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# Non-masticatory striations on human teeth from the British Upper Palaeolithic to the Neolithic

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Non-masticatory labial striations on human anterior teeth are a form of cultural dental wear well recorded throughout the Pleistocene, which has been interpreted as resulting from the use of the mouth as a ‘third hand’ when processing different materials during daily activities, such as cutting meat or working hides with stone tools. Non-masticatory scratches have also been reported on the buccal surface of molars and premolars, although at a far lower frequency compared to the anterior dentition. Previous studies observed an apparent decrease through time in the occurrence of non-masticatory scratches on human teeth, with labial striations appearing to be rare for the Neolithic compared to earlier periods. This study further tests this previously observed pattern through the analysis of over 900 human teeth from 20 sites across England and Wales dating from the Upper Palaeolithic, Mesolithic, and Neolithic, to discuss the distribution and aetiology of non-masticatory striations in the British archaeological record. To record and assess the micro-morphometric characteristics of these dental alterations, macroscopic and microscopic analytical techniques were used. Results show that non-masticatory labial striations are still found on Neolithic teeth, although at a decreased frequency when compared to hunter-gatherer (Upper Palaeolithic and Mesolithic) samples. This may be partly due to changes in diets and food processing methods, as well as types of processed materials and changes in manual handling arising from the inception of the Neolithic in Britain. The sample also includes Upper Palaeolithic, Mesolithic and Neolithic teeth with non-masticatory striations likely associated with funerary practices or cannibalistic treatment of cadavers. Analyses of these marks suggest that striations inflicted during the post-mortem cutting of cadavers from cannibalism or funerary practices differ in their location and micro-morphology, compared with non-masticatory striations produced during the life of an individual using the mouth as a ‘third hand’.

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## Introduction

Marks and alterations on archaeological human dentitions can be caused by various factors, such as dental wear during the life of the individual, anthropogenic ante-mortem and post-mortem modifications, or taphonomical processes damaging the remains after their deposition (Hillson, 1990). Although it is essential to identify surface damage due to natural processes such as weathering or trampling which might polish or abrade dental surfaces (King et al., 1999; Micó et al., 2023), what is of particular interest is the identification of dental alterations due to human activities. The latter can be summarized into four main alteration types related to particular behaviours: (1) dietary dental wear, caused by food consumption (Grine et al., 2006; Mahoney, 2006; Scott, 2005; Ungar et al., 2006; Walker et al., 1978); (2) culturally driven dental alteration, such as dental modification and evulsion (e.g., Burnett and Irish, 2017; Humphrey and Bocaage, 2008); (3) post-mortem dental alterations, caused by the cutting of a body after death during funerary rituals or cannibalism; and (4) non-masticatory dental alterations produced by daily activities such as tooth picking or the use of the mouth as a ‘third hand’. This paper focuses on the two latter types of dental alteration, and most particularly on the scratches produced when using the mouth as a ‘third hand’.

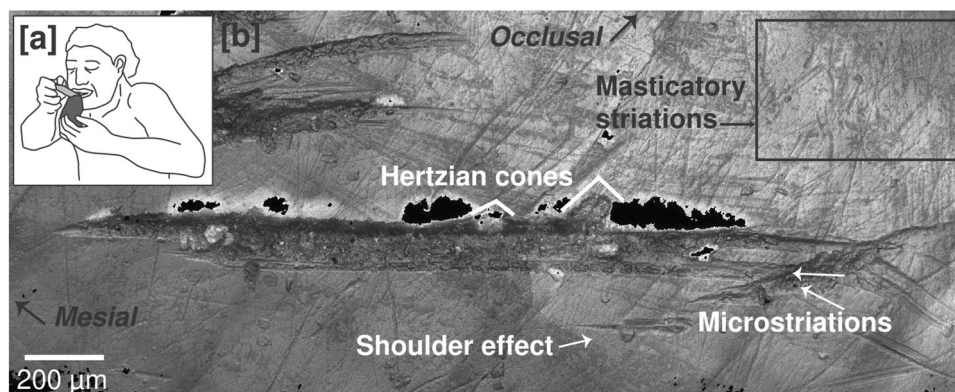
Non-masticatory dental alterations associated with the use of the mouth as a ‘third hand’ are usually observed as striations on the labial surface of anterior teeth (i.e., incisors and canines). These labial striations have been interpreted as accidental damage of the dentition inflicted during daily activities involving the teeth, such as the ‘stuff and cut’ technique where the mouth is used to grip a material at one end, usually meat, and held by the non-dominant hand at the other end to stretch it. The free, dominant hand is then used to wield a sharp object to slice the material close to the mouth and cut it into smaller sections for further processing or consumption (Estalrich and Marín-Arroyo, 2021; Lalueza Fox and Pérez-Pérez, 1994; Lozano et al., 2017b; Willman, 2016), (Fig. 1a). On occasion, the cutting edge of the tool might come into contact with the anterior teeth before cutting the material or when piercing through it, leaving a scratch on the dental surface, known as a non-masticatory (NM) labial striation (Hillson et al., 2010; Lozano et al., 2008). Such non-masticatory use of the teeth leaves specific damage on the dentitions which can be identified through microscopic and 3D analyses (Bello, 2011; Bello et al., 2011b; Lalueza Fox and Frayer, 1997; Lozano et al., 2008). Non-masticatory striations can be differentiated from taphonomic damage and dietary alterations by their larger size (width, length), their orientation, their

location, and their regularity (Lalueza Fox, 1992; Lozano et al., 2008; Lozano-Ruiz et al., 2004).

NM striations tend to be localized on the crown of anterior teeth, and are rare on the premolars and molars, which are better protected by soft tissue during the lifetime of the individual (Lozano et al., 2008; Lozano et al., 2017a). When present, they tend to be horizontal or vertical to the occlusal plane and are sometimes associated with micro-chipping of the enamel (Lalueza Fox and Frayer, 1997). Some NM striations have been interpreted as a result from the use of toothpicks; these marks have distinctive morphology, and they are typically located as interproximal grooves (Estalrich et al., 2017; Frayer, 1991; Formicola, 1988; Lalueza Fox and Frayer, 1997; Ungar et al., 2001). Likewise, NM scratches are rare on dental roots, which are usually covered by the gums. Nevertheless, incisions were observed on the roots of two middle Pleistocene incisors from Boxgrove (UK; Hillson et al., 2010). Two possible explanations have been given to interpret these multiple overlapping labial striations on the Boxgrove incisors: (1) the roots were exposed due to the recession of the gums associated with an infection; (2) the striations on the roots were produced after the death of the individual and could potentially be associated with the butchery of the cadaver.

Labial scratches, vestibular-lingual striations, enamel chipping, and pits and polished enamel on occlusal surfaces are the most commonly observed dental features resulting from non-masticatory processes (Constantino et al., 2010; Lozano et al., 2008; Lozano-Ruiz et al., 2004; Puech, 1982; Scott and Winn, 2011). It has been suggested that dental alterations such as vestibular-lingual striations and, in some cases, enamel chipping might result from the working of plant fibres, where fibres are repetitively moved back and forth in the mouth (Lozano et al., 2008). Similarly, the working of leather and skins, while using the mouth to hold the material clenched between the teeth, has been suggested to produce areas of polished enamel and bevelling of the occlusal surface of the teeth from the friction between the teeth and the material being worked (Lozano et al., 2008; Puech, 1982). This polishing process can also attenuate and smooth over any pre-existing modification present on the teeth.

NM labial striations on human teeth attributed to the ‘stuff and cut’ technique are reported among contemporary hunter-gatherers (Bax and Ungar, 1999; Clement, 2008; Lalueza Fox, 1992; Merbs, 1968; Molnar, 1972), as well as in the palaeoanthropological record. The earliest example of this behaviour is recorded on anterior teeth of the ~1.8 Ma *Homo habilis* (OH-65 maxilla) from Olduvai Gorge (Clarke, 2012). A detailed study of



**Fig. 1** The ‘stuff and cut’ technique and non-masticatory striations. **a** Illustration of the ‘stuff and cut’ technique, in which an object is held at one end by the anterior teeth, stretched taut using the non-dominant hand and cut with a tool held in the other hand. **b** Example of a non-masticatory striation on the lingual surface of a left maxillary first incisor from Gough’s Cave (NHMUK PV M 54131), illustrating key microscopic features (Alicona Infinite Focus image; lens: 50x).

the >550 mostly oblique NM striations on these teeth suggests that the individual was right-handed (Frayer et al., 2016). Labial striations are one of the most common cultural dental features in the large hominin collection of Sima de los Huesos (SH; Sierra de Atapuerca, Spain; ~430,000 BP), where they are recorded on 94.5% of the anterior teeth of 20 Neanderthals (Lozano et al., 2008; Lozano et al., 2017a). These striations are interpreted as marks resulting from the processing of meat and plant foods, as the associated archaeological record provides primarily evidence for activities centred around food acquisition and processing (Carbonell et al., 1999; Saladié et al., 2011). A survey of the literature identifies this behaviour as a feature of other European Middle Pleistocene populations (Bello, 2011; Hillson et al., 2010) in association with lithic technologies allowing to work different materials such as wood, plant fibres and leather (Haidle, 2010; Moncel et al., 2012; Rodríguez, 2004). NM scratches have been commonly observed on Neanderthal teeth, for example on specimens from Le Regourdou, La Quina, Hortus, Krapina, Vindija, Shanidar, Cova Negra, El Sidrón and Valdegoba (Estalrich and Rosas, 2013; De Lumley-Woodyear, 1973; Frayer et al., 2010; Frayer et al., 2012; Lalueza Fox and Frayer, 1997; Lalueza Fox and Pérez-Pérez, 1994; Lozano et al., 2008; Puech, 1979; Trinkaus, 1983; Volpato et al., 2012). The orientation of these dental striations has been suggested to relate to lateralized activities among Neanderthals, with observed patterns of lateralized use-wear on stone and bone tools, and tooth striations dominated by oblique striations oriented downward to the right (i.e., from the upper left part of the dental surface to the lower right part of the tooth) consistent with right-handedness (Bermúdez de Castro et al., 1988; Fernández-Jalvo and Bermúdez de Castro, 1988; Uomini, 2011). At Sierra de Atapuerca, labial striations have been observed on human teeth dating from the Lower Palaeolithic to the Bronze Age, suggesting the common occurrence of this behaviour across several hominin species (i.e., *Homo* sp., *H. antecessor*, *H. neanderthalensis*, and *H. sapiens*), (Lozano et al., 2008; Lozano et al., 2017a).

NM labial striations are rarely reported from the Neolithic and later archaeological contexts, although some forms of cultural dental wear such as polishing, chipping and vestibular-lingual striations persist (Lozano et al., 2017a; Lozano et al., 2017b). For instance, polishing and vestibular-lingual striations on human dentitions from the Spanish Chalcolithic site of El Mirador Cave have been attributed to the manipulation of sinew and wool while using the mouth as a 'third hand' (Vergès et al., 2016). Overall, few examples of NM labial striations have been documented for the Neolithic and Chalcolithic, with the exception of Neolithic individuals from Ash Tree Shelter (UK) and Sant Pau (Spain), and Chalcolithic remains from Mehgarh (Pakistan) (Dinnis et al., 2014; Lalueza Fox, 1992; Lalueza Fox and Pérez-Pérez, 1994; Lukacs and Pastor, 1988). This apparent decrease in the occurrence of NM labial striations from the Upper Palaeolithic to the Mesolithic and Neolithic could relate to changes in diet (e.g., Bickle, 2018; Molleson et al., 1993; Richards et al., 2003), food processing methods and cultural behaviours, with a modification of the daily tasks performed and of the toolkit used for these purposes. Alternatively, it could also be due to a lack of identification of these marks on more recent, larger collections, which can seldom be scrutinized for microscopic details compared to older human remain collections, often rarer and smaller, which tend to benefit from more systematic microscopic studies.

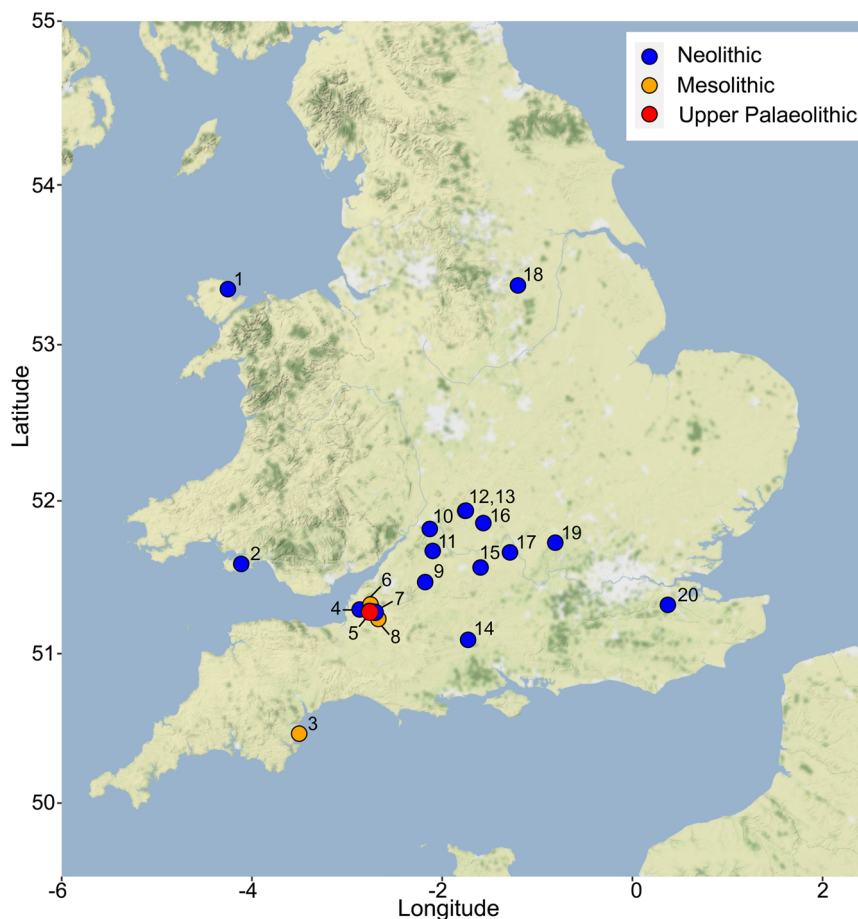
This paper records the occurrence of NM striations on human teeth from the Upper Palaeolithic to the Neolithic in Britain, and assesses their prevalence through time in a context of changing lifestyles with the rise of sedentism and farming practices. Near 1,000 anterior and posterior teeth from 20 sites were examined to evaluate the occurrence of both labial and buccal NM striations

within the assemblage and discuss their distribution and possible aetiology. Focus-variation microscopy was used on selected specimens to conduct exploratory measurements and assess the micro-morphometric characteristics of these dental alterations in 3-dimensions.

## Material and methods

A total of 974 teeth from 20 archaeological sites from England and Wales were examined: one site dates to the Upper Palaeolithic, three to the Mesolithic, and 16 to the Neolithic (Fig. 2, Table 1). Two of the Mesolithic assemblages (Aveline's Hole, Somerset, and Kent's Cavern, Devon) may include some Neolithic human remains. A full description of the sites is presented in the Supplementary Note. The majority of the dental remains examined are housed at the Natural History Museum, London (UK). All but three of the Aveline's Hole specimens (i.e., NHMUK PA EM 504, 505 and 506) are stored at the University of Bristol Speleological Society Museum. The Badger Hole and Totty Pot human collections are curated at the Wells and Mendip Museum. Both anterior (i.e., incisors and canines) and posterior (i.e., premolars and molars) dentitions were assessed. Tooth types are described using the following nomenclature: I1 for central incisors, I2 for lateral incisors, C for canines, Pm3 and Pm4 for third and fourth premolars, and M1, M2, and M3 for first, second and third molars. To distinguish upper from lower dentition where relevant, the tooth number is indicated in subscript for lower teeth (i.e., I<sub>1</sub>, I<sub>2</sub>, C<sub>1</sub>, Pm<sub>3</sub>, Pm<sub>4</sub>, M<sub>1</sub>, M<sub>2</sub>, and M<sub>3</sub>) and in superscript for upper teeth (i.e., I<sup>1</sup>, I<sup>2</sup>, C<sup>1</sup>, Pm<sup>3</sup>, Pm<sup>4</sup>, M<sup>1</sup>, M<sup>2</sup>, and M<sup>3</sup>). The assemblage contains isolated teeth as well as specimens with several teeth or the entire dentition preserved. For specimens with multiple teeth, each tooth was assessed individually to evaluate the prevalence of striations for each tooth category. Our analysis did not attempt to determine the age, sex or minimum number of individuals based on the dental remains due to the representation/preservation heterogeneity of the samples; however, details of MNI and palaeodemographic structure of the sites can be found in the relevant literature cited for each site when available (see references in Table 1 and Supplementary Note).

To identify NM striations, we followed the methodology proposed by Lozano et al. (2008). NM striations are scratches which generally range between 20–100 µm in width, contrary to scratches produced by phytoliths, dust or grit (<5–20 µm in width), which are more typical of the damage incurred from mastication (e.g., consumption of fruits or grasses rich in silica/phytoliths) or from taphonomical processes such as sediment abrasion during burial, trampling and weathering (Bermúdez de Castro et al., 1988; Hillson et al., 2010; Lalueza Fox and Frayer, 1997; Lalueza Fox and Pérez-Pérez, 1994; Maas, 1991; Martínez and Pérez-Pérez, 2004; Puech, 1982). Because of their larger dimensions compared to dietary microwear, NM striations can usually be identified through simple visual inspection using a hand lens or microscope with illumination from a fibre optic light. Microscopically, NM striations are comparable to cutmarks found on bone, with a √ or V-shaped profile (which depends on the inclination of the tool making the cut), often accompanied by lateral or internal microstriations (resulting from irregularities along the edge of the cutting tool), and the presence of Hertzian cones (Bello and Soligo, 2008; Lalueza Fox and Pérez-Pérez, 1994; Lozano-Ruiz et al., 2004; Shipman and Rose, 1984), (Fig. 1b). NM striations which occurred during life tend to appear worn and smoothed over due to masticatory actions (i.e., chewing, tongue action, or saliva), in contrast to post-mortem cutmarks which tend to have sharper, clearer edges (Lalueza Fox and Frayer, 1997; Lozano et al., 2008).



**Fig. 2 Map of the sites examined across Britain.** 1: Lligwy Cromlech; 2: Cathole Cave; 3: Kent's Cavern; 4: Picken's Hole; 5: Gough's Cave; 6: Aveline's Hole; 7: Totty Pot; 8: Badger Hole; 9: Lanhill; 10: West Tump; 11: Windmill Tump; 12: Swell IV; 13: Swell V; 14: Fussell's Lodge; 15: Wayland's Smithy; 16: Ascott-under-Wychwood; 17: Abingdon; 18: Dinnington; 19: Whiteleaf; 20: Coldrum. See Table 1 and Supplementary Note for more detail on these sites. Map made in R Studio (v 2022.12.0) using the ggmap package (v3.0.2; Kahle and Wickham, 2013) and map tiles by Stamen Design (data by OpenStreetMap, <https://www.openstreetmap.org/>).

Each tooth was first examined macroscopically (by CD, SAP, and SAB), using a Digiflex Jewellers Loupe (Glass lens; Lens diameter: 21 mm; magnification: 30x). Any tooth that had preserved enamel, however damaged, was assessed, but the teeth with extensively damaged enamel were excluded from the calculations of striation prevalence. We selected 10 specimens for exploratory microscopic analysis (5 for the Upper Palaeolithic, 1 for the Mesolithic, and 4 for the Neolithic), based on material availability, tooth type representation (i.e., prioritizing specimens with multiple teeth preserved on a tooth row), and preservation of the enamel surface. The selected specimens were analysed using a Focus Variation microscope, the Alicona InfiniteFocus G5+ (AIF) optical surface measurement system (Optimax Ltd, Market Harborough, UK), housed at the Imaging and Analysis Centre, Science Innovation Platforms, at the Natural History Museum (London, UK). This optical microscope allows for the three-dimensional (3D), non-invasive and non-destructive analysis of microscopic surface features by creating a series of individual image planes and overlapping focus levels to construct a 3D 'true colour' virtual reproduction of the object. The x, y and z coordinates of each reproduced pixel can be subsequently used to conduct linear and volumetric measurements of the surface features using the AIF software IF-MeasureSuite (Bello and Galway-Witham, 2019; Bello and Soligo, 2008). To obtain different degree of magnification and capture finer details, three lenses were used: 20x (working distance: 19 nm; lateral resolution: 0.82  $\mu\text{m}$ ; vertical

resolution: 50 nm), 50x (working distance: 11 nm; lateral resolution: 0.54  $\mu\text{m}$ ; vertical resolution: 20 nm), and 100x (working distance: 4.5 nm; lateral resolution: 0.41  $\mu\text{m}$ ; vertical resolution: 10 nm). Where the quality of the produced 3D images allowed it, the overall length and profile parameters (width of the incision at the surface, WIS; opening angle, OA; and depth of the incision, D) were measured following the method proposed by Bello and colleagues (2013), (Fig. 3). Some areas of the enamel were too translucent or highly reflective to be captured by the AIF and appeared as 'black areas' in the 3D reconstructions, indicating the absence of recorded data points on these parts of the dental surface (e.g., Fig. 1b). As these areas could not be measured, they were not considered for profile measurements. Descriptive statistics and plots were computed using R Studio (version 2022.12.0 + 253; R Core Team, 2022) using the dplyr and ggplot2 packages (Wickham et al., 2016; Wickham et al., 2019).

The orientation of the striations was recorded using the method proposed by Pérez-Pérez and colleagues (1994) who recognized four categories of orientation based on the measurement of the angle of a striation relative to the occlusal (mesio-distal) plane: left/oblique (a) (22.5°–67.5°), vertical (b) (67.5°–112.5°), right/oblique (c) (112.5°–157.5°) and horizontal (d) (0°–22.5° and 157.5°–180°) (Supplementary Information Fig. S1). These measurements were obtained from drawings locating the NM striations on each tooth. The total number of striations was not counted on each tooth, regardless of their orientation, to

**Table 1 Sites, number of teeth examined, and key references.**

Map N°	Site	Site type	Number of teeth [Total (anterior/ posterior)]	Collection	Key references
Upper Palaeolithic					
5	Gough's Cave, Somerset	Cave	40 (15/25)	NHM	Stringer, 2000; Humphrey and Stringer, 2002
Mesolithic					
6	Aveline's Hole <sup>a</sup> , Somerset	Cave	86 (22/64)	UBSSM/NHM	Schulting et al., 2019
8	Badger Hole, Somerset	Cave	6 (1/5)	WMM	Hedges et al., 1989
3	Kent's Cavern <sup>a</sup> , Devon	Cave	7 (0/7)	NHM	Meiklejohn et al., 2011
Neolithic					
17	Abingdon, Oxfordshire	Burial	8 (3/5)	NHM	Leeds, 1928
16	Ascott-under-Wychwood, Oxfordshire	Long barrow	159 (66/93)	NHM	Bayliss et al., 2007
2	Cathole Cave, Gower	Cave	8 (1/7)	NHM	Walker et al., 2014
20	Coldrum, Kent	Long barrow	39 (13/26)	NHM	Wysocki et al., 2013
18	Dinnington, Yorkshire	Long barrow	75 (8/67)	NHM	Thurnam, 1869; Schulting and Wysocki 2005
14	Fussell's Lodge, Wiltshire	Long barrow	196 (35/161)	NHM	Wysocki et al., 2007
9	Lanhill, Wiltshire	Long barrow	10 (3/7)	NHM	Keiller et al., 1938
1	Lligwy Cromlech, Anglesey	Megalithic tomb	61 (21/40)	NHM	Baynes, 1909
4	Picken's Hole, Somerset	Cave	2 (1/1)	UBSSM	ApSimon and Mullan, 2018
12	Swell IV, Gloucestershire	Long barrow	71 (9/62)	NHM	O'Neil and Grinsell, 1960
13	Swell V, Gloucestershire	Long barrow	113 (26/87)	NHM	Grinsell and O'Neil, 1961
7	Totty Pot, Somerset	Cave	2 (2/0)	WMM	Schulting et al., 2010
15	Wayland's Smithy, Oxfordshire	Long barrow	10 (2/8)	NHM	Whittle et al., 2007
10	West Tump, Gloucestershire	Long barrow	58 (13/45)	NHM	Smith and Brickley, 2004
19	Whiteleaf, Buckinghamshire	Oval barrow	2 (0/2)	NHM	Childe and Smith, 1955; Hey et al., 2007
11	Windmill Tump, Gloucestershire	Long barrow	21 (2/19)	NHM	Clifford and Daniel, 1940

<sup>a</sup>Map N° indicates the site number plotted in Fig. 2. For site details and additional references see Supplementary Note.  
 NHM Natural History Museum, London, UK, UBSSM University of Bristol Speleological Society Museum, WMM Wells and Mendip Museum  
<sup>a</sup>These collections include Neolithic human remains.

avoid potential taphonomic bias due to enamel preservation heterogeneity across the assemblage. However, when striations of different orientations were present on the same tooth, we recorded the presence of these different orientations, to account for instances where two or more striation orientations can be present on an individual tooth.

**Results**

Of the 974 teeth studied from the 20 sites, 82 (8.42%) bear clear incisions on the enamel. Fifty-six teeth show NM labial striations on the incisors and canines, and 26 show NM buccal striations on the premolars and molars (Fig. 4; Supplementary Table S1). NM striations were also observed on the lingual surface of one tooth (i.e., Gough's Cave, NHMUK PV M 54131). NM striations were not observed on any of the teeth in the Badger Hole Mesolithic sample. Similarly, NM striations were absent on teeth from six Neolithic sites (Picken's Hole, Swell IV, Totty Pot, Wayland's Smithy, Whiteleaf, and Windmill Tump). The Mesolithic sample from Kent's Cavern only shows buccal striations on the posterior dentition, while the majority of the Neolithic assemblage (12 sites) shows no evidence of buccal striations.

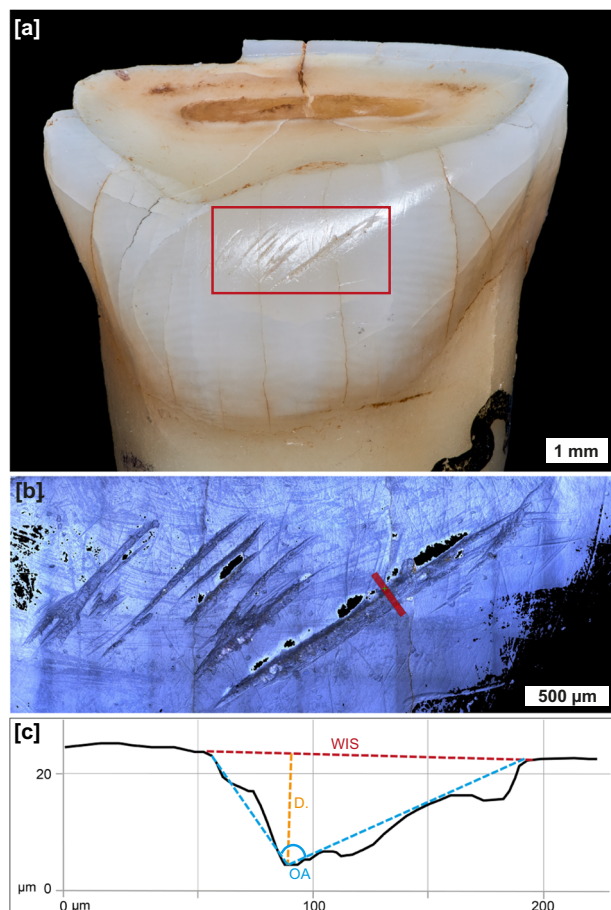
**Frequency and orientation of non-masticatory striations by tooth types.** The most commonly marked teeth are the I<sup>1</sup> (52.38% of the 21 I<sup>1</sup> assessed) and the C' (27.78% of the 36 C' assessed), (Table 2; Supplementary Fig. S2). Across all assemblages, NM striations are slightly more frequent on upper teeth (10.55%, n = 379) than lower teeth (7.06%, n = 595) (Supplementary Table S2). When only the anterior dentition is considered, 33.75% of the upper teeth show labial striations, against 17.79% of the lower

anterior teeth. Posterior teeth also display buccal striations more frequently on the upper dentition (4.35%) compared to the lower dentition (3.01%).

Fifty-six anterior teeth bear labial striations (23.05% of all anterior teeth assessed), which are dominated by vertical and right/oblique striations (66.07% and 46.43% of the labial striations observed, respectively), (Fig. 4, Table 3, and Supplementary Table S1). Only 3.56% of the posterior teeth assessed show buccal striations, clearly dominated by vertical (69.23%) and right/oblique striations (30.77%). Horizontal striations were not found in the samples we examined.

**Frequency of non-masticatory striations by time period**

*Upper Palaeolithic.* NM labial striations are present on 80% of the Gough's Cave anterior teeth studied, with a predominance of right/oblique scratches (91.67%), (Table 3). For the posterior dentition, 32% of the assessed teeth show buccal striations, dominated by vertical striations (50%). Within this assemblage, NM striations were observed on all assessed upper and lower I1 (n = 8), (Table 2). A high incidence of NM striations was also observed on C' (50%, n = 4), P<sup>4</sup> (66.67%, n = 3), P<sub>4</sub> (66.67%, n = 3), and M<sub>1</sub> (50%, n = 4). Across the entire Gough's Cave dental assemblage (n = 40), NM striations are more frequent on the lower dentition (62.5%, n = 16) compared to the upper dentition (41.67%, n = 24), (Supplementary Table S2). When considering the upper dentition only, labial striations are noted more frequently on anterior teeth (80%, n = 10) than buccal striations on posterior teeth (14.29%, n = 14). On the lower dentition, similarly, NM striations are more frequent on anterior teeth (80%, n = 5) than on posterior teeth (54.55%,



**Fig. 3** Example of non-masticatory lingual striations on an Upper Palaeolithic maxillary first incisor (Gough's Cave; NHMUK PV M 54131).

**a** location of the surface area scanned using the Alicona Infinite Focus G5+; **b** 3D reconstruction of the surface with a red line showing where profile measurements were taken using the AIF MeasureSuite; **c** profile diagram with the measurements taken for the width of the incision on the surface (WIS), the depth of the incision (D), and the opening angle of the incision (OA). Photo © Longleat Estate and Trustees of the Natural History Museum.

$n = 11$ ). Buccal striations are more common on the lower dentition (54.55%,  $n = 11$ ) than on the upper dentition (14.29%,  $n = 14$ ).

**Mesolithic.** NM labial striations were observed on 43.48% of the Mesolithic anterior teeth sample, with a predominance of vertical striations (70%), (Table 3). Buccal NM striations were found on 9% of the posterior teeth, dominated by vertical striations (71.43%). Within the Aveline's Hole sample, NM striations were observed more frequently on upper and lower I1 (100%,  $n = 2$ , and 60%,  $n = 5$ , respectively), (Table 2). NM striations were also identified on Mesolithic posterior dentition, most particularly on M<sup>1</sup> (16.67%,  $n = 6$ ) and P<sub>4</sub> (16.67%,  $n = 6$ ). Across the whole Mesolithic assemblage, NM striations are slightly more frequent on the lower dentition (18.46%,  $n = 65$ ) compared to the upper dentition (14.71%,  $n = 34$ ), (Supplementary Table S2). Similarly to the Upper Palaeolithic sample, labial NM striations on anterior teeth appear to be more frequent than buccal striations on posterior teeth when assessing the upper dentition only (75%,  $n = 40$  and 6.67%,  $n = 30$ , respectively). On the lower dentition, NM striations show higher frequencies on anterior teeth (36.84%,  $n = 19$ ) than on posterior dentition (10.87%,  $n = 46$ ). Buccal

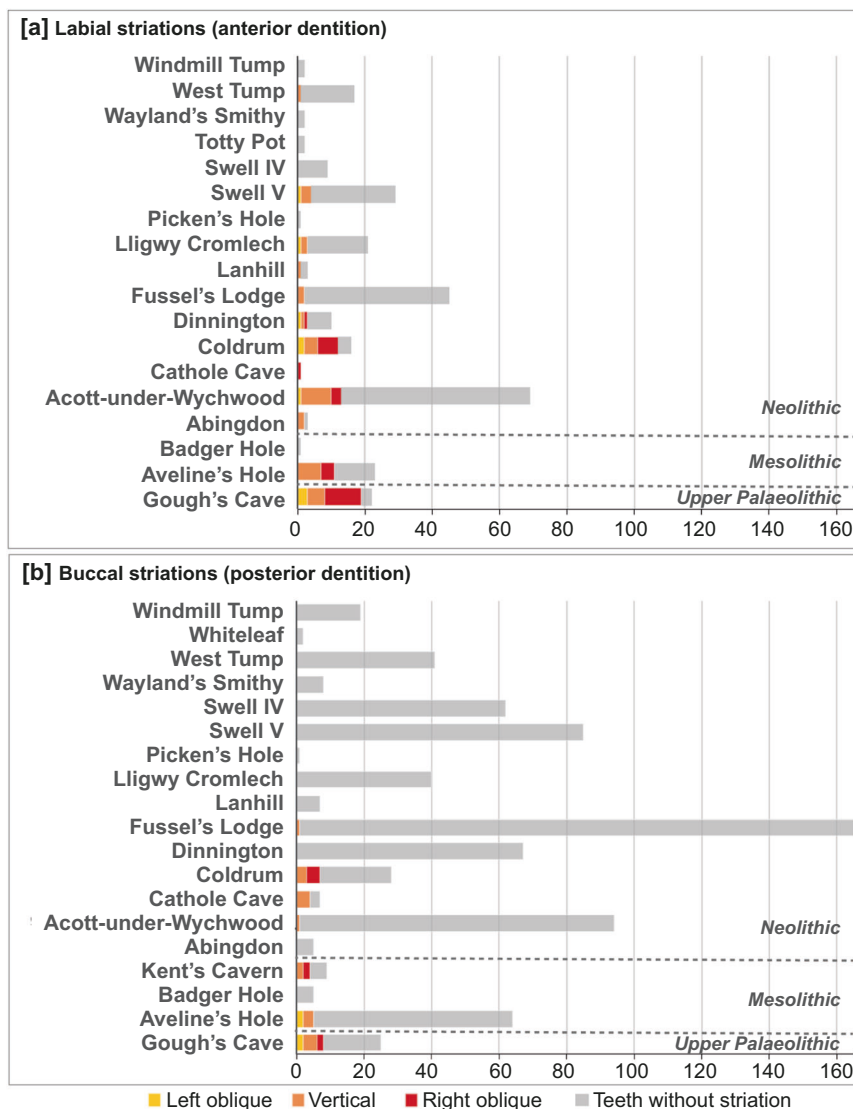
striations are more common on the lower dentition (10.87%,  $n = 46$ ) than on the upper dentition (6.67%,  $n = 30$ ).

**Neolithic.** Within the Neolithic assemblage, NM labial striations were observed on 15.70% of the anterior teeth, 71.43% of which are oriented vertically (Table 3). Only 1.75% of the posterior teeth display buccal striations, with a prevalence of vertical striations (81.82%). The highest proportions of NM striations observed within the Neolithic assemblage are located on I<sup>1</sup> (33.33%,  $n = 15$ ) and C' (23.33%,  $n = 30$ ), (Table 2). Few occurrences of NM striations were identified on the posterior dentition, predominantly on M<sup>1</sup> (7.25%,  $n = 69$ ) from the sites of Coldrum and Cathole Cave (Table 2). Across the entire Neolithic assemblage, NM striations are more frequently present on the upper dentition (7.79%,  $n = 231$ ) than on the lower dentition (3.89%,  $n = 514$ ), (Supplementary Table S2). When considering the upper dentition only, labial striations are observed more frequently on anterior teeth (24.24%,  $n = 66$ ) than buccal striations on posterior teeth (3.53%,  $n = 255$ ). On the lower dentition, similarly, NM striations are more frequent on anterior teeth (12.95%,  $n = 139$ ) than on posterior teeth (0.53%,  $n = 375$ ).

**Micro-morphometrics of non-masticatory striations.** A total of 55 NM striations were measured with the AIF software across the 10 specimens scanned using the AIF Focus Variation microscope (Supplementary Table S3). The length of the striations ranges between 0.23 and 3.5 mm, with a mean value of 1.10 mm for the scratches found on Upper Palaeolithic teeth (s.d. = 0.93), 1.40 mm for Mesolithic teeth (s.d. = 0.98), and 0.86 mm for Neolithic teeth (s.d. = 0.46), (Table 4). The shortest mean lengths are observed on molars (means < 0.9 mm), with the exception of the striations measured on the M<sub>1</sub> from Gough's Cave (mean = 1.87 mm), which yields the highest values and largest standard deviation (s.d. = 2.26) compared to the rest of the assemblage (Supplementary Fig. S3). Most incisors and canines tend to exhibit relatively high mean length values (means > 0.85 mm) compared to most of the posterior dentition (Supplementary Fig. S3). When comparing lengths between sites, a similar range of high values are observed for buccal and lingual surfaces on teeth from Gough's Cave (Upper Palaeolithic) and Aveline's Hole (Mesolithic), while the lowest values are found for the Neolithic specimens from Cathole Cave and Lligwy Cromlech (Fig. 5a).

When considering the width at the surface of each incision (WIS), the values display a very large range, between 4.85  $\mu\text{m}$  and 135.57  $\mu\text{m}$  (Supplementary Table S3), with a much larger mean value for the Upper Palaeolithic sample (mean = 53.49  $\mu\text{m}$ , s.d. = 37.78) compared to the Neolithic sample (19.89  $\mu\text{m}$ , s.d. = 17.45), (Table 4). The largest WIS measures were observed on the Gough's Cave first incisors and first molars. The mean WIS of the Mesolithic canine from Aveline's Hole (48.95  $\mu\text{m}$ ; s.d. = 21.21) is most similar to the values observed on the Upper Palaeolithic second and third molars, and higher than the mean values of the Neolithic sample (Supplementary Fig. S3). When comparing widths between sites, a similar range of high values are observed for the teeth from Gough's Cave and Aveline's Hole, while the Neolithic teeth present a range of distinctly narrower incisions (Fig. 5).

The depths of the incisions ranged between 0.07  $\mu\text{m}$  and 42.72  $\mu\text{m}$  (Supplementary Table S3), with deeper scratches occurring on the Upper Palaeolithic specimens (mean = 8.11  $\mu\text{m}$ , s.d. = 11.78) compared to the Mesolithic (mean = 5.22  $\mu\text{m}$ , s.d. = 3.06) and the Neolithic (mean = 1.06  $\mu\text{m}$ , s.d. = 1.54) samples (Table 4). The deepest incisions were observed on the Gough's Cave first incisors, first and second molars, as well as on



**Fig. 4** Number of teeth with identified non-masticatory striations in the studied British samples, and the striation orientation types observed. Results for (a) anterior dentitions, and (b) posterior dentitions, with striation orientations represented by the following colour key: left oblique = yellow; vertical = orange; right oblique = red.

the canine from Aveline's Hole (i.e., depths > 5 µm), (Supplementary Fig. S3). Similarly to the trend observed for WIS, NM scratches are deeper for the teeth from Gough's Cave and Aveline's Hole, while they are shallower on the Neolithic teeth (Fig. 5b).

The values for the opening angle of the incision (OA) vary between 108.07° and 176.65° (Supplementary Table S3), with a mean value of 157.06° for the Upper Palaeolithic (s.d. = 17.86), 150.01° for the Mesolithic (s.d. = 12.98), and 168.36° for the Neolithic (s.d. = 5.31), (Table 4). The smallest OA values were observed on the Gough's Cave first incisors and first molars, as well as on the canine from Aveline's Hole (Supplementary Fig. S3). When comparing opening angles across sites, there is no overlap between the range of relatively low values observed for the Upper Palaeolithic sample from Gough's Cave and the Mesolithic teeth from Aveline's Hole, compared with the much higher OA values observed for the Neolithic sample (Fig. 5c).

For all measured variables, a wide range of values can be observed for the buccal striations of the first molars from Gough's Cave (Supplementary Fig. S3). Upon closer examination of the dataset (Supplementary Table S3), this seems to be due to an outlier, specimen NHM UK PV M 54130, which is marked by

much longer, wider and deeper striations compared to the NM scratches on the rest of the assemblage. This singularity is also observed for the Gough's Cave second molars when assessing the depth of the striations, also due to specimen NHMUK PV M 54130, which presents deeper incisions compared to other samples.

**Discussion**

**Frequency of labial vs buccal non-masticatory striations.** Previous studies have suggested that NM striations tend to be predominantly localised on anterior teeth (i.e., labial striations), with this preferential location of the marks on labial surfaces being one of the identifying characteristics of NM striations resulting from the use of the mouth as a 'third hand', in addition to their size, regularity, and their micro-morphological features (Lozano et al., 2008; Lozano et al., 2017a). For example, at Atapuerca (Spain), 94.5% of the anterior teeth from the Sima de Los Huesos hominins are marked by labial alterations, compared to only 6% of the posterior teeth (Lozano et al., 2008). Results from our study confirm this trend and show a similar pattern of NM striation distribution along the tooth row in the British assemblage, with

**Table 2 Counts and relative proportion (%) of the teeth examined bearing non-masticatory (NM) striations, according to tooth type, dentition, and assemblage.**

Site	Number of teeth with striations / total number of teeth									% of teeth with NM striations						
	I1	I2	C	P3	P4	M1	M2	M3	I1	I2	C	P3	P4	M1	M2	M3
(a) Upper dentition																
<b>Upper Palaeolithic</b>																
Gough's Cave	4/4	2/2	2/4	0/4	2/3	0/3	0/4	-	100	100	50	0	66.67	0	0	-
<b>Mesolithic</b>																
Aveline's Hole	2/2	-	1/2	0/2	0/7	1/6	1/10	0/5	100	-	50	0	0	16.67	10	0
Badger Hole	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kent's Cavern	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<b>Mesolithic - total</b>	<b>2/2</b>	<b>-</b>	<b>1/2</b>	<b>0/2</b>	<b>0/7</b>	<b>1/6</b>	<b>1/10</b>	<b>0/5</b>	<b>100</b>	<b>-</b>	<b>50</b>	<b>0</b>	<b>0</b>	<b>16.67</b>	<b>10</b>	<b>0</b>
<b>Neolithic</b>																
Abingdon	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	-	-	-	-	-	-	-	-
Ascott-under-Wychwood	2/4	1/6	0/7	0/6	0/10	0/8	0/7	0/3	50	16.67	0	0	0	0	0	0
Cathole Cave	0/0	0/0	0/0	0/0	0/0	2/2	2/2	0/0	-	-	-	-	-	100	100	-
Coldrum	2/3	3/4	4/5	2/6	0/6	3/7	0/3	0/0	66.67	75	80	33.33	0	42.86	0	-
Dinnington	0/0	0/2	1/2	0/4	0/4	0/10	0/8	0/6	-	0	50	0	0	0	0	0
Fussell's Lodge	0/6	0/4	0/6	0/16	0/14	0/18	0/15	0/10	0	0	0	0	0	0	0	0
Lanhill	0/0	0/0	0/0	0/0	0/0	0/1	0/0	0/0	-	-	-	-	-	0	-	-
Lligwy Cromlech	1/1	0/1	1/2	0/1	0/2	0/2	0/2	0/0	100	0	50	0	0	0	0	-
Picken's Hole	0/0	0/0	0/0	0/0	0/1	0/0	0/0	0/0	-	-	-	-	0	-	-	-
Swell IV	0/0	0/0	0/2	0/7	0/4	0/7	0/6	0/2	-	-	0	0	0	0	0	0
Swell V	0/0	0/3	0/3	0/6	0/7	0/9	0/6	0/5	-	0	0	0	0	0	0	0
Totty Pot	0/0	0/0	0/1	0/0	0/0	0/0	0/0	0/0	-	-	0	-	-	-	-	-
Wayland's Smithy	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	-	-	-	-	-	-	-	-
West Tump	0/1	0/1	1/1	0/1	0/2	0/2	0/2	0/2	0	0	100	0	0	0	0	0
Whiteleaf	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	-	-	-	-	-	-	-	-
Windmill Tump	0/0	0/0	0/1	0/2	0/3	0/3	0/3	0/2	-	-	0	0	0	0	0	0
<b>Neolithic - total</b>	<b>5/15</b>	<b>4/21</b>	<b>7/30</b>	<b>2/49</b>	<b>0/53</b>	<b>5/69</b>	<b>2/54</b>	<b>0/30</b>	<b>33.33</b>	<b>19.05</b>	<b>23.33</b>	<b>4.08</b>	<b>0</b>	<b>7.25</b>	<b>3.70</b>	<b>0</b>
<b>Grand Total</b>	<b>11/21</b>	<b>6/23</b>	<b>10/36</b>	<b>2/55</b>	<b>2/63</b>	<b>6/78</b>	<b>3/68</b>	<b>0/35</b>	<b>52.38</b>	<b>26.1</b>	<b>27.78</b>	<b>3.64</b>	<b>3.17</b>	<b>7.69</b>	<b>4.41</b>	<b>0</b>

(b) Lower dentition																
Site	Number of teeth with striations / total number of teeth									% of teeth with NM striations						
	I1	I2	C	P3	P4	M1	M2	M3	I1	I2	C	P3	P4	M1	M2	M3
<b>Upper Palaeolithic</b>																
Gough's Cave	4/4	0/1	-	-	2/3	2/4	1/3	1/1	100	0	-	-	66.67	50	33.33	100
<b>Mesolithic</b>																
Aveline's Hole	3/5	1/2	3/11	2/10	0/5	0/6	1/8	0/5	60	50	27.27	20	0	0	12.5	0
Badger Hole	-	-	0/1	-	-	0/2	0/3	-	-	-	0	-	-	0	0	-
Kent's Cavern	-	-	-	-	1/1	1/2	0/2	0/2	-	-	-	-	100	50	0	0
<b>Mesolithic - total</b>	<b>3/5</b>	<b>1/2</b>	<b>3/12</b>	<b>2/10</b>	<b>1/6</b>	<b>1/10</b>	<b>1/13</b>	<b>0/7</b>	<b>60</b>	<b>50</b>	<b>25</b>	<b>20</b>	<b>16.67</b>	<b>10</b>	<b>7.69</b>	<b>0</b>
<b>Neolithic</b>																
Abingdon	1/1	1/1	0/1	0/2	0/1	-	0/1	0/1	100	100	0	0	0	-	0	0
Ascott-under-Wychwood	3/16	2/17	4/16	0/10	1/11	0/16	0/13	0/9	18.75	11.76	25	0	9.09	0	0	0
Cathole Cave	-	-	1/1	0/1	-	0/1	-	0/1	-	-	100	0	-	0	-	0
Coldrum	0/1	-	-	0/2	0/1	0/1	-	-	0	-	-	0	0	0	-	-
Dinnington	0/2	-	0/2	0/1	0/4	0/11	0/10	0/9	0	-	0	0	0	0	0	0
Fussell's Lodge	0/5	0/7	1/7	1/10	0/15	0/26	0/21	0/16	0	0	14.29	10.00	0	0	0	0
Lanhill	1/1	0/1	0/1	-	0/1	0/2	0/2	0/1	100	0	0	-	0	0	0	0
Lligwy Cromlech	0/7	0/6	1/4	0/2	0/6	0/11	0/9	0/5	0	0	25	0	0	0	0	0
Picken's Hole	-	0/1	-	-	-	-	-	-	-	0	-	-	-	-	-	-
Swell IV	0/2	0/3	0/2	0/5	0/10	0/7	0/8	0/6	0	0	0	0	0	0	0	0
Swell V	0/6	2/7	1/7	0/10	0/9	0/13	0/13	0/9	0	28.57	14.29	0	0	0	0	0
Totty Pot	0/1	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-
Wayland's Smithy	-	0/1	0/1	0/2	0/1	0/2	0/2	0/1	-	0	0	0	0	0	0	0
West Tump	0/2	0/3	0/5	0/3	0/5	0/13	0/9	0/6	0	0	0	0	0	0	0	0
Whiteleaf	-	-	-	-	-	-	0/2	-	-	-	-	-	-	-	0	-
Windmill Tump	-	-	0/1	0/1	0/1	0/2	0/1	0/1	-	-	0	0	0	0	0	0
<b>Neolithic - total</b>	<b>5/44</b>	<b>5/47</b>	<b>8/48</b>	<b>1/49</b>	<b>1/65</b>	<b>0/105</b>	<b>0/91</b>	<b>0/65</b>	<b>11.36</b>	<b>10.64</b>	<b>16.7</b>	<b>2.04</b>	<b>1.54</b>	<b>0</b>	<b>0</b>	<b>0</b>
<b>Grand Total</b>	<b>12/53</b>	<b>6/50</b>	<b>11/60</b>	<b>3/59</b>	<b>4/74</b>	<b>3/119</b>	<b>2/107</b>	<b>1/73</b>	<b>22.64</b>	<b>12</b>	<b>18.33</b>	<b>5.08</b>	<b>5.41</b>	<b>2.52</b>	<b>1.87</b>	<b>1.37</b>

Results for (a) upper dentition, (b) lower dentition, with counts presented as the number of teeth with striations/total number of teeth.  
M molar, Pm premolar, C canine, I incisor  
Bold values in the tables are the lines representing totals for the whole assemblage or for sub-samples, to differentiate them visually from the lines representing values for each site.



**Table 3 Relative proportion (%) of anterior (labial) and posterior (buccal) teeth presenting non-masticatory striations for each sample, and relative proportions (%) of the striation orientation types observed on the teeth bearing striations (Left oblique; Vertical; Right Oblique).**

Site	% of anterior teeth with labial striations					% of posterior teeth with buccal striations				
	n	Teeth with striations	Left oblique	Vertical	Right oblique	n	Teeth with striations	Left oblique	Vertical	Right oblique
<b>Upper Palaeolithic</b>										
Gough's Cave	15	80.00	25.00	41.67	91.67	25	32	25	50	25
<b>Mesolithic</b>										
Aveline's Hole	22	45.45	0	70	40	64	7.81	40	60	0
Badger Hole	1	0	-	-	-	5	0	-	-	-
Kent's Cavern	0	-	-	-	-	7	28.57	0	100	100
<b>Mesolithic - total</b>	<b>23</b>	<b>43.48</b>	<b>0</b>	<b>70</b>	<b>40</b>	<b>76</b>	<b>9</b>	<b>28.57</b>	<b>71.43</b>	<b>28.57</b>
<b>Neolithic</b>										
Abingdon	3	66.67	0	100	0	5	0	-	-	-
Ascott-under-Wychwood	66	18.18	8.33	75.00	25.00	93	1.08	0	100	0
Cathole Cave	1	100	0	0	100	7	57.14	0	100	0
Coldrum	13	69.23	22.22	44.44	66.67	26	19.23	0	60	80
Dinnington	8	12.50	100	100	100	67	0	-	-	-
Fussell's Lodge	35	2.86	0	200.00	0	161	0.62	0	100	0
Lanhill	3	33.33	0	100	0	7	0	-	-	-
Lligwy Cromlech	21	14.29	33.33	66.67	0	40	0	-	-	-
Picken's Hole	1	0	-	-	-	1	0	-	-	-
Swell V	9	0.00	33.33	100	0	62	0	-	-	-
Swell IV	26	11.54	-	-	-	87	0	-	-	-
Totty Pot	2	0	-	-	-	0	-	-	-	-
Wayland's Smithy	2	0	-	-	-	8	0	-	-	-
West Tump	13	7.69	0	100	0	45	0	-	-	-
Whiteleaf	0	-	-	-	-	2	0	-	-	-
Windmill Tump	2	0	-	-	-	19	0	-	-	-
<b>Neolithic - total</b>	<b>205</b>	<b>15.70</b>	<b>17.14</b>	<b>71.43</b>	<b>31.43</b>	<b>630</b>	<b>1.75</b>	<b>0</b>	<b>81.82</b>	<b>36.36</b>
<b>Grand total</b>	<b>243</b>	<b>23.05</b>	<b>16.07</b>	<b>66.07</b>	<b>46.43</b>	<b>731</b>	<b>3.56</b>	<b>15.38</b>	<b>69.23</b>	<b>30.77</b>

'n' represents the total number of teeth assessed in each sample.  
 Bold values in the tables are the lines representing totals for the whole assemblage or for sub-samples, to differentiate them visually from the lines representing values for each site.

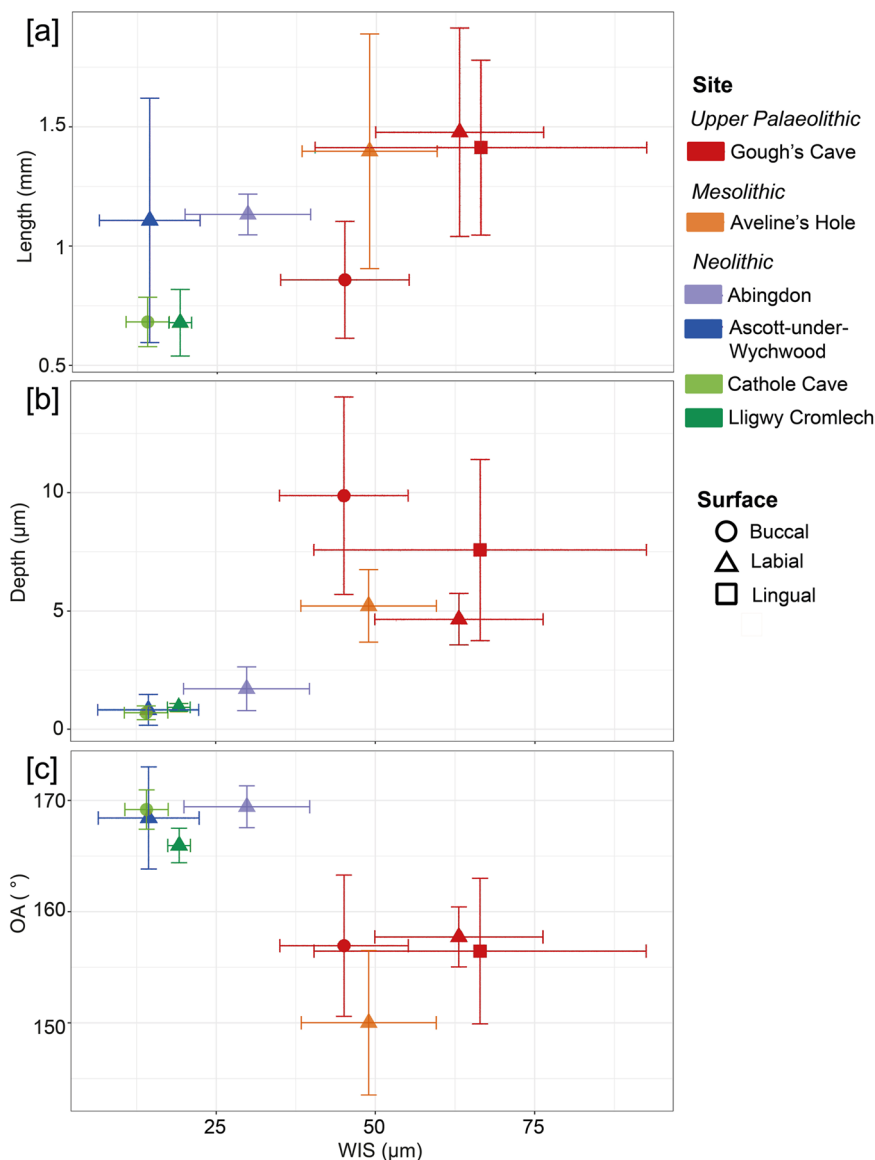
**Table 4 Descriptive statistics summarising the measurements taken on the specimens scanned with the Alicona Infinite Focus G5+, with mean and standard deviation (s.d.) for each measured variable: Length of the incision (Length), width of the incision on the surface (WIS), opening angle of the incision (OA), and depth of the incision (Depth).**

Period	Tooth	Surface	Dentition	n	Length (mm)		WIS (µm)		OA (°)		Depth (µm)	
					mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.
<b>Upper Palaeolithic</b>				<b>23</b>	<b>1.10</b>	<b>0.93</b>	<b>53.49</b>	<b>37.78</b>	<b>157.06</b>	<b>17.86</b>	<b>8.11</b>	<b>11.78</b>
	I1	Labial	Lower	2	0.62	0.18	24.24	15.61	162.49	1.28	1.32	0.74
		Labial	Upper	4	1.91	1.08	82.54	12.16	155.35	7.05	6.32	0.64
		Lingual	Upper	4	1.41	0.73	66.43	52.09	156.46	13.09	7.58	7.66
	M1	Buccal	Lower	2	1.87	2.26	95.60	38.48	141.33	41.78	18.47	23.06
	M2	Buccal	Lower	8	0.62	0.33	35.73	32.46	159.01	23.47	10.82	16.19
	M3	Lingual	Lower	3	0.83	0.72	36.28	22.35	161.84	6.64	1.61	0.87
<b>Mesolithic</b>	<b>C</b>	<b>Labial</b>	<b>Lower</b>	<b>4</b>	<b>1.40</b>	<b>0.98</b>	<b>48.95</b>	<b>21.21</b>	<b>150.01</b>	<b>12.98</b>	<b>5.22</b>	<b>3.06</b>
<b>Neolithic</b>				<b>28</b>	<b>0.86</b>	<b>0.46</b>	<b>19.89</b>	<b>17.45</b>	<b>168.36</b>	<b>5.31</b>	<b>1.06</b>	<b>1.54</b>
	I1	Labial	Lower	12	0.89	0.61	22.20	24.36	168.81	5.90	1.30	2.21
	I2	Labial	Lower	5	1.02	0.20	25.98	4.18	166.84	3.21	1.23	0.45
	C	Labial	Upper	1	-	-	19.96	-	162.35	-	0.90	-
	M1	Buccal	Upper	5	0.64	0.35	11.46	5.47	170.02	4.98	0.37	0.29
	M2	Buccal	Upper	5	0.87	-	16.70	14.58	168.34	6.58	1.02	1.26

Bold values in the tables are the lines representing totals for the whole assemblage or for sub-samples, to differentiate them visually from the lines representing values for each site.

23.05% of the anterior teeth examined presenting NM scratches, as opposed to only 3.56% of the posterior teeth (Table 3). Such differences between anterior and posterior dentitions may relate to practical limitations of the 'stuff and cut' technique, as this type

of behaviour would likely cause little damage to the posterior teeth due to the presence of sensitive soft tissues, the cheeks, protecting the buccal side of the crowns from accidental damage, most particularly for the molars.



**Fig. 5 Summary statistics of non-masticatory striations measurements per site and dental surface.** Width of the incision at the surface (WIS) plotted against (a) the length of the incision, (b) the depth of the incision, and (c) the opening angle of the incision (OA). Points represent the mean of each variable, and the error bars represent the standard error of the mean. Symbols represent the different dental surfaces examined (buccal: circle; labial: triangles; lingual: squares). The colour key specifies the provenance sites of each sample.

The presence in our assemblage, although at a low frequency, of scratches on the posterior dentition could be an indication of other forms of behaviour that are distinct from the use of the mouth as a 'third hand', since it would seem unlikely for 'stuff and cut' activities to be carried out so far back in the mouth that the cutting action would inflict striations on the molars without significantly damaging the surrounding tissues of the cheeks. Instead, NM striations occurring on the posterior dentition could result from activities such as the post-mortem defleshing and cutting of the *masseter* muscle of cadavers, either as part of burial rites or in relation to cannibalism (e.g., Bello et al., 2011a; Bello et al., 2016; Boulestin and Henry-Gambier, 2012; Toussaint, 2011). Likewise, the NM striations observed on the lingual surface of one of the I<sup>1</sup> from Gough's Cave (NHMUK PV M 54131; shown in Fig. 3) would be more consistent with post-mortem defleshing and cutting of the body rather than with accidental damage resulting from 'stuff and cut' activities. Indeed, the tool edge could have damaged the lingual surface of the tooth during

the cutting of the facial muscles, tongue or lips of the deceased individual, a behaviour that has been previously recorded for the Gough's Cave collection (Andrews and Fernández-Jalvo, 2003; Bello et al., 2011a; Cook, 1986). Evidence of post-mortem treatment of the cadaver has also been reported for the Mesolithic human remains from Kent's Cavern (Devon), with an ulna exhibiting butchery traces indicative of disarticulation and marrow extraction (Schulting et al., 2015). Since the post-mortem manipulation of human bodies has been previously reported for several Magdalenian and Mesolithic sites (e.g., Buisson and Gambier, 1991; Le Mort and Gambier, 1991; Marsh and Bello, 2023; Schulting et al., 2015 and references therein; Wysocki et al., 2013), we suggest that the NM buccal striations observed on the posterior teeth of our British Upper Palaeolithic and Mesolithic samples could be further evidence of cannibalism or funerary rituals. This could explain the relatively high frequency of buccal striations observed on the Upper Palaeolithic material from Gough's Cave (32% of posterior teeth), and within

the Mesolithic assemblage from Kent's Cavern (28.57% of posterior teeth).

The post-mortem treatment of bodies is not exclusive to the Upper Palaeolithic and the Mesolithic, and is a behaviour also known during the Neolithic (Schulting et al., 2015; Carbonell et al., 2010), with some examples from the site of Herxheim (Germany; Boulestin et al., 2009), as well as various examples from British Neolithic burial sites (Smith and Brickley, 2009). Two Neolithic sites in our assemblage showed evidence of post-mortem manipulation of the cadavers, with the presence of cutmarks on human remains on cranial and post-cranial elements at Coldrum, and on a clavicle at West Tump (Smith and Brickley, 2004; Smith and Brickley, 2009; Wysocki et al., 2013). At Coldrum, for example, the relatively high frequency of buccal striations (19.23% of the 26 posterior teeth examined) compared to the majority of our Neolithic samples may be explained by the defleshing and cutting of the heads and mandible, as demonstrated by the presence of cutmarks on the left temporal bone of an adult individual which also exhibited an unhealed injury to its left frontal (Wysocki et al., 2013). It could, therefore, be hypothesized that some of the NM buccal striations observed within our Neolithic sample relate to post-mortem treatment of the bodies rather than to ante-mortem 'stuff and cut' behaviours. We argue that NM buccal striations on posterior teeth, due to their location in the mouth and to their relatively low frequency compared to NM labial striations on anterior teeth, may be a further indication of such post-mortem practices, and therefore provide evidence for cultural behaviours very distinct from the use of the mouth as a 'third hand'.

However, current knowledge on the precise aetiology of these marks remains limited, and differentiating confidently NM striations which occurred during life from those inflicted after death is challenging. Indeed, if we hypothesise that buccal striations on the posterior dentition could be due to the post-mortem treatment of the bodies in human groups known to practice this type of behaviour, we could expect that the defleshing and cleaning of the cadavers could result in striations on the anterior dentition as well. In that case, some of the labial NM striations observed on anterior teeth could have been produced post-mortem but be misinterpreted as striations inflicted during life. This highlights a need for future studies to further our understanding of these types of dental alterations, their causes, and their specific micro-morphometric properties. We suggest that 3D microscopy (such as the use of focus-variation microscopy, as in the present study, or of confocal microscopy, for example) could prove to be a useful tool to help better distinguish the different types of NM striations (i.e., in-life vs post-mortem), and help identify more confidently the behaviours involved. High-resolution profile analyses of these striations, in particular, could potentially allow to differentiate in-life from post-mortem striations by exploring the micro-morphometric differences between these dental alteration types.

For instance, the measurements conducted on selected specimens in this study suggest micro-morphometric differences between labial and buccal NM striations. Labial striations appear to be longer and to have a narrower, shallower, and more open profile compared to buccal striations (with the exception of the Gough's Cave assemblage, in particular for specimen NHMUK PV M 54130, further discussed below), (Figs. 6–7 and Table 4; Supplementary Fig. S3). Although this is only a preliminary study, and more measurements need to be undertaken on a larger sample to confirm this trend with more confidence, we suggest that the micro-morphometric differences observed between labial and buccal NM striations could relate to actual differences between the behaviours that produced them, and to whether it was inflicted during life or after death. If, as hypothesized above, labial NM striations are more commonly produced during the

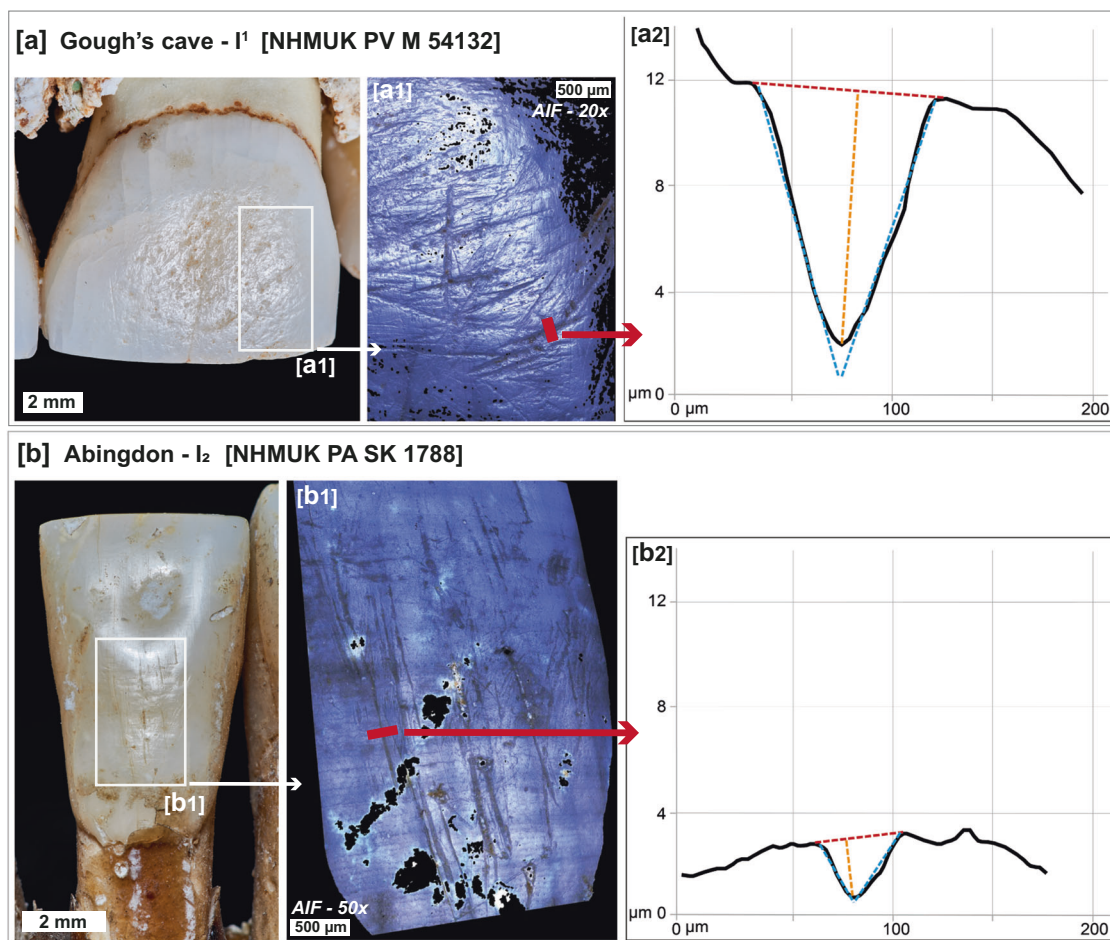
life of the individual as result of the 'stuff and cut' technique, a reduced and controlled force was likely applied on the tool to reduce the risk of accidentally damaging nearby sensitive living tissues. This would have resulted in shallower and narrower striations, as those observed on the labial striations measured from our anterior teeth assemblage (Fig. 6). Conversely, the cutting of facial muscles and the disarticulation of the mandible from the skull during post-mortem treatment of cadavers would involve more forceful actions and handling of the tool at different angles, with possibly short and repeated movements. This would likely result in shorter, but deeper and wider striations, as those recorded on the posterior teeth selected for profile measurements (Table 4; Supplementary Fig. S3). Micro-morphometric differences between labial and buccal NM striations could also reflect the use of different tools for the 'stuff and cut' technique compared with those marked by the post-mortem processing of the remains.

Another explanation could more simply relate to differing wear processes of the enamel, with striations occurring during life appearing more worn and shallower having been subjected to abrasion of the enamel from food and tooth-on-tooth contact during mastication, saliva, and surrounding tissues during life, as opposed to post-mortem striations, which were the last made and therefore were not subjected to such processes. This latter hypothesis aligns with previous studies suggesting that NM striations tend to appear worn and smoothed over due to masticatory actions, as opposed to the sharper and clearer edges observed on post-mortem alterations (Lalueza Fox and Frayer, 1997; Lozano et al., 2008).

The example of the Gough's Cave mandible NHMUK PV M 54130 illustrates further our argument, due to the presence of both buccal striations on its posterior teeth, and cutmarks on its right mandibular ramus running antero-posteriorly, in near-alignment with the striations observed on the right molars (Fig. 7a). As previously mentioned in the results from our micro-morphometric analysis, this specimen was identified as an outlier within the Upper Palaeolithic assemblage, due to significantly longer, wider, and deeper striations compared with those other specimens, most particularly on its  $M_1$  and  $M_2$ . When comparing the profiles of the cutmarks on the mandibular ramus with those recorded on the molars, similar patterns can be observed, in both dimensions and cutmark morphology. We suggest that this indicates that the striations observed on both the ramus and the molars of this specimen were produced as a single event, probably inflicted as a result of cutting the *masseter* muscle and removing and/or detaching the *temporalis* muscle from the mandible, accidentally damaging the buccal surface of the molars in the process.

It is also interesting to note that among the specimens selected for micro-morphometric analysis, the Mesolithic canine from Aveline's Hole (NHMUK EM 504) has incisions with WIS values similar to those observed on the Gough's Cave second and third molars, as well as higher values for the depth of the incisions compared to most Neolithic specimens. It is possible that these wider and deeper striations could be a feature of post-mortem treatment of the head, similarly to the example from Gough's Cave. Future studies would benefit from further exploration of the micro-morphometric characteristics of both buccal and labial NM striations, to better understand if some of their characteristics might indeed relate to specific practices and activities, hence potentially providing us with further tools to study ancient behaviours from dental remains.

**Location of labial non-masticatory striations: upper vs lower dentition.** The anterior teeth examined in our study show that the upper dentition is more frequently damaged (33.75% of cases) than the lower dentition (17.79% of cases), with the highest



**Fig. 6** Examples of non-masticatory labial striations [photos, Alicona Infinite Focus (AIF) 3D reconstruction, and 3D profiles]. (a) Labial striations on an upper first incisor from Gough's Cave (NHMUK PV M 54132) with [a1] showing an AIF 3D reconstruction (objective: 20x) and [a2] showing a reconstructed 3D profile used for measurements. (b) Labial striations on a lower second incisor from Abingdon (NHMUK PA SK 1788), with [b1] showing an AIF 3D reconstruction (objective: 50x) and [b2] showing a reconstructed 3D profile used for measurements. Thick red lines show the locations of measured profiles. Photo © Longleat Estate and Trustees of the Natural History Museum.

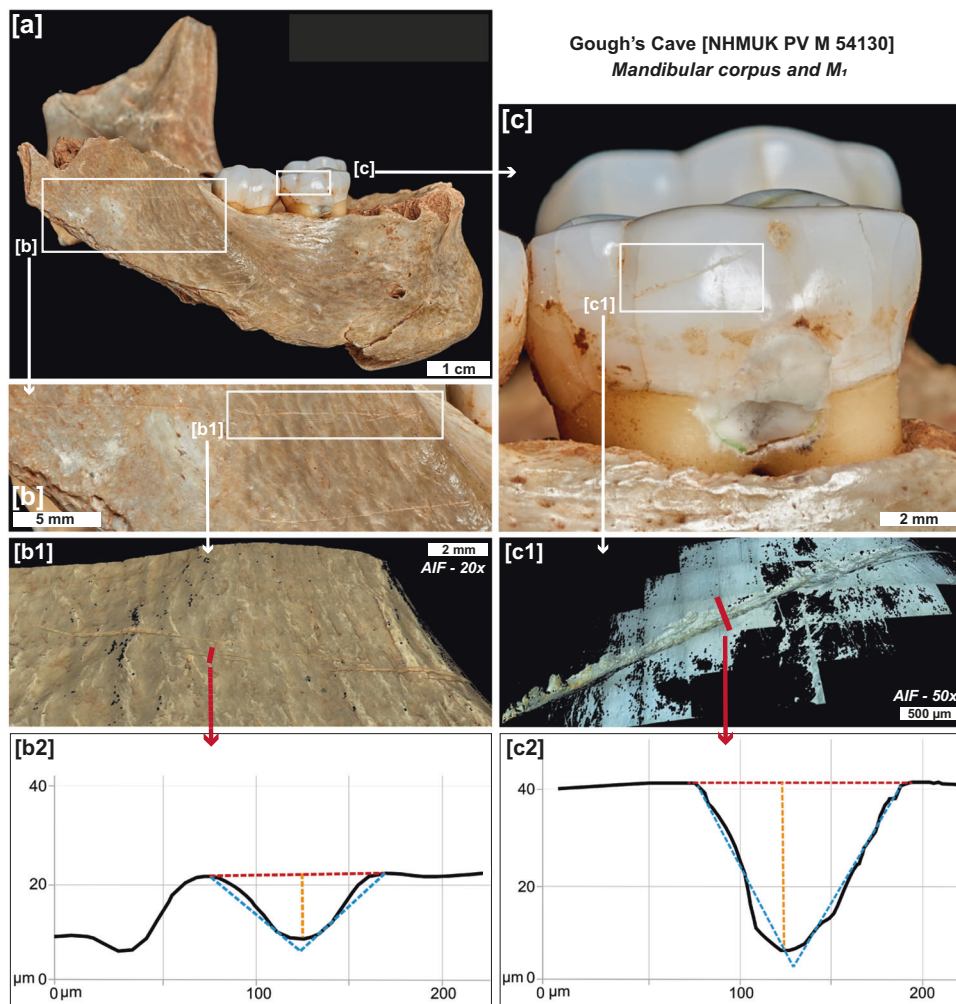
frequency of labial NM marks on the upper central incisors (Table 2 and Supplementary Table S2). This is consistent with the hypothesis formulated by Lozano et al. (2008) suggesting that upper teeth are likely to be more exposed to accidental scratches inflicted by a cutting tool than lower teeth due to the natural position of the dentitions during occlusion. Indeed, when material is held in the mouth, the upper teeth, particularly the incisors, are the more exposed to receiving a potential tool impact, whereas the lower teeth are partially covered by the material being held.

When evaluating the location of specific scratch orientations, results from our Neolithic and Mesolithic samples echo those from Lozano et al. (2008) for the Sima de los Huesos (Atapuerca) hominins, in which a predominance of vertical striations was observed on the lower dentition. Although the Upper Palaeolithic assemblage from Gough's Cave is dominated by right oblique/striations (91.67%), both our Mesolithic and Neolithic samples were dominated by vertical striations (70% and 71.43%, respectively), (Table 3). These vertical striations are likely marks left by the cutting tool as the material was cut and severed when the tool was descending vertically towards the lower incisors. Similar modifications have been observed among Inuits, who have been recorded clenching different types of materials in their mouth while cutting it from above with a vertical downward movement (Faurie and Raymond, 2005).

When measuring the profiles of this type of striations, we might expect to find deeper scratches on the lower dentition compared with those of the upper dentition, as a result of a sudden excess of force when the material gives way and the tool cuts through. However, no such pattern could be observed in our preliminary micro-morphometric exploration of NM labial striations on anterior teeth.

#### Frequency of labial non-masticatory striations through time.

The frequency of labial striations on anterior teeth appears to gradually decrease through time within our British assemblage, with frequencies declining from 80% in the Upper Palaeolithic Gough's Cave sample, to 43.48% in the pooled Mesolithic sample, and 15.70% in the combined Neolithic sample. These results show that NM labial striations (and by extension, the 'stuff and cut' behaviour as well, potentially) were still occurring during the British Neolithic. These findings bring nuance to previous statements suggesting that such dental alterations and their associated behaviours were 'rare' in the Neolithic (Dinnis et al., 2014, p.116) or 'few' in *Homo sapiens* (Lozano et al., 2017a, p.247; Lozano et al., 2017b, p.314), but remain in agreement with previous studies such as the diachronic study of the Atapuerca material by Lozano and colleagues (Lozano et al., 2017a) which demonstrated



**Fig. 7** Examples of cutmarks on the Gough's Cave specimen NHMUK PV M 54130 [photos, Alicona Infinite Focus (AIF) 3D reconstruction, and 3D profiles]. (a) General photo of the specimen. (b) Photo of cutmarks on the right mandibular ramus, with [b1] showing an AIF 3D reconstruction (objective: 20x) and [b2] showing a reconstructed 3D profile used for measurements. (c) Photo of buccal striations on the right lower first molar, with [c1] showing an AIF 3D reconstruction (objective: 50x) and [c2] showing a reconstructed 3D profile used for measurements. Thick red lines represented in images [b1] and [c1] show the location of the measured profiles on each surface. Photo © Longleat Estate and Trustees of the Natural History Museum.

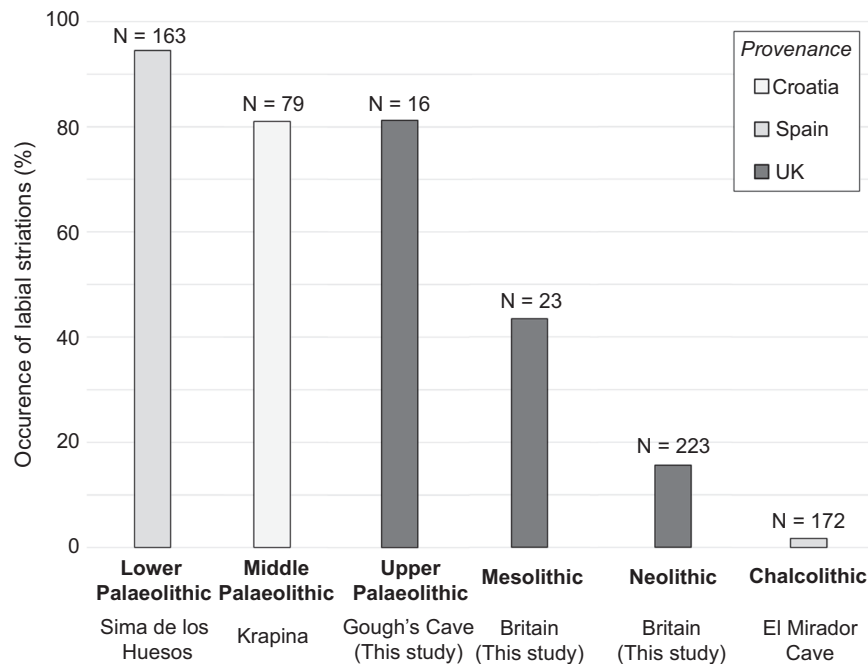
a gradual decline through time in the occurrence of NM labial striations (Fig. 8).

The 'rarity' of NM labial striations during the Neolithic could be attributed to different causes. Firstly, it is possible that labial striations may have been 'missed' or overlooked when assessing large collections, particularly if this type of feature was not specifically looked for. Teeth defects are not easily visible using hand lenses alone, particularly if the light is not appropriate. Scanning teeth under a microscope is the most appropriate method for assessing the presence and type of NM striations, although this may be difficult to implement in the case of large human assemblages as the process is time consuming.

Secondly, although NM labial scratches may have been under-represented in Neolithic assemblages because of the difficulty in identifying these modifications macroscopically, it is also possible that their frequencies might also have been 'over-estimated' for Palaeolithic and Mesolithic material, by wrongly attributing post-mortem cutmarks on teeth to the 'stuff and cut' behaviour. As previously mentioned, cannibalism is a practice more often recognized for the Upper Palaeolithic (specifically the Magdalenian period) and the Mesolithic, with less evidence, but also occurring, during the Neolithic. Several of the sites analysed in this study showed evidence of cutmarks on bones, such as in Gough's Cave and

Kent's Cavern (Bello et al., 2011a; Bello et al., 2015; Schulting et al., 2015). These sites are likely to have an inflated number of NM striations recorded as a result of a combination of the ante-mortem 'stuff and cut' behaviour and the post-mortem processing of the bodies during cannibalistic practices. The same could be hypothesized from previously studied collections where both labial striations and cutmarks on human remains were identified.

Finally, the inception of the Neolithic period in Britain c.6000 BP, with the introduction of domestic plants and animals, could also offer a possible explanation for the reduced frequency of non-masticatory labial striations. Labial striations resulting from the 'stuff and cut' technique have been primarily suggested to relate to the preparation and processing of meat, as opposed to the working of other types of organic materials such as skin, leather and fibres (Lalueza Fox and Pérez-Pérez, 1994). With the transition from hunting-gathering societies to farming, the decrease in labial NM striations could possibly relate to a more plant-based diet for Neolithic groups, as the domestication and processing of plants played a vital role with the rapid population expansion during this period (Bickle, 2018; Downey et al., 2016; Gkiasta et al., 2003; Richards et al., 2003). This would have likely resulted in a predominance of different dental alteration morphologies compared with those observed for the Palaeolithic



**Fig. 8** Relative proportion (%) of labial striations observed on anterior teeth through time from the Lower Palaeolithic to the Chalcolithic. 'N' indicates the total number of anterior teeth assessed for each sample. This chart combines results from this study for Britain and results previously published for the Atapuerca sites, Spain (Lozano et al., 2017a, 2017b), and Krapina, Croatia (Lalueza Fox and Frayer, 1997).

and Mesolithic, as daily activities might have been less focused on the processing of animal carcasses compared to earlier hunter-gatherers. This assumption is coherent with previous studies of Chalcolithic and Neolithic populations which observed a reduced rate of labial NM striations, but also a higher rate of specific dental alterations such as vestibular-lingual striations and enamel chipping usually associated with the working of plant fibres (Lozano et al., 2008). In addition, the larger population sizes of the Neolithic might have provided with more opportunities to process foods and materials as a group, without requiring one individual to systematically use its mouth as a 'third hand'.

It would be interesting to explore further the temporal frame of the appearance of labial NM striations through the analysis of Bronze and Iron Age archaeological collections to evaluate whether labial striations still occur through the Holocene, and if so, in which proportions and alongside which other types of dental alterations. We would also expect different striation micro-morphologies from 'stuff and cut' activities when stone cutting tools were replaced by metal knives.

### Conclusion

Our analyses indicate a reduction in the frequency of labial non-masticatory (NM) striations through time, with frequencies decreasing from 80% in the Upper Palaeolithic, to 43.48% in the Mesolithic, and 15.70% in the Neolithic. Although the use of the mouth as a 'third hand' has been considered a 'rare' occurrence during the Neolithic, our results show that NM striations were still present in the British Neolithic, despite drastic cultural and economic changes. The reduction of labial NM striations during the Neolithic is likely associated with behavioural changes during a period when societies moved from hunting and gathering towards farming, resulting from a new primary subsistence base (i.e., less meat and more plant-based diet), new tools and techniques for processing foods and raw materials, and growing population sizes (Bickle, 2018; Schulting, 2000; Richards et al., 2003). It must be noted, however, that while labial NM striations have been generally interpreted as resulting from the 'stuff and cut' technique, this

cultural signal might be blurred by the occurrence of post-mortem NM striations in assemblages associated with evidence of cannibalism or funerary rituals. Indeed, the defleshing and processing of the body after death might have produced labial NM striations that could be difficult to differentiate from NM striations produced during life by using the mouth as a 'third hand', as demonstrated in our assemblage by the Magdalenian examples from Gough's Cave.

Although less frequent than labial NM striations on the anterior dentition, buccal NM striations were also observed on posterior teeth, more particularly within the Upper Palaeolithic and Mesolithic assemblages, as well as in some of our Neolithic samples. Due to the location of these dental alterations in the mouth and to their micro-morphometric characteristics, we suggest that these might relate primarily to post-mortem treatment of the bodies, rather than to the use of the mouth as a 'third hand'. Our observations and analysis of the profiles of selected labial and buccal NM striations agree with previous studies suggesting that striations resulting from the 'stuff and cut' behaviour differ in their micro-morphologies when compared to post-mortem cutmarks. This opens interesting avenues for future research to further our understanding of NM dental striations, their aetiology, and their specific micro-morphometric characteristics, and to assist in differentiating ante-mortem from post-mortem marking and scratching of teeth.

It is, therefore, essential to keep exploring the fossil record to better identify and characterize these dental alterations, taking advantage of recent advances in the field of 3D microscopy to conduct further micro-morphometric analyses of NM striations. This could facilitate the identification of NM striations, allowing to distinguish them more systematically and more confidently from other dental alterations produced by diet, post-mortem treatment of the dead, or taphonomic damage, which can blur this important cultural signal.

### Data availability

All data generated or analysed during this study are included in this published article [and its supplementary information files].

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### Author contributions

Conceptualization: SMB, SAP, and LC; Data curation: SMB, LC, CD, and SAP; Formal analysis: CD and LC; Methodology: SMB; Supervision: SMB and SAP; Writing – original draft: LC and CD. Writing – review and editing: LC, CD, SMB, and SAP.

### Competing interests

The authors declare no competing interests.

### Ethical statement

Ethical approval was not required as the study did not involve human participants.

### Informed consent

This article does not contain any studies with human participants performed by any of the authors.

### Additional information

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