account variations in the prevalence of the markers, such as number of carious lesions per tooth, location of carious lesion, or location of abscess or AMTL, these methods have been widely applied in bioarchaeological studies (and widely applied to subsequent interpretations), allowing for the type of comparative analysis engaged herein. Moreover, they are assumed to have low rates of interobserver error (e.g., Steckel and Rose 2002), a crucial point to allow for reliable interpretations of our comparisons. Only samples explicitly classified as agriculturists/horticulturists or hunter-gatherers were included in the analyses. Fisher-hunter-gatherers, modern (postindustrial revolution), and mixed-subsistence samples were not included in the data set, in an attempt to be as conservative as possible in the definition of the broad categories studied here. We also acknowledge the high preexisting heterogeneity within agricultural and hunter-gatherer populations, but we maintain and consider these categories as homogeneous for this exercise, in the same way they have been constructed and analyzed in previous studies (e.g., Turner 1979). Finally, all analyses were done on the overall prevalence of dental lesions as reported for the sites, without detailed consideration of sex or age composition of the populations. Although both sex and age are important covariates in the prevalence of the three dental markers analyzed here (see review in Larsen 2015 and references therein), the division of the samples according to sex, age, and tooth type would reduce the number of series in the analyses substantially, since many of the articles do not present this information, thereby limiting the power of our comparisons. However, while we acknowledge this as a potential limitation to our analyses, we argue that it does not significantly affect our conclu sions because the hypothesis tested here states that the adoption of agriculture is a stronger contributing factor to the prevalence of caries, abscesses, and AMTL than other demographic and morphological parameters. The central paradigm tested here, namely, that increases in dental lesions reflect shifts to agricultural subsistence, bases its argument on gross prevalence data of these dental indicators of oral health, irrespective of tooth type, sex, and age variables. Therefore, although variation due to demographic differences is certainly not being considered here, accordingly, it should be orders of magnitude smaller than the impact of the adoption of agriculture and as such should not invalidate the test of our hypothesis.

Prevalence data for each dental trait from agricultural and hunter-gatherer populations were compared using one-way analyses of variance (ANOVAs). Since ANOVAs are general linear models, they allow us to calculate the proportion of the total variance in the data that is due to differences between groups (R^2), providing a better quantification of the importance of subsistence strategies in the definition of each of the markers' prevalence. ANOVAs were calculated independently for prevalences calculated based on teeth/alveoli count and on individual count for each of the dental markers. To better understand the relationship between these markers and the strength of the association between them and broad subsistence pattern, Pearson correlations between traits were also calculated.

To test the alternative hypothesis that environmental factors explain a significant portion of the variation in the prevalence of dental pathological lesions across regions, climatic and geographical variables (annual mean temperature, annual temperature range, annual precipitation, and latitude) were obtained for all agricultural and hunter-gatherer populations with defined settlement or home range locations. These four variables are commonly used climatic variables and are easy to extrapolate from worldwide climate databases. Data are restricted to modern climates, recovered from the WorldClim spatial database (Hijmans et al. 2004), and therefore do not take into consideration climatic oscillations in the past. Again, while this is a potential limitation to our analyses, it is expected that climate variation during the last half of the Holocene (time frame of the majority of the series in our samples) is smaller than differences between regions and therefore any significant association between climate variables and the dental markers will not be strongly affected by diachronic changes in regional climate.

The association between dental indicators of oral health prevalences and climatic variables were analyzed using univariate linear regressions. The strength of the association is reported here as the amount of the variance in the data that is due to the relationship between variables (R^2), which is a statistic that is directly comparable to the one obtained from the ANOVAs and, as such, allows for the comparison of the relative importance of both factors in the definition of the dental traits prevalences. All statistical analyses were conducted in SPSS 22 (IBM 2013).

Results

Oral Health and Subsistence Practices

Among the 185 skeletal assemblages included in this study, caries prevalence per tooth and per individual were available for 104 agricultural and 53 hunter-gatherer groups and 17 agriculturalist and 12 hunter-gatherer populations, respectively (table 1). The comparison between subsistence pattern shows that, as expected, agriculturalists have significantly higher ($P <$ .001) caries prevalence (average of 12.32% of teeth affected and 40.95% of individuals affected) than hunter-gatherers (average of 3.3% of teeth affected and 14.7% of individuals affected). However, despite the significant differences, there is a strong overlap when the range of variation within each subsistence strategy is considered (table 1; figs. 2, 3), with a very broad range in agricultural populations (0.97%–79.5% of teeth affected; 15.0%–87.5% of individuals affected) when compared to hunter-gatherers groups (0.0%–17.7% of teeth affected and 0.0%–43.48% individuals affected). For caries prevalence according to teeth, 62.2% (33 of 53) of hunter-gatherer populations exhibited percentages that fall within the range of agricultural caries percentages and 81.7% (85 of 104) of agricultural values fall within the hunter-gatherer range. Similarly, preva-

Table 1. Prevalence, sample size, and ANOVA results for each of the dental lesions compared between subsistence patterns

Trait	Teeth/alveoli prevalence		Individual prevalence	
Caries:	Agriculturists	Hunter-gatherers	Agriculturists	Hunter-gatherers
Prevalence (%)	12.32 ± 12.98	3.30	40.95 ± 22.90	14.70 ± 14.47
Range (%)	.97–79.50	.00–17.70	15.00–87.50	.00–43.48
95% CI (%)	9.80–14.84	2.20–4.39	29.18–52.72	5.51–23.89
n	104	53	17	12
ANOVA	$F = 24.411, P < .001, R^2 = .136$	. . .	$F = 12.239, P = .002, R^2 = .312$	. . .
Abscesses:	Agriculturists	Hunter-gatherers	Agriculturists	Hunter-gatherers
Prevalence (%)	9.33 ± 13.34	3.03 ± 3.08	37.73 ± 15.23	37.87 ± 17.01
Range (%)	1.60–70.90	.00–7.90	14.60–62.00	20.00–66.67
95% CI (%)	28.06–47.40	.83–5.24	28.06–47.41	28.56–47.30
n	26	10	12	15
ANOVA	$F = 2.142, P = .152, R^2 = .059$	. . .	$F = .001, P = .982, R^2 = .000$	. . .
Antemortem tooth loss:	Agriculturists	Hunter-gatherers	Agriculturists	Hunter-gatherers
Prevalence (%)	17.76 ± 14.04	15.17 ± 10.36	52.53 ± 21.97	32.17 ± 19.10
Range (%)	2.80–55.00	2.80–38.70	13.30–90.90	.00–73.68
95% CI (%)	12.61–22.92	7.76–22.58	39.26–65.81	22.35–41.99
n	31	10	13	17
ANOVA	$F = .288, P = .595, R^2 = .007$	. . .	$F = 7.354, P = .011, R^2 = .208$	. . .

Note. CI = confidence interval.

lence of individuals with carious lesions show that all 50% (six of 12) of hunter-gatherer populations fall within the agricultural percentage range, while 64.7% (11 of 17) of agricultural groups fall within the hunter-gatherer percentage range. Histograms of the caries prevalence by subsistence pattern (figs. 2, 3) show that both distributions are similarly skewed toward low values of caries, with agricultural series showing a larger number of series with high values, which explains the nature of the overlap seen for this marker. This overlap of the distributions is clearly reflected in the R^2 values for the ANOVA (table 1), which show that 13.6% and 31.2%, respectively, of the variation in prevalence of caries is explained by subsistence strategy. In other words, even though differences between broad subsistence patterns affect the average expected prevalence of caries, broad subsistence categories explain only a minor portion of the total variance in the data set, and the largest portion of the variance is explained by differences within categories.

For abscesses and AMTL, sample sizes were considerably lower, due to the lack of information about these pathological markers in the literature (table 1). For abscesses, prevalence per alveoli show higher average frequency among agricultural (9.33%; $n = 26$) than hunter-gatherer (3.03%; $n = 10$) groups, but this difference is not statistically significant ($P = .15$). Individual prevalence of abscesses were virtually identical between subsistence groups (37.7% and 37.9%; $P = .982$). As with caries data, there is a large overlap of prevalence ranges when both affected alveoli and individuals were considered (table 1; figs. 4, 5). For percentages of affected alveoli, 16 of the 26 (61.5%) agricultural populations fall within the hunter-gatherer range (0.0%–7.9% alveoli affected), while five of the 10 (50%) hunter-gatherer groups are within the agricultural range (1.6%–70.9% alveoli affected). A similar pattern of overlap occurs when percentage of individuals affected is observed: with ranges of 14.6%–62.0% for agriculturalists and 20.0%–66.7% for hunter-gatherers, 86.7% (13 of 15) of hunter-gatherer groups fall within the agriculturists' range and 83.3% (10 of 12) of agricultural groups fall within the hunter-gatherers' range.

The observed prevalence of AMTL based on alveoli counts (table 1) was greater among agricultural populations (17.8%; $n = 31$) than hunter-gatherers (15.2%; $n = 10$), although not statistically significant ($P = .595$). When percentages of individuals with AMTL were considered, the agricultural prevalence (52.5%; $n = 13$) was statistically higher than the hunter-gatherer prevalence (32.2%; $n = 17$; $P = .011$). Hunter-gatherers' AMTL percentage ranges for alveoli count overlapped with agricultural ranges for 90.0% (nine of 10) of the sites, while 83.9% (26 of 31) of agriculturists fall within the hunter-gatherers range (fig. 6). For individuals affected, despite the statistical difference 88.2% (15 of 17) of hunter-gatherers show prevalence within the agricultural range and 84.6% (11 of 13) of agricultural AMTL prevalences fall within the hunter-gatherer range (fig. 7). The prevalence of AMTL by individuals shows a somewhat higher but still small amount of variance explained by differences in subsistence pattern ($R^2 = 0.208$), although the prevalence by alveoli show the percentage of variance explained by subsistence pattern to be close to zero ($R^2 = 0.007$).

The lack of concordance in the association between the different dental markers and subsistence pattern is evident in the results from the correlation analyses between dental traits' prevalence (table 2). There is a significant correlation between the prevalence based on alveoli count and individuals count for of AMTL ($R = 0.64$, $P = .033$) and abscesses ($R = 0.66$, $P = .010$). However, the same is not true for carious lesions ($R = -0.06$, $P = .802$), which is surprising given that both methods of caries analysis are assumed to measure similar phenomena in bioarchaeological samples. Between markers, AMTL and

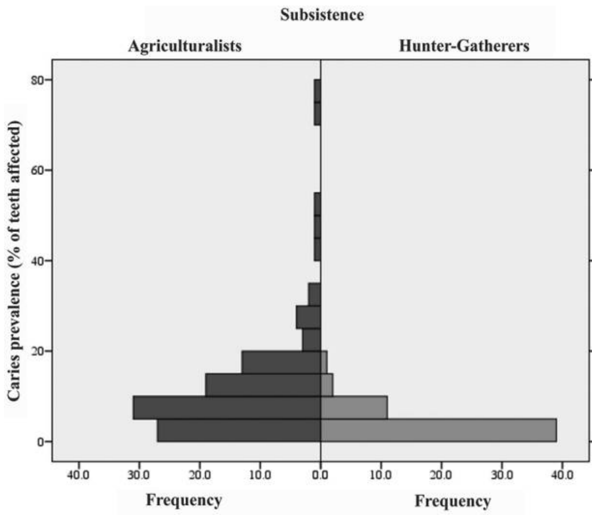

Figure 2. Distribution of carious lesion prevalence by teeth among agriculturalists and hunter-gatherers. A color version of this figure is available online.

abscesses show significant correlation when alveoli ($R = 0.75$, $P < .001$) and individuals ($R = 0.76$, $P < .001$) are used as the unit of analysis, supporting the association between the formation of abscesses and subsequent tooth loss assumed in the literature (e.g., Hillson 1996). The association between caries and the other markers, however, is less evident. When individuals are considered as the unit of analysis, there is a negative significant correlation between caries and abscesses ($R = -0.643$, $P = .008$), but this is not observed in the data based on tooth/alveoli count. The negative nature of the association is unexpected, especially considering that one of the sources of infection that results in abscesses reported in the literature is pulp exposure due to severe carious processes (e.g., Hillson 1996; Lukacs, 1992, 1995). No association between carious lesions and AMTL prevalence is observed in this data.

Oral Health and Climate

Table 3 shows the results of the regression between the oral health markers and the four climatic variables collected in this study. As captured in the table, climate is not a good predictor of the dental health markers, with a few exceptions. Prevalence of carious lesions shows a positive correlation with mean temperature ($r = 0.48$, $P = .010$), explaining 22.7% the variance in the data. Mean temperature is also negatively correlated with the prevalence of abscesses measured by individuals ($r = -0.495$, $P = .022$, $R^2 = 0.245$). Finally, AMTL shows a negative correlation with precipitation ($r = -0.358$, $P = .023$ for prevalence in alveoli, and $r = -0.473$, $P = .019$ for prevalence in individuals), with precipitation explaining 12.8% and 22.4% of the variance in the prevalence of AMTL, respectively.

Discussion

The impossibility of establishing absolute quantifications for many aspects of life in past human societies mandates the creation of comparative frameworks defined by meaningful categories. Therefore, the definition of comparative categories is more than a useful tool in the study of the past; it is a necessary analytical recourse to discuss the changes observed among human societies past and present. Indeed, bioarchaeology, arguably, became a mature scientific field with the advent of cross-populational comparative studies that incorporated into their contextual discussion broad subsistence categories from archaeological, cultural, and biological literature (Cohen and Armelagos 2013; Knüsel 2010). The adoption and subsequent use of these meaningful categories, such as agriculturalists and hunter-gatherers, allowed for discussion and interpretations of otherwise geographically and chronologically disparate groups. Notably, the first comparative research into agricultural transitions marked a major development in bioarchaeology, transforming the early discipline of individual case studies and regional osteological reports into its current national and international collaborations (Armelagos 2003; Buikstra and Beck 2006; Knüsel 2010; Larsen 2015; Martin, Harrod, and Pérez 2013; Zuckerman and Armelagos 2011).

However, it cannot be ignored that the categories created by researchers to study the past can become analytical subterfuges, and as such are not true reflections of the reality we aspire to reconstruct. As such, comparative categories need to be constantly reassessed and reviewed in light of the accumulated knowledge directly or indirectly acquired in the field. In recent years, many articles have highlighted the complex bases of bioarchaeological skeletal stress markers commonly used to

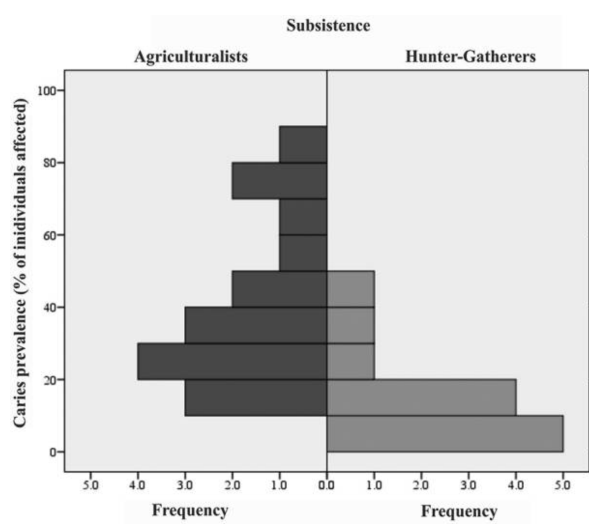

Figure 3. Distribution of carious lesion prevalence by individual among agriculturalists and hunter-gatherers. A color version of this figure is available online.

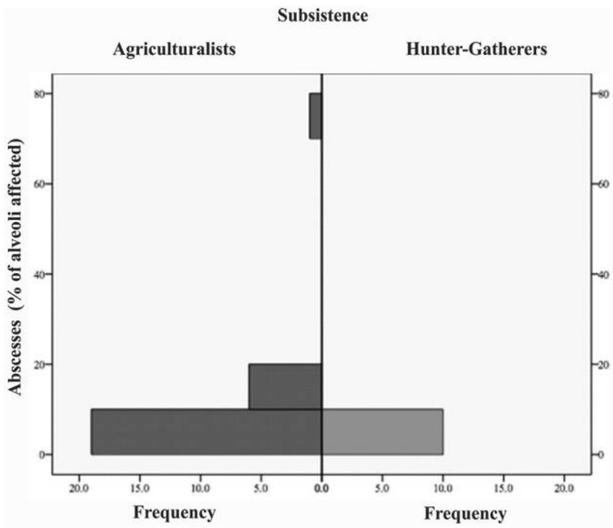

Figure 4. Distribution of abscess prevalence by alveoli among agriculturalists and hunter-gatherers. A color version of this figure is available online.

reconstruct past human lifeways, in many cases challenging the validity of some of the interpretations about past lifestyles (e.g., DeWitte and Stojanowski 2015; Reitsema and McIlvaine 2014). Interestingly, though, comparative categories have strong inertia, and despite the cautionary nature of these studies, linear, causal relationships between osteological and dental markers and specific life conditions continue to be accepted throughout the field. It is possible this results from the necessity to have a valid comparative framework; meaningful broad comparative categories become harder to establish as the complex nature of skeletal markers becomes better understood. Skeletal and dental lesions, which have been applied throughout bioarchaeology as pathognomonic indicators of individual and group behaviors, are ultimately multifactorial entities of overlapping biological, environmental, and cultural practices (Lukacs 2008, 2011*a*). For this reason, changes to the biological human landscape, such as increases in disease prevalence, cannot be easily conflated with overall changes to the sociopolitical, sociocultural, and economic landscape without complementary archaeological data. Applying categorical subsistence nomenclature to complex biocultural relationships and contexts increases the risk of oversimplifying local/regional patterns and reducing complicated human behaviors and interactions into universal socio-evolutionary stages.

The results of our global analysis of dental lesion prevalence contributes to this discussion by highlighting that variation within subsistence categories can be as large as, if not larger than, variation due to differences between categories. As such, our results should be read as another cautionary note on the validity of subsistence categories as a comparative framework to study past human societies. Ultimately, this exercise showed that the interpretation of the prevalence of dental indicators of oral health in the past requires a greater emphasis on biocultural and environmental contexts of the populations under study. While this argument toward a better inclusion of local factors is not new and has been explored by other researchers (Lukacs 2011; Lee et al. 2012; Russell et al. 2013), our study illustrates the worldwide pattern of overlap between the prevalences of dental stress markers. Although categorical lifestyle patterns may sometimes be inferred from skeletal and dental remains, we join recent colleagues (e.g., Martin, Burr, and Sharkey 2013; Temple and Goodman 2014) in emphasizing that such conclusions require a deeper understanding of the biocultural context of the groups, since the variance in the prevalence of markers between groups is not well partitioned according to the subsistence or even climate differences among them.

The Impact of Agriculture on Oral Health

Turner's (1979) cross-population study of archaeological dental collections set a precedent for the relationship between carious lesions, dietary components, and subsistence strategies. Since this publication, subsequent studies in bioarchaeology, for the most part across the world, have upheld this paradigm that increases in the prevalence of caries coincided with the adoption of agriculture, although regional studies have explored nuances in carious lesion prevalences (e.g., Temple and Larsen 2007). A general comparison of caries mean prevalences between subsistence groups confirms this tendency, yielding a statistically significant difference in total teeth and individual caries averages between agriculturalist and hunter-gather societies. Nevertheless, this comparison also exposes the linear association between caries and agriculture as probably too sim-

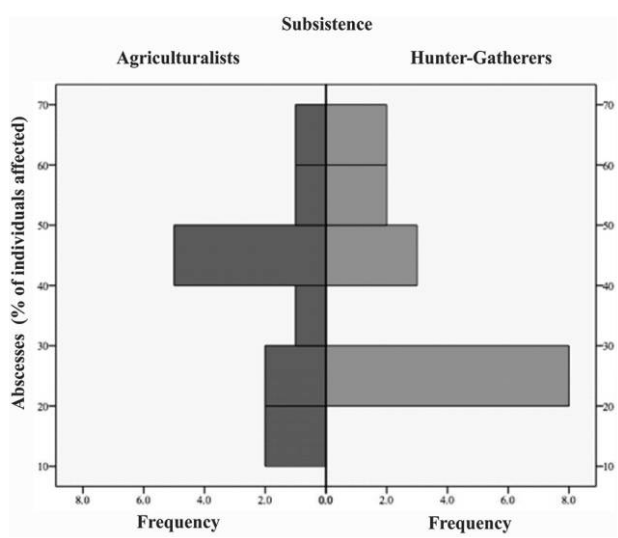

Figure 5. Distribution of abscess prevalence by individual among agriculturalists and hunter-gatherers. A color version of this figure is available online.

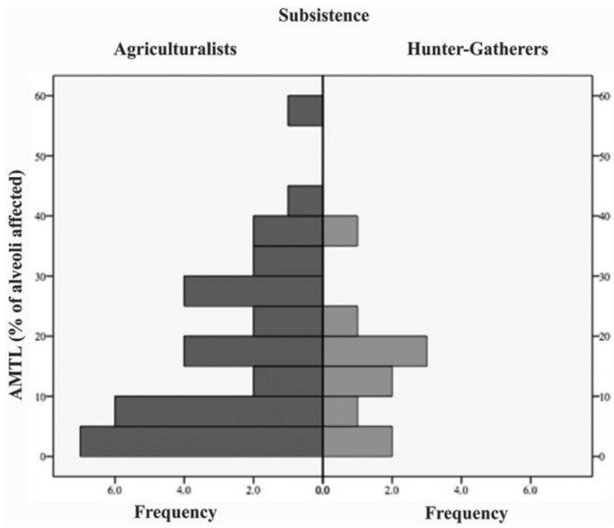

Figure 6. Distribution of antemortem tooth loss (AMTL) prevalence by alveoli among agriculturalists and hunter-gatherers. A color version of this figure is available online.

plistic, since the variation in carious lesion prevalence within each broad diet subsistence category shows considerable overlap, with differences in lifestyle explaining a small percentage of the total variance observed in caries prevalence (13.0% of variation in teeth and 28.0% of variation in individuals). In other words, our analysis of these bioarchaeological publications highlights the fact that the majority of the overall variance in this specific dental pathological lesion is the result of other factors, ranging from environmental to other biocultural factors. This notion of caries as multifactorial is not a new concept proposed here, but is rather one that has been widely explored in recent anthropological literature but not integrated into these larger discussions (Lukacs 2008; Lukacs and Largaespada 2006; Tayles, Domett, and Nelsen 2000). Despite bioarchaeologists acknowledging the multifactorial nature of caries, many studies still make the unilinear association between dietary shifts and caries prevalence, explaining increased caries prevalence through a presumed increase in nonspecific carbohydrate consumption (Bonfiglioli, Brasili, and Belcastro 2003; Hubbe et al. 2012; Mant and Roberts 2015). Our results and discussion do not negate diet as a contributing factor to caries development, but they critique the use of diet as the sole contributing component in caries expression. Indeed, many studies show empirical evidence that diet is de facto one of the main promoters of caries in many situations (Zero 1996; Hillson 2008; Hara and Zero 2010; Larsen 1997). What we are arguing, therefore, is that it is possible that the variation in diet composition among agriculturists may be just as or more important in the expression of carious lesions than the fact that societies rely broadly on domesticated plants. Other factors related to types of food availability, food preparation, food access, and tooth morphology (among many others) may also explain transitional increases in caries, not simply the gradual adoption of agriculture (Harris 1963; Hoover and Williams 2016; Temple 2011*a*; Temple and Larsen 2007). While our results do not reject the assumption that diet contributes to the distribution of caries, we reevaluate using the adoption of agriculture as a static, analytical category and suggest that bioarchaeological studies reconsider/represent subsistence (e.g., agricultural) transitions in terms of more contextualized lifestyle reconstructions rather than binary revolutions.

A similar pattern to caries is observed with the prevalence of the other two markers observed here: abscesses and AMTL. Analogous to (although more demonstrative than) carious lesions, ranges for affected alveoli and individuals show considerable overlap between agriculturalists and hunter-gatherers. With the exception of AMTL prevalence by individual, there are no statistical differences observed among hunter-gatherer and agricultural groups. In all statistics compared for abscesses and AMTL, the amount of variance explained by subsistence difference for AMTL (18%) is minimal, reinforcing the argument made above for caries, although the sample of skeletal series in these analyses is reduced and therefore the results should be taken as preliminary. Once again, our results do not necessarily contradict these associations (but see below), but they do question the validity of the adoption of agriculture as a meaningful monolithic comparative category with which to study the past. As with caries, these data support the growing consensus that the etiological bases of abscesses and tooth loss are complex and not linear, even though caries is regarded as one of the major causes for abscesses and AMTL (Lukacs 1995), therein linking these markers indirectly to diet. Results from this study reveal no significant correlations between caries and either abscesses or AMTL, when both individuals and teeth/alveoli are considered, although such correlations have been ob-

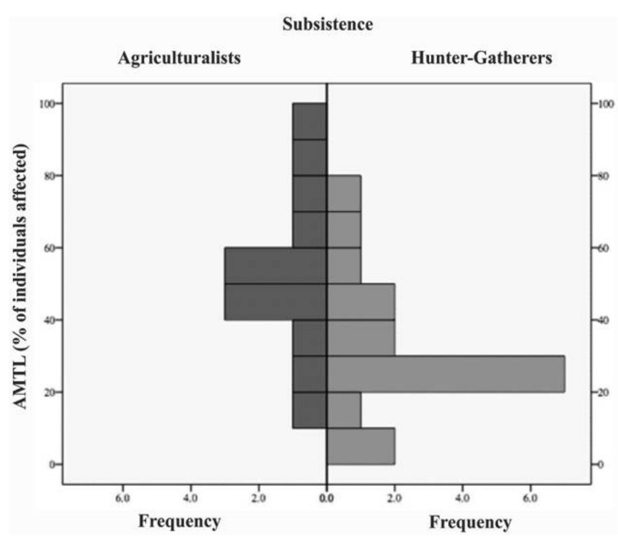

Figure 7. Distribution of antemortem tooth loss (AMTL) prevalence by individual among agriculturalists and hunter-gatherers. A color version of this figure is available online.

Table 2. Pearson correlations between dental lesions

	Caries (% teeth affected)	Caries (% individuals affected)	Abscesses (% alveoli affected)	Abscesses (% individuals affected)	AMTL (% alveoli affected)	AMTL (% individuals affected)
Caries (% teeth affected):						
R	1					
P						
n	157					
Caries (% individuals affected):						
R	−.062	1				
P	.802					
n	19	29				
Abscesses (% alveoli affected):						
R	.354	−.227	1			
P	.059	.501				
n	29	11	36			
Abscesses (% individuals affected):						
R	−.249	**−.635**	**.660**	1		
P	.435	**.008**	**.010**			
n	12	**16**	**14**	27		
AMTL (% alveoli affected):						
R	.207	−.015	**.753**	.592	1	
P	.205	.964	**<.000**	.055		
n	39	11	**27**	11	41	
AMTL (% individuals affected):						
R	.405	.251	.412	**.764**	**.643**	1
P	.120	.273	.208	**.000**	**.033**	
n	16	21	11	**21**	**11**	30

Note. Significant correlations, $P < .05$, shown in boldface. AMTL = antemortem tooth loss.

served in previous studies (Cucina and Tiesler 2003). However, significant correlations exist within and between individual abscess and AMTL data. No such correlation occurs between the prevalences of caries for individuals and teeth, demonstrating that there are differing sources of variation in the manifestation of caries at an individual level than on a population level. This nonrelationship also attests to the extensive variability in predisposition, progression, and severity of caries among individuals. Overall, this study showed no strong correlation between caries and other pathological lesions, suggesting that the biological processes that terminate in dental abscesses and AMTL may not require or be predicated on the presence of caries (Hillson 2001). Without being able to confidently identify the contributing factors between dental variables, we suggest that all oral lesion data should not be employed as single diagnostic tools for past diet and subsistence. Rather, the prevalences and distributions of these conditions should be explored separately and in relation to one another with their respective biocultural and environmental contexts.

Finally, our exercise of looking for alternative sources of variation for the prevalence of these dental markers showed only a few strong associations between climate variables and dental markers. Mean temperature showed a positive correlation with caries prevalence and a negative correlation with abscesses, while precipitation was negatively correlated with antemortem tooth loss. Previous work observing dental conditions in past populations have noted clinal trends in carious lesion prevalence, namely, increases correlated with proximity to warmer, humid climates around the Mediterranean (Lukacs and Pal 1993; Meiklejohn and Zvelebil 1991). Our results, especially relating to carious lesions and temperature, coincide with these earlier regional studies and expand the pattern observed to a global scale. The main point to be taken from these results is that the climatic variables that contributed to variation in oral lesion prevalences show an equal or greater explanatory power (as measured by R^2; cf. tables 1 and 3) than subsistence. While it is not the intention of this paper to thoroughly dissect each of these associations, these results clearly attest to the important role climate assumes in not only the development of subsistence strategies but also in the development of communities.

Throughout hominin evolution and modern human dispersal and variation, climatic variables have influenced survival and adaptive shifts (Auliciems 2009; Coombes and Barber 2005). The sustained adoption of agriculture lifeways, in fact, was found to correlate with a global rise and plateau in temperature at the end of the Pleistocene and beginning of the Holocene (Bettinger, Richerson, and Boyd 2009; Richerson, Boyd, Bettinger 2001). Temperature, precipitation, and sunlight exposure all contribute to various biomes in which humans live and extract resources. Consequently, these factors determine what con-

Table 3. Linear regressions between dental lesions and climatic variables

	Latitude	Mean temperature	Annual temperature range	Precipitation
Caries (% teeth affected):				
R	.059	.009	−.175	.001
P	.526	.927	.057	.991
n	119	119	119	119
Caries (% individuals affected):				
R	−.362	**.476**	−.240	.259
P	.058	**.010**	.218	.183
n	28	**28**	28	28
Abscesses (% alveoli affected):				
R	.354	.271	−.040	−.252
P	33	.127	.825	.157
n	.402	33	33	33
Abscesses (% individuals affected):				
R	.402	**−.495**	.018	.034
P	.071	**.022**	.938	.885
n	21	**21**	21	21
Antemortem tooth loss (AMTL; % alveoli affected):				
R	−.288	.253	−.176	**−.358**
P	.071	.115	.278	**.023**
n	40	40	40	**40**
AMTL (% individuals affected):				
R	−.038	−.067	.062	**−.473**
P	.858	.757	.773	**.019**
n	24	24	24	**24**

Note. Significant correlations, $P < 0.05$, shown in boldface.

sumable plant and animal species may exist naturally and be domesticated within a region. For example, contemporary climate change research has demonstrated significant declines in crop yields in areas of Africa over the past 30 years as a result of temperature increases (Ramirez-Villegas and Thornton 2015). Fluctuating temperatures and rainfalls also affect marine, riverine, and terrestrial ecosystems, thereby affecting how humans exploit their local food webs (Allison, Andrew, and Oliver 2007; Meze-Hausken 2004). Furthermore, human populations culturally and economically process, store, and prepare foodstuffs according to the quantity, quality, and annual availability of domesticated and wild animal and plant resources. Studying Paleolithic diets should not be constrained to discovering what past people ate, but inasmuch as possible should also consider how they prepared and consumed these foods. In addition to climates' direct effects on local food landscapes, it also affects socioeconomic, political, and cultural interactions, which determine what food resources are available and to which persons (Berglund 2003; Kennett and Kennett 2000; Kirch 2005). Climate is inextricably bound with subsistence and the societal mores and practices that uphold, tend, and ultimately transform subsistence lifestyles. In this way, climate represents one of the many confounding variables influencing human behavior and subsistence, which ultimately generate the observed dental lesions, and poses another variable to consider in addition to dietary forces affecting oral health.

Concluding Remarks

It would be a gross oversimplification of human history and adaptation to assume that the adoption and transition to agricultural subsistence was an identical, universal process with similar impacts on populations throughout the world. Minute changes ranging from the cariogenic potential of the local resources, to the ways foods were prepared, to physiological, and environmental (e.g., climate) factors contribute to the variation in oral lesion distributions across the planet. The foremost issue our study addresses is the continued belief that diet is "the main driver of the caries process" (Hara and Zero 2010:459). Our results acknowledge that subsistence does factor significantly into differences in caries and AMTL, whereby agriculturalists tend to exhibit higher averages for these dental lesions than hunter-gatherer populations; however, these results also allude to important levels of variation internal to these broad subsistence groups. While researchers may define populations as agriculturalists or hunter-gatherers according to their primary dietary and economic components, these categorizations overshadow the uniqueness of variable subsistence contexts. With regard to subsistence and social practices, it is well established that hunter-gatherers are highly variable and specialized (Kelly 2007); for example, communities inhabiting the Arctic Circle and living within its extreme climes vary markedly (Chance 2002; Lee 2013). Similar disparities may be noted among Japanese Yayoi rice cultivators and farming Guale Indians of coastal Georgia (Temple and Larsen 2007; Thomas 1988; Tsude 2001). Within these categorized agricultural and hunter-gatherer populations are variations in not only the type of food—domesticated crops, cultigens, wild vegetation, and animal products—but also the cultural and environmental constituents affecting the preparations of these foods and, more importantly, the sociocultural and political environs in which these foods are collected, distributed, and consumed. All agricultural and all hunter-gatherer populations do not live and behave according to standardized societal codes and constraints, divisions of labor, and established hierarchical or egalitarian systems. For these reasons, the pathogeneses of skeletal and dental biomarkers also vary within subsistences, and we would be remiss to aggregate so many contextually diverse populations under a singular dietary/subsistence label. In this way, we recommend that researchers reevaluate the validity of some of our comparative frameworks to questions in past human behavior. Following the suggestions of Temple and Goodman (2014), a deeper, processual, biocultural understanding of the proximate and indirect factors affecting biological traits is essential for bringing about more accurate interpretations of regional and global phenomena that have shaped human life in the past. We advocate for the analysis and thorough interpretation of dental (and skeletal) pathological lesions within the scope of a population's archaeological, biocultural, sociopolitical, paleoclimatic, and regional-global context. Many recent regional paleopathological studies have adopted holistic, contextualized investigations, studies that incorporate multiple lines of evidence—historical text, ethnoarchaeological, artifactual, archaeobotanical/zooarchaeological, genetic/biological distance, craniometric, and stable isotope analyses (among others)—to fully elucidate synchronic and diachronic, intrapopulational, and interpopulational variations in subsistence lifeways (Cohen and Crane-Kramer 2007; Larsen et al. 2001; Powell 1985; Temple and Larsen 2007; Triantaphyllou 2015; Turner 2013). It is our hope that the promotion of a broader biocultural approach in our field (Buikstra and Beck 2006), which advocates for more nuanced and accurate reconstructions of adaptive processes and transitions, characterizes the future of our studies in human history.

Acknowledgments

We dedicate this work to George Armelagos, a founding scholar in paleopathology who taught the first author (and many others) to think critically about bioarchaeology in order to best appreciate its capacity for understanding and illuminating human history. We thank also Mark Cohen, Daniel Temple, and another anonymous reviewer for their insightful and encouraging comments and critiques throughout the review process. The final paper has been significantly improved from its initial submission as a result. We would also like to acknowledge the helpful input from the former Editor, Mark Aldenderfer. This work was sponsored by FONDECYT (no. 1120376) and the National Science Foundation (no. 1359644).

Comments

Andrea Cucina
Facultad de Ciencias Antropológicas, Universidad Autónoma de Yucatán, KM 1 Carretera Merida-Tizimin, Merida, Yucatán, 97305 Mexico (cucina@correo.uady.mx). 25 IX 18

This paper critically presents a metadata analysis of oral health markers (carious lesions, periapical defects, and antemortem tooth loss) with the goal to rediscuss their stereotyped use as indicator of diet and subsistence in past human populations. It is definitely a topic that is worthy of being more thoroughly explored.

It is true that some oversimplified explanations exist between some pathological conditions and their causative factors (i.e., porotic hyperostosis and anemia, LEH and nutritional stress, caries and carbohydrates, etc.); however, the authors' statement throughout the text is also an oversimplification that may erroneously lead readers to think that bioarchaeology only finds the most common way to explain the presence of certain pathological conditions. A large number of publications have already discussed such weak association. For example, we no longer consider LEH as an indicator of nutritional stress but rather one of developmental stress, which is a completely different issue.

As regards caries, in my opinion our discussion (as bioarchaeologists) should address a different point. Leaving momentarily aside the timing and ways of carbohydrate consumption, which are no doubt important elements in the insurgence of oral lesions, the problem is that caries are indeed associated with such consumption; that's unquestionable. Instead, the point is how we define and what we mean by carbohydrates. I agree that it is a big mistake (and an oversimplification) to think of carbohydrates in terms of agriculture only, and that higher frequencies of caries automatically indicate a subsistence relying (almost) exclusively on staple crops (maize, corn, rice, etc.). Yet caries are triggered by carbohydrates—the matter is which carbohydrates. In a paper I published in 2011 (it is cited in the text, but strangely data were not included in the analysis), we found that caries significantly increased in a Late Classic period Maya coastal population, but we went against the theoretical mainstream and ruled out the possibility that such an increase was indicative of worsening socioeconomic conditions that forced these people to rely on maize instead of the wide variety of foodstuff that they had access to. Instead, worsened oral conditions were associated with the (likely) consumption of cariogenic exotic foods (like honey), which are rich in sugars and are themselves carbohydrates. In my opinion, this is the point that should be more thoroughly discussed in academia (and in a forum like this). To do that, as the text mentions, we must have a clear picture of the past populations' dietary, socioeconomic, political, and environmental conditions, as well as understand more deeply daily habits, because all these variables affect oral health. I am well aware that very often we do not have such detailed bioarchaeological evidence; in such case(s), we should refrain from making oversimplified statements that may eventually not correspond to what really occurred in the past.

Other points also need to be discussed. First, even though the authors briefly stated that they were not going to take into consideration variables like sex and age at death, due to reduced sample size, I think that ignoring them (or at least sex) has led to a very partial and skewed view of the situation. So, in my opinion, the authors themselves somehow fell into the trap of oversimplification. Again, I know that oftentimes publications do not present such detailed analyses, but whereas they did, they should have been taken into consideration, even if it meant to handle a smaller sample size. It would have made the metadata analysis more compelling and allowed a more thorough bioarchaeological (and not skeletal biological) discussion and understanding of sex-based gender issues.

Second, the manuscript takes into consideration frequencies based on the tooth-count method and on the individual-count method. It is not surprising to me that correlations were fairly random, and real, consistent patterns (between tooth frequencies and individual frequencies) did not show up. Honestly, I have major and serious concerns about the individual-count approach. The tooth is the unit of analysis in the tooth-count method (the same applies to the alveolar bone), so the researcher has two options: the tooth can be scored or not. If not, that dental piece will not form part of the final results. Instead, for the individual-count method, it is almost impossible to assess when an individual was free from lesions. This is a problem that is mainly related to preservation. While in perfectly preserved specimens it is fairly easy to assess whether they presented any of the oral health indicators, in poorly preserved ones the same cannot be done. Specimens represented by just a portion of the mandible or maxilla, and assuming that such skeletal portion is free from lesions, cannot be assigned to the free-from-lesions category because the researcher has absolutely no way to know whether the segment missing is indeed free. The individual-count method generates two different problems: first, a marked underestimation of the real frequencies, and second, how each individual weights in the final outcome. The latter can be a confounding variable, because one individual with only one carious lesion will weight the same as one individual with all his/her teeth showing caries. As I mentioned above, these are the reasons for a weak correlation between tooth count and individual count.

Last, the weak association between oral lesions and climate did not surprise me. Oral lesions are multifactorial, which leads to intraregion variability; at the same time, each climate hosts a wide range of ecological and cultural variables that differentially affect frequencies of oral lesions. In fact, for example, in the subtropical environment where I have been carrying out my research for the last 15 years, frequencies of caries range between about 6% and almost 40%, and all were maize dependent. In this perspective, the manuscript lacks a strong theoretical hypothesis to sustain the assumption of correlation between climate and oral lesions. As the authors state in the manuscript, a thorough and clear picture of the archaeological populations, both from a biological and cultural perspective, is needed in order to assess oral pathological conditions and to assess the extent to which they are linked to diet and subsistence.

Pedro Da-Gloria
Programa de Pós-Graduação em Antropologia, Universidade Federal do Pará, Cidade Universitária Professor José Rodrigues da Silveira Netto, Instituto de Filosofia e Ciências Humanas, 66075-110, Belém, Pará, Brazil (da-gloria@ib.usp.br). 19 IX 18

The authors wrote an article reevaluating the significance of the categorization in modes of subsistence of human dental pathological lesions. They criticized the essentialization of the agriculturalist and hunter-gatherer modes of subsistence and defended the inclusion of other contextual factors in the analyses, such as political, economic, biological, and environmental. They argued that the risks of using simple modes of subsistence typologies for interpreting dental markers are ignoring the etiology of these markers, confounding correlation with causation, and creating a typologization of human lifeways. To test the argument, they compiled a database of caries, abscesses, and antemortem tooth loss (AMTL) from populations across the globe, applying tests of variance and correlation to the samples.

Their article is an important contribution to biological anthropology in several aspects. First, they highlighted the high degree of overlapping between different modes of subsistence regarding prevalence of dental pathologies. Second, they recognized the multifactorial and complex nature of the etiology of these dental pathologies, pointing to the risks of oversimplifying their interpretation. Third, they identified some additional factors contributing to their prevalence, such as temperature and precipitation.

Some of the unexpected results of the article, such as the lack of correlation between caries and AMTL, can be discussed—including the analysis of tooth wear. One of the causes of AMTL is high degree of tooth wear, which can expose the dental pulp and open the area for infection (Lukacs 1995). Lagoa Santa hunter-gatherers, for example, had 53.85% (21/39) of the teeth with exposed pulp caused by tooth wear (see Da-Gloria and Larsen 2014). In addition, very high degrees of tooth wear usually found in foragers can in some cases be negatively correlated with dental caries, since occlusal wear eliminates previous cavities and decreases the area of attachment for dental plaque. In that sense, tooth wear is another element of the complex interaction among dental markers, which may contribute to making the distinction between subsistence modes less clear.

Even agreeing with the authors in their main conclusions, I approach this discussion in a slightly different manner. Debates in the broad field of anthropology have been historically marked by dichotomies between particular versus universal, biological versus social, and nature versus nurture, among others. In this regard, I see the break of these dichotomies as a better approach for our anthropological questions. The article showed that on a more general level, by using averages, it is possible to distinguish general differences between modes of subsistence, which are more marked in caries, and less marked (and not statistically significant) in AMTL and abscesses, depending on the unit of analysis, but always pointing to a trend of lower values for hunter-gatherers. These general conclusions, as cited by the text, are well supported by previous work that compiled a large number of studies across the globe, showing consistently the occurrence of health changes in human populations with the advent of agriculture. The classification of populations in subsistence strategies is an important way to compare populations not sharing historical connection, since the subsistence strategies influence consistently not only diet but also demography, food distribution and preparation, social organization, and religious understanding of the human-environment connection. Explaining 10%–30% of the variability of the data, which can be apparently interpreted as a low proportion, it is a reasonable amount considering the complexity of the traits analyzed in broad temporal and spatial contexts. At this general level, I disagree with the sentence that "we would be remiss to aggregate so many contextually diverse populations under a singular dietary/subsistence label." A different but equally relevant question is the explanation of the variability within these modes of subsistence, in order to understand other causal factors associated with the dental pathologies, such as environmental and biological ones. In fact, to explain in detail particular situations, the best approach is going further in the biocultural context of each population, improving the specificity of the explanation and taking into account multiple, complex, and unique combinations of factors. These two sides of the same coin, that is, generalizations using broad and meaningful categories and particular biocultural contexts, should be integrated in an interpretation that does not dichotomize general/particular and average/variability. I defend an interpretation similar to the one undertaken in Da-Gloria and Larsen (2014), which uses subsistence categories as analytical tools and at the same time explores the biocultural context and the position of a particular population within the modes of subsistence, understanding that these two approaches should be integrated.

Finally, we should be prepared to face one of the most relevant questions regarding the osteological markers of health and lifestyle in the past: the construction of complex interpretative models of stress and disease. We need to build models that help us to interpret prevalence of osteological markers in a way that goes beyond simple descriptions of traits and reports of prevalence. In that task, interpreting osteological markers in a case-by-case basis faces the problem of the lack of enough information in the archaeological record, while oversimplifying interpretation brings the problem of ignoring the complex nature of biocultural adaptation. One of the solutions for this problem is constructing robust interpretive models using clinical, ethnographic, and archaeological data that include the relative importance of genetics, bacteria, biochemistry, morphology, diet, and sociocultural factors for explaining dental pathologies, always giving special attention to variables observable in the past record. In that sense, this article brings an important contribution to provide additional interpretive factors to explain dental markers and to show the complex interrelations among them. On the other hand, we should not dismiss the important role that subsistence has on providing a general level of explanation for dental markers. Instead, we need to build on it to create more complex models.

Kate Domett
College of Medicine and Dentistry, James Cook University, Townsville, Queensland 4811, Australia (kate.domett@jcu.edu.au). 27 IX 18

Marklein et al.'s study will invigorate discussion on a number of issues in bioarchaeology, both those specific to the relationship of caries and subsistence but also those of a broader nature, including the nonlinearity of many pathologies and human behavior and the importance of variation in human responses to change. To some degree, behind these issues is the lack of (or token) engagement with advancement in clinical studies that has led to the overgeneralization of, or now outdated, links between paleopathology and behavior. As many bioarchaeologists are recognizing, with advancements in our understanding of pathogenesis and the link between genetics and disease it is no longer valid to purport singular links between, for example, caries and diet (Newton et al. 2013; Tayles, Domett, and Halcrow 2009) or osteoarthritis and physical activity (Domett et al. 2017).

This study provides further proof of the highly variable nature of dental health, not only geographically and temporally, but also between closely related populations. It is clear, and has been clear for some time, that dental health, including caries, is not solely linked to diet. It is also not a new concept that we cannot use a particular caries prevalence rate to suggest the consumption of a carbohydrate staple (Tayles, Domett, and Halcrow 2009). Evidence for the consumption of particular foods can only come from direct paleobotanical and archaeological evidence, with supporting molecular research. We also have evidence that not all carbohydrates are equally cariogenic: wheat, maize, and rice, for example, have quite different properties and effects. In addition, carbohydrate processing should be considered; highly processed and polished white rice will have a different cariogenic ability than partially husked brown rice. The latter will also more likely accelerate dental attrition, thereby removing potential and developing sites of caries (see reviews in Tayles, Domett, and Nelsen 2000; Willis and Oxenham 2013). When we compare caries rates globally, not only are we not comparing like with like but also much of the context is obscured through the somewhat forced categorization of samples to subsistence categories. Marklein et al.'s study highlights that our desire to categorize often leads to oversimplification and a disregard for variation.

In mainland Southeast Asia, it is clear from paleobotanical and isotope evidence that the consumption of rice has changed over the last ca. 4,000 years (Castillo et al. 2018; King et al. 2013) and that there is no simple linear relationship with caries prevalence and rice consumption. In our initial work (Tayles, Domett, and Nelsen 2000) there was evidence for decreasing caries prevalence with increasing rice agriculture. This linked well with the scientific evidence for the low cariogenicity of rice compared with other carbohydrate staples and, importantly, as Marklein et al. emphasizes, there cannot be worldwide rules or patterns in caries prevalence and subsistence mode. Caries rates are dependent on individual population parameters not only from the type of stable carbohydrate consumed but also its processing, the consumption of other foods, and also genetic and environmental factors, such as the shape of the teeth and the genera of bacteria a person acquires from their environment. Lukacs's work highlighting the predisposition to caries in females is also of importance (Lukacs 2008, 2011*a*, 2011*b*; Lukacs and Largaespada 2006).

New evidence of dental health in prehistoric Southeast Asia showed that our original conclusion that increasing rice consumption had an inverse relationship with caries no longer held; analysis of new skeletal samples highlighted the nonlinear and multifactorial nature of this relationship. Oxenham, Nguyen and Nguyen (2006) concluded that there was no clear decline in oral health as rice agriculture intensified; in fact, no clear pattern of increase or decrease was identified for mainland Southeast Asia. Interestingly, Oxenham, Nguyen and Nguyen (2006) suggested that the inclusion of later Iron Age sites may help elucidate the relationship of rice consumption and oral health as rice consumption further intensified. Newton et al. (2013) followed up this hypothesis when new late Iron Age sites were excavated in northwest Cambodia. Again evidence showed the wide variation within mainland Southeast Asia skeletal samples in dental health but did indeed show some of the later Iron Age sites with higher caries rates and overall declining dental health. Furthermore, Shkrum (2014) showed that even when we can control for a number of variables by studying dental health through time at one site, there can be a lack of consistent patterns and no linear relationship with rice agriculture. There is also increasing evidence for millet consumption in the region (Weber et al. 2010) that needs to be factored into the picture. There is the continued need for reevaluation of past research as new evidence, both archaeological and clinical, is discovered.

Marklein et al.'s current metastudy, by its nature, fails to incorporate the importance of variable demography globally. Notably, most dental pathologies are strongly age progressive; thus, samples with high proportions of older adults will typically show poorer dental health. Willis and Oxenham (2013) also raised the issue of the influence of demography and fertility on oral health using Southeast Asian data. Using up-to-date clinical evidence for the link between female anatomy and physiology, including fluctuating hormonal levels in pregnancy, and dental health, Willis and Oxenham (2013) discussed the potential link for the frequent evidence of higher caries rates, and poorer general dental health, in females and the increasing fertility through the Neolithic demographic transition. This pattern, though, is not universal across prehistoric Southeast Asia; not all sites with high fertility show high caries rates—it is just one more piece of the puzzle to consider (Newton et al. 2013). Marklein et al. rightly note the lack of inclusion of demographic variables, due to a lack of data divided by sex or age at death, or both, in a number of their chosen studies, is a limitation of their study. The fact that these data are not presented in some studies further advocates Marklein et al.'s final conclusion: future studies must truly embed their conclusions in the distinctive biocultural context of each sample before attempting any wider comparisons.

Alan Goodman
Cole Science Center 110, Hampshire College, Amherst, Massachusetts 01002, USA (agoodman@hampshire.edu). 1 XI 18

Marklein and colleagues have done us all a big favor by compiling much or perhaps even all of the existing data on caries prevalence and the prevalence of other dental lesions in skeletal remains. They focus on the prevalence of lesions in hunter-gatherer (preagricultural) groups and agricultural-based subsistence societies. They find that caries lesions do tend to be greater in agriculture than hunter-gatherer societies. However, the variation in rates within agricultural groups is great, and they show substantial overlap in prevalence rates with hunter-gatherers. Certainly, caries is not just a lesion of civilization or a disease of agriculture. It is one of humanity's older and most ubiquitous afflictions.

To be honest, I do not find these results to be at all surprising. I read the results as showing that agriculture is a predictor of increased caries rates. It is not perfect. I do not think anyone would have expected that. Agriculture seems to be a predictor, and other factors yet to be firmly determined also explain a great deal of the variation in caries rates.

As for other defects, such as periapical abscesses and antemortem tooth loss, the trends are much less certain. This may be because these defects are less clearly related to the inclusion of grains and other agricultural products into diets. It might also be that the data are not collected in a reliable way. I am skeptical that these data have been well collected to say much of anything about dental abscessing and tooth loss across so many studies. This remains to be seen.

Cavities rates, indeed, have often been employed a sign of changing subsistence patterns. But caries etiology is far from just what one eats. It is related to, among many other things, food preparation, sugar content, the biome, genetics, age, and dietary consistency. Thus, for example, a group with high rates of attrition might display few caries but not necessarily be less cariogenic. I do not think the authors would disagree with any of this. I do not find their interpretations to be surprising.

What I find most useful is not the unsurprising interpretation. What I find super useful is the compilation of data across so many studies. It is rare to see such a thorough job of working across studies. This should set up for future research and hypothesis testing. I look forward to more. But for the moment—thank you.

Clark Spencer Larsen
Department of Anthropology, Ohio State University, 4034 Smith Laboratory, 174 West 18th Avenue, Columbus, Ohio 43210-1106, USA (larsen.53@osu.edu). 23 IX 18

Marklein et al.'s meta-analysis presents a big-picture perspective on oral pathological conditions and an assessment of dietary and other contexts for their interpretation from a wide range of bioarchaeological settings as reported in the literature. Their ambitious analysis and thoughtful discussion highlight the downside of drawing simple conclusions from the study of complex data sets. To be sure, there are drawbacks to using categorical temporal, economic, and other standards for identifying patterns of variation. Informed investigators, however, are well aware that comparative approaches have limitations, including the risks of typologizing or essentializing health outcomes and conflating correlation with causation, for example. Good science prevails, however, especially in regard to formulation of informed hypotheses, assumptions made, limitations (and strengths) of data sets, and the complex array of causal factors as reconstructed from social, cultural, ecological, and other complex circumstances. Moreover, over the past several decades, investigators have successfully presented patterns of oral pathology in relation to local, regional, and global frameworks; the relative dependence on domesticated versus nondomesticated sources (ranging from slight to dominant); and the degree of cariogenicity of some plant carbohydrates (e.g., rice vs. maize). I do not think we know enough about the variation in cariogenicity of plants, such as the apparent consensus that rice is less cariogenic than maize. Moreover, some settings show no change in dental caries prevalence with increased focus on rice, whereas other settings do (see Pechenkina et al. 2013).

Their article makes clear the global variability in the impact shift in dietary focus on oral health during the last 10,000 years. On the other hand, oral health outcomes meet expectation for those populations having a record of increased carbohydrate consumption. That is, once ingested, carbohydrates are metabolized by endogenous oral bacteria (e.g., *Streptococcus mutans*), the acid by-product of which results in the focal demineralization of tooth enamel and associated hard tissues. There is much we do not know about the history of oral health, but we do know in general the outcome of carbohydrate consumption. Researchers, however, account for a number of multiple confounding circumstances that influence oral health and disease, but the direct and indirect effects of diet and access to plant carbohydrates are the drivers of dental caries. Marklein et al. are careful to underscore the mitigating factors influencing prevalence and pattern of dental caries, including but not limited to potential variability in cariogenic properties of different cultigens. As they point out, cariogenic nondomesticated plants were exploited by a number of foraging societies, including prefarming, late Pleistocene, and early Holocene populations in South America and elsewhere (e.g., Da-Gloria and Larsen 2014; see discussion in Larsen 2015). As the record currently shows, however, relatively few prehistoric settings inhabited by foragers had available the kinds of carbohydrate-enriched diets that would promote elevated dental caries.

Of the three pathological conditions discussed by Marklein et al., dental caries has received the most attention by bioarchaeologists. Carious lesions are readily identifiable, whereas the diagnosis of antemortem tooth loss and periapical abscesses are more nuanced. In comparison with dental caries, the diagnostic methods are more diverse and less comparable across studies undertaken by different investigators.

Not surprisingly, Marklein et al.'s analysis reveals an overall higher prevalence of carious lesions in farmers than in foragers but with considerable overlap in the range of variation. That record includes diverse populations expressing different levels of commitment to farming and a range of other contextual circumstances. Interestingly, the analysis indicates a positive relationship between higher temperatures/greater humidity and elevated prevalence of carious lesions. This finding is consistent with the notion that regions of the world amenable to productive farming would be expected to include populations having relatively greater dental caries prevalence. More importantly, this emphasizes the range of dietary and nondietary circumstances that may influence the development of carious lesions.

Marklein et al. encourage bioarchaeologists to shift their emphasis from simple characterizations of oral health—for example, oral pathology is high in farmers and low in foragers—to more detailed investigations accounting for variability in landscape, climate, degree of dependence on farming, social and cultural contexts, and other factors. They make excellent points regarding interpretation of the record based on their first-of-a-kind analysis. It is certainly the case that much of the older literature is simplistic, presenting in a number of instances all-or-nothing kinds of summary statements regarding trends in oral health. On the other hand, the newer literature is considerably more informed by its analysis of context—socioeconomic, political, and environmental—and level of commitment to farming. For example, stable isotope analysis and other methodological advances have been critical for identifying presence and level of dependence on some cultigens and the range of issues that contextualize oral health in communities and regions globally. The fact remains that the newer research and the science behind it are successfully characterizing the complexity of oral health outcomes via more informed interpretations of patterns observed in archaeological contexts.

Marklein et al.'s study emphasizes the importance of regionally based investigations in order to piece together larger patterns. Regional investigations provide greater control owing to shared contextual elements, such as common cultigens and relative degree of reliance on them (e.g., maize in various regions of the Western Hemisphere, millet in East Asia); food preparation practices; living conditions; and social, cultural, and behavioral dynamics. Broad patterns of oral health have been characterized by biological anthropologists and others over the last half-century of study. The earlier record of oral health is important to know because it is the health outcomes in prehistory and later that set the stage for today's oral health.

I may be overly optimistic, but I believe that their recommended "broader biocultural approach" is now well underway in the practice of bioarchaeology. Be that as it may, Marklein et al. set a high bar for future study of oral health viewed in all of its complexity and, as the field continues to develop, best practices for building an increasingly informed understanding of the history and evolution of life conditions.

John Lukacs
Department of Anthropology, University of Oregon, 1218 University of Oregon, Eugene, Oregon 97403, USA (jrlukacs@uoregon.edu). 9 X 18

This review evaluates the association of pathological dental lesions, mode of subsistence, and climatic variation in a sample of 185 archaeological skeletal series. The focus of this critical meta-analysis is the prevailing and widely accepted view that dental pathology profiles differ among foragers versus farmers. Reevaluation of consensus views and oversimplified interpretation of key variables is critical to the growth and maturation of any field of study. The critique questions the logic of making direct linear associations between the prevalence of dental caries, antemortem tooth loss (AMTL), and mode of subsistence. The review is timely and comprehensive and will promote deeper critical analysis of the complex and synergistic factors influencing the expression of dental disease in groups with dissimilar modes of subsistence and diet. Although shortcomings of the article are few and small (e.g., criteria for including studies in the meta-analysis, priority of citations in literature review, fully integrating demographic variables), my comments are limited to topics mentioned in this study that deserve further consideration. Below I show how intergroup variation affects the complex etiology and diversity of expression of pathological dental lesions.

a) Etiological pathways. Diagrammatic representation of the relationship between causal agents and dental pathological lesions are complex and may result in multiple etiological pathways to the same pathological lesion (Lukacs 1989; fig. 1). An informative example is the etiology of AMTL, a lesion caused by penetrating dental caries in Harappan farmers and by severe occlusal tooth wear in foragers of Damdama (Lukacs 2017*b*).

b) Demographic factors and reproductive biology. The demographic structure of a population is closely linked to aspects of reproductive biology, especially fertility. The adoption of farming is associated with increased sedentism, reduced dietary diversity, and an increase in total fertility.

Explaining the decline in women's oral health with the advent of agriculture as the exclusive result of dietary change and division of labor is shortsighted and incomplete. Biological aspects of pregnancy are involved and the relative impact of diet and biology should be considered (Lukacs 2008). Since this argument was made, some researchers have given attention to demographic parameters of past populations in explaining the prevalence of pathological dental lesions. Beyond diet and subsistence, I encourage routine consideration of demographic variables, especially fertility, when explaining the prevalence of dental caries and AMTL in archaeological skeletal samples.

The authors acknowledge the triad model for the etiology of pathological dental lesions (tooth, oral microbiome, and diet); two of the variables (the tooth and the microbiome) are not given sufficient attention (Keyes 1968). Features of cariogenesis that benefit from further comment include (i) the microstructure of enamel and its genetic basis and (ii) differences in the human oral microbiome and subsistence.

c) Genetics of enamel microstructure. Several genes are involved in enamel formation in humans: ameloblastin, amelogenin, enamelin, tuftelin 1 and tuftelin interacting protein 11. In the modern era of diets with abundant highly refined carbohydrates and sugars, variation in individual caries experience ranges from those highly affected to those who are resistant and caries free. Variation in caries experience in similar dietary environments may result from differences in genetically controlled variation in enamel microstructure. Genetic, experimental, and clinical research suggests that weaker enamel may explain dental decay (Vieira et al. 2015). Enamel formed under lower amelogenin expression was more susceptible to caries formation because it is weaker or softer than enamel formed under conditions of amelogenin overexpression. Studies of single nucleotide polymorphisms (SNPs) identified candidate genes linked to the etiology of dental caries resistance or susceptibility (Piekoszewska-Zietek et al. 2017). A list of enamel formation genes, immune resistance genes, and saliva genes is informative (Vieira et al. 2014). Studies of SNPs in dispersed populations (Guatemala Mayan [Deeley et al. 2008]; Iranian [Koohpeima et al. 2018], Polish [Gerreth et al. 2017], and Turkish [Patir et al 2008]) suggest that different candidate genes influence caries susceptibility or resistance occurrence in diverse groups (Vieira et al. 2008). Investigators hypothesize that variation in enamel formation genes contributes to microstructural alterations in enamel, resulting in higher mineral loss under acidic conditions and facilitating bacterial attachment to biofilms (Patir et al. 2008). Variation in the genetics of enamel formation should be investigated in foragers and farmers to determine whether differences exist and whether they contribute to divergence in prevalence of pathological dental lesions.

d) Subsistence and the human oral microbiome. Global studies of oral microbiome reveal great variation in species diversity and abundance that are associated with mode of subsistence (Nasidze et al. 2009) and are linked with major transitions in subsistence—from hunting and foraging, to traditional farming, to postindustrial farming (Gupta et al. 2017; Schnorr et al. 2016). The Batwa Pygmies, formerly a hunger-gather group of Uganda, have significantly higher oral biome diversity than Bantu farmers from Sierra Leone and the Democratic Republic of Congo (Nasidze et al. 2011). The two farming groups were similar to one another in having less diverse oral microbiomes than the Batwa. The Batwa also had a very low prevalence of dental caries and reduced rate of tooth loss. Differences in oral pathology between Batwa and Bantu farmers result in part from the dietary regimens of these groups. The Batwa have a greater proportion of protein in their diet, while Bantu have more access to cariogenic refined carbohydrates. Nasidze et al. (2011) found a higher frequency of *Haemophilus* in Batwa saliva and biofilm than in the farming groups. Because *Haemophilus* is responsible for alkali generation in the oral cavity and regulation of pH homeostasis, the authors hypothesize that its high frequency in Batwa affects their low rates of caries and tooth loss. In a global survey of the oral microbiome, Gupta et al. (2017) found higher species diversity in the oral cavities of hunter-gatherers, coupled with higher prevalence of *Haemophilus* in hunter-gatherers than in farmers (Gupta et al. 2017). The oral microbiome of six groups, pairs of foragers, and farmers living in close proximity in the Philippines revealed that core species were significantly correlated with subsistence strategy (Lassalle et al. 2018). Collectively, these results are suggestive: the oral microbiome of foragers and farmers is significantly distinctive in both species composition and diversity. These differences affect the prevalence in dental caries and its pathological sequellae, including the frequency of AMTL and periapical abscesses.

Anastasia Papathanasiou
Greek Ministry of Culture, Ephorate of Paleoanthropology and Speleology, 34B Ardittou Street, Athens 11634, Greece (anastasia.papathanasiou@gmail.com). 1 X 18

The Marklein et al. paper starts with an extensive introduction, summarizing the debate on the transition to agriculture over a century, and especially during the second half of the twentieth century, then it describes the trajectory that led to the overturn of the "simplistic view that the adoption of food production by human societies led to improvements in all aspects of human life" to the acknowledgement of the diversity of the effects brought by the agricultural transition and, moreover, to the significant overlapping of the prevalence of the indicative lesions when comparing agricultural to hunter-gatherer groups, and finally to the acknowledgment of the multifactorial nature of the issue.

The paper describes and critiques the theoretical framework that has shaped research on the transition to agricultural subsistence as well as the oversimplified way evidence was used to substantiate the changes underlying the transition, namely, the essentialized use of specific indicators of oral health and the subsequent conflation of those health indicators with broad global transitions and production systems. However, although this paper focuses specifically on the transition to agriculture, at the same time it describes a more general theme prevalent in the majority of the bioarchaeological studies today. Although the authors refer to a specific transition and its assessment, it is hard not to recognize how their discussion relates to the broader field of bioanthropology today. The points raised by Marklein et al. apply as well in many other specific subfields, including health stress indicators, stable isotopes, and aDNA, research. This is the major theoretical merit of this work.

Marklein et al. explicitly make the following points: (*a*) how early bioanthropology as a discipline was asserting its efficacy in identifying patterns, codifying demographic and pathological standards, building comparative databases, and standardizing methodologies globally; (*b*) that through this maturation period, bioarchaeological research risked essentializing and oversimplifying the etiologies of the observed health indicators and, moreover, it was susceptible to conflating the existence of specific skeletal lesions and biomarkers with political, economic, and social systems; and (*c*) that the construction of analytical categorical typologies, under which all the existing variation needed to fit, in order to be comparable, ultimately masked diversity.

These realizations characterize both the research on the food production transition and bioarchaeology as a whole. However, the field needed its infancy period to establish and standardize its methodologies and to compile its databases, and it should not be critiqued for it. Essentialization offered validity to the interpretations, and categorization offered global comparability at that point. Today's research, since the field is established, very correctly and reasonably has to question the causal and often dichotomized relationships between lifeways and observed lesions, and it has to proceed to finer distinctions when making comparisons and to introduce and account for more biological and cultural parameters.

Large-scale interregional global projects of the past years have widely and routinely applied standardized methodologies, produced patterns and models, debated ideas, and tested hypotheses, but always in a broad generalized way, away from the cultural context. Inter-and intrapopulation variation was masked, ignored, or remained unstudied, as it was extremely complex to incorporate into global studies. Even metastudies of data compiled by such large projects suffer the same problems, which even this paper does not escape. Despite its sound theoretical structure and orientation, it is detached from an extremely chronologically and culturally heterogeneous broad and unrelated database that extends from the Upper Paleolithic to 500 BP and from 7000 BC to modern times. Categorizing the data only in terms of the subsistence strategy misses any cultural characteristic or sometimes the names of sites, a pattern that is common and unavoidable when we use past material. This way of categorizing the data has to be eliminated, as it jeopardizes the objectivity and validity of our interpretations. The second, climatic, hypothesis is useful but again is overly general and weakly tied to the materials and the underlying mechanism in correlation to the etiology.

Marklein et al. raised several crucial points for bioarchaeologists to consider: oversimplification of etiologies, conflation of lesions with systems, construction of analytical categories insensitive to inter and intragroup variation, multifactorial biological etiologies. Two additional points need to be mentioned:

First, current researchers need to move away from overgeneralizations and overstated ideas based on too little empirical data and too few samples, for which the contextual significance may be not reported or known as well as the significance of the cultural period or region they represent. Especially, when older material is used, the assumptions should not be repeated simplistically and uncritically, without checking. It is often the case that the research questions are clearly defined and the methods can answer the research questions but the theoretical assumptions oversimplify and overstate the potential of the proposed materials, particularly in relation to the number and representativeness of samples. When it would only be possible to show possible trends, researchers proceed to incautious quantitative or chronological generalizations.

Second, current research will greatly benefit from systematic adherence to the archaeological context and the cultural component and by seeing past communities as parts of the political and economic landscapes (Wood et al. 1992). It is refreshing to see studies with a well-informed contextual cultural background that bridge the gap between the material and various bigger interpretations (Robb 2014:28), usually in dialogue with the archaeological particularities, which result in nuanced interpretations of the observed diversity and the patterns of group exclusion or inclusion.

Finally, as a bioarchaeologist working with Mediterranean archaeological sites, I believe that current bioarchaeology may generate new questions to approach prehistoric and historic societies as integrative and evolving institutions rather than as arenas of social antagonism. This approach can contribute to the understanding of the organizing principles of ancient societies if the work is embedded into a socio-archaeological framework that takes into account both the ideological and symbolic parameters that govern human behavior and social relations and the cultural specificities that shape ideology and symbolism in each period (Papadimitriou 2018:183).

Daniel H. Temple
Department of Sociology and Anthropology, George Mason University, 4400 University Drive, Fairfax, Virginia 22040, USA (dtemple3@gmu.edu). 17 X 18

Marklein and colleagues challenge long-standing paradigms in bioarchaeology. There are problems with typology and linear thinking in the construction of hunter-gatherer and agricultural systems, as well as the reconstruction of subsistence economy based entirely on carious lesion prevalence. These reconstructions are embedded in the concept of mutual reliance between humans and agricultural products, one that envisions intensive food consumption as entirely based upon levels of dependence only observed in agricultural populations. The authors argue that heredity in oral biofilm, malocclusion, atomization of dietary molecules, intervals between food consumption, and reproductive ecology all produce complexities in carious lesion frequencies and other indicators of oral health. Thusly, bioarchaeological research should express caution in interpretations of caries prevalence as a marker for subsistence economy. This is a timely observation, as bioarchaeologists have questioned this paradigm over the past 20 years. For example, the lack of association between carious lesion frequencies concurrent with the advent of wet rice agriculture in Southeast and East Asia demonstrates that the relationship between subsistence economy and carious lesions is not straightforward (Pietrusewsky and Douglas 2001; Willis and Oxenham 2013). Even when carious lesion prevalence increases in response to wet rice agriculture, scientists propose that factors such as gelatinization may have increased the cariogenecity of starch molecules, while malocclusion attendant with migration may have trapped food particles in the oral cavity (Inoue et al. 1986; Temple and Larsen 2007). These findings suggest complexity in the formation of carious lesions and, as the authors seek to demonstrate, that caries prevalence alone cannot be reduced to subsistence economy.

The authors explore caries prevalence, periapical abscesses, and antemortem tooth loss (AMTL) through two comparative meta-analyses. The samples encompass a broad geographic (60 countries) and temporal (6000 years) range. The first treatment uses ANOVA to compare frequencies of carious lesions, periapical abscesses, and AMTL between hunter-gatherers and agriculturalists. The second treatment uses linear regression to evaluate the relationship between carious lesions, periapical abscesses, and AMTL with environmental variables including annual temperature range, annual precipitation, and latitude. Significantly greater carious lesion frequencies are found in agriculturists compared with hunter-gatherers, but the samples overlap in the range of caries prevalence. The R^2 values support this point by demonstrating that only a small percentage of carious teeth are found between subsistence economies, while greater variation is observed within each category. Statistically significant differences in AMTL and periapical abscesses were not found, and both indicators of oral health produced small R^2 values, also indicating greater within-group than between-group variation. Positive relationships were found between dental caries prevalence and mean annual temperature. Negative correlations were found between periapical abscess frequency and mean temperature, while AMTL is negatively correlated with precipitation. The authors draw several conclusions from these results: (1) subsistence economies should not be used as a de facto contributor to oral health, (2) assumptions tying oral health to subsistence category may inadvertently produce unilineal thinking as it relates to human cultural evolution and variation, and (3) there exist many factors that influence subsistence economies, particularly interactions with local biomes.

The development of hypotheses, levels of independent variables, and conclusions of the study demonstrate interdependence between dental caries prevalence and adaptation to local environments, rather than subsistence categories. Such results help move bioarchaeology toward a critical synthesis where greater caution is exercised in interpretations of caries prevalence. However, there exists some circularity in the progression of ideas and conclusions of the study. The authors argue for complexity in carious lesion formation by emphasizing heredity in oral biofilm, malocclusion, atomization of food molecules, intervals between food consumption, and reproductive ecology. However, the independent variables of this study do not reflect these complexities. While it was of interest to compare oral health indicators between subsistence groups to test the hypothesis that the greatest amount of variation occurred within each category, the use of climatic variables feels haphazard, as the hypotheses were not developed on this basis. In particular, the authors argue against environmentally deterministic models of human social organization, yet chose independent variables that measured the association between oral health indicators and the environment (i.e., climate). To further emphasize this point, the authors discuss climate as an accentuating or mitigating factor surrounding dietary choices and resultant subsistence economies.

While climate is an important variable that allows bioarchaeologists to cast aside the veneer of teleology in reconstructing diet, there exists autocorrelation between climate and diet that fails to argue against the use of subsistence categories as a primary basis for comparison. A careful review of the metadata supports this contention. The large majority of hunter-gatherers with elevated carious lesion frequencies (i.e., those who overlap with the agricultural data set) are derived from temperate and tropical environments, specifically locations where the care and maintenance of cariogenic foods are possible. In this sense, the authors have committed a tautological error in argumentation by demonstrating that dental caries prevalence has greater within-group than between-group variation when subsistence categories are used as a basis for comparison, then establishing that factors closely allied with subsistence economies, namely, climate, are associated with dental caries prevalence as supporting evidence.

In addition, dietary choices among hunter-gatherers and agricultural populations frequently transcend environmental categories and remain tethered to identity (Schulting 2014). Hunter-gatherers of the Pacific Northwest maintained salmonid fishing during periods of dearth in these species due to spiritual affiliations with these animals (Campbell and Butler 2010). Religious proscriptions regarding conservation were used to maintain local populations of salmonids during times of resource stress, although salmon were continuously consumed over 7,500 years. Similarly, prehistoric hunter-gatherers of the Late/Final Jomon period incorporated terrestrial mammal bones into mortuary rituals following reduction in the consumption of these foods, creating persistent relational interactions with these animals (Temple 2018). The point here is to say that dietary behavior is highly symbolic and often transcends resource availability and ecological conditions. These factors should also be considered when evaluating carious lesion prevalence in a sample—food may be consumed in greater or lesser amounts based on adaptation to local environments, but there exist many instances where population identity is maintained through continued interaction with these items in life through diet or in death through mortuary ritual. Bioarchaeologists must find unique and creative ways to use indicators of oral health as a reflection of community identity (e.g., Stojanowski 2018). That said, this work represents a contribution toward untangling the deeply typological that human cultural variation is envisioned, and this is laudatory. The authors should be commended for producing a deeply engaging and thought-provoking article.

James T. Watson
Arizona State Museum, University of Arizona, 1013 East University Boulevard, PO Box 210026, Tucson, Arizona 85721, USA (watsonjt@email.arizona.edu). 18 IX 18

Variability in caries experience (and more broadly in oral pathology) is well documented by time, space, and subsistence regime. Carious lesions have been found on fossil hominins as far back as 1.77 Ma, including several individuals from Dmanisi (Margvelashvili et al. 2016) or even further back to 12.5 Ma on the type specimen of *Dryopithecus carinthiacus* (Fuss, Uhlig, and Böhme 2018). Instead of using the presence, distribution, and severity of oral pathology lesions in individuals or across skeletal samples such as these paleontological cases illustrate, bioarchaeologists are generally obsessed with broad comparisons of pathology frequencies to make assumptions about, and link, pathology to diet and subsistence patterns in past human groups. I believe the two principal reasons for this are (1) a limited understanding of oral pathophysiology and (2) Turner's (1979) seminal paper on the global distribution of caries rates between foraging, mixed-subsistence, and agricultural groups. Marklein and colleagues present a cautionary tale about relying on sweeping metadata studies and the blind application of their interpretations. Their conclusions express a principal concern for interpretation and theoretical approaches in bioarchaeology in stating that "applying categorical subsistence nomenclature to complex biocultural relationships and contexts increases the risk of oversimplifying local/regional patterns and reducing complicated human behaviors and interactions into universal socioevolutionary stages."

One of the reasons that Turner's (1979) study was so important was because it provided a broad framework within which to compare and situate subsequent research. Good science formulates hypotheses that can be replicated and tested under varying or experimental circumstances, and that is exactly what Turner's work did. Dozens of bioarchaeologists have now tested their hypotheses against Turner's original metadata results and gained insights into local conditions, developing nuanced interpretations of the past on individual case bases. I would be concerned if succeeding researchers had not found greater variation in caries experience across global space and time. As Marklein and colleagues correctly point out, metadata studies are important for providing a broader perspective and framework to work from—as their study further demonstrates; however, inherent bias, inaccuracy, and problematic generalizations commonly increase with larger data sets.

Marklein and colleagues provide a series of caveats that facilitate the creation of a larger global sample for analysis, and specifically argue that "it does not significantly affect our conclusions because the hypothesis tested here states that the adoption of agriculture is a stronger contributing factor to the prevalence of caries, abscesses, and AMTL [antemortem tooth loss] than other demographic and morphological parameters." After arguing against the issues with comparing conglomerated data that obfuscates local nuances in behavior and environmental variability, they use the same (expanded) type of data set to test their hypotheses. The primary utility of regional studies that consider contextual detail in their analysis of oral pathology is that they provide greater detail to interpret past human behavior and biocultural consequences.

The conclusions of Marklein and colleagues are important and need to be heeded by researchers moving forward, and I completely agree that looking beyond diet is a critical perspective when considering oral pathology. However, I feel the authors focus on the perceived dominance of diet in interpretations to the detriment of two equally important considerations that are often underconsidered: age and heterogeneity in susceptibility. Age, more than any other variable, should play the greatest role in caries experience across human groups. Caries and tooth loss (and secondarily abscesses) result from age-progressive disease processes, accumulating throughout the life course. If, for example, a large proportion of the hunter-gatherer sample examined by Marklein and colleagues consisted of older demographic samples (older age-at-death profiles) compared with most of the agricultural sample, then caries rates would minimally equalize across a subsistence dichotomy—a scenario that is conceivable given the significant differences in mortality profiles between these broadly defined subsistence regimes. Several authors have considered how to treat demographic variation when comparing oral pathology (see Pechenkina, Benfer, and Zhijun 2002, e.g.), yet few researchers incorporate this basic consideration into comparative analyses.

The other factor that needs to be considered, and attempted to control for, in comparative studies of oral pathology is individual-level heterogeneity in susceptibility. Despite the call of Wood and colleagues (1992) for greater attention to this topic as part of the osteological paradox, few practitioners have answered with reasonable attempts. Pathology rates, especially those calculated by tooth or alveolar segment, are prone to inflation from individuals that are particularly susceptible to oral diseases that could result from a myriad of etiologies, varying from fluctuations in pH to inheriting a phenotype for thin enamel. In addition, pathology experience related to individual susceptibility is further exacerbated by increasing age.

The conclusions of Marklein and colleagues that climatic variables "contributed to variation in oral lesion prevalences show an equal or greater explanatory power . . . than subsistence" is an important test, and rebuke, of traditional approaches, and I laud their attempt to highlight the limitations in our discipline. The continued use of linear associations between oral lesions and behavior, specifically focused on diet/subsistence dichotomies, is flawed and needs to be discontinued. However, I would extend their call for a more encompassing perspective to argue that age and heterogeneity in susceptibility are equally important to the consideration of the complex biocultural etiologies of oral pathology.

Reply

Before addressing the provocative comments put forth by our colleagues, we would like to express our gratitude to all the commentators for their thoughtful responses to our paper. Our main objective with this comparative analysis was to provoke a constructive discussion, and we are indebted to the respondents for recognizing the contribution of this work to the broader anthropological literature, as well as more specialized fields, and for highlighting the limitations and shortcomings in our article. As Papathanasiou highlights in her response, while our analysis focuses on agricultural transitions and oral (notably, carious) lesions, the more general themes of the paper harken back to broader concerns in bioanthropology. In that sense, we believe that we achieved our most ambitious goal. Although we dwell primarily on the research in oral health, with a focus on caries due to the amount of data in the literature available, our analyses can be seen as cautionary tales for all skeletal and dental conditions included in paleopathological, epidemiological, and bioarchaeological research agendas.

It was our hope to generate a conversation that would expand beyond these journal pages, so it was a pleasure subsequently to read the different perspectives and insights put forth by scholars across the world. We would like to add this reply as a continuation of that discussion, rather than a conclusion, hoping to continue spurring "future research and hypothesis testing" (Goodman) in bioarchaeology and biological anthropology.

Although commentators addressed specific theoretical or methodological points (and limitations) throughout the paper, we observed a consensus among several of the comments, namely, that oral health markers do represent important evidence of dietary contributions to past populations but that the precision and value of these analyses are best interpreted within demographic, archaeological, ecological, and epidemiological contexts. We are pleased to see that our metastudy, which by nature of its geographically and chronologically expansive and varied sample size did not apply such a rigorous context to its findings, was able nonetheless to stimulate a dialogue about the importance and necessity of context in bioarchaeology. We appreciate that commentators generally saw beyond these inherent shortcomings in our paper necessitated by our holistic perspective—lack of associated demographic data, generalized prevalence reporting (presence-absence), and purposeful oversight of correlative, confounding variables (i.e., antemortem tooth loss and tooth wear)—and focused on the broader theoretical implications presented.

As most of the commentators rightly pointed out, there can be no question as to the multifactorial and complex etiology of dental and oral lesions, especially the foregrounded carious lesions. Without conclusive data about cariogenic processes in modern oral pathology, how are we supposed to extrapolate behavior in past populations? It is not a hopeless endeavor, and as respondents demonstrate, there are clinical and genetic research projects devoted to understanding predilections to and patterns in oral lesions (Da-Gloria, Larsen, and Lukacs). We want to highlight this point here, as we believe as well that embracing what genetics can tell us about populations and individual microbiomes and oral biologies will become tantamount to future studies in carious lesion research. In the meantime, it is imperative to factor what observable variables in the skeleton we know into our local, regional, and interregional studies: biological age and sex estimations, number of lesions per individual, location of lesion on the tooth or alveolar bone, and severity of lesions, especially as they inform other conditions. While our metastudy deliberately chose to exclude these variables, so as to include more sites in the analysis, this decision was not intended to discount the importance of such factors; in fact, it is quite the contrary.

Another point of interest that deserves some clarification on our part was the use of climatic variables to explain lesion variation. Originally, we designed this inclusion in the analysis as an exercise to show that there are alternative observable variables that can have similar explanatory powers than diet per se to explain the different prevalence of oral pathological lesions. The presented results are not intended to shake the foundations of dietary contributions to oral pathogenesis (nor would our results argue to that effect) but rather to underline our point that broad lifestyle categories, even though statistically significant, can demonstrate relatively weak explanatory powers in a larger regional context. The climatic variables, therefore, were not presented to argue that we should include climate in our analyses but rather to add a reference to the explanatory power of what are seen as major contributors to the prevalence of oral health. This comparative perspective helps to illustrate how population variation and pathological lesions may correlate with, but not necessarily be determined by, their environments.

To bring to the forefront another of our concerns, our comparative exercise was designed exactly to illustrate how we frequently run the risk of further simplifying and essentializing biological, cultural, and archaeological components to pathogeneses. Categorizing variables has heuristic benefits, as Da-Gloria notes, as long as these findings are situated in biocultural reality. Providing this context will help us avoid falling into a teleological trap of biomarkers and self-affirming behaviors.

Another aspect to consider in this study, especially regarding agricultural transitions, is the interconnectedness and embeddedness of environment, biology, and culture. To address Temple's tautological error statement, there can be no doubt, for example, as to the inextricable association between climatic variables, such as annual precipitation and temperature, and subsistence strategies. Temple provides detailed commentary about climate in terms of its pervasiveness in agricultural and hunter-gatherer food availabilities and subsistence decisions. He also reminds us how profoundly cultural identity affects dietary decisions from a religious and symbolic standpoint with examples from Late/Final Jomon period Japan and Pacific Northwest hunter-gatherer communities. We wholeheartedly agree with his points. As we noted above, the reason for our climatic analysis was not to overshadow the importance of subsistence and other cultural variables but to demonstrate that even climate, as an example, could be shown to have the same magnitude of impact on carious lesion distribution as subsistence categories. In our quest to explain skeletal and dental variation within and between samples, we should always be mindful of the ecological contexts in which populations adapted cultural behaviors and subsistence economies.

Constructing and scrutinizing the physical and social landscape in which past peoples lived, through extensive archaeological, paleoenvironmental, and biochemical research, is critical not only to understanding human behavior but also to contextualizing patterns of skeletal and dental biomarkers observed throughout population samples. The most recent research in Southeast Asia on carious lesions, as expounded upon by Domett, is significantly enriched by the incorporation of supportive paleobotanical, archaeological, and stable isotopic evidence. These complementary data sets are especially crucial for bioarchaeological results with "no clear pattern" (Domett) of carious lesions over time.

Even where more demonstrative patterns of dental lesions have been associated with agricultural transitions (e.g., maize agriculture in the Americas) and substantiated with archaeological and ethnographic evidence, interpretations have been recently reevaluated with biological, demographic, and genetic considerations in mind. As Lukacs comments, these considerations are important for explaining specifically declines in oral health among females at the advent of agriculture. Clinical research has demonstrated how significantly oral environments and microbiomes fluctuate in females throughout their lifetimes, especially during reproductive years. While we may not be able to quantify the direct effects of female reproductive biology on carious lesion prevalence, researchers have demonstrated how fertility and demography (both sex and age considerations) can be factored into a bioculturally informed interpretation of a population's oral health distribution (Lukacs 2018; Temple 2018). These complementary biological data will help to both strengthen and enrichen future analyses in bioarchaeological oral health research.

The future of bioarchaeological (and bioanthropological) research, as the commentators have projected, is a promising one, with remarkable potential for continued interdisciplinary studies and dialogues. One of the avenues for progress exists in the clinical, epidemiologic, and genetic and epigenetic fields, teasing apart the observable and quantifiable etiological components to caries. Not only will further dissecting of dental (and skeletal) pathological etiologies inform bioarchaeological research about contributing and confounding variables but these data will enhance our understanding of phenotypic variability (e.g., dental morphology, enamel microstructure) and help explain differential lesion susceptibility among peoples and populations. As Da-Gloria suggests, future bioarchaeological approaches should include "robust interpretative models"—as have been employed in archaeological, epidemiological, and ethnographic studies—into which we can agglomerate and analyze the many variables that directly or indirectly contribute to pathological conditions. While this new standard may demand considerable efforts in gathering experimental data, as well as in conducting rigorous analyses of data, there can be no doubt as to the ultimate value such undertakings will have for the field.

Epidemiological, archaeological, and cultural modeling brings us only so far with understanding and explaining skeletal and dental conditions, however. We also need to impress upon researchers greater consideration of individual-level heterogeneity and susceptibility, hallmarks of the osteological paradox that still mandate further attention. As a metastudy, this paper knowingly avoided this important issue in the analysis, but, as Watson reflected, this concept nonetheless is critical to all studies that evaluate ancient health and disease, especially studies, like agricultural transitions, where so much variability is observed.

Novel cross-disciplinary work seeks to address individual heterogeneity. In particular, recent experiments in applied immunology, and the genesis of archaeoproteomic research, provide a way to not only recognize immunological shifts but also quantify inflammatory responses in individuals with chronic disease (Crespo and Lawrenz 2014; Crespo et al. 2017). If we are able to complement skeletal and dental lesion data with information about individual immunological responses, therein lies the potential to directly connect our suite of biomarkers with systemic heterogeneity and susceptibility. Osteoimmunology follows the vast and continually growing fields of histology, molecular anthropology, and archaeogenetics, which have already been adopted into the paleoanthropological and bioarchaeological canons (Klaus 2014; Ragsdale et al. 2012; Weyrich et al. 2017) as additional lines of evidence to elucidate hidden heterogeneity. While progressive paleodemographic and paleoepidemiological work on the Black Death and outbreaks of Medieval plague (DeWitte 2014*a*, 2015) has demonstrated how, with historically contextualized skeletal series, bioarchaeologists have addressed overall population trends in risk of mortality and epidemic susceptibility, biomolecular and genetic data may add a further dimensional approach to accounting for individual heterogeneity. However, these attempts to identify individual heterogeneity should not be limited to epidemic bioarchaeological studies but become part and parcel of all bioarchaeological studies. When trying to reconstruct past population lifeways, we must also reconstruct the individual lifeways within that population. This is not a new reflection for our discipline; it reiterates justified critiques enumerated by Wood and colleagues (1992), which are nonetheless recognized as present shortcomings in our field (DeWitte and Stojanowski 2015). Rather than include a cursory caveat in publications that individual heterogeneity exists, bioarchaeologists need to make more earnest efforts to identify, explain, and contextualize hidden heterogeneity in their discussions of results and conclusions. This is not a universal failing of bioarchaeological studies—progress has been made in the way of well-developed hypotheses that test intra- and interpopulation heterogeneity (DeWitte 2014*b*; Kyle et al. 2018; Redfern et al. 2018)—but we believe it should be a major course for improvement (Boldsen and Milner 2012).

While the respondents and we have indicated many and various avenues for research potential and improvement in our field, the path forward is a positive one, and we wish to end our current contribution to the dialogue on an optimistic (Larsen) note. An immediate course for change, which is already well underway, is the scrutinized interpretation of pathological lesions in an informative demographic and archaeological context. But this scrutiny must transcend general percentages and distributions (e.g., males and females, general and age categories) to understand the etiological, sociocultural, and biocultural processes affecting the presence (or absence) of pathological lesions and conditions. Fortunately, we are in a technological and scientific age in which these processes can be thoroughly and more accurately dissected. Modern and historical clinical and epidemiological accounts of skeletal and dental conditions can be complemented by the synchronic snowballing fields of archaeogenetics and paleomicrobiology to better explain how diseases differentially evolve and manifest in populations throughout history and the globe. These data will also be essential to modeling population susceptibility and individual-level heterogeneity. Additionally, and what this paper sought most to foreground, bioarchaeology is a study of past peoples interacting in and engaging with unique local, regional, and interregional contexts and individuals. To truly understand these peoples, we need to fully understand the interwoven environmental, political, and sociocultural variables contributing to their biological health and embodied identities. If we essentialize complex lifeways and do not acknowledge, present, and explain the variability embedded in the people, the cultures, the politics, and the subsistence economies that bioarchaeologists dedicatedly study, the humanistic quality of our scientific research may be compromised. We have great hope that researchers and scholars will continue to rise to the current theoretical and methodological challenges with innovative, collaborative, and inspiring results.

—Kathryn E. Marklein, Christina Torres-Rouff, Laura M. King, and Mark Hubbe

References Cited

Allison, Edward H., Neil L. Andrew, and Jamie Oliver. 2007. Enhancing the resilience of inland fisheries and aquaculture systems to climate change. *Journal of Semi-Arid Tropical Agricultural Research* 4(1):35.

Armelagos, George J. 2003. Bioarchaeology as anthropology. *Archeological Papers of the American Anthropological Association* 13(1):27–40.

Aufderheide, Arthur C., and Conrado Rodrigues-Martin. 1998. *The Cambridge encyclopedia of human paleopathology*. Cambridge: Cambridge University Press.

Auliciems, Andris. 2009. Human adaptation within a paradigm of climatic determinism and change. In *Biometeorology for adaptation to climate variability and change*. K. L. Ebi, I. Burton, and G. McGregor, eds. Pp. 235–267. New York: Springer.

Baadgsaard, Aubrey, Alexis T. Boutin, and Jane E. Buikstra, eds. 2012. *Breathing new life into the evidence of death: contemporary approaches to bioarchaeology*. Santa Fe, NM: School for Advanced Research.

Bass, William. 1987. *Human osteology: a laboratory and field manual*. 3rd edition. Springfield: Missouri Archaeological Society.

Beckett, Sean, and Nancy C. Lovell. 1994. Dental disease evidence for agricultural intensification in the Nubian C-Group. *International Journal of Osteoarchaeology* 4(3):223–239.

Berbesque, J. Colette, Frank W. Marlowe, and Alyssa N. Crittenden. 2011. Sex differences in Hadza eating frequency by food type. *American Journal of Human Biology* 23(3):339–345.

Berglund, Björn E. 2003. Human impact and climate changes: synchronous events and a causal link? *Quaternary International* 105(1):7–12.

Bettinger, Robert, Peter Richerson, and Robert Boyd. 2009. Constraints on the development of agriculture. *Current Anthropology* 50(5):627–631.

Bocquet-Appel, Jean-Pierre, and Ofer Bar-Yosef. 2008. *The Neolithic demographic transition and its consequences*. New York: Springer.

Boldsen, Jesper L., and George R. Milner. 2012. An epidemiological approach to paleopathology. In *A companion to paleopathology*. A. L. Grauer, ed. Pp. 114–132. Chichester: Blackwell.

Bonfiglioli, B., P. Brasili, and M. G. Belcastro. 2003. Dento-alveolar lesions and nutritional habits of a Roman Imperial age population (1st–4th c. AD): Quadrella (Molise, Italy). *Homo* 54(1):36–56.

Boserup, Ester. 1965. *The conditions of agricultural growth: the economics of agrarian change under population pressure*. London: Allen & Unwin.

Braidwood, Robert J. 1960. The agricultural revolution. *Scientific American* 203:130–148.

Brickley, Megan, and Jacqueline I. McKinley, eds. 2004. *Guidelines to the standards for recording human remains*. Southampton, UK: British Association for Biological Anthropology and Osteoarchaeology.

Brothwell, Don R. 1963. *Digging up bones: the excavation, treatment, and study of human skeletal remains*. London: British Museum.

Buikstra, Jane E., and Douglas H. Ubelaker. 1994. *Standards for data collection from human skeletal remains*. Fayetteville: Arkansas Archaeological Society.

Buikstra, Jane E., and Lane A. Beck, eds. 2006. *Bioarchaeology: the contextual analysis of human remains*. Amsterdam: Academic Press.

Burt, Brian A., and Satishchandra Pai. 2001. Sugar consumption and caries risk: a systematic review. *Journal of Dental Education* 65(10):1017–1023.

Campbell, Sarah K., and Virginia Butler. 2010. Archaeological evidence for resilience of Pacific Northwest salmon populations and the socioecological system over the last ~7500 years. *Ecology and Society* 15:17. [DHT]

Carlson, David S., and Dennis P. Van Gerven. 1977. Masticatory function and post-Pleistocene evolution in Nubia. *American Journal of Physical Anthropology* 46(3):495–506.

Castillo, C. C., C. F. W. Higham, K. Miller, N. Chang, K. Douka, T. F. G. Higham, and D. Q Fuller. 2018. Social responses to climate change in Iron Age northeast Thailand: new archaeobotanical evidence. *Antiquity* 365 (92):1274–1291. [KD]

Chance, Norman A. 2002. *The Inupiat and Arctic Alaska: an ethnography of development*. Fort Worth, TX: Thomas.

Childe, V. Gordon. 1950. The urban revolution. *Town Planning Review* 21:3–17.

———. 1957. Civilizations, cities, and towns. *Antiquity* 31(121):36–38.

Cohen, Mark N. 1977. *The food crisis in prehistory: overpopulation and the origins of agriculture*. New Haven, CT: Yale University Press.

———. 1989. *Health and the rise of civilization*. New Haven: Yale University Press.

Cohen, Mark N., and George J. Armelagos, eds. 1984. *Paleopathology at the origins of agriculture*. Orlando, FL: Academic Press.

———. 2013. *Paleopathology at the origins of agriculture*. 2nd edition. Orlando, FL: Academic Press.

Cohen, Mark N., and Gillian M. M. Crane-Kramer, eds. 2007. *Ancient health: skeletal indicators of agricultural and economic intensification*. Gainesville: University Press of Florida.

Cole, Michael F., Katherine A. Wirth, and George H. Bowden. 2013. Microbial populations in oral biofilms. In *Oral microbial ecology: current research and new perspectives*. N. S. Jakubovics, and R. J. Palmer Jr., eds. Pp. 1–26. Norfolk, VA: Caister Academic.

Cook, Della C., and Jane E. Buikstra. 1979. Health and differential survival in prehistoric populations: prenatal dental defects. *American Journal of Physical Anthropology* 51(4):649–664.

Coombes, Paul, and Keith Barber. 2005. Environmental determinism in Holocene research: causality or coincidence? *Area* 37(3):303–311.

Costa, Raymond L. 1980. Incidence of caries and abscesses in archeological Eskimo skeletal samples from Point Hope and Kodiak Island, Alaska. *American Journal of Physical Anthropology* 52(4):501–514.

Crespo, Fabian A., Christopher K. Klaes, Andrew E. Switala, and Sharon N. DeWitte. 2017. Do leprosy and tuberculosis generate a systemic inflammatory shift? setting the ground for a new dialogue between experimental immunology and bioarchaeology. *American Journal of Physical Anthropology* 162(1):143–156.

Crespo, Fabian A., and Matthew B. Lawrenz. 2014. Heterogeneous immunological landscapes and medieval plague: an invitation to a new dialogue between historians and immunologists. *Medieval Globe* 1(1):229–258.

Crittenden Alyssa N., John Sorrentino, Sheniz A. Moonie, Mika Peterson, Audax Mabulla, and Peter S. Ungar. 2017. Oral health in transition: the Hadza foragers of Tanzania. *PLoS ONE* 12(3):e0172197.

Cucina, Andrea, Cristina P. Cantillo, Thelma S. Sosa, and Vera Tiesler. 2011. Carious lesions and maize consumption among the prehispanic Maya: an analysis of a coastal community in northern Yucatan. *American Journal of Physical Anthropology* 145(4):560–567.

Cucina, Andrea, and Vera Tiesler. 2003. Dental caries and antemortem tooth loss in the Northern Peten area, Mexico: a biocultural perspective on social status differences among the Classic Maya. *American Journal of Physical Anthropology* 122(1):1–10.

Da-Gloria, Pedro, and Clark Spencer Larsen. 2014. Oral health of the Paleoamericans of Lagoa Santa, central Brazil. *American Journal of Physical Anthropology* 154(1):11–26.

Deeley, K., A. Letra, E. K. Rose, C. A. Brandon, J. M. Resick, M. L. Marazita, and A. R. Vieira. 2008. Possible association of amelogenin to high caries experience in a Guatemalan-Mayan population. *Caries Research* 42:8–13. [JL]

DeWitte, Sharon N. 2014*a*. The anthropology of plague: insights from bioarchaeological analyses of epidemic cemeteries. *Medieval Globe* 1(1):97–124.

———. 2014*b*. Differential survival among individuals with active and healed periosteal new bone formation. *International Journal of Paleopathology* 7:38–44.

———. 2015. Setting the stage for medieval plague: pre-black death trends in survival and mortality. *American Journal of Physical Anthropology* 158(3): 441–451.

DeWitte, Sharon N., and Christopher M. Stojanowski. 2015. The osteological paradox 20 years later: past perspectives, future directions. *Journal of Archaeological Research* 23:397–450.

Domett, Kathryn M., Caitlin Evans, Nigel Chang, Nancy Tayles, and Jennifer Newton. 2017. Interpreting osteoarthritis in bioarchaeology: highlighting the importance of a clinical approach through case studies from prehistoric Thailand. *Journal of Archaeological Science: Reports* 11:762–773. [KD]

Domett, Kathryn M. 2001. *Health in late prehistoric Thailand*. British Archaeological Reports, vol. 946. Oxford: BAR.

Dymock, D., A. J. Weightman, C. Scully, and W. G. Wade. 1996. Molecular analysis of microflora associated with dentoalveolar abscesses. *Journal of Clinical Microbiology* 34(3):537–542.

Edgar, W. M., B. G. Bibby, S. Mundorff, and J. Rowley. 1975. Acid production in plaques after eating snacks: modifying factors in foods. *Journal of the American Dental Association* 90(2):418–425.

Edgar, W. M., S. M. Higham, and R. H. Manning. 1994. Saliva stimulation and caries prevention. *Advances in Dental Research* 8(2):239–245.
Eshed, Vered, Avi Gopher, and Israel Hershkovitz. 2006. Tooth wear and dental pathology at the advent of agriculture: new evidence from the Levant. *American Journal of Physical Anthropology* 130(2):145–159.
Frayer, D. W. 1989. Oral pathologies in the European Upper Paleolithic and Mesolithic. In *People and culture in change*. I. Hershkovits, ed. Pp. 255–281. Oxford: British Archaeological Reports International Series 508(1).
Fuss, J., G. Uhlig, and M. Böhme. 2018. Earliest evidence of caries lesion in hominids reveal sugar-rich diet for a Middle Miocene dryopithecine from Europe. *PLoS ONE* 13(8):e0203307. [JTW]
Gerreth, K., K. Zaorska, M. Zabel, M. Borysewicz-Lewicka, and M. Nowicki. 2017. Chosen single nucleotide polymorphisms (SNPs) of enamel formation genes and dental caries in a population of Polish children. *Advances in Clinical and Experimental Medicine* 26:899–905. [JL]
Gehlsen, Duane. 2009. *Social complexity and the origins of agriculture: the complex-systems theory of culture*. Saarbrücken, Germany: VDM.
Gill, Y., and C. Scully. 1990. Orofacial odontogenic infections: review of microbiology and current treatment. *Oral Surgery, Oral Medicine, Oral Pathology* 70(2):155–158.
Goodman, Alan H., and George J. Armelagos, and Jerome C. Rose. 1980. Enamel hypoplasias as indicators of stress in three prehistoric populations from Illinois. *Human Biology* 52(3):515–528.
Goodman, Alan H., John Lallo, George J. Armelagos, and Jerome C. Rose. 1984. Health changes at Dickson Mounds (AD 950–1300). In *Paleopathology at the origins of agriculture*. M. N. Cohen and G. J. Armelagos, eds. Pp. 271–305. Orlando, FL: Academic Press.
Gosman, James H., Samuel D. Stout, and Clark S. Larsen. 2011. Skeletal biology over the life span: a view from the surfaces. *American Journal of Physical Anthropology* 146(S53):S86–S98.
Grmek, Mirko D. 1989. *Diseases in the ancient Greek world*. Baltimore: Johns Hopkins University Press.
Gross, Erin L., Clifford J. Beall, Stacey R. Kutsch, Noah D. Firestone, Eugene J. Leys, and Ann L. Griffen. 2012. Beyond *Streptococcus mutans*: dental caries onset linked to multiple species by 16S rRNA community analysis. *PLoS ONE* 7(10):e47722.
Gupta, V. K., S. Paul, and C. Dutta. 2017. Geography, ethnicity or subsistence-specific variations in human microbiome composition and diversity. *Frontiers in Microbiology* 8. https://doi.org/10.3389/fmicb.2017.01162. [JL]
Gustafsson, Bengt E., Carl-Erik Quensel, Lisa Swenander Lanke, Claes Lundqvist, Hans Grahnen, Bo Erik Bonow, and B. O. Krasse. 1953. The effect of different levels of carbohydrate intake on caries activity in 436 individuals observed for five years. *Acta Odontologica Scandinavica* 11(3–4):232–364.
Hara, Anderson T., and Domenick T. Zero. 2010. The caries environment: saliva, pellicle, diet, and hard tissue ultrastructure. *Dental Clinics of North America* 54(3):455–467.
Harris, Robert. 1963. Biology of the children of Hopewood House, Bowral, Australia. 4. Observations on dental-caries experience extending over five years (1957–61). *Journal of Dental Research* 42:1387–1399.
Hayden, B. 1981. Research and development in the Stone Age. *Current Anthropology* 22:519–548.
Helm, Sven, and Poul Erik Petersen. 1989. Causal relation between malocclusion and periodontal health. *Acta Odontologica Scandinavica* 47(4):223–228.
Henne, K., A.-P. Gunesch, C. Walther, H. Meyer-Lueckel, G. Conrads, and M. Esteves-Oliveira. 2016. Analysis of bacterial activity in sound and cariogenic biofilm: a pilot in vivo study. *Caries Research* 50:480–488.
Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2004. The WorldClim interpolated global terrestrial climate surfaces. Version 1.3.
Hillson, Simon. 1996. *Dental anthropology*. Cambridge: Cambridge University Press.
———. 2001. Recording dental caries in archaeological human remains. *International Journal of Osteoarchaeology* 11(4):249–289.
———. 2008. Dental pathology. In *Biological anthropology of the human skeleton*. 2nd edition. M.A. Katzenberg and S. R. Saunders, eds. Pp. 299–340. Hoboken, NJ: Wiley.
———. 2014. *Tooth development in human evolution and bioarchaeology*. Cambridge: Cambridge University Press.
Hixon, Ernest H., Philip J. Maschka, and Paul T. Fleming. 1962. Occlusal status, caries, and mastication. *Journal of Dental Research* 41(3):514–524.
Hoover, Kara C., and Frank L. Williams. 2016. Variation in regional diet and mandibular morphology in prehistoric Japanese hunter-gatherer-fishers. *Quaternary International* 405:101–109.
Hubbe, Mark, Christina Torres-Rouff, Walter Alves Neves, Laura M. King, Pedro Da-Gloria, and Maria Antonietta Costa. 2012. Dental health in northern Chile's Atacama oases: evaluating the Middle Horizon (AD 500–1000) impact on local diet. *American Journal of Physical Anthropology* 148 (1):62–72.
Humphrey, Louise T., Isabelle De Groote, Jacob Morales, Nick Barton, Simon Collcutt, Christopher Bronk Ramsey, and Abdeljalil Bouzouggar. 2014. Earliest evidence for caries and exploitation of starchy plant foods in Pleistocene hunter-gatherers from Morocco. *Proceedings of the National Academy of Sciences of the USA* 111(3):954–959.
IBM. 2013. IBM SPSS statistics for Windows, version 22.0. Armonk, NY: IBM Corp.
Ilie, Olga, Mark C. M. van Loosdrecht, and Cristian Picioreanu. 2012. Mathematical modelling of tooth demineralisation and pH profiles in dental plaque. *Journal of Theoretical Biology* 309:159–175.
Inoue, Naohiko, Gakuji Ito, and Tetsuya Kamegai. 1986. Dental pathology of hunter-gatherers and early farmers in prehistoric Japan. In *Prehistoric hunter-gatherers of Japan: new research methods*. C. M. Aikens and T. Akazawa, eds. Pp. 163–198. University of Tokyo Bulletin 27. Tokyo: University Museum. [DHT]
Keenleyside, Anne. 2008. Dental pathology and diet at Apollonia, a Greek colony on the Black Sea. *International Journal of Osteoarchaeology* 18(3): 262–279.
Kelly, Robert L. 2007. *The foraging spectrum: diversity in hunter-gatherer lifeways*. Clinton Corners, NY: Percheron.
Kennett, Douglas J., and James P. Kennett. 2000. Competitive and cooperative responses to climatic instability in coastal southern California. *American Antiquity* 65(2):379–395.
Keyes, P. H. 1968. Research in dental caries. *Journal of the American Dental Association* 76(6):1357–1373. [JL]
Kidd, Edwina A., and S. Joyston-Bechal. 1997. Diet and caries. In *Essentials of dental caries*. 2nd edition. E. A. M. Kidd, ed. Pp. 79–103. Oxford: Oxford University Press.
King, Charlotte L., R. Alexander Bentley, Nancy Tayles, Una Strand Viðarsdóttir, Geoff Nowell, and Colin G. Macpherson. 2013. Moving peoples, changing diets: isotopic differences highlight migration and subsistence changes in the Upper Mun River Valley, Thailand. *Journal of Archaeological Science* 40(4):1681–1688. [KD]
Kirch, Patrick V. 2005. Archaeology and global change: the Holocene record. *Annual Review of Environment and Resources* 30:409–440.
Klaus, Haagen D. 2014. Frontiers in the bioarchaeology of stress and disease: cross-disciplinary perspectives from pathophysiology, human biology, and epidemiology. *American Journal of Physical Anthropology* 155(2):294–308.
Knüsel, Christopher J. 2010. Bioarchaeology: a synthetic approach. *Bulletins et mémoires de la Société d'anthropologie de Paris* 22(1):62–73.
Koohpeima, F., F. Hashemi-Gorji, and M. J. Mokhtari. 2018. Evaluation of caries experience in two genders and enam polymorphism in Iranian adults. *Meta Gene* 17:78–81. [JL]
Kyle, Britney, Laurie J. Reitsema, Janelle Tyler, Pier Francesco Fabbri, and Stefano Vassallo. 2018. Examining the osteological paradox: skeletal stress in mass graves versus civilians at the Greek colony of Himera (Sicily). *American Journal of Physical Anthropology* 167(1):161–172.
Lambert, Patricia, ed. 2000. *Bioarchaeological studies of life in the age of agriculture: a view for the Southeast*. Tuscaloosa: University of Alabama Press.
Larsen, Clark S. 1982. The anthropology of St. Catherines Island. 3. Prehistoric human biological adaptation. *Anthropological Papers of the American Museum of Natural History* 57(3).
———. 1995. Biological changes in human populations with agriculture. *Annual Review of Anthropology* 24:185–213.
———. 1997. *Bioarchaeology: interpreting behavior from the human skeleton*. 1st edition. Cambridge: Cambridge University Press.
———. 2015. *Bioarchaeology: interpreting behavior from the human skeleton*. 2nd edition. Cambridge: Cambridge University Press.
Larsen, Clark S., Mark C. Griffin, Dale L. Hutchinson, Vivian E. Noble, Lynette Norr, Robert F. Pastor, Christopher B. Ruff, et al. 2001. Frontiers of contact: bioarchaeology of Spanish Florida. *Journal of World Prehistory* 15 (1):69–123.
Lassalle, F., M. Spagnoletti, M. Fumagalli, L. Shaw, M. Dyble, C. Walker, M. G. Thomas, A. B. Migliano, and F. Balloux. 2018. Oral microbiomes from hunter-gatherers and traditional farmers reveal shifts in commensal balance and pathogen load linked to diet. *Molecular Ecology* 27:182–195. [JL]
Lee, Hoo-Yeon, Youn-Hee Choi, Hyoung Wook Park, and Sang Gyu Lee. 2012. Changing patterns in the association between regional socio-economic con-

text and dental caries experience according to gender and age: a multilevel study in Korean adults. *International Journal of Health Geographics* 11(1):30.
Lee, Richard B. 2013. *The Dobe Ju/'hoansi*. 4th edition. Belmont, CA: Wadsworth.
Lee, Richard B., and Irven DeVore, eds. 1968. *Man the hunter*. Piscataway, NJ: Aldine.
Legler, D. W., and L. Menaker. 1980. Definition, etiology, epidemiology and clinical implication of dental caries. In *The biological basis of dental caries*. L. Menaker, ed. Pp. 217. New York: Harper & Row.
Leverett, Dennis H. 1982. Fluorides and the changing prevalence of dental caries. *Science* 217(4554):26–30.
Lieberman, Daniel E., Gail E. Krovitz, Franklin W. Yates, Maureen Devlin, and Marisa St Claire. 2004. Effects of food processing on masticatory strain and craniofacial growth in a retrognathic face. *Journal of Human Evolution* 46(6):655–677.
Lubell, David, Mary Jackes, Henry Schwarcz, Martin Knyf, and Christopher Meiklejohn. 1994. The Mesolithic-Neolithic transition in Portugal: isotopic and dental evidence of diet. *Journal of Archaeological Science* 21(2):201–216.
Lukacs, John R. 1989. Dental paleopathology: methods for reconstructing dietary patterns. In *Reconstruction of life from the skeleton*. M. Yaşar İşcan and Kenneth A. R. Kennedy, eds. Pp. 261–286. New York: Liss.
———. 1992. Dental paleopathology and agricultural intensification in South Asia: new evidence from Bronze Age Harappa. *American Journal of Physical Anthropology* 87:133–150.
———. 1995. The "caries correction factor": a new method of calibrating dental caries rates to compensate for antemortem tooth loss. *International Journal of Osteoarchaeology* 5:151–156.
———. 1996. Sex differences in dental caries rates with the origin of agriculture in South Asia. *Current Anthropology* 37(1):147–153.
———. 2007. Dental trauma and antemortem tooth loss in prehistoric Canary Islanders: prevalence and contributing factors. *International Journal of Osteoarchaeology* 17(2):157–173.
———. 2008. Fertility and agriculture accentuate sex differences in dental caries rates. *Current Anthropology* 49(5):901–914.
———. 2011*a*. Gender differences in oral health in South Asia: metadata imply multifactorial biological and cultural causes. *American Journal of Human Biology* 23(3):398–411.
———. 2011*b*. Sex differences in dental caries experience: clinical evidence, complex etiology. *Clinical Oral Investigations* 15:649–656. [KD]
———. 2017*a*. Bioarchaeology of oral health: sex and gender differences in dental disease. In *Exploring sex and gender in bioarchaeology*. S. C. Agarwal and J. K. Wesp, eds. Pp. 263–290. Albuquerque: University of New Mexico Press.
———. 2017*b*. Dental adaptations of Bronze Age Harappans: occlusal wear, crown size, and dental pathology. *International Journal of Paleopathology* 18:69–81. [JL]
———. 2018. Dental caries and other dental diseases. In *The International encyclopedia of biological anthropology*. W. Trevathan, ed. Chichester: Wiley.
Lukacs, John R., and Leah H. Largaespada. 2006. Explaining sex differences in dental caries prevalence: saliva, hormones and "life-history" etiologies. *American Journal of Human Biology* 18:540–555.
Lukacs, John R., and J. N. Pal. 1993. Mesolithic subsistence in north India: inferences from dental attributes. *Current Anthropology* 34(5):745–765.
Mandel, Irwin D. 1989. The role of saliva in maintaining oral homeostasis. *Journal of the American Dental Association* 119(2):298–304.
Mant, Madeleine, and Charlotte Roberts. 2015. Diet and dental caries in post-medieval London. *International Journal of Historical Archaeology* 19:188–207.
Margvelashvili, A., C. P. E. Zollikofer, D. Lordkipanidze, P. Tafforeau, and M. A. Ponce De León. 2016. Comparative analysis of dentognathic pathologies in the Dmanisi mandibles. *American Journal of Physical Anthropology* 160(2):229–253. [JTW]
Marlowe, Frank W. 2010. *The Hadza: hunter-gatherers of Tanzania*, vol. 3. Berkeley: University of California Press.
Martin, Bruce, David Burr, and Neil A. Sharkey. 1998. *Skeletal tissue mechanics*. New York: Springer.
Martin, Debra L., Ryan P. Harrod, and Ventura R. Pérez. 2013. *Bioarchaeology: an integrated approach to working with human remains*. New York: Springer.
Meiklejohn, Christopher, and Marek Zvelebil. 1991. Health status of European populations at the agricultural transition and the implications for the adoption of farming. In *Health in past societies: biocultural interpretations of human skeletal remains in archaeological contexts*. H. Bush and M. Zvelebil, eds. Pp. 129–145. Oxford: Archaeological and Historical Associates.
Meze-Hausken, Elisabeth. 2004. Contrasting climate variability and meteorological drought with perceived drought and climate change in northern Ethiopia. *Climate Research* 27:19–31.
Morgan, Lewis H. 1877. *Ancient society or researches in the lines of human progress from savagery through barbarism to civilization*. New York: Holt.
Nair, P. N. R. 2004. Pathogenesis of apical periodontitis and the causes of endodontic failures. *Critical Reviews in Oral Biology and Medicine* 15(6): 348–381.
Nasidze, I., J. Li, D. Quinque, K. Tang, and M. Stoneking. 2009. Global diversity in the human salivary microbiome. *Genome Research* 19:636–643. [JL]
Nasidze, I., J. Li, R. Schroeder, J. L. Creasey, M. K. Li, and M. Stoneking. 2011. High diversity of the saliva microbiome in Batwa Pygmies. *PLoS ONE* 6(8): e23352. doi:10.1371/journal.pone.0023352. [JL]
Navia, Juan M. 1994. Caries prevention in infants and young children: which etiologic factors should we address? *Journal of Public Health Dentistry* 54 (4):195–196.
Newton, J., K. Domett, D. J. W. O'Reilly, and L. Shewan. 2013. Dental health in Iron Age Cambodia: temporal variations with rice agriculture. *International Journal of Paleopathology* 3:1–10. [KD]
Ortner, Donald J. 2003. *Identification of pathological conditions in human skeletal remains*. New York: Academic Press.
Ortner, Donald J., and Walter G. J. Putschar. 1985. *Identification of pathological conditions in human skeletal remains*. Washington, DC: Smithsonian Institution.
Oxenham, Marc. 2006. Biological responses to change in prehistoric Viet Nam. *Asian Perspectives* 45(2):212–239.
Oxenham, Marc, Nguyen Lan Cuong, and Nguyen Kim Thuy. 2006. The oral health consequences of the adoption and intensification of agriculture in Southeast Asia. In *Bioarchaeology of Southeast Asia*. M. Oxenham and N. Tayles, eds. Pp. 263–289. Cambridge: Cambridge University Press.
Papadimitriou, N. 2018. Counting individuals, reconstructing groups: a critical review of bioarchaeological data from Middle Helladic and Mycenaean graves. In *Gathered in death: archaeological and ethnological perspectives on collective burial and social organisation*. A. Schmitt, S. Déderix, and I. Crevecoeur, eds. Pp. 159–188. Louvain-la-Neuve: Presses universitaires de Louvain. [AP]
Patir, A., F. Seymen, M. Yildirim, K. Deeley, M. E. Cooper, M. L. Marazita, and A. R. Vieira. 2008. Enamel formation genes are associated with high caries experience in Turkish children. *Caries Research* 42:394–400. [JL]
Pechenkina, E. A., R. A. Benfer, and W. Zhijun. 2002. Diet and health changes at the end of the Chinese Neolithic: the Yangshao/Longshan transition in Shaanxi province. *American Journal of Physical Anthropology* 117:15–36. [JTW]
Pechenkina, Kate, Ma Xiaolin, and Fan Wenquan. 2013. Trajectories of health in early farming communities in East Asia. In *Bioarchaeology of East Asia: movement, contact, health*. K. Pechenkina and M. Oxenham, eds. Pp. 444–481. Gainesville: University Press of Florida. [CSL]
Piekoszewska-Zietek, P., A. Turska-Szybka, and D. Olczak-Kowalczyk. 2017. Single nucleotide polymorphism in the aetiology of caries: systematic literature review. *Caries Research* 51:425–435. [JL]
Pietrusewsky, Michael, and Michele Toomay Douglas. 2001. Intensification of agriculture at Ban Chiang: is there any evidence in the skeletons? *Asian Perspectives* 40:157–178. [DHT]
Pinhasi, Ron, and Jay T. Stock, eds. 2011. *Human bioarchaeology of the transition to agriculture*. Hoboken, NJ: Wiley.
Powell, Mary Lucas. 1985. Dental wear and caries in dietary reconstruction. In *The analysis of prehistoric diets*. R. I. Gilbert Jr. and J. H. Mielke, eds. Pp. 307–338. Orlando, FL: Academic Press.
Ragsdale, Bruce D., and Larisa M. Lehmer. 2012. A knowledge of bone at the cellular (histological) level is essential to paleopathology. In *A companion to paleopathology*. A. L. Grauer, ed. Pp. 225–249. Chichester: Blackwell.
Ramirez-Villegas, Julian, and Philip K. Thornton. 2015. *Climate changes impacts on African crop production*. CCAFS Working Paper no. 119. Copenhagen: CGIAR Research Program on Climate Change, Agriculture and Food Security (CCAFS).
Redfern, Rebecca, Sharon DeWitte, Janet Montgomery, and Rebecca Gowland. 2018. A novel investigation into migrant and local health statuses in the past: a case study from Roman Britain. *Bioarchaeology International* 2(1):20–43.
Reitsema, Laurie J., and Britney Kyle McIlvaine. 2014. Reconciling "stress" and "health" in physical anthropology: what can bioarchaeologists learn from the other subdisciplines? *American Journal of Physical Anthropology* 155(2):181–185.

Richerson, Peter J., Robert Boyd, and Robert L. Bettinger. 2001. Was agriculture impossible during the Pleistocene but mandatory during the Holocene? a climate change hypothesis. *American Antiquity* 66(3):387–411.

Robb, J. 2014. The future Neolithic: a new research agenda. In *Early farmers: the view from archaeology and science*. A. Whittle and P. Bickle, eds. Pp. 21–38. Proceedings of the British Academy, no. 198. Oxford: Oxford University Press. [AP]

Robertson, D., and A. J. Smith. 2009. The microbiology of the acute dental abscess. *Journal of Medical Microbiology* 58(2):155–162.

Rose, Jerome C., Barbara A. Burnett, Mark W. Blaeuer, and Michael S. Nassaney. 1984. Paleopathology and the origins of maize agriculture in the Lower Mississippi Valley and Caddoan culture areas. In *Paleopathology at the origins of agriculture*. M. N. Cohen and G. J. Armelagos, eds. Pp. 393–425. Gainesville: University Press of Florida.

Rowe, Nathaniel H. 1975. Dental caries. In *Dimensions of dental hygiene*. 2nd edition. P. F. Steele, ed. Pp. 198–122. Philadelphia: Lea & Febiger.

Russell, Stefanie L., Sara Gordon, John R. Lukacs, and Linda M. Kaste. 2013. Sex/gender differences in tooth loss and edentulism: historical perspectives, biological factors, and sociologic reasons. *Dental Clinics of North America* 57:317–337.

Schnorr, S. L., K. Sankaranarayanan, C. M. Lewis, and C. Warinner. 2016. Insights into human evolution from ancient and contemporary microbiome studies. *Current Opinion in Genetics and Development* 41:14–26. [JL]

Schulting, Rick. 2014. Hunter-gatherer diet, subsistence, and foodways. In *Oxford handbook of the archaeology and anthropology of hunter-gatherers*. V. Cummings, P. Jordan, and M. Zvelebil, eds. Pp. 1266–1287. Oxford: Oxford University Press. [DHT]

Shkrum, S. 2014. Oral health and the intensification of agriculture at Ban Non Wat, Thailand. PhD thesis. University of Otago, Dunedin, New Zealand. [KD]

Soames, J. V., and J. C. Southam. 2005. *Oral pathology*. 4th edition. Oxford: Oxford University Press.

Stahl, F., and R. Grabowski. 2004. Malocclusion and caries prevalence: is there a connection in the primary and mixed dentitions? *Clinical Oral Investigations* 8(2):86–90.

Steckel, Richard H., and Jerome C. Rose, eds. 2002. *The backbone of history: health and nutrition in the Western hemisphere*. Cambridge: Cambridge University Press.

Steckel, Richard H., Jerome C. Rose, Clark Spencer Larsen, and Phillip L. Walker. 2002. Skeletal health in the Western Hemisphere from 4000 BC to the present. *Evolutionary Anthropology: Issues, News, and Reviews* 11(4):142–155.

Stojanowski, Christopher M. 2018. Persistence or pastoralism? the challenges of studying hunter-gatherer resilience in Africa. In *Hunter-gatherer adaptation and resilience: a bioarchaeological perspective*. D. H. Temple and C. M. Stojanowski, eds. Pp. 193–226. Cambridge: Cambridge University Press. [DHT]

Tayles, Nancy, Kathryn Domett, and Siân Halcrow. 2009. Can dental caries be interpreted as evidence of farming? the Asian experience. In *Comparative dental morphology*. T. Koppe, G. Meyer, and K. W. Alt, eds. Pp. 162–166. Basel: Karger.

Tayles, Nancy, Kathryn Domett, and Kirsten Nelsen. 2000. Agriculture and dental caries? the case of rise in prehistoric Southeast Asia. *World Archaeology* 32(1):68–83.

Temple, Daniel H. 2018. Persistence of time: resilience and adaptability in prehistoric Jomon hunter-gatherers from the Inland Sea Region of southwestern Honshu, Japan. In *Hunter-gatherer adaptation and resilience: a bioarchaeological perspective*. D. H. Temple and C. M. Stojanowski, eds. Pp. 85–109. Cambridge: Cambridge University Press.

———. 2011*a*. Evolution of postcranial morphology during the agricultural transition in prehistoric Japan. In *Human bioarchaeology of the transition to agriculture*. R. Pinhasi and J. T. Stock, eds. Pp. 235–262. Hoboken, NJ: Wiley.

———. 2011*b*. Variability in dental caries prevalence between male and female foragers from the Late/Final Jomon Period: implications for dietary behavior and reproductive ecology. *American Journal of Human Biology* 23(1):107–117.

Temple, Daniel H., and Alan H. Goodman. 2014. Bioarcheology has a "health" problem: conceptualizing "stress" and "health" in bioarcheological research. *American Journal of Physical Anthropology* 155(2):186–191.

Temple, Daniel H., and Clark Spencer Larsen. 2007. Dental caries prevalence as evidence for agriculture and subsistence variation during the Yayoi period in prehistoric Japan: biocultural interpretations of an economy in transition. *American Journal of Physical Anthropology* 134:501–512.

Thibodeau, Edward A., and David M. O'Sullivan. 1999. Salivary mutans streptococci and caries development in the primary and mixed dentitions of children. *Community Dentistry and Oral Epidemiology* 27(6):406–412.

Thomas David H. 1988. *St. Catherines: an island in time*. Athens: University of Georgia Press.

Triantaphyllou, Sevasti. 2015. Stable isotope analysis of skeletal assemblages from prehistoric northern Greece. In *Archaeodiet in the Greek world: dietary reconstruction from stable isotope analysis*. A. Papathanasiou, M. P. Richards, and S. C. Fox, eds. Pp. 57–76. Hesperia Supplement 49. Princeton, NJ: American School of Classical Studies.

Truhe, T. 1996. Diet and caries. *Dentistry Today* 15(9):60–62.

Tsude, Hiroshi. 2001. Yayoi farmers reconsidered: new perspectives on agricultural development in East Asia. *Bulletin of the Indo-Pacific Prehistory Association* 5:53–59.

Turner, Bethany L. 2013. Interpreting oral pathology at Machu Picchu, Peru. *International Journal of Osteoarchaeology* 25(4):502–514.

Turner, Christy G. 1979. Dental anthropological indications of agriculture among the Jomon people of central Japan. X. Peopling of the Pacific. *American Journal of Physical Anthropology* 51(4):619–635.

Turner, J. E., D. W. Moore, and B. S. Shaw. 1975. Prevalence and antibiotic susceptibility of organisms isolated from acute soft-tissue abscesses secondary to dental caries. *Oral Surgery, Oral Medicine, Oral Pathology* 39(6):848–857.

Vieira, A. R., A. Modesto, and M. L. Marazita. 2014. Caries: review of human genetics research. *Caries Research* 48:491–506. [JL]

Vieira, A. R., C. W. Gibson, K. Deeley, H. Xue, and Y. Li. 2015. Weaker dental enamel explains dental decay. *PLoS ONE* 10(4):e0124236. doi: 10.1371/journal.pone.0124236. [JL]

Vieira, A. R., M. L. Marazita, and T. Goldstein-McHenry. 2008. Genome-Wide scan finds suggestive caries loci. *Journal of Dental Research* 87:915–918. [JL]

Waldron, Tony. 2009. *Palaeopathology*. Cambridge: Cambridge University Press.

Watson, James T. 2008. Prehistoric dental disease and the dietary shift from cactus to cultigens in northwest Mexico. *International Journal of Osteoarchaeology* 18(2):202–212.

Weber, S., H. Lehman, T. Barela, S. Hawks, and D. Harriman. 2010. Rice or millets: early farming strategies in prehistoric central Thailand. *Archaeological and Anthropological Sciences* 2(2):79–88. [KD]

Weyrich, Laura S., Sebastian Duchene, Julien Soubrier, Luis Arriola, Bastien Llamas, James Breen, Alan G. Morris, Kurt W. Alt, David Caramelli, and Veit J. Dresely. 2017. Neanderthal behaviour, diet, and disease inferred from ancient DNA in dental calculus. *Nature* 544(7650):357.

Willis, Anna, and Marc F. Oxenham. 2013. The Neolithic demographic transition and oral health: the Southeast Asia experience. *American Journal of Physical Anthropology* 152(2):197–208.

Wood, James W., George R. Milner, Henry C. Harpending, and Kenneth M. Weiss. 1992. The osteological paradox: problems of inferring prehistoric health from skeletal samples (and comments and reply). *Current Anthropology* 33(4):343–370.

Zero, Domenick T. 1996. Etiology of dental erosion-extrinsic factors. *European Journal of Oral Sciences* 104(2):162–177.

Zuckerman, Molly K., and George J. Armelagos. 2011. The origins of biocultural dimensions in bioarchaeology. In *Social bioarchaeology*. S. C. Agarwal and B. A. Glencross, eds. Pp. 15–43. Hoboken, NJ: Wiley.