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John C Willman, Raquel Hernando, Marie Matu, Isabelle Crevecoeur. Biocultural diversity in Late Pleistocene/Early Holocene Africa: Olduvai Hominid 1 (Tanzania) biological affinity and intentional body modification. American Journal of Physical Anthropology, 2020, 172, pp.664 - 681. 10.1002/ajpa.24007. hal-02990216

HAL Id: hal-02990216

https://hal.science/hal-02990216

Submitted on 5 Nov 2020

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RESEARCH ARTICLE



Biocultural diversity in Late Pleistocene/Early Holocene Africa: Olduvai Hominid 1 (Tanzania) biological affinity and intentional body modification

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Funding information

Agence Nationale de la Recherche, Grant/ Award Number: ANR-14-CE31; Agència de Gestió d'Ajuts Universitaris i de Recerca, Grant/Award Number: 2017SGR1040; H2020 Marie Skłodowska-Curie Actions, Grant/ Award Number: H2020-MSCA-IF-2016 No. 749188; Ministerio de Ciencia e Innovación, Grant/Award Number: PGC2018-093925-B-C32; Universitat Rovira i Virgili, Grant/Award Number: 2017PFR-URV-B2-91; Martí-Franqués Research Grant, Grant/ Award Number: 2019PMF-PIPF-59

Abstract

Objectives: The dentition of Olduvai Hominid 1 (OH1) exhibits an anomalous pattern of dental wear that was originally attributed to either intentional cultural modification (filing) or plant processing behaviors. A differential diagnosis of the wear and assessment of the biological affinity of OH1 is presented.

Materials and Methods: Macroscopic and microscopic observations of all labial and buccal tooth surfaces were undertaken to assess wear patterns. A multivariate analysis of mandibular morphology of OH1 compared to other Late Pleistocene, Holocene, and recent modern humans was used to ascertain biological affinity.

Results: The morphological variation of the OH1 mandible is closely aligned with variation in penecontemporaneous fossils from Africa and outside that of recent humans. The concave wear facets exposing dentin on the labial surfaces of all three preserved mandibular incisors is confirmed. Substantial loss of labial/buccal surfaces was documented on the surfaces of all in situ maxillary and mandibular canines, premolars, and molars ranging from distinct facets with well-defined edges, to blunting or "polishing" around areas of maximum buccal curvature. The wear on both the anterior and postcanine teeth closely resemble that caused by adornments ("labrets") worn in lower-lip and buccal facial piercings known from bioarchaeological and ethnographic contexts. The wear pattern suggests that the OH1 wore three facial piercings—two buccal/lateral and a medial one in the lower lip.

Discussion: Our findings suggest that the expression of social identities through intentional body modification is more diverse than previously documented elsewhere in Africa during the Late Pleistocene (i.e., ablation) and Early Holocene (i.e., ablation, chipping, and filing).

KEYWORDS

dental wear, facial piercing, labret, Later Stone Age, social identity

1 | INTRODUCTION

Human morphological variation across Africa during the Late Pleistocene and Early Holocene is poorly understood despite its importance for understanding prehistoric population dynamics within the continent and the transition from anatomically archaic to modern human morphology. This can be partly attributed to the sparse, highly fragmentary, and often indirectly dated Late Pleistocene human fossil record of Africa (Crevecoeur, 2008; Crevecoeur, Brooks, Ribot, Cornelissen, & Semal, 2016; Crevecoeur, Rougier, Grine, & Froment,

2009; Grine, 2016; Grine et al., 2017; Stojanowski, 2014; Tryon et al., 2015). Human remains from MIS 2 and early MIS 1 are more common than fossils from the preceding MIS 6 to MIS 3 (Grine 2016), but the regional distribution of human remains are skewed by a few, large mortuary contexts from more recent periods in North Africa (e.g., Afalou-bou-Rhummel and Grotte des Pigeons [Taforalt]) and the Nile Valley (e.g., Jebel Sahaba, Wadi Halfa, Tushka, Al Khiday) (Arambourg, Boule, Vallois, & Verneau, 1934; Ferembach, Dastugue, & Poitrat-Targowla, 1962; Hachi, 1996; Humphrey, Bello, Turner, Bouzouggar, & Barton, 2012; Stojanowski, Carver, & Miller, 2014; Stojanowski, Johnson, Paul, & Carver, 2016; Usai et al., 2010; Wendorf, 1968). With so few human fossils dated to the Late Pleistocene and Early Holocene in Africa, and concomitant biases in regional representation, the ones that are available for detailed analyses are of great importance for understanding issues of human biocultural variation in African prehistory (Crevecoeur et al., 2016; Mounier et al., 2018; Sawchuk & Willoughby, 2015; Scerri et al., 2018). Cranial, dental, and postcranial analyses of Pleistocene and Holocene humans provide meaningful insights into population dynamics within Africa (Armelagos, Van Gerven, Martin, & Huss-Ashmore, 1984; Benoiston, Bayle, & Crevecoeur, 2018; Crevecoeur, 2008; Crevecoeur et al., 2016; Crevecoeur et al., 2009; Greene, Ewing, & Armelagos, 1967; Holliday, 2015; Irish, 2000, 2005; Irish, Black, Sealy, & Ackermann, 2014; Irish & Guatelli-Steinberg, 2003; Irish & Konigsberg, 2007; Mounier et al., 2018; Pfeiffer & Harrington, 2018; Ponce de León et al., 2018; Sawchuk & Willoughby, 2015; Stojanowski, 2014; Warren, Hall, & Ackermann, 2015), but biocultural approaches emphasizing intentional body modification have also proven useful as markers of population movement, continuity, and replacement in African prehistory (Barton et al., 2008: De Groote & Humphrey, 2016: Finucane. Manning, & Touré, 2008; Humphrey & Bocaege, 2008; Irish, 2017; Mercader, Garralda, Pearson, & Bailey, 2001; Stojanowski et al., 2014, 2016). Biocultural approaches also provide an additional level of information on human lifeways and social identities that may otherwise be ignored in pursuit of data on biological affinity alone.

Renewed interest in the paleobiology of Olduvai Hominid I (OH1, Olduvai [Oldupai] Gorge, northern Tanzania)—principally concerning morphological variation and burial taphonomy (Crevecoeur et al., 2016; Matu, Crevecoeur, & Huchet, 2017; Tryon et al., 2015)provided an opportunity to reexamine the entire dentition with an emphasis on the anomalous pattern of dental wear on the labial surfaces of the mandibular incisors and canine of this individual, which was only briefly discussed elsewhere (Mollison, 1929; Parsche, 1993). This study aims to provide a differential diagnosis of the OH1 dental wear in light of literature now replete with examples of idiosyncratic and non-dietary dental wear features (Bonfiglioli, Mariotti, Facchini, Belcastro, & Condemi, 2004; d'Incau, Couture, & Maureille, 2012; Milner & Larsen, 1991; P. Molnar, 2011; S. Molnar, 1972; Scott & Jolie, 2008; Stojanowski et al., 2016), and a growing literature on intentional body modification in the African archaeological record (Barton et al., 2008; De Groote & Humphrey, 2016; Finucane et al., 2008; Honegger, 2004; Humphrey & Bocaege, 2008; Irish, 2017; MacDonald, 1999; Mercader et al., 2001; Petit-Maire & Riser, 1983; Salvatori & Usai, 2009, 2014, 2016; Santoni, Sakka, & Garcier, 2006; Stojanowski et al., 2014, 2016).

1.1 | Archaeological and paleobiological context

The archaeological context of the OH1 was initially published over 100 years ago (M. D. Leakey, 1978; Reck, 1914), and few studies concerning this relatively complete skeleton have been published since the 1930s (Boswell, 1932; Crevecoeur et al., 2016; Gieseler and Mollison, 1929; L. S. B. Leakey, 1928; Matu et al., 2017; Mollison, 1929; Parsche, 1993; Protsch, 1974; Twiesselman, 1973; Reck, 1926, 1933). Direct dating provided an age of 16,920 \pm 920 BP for the skeleton (Protsch, 1974, 1975), but doubts have been cast on the dates acquired through the radiocarbon and/or amino acid racemization dating by Protsch in the 1970s (Grine, 2016). A new attempt to re-date OH1 was undertaken in 2018 on a fragment of femoral diaphysis that was not varnished. Unfortunately, despite a careful pretreatment, no reliable collagen fraction could be isolated and purified. The sample could not be dated nor a $\delta^{15} N/$ $\delta^{14} N$ measurement be done due to this absence of collagen.

Previous analyses indicate that OH1 was a young adult male (~20-35 years old at death) and deliberately buried (Matu et al., 2017). Morphological analyses have been more illustrative of the biological and probable chronological affinity of the OH1 individual relative to other Later Stone Age human remains. For instance, morphological analyses show that the mandibular and distal humeral morphology of OH1 are outside of the 95% confidence interval ellipse for recent African human comparative samples (Crevecoeur et al., 2016). Furthermore, the OH1 mandibular metrics cluster with penecontemporaneous Later Stone Age humans from Ishango and Mumbwa, and distal humeral morphology follows the general pattern of Late Pleistocene humans (Crevecoeur et al., 2016). The presence of microlithic fragments found in potentially associated layers (Protsch, 1974) can be attributed to the temporospatially diverse Later Stone Age of East Africa, regardless of what "industry" or technocultural variant it was, or is currently, attributed to (Wilshaw, 2016). Thus, the skeletal morphology and artifacts associated with the skeleton provide support for a Late Pleistocene/Later Stone Age context for OH1.

1.2 | Previous assessments of the anomalous anterior dental wear

The OH1 dentition is incomplete, but the mandibular anterior dentition does preserve the left I_1 and right I_1 , I_2 , and C_1 —all of which exhibit marked wear facets on the labial surfaces of each tooth. The wear is most marked on the labial incisor surfaces, exposing dentin on each tooth, and a flat labial facet is also apparent on the left C_1 (Figure 1).

Early observations by Leakey (1928) report a lack of anterior tooth chipping or filing commonly affiliated with Bantu populations, and the observation was later confirmed by Mollison (1929) for both



FIGURE 1 Macroscopic details of anterior mandibular dentition in lateral and labial views. Note marked concave facets on each incisor. Modest canine facet is faint and difficult to view here. Scale is 10 mm

the maxilla and mandible. However, Mollison (1929) noted the presence of the labial surface wear on the anterior mandibular dentition. Mollison attributed this wear to the probable use of a sandstone file through an analogy with dental filing practices among the Proto-Malay, since similar labial abrasion had not yet been documented in Africa. A subsequent investigation by Parsche (1993) also agreed that the labial wear on the OH1 mandible has no equivalent among ethnographically known examples of intentional dental modification in Africa.

However, Parsche (1993) emphasized the high degree of asymmetry of labial surface wear between anterior teeth and challenged Mollison's assertion that the wear was derived from sandstone filing. Parsche (1993) pursued two experiments to replicate the labial wear pattern—the first, abrasion with sandstone, and the second, abrasion with moist sisal fibers. After 30 minutes of abrasion with each material, scanning electron microscopy (SEM) was used to examine the experimentally worn teeth and comparisons with the incisors of OH1 were also made. He determined that the micro-grooving on the OH1 teeth was more consistent with wear induced by sisal fibers and rejected the possibility of wear from a sandstone file. Parsche (1993) ultimately attributed the labial wear to non-masticatory uses of the anterior teeth as tools for fiber processing rather than any form of intentional dental modification.

There are several major criticisms concerning the methods and conclusions of Parsche (1993). First, the surfaces of the experimentally worn teeth were not cleaned of residues to improve visualization of the microwear patterns produced (Parsche 1993). Second, the orientation of striations in the sandstone experiment are oblique and the sisal fiber experiment produced horizontal striations (Parsche 1993), which indicates that motions used to produce abrasion between experiments lacked uniformity. Third, the microscopic examination of each labially-facetted tooth was not conducted, and purportedly unworn premolars and molars were not examined to determine baseline levels of buccal preservation and wear across tooth types. Furthermore, at the time of publication, the broad literature on nonmasticatory wear caused by manipulative behaviors (Barrett, 1977; Formicola, 1988; Irish & Turner, 1987; Larsen, 1985; Milner & Larsen, 1991; S. Molnar, 1972; Pedersen & Jakobsen, 1989; Taylor, 1986; Turner & Machado, 1983; Ubelaker, Phenice, & Bass, 1969) contained a paucity of references to mandibular labial surface modification aside from instrumental striations attributed to "stuff-and-cut" behaviors (Arsuaga et al., 1989; Bermúdez de Castro, Bromage, & Jalvo, 1988; Brace, 1975; Koby, 1956). Therefore, we suggest that there is little ethnographic, bioarchaeological, or paleobiological support for non-dietary manipulative behaviors that would produce the pattern of labial wear exhibited on the anterior mandibular teeth of OH1.

We agree with Parsche (1993) that the OH1 labial dental wear is unintentional; however, we argue that it is an unintentional byproduct of intentional body modification. One such form of body modification that produces unintentional dental (and occasionally, osseous) modification is the use of facial piercings (e.g., "labrets", "lip plugs", "lipstuds", "lip discs", etc.; henceforth: labrets) (Alt & Pichler, 1998; Cybulski, 1974, 2010; Cybulski, Balkwill, Young, & Sutherland, 1992; Dietze et al., 2007; Garve, Garve, Türp, & Meyer, 2017; MacDonald, 1999; Mukherjee, Trevor, & Rao, 1955; Pedersen, 1952, 1955; Santoni et al., 2006; Torres-Rouff, 2003, 2011). Indeed, facial piercings were documented historically (Colette, 1933; Gupta, 1986; Huntingford, 1961: Labouret, 1952: Schweinfurth, 1875: also see citations in Insoll, 2015; MacDonald, 1999; Seligman, 2015) and archaeologically in Africa (Addison, 1949; Mukherjee et al., 1955; Petit-Maire & Riser, 1983; also see citations in Insoll, 2015; MacDonald. 1999) when Parsche (1993) conducted his analysis, but were not considered in any previous evaluation of the OH1 labial wear. Thus, a re-analysis is warranted.

2 | MATERIALS AND METHODS

2.1 | Morphometric analysis of biological affinity

Five measurements were taken on the relatively complete OH1 mandible following Martin (in Bräuer, 1988) for mandibular corpus length (M68), bimental breadth (M67), symphyseal height (M69), breadth of the corpus at the level of the mental foramen (M69[3]), and minimum anteroposterior width of the ramus (M71a). Previously analyses show that these measurements are a good proxy for overall mandibular morphology, and are discriminant between groups (e.g., Crevecoeur, 2008; Crevecoeur & Trinkaus, 2004; Crevecoeur et al., 2009, 2016). The use of only five measurements also ensures a large comparative sample of fossil and recent human remains. A principle component analysis (PCA) is used to assess the mandibular morphology of OH1 compared to geographically and chronologically defined groups comprised of Middle Stone Age humans (Loyangalani and Mumbwa X); Middle Paleolithic modern humans from Southwest Asia (Skhul VI and V, and Qafzeh 9); Late Pleistocene Homo sapiens from Nazlet Khater (NK2), Ishango (#Ish15), Northeast Africa (Jebel Sahaba, Wadi Kubbaniya, and Wadi Halfa), Northwest Africa (Taforalt), Southwest Asia (Ohalo II H2, Mallaha, and Nahal Oren); Neolithic individuals from Northwest Africa (Mechta el Arbi), East Africa (Gamble's Cave and Lothagam), South Africa (Fish Hoek); and recent modern humans from Africa. Morphological data from fossil and bioarchaeological materials were collected by one of us (I. Crevecoeur) on original specimens except for Wadi Kubbaniya (cast at the Smithsonian

Institution, Washington D.C.). Recent modern human data are from Ribot (2011).

2.2 | Dental wear and oral pathology

Digital photography and macroscopic observations were made on the original specimen. High resolution molds of all teeth were made using President Light Body polyvinylsiloxane (Coltene Whaledent), and epoxy resin (Epo-Tek 301: Epoxy Technologies, Inc.) was used for positive casts (Galbany, Martínez, & Pérez-Pérez, 2004). Casts were prepared for environmental scanning electron microscopy (ESEM: FEI Quanta 600) by sputter-coating with approximately 20 nm layer of gold to improve the conductivity. Macroscopic observations were also made to assess presence or absence of various dental wear features (e.g., interproximal grooving, antemortem enamel chipping) and oral paleopathological conditions (e.g., caries and periodontal status).

3 | RESULTS

3.1 | Biological affinity

The first three principle components (PC1, PC2, and PC3) for the PCA on mandibular metrics account for 83.6% of total sample variation (54.6%, 15.5%, and 13.5%, respectively; Table 1, Figures 2 and 3). OH1 and most of the Late Pleistocene individuals plot in the upper left quadrant of each projection and many of these individuals, including OH1, are outside of the 95% concentration ellipse of recent modern human variation. The position of OH1 relative to other specimens is driven by the absolute dimensions of the mandible, particularly corpus length for PC1, symphysis height for PC2 (Figure 2), and corpus breadth for PC3 (Figure 3). The Early Holocene East African individuals from Lothagam (notably, KNM-LT 13704B) overlap with OH1 along PC1, but diverge along PC2 and PC3, reflecting shorter symphyseal height and thinner corpus breadth, respectively. Concentration

TABLE 1 Principle Component Analysis eigenvalues and factor loadings

<u> </u>	,					
Factors	Eigenvalue	% Total				
PC1	2.730317	54.60634				
PC2	0.773816	15.47631				
PC3	0.674325	13.48649				
PC4	0.475479	9.50957				
PC5	0.346064	6.92128				
Variable (Martin no.)	Raw measurement (mm)	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Corpus length (M68)	98.00	-0.648200	0.447773	0.601108	-0.033152	0.130024
Bimental breadth (M67)	50.60	-0.800955	-0.110379	-0.027889	0.564091	-0.165260
Minimum anteroposterior breath of the ramus (M71a)	41.22	-0.836580	-0.085194	-0.032869	-0.374825	-0.388976
Symphysis height (M69)	39.89	-0.670990	0.445330	-0.555887	-0.051454	0.199487
Corpus breadth at the level of the mental foramen (M69[3])	14.97	-0.720091	-0.596284	0.046094	-0.114190	0.332791

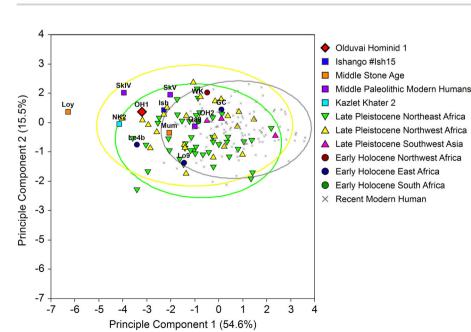


FIGURE 2 Bivariate projection of component 1 and 2 from the principle components analysis of mandibular morphology. The 95% concentration ellipses for Late Pleistocene Northeast Africa, Late Pleistocene Northwest Africa, and recent modern humans are shown. Abbreviations not indicated in legend: Loy = Loyangalani, Mum = Mumbwa X, Sk = Skhul, Qa = Qafzeh, OH2 = Ohalo 2, WK = Wadi Kubbaniya, Lo = Lothagam, GC = Gamble's Cave

ellipses for the two largest fossil groups (Late Pleistocene Northeast and Northwest Africa) are also provided. When PCA is performed with size-adjusted data (the logged ratio of each variable by the geometric mean of all variables; see: Darroch and Mosimann, 1985; Jungers, Falsetti, Wall, 1995), no meaningful patterning is shown between individuals and the various subgroupings. Overall, the PCA reflects a massive, elongated mandible with a tall mandibular symphysis and thick corpus for OH1.

3.2 Dental wear and oral pathology

There are three large, concave facets exposing dentin on the labial surfaces of each of the preserved mandibular incisors (Figures 1 and 4a,b). The incisor facets are most deeply faceted on the central incisors and less so on the left I_2 where only a small dentin exposure is present on the mesial half of the cervical two-thirds of the labial face.

The cervical borders of each facet are the shape of inverted crescents. The enamel surrounding each labial dentin exposure exhibits mesiolaterally oriented microgrooves (Figure 4b). A shallow, concave facet without dentin exposure is also present on the left mandibular canine (Figure 4c). The canine facet is located on the middle third of the labial face. The canine is less worn than the left I_2 , which further emphasizes the diminishing wear gradient from the central incisors to lateral incisor and canine. The right I^1 exhibits normal occlusal wear but lacks the labial wear of its mandibular antagonists.

Contrary to previous studies, we document marked buccal faceting, blunting of buccal curvatures, and "polish" on most of the postcanine teeth (Figure 5). All premolars display a substantial loss of buccal enamel with flat facets where the crown should exhibit its greatest buccal curvature, and with well-defined facet margins. The buccal facets of maxillary and mandibular premolars form a continuous, flat wear plane with adjacent first molars (Figure 6a). The maxillary canines display blunting of their buccal surfaces, but it is less

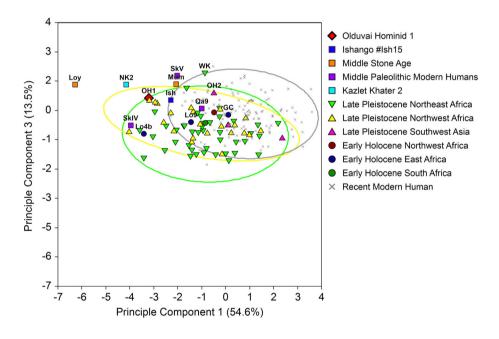


FIGURE 3 Bivariate projection of component 1 and 3 from the principle components analysis of mandibular morphology. The 95% concentration ellipses for Late Pleistocene Northeast Africa, Late Pleistocene Northwest Africa, and recent modern humans are shown. Abbreviations same as Figure 2

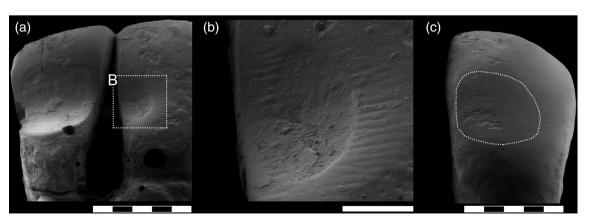


FIGURE 4 (a) ESEM micrograph of left I_1 and I_2 concave facets on labial surface. (b) Closer view of horizontal microgrooving around dentin exposure on the left I_2 . (c) Left C_1 with subtle facet concavity outlined. Scale increments are 10 mm

marked than that of premolars and first molars (Figure 6b). Maxillary second molars exhibit marked buccal facets (Figure 6c,d), albeit, slightly less defined than in M^1 s. Similarly, the mesiobuccal faces of each M^3 exhibit subtle flattening. Together, this suggests a

decreasing gradient of buccal wear from M^1 to M^2 to M^3 , in both the total area worn and depth of wear, which is also evident in the decreasing visibility of the buccal grooves across the maxillary molars (Figure 6c).



FIGURE 5 Approximate outlines of buccal wear on OH1 dentition. Blue shapes indicate strongly marked facets and red shapes indicate less-marked buccal wear exhibited as modest blunting of buccal curvatures and polish. Anterior dentition not outlined in this view. Scale increments are 10 mm

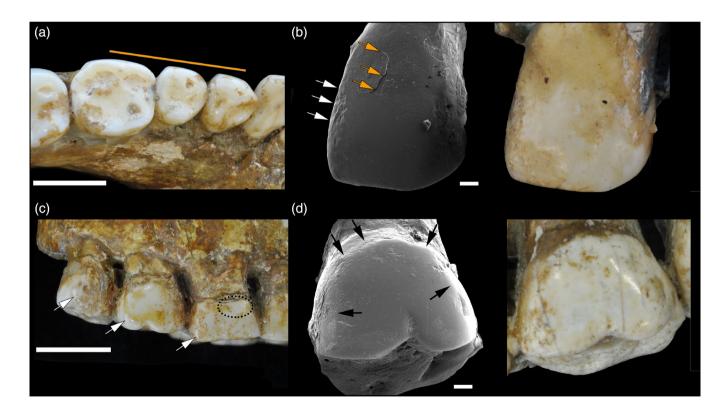


FIGURE 6 (a) Continuous buccal wear plan on left P_3 , P_4 , and M_1 emphasized by orange line. Note that wear is most accentuated on premolars. Scale is 10 mm. (b) ESEM micrograph of left C^1 showing modest flatness to buccal curvature and rugose area (white areas) that border facet margin. Rugosity is unaffected by buccal wear agent. Orange arrows point to partially exfoliated shellac. Macrophotograph of same surface in similar orientation. Scale is 1 mm. (c) Right M^1 to M^3 showing gradient of buccal wear. Note the decreasing visibility of buccal grooves from M^1 to M^3 . Arrows indicate distobuccal margin of buccal wear facets. Dotted ellipse surrounds a white dentin exposure. Scale is 10 mm. (d) ESEM micrograph of left M^2 showing well defined buccal facet (black arrows). Note flatness of surface surrounding the buccal groove. Macrophotograph of the same surface with slightly different orientation. Scale is 1 mm

Dentin exposure is present near the mesiobuccal cervix of the right M¹, emphasizing the exceptional loss of buccal enamel on the tooth (Figure 6c). Similar loss of enamel seems to be present on at least the left P^4 and M^1 (Figure 7a). The damage to root and alveolar surfaces, and the conspicuous glue/shellac coating them, makes it particularly difficult to identify antemortem features on non-enamel surfaces. However, the buccal wear penetrating into the dentin near the cervix of the M¹s and left P⁴ may be continuous from the enamel/dentin to the surfaces of roots. However, it is unclear if this is a taphonomic artifact associated with postmortem breakage, the presence (or localized exfoliation) of adhesive materials, or some combination of these factors (Figure 7a). The buccodistal cervical root surface of the left M¹ exhibits a wide, shallow grooved appearance that could be attributed to any of the factors listed above, or possibly attributable to actions associated with the formation of an interproximal groove (Figure 7a). Unfortunately, the condition of the root is poor, and diagnosis of etiology uncertain.

The only possible evidence of root surface caries is present on lingual surface of the left M^1 , but again, this could be a product of postmortem breakage and repair, but the preservation is simply too poor to be certain (Figure 7b). No other caries are identified, but it must be reiterated that various forms of adhesive (glue, shellac, etc.), as well as some postdepositional exfoliation of the left maxillary occlusal surfaces, prevented a thorough investigation of many surfaces. Most of the discoloration of the enamel visible in photos can be attributed to aging adhesives rather than decay.

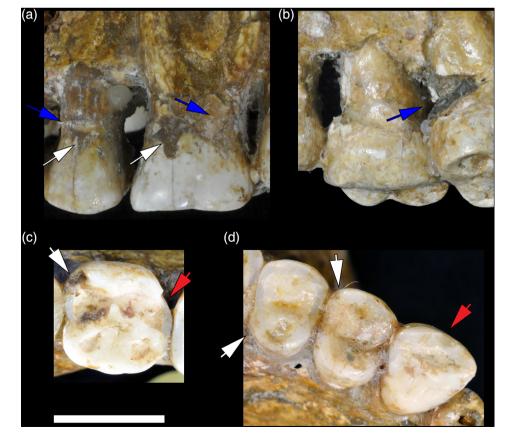
Periodontal status is also difficult to assess due to damage and reconstruction. Most *in situ* teeth were broken postmortem near the

cervix and glued into their current positions, which complicates observations of root and alveolar surfaces and distorts measurements. Cementoenamel junction to alveolar crest distances (CEJ-AC) are best preserved on the postcanine teeth—especially for the mandible and the left maxilla. The degree of alveolar remodeling and CEJ-AC distances suggest mild to moderate periodontal disease for the right maxilla and mandibular postcanine dentition (Lavigne & Molto, 1995; Ogden, 2008), but observations of alveolar bone and CEJ-AC distances in the anterior dentitions are too poorly preserved to assess.

Antemortem and postmortem dental chipping is documented on several teeth, but conclusions about diet or behavior drawn from antemortem chipping should be cautious given overall enamel preservation (Figure 7c,d). For instance, the surface exfoliation on some teeth and adhesive on others makes the identification of some chips impossible. Interproximal chips are the most difficult to identify given the concentration of adhesive at the interface of the interstitial spaces and the occlusal surface. Most antemortem enamel chips are small (Grade 1: Bonfiglioli et al., 2004), but there is one large (Grade 3) antemortem chip on the mesiobuccal cusp of the right M_1 (Figure 7c).

To summarize, the buccal faceting, substantial blunting of buccal curvature, and/or polish is present on the labial/buccal surfaces of all in situ maxillary and mandibular canines and premolars, and first and second molars. Buccal faceting is either less distinct, or absent, on third molars. The pattern suggests that wear affected the buccal surfaces of the maxillary premolars and first molars most heavily, less so anteriorly (C¹), and also decreases from M¹ to M³. The pattern of buccal wear in the mandible is like that of the maxilla, but the wear angles

FIGURE 7 (a) Detail buccal enamel and root surfaces of right P4-M¹. Blue arrows point to areas of possible root features continuous with dentin exposure (white arrows) and buccal faceting. The M¹ example appears as a wide, shallow groove. (b) Lingual surface of left M¹-M². Blue arrow pointing to possible taphonomic damage or root surface caries. (c) Antemortem (white) and postmortem (red) enamel chipping on right M₁. The chip is the largest documented in the dentition. D: Antemortem (white) and postmortem (red) enamel chipping on the right C¹-P⁴. Also note the presence of adhesive on the occlusal surfaces and interstitial spaces that make identification of features difficult. Scale is 10 mm



toward the occlusal surface. The premolars exhibit well-defined facets in both jaws, but facets are better defined in maxillary molars than mandibular ones. OH1 exhibits mild to moderate periodontal disease, some enamel chipping, but no conclusive evidence of caries. Unfortunately, significant use of shellac and glue obscures most surfaces, making the detailed microscopic examination of surfaces difficult.

4 | DISCUSSION

Biological affinity: The present study shows that the mandibular morphology of OH1 aligns with other Late Pleistocene African fossils in terms of absolute size, while remaining outside of the 95% concentration ellipse for multidimensional mandibular variability observed in recent modern humans. Indeed, the PCA confirms patterns shown in previous metric assessments of bimental breadth and corpus length that created a cluster among OH1, Ishango (#Ish15), Mumbwa X, Wadi Kubbaniva, and other Late Pleistocene individuals from Northeast and Northwest Africa while remaining outside the 95% confidence intervals for recent human variation (Crevecoeur et al., 2016). Interestingly, an individual from the Early Holocene site at Lothagam (KNM-LT 13704B) has an absolutely wider bimental breadth, but shorter mandibular corpus than all other Late Pleistocene African fossils previously observed (Crevecoeur et al., 2016). Mounier et al. (2018) also documented larger centroid size for the Lothagam individuals using mandibular geometric morphometrics, albeit with substantial overlap, compared to Early Holocene individuals from Nataruk (West Turkana, Kenya) and Pleistocene North Africa (i.e., Afalou, Taforalt, and Nazlet Khater 2). However, relatively little difference in centroid size between a diverse, global sample of recent humans and pre-dynastic African groups was found; and both Early Holocene and Late Pleistocene African fossil groups exhibit absolutely larger centroid sizes than the former (Mounier et al., 2018). These results are like those in the present study, showing some overlap between Late Pleistocene and Early Holocene individuals, but much less overlap between the Late Pleistocene and recent modern human groups.

Together, these analyses provide a sense of regional and chronological mosaicism in mandibular morphology of Late Pleistocene and Early Holocene humans of Northwest, Northeast, Central, and East Africa. Not only is there a high level of morphological diversity documented in Late Pleistocene and Early Holocene humans from Africa, but this diversity is also relatively distinct from the morphological diversity of later Holocene and recent modern humans (Crevecoeur et al., 2009, 2016; Harvati et al., 2011; Mounier et al., 2018; Tryon et al., 2015), which has been attributed to a "Holocene filter" shaping patterns of recent human diversity in Africa (Mirazón Lahr, 2016; Mounier et al., 2018).

Differential diagnosis of dental wear: The wear on the labial and buccal surfaces of the teeth of OH1 affect far more teeth than initially acknowledged (Mollison, 1929; Parsche, 1993), but the patterning of wear shows remarkable symmetry and patterning across tooth types.

The use of a sandstone file (Mollison, 1929) is an unlikely cause of the labial wear. This is due, in part, to maxillary overbite and overjet

which can prevent ease of filing of the mandibular incisor and canine labial surfaces (Burnett & Irish, 2017), and is seldom documented compared to the filing and modification of the labial surfaces of maxillary anterior tooth surfaces (Arcini, 2005; Bocquentin, Crevecoeur, & Semal, 2013; Ikehara-Quebral et al., 2017; Milner & Larsen, 1991). Second, the practice of intentional filing is generally related to the expression of individual and group-level social identities, and therefore, outwardly visible. Filed mandibular (and cheek) teeth would be a nondescript signal to others, thus making it difficult to ascribe such a practice to the intentional marking and display of one's social identity.

Non-masticatory preparation of vegetal fibers (Parsche, 1993) is also difficult to attribute to the mandibular labial surface wear of OH1. The manipulation of vegetal fibers, sinews, cordage, thread, and similar materials with the dentition is well-documented in both ethnographic and bioarchaeological contexts, but commonly produces occlusal and/or interproximal grooves (Brown & Molnar, 1990; Cybulski, 1974; Erdal, 2008; Formicola, 1988; Lorkiewicz, 2011; Lukacs & Pastor, 1988: Molleson, 2016: Schulz, 1977: Scott & Jolie, 2008; Sperduti et al., 2018; Ubelaker, 1969; Waters-Rist, Bazaliiskii, Weber, Goriunova, & Katzenberg, 2010; Wheat, 1967). Most fiber processing behaviors are reconstructed as pulling fibers across the occlusal surfaces or around the lingual and interproximal surfaces of teeth (see references above). However, the form of wear documented on the mandibular labial surfaces of OH1 has no parallel with any wear features documented in the bioarchaeological literature that have been attributed to non-masticatory manipulative behaviors.

Holding fibrous materials between the teeth and lower lip to soften them or to remove nutrients before expectorating an indigestible, fibrous quid (e.g., Schoeninger, Bunn, Murray, & Marlett, 2001) could produce localized abrasion or corrosion depending on the physical and chemical properties of the material placed between the lip and teeth. However, it is difficult to reconstruct a scenario in which fibers held between the lip and teeth would relate to the mediolateral movements hypothesized by Parsche (1993) for the wear on the anterior mandibular dentition. Furthermore, erosive wear can be ruled out since there is a lack of macroscopic scooping of dentin on the labial surfaces of the mandibular incisors (in addition to the buccal dentin exposure on the right M1). Erosive wear is commonly found on the lingual surfaces of the maxillary anterior teeth (Johansson, Omar, Carlsson, & Johansson, 2012), but none is evident on the well-preserved right I1 or either C1. There is modest cupping of the exposed dentin on the first and second molars, which is often a sign of erosive processes in clinical studies (d'Incau et al., 2012; Johansson et al., 2012), but there is no cupping of anterior tooth dentin, and cupping of exposed dentin on postcanine teeth is also a common outcome of abrasive dentin wear in archaeological contexts (Hinton, 1981; Kaidonis, 2008; Molnar, 1971). Likewise, the labial anterior dental wear is most prominent on the incisal and middle third of each tooth, exhibits sharp lateral edges, and terminates near the cervix-a pattern that is at odds with the position of non-carious cervical lesions (Michael, Kaidonis, & Townsend, 2010). Furthermore, the sharp cervical edge of the concave wear facet would be rounded in a corrosive situation (d'Incau et al., 2012). Furthermore, there is a predominance of

abrasive dietary and non-dietary wear on the labial and buccal surfaces that strongly favor mechanical (abrasive) wear over chemical erosion of the surfaces (Coupal & Sołtysiak, 2017; Kieser et al., 2001). The pattern of labial and buccal wear is also inconsistent with hard tissue correlates of behaviors related to the use of materials like coca (Indriati & Buikstra, 2001), betel nut (Reichart, Creutz, & Scheifele, 2006), or chewing sticks (Cook, Bastos, Lopes, Mendonça de Souza, & Santos, 2015).

The pattern of diminishing wear from the mandibular central incisors to the left C₁ suggests a uniform pattern of wear by a fixed object if one assumes the missing right I₂ and C₁ exhibited symmetrical wear. Wear of this form is commonly documented among wearers of ornaments fixed in piercings through the lower lip in ethnographic, clinical, and bioarchaeological contexts (Addison, 1949; Aigner & Veltre, 1976; Alt & Pichler, 1998; Croucher, 2012; Cybulski, 1974, 2010; Cybulski et al., 1992; Dietze et al., 2007; Erdal, 2013; Garve et al., 2017; Hole, Flannery, & Neely, 1969; Keddie, 1981; MacDonald, 1999: Mattingly et al., 2009: Mukheriee et al., 1955: Pedersen, 1952. 1955; Salvatori & Usai, 2009, 2016; Santoni et al., 2006; Torres-Rouff, 2003, 2011). The symmetry and depth of wear-decreasing from central to lateral incisor and canine-are common characteristics of midline, or "medial" (following Keddie, 1981), lower lip piercings in North American bioarchaeological remains (Cybulski, 2010; Willman, personal observation). Such facial ornamentation is documented in archaeological contexts across the African continent (Addison, 1949: Honegger, 2004; MacDonald, 1999; Mattingly et al., 2009; Mukherjee et al., 1955; Petit-Maire & Riser, 1983; Salvatori & Usai, 2016; Santoni et al., 2006) and is well-known in African ethnohistoric records in numerous forms (Aanestad & Poulsen, 1996; Garve et al., 2017; Gauthier & Wangermez. 1964: Labouret. 1952: LaToskv. 2006: Mac-Donald, 1999; Schweinfurth, 1874; Seligman, 2015; Wayland, 1931).

The microgrooves bordering the exposed dentin on the mandibular anterior facets may relate to the abrasive properties and form of an adornment worn through the lower lip. While we cannot be certain of the exact shape or surface texture of the portion of the adornment abutting the teeth of OH1, but an adornment suspended in a piercing that constrained its movement is a reasonable explanation for the local formation of wear facets and microgrooves on the labial surfaces of the anterior mandibular dentition.

The buccal faceting and wear of postcanine teeth is far less commonly documented in the literature, and is largely confined to examples from bioarchaeological contexts in North America where there is cultural and direct evidence of "lateral" piercings (after Keddie, 1981) for wearing labrets (Aigner & Veltre, 1976; Curtin, 1984; Cybulski, 2010; Murray, 1981; Pedersen, 1955; Severs, 1974), and archaeological sites of the Mid-Upper Paleolithic (Gravettian, sensu *lato*) of Central Europe (Drozdová, 2002; Hillson, 2006; Matiegka, 1924, 1929, 1934; Trefný, 2008; Vlček, 1991, 1997; Willman, 2016). They have been attributed to holding objects between the cheek and buccal surfaces of teeth, such as small pebbles to alleviate thirst (Matiegka, 1924, 1929, 1934; Vlček, 1991), to a range of other possible behaviors (Hillson, 2006), and labret-use (Willman, 2016). However, the archaeological examples from North America that occur in the context

of labret-use exhibit markedly similar patterns of buccal wear to OH1 (Aigner & Veltre, 1976; Curtin, 1984; Cybulski, 2010; Murray, 1981; Pedersen, 1955; Severs, 1974) which lends support for the attribution of labret use by OH1. Lukacs and Pastor (1988) documented a type of interproximal groove on distal maxillary molar roots that was associated with buccal cervical abrasion of teeth proximal to the groove. This form of manipulative wear superficially matches the cervical features on the left side of the OH1 dentition. However, there is a lack of right/left symmetry and a greater involvement of enamel (and dentin) than root surface for OH1. While the left M¹ distal root surface may exhibit an interproximal groove, it is not likely caused by the same agent producing the blunting and faceting of the buccal surfaces.

The more extreme buccal wear on the premolars and first molars, compared to second and third molars, suggests that an object was in contact with the more anterior postcanine teeth for a long enough period of time to create a continuous, flat wear plane across multiple adjacent teeth. Furthermore, the M^1 's exhibit greater buccal wear than the M_1 's which is less probable if an object was placed inside the mouth to rest between the buccal surfaces of the teeth and cheek. This is because a small, hard object would preferentially settle against the mandibular molars. Thus, both the consistent wear planes, and wear patterning along the tooth row and between jaws, is more consistent with ornaments that are fixed through piercings in the cheeks.

Periodontal disease is not uncommon in Late Pleistocene contexts (Cucina, Herrera Atoche, & Chatter, 2019; Lacy, 2014, 2015; Trinkaus, Lacy, & Willman, 2016; Villotte, Ogden, & Trinkaus, 2018), so it is relatively unsurprising for OH1. However, the mild to moderate periodontal disease of OH1 co-occurs with the unique pattern of buccal wear. Likewise, the largest enamel chip is also located on the buccal edge of a mandibular, which is not only facetted, but situated between, and in occlusion with, other facetted teeth. While a number of factors can produce dental chipping and periodontal problems, contemporary clinical literature notes high rates of tooth damage and periodontal issues associated with facial piercings (Hennequin-Hoenderdos, Slot, & Van der Weijden, 2016; Otzel & Birch, 2016; Schmidt, Calderaro, Weiger, & Walter, 2019). If the groove on the buccal roots of the left M¹ is not a taphonomic artifact, it too may relate to gingival irritation caused by facial piercings.

Whether one agrees with the interpretation we present, the buccal facets are a previously undocumented form of dental wear in Late Pleistocene and Early Holocene contexts in Africa. Whatever the ultimate cause of the buccal wear is, it does document a temporospatially unique biocultural marker of past human behavior (Willman, 2016).

Labrets and social identity: Comparative analyses of facial ornaments in conjunction with dental wear are still needed to determine how the number of labrets, material they are composed of, and their style influences idiosyncratic patterns of dental wear. Such comparative analyses are necessary because facial ornaments are often absent in burials, as is the case here, either because they were not included as burial goods, were made of organic material that decomposed, or were not documented due to excavation techniques. However, the pattern of wear can still be used to infer information about the type(s)

TABLE 2 Temporal and spatial distribution of cultural dental modification in Africa and Southwest Asia during the Pleistocene to Early and Middle Holocene^a

Maghreb		Sahara		Nile Valley		East Africa		West Africa		Southwest Asia	
Present	Absent	Present	Absent	Present	Absent	Present	Absent	Present	Absent	Present	Absent
Terminal Pleistocene (~20-12 kya)	(~20–12 kya)										
Ablation (sources: Boc	Ablation (sources: Bocquentin, 2011; Stojanowski, Carver, & Miller, 2014, 2016; this study)	Carver, & Miller,	2014, 2016; this study)								
Khef el Hammar, Hattab II, İfri n'Ammar, Taforalt, La Mouillah, Columnata, Grotte du Polygone, Grotte de la Tranchée, Abri Alain, Djemar Schkra, Rachgoun, cap Tènes, Champlain, Taza 1, Afalou Wechta el Arbi, Djebel Taya, Kef-Oum-Touliza	Rabat, Kifan Bel Ghomari, El-Bachir, Chenoua, Pointe Pescade, Bains Romains, Ali Sacha, e Ternifine, Gambetta i				Soleb, Taramsa Hill, Esna, Wadi Kubbaniya, Tushka, Wadi Halfa, Jebel Sahaba		Kabua, Ishango, Guli Waabayo, Mlambalasi, Olduvai Hominid 1		Iwo Eleru	Shukbah, El Wad, Kebara, Nahal Oren, Mallaha	Ohalo II ^b , Erg-el-Ahmar, Hayonim, Raqefet
Abrasion of maxillary c	Abrasion of maxillary central incisor labial surfaces (source: Bocquentin, Crevecoeur, & Semal, 2013)	source: Bocquen	tin, Crevecoeur, & Semal, 2	013)							
										Wadi Hammeh ^c	Erg-el-Ahmar, Hayonim, Raqefet, Shukbah, El Wad, Kebara, Nahal Oren, Mallaha
Labret wear (source: This study)											
					J	Olduvai Hominid 1					
Early Holocene (~10-7 kya)	7 kya)										
Ablation (sources: Stoja Rachgoun, Columnata, Ain Keda, Mesloug 1, Medjez II, Mechta el Arbi, Grotte des Hyènes, El Mahder, Koudiat Kherrouba, Faid Souar, Aioun Berriche, Khanguet el-Mouhaad, Kilomètre 3,200, Ain Boucherit	janowski et al., 2014, 2016; i Medjez I, Site 59, Ain Misteheyia, Damous a el-Ahmar, Bekkaria, Ain Meterchem, Bir Oum Ali, Ain Dokkara, Ani Bahir, El-Mekta, Abri Clariond, Site 51, Oued Medfoun,	ihis study) Gobero, Asselar Hassi-el-Abiod.		Saggai 1, Early Khartoum, Al- Khiday, El-Barga (Mesolithic)	Wadi Halfa		Galana Boi, Lopoy, Lothagam, Gamble's Cave		Shum Laka ^d		
											(Continues)

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Maghreb	Sal	Sahara		Nile Valley		East Africa		West Africa		Southwest Asia	
Present	Absent Pre	Present A	Absent	Present	Absent	Present	Absent	Present	Absent	Present	Absent
Labret wear (source: This study)	iis study)										
				el-Barga (Neolithic), el-Barga (Mesolithic) Al Khiday 1 (16-D-4), Al Khiday 2 (16-D-5)	el-Barga (Mesolithic)						
Middle Holocene (~7–3 kya ^d) Ablation (sources: Stojanowsk	Middle Holocene (~7-3 kya ⁴) Ablation (sources: Stojanowski et al., 2014, 2016; this study)	s study)									
Douar Debagh, Dar- Mugharet el'Ali es-Soltan 16. Sebkha Laas. Sebkha Mah Tintan, Chami, Rio Sebkha Edjai Salado, Grotte des Lemheiris, Al troglodytes, El La Meskiana Cuartel, Champlain, Djebel Fartas, kef el Agab	ya, Izriten, Tailia, ariat, la Sebkha i Bacha, Racha, K	Tessalit-Reg de L Zaki, Kesret- el-Ganl, Amekni 1, Ibalaghen, Kobadi, Gobero, Wadi Howar, Yao	Uan Muhuggiag, Emi Lulu, Adrar Bous, Iwelen, Hassi-el- Abiod, Mentes, Tamaya Mellet, in Tuduf, Chin Tafidet, Afunfun, Areschima, Kourounkorokale	Nabta Playa, Jebel Shaqadud, Jebel Moya, El-Barga (Neolithic)	Wadi Halfa, R12	Njoro River Cave, Willey's Kopje, Naivasha Railway Site, Lukenya Hill (GvJm 202), Ngorongoro Crater	Lowasera, Laikipia, Hyrax Hill, Cole's Burial Site, Makalia Burial Site, Bromhead's Site, Mt. Suswa	Mouhoun	Rop, Laakpa, Shum Laka?e		
Labret wear (source: This study)	is study)										
	E T	Tagnout Chaggeret		Jebel Moya, Al Khiday 2 (16-D-5), UA 53							

a"Present" or "Absent" columns indicates whether there is documented evidence (present) or not (absent) of a given form of dental modification at that site. Presence of labrets is limited to accounts in the literature that explicitly note wear caused by ornaments worn in facial piercings, or at least the mention of an in situ labret, in close association with the jaws, that cannot be confused with ornaments worn in ear piercings (MacDonald, 1999).

^bObservations by one of us (J. C. Willman) suggest that intentional incisor ablation cannot be ruled out for Ohalo II H2.

The labial surface abrasion on the 11's of Wadi Hammeh 26 Homo 4 is suggestive of intentional body modification, but task-related behaviors cannot be ruled out (Bocquentin et al., 2013).

 $^{\rm d}$ West African sites are as young as 2 kya given how few sites are documented in the region (Stojanowski et al., 2016).

elrish (2017) notes "potential" UI1 ablation for Shum Laka.

of ornaments and way(s) in which the ornaments are worn—key information for understanding the temporospatial patterning of labret use and its cultural significance to the wearer(s). In this vein, we posit that it is unlikely that numerous, small labrets—like those from Jebel Moya (see below)—would have produced the broad and uniform wear planes on the OH1 dentition. Instead, we propose that three ornaments were worn in three separate piercings (two buccal and one lower lip or "medial").

The precursor to wearing labrets is the act of facial piercing—an event, or events, that are often associated with initiatory rites and the transformation of one's social identity (Seeger, 1975; Turner, 1980; LaTosky, 2006; Torres-Rouff, 2011; Reddish, 2013). Furthermore, the piercings were likely to have been small at first but stretched over time to incorporate increasingly larger labrets (e.g., Seeger, 1975; Turner, 1980; LaTosky, 2006; Reddish, 2013). The degree of wear

across all three proposed piercing sites indicates that OH1 wore ornaments for long enough to create the substantial wear facets. The labrets worn by OH1 not only mark an outwardly visible marker of social identity but also the embodiment of the process of identity transformation and/or social maturation.

Temporospatial distribution of body modification in African prehistory: Body modification practices that result in observable transfigurement of skeletal and dental tissues have long been of interest to scholars of prehistoric population movements, biological affinity, and cultural practices in Africa (De Groote & Humphrey, 2016; Humphrey & Bocaege, 2008; Irish, 2017; L. S. B. Leakey, 1928; Mollison, 1929; Parsche, 1993; Stojanowski et al., 2014, 2016; van Reenen, 1978, 1986). A particularly prominent practice of body modification in Late Pleistocene and Holocene Africa is ablation, or the culturally motivated practice of anterior tooth (incisor, canine, and sometimes

TABLE 3 Late Pleistocene to mid-Holocene facial piercings documented through dental wear and/or ornaments found in association with burials

Site	Location	Chronology	¹⁴ C years	Evidence of labret use/description from literature	Sources
Olduvai (Oldupai)	Northern Tanzania	Late Pleistocene	n/a	Anterior and buccal faceting suggestive of one medial and two lateral piercings for OH1. No ornaments recovered from burial.	This study
16-D-5 (Al-Khiday 2)	Central Sudan	Early Mesolithic	7,980 ± 40-7,710 ± 40	Stone lip plugs recovered that are typologically different from el-Barga types.	Salvatori & Usai, 2016; Salvatori, Usai, & Zerboni, 2011
16-D-4 (Al-Khiday 1)	Central Sudan	Middle Mesolithic	7,760 ± 90-7,530 ± 100	Lip-plug found in situ with mandible in burial.	Salvatori & Usai, 2009; Salvatori et al., 2011
el-Barga	Northern Sudan	Early Neolithic	7,045 ± 70-6,605 ± 60	Lip plugs in situ near upper and/or lower lips. Most commonly one lip plug, although 2, 4, or 6 were found in some burials. Elongated, thickened at ends, carved from ivory or stone (amazonite).	Honegger, 2004; Honegger & Williams, 2015
16-D-5 (Al-Khiday 2)	Central Sudan	Neolithic	5,470 ± 50	Lip plugs associated with grave 103 typical of Khartoum Neolithic. Very rich grave offerings.	Salvatori & Usai, 2014; Salvatori et al., 2011
Tagnout Chaggeret	Mali	Neolithic	4,520 ± 100	Quartz labret associated with burial.	MacDonald, 1999; Petit-Maire & Riser, 1983
UA 53	Eastern Sudan	Late Butana Group	Fourth to early third millennium BC	9 lip plugs associated with burial.	Manzo, 2017
Jebel Moya	South-Central Sudan	Multi-phase pastoralist cemetery	3,245 ± 755-1,545 ± 535°	1 to 6 polished stone, ceramic, bone, or ivory labrets found in 27% of graves. Labret wear on 47% of females, but 14% of these individuals had no labrets in graves. Labret wear and mandibular incisor ablation co-occur in some individuals.	Addison, 1949; Brass & Schwenniger, 2013; MacDonald, 1999

^aOptically stimulated luminescence (OSL) dates obtained from ceramics calibrated to years before 2012 (Brass & Schwenniger, 2013).

premolar) removal during an individual's lifetime. Ablation is well-documented in the Late Pleistocene Old World (Willman, Shackelford, & Demeter, 2016), and most thoroughly documented in Africa (De Groote & Humphrey, 2016; Humphrey & Bocaege, 2008; Stojanowski et al., 2014, 2016) and Natufian contexts in Southwest Asia (Bocquentin, 2011). Another prominent pattern of body modification involves the chipping and filing of the anterior dentition, which is frequently associated with the "Bantu Expansion" (Irish, 2017; L. S. B. Leakey, 1928; van Reenen, 1978, 1986). Despite extensive discussion of ablation, chipping, and filing of teeth, very little discussion of facial piercing is found in the literature. What follows is a brief review of prehistoric labret-use in Africa and an integration of its temporospatial distribution into the discussion of body modification in African prehistory.

The temporal and spatial trends for ablation strongly support a Terminal Pleistocene (~18–12 kya) origin for the practice in the Maghreb, subsequent diffusion into the Sahara and Nile Valley during the Early Holocene (~10–7 kya), and a widespread distribution throughout Africa during the Middle Holocene (~7–3 kya) (Stojanowski et al., 2014, 2016) (Table 2). In contrast, there is complete absence of incisor and canine chipping and filing in Africa until the Middle Holocene when examples are first documented in the Sahara and West Africa (Finucane et al., 2008; Irish, 2017; Maes, Irish, Holl, Walker, & Armelagos, 2004) (Table 2). Following the "Bantu Expansion," chipping and filing become widespread despite being largely absent in sub-Saharan Africa prior to the Bantu expansion (Irish, 2017).

The spatial distribution of prehistoric labret-use is limited to several sites in the Nile Valley, Tagnout Chaggeret in the Sahara, and Olduvai Gorge in East Africa (Tables 2 and 3). The probable Late Pleistocene affiliation of OH1 makes it either the earliest case or penecontemporaneous with Early and Middle Mesolithic examples from Al-Khiday (Salvatori & Usai, 2009, 2016). Labrets from Neolithic contexts differ in style from those of early periods in the Nile Valley (Salvatori & Usai, 2016), and both labrets and dental wear associated with labrets are found in great quantities among individuals interred in the later pastoralist cemeteries at Jebel Moya (Addison, 1949; Brass & Schwenniger, 2013; MacDonald, 1999) (Tables 2 and 3). Interestingly, some degree of replacement between the Mesolithic and Early Neolithic populations is probable at el-Barga on the basis of skeletal and dental morphology between the Mesolithic and Early Neolithic individuals (Benoiston et al., 2018; Crevecoeur, Desideri, Chaix, & Honegger, 2012), which corresponds well with distinct differences in labret styles recorded between Sudanese Mesolithic and Neolithic sites summarized here (Table 3). Labrets, defined on stylistic grounds, rather than association with burials or dental wear, are frequently documented in archaeological contexts within the Nile Valley (e.g., Arkell, 1949; Bobrowski, Jórdeczka, Sobkowiak-Tabaka, & Binder, 2016; Chłodnicki & Kabaciński, 2015; Dachy et al., 2018; Fernández, Jimeno, & Menéndez, 2003; Geus & Lecointe, 2003; McDonald, 2016), and elsewhere in Africa (Gaussen & Gaussen, 1962; MacDonald, 1999), and largely reinforce the temporospatial distribution presented here on the basis of labret-induced wear and labrets associated with burials.

OH1 is one of the earliest examples of labret-use in Africa and marks the southern-most extent of the currently known distribution for the practice during the Late Pleistocene and early Holocene. Furthermore, OH1 exhibits a unique labret configuration of buccal and lower lip piercings—a markedly different pattern than that documented at sites from the Mesolithic and Neolithic Nile Valley (Table 3). Thus, the OH1 body modification practices are temporally, geographically, and stylistically idiosyncratic when compared to penecontemporaneous body modification practices in Africa.

5 | CONCLUSION

Little had been known about the paleobiology of OH1 prior to recent analyses indicating that the young adult male (~20–35 years old at death) was deliberately buried (Matu et al., 2017), and shares aspects of cranial and postcranial morphology with other Late Pleistocene fossils from Africa (Crevecoeur et al., 2016; Tryon et al., 2015). The osteobiography of OH1 now provides evidence for the use of multiple ornaments worn through facial piercings that would have outwardly expressed, and embodied, aspects of individual and/or group-level social identity.

Extensive morphological variation has been documented within the sparse human fossil record from Late Pleistocene and Early Holocene Africa, which suggests that we are only beginning to understand how much variation existed prior to the biological homogenization that occurred during the late Holocene and historic periods. Likewise, the evidence for labret-use presented here adds to the diversity of body modification practices already documented elsewhere in Africa during the Late Pleistocene (e.g., dental ablation) and Early to Middle Holocene (e.g., dental ablation, chipping, filing, and labret use). We have provided a detailed analysis of labret wear, and a review of similar cases, to stimulate further documentation of this cultural practice that together with inferences from biological variation and archeological investigations, can provide additional means of understanding inter- and intraregional population dynamics and interactions among prehistoric peoples across Late Pleistocene and early Holocene Africa.

ACKNOWLEDGMENTS

George McGlynn and Mike Schweissing (Staatssammlung für Anthropologie und Paläoanatomie) provided access to and assistance with the OH1 skeletal material. Donatella Usai generously provided information on the Al Khiday material, and G. Richard Scott provided helpful suggestions and encouragement during the early stages of research. The reassessment of the morphometric data of OH1 was funded by the project "Big Dry: Ruptures et continuité dans le peuplement de l'Afrique à la fin du Pléistocène: paléoanthropologie, paléoenvironnement et archéologies comparées du Rift et du Nil dans leur cadre continental" of the Agence Nationale de la Recherche (ANR-14-CE31). JCW is supported by funding from the Marie Skłodowska-Curie Actions (H2020-MSCA-IF-2016 No. 749188), AGAUR (Ref. 2017SGR1040) and URV (Ref. 2017PFR-URV-B2-91) Projects, and MICINN/FEDER (Ref. PGC2018-093925-B-C32). RH is

supported by a Martí i Franquès doctoral research fellowship (2019PMF-PIPF-59). An associate editor and two anonymous reviewers provided critical insights that greatly improved this article. To all we are grateful.

DATA AVAILABILITY STATEMENT

All data related to the description and measurement of Olduvai Hominid 1 are published in this manuscript. The comparative fossil human dataset is not publicly available but may be made available to researchers on a case-by-case basis by contacting Isabelle Crevecoeur.

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How to cite this article: Willman JC, Hernando R, Matu M, Crevecoeur I. Biocultural diversity in Late Pleistocene/Early Holocene Africa: Olduvai Hominid 1 (Tanzania) biological affinity and intentional body modification. *Am J Phys Anthropol.* 2020;1–18. https://doi.org/10.1002/ajpa.24007