Dental scratches and handedness in East Asian Early Pleistocene hominins

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Abstract

The current study aims to characterize dental scratches found on an East Asian hominin upper left central incisor (I^1) and lower left lateral incisor (I_2) from the Early Pleistocene (Meipu site, Yunxian County), and infer the preference for handedness of this two individuals by quantifying the orientation of dental scratches. The labial surfaces of these two teeth were observed and imaged using light microscopes and/or scanning electron microscope (SEM) under different magnifications (5x-70x). The angle, width, and length of each dental scratch was measured and analyzed. The dental scratches described and quantified on the labial enamel surface of Meipu I^1 and I_2 fit the description of cutmarks caused by "stuff and cut" behavior. Most scratches are oriented in the right oblique direction, averaging 47.11 degrees in I^1 and 44.60 degrees in I_2. This result indicates preference for the right hand as the dominant one in holding a tool during "stuff and cut" behaviors. This is the earliest reported "stuff and cut" behavior and inferred right-handedness in East Asia. It fills a temporal gap between the earliest known example in the African Early Pleistocene (~1.8 Ma) and the next known instance in the European Middle Pleistocene. This is also the first time the "stuff and cut" behavior and right-handedness has been reported in a hominin assigned to *Homo erectus sensu lato*.

Introduction

Ninety percent of individuals in modern human populations are right handed (Annett, 1985). Such high lateral preference is genetically controlled and is unique to modern humans (Levy & Nagylaki, 1972; McKeever, 2000; Francks *et al*., 2002). To varying degrees, handedness has been related to both cerebral lateralization and the development of language (Ocklenburg *et al*., 2014).

While it is possible to study handedness directly in living populations, uncovering manual lateralization in prehistoric populations requires a more deductive approach (see Cashmore *et al*., 2008). Studies of handedness in past populations rely on the assumption that a behavior's directional laterality will leave traceable markers in bone or artefacts such as morphological asymmetry of the upper limbs and cranial endocasts (e.g. Holloway & De La Coste-Lareymondie, 1982; Trinkaus *et al*., 1994; Sparacello *et al*., in press), orientation of the cortex on lithic flakes (e.g. Toth, 1985; Rugg & Mullane, 2001), and polarity of rock art (e.g., Faurie & Raymond, 2004). Additionally, the orientation of cutmarks on the labial enamel surface of human anterior teeth has been recognized as evidence of handedness (Bérmudez de Castro *et al*., 1988; Fox & Frayer, 1997; Lozano-Ruiz *et al*., 2004; Hillson *et al*., 2010; Frayer *et al*., 2012, 2016; Volpato *et al*., 2012; Estalrrich & Rosas, 2013, 2015; Willman, 2016).

Oblique scratches are formed on anterior teeth during a bimanual task referred to as "stuff and cut" behavior when lithic tools inadvertently contact and scratch dental enamel (Brace, 1975, 1991). During this process, the non-dominant hand and the anterior teeth (sometimes referred to as the "third hand") clench the object in the mouth, while the dominant hand cuts the object with an instrument. If the cutting instrument scratches the labial enamel surface, it will leave cutmarks that are oriented at certain oblique angles. The orientation of the oblique scratches can indicate which hand was used to cut the object. Oblique scratches, purported to represent the "stuff and cut" behavior using the right hand, have been described in approximately 90% of *H. heidelbergensis* and *H. neanderthalensis* studied (Bermúdez de Castro *et al*., 1988; Fox & Frayer, 1997; Lozano-Ruiz *et al*., 2004;

Hillson *et al*., 2010; Frayer *et al*., 2012; Volpato *et al*., 2012). However, considering the limited sample size of hominin teeth in most fossil sites that bear oblique scratches, it is often difficult to identify frequencies of handedness in past populations. Morphological asymmetries of humeri also attest to right-handed dominance in several Neanderthals (Trinkaus, 1994); in one Neanderthal, Regourdou I, both oblique striations in anterior teeth and humeral asymmetry were identified (Volpato *et al*., 2012).

Through the extensive characterization of oblique scratches and their orientations, right-handedness and related "stuff and cut" behavior has been well established in the fossil record of Middle and Late Pleistocene Neanderthal-lineage hominins (e.g. Bérmudez de Castro *et al*., 1988; Fox & Frayer, 1997; Trinkaus, 1994). Frayer *et al*. (2016) recently documented the orientation of cutmarks on the anterior teeth of OH 65, a maxilla specimen of African early *Homo* dated to ~1.8 Ma. This work revealed the earliest evidence for right-handedness in human history. While right-handedness and related "stuff and cut" behavior is well-documented in European Middle Pleistocene and existed as early as the Early Pleistocene in Africa, little is known about this type of behavior in East Asia.

Recently, we identified dental scratches macroscopically on the labial enamel surface of the upper left central incisor (I^1) and lower left lateral incisor (I_2) from two East Asian *Homo erectus sensu lato* individuals. The teeth were recovered from the Meipu site of southern China. The present study aims to document in detail the number, length, width, and orientation of the dental scratches present on the labial enamel surface of the Meipu I^1 and I_2. Through this analysis, we provide the earliest evidence of "stuff and cut" behavior as well as right-hand dominance in East Asia.

The Meipu site

In 1975, four isolated teeth (I^1, P^4, M^1, and I_2) were recovered from the Meipu site, Yunxian County, southern China (33°0' 6.49''N, 111° 8' 57.88''E, 263 m) (Xu, 1978; Wu & Dong, 1980; Dong, 2016). According to standards of Molnar (1971), the degree of occlusal wear is 3, 2, 3, and 4, respectively. Based on this, these four isolated teeth probably represent at least three individuals (Individual I: I^1, Individual II: P^4 and M^1, and Individual III: I_2). The

Meipu site is located in the same county as the Quyuanhekou site (56.4 km southwest to Meipu), where two almost complete hominin crania (EV9001 and EV9002), classified as *Homo erectus*, were recovered (Li & Etler, 1992). Early reports compared the Meipu teeth to *Paranthropus*, *Australopithecus*, *H. erectus*, Neanderthals, and recent Chinese (Wu & Dong, 1980). Wu & Dong (1980) found that the Meipu hominins had large tooth crowns, complex occlusal surfaces on the posterior teeth, a shovel-shaped I^1 with a strong basal eminence, and a sub-square M^1 crown outline. Wu & Dong (1980) assigned the Meipu material to the group *H. erectus sensu lato* based on this preliminary description and comparison, although more work is needed to confirm the taxonomy and phylogenetic relationship to other hominins.

The Meipu site can be stratigraphically divided into three layers from top to bottom: ~0.3 m calcareous layer, 0.5-2.5m of yellow silty clay, and 0-0.6m of yellow, highly calcareous-cemented silt layer containing small limestone breccia. All human and faunal remains were recovered from Layer 2, the layer of yellow silty clay. The Meipu fauna includes 25 species, including several Neogene relics or primitive species of the Pleistocene, such as *Pachycrocuta licenti*, *Leptobos brevicornis*, and *Gomphotherium* (*Sinomastodon*). This biostratigraphic context suggests a late Early Pleistocene age for the Meipu teeth (present study; Xu, 1978). Recently, 11 oriented block samples at ~20 cm intervals were collected along the depositional sequence of Layer 2 at Meipu, and paleomagnetic measurements were carried out. Preliminary results show that a reversal magnetozone can be defined from top to ~40 cm along the upper portion of the Layer 2, which can be possibly interpreted as the Jaramillo or Olduvai. This result agrees well with the Early Pleistocene age for the Meipu hominin fossils indicated by the faunal assemblage. With the combination of biostratigraphic and paleomagnetic results, the Meipu hominins are likely to have lived in the Early Pleistocene, at least ~1.0 Ma before present.

Material and methods

The present study describes and quantifies dental scratches on the labial enamel surface of an upper left central incisor (I^1) and lower left lateral incisor (I_2) from Early Pleistocene of the Meipu site in southern China.

Microscopic observation and imaging: The labial, mesial, lingual, and distal aspects of the Meipu teeth were observed under light microscopes (Olympus SZX7 and HIROX KH-8700) for the existence of scratches and their morphologies. The magnification ranged from 8x to 75x.

SEM imaging: A scanning electron microscope (Hitachi S-3700 N), housed at the Institute of Vertebrate Paleontology and Paleoanthropology (Beijing), was used to image the labial enamel surface of the Meipu I^1 and I_2. A voltage of 3.00 kV was used under magnifications ranging from 5× to 75×. The tooth was adjusted with the labial surface being orientated perpendicularly to the microscope's optical axis before imaging. SEM images were saved in TIFF format.

Measurement: The SEM images of Meipu I^1 and I_2 were rotated into anatomical position with the sagittal axis of its crown being vertically aligned. Next, the angles, widths, lengths of the dental scratches were measured with ImageJ 1.50i. As in other studies of dental scratches (e.g. Lozano-Ruiz *et al*., 2004; Volpato *et al*., 2012), the angle is defined as the degree to which the dental scratch (line *b* in Figure 1) deviates away from the horizontal line of the crown (line *a* in Figure 1) when rotated counterclockwise.

Statistics: The angle, width, and length measurements of the dental scratches were imported into SPSS 20.0 for descriptive statistics. The dental scratches recorded here were those have the typical micromorphology characteristic of cutmarks, that is, parallel edges, "V"-shaped cross-section, microstriations running along the orientation of scratch, and the presence of Hertzian cones (Lozano *et al*., 2004). For some thin striations, micromorphologies were unclear due to the possible ante-mortem or post-mortem erosion or abrasion and were therefore not included in this study. In addition, abrasive particles in food can generate striations with widths ranging from 1 to 20 μm during mastication (Bermúdez

de Castro *et al*., 1988; Puech, 1982). In view of these findings, only the cutmarks with widths exceeding 20 μm were taken into consideration in the statistical analysis of the dental scratches for Meipu I^1 and I_2. The orientation and width of the scratches were displayed in a rose diagram, generated in the R 3.2.5 program (ref.) with the openair package (Carslaw and Ropkins, 2012). Additionally, to compare our results with those previously published, all scratches were grouped into four categories according to their orientation, following Bermúdez de Castro *et al*. (1988): 1) Right Oblique (22.5°-67.5°), 2) Vertical (67.5°-112.5°), 3) Left Oblique (112.5°-157.5°), and 4) Horizontal (0°-22.5° and 157.5°-180°), The categories for the horizontal orientation were listed in Table 1 as two separated groups based on the different angles (0°-22.5° and 157.5°-180°).

[Insert Figure 1 here]

Results

Occurrence of dental scratches by tooth category: The labial surface of the Meipu I^1 is covered by numerous scratches that were visible to the naked eye and more obvious under the light microscope and SEM. Comparatively, the distribution of scratches is sparser in the labial surface of I_2. No similar scratches were present in the other two teeth (P^4 and M^1).

Location of scratches in the I^1 and I_2: The dental scratches are primarily distributed on the mesial aspects of the I^1 and I_2 labial surfaces. The cervical third of the tooth is mostly devoid of scratches (Figure 2 and 3). The middle third is the most heavily scratched, possibly due to the fact that this section of the tooth would have been the most likely to be accidentally hit by a tool. Comparatively, the dental scratches like those on the labial aspect were absent from the mesial, lingual, and distal aspects.

Morphology of the I^1 and I_2 **scratches**: The majority of the scratches have probably been rounded by food particle abrasion or saliva erosion (Frayer *et al*., 2012; Volpato *et al*., 2012). Scratches with a sharp edge were rarely seen in Meipu I^1 and I_2 (Figure 3 and 4). The edges of the scratches are generally parallel with each other and, in a few of cases, intersect in a sharp end (Blue arrow in Figure 4). The scratches are generally straight, but a curved or "S"-shaped scratch can be found (green arrow in Figure 4). Most scratches consist of a single

furrow, but some include multiple parallel furrows, as indicated by the red arrow in Figure 4. A "V" or "U"-shaped cross-section is typical for most scratches (Figure 5a). Along a few scratches, Hertzian cones remain (Figure 5c), although the edges are rounded, likely due to food particles or erosion by saliva. Additionally, fine striations can be observed running along the walls of a scratch (Figure 5b and yellow arrows in Figure 4). On the labial enamel surface, dental scratches with varying widths and lengths intersect and overlap with one another, especially in the most intensely scratched area (the middle third of the mesial aspect) (see Figure 4 and 5).

Count and orientation of the I^1 and I_2 scratches: As shown in Figure 6, most scratches wider than 20 µm (88.11% for I^1 and 81.81% for I_2) are oriented in the lower left quadrant of the diagram (0-90°). Following the categories described by Bermúdez de Castro *et al*. (1988), the right oblique is the most common (47.55% for I^1 and 54.55% for I_2, Table 1 and 2). In comparison, the percentage of horizontal, vertical, and left-oriented I^1 scratches are 16.78%, 30.77%, and 2.79%, respectively. For the I_2, these values are 4.55%, 31.82%, and 9.09%, respectively.

Width and Length of the I^1 scratches: In Table 1 and 2, the mean and variation of the width and length of the dental scratches are provided. The mean width of all the dental scratches is 38.41 µm in I^1 and 44.53 µm in I_2. Following the categories described by Bermúdez de Castro *et al*. (1988), the mean width by category falls closely around the overall mean, with the exception of the horizontal group (157.5°-180°) in I^1 that has a mean of 51.13 µm. The mean length of dental scratches by category falls between 1000-1600 µm in I^1 and 350-601 µm in I_2, although the full range extends from 310-4037 µm in I^1 and 246-974 µm in I_2.

[Insert Figure 2 here]

[Insert Figure 3 here]

[Insert Figure 4 here]

[Insert Table 1 here]

[Insert Table 2 here]

[Insert Table 3 here]

[Insert Figure 5 here]

[Insert Figure 6 here]

Discussion

Ante-mortem versus post-mortem nature of the dental scratches: In addition to the ante-mortem causes of dental scratches (such as the stuff and cut behavior), post-mortem factors like the taphonomic environment and the cleaning of the fossils can also produce dental scratches (Bermúdez de Castro *et al*., 1988; Fox & Pérez-Pérez, 1994). If taphonomic factors (e.g., trampling or transportation) were the cause, we would expect the other specimens deposited at the site to have similar scratches and for the scratches to be distributed randomly on the surface of the tooth (Bermúdez de Castro *et al*., 1988), particularly because all the hominin Meipu teeth came from Layer 2. However, for the Meipu teeth, only the I^1 and I_2 have clear scratches and the scratches are mainly restricted to the middle third area of their labial surfaces. This situation excludes the possibility that the dental scratches of Meipu I^1 and I_2 can be explained fully by taphonomic processes. Second, damage during post-excavation cleaning process could also scratch the tooth surface, but would leave fresh striations with sharp edges (Fox & Frayer, 1997). In contrast to this, the edges of most scratches in Meipu I^1 and I_2 have been rounded, probably by the abrasion from food particles and/or eroded by saliva, indicating their age (Frayer *et al*., 2012; Volpato *et al*., 2012). In sum, the dental scratches quantified and documented in the present study are most likely to be generated by ante-mortem behaviors.

Dietary versus non-dietary scratches: Over an individual's lifetime, food items or other particles can leave scratches on a tooth's surface (Bermúdez de Castro *et al*., 1988; Estalrrich & Rosas, 2015). Compared to the non-dietary scratches or cutmarks documented in the present study, scratches related to chewing behavior are usually thin (<20 microns in width according to Puech, 1982). In the present study, we only record those scratches of width >20 microns in order to eliminate all the possible dietary scratches. Additionally, the Meipu I^1 and

I_2 display a series of morphological traits typical of cutmarks, that is, parallel edges, "V" or "U"-shaped cross-section, microstriations running along the orientation of scratch, the presence of Hertzian cones (Lozano *et al*., 2004) (see Figure 4). Besides these aspects, the distribution of the Meipu I^1 and I_2 dental scratches is inconsistent with dietary causes. Most scratches on the Meipu I^1 and I_2 are confined to the middle third of the mesial half of the crown, corresponding to the most bulging area of upper central incisor when situated in the maxilla. The size, morphology, directionality, and location of the Meipu I^1 and I_2 scratches fit the criteria of non-dietary marks or cutmarks usually left on enamel surface by "stuff and cut" behavior (Bermúdez de Castro *et al*., 1988; Lozano-Ruiz *et al*., 2004).

Handedness of Meipu hominin: Most scratches (88.11% in I^1 and 81.81% in I_2) identified on the Meipu teeth are oriented in the right oblique direction, with the right oblique (22.5°-67.5°) being the most common type (47.55% for I^1 and 54.55% for I_2, Tables 1 and 2). Therefore, the individuals represented by the I^1 and I_2 were likely right-handed or at least used the right hand to perform the "stuff and cut" activity. The right oblique scratches are observed to extensively overlap with others, indicating or implying a repetitive and "habitual" use of the right hand as the dominant one.

Comparing Meipu and other hominins: Oblique scratches likely generated by right-handed "stuff and cut" behavior have been identified in other hominins using quantifiable characteristics of scratches, similar to those measurements used in this study (Table 3). The average direction of 47.11° in the Meipu I^1 and 44.60° in the Meipu I_2 is close to the value of 50.66° in Sima de los Huesos (SH site) and falls into the range of variation from Regourdou 1 (Table 3). The mean width of all scratches is 38.41 μm in Meipu I^1 and 44.53 μm in Meipu I_2, very close to the mean of Sima de los Huesos (SH), Boxgroves, El Sidrón, and within the range of variation from the Krapina Neanderthals (Table 3). However, the present study only considered those cutmarks wider than 20 microns, and may have shifted the distribution of the scratch width. The Meipu I^1 average scratch length is only slightly smaller than that of the SH specimens. The Meipu I_2 average scratch length is smaller than those of the Regourdou 1 mandible and Boxgroves lower anterior teeth (Table 3).

In addition to the scratches, there are two pieces (chips) of enamel broken from the

incisal edge of the Meipu I^1 (Figure 2). In Krapina teeth (Fox & Frayer, 1997), this type of microchip has been associated with scratches and is thought to be produced when using the teeth as the third hand during "stuff and cut" behavior. As revealed by previous studies, the dental scratches are usually concentrated in the central part of the labial face (Fox & Frayer, 1997, Hillson *et al*., 2010). And, the scratches left by right-handed individuals are generally clustered in the mesial half of a left tooth and the distal half of a right tooth (Fox & Frayer, 1997). The distribution of the scratches on the Meipu incisors, an upper left and a lower left incisor, matches the expected pattern. The scratch number in the Meipu I^1 is less than those in Vindja 290 (Frayer *et al*., 2010) and OH65 (Frayer *et al*., 2016). However, number of scratches on the Meipu I^1 is greater than most other specimens of *H. heidelbergensis* and *H. neanderthalensis* (Lozano *et al*., 2008; Hillson *et al*., 2010; Estalrrich & Rosas, 2013). The great number and overlapping pattern of the dental scratches in Meipu I^1 imply a highly frequent "stuff and cut" activity during the lifetime of this individual.

Although Bax and Ungar (1999) questioned the use of labial striations to infer handedness, experimental studies (Bermúdez de Castro *et al*., 1988; Lozano-Ruiz *et al*., 2004) as well as multiple detailed analyses of these scratches on fossil teeth have established that dental scratch orientation is a reliable indicator of handedness in "stuff and cut" behavior (Bérmudez de Castro *et al*., 1988; Fox & Frayer, 1997; Lozano-Ruiz *et al*., 2004; Frayer *et al*., 2012, 2016; Volpato *et al*., 2012; Condemi *et al*., 2017). These studies show that the morphologies and sizes of the scratches correspond with cutmarks produced by lithic tools. The location-specific distribution within a tooth (normally the middle section of the labial enamel), and tooth-specific presence within the individual dentition (normally in anterior teeth, especially in the upper incisors) (the present study, see also Lozano-Ruiz *et al*., 2004), indicate the non-random occurrence of oblique scratches. Tests with porcelain or real teeth during the activity of "stuff and cut" generate a similar pattern of scratches as those identified in fossil hominins (Bermúdez de Castro *et al*., 1988; Lozano-Ruiz *et al*., 2004).

With the presence of predominant right-oblique scratches on the labial enamel surface, the Meipu I^1 and I_2 from Early Pleistocene of southern China provides the earliest evidence of "stuff and cut" behavior and right-handedness in East Asia. There are only two anterior teeth

recovered from the Meipu site, but all of them display the dental scratches. It might imply that the "stuff and cut" behavior and inferred right-handedness were not uncommon among this population. However, the estimation of frequency of handedness or "stuff and cut" behavior in *Homo erectus* or East Asia requires more evidences. The present study extends the known range of right-handedness and "stuff and cut" behavior within the *Homo* lineage, in temporal, spatial, and taxonomic contexts.

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References

Annett M. 1985. *Left, Right, Hand and Brain: The Right Shift Theory*. Lawrence Erlbaum Associates: London.

Bax JS, Ungar PS. 1999. Incisor labial surface wear striations in modern humans and their implications for handedness in Middle and Late Pleistocene hominids. *International Journal of Osteoarchaeology*, 9:189-198.

Bermúdez de Castro JM, Bromage TG, Fernández-Jalvo Y. 1988. Buccal Striations on fossil human anterior teeth: evidence of handedness in the middle and early Upper Pleistocene. *Journal of Human Evolution* 17:403-412.

Brace CL. 1975. Comment on ‘‘Did La Ferrasie I use his teeth as tools?’’. *Current Anthropology* 16:396-397.

Brace CL. 1991. The stages of human evolution. Englewood Cliffs (NJ): Prentice-Hall. 200p.

Carslaw DC, Ropkins K. 2012. Openair—an R package for air quality data analysis. *Environmental Modelling & Software* 27:52-61.

Cashmore L, Uomini N, Chapelain A. 2008. The evolution of handedness in humans and great apes: a review and current issues. *Journal of anthropological sciences* 86:7-35.

Condemi S, Monge J, Quertelet S, Frayer DW, Combier J. 2017. Vergisson 4: a left-handed Neandertal. *American Journal of Physical Anthropology 162*:186-190.

Dong W. 2016. Biochronological framework of *Homo erectus* horizons in China. *Quaternary International* 400:47-57.

Estalrrich A, Rosas A. 2013. Handedness in Neandertals from the El Sidron (Asturias, Spain): Evidence from instrumental striations with ontogenetic inferences. *PLoS ONE* 8: e62797.

Estalrrich A, Rosas A. 2015. Division of labor by sex and age in Neandertals: an approach through the study of activity-related dental wear. *Journal of Human Evolution* 80:51-63.

Faurie C, Raymond M. 2004. Handedness frequency over more than ten

thousand years. *Proceedings of the Royal Society of London B: Biological Sciences* 271:S43-S45.

Francks C, Fisher SE, MacPhie IL, Richardson AJ, Marlow AJ, Stein JF, Monaco AP. 2002. A genomewide linkage screen for relative hand skill in sibling pairs. *The American Journal of Human Genetics* 70:800-805.

Fox CL, Frayer DW. 1997. Non-dietary Marks in the Anterior Dentition of the Krapina Neanderthals. *International Journal of Osteoarchaeology* 7:133-149.

Fox CL, Pérez-Pérez A. 1994. Cutmarks andpost-mortem striations in fossil human teeth. *Human Evolution* 9:165-172.

Frayer DW, Fiore I, Laluezafox C, Radovcić J, Bondioli L. 2010. Right handed Neandertals: vindija and beyond. *Journal of Anthropological Sciences*, 88:113-127.

Frayer DW, Lozano M, Bermúdez de Castro JM, Carbonell E, Arsuaga JL, Radovčić J, Fiore I, Bondioli L. 2012. More than 500,000 years of right-handedness in Europe. *Laterality: Asymmetries of Body, Brain and Cognition* 17:51-69.

Frayer DW, Clarke RJ, Fiore I, Blumenschine RJ, Pérez-Pérez A, Martinez LM, Estebaranz F, Holloway R, Bondioli L. 2016. OH-65: The earliest evidence for right-handedness in the fossil record. *Journal of Human Evolution* 100:65-72.

Hillson S, Parfitt SA, Bello SM, Roberts MB, Stringer CB. 2010. Two hominin incisor teeth from the Middle Pleistocene site of Boxgrove, Sussex, England. *Journal of Human Evolution* 59: 493-503.

Holloway RL, De La Coste-Lareymondie MC. 1982. Brain endocast asymmetry in pongids and hominids: some preliminary findings on the paleontology of cerebral dominance. *American Journal of Physical Anthropology* 58:101-110.

Levy J, Nagylaki T. 1972. A model for the genetics of handedness. Genetics 72: 117-128.

Li T, Etler DA. 1992. New middle Pleistocene hominid crania from Yunxian in China. *Nature* 357:404-407.

Lozano-Ruiz M, Bérmudez De Castro JB, Martinón-Torres M, Sarmiento S. 2004. Cutmarks on fossil human anterior teeth of the Sima de los Huesos site (Atapuerca,

Spain). Journal of Archaeological *Science* 31:1127-1135.

McKeever WF. 2000. A new family handedness sample with findings consistent with X-linked transmission. *British Journal of Psychology* 91:21-39.

Molnar S. 1971. Human tooth wear, tooth function and cultural variability. *American Journal of Physical Anthropology* 34:175-189.

Ocklenburg S, Beste C, Arning L, Peterburs J, Güntürkün O. 2014. The ontogenesis of Language lateralization and its relation to handedness. *Neuroscience & Biobehavioral Reviews* 43:191-198.

Puech PF. 1982. L'usure dentaire de I'Homme de Tautavel. In *L'Homo erectus et laplace de 1'Homme de Tautavel parmi les hominidés fossiles*. *Congrés International de Paléontologie Humaine,* 1^0 Congrés, Nice. CNRS. Pretirage, Tome 1.

Rugg G, Mullane M. 2001. Inferring handedness from lithic evidence. *Laterality* 6:247- 259.

Sparacello VS, Villotte S, Shackelford LL, Trinkaus E. Patterns of humeral asymmetry among Late Pleistocene humans. *Comptes Rendus Palevol* http://dx.doi.org/10.1016/j.crpv.2016.09.001

Toth N. (1985). Archaeological evidence for preferential right-handedness in the Lower and Middle Pleistocene, and its possible implications. *Journal of Human Evolution* 14:607-614.

Trinkaus E, Churchill SE, Ruff CB. 1994. Postcranial robusticity in Homo II: Humeral bilateral asymmetry and bone plasticity. *American Journal of Physical Anthropology* 93:1-34.

Volpato V, Macchiarelli R, Guatelli-Steinberg D, Fiore I, Bondioli L, Frayer DW. 2012. Hand to mouth in a Neandertal: Right-handedness in Regourdou 1. PLoS One 7:e43949.

Willman JC. 2016. Dental wear at Dolní Věstonice II: Habitual behaviors and social identities written on teeth. In: Svoboda J, editor. *Dolní Věstonice II: Chronostratigraphy, Paleoethnology, Paleoanthropology Dolní Věstonice Studies 21*. Brno: Archeologický ústav AV ČR. p 353-371.

Wu RK, Dong XR. 1980. The fossil human teeth from Yunxian, Hubei. *Vertebrata Palasiatica* 18:142-149.

Xu C. 1978. The excavation of *Homo erectus* site at Meipu, Yunxian, Hubei (in Chinese). In: *Proceedings of Paleoanthropology of the Institute of Vertebrate Paleontology and Paleoanthropology. Chinese Academy of Sciences* (pp. 175-179). Science Press: Beijing.

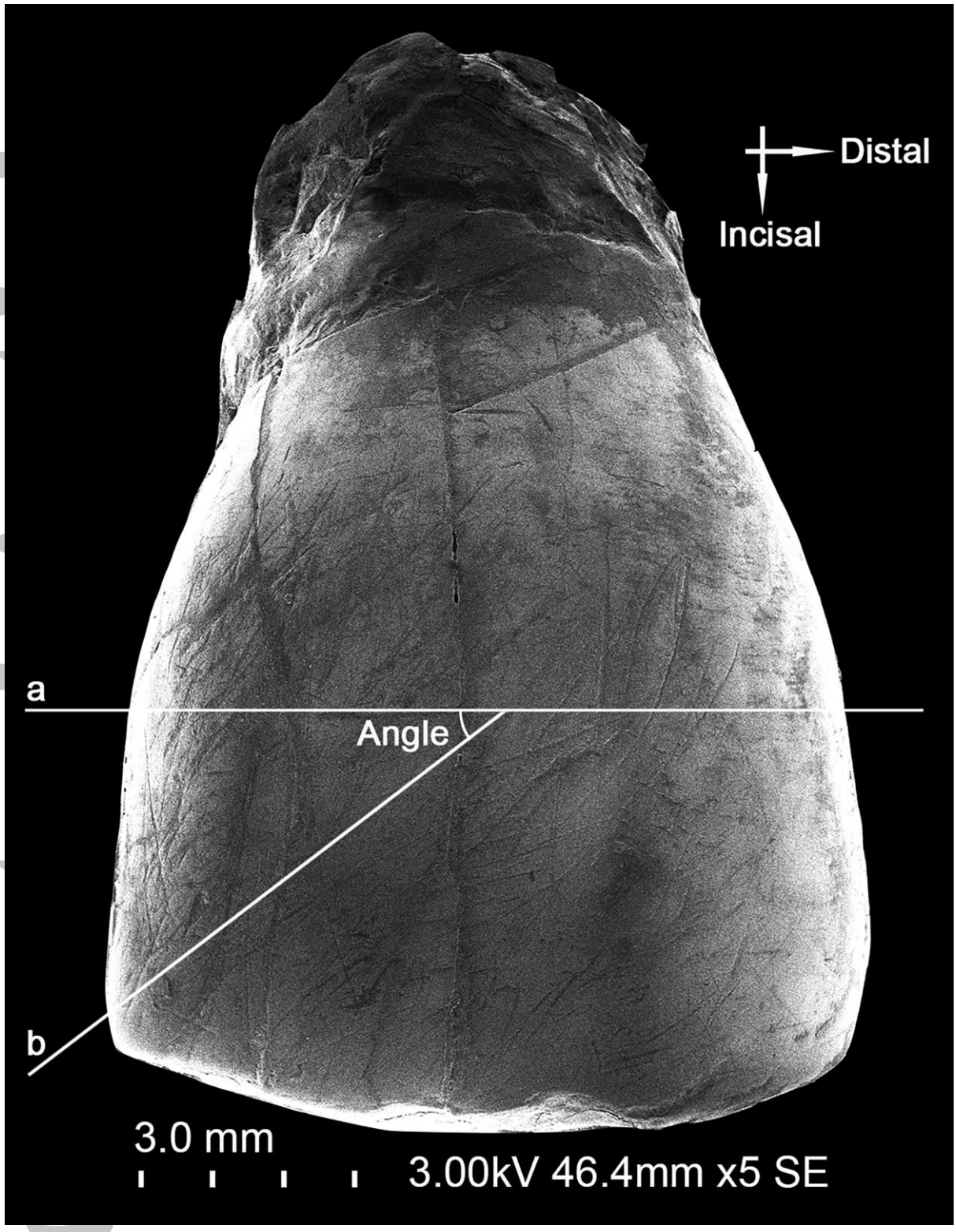

Figure 1. SEM image of the Meipu I[1], showing the whole labial surface and the way of measuring the angles of dental scratches (a: a horizontal line; b: an example line tracing one of the scratches).

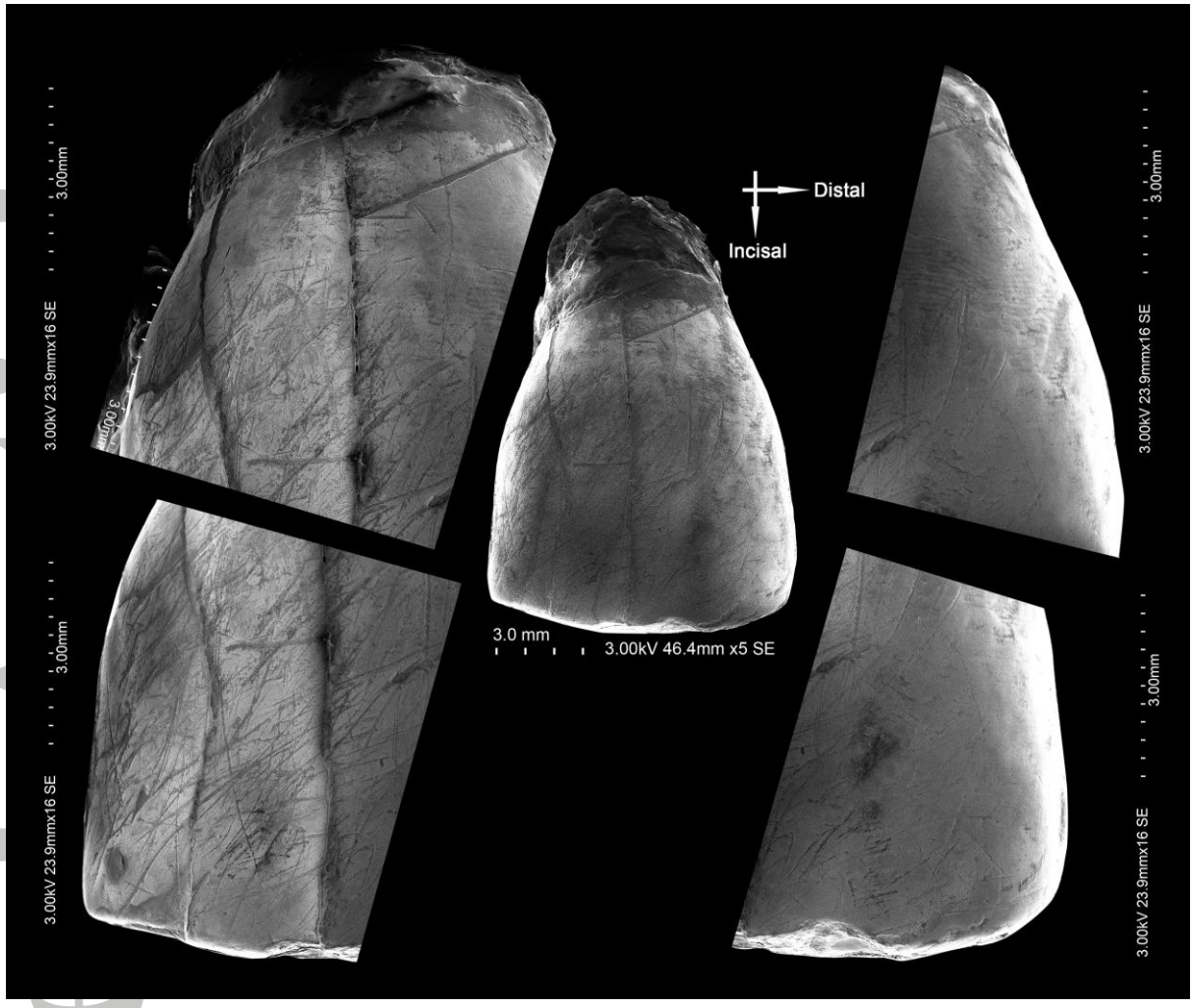

Figure 2. SEM images of the labial surface of Meipu I[1], showing the distributions and orientations of the dental scratches. Four SEM images of higher magnification (16 x) representing each quarter of the labial surface were added.

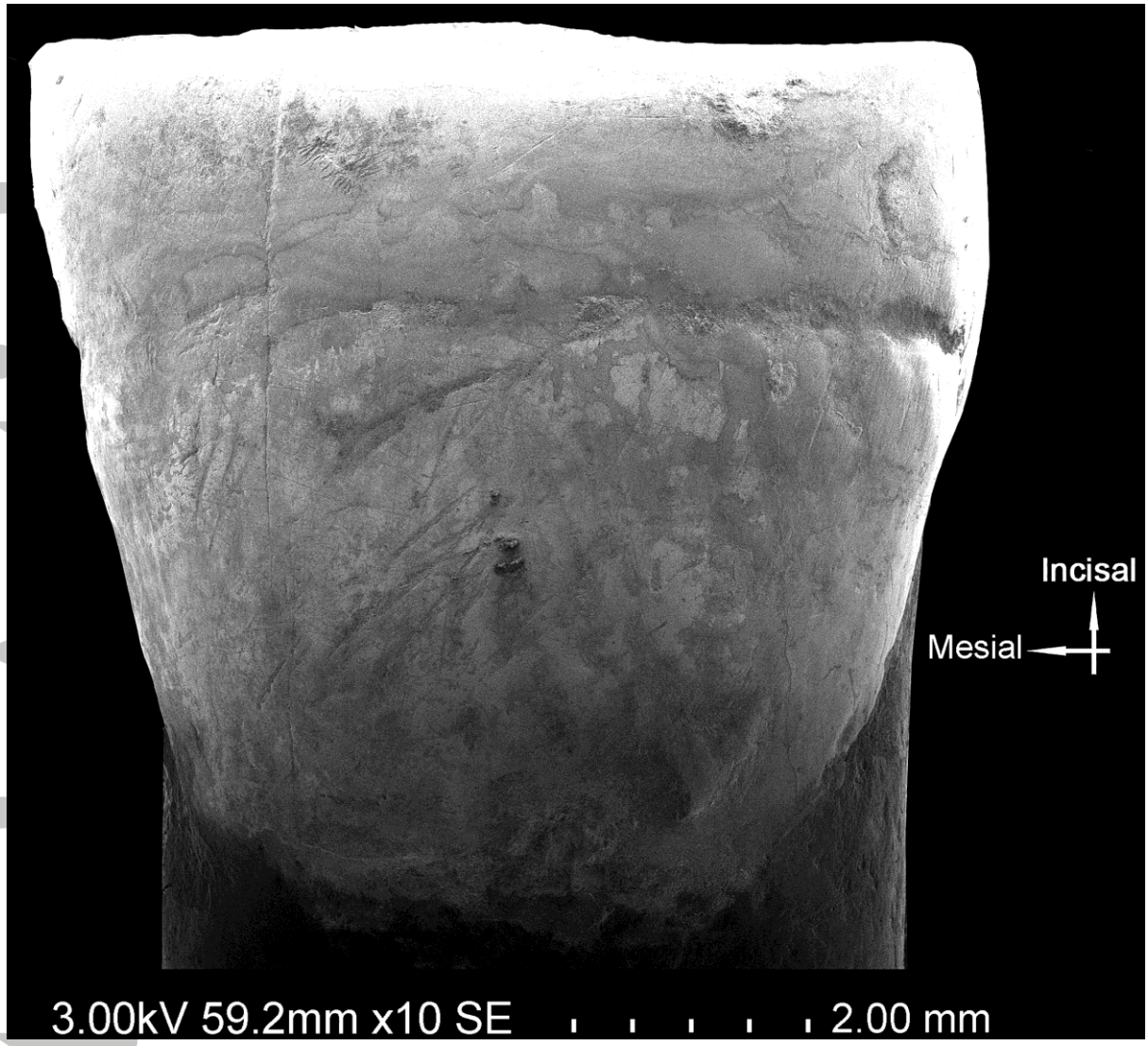

Figure 3. SEM images of the labial surface of Meipu I_2, showing the distributions and orientations of the dental scratches.

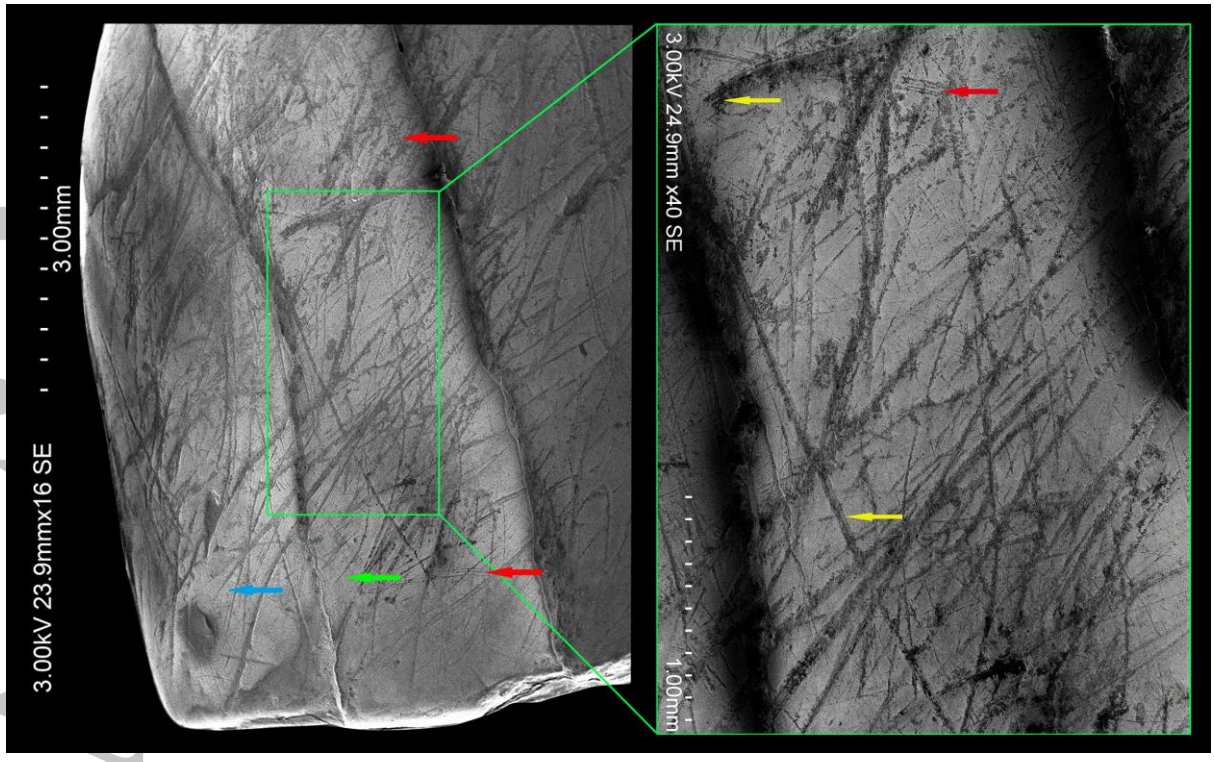

Figure 4. SEM images of the labial surface of Meipu I[1], showing the details of the dental scratches under a higher magnification (16x and 40x). The following features are indicated: a scratch with a sharp end (blue arrow), S-shaped scratch (green arrow), fine striations inside a larger scratch (yellow arrow), and multiple-furrow parallel scratches (red arrows).

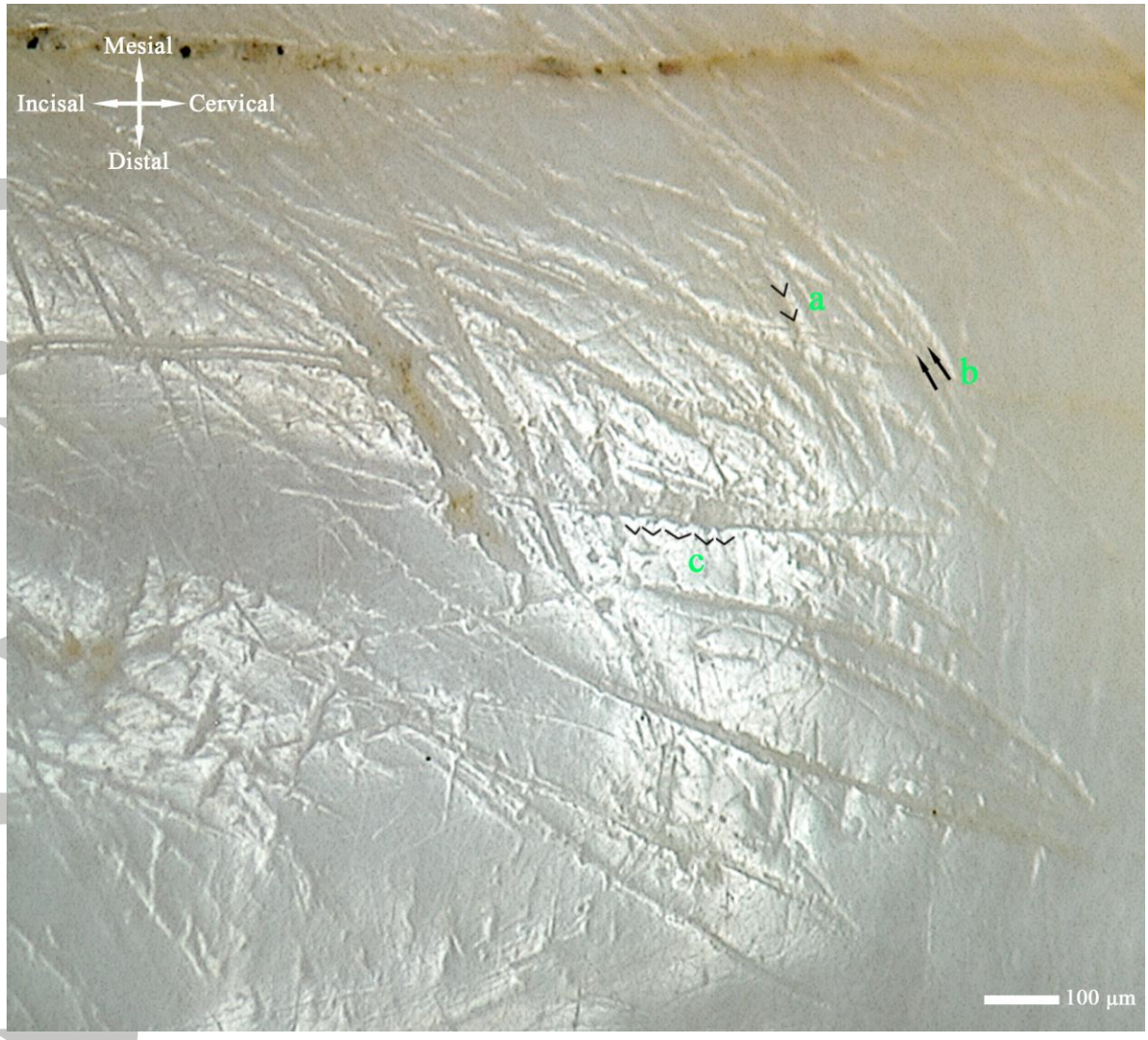

Figure 5. Microscopic images of the labial surface of Meipu I[1], showing the micromorphologies of the dental scratches.

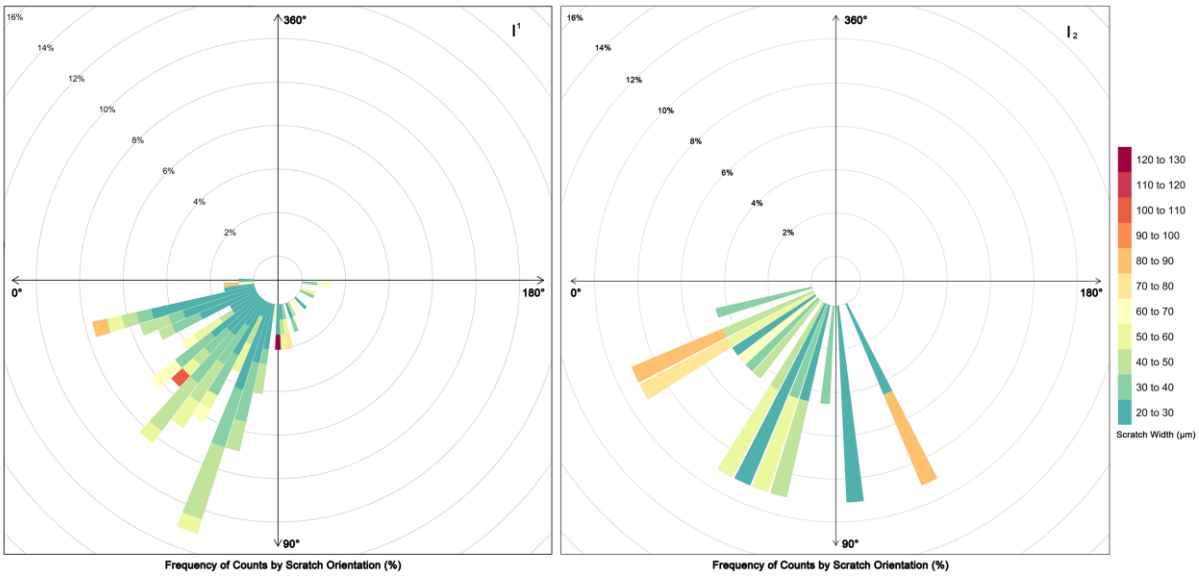

Figure 6. A rose diagram of the orientations (frequency indicated by the length of the bin) and widths (indicated by a color gradient) of the dental scratches. The scratches are grouped by every 5°.

Table 1. The descriptive statistics of angles, widths, and lengths of dental scratches in Meipu I[1]. The scratches are classified into four categories (horizontal, right oblique, vertical, and left oblique) according to their orientation following Bermúdez de Castro et al. (1988). The categories for the horizontal orientation was listed here as two separated groups based on the different angles (0°-22.5° and 157.5°-180°).

	Number	Frequency	Angle (Mean±SD)	Width (Mean±SD)	Length (Mean±SD)
Total	143	100%	56.71 ± 32.36	38.41 ± 17.02	1276.28 ± 710.76
Horizontal (0°-22.5°)	24	16.78%	14.98 ± 5.71	36.32 ± 19.44	1028.52 ± 557.51
Right Oblique (22.5°-67.5°)	68	47.55%	47.11 ± 11.61	38.72 ± 15.61	1233.69 ± 643.98
Vertical (67.5°-112.5°)	44	30.77%	79.80 ± 11.43	37.95 ± 18.16	1467.33 ± 811.58
Left Oblique (112.5°-157.5°)	4	2.79%	131.92 ± 17.39	41.48 ± 15.80	1524.99 ± 1250.96
Horizontal (157.5°-180°)	3	2.10%	169.23 ± 10.05	51.13 ± 16.43	1090.04 ± 339.03

Table 2. The descriptive statistics of angles, widths, and lengths of dental scratches in Meipu I_2. The scratches are classified into four categories (horizontal, right oblique, vertical, and left oblique) according to their orientation following Bermúdez de Castro et al. (1988). The categories for the horizontal orientation was listed here as two separated groups based on the different angles (0°-22.5° and 157.5°-180°).

	Number	Frequency	Angle (Mean±SD)	Width (Mean±SD)	Length (Mean±SD)
Total	22	100%	61.10±29.02	44.53±20.18	570.50±255.10
Horizontal (0°-22.5°)	1	4.55%	15.55	32.07	349.56
Right Oblique (22.5°-67.5°)	12	54.55%	44.60±16.13	48.95±21.09	592.98±285.55
Vertical (67.5°-112.5°)	7	31.82%	79.87±11.00	36.02±8.92	601.11±245.23
Left Oblique (112.5°-157.5°)	2	9.09%	117.16±0.18	53.98±45.90	438.95±113.07
Horizontal (157.5°-180°)	0	0.00%	--	--	--

* "--" indicates missing value.

Table 3. The parameters of Meipu I[1], I_2, and comparative specimens[*].

	Meipu I[11]	Meipu I_2[1]	*H. heidelbergensis*		*H. neanderthalensis*			
			Sima de los Huesos[2,3]	Boxgroves[4]	Krapina[5]	Regourdou[6]	El Sidrón[7]	Vindija[8]
Average value of the angle degree of the right oblique angle (°)	47.11 ± 11.61	44.60±16.13	50.66		---	41.92±11.69-54.85±12.38		
Maximum width (μm)	122.29	89.01	62.6	93.60	122.20	---		
Average width ± SD (μm)	38.41 ± 17.02	44.53±20.18	43.20±17.8	45.00±15.10 or 50.00±16.80	25.50±7.10 -67.70±37.10	---	43.50± 16.00	
Maximum length (μm)	4036.88	1236.50	1960.60	2380.00	6000.00	4362.00		2970.00
Average length ± SD (μm)	1276.28 ± 710.76	570.50±255.10	1507.30±597.50	884.10±485.50 or 852.30±365.10	---	1098.25±759.78-5066.70±371.71		

* 1: present study; 2: Lozano-Ruiz *et al*., 2004, 2008; 3: Lozano *et al*., 2008; 4: Hillson *et al*., 2010; 5: Fox & Frayer, 1997; 6: Volpato *et al*., 2012; 7: Estalrrich & Rosas, 2013; 8: Frayer *et al*., 2010.