Oral pathological conditions of an Early Epipaleolithic human from Southwest Asia: Ohalo II H2 as a probable case of intentional dental ablation

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Running head: Ohalo 2 Early Epipaleolithic dental ablation

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Abstract

Objective: To describe the oral pathological conditions of Ohalo II H2, an Early Epipaleolithic human from southwest Asia.
Materials: The dentognathic skeleton of Ohalo II H2 and relevant comparative data from similar chronological and/or geographic contexts.
Methods: Gross and x-ray observations of oral pathological conditions and occlusal wear were made following published protocols. A differential diagnosis of antemortem tooth loss is provided.
Results: Ohalo 2 has two carious lesions on the right M^3, pulpal exposure of left M_1, mild to moderate anterior alveolar bone loss. The right I^1 was lost antemortem and there is probably agenesis of the left M^3.
Conclusions: The pathological conditions noted are not exceptional for a Late Upper Paleolithic forager. However, the antemortem missing right I^1 is most parsimoniously explained by intentional dental ablation.
Significance: Ohalo 2 could represent the oldest example of dental ablation from the Late Pleistocene circum-Mediterranean world – predating the earliest examples from both North Africa and southwest Asia by several thousand years. The similarity of the Ohalo 2 ablation pattern with later Natufians provides further evidence of potential long-term behavioral trends related to the embodiment of social identities through international body modification within the Epipaleolithic of southwest Asia.
Limitations: The pre-Natufian (~23,000-14,500 cal BP) human fossil record is relatively sparse, making comparisons with the Natufian (~14,500-11,500 cal BP) phases of the Epipaleolithic difficult.
Suggestions for Further Research: Documentation of oral pathological conditions for other pre-Natufian fossils would provide greater resolution of the temporospatial patterning of oral health and embodied social identities during the Epipaleolithic of southwest Asia.

1 Introduction

The human fossil record from the Upper Paleolithic and earlier Epipaleolithic (Early and Middle phases, ~23,000-14,500 cal BP) of southwest Asia is sparse (Arensburg, 1977; Arensburg and Bar-Yosef, 1973; Arensburg et al., 1990; Bocquentin et al., 2011; De Groote et al., 2014; Hershkovitz et al., 1995; Maher et al., 2012; McCown and Keith, 1939; Richter et al., 2010; Rolston, 1982; Stock et al., 2005; Trinkaus, 2018b, c; Vandermeersch et al., 2013) compared to the Late Epipaleolithic (~14,500-11,500 cal BP) phases of the Natufian that immediately precede the onset of food production in the region (Bar-Yosef et al., 1971; Bar-Yosef and Goren, 1973; Bocquentin, 2007; Crognier and Dupouy-Madre, 1974; De Groote et al., 2014; Ferembach, 1961; Garrod, 1932; Garrod and Bate, 1937, 1942; Grosman et al., 2016; Nadel et al., 2013; Vallois, 1936; Webb and Edwards, 2002). Given this dichotomy in human fossil abundance, it is not surprising that the less abundant pre-Natufian fossils of southwest Asia are generally analyzed within the context of Eurasian Late Pleistocene/Upper Paleolithic human variation and paleobiology (Schmidt et al., 2019; Shackelford, 2007; Sparacello et al., 2017; Trinkaus, 2018b, c; Trinkaus and Ruff, 2012), or are not directly compared to, or treated separately from, their Natufian counterparts (e.g., Schmidt et al., 2019; Shackelford, 2007). Likewise, Natufian paleobiology is discussed within the context of the transition to food production in the Neolithic (Cheronet et al., 2016; Eshed et al., 2006; Eshed et al., 2010; Mahoney, 2006; May and Ruff, 2016; May et al., 2018; Pinhasi et al., 2008; Pinhasi et al., 2015) rather than understood within the context of the regional Epipaleolithic as a whole. A growing body of research documents not only long-term behavioral trends between the pre-Natufian and Natufian phases of the Epipaleolithic, but also greater behavioral variability than previously appreciated (reviewed in Maher et al., 2012). This archaeologically documented trend has a paleobiological parallel in that there is both considerable morphological and paleobiological heterogeneity among Epipaleolithic humans of southwest Asia, but also some morphological continuity between earlier Epipaleolithic humans and later Natufians in other ways (Arensburg, 1981; Arensburg and Bar-Yosef, 1973; Bocquentin, 2011; Hershkovitz and Arensburg, 2017; Hershkovitz et al., 1995; Lahr and Arensburg, 1995; Mahoney, 2007; Richter et al., 2010; Stock et al., 2005). Thus, the current state of archaeological and paleobiological research on Epipaleolithic human behavioral variability in southwest Asia emphasizes a need to evaluate biological affinity, paleobiology, and biocultural trends within and between the Early, Middle, and Late phases of the Epipaleolithic.

With the above context in mind, we provide a differential diagnosis for antemortem loss of the right maxillary central incisor (I^1) exhibited by the Early Epipaleolithic human, Ohalo II H2 (henceforth, Ohalo II will be used to refer to the archaeological site and Ohalo 2 will be used to refer to the individual; **Figure 1**), as well as other indicators of oral pathological conditions more generally. Previous analyses are limited to the following statement by Hershkovitz and colleagues (1995, 225): “The right maxillary I1 was lost premortem and the socket resorbed. Loss of the tooth occurred late in life as the lower central incisors both manifest considerable attrition.” However, the aetiology of AMTL is multifactorial – frequently co-occurring with high rates of occlusal wear, trauma, intentional dental modification, and/or oral pathological conditions (De Groote and Humphrey, 2016; Lacy, 2014, 2015; Lukacs, 2007; Russell et al., 2013). Furthermore, intentional dental ablation – the culturally mediated, intentional removal of healthy teeth during the life of an individual – is a salient Late Epipaleolithic/Natufian practice (Bocquentin et al., 2011). While ablation has not been identified in Pre-Natufian contexts, it has not been ruled out for Ohalo 2 (Willman et al., in press). Therefore, the Ohalo 2 AMTL should be re-evaluated and contextualized within the context of Epipaleolithic southwest Asian human biocultural variability to evaluate the temporal uniqueness, or potential long-term biocultural continuity, represented by this paleobiological marker of prehistoric behavior and oral pathological conditions.

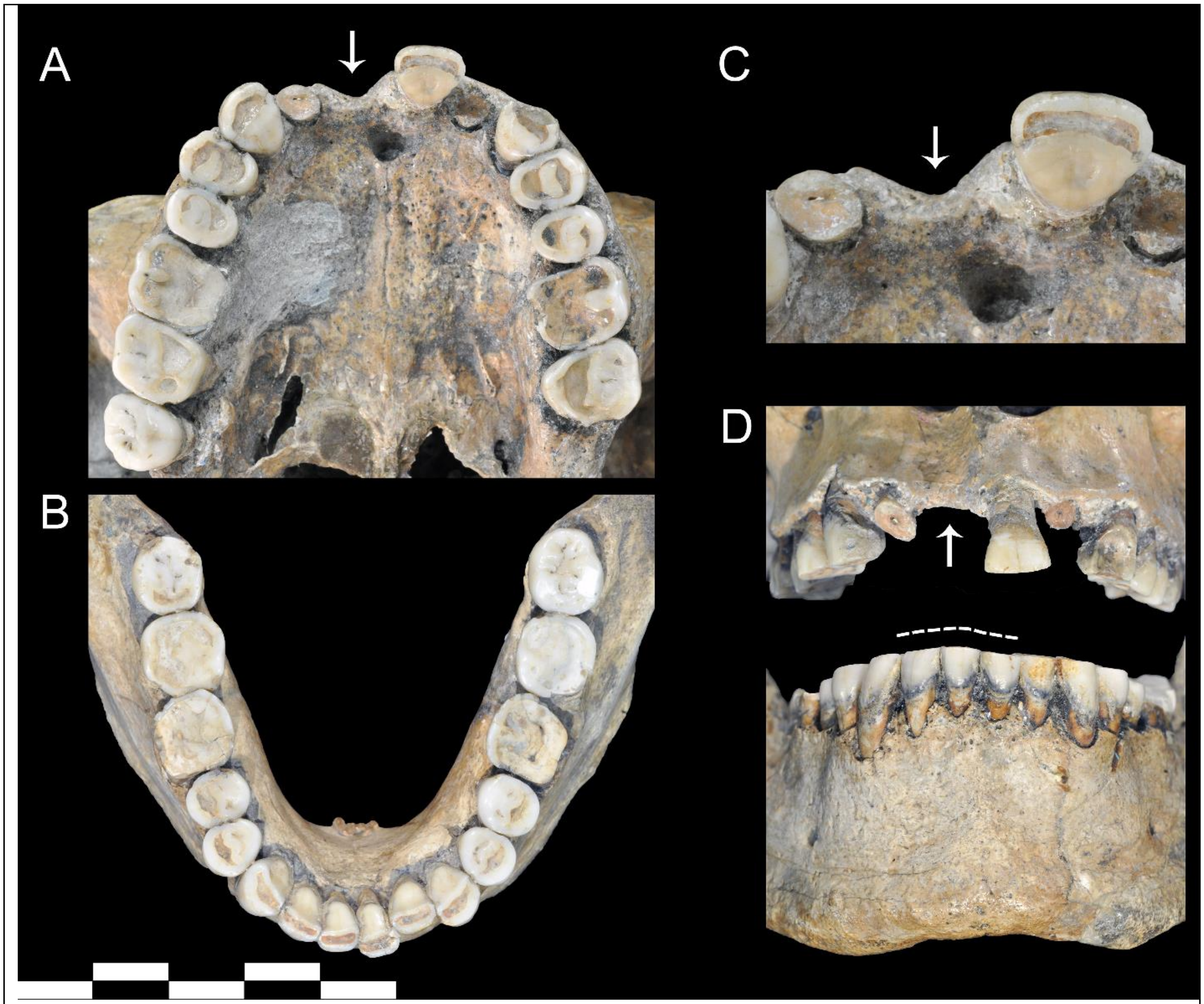

Figure 1. A) Occlusal view of Ohalo 2 maxilla. Arrow pointing at right I1 AMTL. Both I2s are broken at the cervix postmortem. B) Occlusal view of mandible. C) Close-up [2x Figure 1A] of AMTL showing well-resorbed alveolus. D) Anterior view of maxilla and mandible. Arrow pointing to right I1 AMTL and dotted line traces uneven occlusal wear of non-occluding mandibular incisors. Scale increments are 10 mm.

1.1 Brief archaeological and paleobiological context for Ohalo 2

The shallow pit burial of Ohalo 2, a ~35-40 year old male, was one of many archaeological features – including multiple hut structures and outdoor hearths – recovered from the water-logged, hunter-fisher-gatherer site of Ohalo II located on the shore of the Sea of Galilee (Hershkovitz et al., 1993; Hershkovitz et al., 1995; Nadel, 1994; Nadel and Hershkovitz, 1991). Multiple radiocarbon dates (Nadel et al., 1995) around ~22,500 cal. BP correspond to the Early Epipaleolithic at the boundary of Marine Isotope Stage (MIS) 3 and MIS 2.

A wide range of mammal, fish, and bird remains (Rabinovich and Nadel, 2005; Simmons and Nadel, 1998; Zohar et al., 2018) in addition to an extensive and diverse record of plant remains and processing implements were recovered and emphasize subsistence strategies based on a wide array of plant and animal resources (Nadel et al., 2012; Piperno et al., 2004; Snir et al., 2015; Weiss et al., 2004).

The dental microwear signature from Ohalo 2 indicates a tough and abrasive diet that is more similar to that of later Pre-Pottery Neolithic A and Chalcolithic food producers than to Natufian foragers and individuals from the Pre-Pottery Neolithic B (Mahoney, 2007).

The upper and lower limb robusticity, hypertrophy, and asymmetry of Ohalo 2 are typical of an Upper Paleolithic forager in general, and a Pre-Natufian forager from southwest Asia specifically (Trinkaus, 2018b, c). However, some evidence for greater robusticity among earlier Epipaleolithic foragers (including Ohalo 2) in comparison to later Natufian foragers has been proposed (Hershkovitz et al., 1995; Stock et al., 2005).

Ohalo 2 exhibits a major injury to the lower thorax that caused a large ossification on portions of the sternum, ribs, and corresponding costal cartilages (Hershkovitz et al., 1993; Trinkaus, 2018c). The injury would have prevented adequate oxygen intake during prolonged periods of elevated activity (Trinkaus, 2018c) and indicates that Ohalo 2 would have received some level of social support from the time the injury was sustained until death (Hershkovitz et al., 1993; Trinkaus, 2018c).

Previously noted oral pathological conditions includes the antemortem loss of the right I^1 but no cause was discussed (Hershkovitz et al., 1995; Trinkaus, 2018c) (**Figure 1**). The left maxillary third molar (M^3) is also missing antemortem but was attributed to agenesis in one instance (Hershkovitz et al., 1995) and AMTL in another (Trinkaus, 2018c). Occlusal macrowear was considered “heavy” and similar to Natufian and early Neolithic groups (Hershkovitz et al., 1995). No other oral pathological conditions were noted. Since AMTL can be caused by intentional dental modification (e.g., ablation), trauma, caries, periodontal disease, extreme dental wear, or a combination of factors (Lukacs, 2007), any number of these factors could have contributed to the Ohalo 2 AMTL. Furthermore, intra- and interindividual patterning of AMTL has the potential to reveal unique insights into biocultural processes contributing to the oral health status of individuals and groups (Lukacs, 2007; Russell et al., 2013). Therefore, a differential diagnosis of Ohalo 2’s AMTL with consideration of overall oral paleopathology and dental wear is warranted.

2 Methods

An assessment of Ohalo 2 oral health is provided to contextualize and provide a differential diagnosis for the previously documented AMTL. Measurements were made with digital calipers, observations were recorded with digital photography, and digital radiographs were produced with a portable x-ray generator (Lacy, 2014). Dental caries was recorded with an eight-stage scoring system (Hillson, 2001). Average cementoenamel junction to alveolar crest (CEJ-AC) distances (Clarke and Hirsch, 1991; Hildebolt and Molnar, 1991; Lavigne and Molto, 1995) and assessments of alveolar septa shape and porosity (Corruccini et al., 1987; Costa, 1982; Kerr, 1988, 1991; Ogden, 2008; Whiting et al., 2019) were scored. Gross observations of alveolar lesions were made and also observed using radiographs (Dias and Tayles, 1997; Dias et al., 2007; Willis and Oxenham, 2013). Dental wear scores were recorded (Smith, 1984) along with alveolar lesions and periodontal disease since non-carious pulpal, root, and furcation exposure can contribute to alveolar lesions and eventual AMTL (Hillson, 2008).

Differential diagnosis of AMTL is essential given the multifactorial nature of tooth loss (De Groote and Humphrey, 2016; Lacy, 2014, 2015; Lukacs, 2007; Pietrusewsky and Douglas, 1993; Robb, 1997; Russell et al., 2013; Stojanowski et al., 2014; Willman et al., 2016). The alveolar status of Ohalo 2 was observed directly, and independently, by both authors. Given the prevalence of culturally mediated ablation practices in Late Epipaleolithic/Natufian contexts (Bocquentin, 2011), an observational protocol for documenting ablation status from Stojanowski and colleagues (2014; Willman et al., 2016) was integrated into the differential diagnosis of AMTL.

A comparative approach to occlusal wear will address the timing of the AMTL during life and whether occlusal wear contributed to AMTL. The first approach uses a modified version of the Scott (1979) occlusal wear scoring system (Littleton et al., 2013) to assess wear in teeth adjacent (i.e., the *in situ* left I^1) to the antemortem missing right I^1 and first molars in the same jaw, since the severity of wear on teeth adjacent to AMTL can be used to discriminate between AMTL due to extreme wear and intentional ablation (Durband et al., 2014). A wear index (tooth adjacent to AMTL / M^1 x 100) is used to compare the value for Ohalo 2 to published values from Roonka (Holocene foragers from South Australia with high prevalence of ablation: Durband et al., 2014).

The second approach uses occlusal wear (percent dentin exposure) gradients standardized to first molar wear to address anterior tooth wear severity in both jaws using comparative data from Late Epipaleolithic contexts (Natufians and Wadi Halfa: Clement, 2008) as well as Iberomaurusian and Capsian individuals from Northwest Africa that exhibit a high prevalence of dental ablation (De Groote and Humphrey, 2016). This approach was chosen because box-plots of dentin exposure relative to first molar wear have been published by tooth type for each of the above groups (Clement, 2008; De Groote and Humphrey, 2016) and allow easy comparison with values calculated for Ohalo 2 in this study. The previously studied groups are also highly relevant to understanding if the anterior dental wear in Ohalo 2 is extensive enough to suggest that the right I^1 was lost late in life (see Hershkovitz et al., 1995) or earlier in life (as is more common in cases of intentional ablation). The Iberomaurusian and Capsian groups both exhibit high rates of anterior tooth ablation (De Groote and Humphrey, 2016), which makes them an example for the expected range of variation in wear gradients for a group exhibiting a high frequency of intentional ablation. Likewise, some of the Natufian individuals also exhibit ablation, but none of the Wadi Halfa sample does (Clement, 2008). This “Epipaleolithic” macrogroup therefore contains mostly individuals with no anterior AMTL, so the variation in anterior relative to posterior tooth wear gradients will approximate an Epipaleolithic hunter-gather control group with low rates of anterior AMTL (whether due to intentional ablation or pathological/wear-induced antemortem loss). We expect Ohalo 2 to be more similar to the Natufian/Wadi Halfa Epipaleolithic group than to the Iberomaurusian or Capsian group if AMTL occurred late in life. We provide wear gradients for each well-preserved anterior tooth in the maxilla (left I^1 and right C^1 versus right M^1) and mandible (right I_1, average of left and right I_2, and average of left and right C_1 versus left M_1) of Ohalo 2.

3 Results

Ohalo 2 has two small carious lesions on the right M^3 (Lacy, 2014) (**Figure 2A**). It is possible that the lesions were initiated in natural pits on the occlusal surface of the tooth, but they show acid etching and can be seen in radiographs suggesting they are more than natural defects in the enamel (**Figure 2A**). The left M_1 also shows pulpal exposure due to extensive wear on the buccal portion of the occlusal surface (**Figure 2B**). This pulpal exposure is most likely the cause of alveolar lesions around each root apex on the same tooth (**Figure 2B**). An open pulp chamber would be the easiest route for bacteria to access the apical region of the alveolar bone (**Figure 2B**).

Hershkovitz and colleagues (1995) noted agenesis of the left M^3, but Trinkaus (2018b) considered the left M^3 to be lost antemortem since he contends that the left M^2 displays a large interproximal facet and the alveolar bone appears resorbed (**Figure 2C**). However, we identify no interproximal facet on the distal surface of the left M^2; instead, there are two large antemortem enamel chips (grade 3: Bonfiglioli et al., 2004) on the distal surface that superficially resemble a distal interproximal facet in occlusal view (**Figure 2D; Supplemental Figure 1**). There is also highly asymmetric occlusal wear between the M_3s (the right M_3 exhibits much greater occlusal wear than the left M_3), and the occlusal wear on the left M_3 is greater on the mesial half of the crown which would have been in contact with the opposing M^2 during mastication (**Figure 2D**). Given the absence of all but modest polishing of the distal portion of the occlusal surface of the left M_3, it is highly unlikely that the left M^3 was ever in occlusion, rather than subject to pathological loss from caries or some form of trauma after eruption. The absence of an impacted left M^3 with no clear evidence of alveolar remodeling in the radiograph (**Figure 2C**), makes the original attribution of agenesis (Hershkovitz et al., 1995) the most likely explanation of the absence of the left M^3.

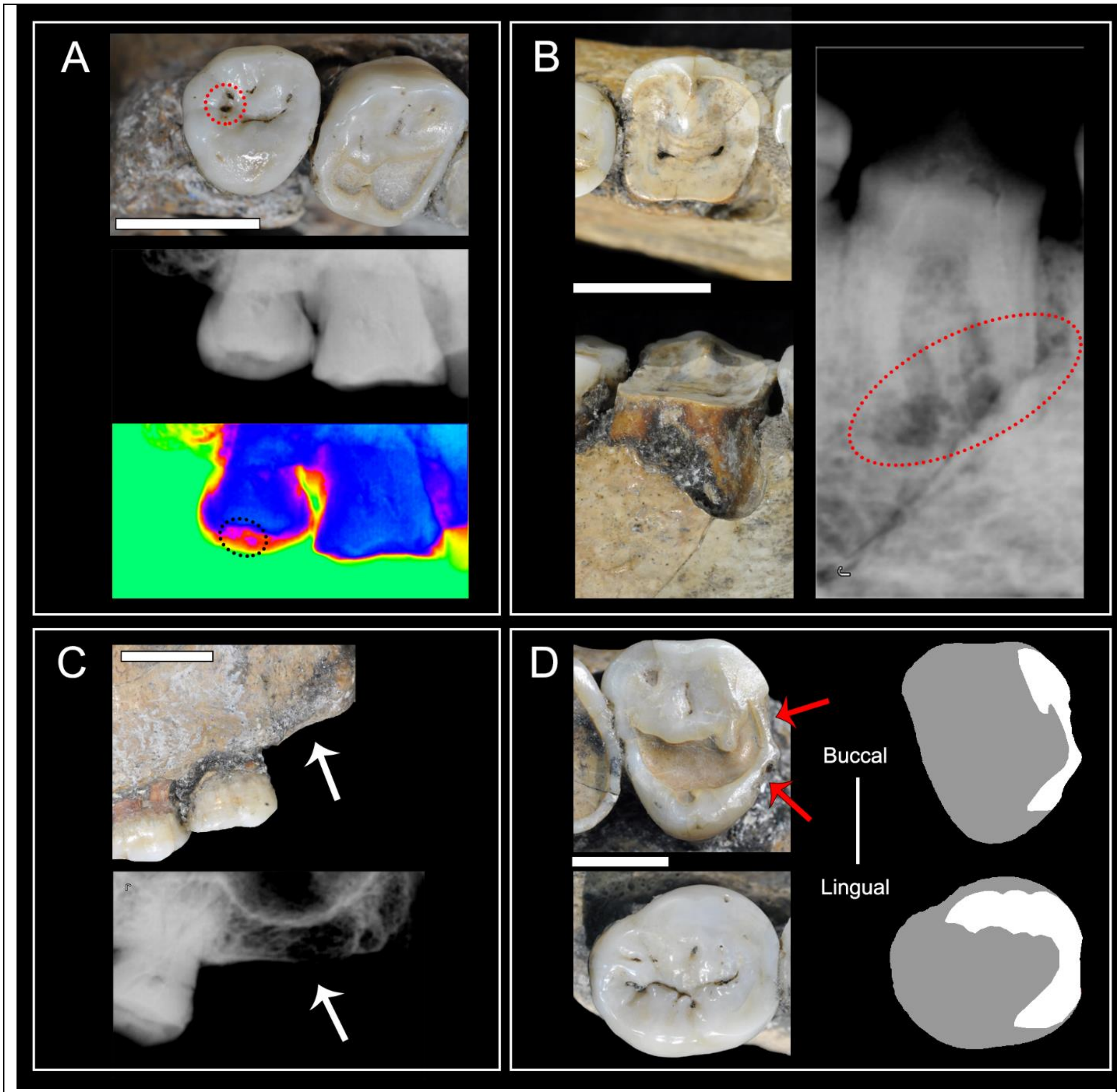

Figure 2. A) Top: small occlusal caries in right M^3; Middle: buccal radiograph of right M^3 and M^2 (not to scale); Bottom: Colorized radiograph emphasizing the occlusal caries (black ellipse) on the right M^3 (not to scale). B) Top Left: Occlusal view of pulpal exposure in left M_1; Lower Left: Buccal view of alveolar lesion; Right; buccal radiograph of left M_1. Note radiotranslucencies around both roots (red ellipse) indicating apical lesions (not to scale). C) Top: Buccal view of left M^1, M^2, and alveolar bone of missing M^3 (Arrow). Bottom: X-Ray of antemortem left M^2 and missing M^3 viewed from occlusal-lingual orientation. Note how thin the bone is without evidence of remodeling. Not to Scale. D) Top Left: Occlusal view of left M^2 with large antemortem enamel chips (red arrows); Bottom Left: Occlusal view of left M_3 showing near modest polish of distal half of occlusal surface and wear facet on the mesial half. Top and Bottom Right: Occlusal outlines of left M^2 and M_3 with corresponding occlusal (distal and mesial, respectively) wear facets indicated in white. All scale bars are 10 mm.

The alveolar bone of Ohalo 2 is generally healthy, though there is a concentration of mild to moderate alveolar bone loss in the anterior portions of the dental arcades. The antemortem missing right I^1 is characterized by a well-healed, remodeled, and non-porous alveolar socket (**Figure 1**). An interproximal contact facet corresponding to the left I^2 is visible on the left I^1, but a facet corresponding to the right I^1 is not visible on the mesial interproximal surface (**Supplemental Figure 2**). The lack of a mesial contact facet on the left I^1 suggests that the right I^1 was not in occlusion long enough to create an interproximal wear facet before it was lost antemortem. Alternatively, if a facet was present between the right and left I^1, it was smaller than the one for the one made between the left I^1 and I^2, and obliterated through occlusal wear. Both scenarios imply that the loss of the right I^1 before it achieved a wear stage similar to the remaining left I^1 at time of death.

There are lingual deposits of dental calculus along the gingival line on most teeth of the mandible. There is also a labial deposit of dental calculus along the gingival line of the I^1. It does not appear as though calculus deposits were large enough to pose as major gingival irritants or contribute to the AMTL of Ohalo 2 (Lukacs, 2007).

The Ohalo 2 occlusal wear (Littleton et al., 2013) for the left I^1, the tooth adjacent to the antemortem lost right I^1, is scored as a 7 relative to the average of both M^1s which is 8.5. The wear index is 82.4, which is at the lower end of the range of variation of the Roonka individuals (n = 17 [edentulous individuals not included], mean 97.2, median 100, range 125.0-80.0; data from Durband et al., 2014), demonstrating greater molar relative to maxillary incisor wear for Ohalo 2. Tooth wear adjacent to the missing right central incisor of Ohalo 2 is low compared to the moderate to heavy values of Roonka, but both Ohalo 2 and the Roonka individuals exhibit no pulp exposure and strong alveolar bone in teeth adjacent to AMTL (Ohalo 2) and ablated teeth (Roonka) (Durband et al., 2014).

Anterior tooth wear gradients for both the maxillary (I^1 and C^1) and mandibular (I_1, I_2, and C_1) teeth versus first molars from the same jaw are low for Ohalo 2 versus Iberomaurusian and Capsian individuals from Northwest Africa (data from De Groote and Humphrey, 2016) and Late Epipaleolithic individuals from Natufian contexts and Wadi Halfa (data from Clement, 2008) (**Supplemental Figures 3** and **4**). Of all anterior tooth types, the value for the I_1 of Ohalo 2 approaches the median value for the Northwest Africa sample. This sample exhibits high rates of intentional ablation of both I^1s (De Groote and Humphrey, 2016) which corresponds to lower rates of wear in opposing mandibular incisors (De Groote and Humphrey, 2016; Humphrey and Bocaege, 2008; Willman, 2016). This latter point is also illustrated by the occlusal wear angles formed by the right I_1 and I_2 that exhibit an uneven plane of wear corresponding to the void left by the missing right I^1 (**Figure 1D**). The differential dental wear indicates that wear continued long after AMTL occurred, but the lack of occlusal antagonists decreased the rate of wear on the lower right incisors compared to the left ones.

4 Discussion

4.1 Ohalo 2 oral health and AMTL in context

Examples of dentognathic pathological conditions are becoming well-documented in Late Pleistocene contexts and are quite prevalent in many Late Upper Paleolithic/Terminal Pleistocene contexts (Capasso, 2001; Cucina et al., 2019; Da-Gloria and Larsen, 2014; De Groote et al., 2018; Frayer, 1989; Humphrey et al., 2014; Lacy, 2014, 2015; Liu et al., 2017; Oxilia et al., 2017; Oxilia et al., 2015; Trinkaus et al., 2016; Villotte et al., 2018). Prior to the onset of food production, carious lesions were particularly prevalent in the circum-Mediterranean region (Lacy, 2014). Thus, the Ohalo 2 carious lesions are not wholly surprising. The extensive evidence for plant foods at the Ohalo II site (Nadel et al., 2012; Piperno et al., 2004; Snir et al., 2015; Weiss et al., 2004) indicates ready access to carbohydrate-rich, cariogenic foods. Indeed, the Early Epipaleolithic Ohalo II H1 partial mandible (Hershkovitz and Arensburg, 2017) also exhibits caries (Lacy, 2014). Furthermore, the tough and abrasive diet inferred from dental microwear (Mahoney, 2007), and the high degree of occlusal macrowear on molars, would have contributed to the postcanine pulpal exposure and alveolar lesions in Ohalo 2.

The relatively low level of anterior relative to postcanine dental wear is at odds with anterior AMTL caused by pulp exposure and subsequent infection (i.e., pulpitis, alveolar lesions) exhibited by foragers with high rates of anterior tooth wear (Capasso, 2001; Da-Gloria and Larsen, 2014; Oxilia et al., 2017). While there are examples of incisor caries among Middle Paleolithic Neandertals and early modern humans in Southwest Asia (Qafzeh 3 (Trinkaus and Pinilla, 2009); Kebara 27 (Tillier, 2007)), as well as caries more generally (Qafzeh 7, H4, 4, 9, 11 (Lacy, 2014) and Skhul 2 (Sognnaes, 1956)), they are relatively minor lesions that do not penetrate deeply. Furthermore, the overall alveolar resorption is mild to moderate. Thus, neither attrition nor pathological conditions seem to most parsimoniously explain the Ohalo 2 AMTL.

The antemortem missing left M^3 can most likely be attributed to agenesis. While relatively rare, agenesis has been previously documented in other Upper Paleolithic contexts, and most commonly presents as third molar agenesis (Dahlberg and Carbonell, 1961; Hillson, 2006; Lacy, 2014; Trinkaus et al., 2016). Third molar agenesis is relatively rare prior to the Late Upper Paleolithic/Epipaleolithic (Lacy, 2014). A recent analysis shows third molar agenesis in about one quarter of the Late Upper Paleolithic sample analyzed (Lacy, nd). Furthermore, as in Ohalo 2, third molar agenesis is most frequently asymmetrically expressed when present (Lacy, nd). Thus, Ohalo 2 not only belongs on a growing list of Pleistocene individuals exhibiting extensive degenerative abnormalities (i.e., thoracic injury: (Trinkaus, 2018a, c), but also on the extensive list of Pleistocene individuals with developmental anomalies (i.e., third molar agenesis: (Trinkaus, 2018a)).

4.2 The timing of AMTL

Hershkovitz and colleagues (1995) suggested that the right I^1 was lost late in life due to the degree of wear present on the mandibular incisors. However, the degree of wear on all observable maxillary and mandibular anterior teeth of Ohalo 2 is low with respect to first molar wear. Furthermore, the wear on the left mandibular incisors is greater than that of the right side – indicating that wear continued after the antemortem loss of the right I^1. Thus, it is not the degree of wear but the patterning of wear that is more important for understanding the timing of AMTL.

Distinct interproximal wear facets are found on all observable surfaces where they are expected, except for the distal surface of the left M^2 (due to probable agenesis of the M^3), and the mesial surface of the left I^1. The median age of full eruption of an I^1 is 7.5 years (AlQahtani et al., 2010), which provides the expected age at which mesial I^1 interproximal wear would begin in late childhood (and persist until the loss of the right I^1). The loss of the right I^1 could have occurred after eruption, but before a distinct facet could form. Similarly, a small facet may have formed before tooth loss occurred but would be subsequently obliterated by progressive occlusal wear. The left I^1 is also sufficiently mesial to indicate that a midline diastema ("gap") was not present between the I^1s prior to the antemortem loss of the right I^1.

Alveolar remodeling is also relevant to understanding the timing of AMTL. The right I^1 alveolus is completely healed and exhibits a non-porous lamellar bone surface. The alveolus is unlikely to contain a root remnant since the proliferation of alveolar bone around the root is often irregular with a porous appearance (Lukacs, 2007). The labiolingual reduction of alveolar bone through resorption is extensive (**Figure 1**). A mean loss of ~50% of alveolar ridge width is associated with 12 months of post-extraction healing for premolars and molars (Farina and Trombelli, 2012; Schropp et al., 2003), which is comparable to the remodeling seen in Ohalo 2.

The age at death of Ohalo 2 is estimated as the mid to late fourth decade of life (Hershkovitz et al., 1995; Trinkaus, 2018c), and alveolar remodeling suggests that the AMTL occurred a minimum of ~9-12 months prior to death. The lack of an interproximal facet on the mesial I^1 surface strongly suggests that AMTL occurred after eruption of the tooth in mid-childhood, and before a substantial mesial interproximal facet could form. Lastly, the uneven occlusal wear of the mandibular incisors also indicates that occlusal attrition continued after AMTL and continued until the death of Ohalo 2. The most parsimonious timing of the loss of the right I^1 is that it occurred relatively early in life, and substantially earlier than the death of the individual in middle adulthood, contrary to a previous assessment (Hershkovitz et al., 1995).

4.3 A case for traumatic AMTL?

Ohalo 2 exhibits a major, lower thoracic pathological condition attributed to infectious chronic osteomyelitis that probably coincided with localized trauma (Hershkovitz et al., 1993; Hershkovitz et al., 1995; Trinkaus, 2018c). Although this injury was not initially linked to the antemortem loss of the right I^1, the co-occurrence of chest and dental trauma must be considered. Unfortunately, the onset and duration of the chronic osteomyelitis is uncertain as noted by Trinkaus (2018b:149): "the surfaces of the bony growths are largely smoothed over, so it is unclear whether the infection was active at the time of death or how long prior to death." Nevertheless, if the lower thorax trauma and AMTL occurred simultaneously, the injuries would have been sustained early in life (see above). This scenario implies that Ohalo 2 persisted for multiple decades with a significant degenerative pathological condition – one that prevented participation in activities requiring sustained or elevated respiration (Trinkaus, 2018b). Such a scenario appears at odds with appendicular hypertrophy which suggests that mobility and physical activity levels of Ohalo 2 were similar to penecontemporaneous Upper Paleolithic humans from western Eurasia and North Africa (Trinkaus, 2018b), even if these patterns would have been at least partially established during development (Cowgill et al., 2015). Thus, the co-occurrence of traumatic AMTL and chest injury is possible, but it does not seem plausible. If the AMTL is a result of childhood or early adolescence trauma, it is most likely decoupled from a subsequent event related to the lower thorax injury.

4.4 A case for intentional dental ablation?

We place the Ohalo 2 AMTL after mid-childhood, but before substantial mesial interproximal attrition could progress, which probably corresponds to adolescence. Copious ethnographic accounts document ritualized tooth ablation – the culturally mediated, intentional removal of health teeth during the life of an individual – at specific life stages. For instance, ablation often corresponds to signs of physical and social maturation associated with puberty and adolescence, respectively (Bocquentin, 2011; Milner and Larsen, 1991; Willman et al., 2016). Indeed, the youngest individual from Epipaleolithic contexts to exhibit ablation was a Natufian adolescent (Bocquentin, 2011).

Dental ablation has long been documented in Late Epipaleolithic Natufian contexts in southwest Asia (Bocquentin, 2007, 2011; Crognier and Dupouy-Madre, 1974; De Groote et al., 2014; Eshed et al., 2006; Ferembach, 1961; Keith, 1931; McCown and Keith, 1939; Smith, 1989; Smith, 1991), but has not been documented in Early or Middle Epipaleolithic contexts (**Table 1**). In addition to ablation, at least two additional examples of dental modification are known from Natufian contexts: labial surface abrasion of both I^1s of an individual from Wadi Hammeh 27 (Bocquentin et al., 2013) and labial surface polish on a fragment of a maxillary canine or first premolar (Edwards, 2015; Edwards et al., 1999) (**Table 1**). Albeit, whether these latter forms of dental modification (abrasion/polish) were intentional, or byproducts of non-intentional idiosyncratic behaviors, remains to be established.

There is a considerable chronological gap separating Early Epipaleolithic Ohalo 2 from the Late Epipaleolithic Natufian contexts where widespread patterns of incisor ablation are well documented. However, one must also recognize that the Pre-Natufian Epipaleolithic human fossil record from the region is sparse and fragmentary (Hershkovitz and Arensburg, 2017), which makes the identification of ablation prior to the Late Epipaleolithic difficult if it is indeed present in additional individuals. While ablation is quite prevalent in the Natufian, it is not present at every Late Epipaleolithic Natufian site nor necessarily uniformly expressed in the same way (e.g., which teeth are ablated) at each site (Bocquentin, 2011). Thus, finding probable ablation among one of only a few earlier Epipaleolithic humans from southwest Asia is notable, but not at odds with its non-uniform prevalence in the Natufian. Furthermore, the most common ablation pattern during the Natufian – removal of the right I^1 (Bocquentin, 2011) – is precisely the pattern documented for Ohalo 2. As such, Ohalo 2 AMTL provides a strong case for intentional ablation, which could represent a source of biocultural data for long-term behavioral trends within the Epipaleolithic (Maher et al., 2012).

Table 1. Late Upper Paleolithic and Epipaleolithic archaeological sites from southwest Asia bearing human fossils for which the presence or absence of dental modification can be reasonably documented.

Site	*Location*	*Dating*	*Notes on dental modification*	*Sources*[a]
Late Upper Paleolithic/Early Epipaleolithic				
Ohalo II H2	Israel	22,500 cal BP	AMTL of right I^1 as probable ablation.	1-3
Ohalo II H1	Israel	22,500 cal BP	Fragmentary mandible, not applicable	1-2, 4
Nahal Ein Gev I	Israel	27,000-25,000 BP	No AMTL observed.	1-2, 5-6
Ein Gev I	Israel	19,000 cal BP	Fragmentary, not applicable.	3, 7
Qasr Kharaneh IV	Jordan	19,000 cal BP	Fragmentary, heavy occlusal wear, no modification mentioned.	8-9
Ayn Qasiyya	Jordan	20,400-19,800 cal BP	Fragmentary, extremely heavy occlusal wear. No modification mentioned.	10
Moghr el-Ahwal Cave 3	Lebanon	19,200-18,200 cal BP	Mandible fragment with 3 teeth. Not applicable.	11
Middle Epipaleolithic				
Neve David	Jordan	16,000-15,000 cal BP	No modification.	12
Moghr el-Ahwal Cave 2	Lebanon	15,200-14,600 cal BP	Highly fragmentary. Not applicable.	11
Wadi Mataha F-81	Jordan	17,000 cal BP	No AMTL. No modification mentioned.	13
Uyun al-Hammam	Jordan	17,700-14,500 cal BP	Multiple, fragmentary individuals; some with heavy wear. No modification mentioned.	14
Late Epipaleolithic/Natufian[b]				
Wadi Hammeh 27	Jordan	Early Natufian	Abrasion right and left I^1 labial surfaces.	15-16
Wadi Khawwan 1	Jordan	Early Natufian	Isolated tooth (C^1 or P^3) with labial surface polish.	17-18
Kebara	Israel	Early Natufian	Ablation	19-20
Erq-el-Ahmar	Israel	Early Natufian	No modification	19-20
Eynan (Ain Mallaha)	Israel	Early, Late, and Final Natufian	Ablation	19-20
Hayonim	Israel	Early and Late Natufian	No modification	19-20
El-Wad	Israel	Early and Late Natufian	Ablation	19-20
Nahal Oren	Israel	Late Natufian	Ablation	19-20
Raqefet	Israel	Late Natufian	No modification	19-20
Shukbah	Israel	Late Natufian	Ablation	19-21

[a] (1) This study; (2) Hershkovitz et al., 1995; (3) Trinkaus, 2018b; (4) Hershkovitz and Arensburg, 2017; (5) Arensburg, 1977; (6) Belfer-Cohen et al., 2004; (7) Arensburg and Bar-Yosef, 1973; (8) Dalou, et al. 2017; (9) Rolston, 1982; (10) Richter et al., 2010; (11) Garrard et al., 2018; (12) Bocquentin et al., 2011; (13) Stock et al., 2005; (14) Maher et al., 2011; (15) Bocquentin et al., 2013; (16) Webb and Edwards, 2002; (17) Edwards, 2015; (18) Edwards et al., 1999; (19) Bocquentin, 2007; (20) Bocquentin, 2011; (21) De Groote et al., 2014.

[b] The Early Natufian is ~15,000-13,000 cal BP, the Late Natufian is ~13,000-11,500 cal BP, and the latter portion of the Late Natufian (11,800-11,500) is sometimes considered the Final Natufian (Grosman and Munro, 2017).

Although the right I^1 is the most commonly removed tooth during the Natufian, there are variants on this pattern (Bocquentin, 2011), and instances of dental polish and abrasion in the Early Natufian of Jordan are suggestive of additional forms dental modification being practiced (Bocquentin et al., 2013; Edwards, 2015; Edwards et al., 1999). The substantial morphological variation documented throughout the Epipaleolithic of southwest Asia (Arensburg, 1981; Arensburg and Bar-Yosef, 1973; Bocquentin et al., 2011; Hershkovitz and Arensburg, 2017; Hershkovitz et al., 1995; Lahr and Arensburg, 1995; Mahoney, 2007; Richter et al., 2010; Stock et al., 2005) is an interesting backdrop to this evidence for biocultural variation in dental modification practices.

There is a near global distribution of ablation practices in prehistoric and historic contexts, and myriad reasons for performing ablation are documented ethnohistorically (Bocquentin, 2011; Durband et al., 2014; Humphrey and Bocaege, 2008; Milner, 2017; Milner and Larsen, 1991; Pietrusewsky and Douglas, 1993; Robb, 1997; Russell et al., 2013; Stojanowski et al., 2014; Stojanowski et al., 2016; Verger-Pratoucy, 1970; Willman et al., 2016). Nevertheless, a unifying explanation for ablation is that it is an irreversible and conspicuous embodiment of an individual or group-level social identity (Stojanowski et al., 2014; Willman et al., 2016). This conspicuous marker of identity (Humphrey and Bocaege, 2008; Stojanowski et al., 2014; Willman et al., 2016), in addition to other forms of intentional dental modification, are increasingly used as markers of human population dynamics that are independent of, but can be integrated with, other forms of data (e.g., ancient DNA, morphology, linguistic, burial practices, material culture, paleoenvironmental, etc.) to better understand prehistoric human population movements and interactions (Edwards, 2015; Irish, 2017; Stojanowski et al., 2014; Stojanowski et al., 2016; Willman et al., in press; Willman et al., 2016). We suggest that evidence from embodied social identities expressed through intentional body modification can contribute to broader discussions of human population dynamics in the Late Pleistocene southwest Asia (e.g., Bocquentin, 2011), as shown in synthetic works from other regions (De Groote and Humphrey, 2016; Humphrey and Bocaege, 2008; Irish, 2017; Stojanowski et al., 2014; Stojanowski et al., 2016; Willman et al., in press; Willman et al., 2016). When viewed together the evidence from ancient DNA, skeletal morphology, material culture, and embodied social identities can provide a more convincing argument for possible long-term regional behavioral trends, as well as interregional biocultural variability or continuity.

5 Conclusion

The Ohalo 2 antemortem missing right I^1 may have been lost through a non-intentional trauma earlier in life. However, the timing of the AMTL, comparative patterns of dental wear, a lack of major oral pathological conditions that would contribute to AMTL, and comparisons with the intra- and inter-regional cases of dental ablation provides a strong case for intentional incisor ablation for Ohalo 2. If correct, Ohalo 2 would be the oldest example of ablation from the Late Pleistocene circum-Mediterranean world – predating the earliest examples from both North Africa and southwest Asia by multiple thousands of years. The similarity of the Ohalo 2 ablation pattern with Late Epipaleolithic Natufian individuals provides further evidence of potential long-term behavioral trends in the Epipaleolithic of southwest Asia. We speculate that understanding the spatiotemporally patterns of embodied social identities will continue to play an important role in identifying prehistoric population movements and interactions throughout southwest Asia during the Pleistocene and Early Holocene.

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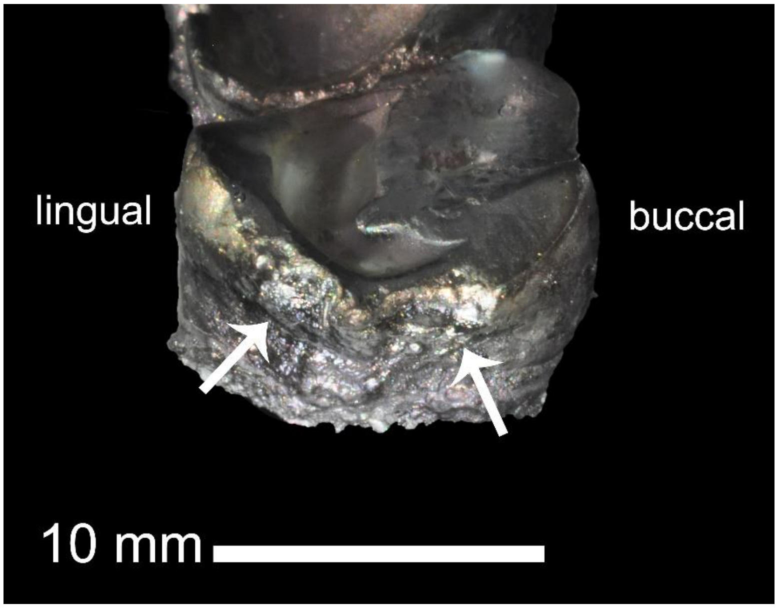
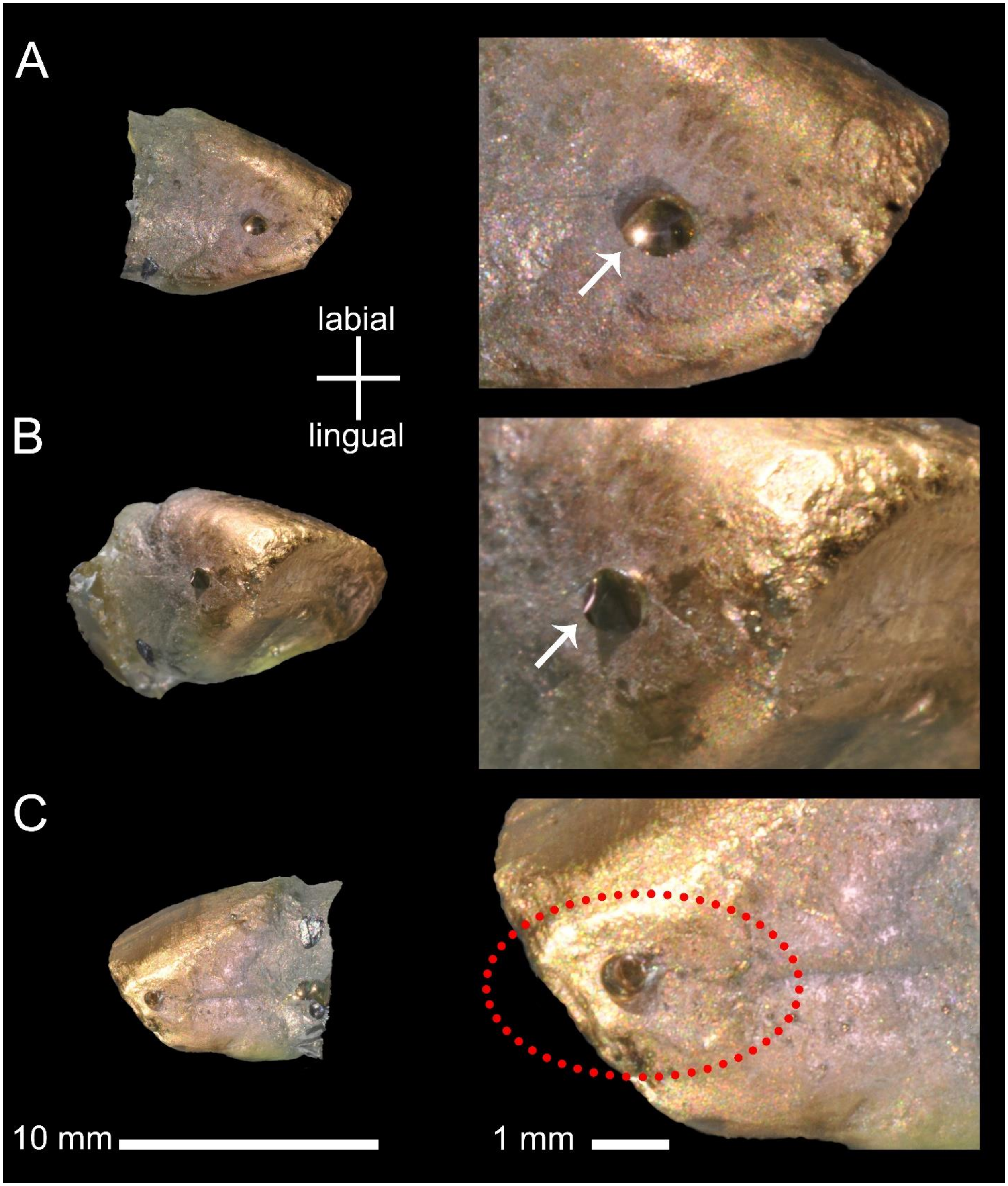
Supplemental Information to accompany:

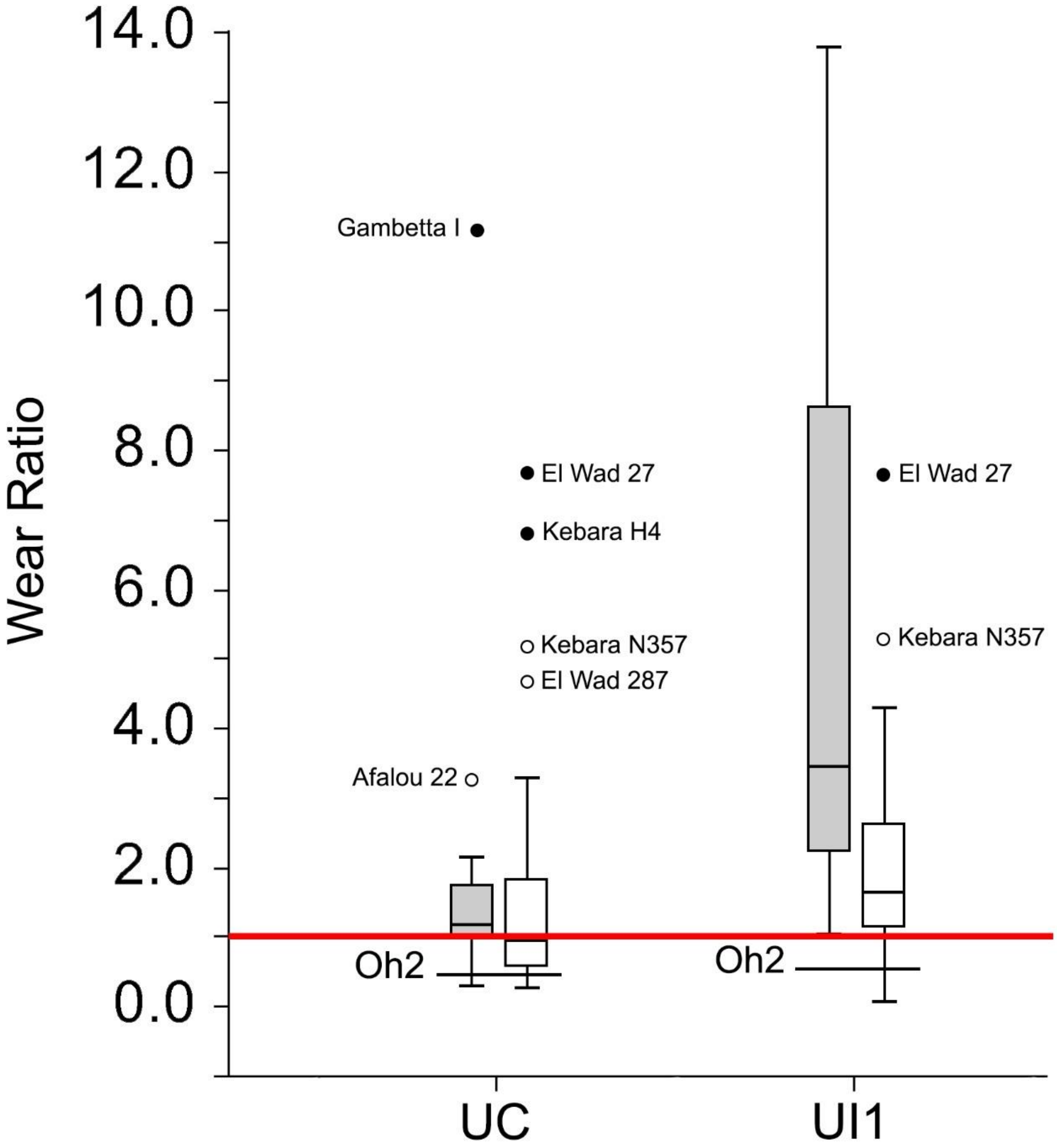
Oral pathological conditions of an Early Epipaleolithic human from Southwest Asia: Ohalo II H2 as a probable case of intentional dental ablation



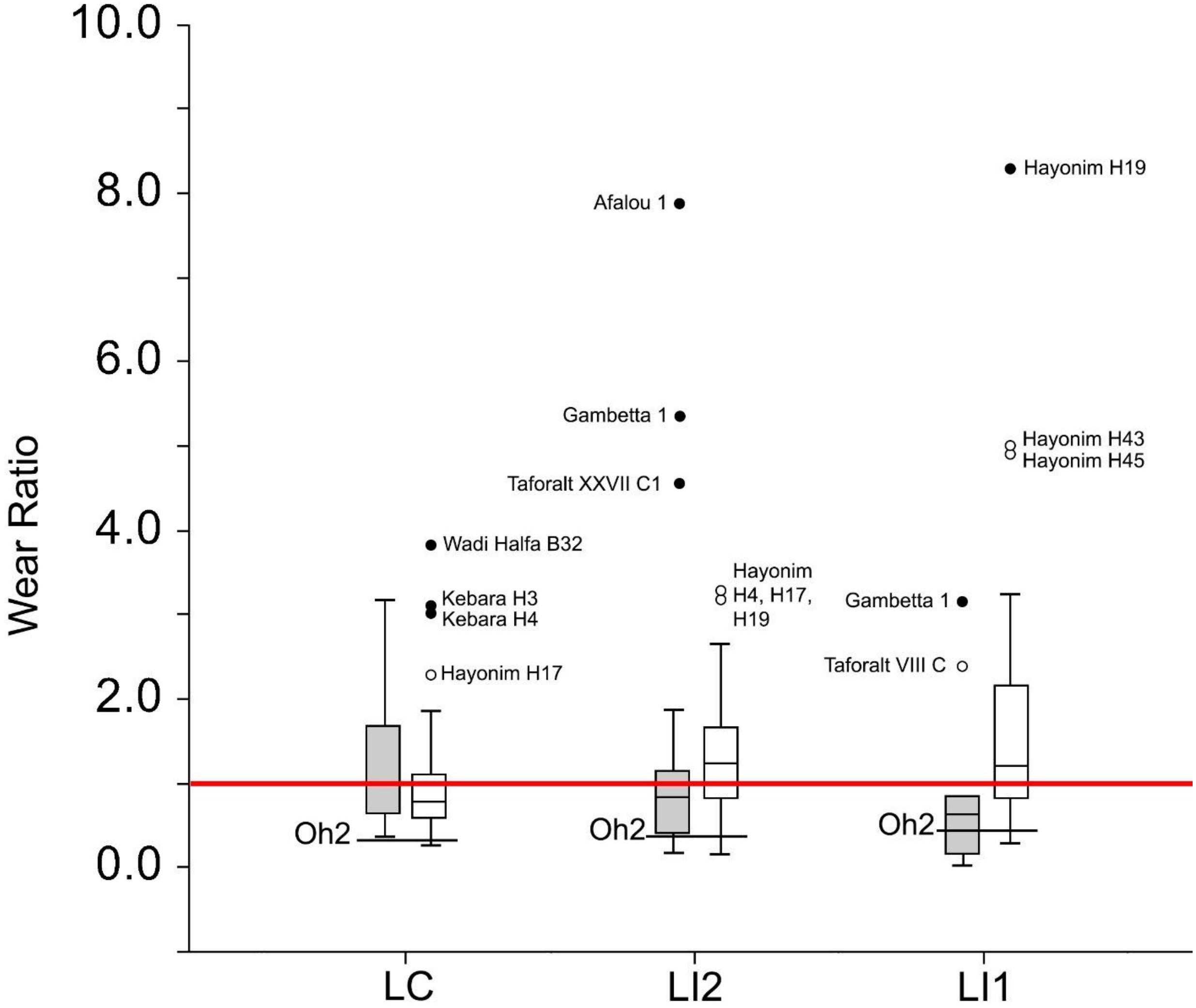
Supplemental Figure 1. Detailed images of distal interproximal surface of Ohalo 2 left M^2. Macrophotographs taken from an epoxy-resin cast of original tooth. Cast has been sputter-coated for scanning electron microscopy analyses unrelated to present study. Occlusal surface is toward top of image. White arrows point toward large antemortem chipping of distal border. Note there is no interproximal facet for the left M^3, only large chips that were likely mistaken for an interproximal facet in occlusal view in a previous analysis (Trinkaus, 2018).



Supplemental Figure 2. Detailed images of interproximal surfaces of Ohalo 2 left I^1. Macrophotographs taken from an epoxy-resin cast of original tooth. Cast has been sputter-coated for scanning electron microscopy analyses unrelated to present study. **A.** Mesial surface of incisor showing no interproximal wear facet for right I^1. White arrow points to small casting defect. Numerous small, antermortem enamel chips are visible along edge. **B.** Mesial suface of incisor at oblique angle to provide additional view of interproximal surface. White arrow points to same casting defect visible in image 1A. **C.** Lateral (distal) interproximal suface with clear interproximal facet (inside red dotted ellipse) for left I^2.



Supplemental Figure 3. Wear ratio (dentine exposure) of C^1 and I^1 relative to M^1 (red line at 1.0). Comparisons of Iberomaurusian and Capsian individuals (grey boxes), Late Epipaleolithic (El-Wad, Kebara, Hayonim, Mallaha, and Wadi Halfa (white boxes), and Ohalo 2 (solids horizontal bars labled "Oh2"). Boxes represent the interquartile range, bars inside boxes represent the median, whiskers represent the range of values, open circles are outliers by more than 1.5x the interquartile range, and closed circles are outliers that are 3.0x the interquartile range. Ohalo 2 anterior relative to first molar wear is low compared to the comparative samples indicating more extreme posterior relative to anterior wear for Ohalo 2. Figures modified from De Groote and Humphrey (2016:58) and Clement (2008:257).



Supplemental Figure 4. Wear ratio (dentine exposure) of C_1, I_2, and I_1 relative to M_1 (red line at 1.0). Comparisons of Iberomaurusian and Capsian individuals (grey boxes), Late Epipaleolithic (El-Wad, Kebara, Hayonim, Mallaha, and Wadi Halfa (white boxes), and Ohalo 2 (solids horizontal bars labled "Oh2"). Boxes represent the interquartile range, bars inside boxes represent the median, whiskers represent the range of values, open circles are outliers by more than 1.5x the interquartile range, and closed circles are outliers that are 3.0x the interquartile range. Ohalo 2 anterior relative to first molar wear is low compared to the comparative samples indicating more extreme posterior relative to anterior wear for Ohalo 2. Figures modified from De Groote and Humphrey (2016:59) and Clement (2008:258).

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