Late Pleistocene hominin teeth from Laoya Cave, southern China

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Abstract Recent fossil finds have complicated the picture of East Asian Late Pleistocene hominin taxonomy and morphology, necessitating analysis of more fossils with secure dates and stratigraphic contexts to better contextualize human evolution during this epoch. Field excavations at the Laoya Cave in Guizhou Province, China in 2013 recovered two isolated human teeth (M_3 and dm^2). The teeth date from ~21–24 kya, according to AMS radiocarbon dating. The present study provides detailed metric and non-metric descriptions of the Laoya teeth, and compares them with the dentition of other Late Pleistocene hominins (Neanderthals and fossil *Homo sapiens* from around the world) as well as chronologically earlier fossil hominins from the same geographical area (East Asian Early/Middle Pleistocene hominins). To achieve this, descriptive morphological observations, geometric morphometric analysis, and micro-computed tomography were employed. The lower third molar (LYC1) is characterized by several derived features, including the absence of a hypoconulid, the lack of C6 and C7, and an 'X'-type cuspal arrangement. The combination of traits expressed by LYC1 is unique, but very similar to other recent *H. sapiens*. However, the LYC1 also displays a suite of dental features that are not common in other East Asian Late Pleistocene fossil *H. sapiens*: the absence of a hypoconulid, the presence of a middle trigonid crest, and a narrowed talonid relative to trigonid. This study of the Laoya teeth expands the known morphological diversity of East Asian Late Pleistocene hominin dentitions, and will contribute to a better understanding of the history of modern humans in this area.

Key words: fossil *H. sapiens*, dental materials, morphology, micro-CT

Introduction

Fossil hominins have been identified at around 50 Late Pleistocene sites across mainland East Asia (Wu and Poirier, 1995; Liu et al., 2010a, b; Li et al., 2017), but the absence of well-defined stratigraphy and/or radioactive dates has made it difficult to place many of these fossils in clear evolutionary contexts. Recently, several reliably dated sites with clear stratigraphy have yielded new *Homo sapiens* fossils, which have revealed an unexpected morphological diversity and a longer chronology of our species in East Asia (Liu et al., 2010a, b, 2015; Curnoe et al., 2012; Bae et al., 2014). In this context, a new Late Pleistocene hominin site, Laoya Cave (LYC), was excavated in 2013. The excavation recovered new human fossil materials, which provide an important opportunity to investigate further the morphological diversity of hominins in the Late Pleistocene.

The Laoya Cave is located in Qingchang Town, Bijie City, Guizhou Province, southern China (27°21'12.57"N, 105°1'8.46"E) (Figure 1). Excavations there between 1983 and 1985 produced an abundance of lithic artifacts and fragmentary mammal bones (Guan et al., 2015). More recently, more than 2000 lithic and bone tools, faunal remains, seed husks, and carbon debris were recovered in the period July–August 2013 (Guan et al., 2015). The deposit is divided into 11 stratigraphic layers (Figure 1), all of which contain mammal fossils, lithic tools, and carbon debris. Among the fossil materials, a fossil hominin isolated upper left deciduous m^2 (dm^2) was recovered from Layer 2 and a fossil hominin isolated lower left third molar (M_3) was recovered from Layer 4 (see the Results section for the classification of the category for this tooth).

The lithic assemblage includes cores, flakes, and retouched pieces such as scrapers, points, choppers, etc. (Guan et al., 2015). To date, 13 mammal species have been identified in the assemblage: *Macaca* sp., *Rhinopithecus* sp., *Rhizomys* sp., *Hystrix* sp., *Ursus* sp., *Ailuropodamelanoleuca*, *Arctonyx* sp., *Tapirus* sp., *Rhinoceros* sp., *Moschus* sp., *Muntiacus* sp., *Capricornis sumatraensis*, and various bovids. These faunal components are typical of southern China in the Late Pleistocene (Wang et al., 2016).

Sixteen samples of mammalian bones and carbon debris

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Figure 1. Geographic locations of Laoya Cave, other major Chinese Late Pleistocene hominin sites, and the stratigraphic sequences of the Laoya Cave (upper left). From top to bottom, the sedimentary compositions of each stratigraphic layer in the Laoya Cave are: (1) grayish yellow travertine, (2) gray-black clay, (3) grayish yellow clay, (4) black clay, (5) gray sandy clay, (6) dark brown ash, (7) yellow sandy clay, (8) yellow sandy clay, (9) dark brown ash, (10) yellow sandy clay, (11) gravel and silt.

Table 1. Radiocarbon dating results from the Laoya Cave site

Layers	Method	Sample; pretreatment method	Uncorrected age (BP)	Corrected age (cal BP)	Maximum layer range (cal BP)
1	AMS-SD	bone collagen; extraction with alkali	12270 ± 50	14285–14065	14285–14065
2	AMS-SD	bone collagen; extraction with alkali	17670 ± 60	21550–21205	
2	AMS-SD	bone collagen; extraction with alkali	17530 ± 60	21360–20995	21550–20995
2	AMS-SD	charred material; acid/alkali/acid	17640 ± 60	21510–21150	
3	AMS-SD	bone collagen; extraction with alkali	19460 ± 70	23605–23295	
3	AMS-SD	bone collagen; extraction with alkali	19760 ± 60	23940–23650	23940–23295
4	AMS-SD	bone collagen; extraction with alkali	19890 ± 70	24085–23790	
4	AMS-SD	bone collagen; extraction with alkali	20150 ± 70	24370–24065	24370–24065
5	AMS-SD	bone collagen; extraction with alkali	22140 ± 80	26525–26140	
5	AMS-SD	bone collagen; extraction with alkali	22910 ± 90	27405–27130	27405–26140
6	AMS-SD	bone collagen; extraction with alkali	23460 ± 90	27740–27525	
7	AMS-SD	bone collagen; extraction with alkali	25480 ± 110	29795–29340	29795–29340
8	AMS-SD	bone collagen; extraction with alkali	26000 ± 120	30630–29875	
8	AMS-SD	bone collagen; extraction with alkali	32640 ± 220	37060–36130	37060–29875

from Layers 1–10 were sent to Beta Analytic Inc. (USA) for radiocarbon dating using the AMS-SD method (Table 1). Two samples failed to provide enough collagen to analyze, but the dating results of the remaining 14 samples are listed in Table 1. The fossil hominin tooth from Layer 2 could be securely assigned to ~21 kya and the tooth from Layer 4 could be assigned to ~24 kya.

In this study, we provide a systematic metric and morphological study of the Laoya Cave teeth to explore how the Laoya hominins fit within the known dental morphological context of East Asian Late Pleistocene *Homo*. This is achieved using descriptive morphological observations, ge-

ometric morphometric analysis, and micro-computed tomography (micro-CT). The Laoya Cave dm² (LYC2) is only partially preserved, so this study will focus mainly on the M₃ (LYC1).

Materials and Methods

The permanent molar (LYC1) was classified as an M₃ rather than an M₂ for two reasons: (i) the geometry of the crown outline shape (see Results); and (ii) the presence of a mesial interproximal wear facet and the absence of a distal facet.

Due to its relatively recent Late Pleistocene age (~24 kya),

Table 2. Comparative specimens used in the present study

		<i>n</i>	Localities	Sources (metrics)
East Asian Early/Middle Pleistocene		26	Lantian, Hexian, Sangiran, Zhoukoudian	Tobias and von Koenigswald, 1964; Grine and Franzen, 1994; Kaifu et al., 2005; Zanolli, 2013
Neanderthal		48	Amud, Arcy Hyene, Arcy Grotte Renne, Arcy Sur Cure (Mousterian), Ehringsdorf, Genay (Côte d'Or), Hortus, Krapina, La Quina, Ochoz, Petit Puymoyen, Regourdou, Shanidar, Spy, St. Césaire, Subalyuk, Tabun, Vindija	Milford Wolpoff, personal communication
Recent <i>H. sapiens</i>	Africa	40	South Africa	This study
	East Asia	107	Xichuan (Henan Province), Yunxian, Danjiangkou, Xiangyang, and Fangxian (Hubei Province)	
Fossil <i>H. sapiens</i>	Africa	2	Klasies River mouth	Rightmire and Deacon, 1991
	West Asia	10	Qafzeh, Skhul	Milford Wolpoff, personal communication
	East Asia	20	Baojiyan, Chuandong, Daoxian, Fusui Nanshan, Huanglong Cave, Huli Cave, Jimuyan, Longlin, Maludong, Tianyuan Cave, Tubo, Zhiren Cave	Wang et al., 1982; Huang, 1989; Wang and Mo, 2004; Liu et al., 2010a, b; Wang et al., 2011; Liu et al., 2015;
	Europe	23	Abri Pataud, Combe Capelle, Dolní Věstonice, Isturitz, Le Rois, Mladeč, Pavlov, Predmostí, SG-LR	Milford Wolpoff, personal communication

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the Laoya Cave M₃ (LYC1) will be compared to several hominin groups: (i) Late Pleistocene hominins (Neanderthals and fossil *H. sapiens* from around the world); (ii) chronologically earlier fossil hominins from the same geographical area (East Asian Early/Middle Pleistocene hominins); and (iii) recent East Asian and African *H. sapiens*. The recent East Asian *H. sapiens* sample comes from archaeological sites in central China, spanning the Neolithic to the Ming-Qing Dynasty. The recent African *H. sapiens* samples were obtained from the Raymond Dart Collection of Human Skeletons housed at the University of the Witwatersrand. Comparisons from other sources will be made throughout the text, particularly from Martínón-Torres et al. (2012). For detailed information of the comparative specimens (both M₂ and M₃), see Table 2. For details of the specimens included in the geometric morphometric analysis, see SI Table 1.

Morphological traits and metrics

All morphological descriptions, scoring, and comparisons were performed following the Arizona State University Dental Anthropology System (ASUDAS) (Turner et al., 1991) and the revised ASUDAS described in Martínón-Torres et al. (2012). Mesiodistal (MD) and buccolingual (BL) dimensions of the crown were measured with standard sliding calipers and recorded to the nearest 0.1 mm, following the methods of Wolpoff (1971). Two box-plots (MD and BL, respectively) were used to display the metric variation among different groups. Additionally, the combination of non-metric traits expressed by each individual tooth in the sample was explored and compared to that of LYC1. A cluster analysis was also performed to compare the non-metric traits of LYC1 to individuals from other taxonomic groups.

Geometric morphometric analysis

Geometric morphometric (GM) analysis was performed on standardized occlusal surface pictures of M₂ and M₃ to examine the crown outline shape for two reasons: first, to classify the permanent molar (LYC1) as either M₂ or M₃

based on its outline shape; and second, to compare LYC1's shape to the other comparative specimens (Figure 2). The camera lens was oriented orthogonally to the plane formed by each tooth's cemento-enamel junction (CEJ) to standardize the pictures. When both anteriors were present, the left was photographed. When an individual was only represented by a right M₂ or M₃, the photograph was mirror-imaged in Adobe Photoshop® so it could be compared to the left M₂s and M₃s. Two landmarks (green circles on Figure 2) representing the intersection points of the mesiobuccal and the lingual occlusal grooves with the crown outline (referred to as Type 1 in Bookstein (1991)) were defined. The outlines of the trigonid and talonid were each divided into 20 equidistant segments using the TpsDig2 program (Rohlf, 1998a). The dividing points were treated as semi-landmarks (blue squares on Figure 2). Overall, two landmarks and 38 semi-landmarks were defined along the M₂ or M₃ crown outline (Figure 2). The TpsDig2 program (Rohlf, 1998a) was used to digitize landmarks and semi-landmarks. The TpsRelw program (Rohlf, 1998b) was employed to superimpose the raw coordinate data and the relative warp analysis (or principal component analysis) of shape variables.

The first 10 relative warp scores were used for Fisher linear discriminant function analyses and a standard cross-validation was conducted in SPSS 20.0. This step allows us to confirm the tooth category (M₂ or M₃) for LYC1, and then to estimate the membership of LYC1 within other taxonomic groups based on the crown outline shape.

Micro-computed tomography and the enamel-dentine junction

High-resolution micro-CT was employed to virtually reconstruct the enamel-dentine (EDJ) (the dentine surface) of LYC1. LYC1 was scanned using a 225 kV micro-CT scanner (designed by the Institute of High Energy Physics, Chinese Academy of Sciences, and housed at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences) equipped with a 1.0 mm aluminum filter

Figure 2. Left: the landmarks (circles) and semi-landmarks (squares) defined in the GM analysis of M_3 . Right: the mesial sectional plane of LYC1. B, buccal; L, lingual; M, mesial.

and using settings of 120 kV, 100 μ A, 0.5° angular increment per step, 360° rotation, with an average of 4 frames. The final isometric voxel size was 15.68 μ m. The images of raw projection generated from the scanner were converted to tomographic slices of RAW format with IVPP225kVCT_Recon software. The size of each slice was 2048×2048 pixels. Multiple slices were put into VGstudio 2.2 and the empty spaces were removed to reduce the file size. The final data was saved as a RAW volume file, which was then imported into Mimics 17.0 to complete the segmentation of enamel and dentine and to visualize the EDJ surface. During the processes of enamel/dentine segmentation, 3D Livewire, single/multiple slice modification, and thresholding tools were employed.

In addition to the visual reconstruction of the EDJ surface, the average and relative enamel thickness of LYC1 were measured on a 2-D standardized section plane of the crown (Figure 2). The plane was prepared following Olejniczak (2006). First, a horizontal plane was fixed by three dentine horn tips (protoconid, metaconid, and hypoconid). Then, a sectional plane, perpendicular to the previous one and simultaneously cutting through the dentine horn tips of protoconid and metaconid, was defined. The area of the enamel cap (c) and dentine (b) were measured as well as the length of the EDJ line (e). The dentine area was defined as the area enclosed by the EDJ line and the shortest connecting line between the two most cervical points.

The occlusal wear was corrected for by virtually reconstructing the missing enamel portion by employing unworn occlusal surfaces as models and by considering the orientations of outer enamel and inner EDJ lines (Figure 2). The mesial plane section was defined in VGstudio 2.2, and then input into ImageJ for measurement of the enamel cap and the dentine area. Average enamel thickness (AET) was defined as c/e , and relative enamel thickness (RET) as $100 (AET/\sqrt{b})$. Both the values calculated using the corrected and uncorrected measurements were recorded. The LYC1 measurements were compared with those obtained by Olejniczak et al. (2008) and Smith et al. (2012). The validity of comparing data from different methods has been discussed in other works (Olejniczak et al., 2008; Smith et al., 2012).

The 3-D average and relative enamel thickness of LYC1

were also measured. The tooth was adjusted to approximate its anatomical position in VGStudio 2.2. Following the method in Olejniczak (2006), a plane (A) was defined along the cervix as the most apical position that contains a continuous ring of enamel. Another cervical plane (B) was defined as the position at the apex of the tooth, carrying the last tip of enamel. The plane separating the crown and root areas was located halfway between planes A and B. Volume (in mm^3) and area (in mm^2) measurements were recorded in the crown part following Kono (2004) and Olejniczak (2006): (i) the volume of the enamel cap (EVOL); (ii) the volume of coronal dentine (including the part of pulp cavity intruded into enamel cap) (DVOL); and (iii) the surface area of the EDJ surface (EDJESA). Average enamel thickness (in mm) (AET3D) was calculated as $\text{EVOL}/\text{EDJESA}$, and relative enamel thickness (RET3D) as $\text{AET3D} \times 100/\sqrt{\text{DVOL}}$ (Kono, 2004; Olejniczak, 2006). Avizo 8.0 was used to visualize the distribution pattern of 3-D enamel thickness for LYC1.

Results

Descriptions

Only the protocone and a small portion of the lingual root are present on the dm^2 , LYC2 (Figure 3). The MD and BL measurements of the remaining part are 5.52 and 5.16 mm, respectively. The occlusal wear is heavy, exposing a large band of dentine (grade 3 or 4 according to Molnar (1971)). There is no sign of Carabelli's cusp on the protocone. Due to the level of wear and broken nature of LYC2, it will not be analyzed extensively in this paper.

The LYC1 M_3 crown is well preserved and while there is some wear (Figure 4), no dentine is exposed (grade 2 wear according to Molnar (1971)). Unfortunately, most of the root is missing. The mesial interproximal wear facet is oval and large and there is no distal interproximal wear facet. LYC1 has a trapezoidal crown outline with a narrowing talonid (Figure 4, Figure 5). All four main cusps (protoconid, metaconid, hypoconid, and entoconid) are present. There is no sign of a hypoconulid, C6, or C7. The protoconid and entoconid are connected so the main groove forms an 'X' pattern (ASUDAS; grade 2 in Martín-Torres et al. (2012)).

Figure 3. The dm^2 from Laoya Cave (o, occlusal; m, mesial; l, lingual; B, buccal; D, distal).

Figure 4. The M_3 from Laoya Cave (o, occlusal; b, buccal; m, mesial; l, lingual; d, distal).

A linear-like anterior fovea is present and well developed (ASUDAS grade 2). Distal to the anterior fovea is a middle trigonid crest (MTC) that is slightly notched by the mesial groove (Type 3 or 5 according to Korenhof (1982); Type A according to Martínez de Pinillos et al. (2014); grade 1 according to Martín-Torres et al. (2012)). There is no distal trigonid crest (DTC) or deflecting wrinkle. The distal accessory ridge of the protoconid is present, as are both the mesial and distal accessory ridges of the hypoconid. A pit is present slightly lingual to the cusp tip of the metaconid (Figure 4, Figure 5). The buccal surface of the crown is featureless and does not include a protostylid. The buccal cervical line is slightly convex at the point where root bifurcation is most likely, and the enamel extension is grade 1 according to ASUDAS.

The occlusal surface of the EDJ is simple, without secondary grooves or ridges (Figure 5 II, III), except the distal accessory ridges of the protoconid and metaconid which are slightly elevated. The essential ridges of both protoconid and metaconid are well developed, but their connections are completely disrupted (no continuous MTC) (Grade 1 according to Bailey et al. (2011); Type 4 according to Martínez de Pinillos et al. (2014)). The dentine horn of the metaconid is accompanied by a shelf-like structure on its distolingual side, corresponding to the large pit on the enamel surface (Figure 5). On the buccal surface of the EDJ, there is a secondary groove originating from the mesial groove and outlining a triangle-like protostylid (grade 4 if ASUDAS was followed, although no protostylid appears on the enamel surface). Mesial to the protostylid, a dentine groove was formed by the elongation of the mesial marginal ridge into

Figure 5. The visual reconstruction of the LYC1 outer enamel and EDJ surfaces reconstructed from micro-CT scanning. (I) Occlusal view of the outer enamel surface. The dotted line indicates the outline of the pit on the metaconid. (II) Enlarged view of the middle trigonid crest (MTC) area enclosed by the cyan rectangle in I; (III) Occlusal view of the EDJ surface. The dotted line points to the shelf-like structure on the metaconid. (IV) Buccal view of the EDJ surface. The dotted line indicates the dentine groove and the dotted triangle marks the protostylid. These images are not scaled.

the buccal area.

The enamel cap area, calculated on the 2-D section of the LYC1, is 18.87 mm²; when the cap is restored to correct for the occlusal wear, the cap area is 20.91 mm². The dentine area is 28.82 mm² and the EDJ length is 17.78 mm. The uncorrected 2-D average enamel thickness (AET2D) and relative enamel thickness (RET2D) are 1.06 mm and 19.74, respectively. The corrected values are 1.18 mm and 21.97, respectively. The volume of the enamel cap (uncorrected) and dentine are 217.51 mm³ and 183.25 mm³, respectively. The area of the EDJ surface is 155.47 mm². The uncorrected 3-D average enamel thickness (AET3D) and relative enamel thickness (RET3D) are 1.40 mm and 24.65, respectively.

Comparisons

Geometric morphometric analysis

Geometric morphometric analysis of M₂ versus M₃ crown shape indicates that the first two relative warps (RW1 and RW2) account for 39.89% and 22.24% of the total shape variation in the crown outline (Figure 6). Although the M₂ and M₃ areas overlap, the M₃ teeth are more displaced towards the negative-value extreme of both RW1 and RW2 axis. LYC1 is located near the lower left border of the M₃s in the graphics, and relatively far away from the area of M₂s. To further support the classification of LYC1 as M₃, discriminant function analysis (cross-validation) also clusters it with M₃s in 100% of cases (Figure 6).

Geometric morphometric analysis of M₃ crown shape (Figure 7) indicates that the first three relative warps (RW1, RW2, and RW3) account for 39.89%, 22.24%, and 15.85%, respectively, of the total shape variation of the crown outline. Specimens at the positive-value extreme of RW1 tend to have a more symmetrical crown contour with a talonid that is reduced in both MD and BL directions, and the mesial part of the crown is markedly wider than the distal end. In

contrast, specimens that fall along the negative end of RW1 tend to have an enlarged talonid in both MD and BL directions. Teeth at both the positive and negative extents of RW2 have an asymmetrical crown outline, with the talonid shifted in lingual and buccal direction related to the trigonid, respectively. Specimens at the negative-value extreme of RW2 tend to have a mesiodistally elongated crown related to those at other end. Compared to those in the negative-value extreme of RW3, teeth plotted against the positive-value end tend to have mesiodistally elongated crowns (SI Figure 1).

Although ranges overlap, there are still some distribution tendencies that can be traced (Figure 7). Most specimens of the East Asian Early/Middle Pleistocene hominins tend to distribute along the positive-value half of RW1, while the Neanderthals mainly plot along the negative-value half of RW1. Most specimens of fossil *H. sapiens* are distributed along the negative-value half of the RW3. The LYC1 plots in the far right side of the graph. Although LYC1 plots outside the distribution area of Neanderthals and *H. sapiens* along the RW1, it completely overlaps with them on the RW2 and RW3 axes.

Based on the discriminant functional analysis of the M₃ crown outline shape (SI Table 2), 29.7% of cross-validated grouped cases were correctly classified. When cross-validated, LYC1 falls into the recent *H. sapiens* group.

Metrics

The MD and BL dimensions of LYC1 are 11.0 mm and 10.1 mm, respectively. The MD measurement of LYC1 is at the upper limit of the first quartile for both East Asian Early/Middle Pleistocene hominins and West Asian fossil *H. sapiens* (Figure 8). It falls into the lower quartile of Neanderthals, the mid-range of fossil *H. sapiens* from Africa and Europe and recent East Asian *H. sapiens*, and the upper quartile of East Asian fossil *H. sapiens*. In the BL dimension,

Figure 6. Left: geometric morphometric analysis of M₂ and M₃. Right: discriminant function analysis of LYC1, M₂, and M₃.

Figure 7. Geometric morphometric analysis of M_3 , with the RW1 and RW2 being shown (TPS grids correspond to the positive-value or negative-value extremes of the RW axis). B, buccal; M, mesial.

Figure 8. Box-plot of the crown sizes of LYC1 and the comparative samples. LYC, Laoya Cave; EAEMP, East Asian Early and Middle Pleistocene hominins; NEA, Neanderthals; AFSAP, African fossil *H. sapiens*; WAFSAP, West Asian fossil *H. sapiens*; EFSAP, European fossil *H. sapiens*; EAFSAP, East Asian fossil *H. sapiens*; SAP, recent *H. sapiens*.

the LYC1 measurement only exceeds the range of African fossil *H. sapiens*. It falls below the median value for every other group, and only falls within the mid-range of recent East Asian *H. sapiens* and fossil *H. sapiens* from Europe and East Asia.

Morphology

Table 3 shows specific frequencies of morphological traits organized by group, geography, and grade; the gray highlighted rows represent the grade characteristic for LYC1.

Early/Middle Pleistocene East Asian hominins and Nean-

derthals typically have a hypoconulid, usually grade 3 or 4; the absence of this cusp in LYC1 is quite rare (present study; Martínón-Torres et al., 2012). Indeed, the presence of a grade 3–4 hypoconulid is common in East Asia across both fossil and recent *H. sapiens*. However, for fossil and recent *H. sapiens* outside of East Asia published by Martínón-Torres et al. (2012), the absence of a hypoconulid is more frequent (33.3% and 50.0%).

LYC1 lacks both a C6 and C7 cusp. The presence and size of these two cusps varies greatly in different groups. C6s and C7s are most frequently found in Early/Middle Pleistocene East Asian hominins. The absence of a C7 increases from 62.5% to 90.0% between fossil and recent East Asian *H. sapiens*.

Although notched by the central groove, an MTC is present in LYC1 (grade 1 in Martínón-Torres et al. (2012), see the description for the grade of this trait according to other scoring system). The presence of a MTC is quite rare in *H. sapiens*, with 89.9–100% of the reported fossil and recent *H. sapiens* missing an MTC (grade 0) (Table 3) (present study; Martínón-Torres et al., 2012). However, more than 50% of Neanderthal individuals had an MTC.

It is noteworthy that the MTC structure is present on the outer enamel surface but absent on the EDJ surface of LYC1 (Figure 5). Previous studies have detected this discrepancy (Bailey et al., 2011; Martínez de Pinillos et al., 2014). Martínez de Pinillos et al. (2014) noticed that the way in which MTC is expressed on the dentine surface is more complicated than on the enamel surface. Bailey et al. (2011) pointed out that the degree to which MTC expression corresponds between the enamel and dentine surfaces was lower

in *H. sapiens* than in Neanderthals, and the authors proposed that the thicker enamel found in *H. sapiens* might be the cause. Bailey et al. (2011) also states that when the discrepancy between enamel and dentine MTC expression occurs, the EDJ always has a higher degree of MTC expression.

The smooth EDJ surface of LYC1 is different from that of Hexian *H. erectus* PA834-2 (Xing et al., 2014). The essential crests of PA834-2 are more elevated or developed than in LYC1. In addition, LYC1 does not have as many accessory ridges as in PA834-2. The NG92.3 and NG0802.2 of Java *H. erectus* display an EDJ surface as simple as that of LYC1 (Zanolli, 2015). However, the EDJ surface of the other M₃ (NG9107.2) is slightly more complicated due to the development of several accessory ridges (Zanolli, 2015).

The frequency of non-Y pattern grooves increases through hominin history. The ‘X’ pattern, as in LYC1, did not become very common until relatively recently (Martínón-Torres et al., 2012; Xing et al., 2014). Only 4 out of 12 specimens of Early/Middle Pleistocene East Asian hominins exhibit the ‘X’ pattern. In comparison, the frequency of the ‘X’ pattern in recent East Asian *H. sapiens* is 90.0%.

The East Asian Early/Middle Pleistocene hominins generally express grades 0–2 (ASUDAS) of enamel extension in the M₃. LYC1 falls into this range, with grade 1 enamel extension. In contrast, about 54% of recent East Asian *H. sapiens* specimens exhibited grade 3 enamel extension. In some cases, the high degree of enamel extension forms a line of enamel extending all the way to the bifurcation point of the root/radical. This linear type of enamel extension has been reported in East Asian early Late Pleistocene fossil *H. sapiens* from Daoxian Fuyan Cave and Huanglong Cave (Liu et

Table 3. Frequencies of the degrees of expression of M₃'s main morphological traits

Grade		Early/Middle Pleistocene	Neanderthal	Fossil <i>H. sapiens</i>		Recent <i>H. sapiens</i>	
		East Asia	Europe and West Asia*	West Asia and Europe*	East Asia	Africa and Europe*	East Asia
Hypoconulid size	0	—**	2 (12.5%)	6 (33.3%)	—	63 (50.0%)	5 (7.1%)
	1	—	—	1 (5.6%)	—	3 (2.4%)	1 (1.4%)
	2	1 (9.1%)	1 (6.3%)	2 (11.1%)	—	14 (11.1%)	4 (5.7%)
	3	3 (27.3%)	7 (43.8%)	6 (33.3%)	3 (37.5%)	17 (13.5%)	14 (20.0%)
	4	6 (54.5%)	5 (31.3%)	2 (11.1%)	3 (37.5%)	17 (13.5%)	24 (34.3%)
	5	1 (9.1%)	1 (6.3%)	1 (5.6%)	2 (25.0%)	12 (9.5%)	22 (31.4%)
C6 size	0	2 (22.2%)	5 (33.3%)	12 (66.7%)	3 (50.0%)	94 (77.7%)	40 (57.1%)
	1	—	1 (6.7%)	—	—	9 (7.4%)	2 (2.9%)
	2	4 (44.4%)	4 (26.7%)	4 (22.2%)	2 (33.3%)	11 (9.1%)	9 (12.9%)
	3	3 (33.3%)	5 (33.3%)	2 (11.1%)	1 (16.7%)	7 (5.8%)	19 (27.1%)
C7 size	0	—	8 (53.3%)	13 (76.5%)	5 (62.5%)	98 (79.0%)	63 (90.0%)
	1	—	1 (6.7%)	1 (5.9%)	—	10 (8.1%)	2 (2.9%)
	2	2 (18.2%)	3 (20.0%)	3 (17.6%)	—	6 (4.8%)	1 (1.4%)
	3	5 (45.5%)	1 (6.7%)	—	1 (12.5%)	7 (5.6%)	2 (2.9%)
	4	4 (36.4%)	2 (13.3%)	—	2 (25.0%)	3 (2.4%)	2 (2.9%)
Middle trigonid crest	0	9 (75.0%)	1 (5.9%)	14 (93.3%)	8 (100.0%)	107 (89.9%)	69 (98.6%)
	1	1 (8.3%)	4 (23.5%)	1 (6.7%)	—	12 (10.1%)	1 (1.4%)
	2	2 (16.7%)	12 (70.6%)	—	—	—	—
Groove pattern	1	8 (33.3%)	9 (60.0%)	2 (14.3%)	2 (22.2%)	21 (19.1%)	7 (10.0%)
	2	4 (66.7%)	6 (40.0%)	12 (85.7%)	7 (77.8%)	89 (80.9%)	63 (90.0%)

* Martínón-Torres et al. (2012).

** ‘—’ means ‘0’.

al., 2010b, 2015), but it is not present in the LYC1 M₃.

When all five traits are considered, no other specimen, extant or extinct, matches the pattern of scores expressed by LYC1 (SI Table 3, SI Table 4). Although no individuals match the suite of all five traits presented in LYC1, three recent Chinese modern humans (SI Table 4) and a *Homo floresiensis* individual (LB6/1) match four of LYC1's scores, but they all lack an MTC (SI Table 4; see Figure 1 in Kaifu et al. (2015)). Aside from LB6/1, no fossil specimen includes this combination of traits (SI Table 3, SI Table 4). Cluster analysis shows that LYC1 clusters with six recent Chinese modern humans and separates from the rest of the individuals in the study (SI Table 4, SI Figure 2).

It is primarily the lack of a hypoconulid and the presence of an MTC that distinguishes LYC1 from all of the other specimens in this sample; no other tooth has that combination of traits (SI Table 4). The combination of a lack of C6, C7, and a non-Y pattern of groove arrangement is fairly common in our sample (33/96 individuals; 30/33 are recent Chinese modern humans).

Enamel thickness

Once the occlusal wear was corrected for by virtually reconstructing the enamel cap (Figure 2, see Methods), the corrected AET2D value for LYC1 is 1.18 mm. This value is slightly above the upper limit of Neanderthals, but falls into the range of fossil and recent *H. sapiens* (Table 4). For RET2D, both corrected and uncorrected values of LYC1 are greater than for Neanderthals. The corrected RET2D of LYC1 falls slightly above the range for fossil *H. sapiens* and is well within the range of recent *H. sapiens*. Neanderthal M₃s generally have thinner enamel than *H. sapiens*, though some overlapping exists in both AET2D and RET2D (Table 4).

The AET3D of LYC1 (Table 5) falls within the range of variation for both Neanderthals and recent *H. sapiens* (values from Pan et al. (2016)). The value of LYC1 is higher than the mean value of Neanderthals provided in Olejniczak et al. (2008). In the RET3D, the value of LYC1 is slightly higher

than the mean of Neanderthals and recent *H. sapiens*, and exceeds the upper limit of the range of variation.

Distribution of 3-D enamel thickness

Although the occlusal surface of LYC1 is slightly worn (no dentine is exposed), the pattern of 3-D enamel thickness distribution could still be observed (Figure 9). Overall, the thickest enamel falls around the buccal groove in the occlusal aspect of the buccal surface. M₃s of recent modern humans show a similar pattern (see also SI Figure 4 in Pan et al. (2016)), with the buccal surface being thicker than the lingual aspect. Typically, the occlusal third of the hypoconid's buccal surface has thick, evenly distributed enamel in recent *H. sapiens*; however, it is the mesial aspect of the hypoconid that shows the thicker enamel in LYC1. Despite this difference, we should be cautious with interpreting it until more data is available. A M₃ from Hexian *H. erectus* (PA831) (unpublished data) and a M₃ from Java (NG0802.2) (see Figure 2 in Zanolli (2015)) are similar to that of recent *H. sapiens* in the distribution pattern of 3-D enamel thickness.

Discussion

M₃ morphology is highly variable among the recent *H. sapiens*, and this tooth category has generally not been included in previous investigations of population history (e.g. Turner, 1987; Matsumura and Oxenham, 2014). However, a suite of M₃ characteristics has been identified as taxonomically and phylogenetically informative, with varying reliability among different taxa (Olejniczak et al., 2008; Bailey et al., 2011; Martín-Torres et al., 2012; Smith et al., 2012; Martínez de Pinillos et al., 2014; Gómez-Robles et al., 2015). Additionally, principal component, canonical variance, and corresponding discriminant function analyses accurately separate M₂ and M₃s in this study. These characteristics were considered in the present study in order to characterize the Laoya Cave permanent molar, and to document the morphological variation among the East Asian

Table 4. Comparisons of AET2D (2-D average enamel thickness) and RET2D (2-D relative enamel thickness) between LYC1 and other fossil hominins and recent *H. sapiens* (parentheses indicate the range when more than one specimen was reported).

Source	LYC1		Neanderthal		Fossil <i>H. sapiens</i>	Recent <i>H. sapiens</i>
	This study corrected	This study uncorrected	Smith et al. (2012)	Olejniczak et al. (2008)	Smith et al. (2012)	Smith et al. (2012)
<i>n</i>	1	1	6	8	2	45
AET (mm)	1.18	1.06	1.01 (0.91–1.16)	0.99	1.28 (1.15–1.41)	1.25 (0.98–1.74)
RET	21.97	19.74	16.8 (14.3–18.3)	16.55	20.5 (19.2–21.9)	21.7 (17.2–31.8)

Table 5. Comparisons of AET3D (3-D average enamel thickness) and RET3D (3-D relative enamel thickness) between LYC1 and other fossil hominins and recent *H. sapiens* (parentheses indicate the range when more than one specimen was reported).

Source	LYC1	Neanderthal		Recent <i>H. sapiens</i>	
	This study uncorrected	Pan et al. (2016)	Olejniczak et al. (2008)	Pan et al. (2016)	Olejniczak et al. (2008)
<i>n</i>	1	5	6	4	9
AET (mm)	1.40	1.38 (1.24–1.54)	1.06	1.38 (1.20–1.47)	1.45
RET	24.65	21.24 (19.11–23.73)	15.43	22.06 (20.52–23.74)	23.79

Figure 9. The distribution pattern of 3-D enamel thickness in LYC1 and four other specimens of recent *H. sapiens*: RMH-1, Yunxian M101; RMH-2, Xichuan M144; RMH-3, Yunxian M263; RMH-4, Yunxian M22. The images are not scaled.

fossil *H. sapiens*.

Given its age and location, the expectation was that LYC1 should have morphological traits most typical of recent *H. sapiens*. As expected, the crown dimensions of LYC1 are fairly small and fall most consistently within the ranges of other Asian and European fossil and recent *H. sapiens*. Similarly, the 2-D relatively thick average and relative enamel thickness values established for LYC1 fall more soundly within the *H. sapiens* range than the Neanderthal range. The discriminant function analysis of the crown outline shape variables and dental non-metrics all assign LYC1 into groups of recent *H. sapiens*.

However, the 3-D enamel thickness displayed a less clear situation based on the comparative data from different sources. Our study also revealed that the variation in recent *H. sapiens* established by our East Asian sample differs slightly from the known modern human variation established by Martínón-Torres et al. (2012). Surprisingly, LYC1 does not always follow the morphological suite of features established for the recent East Asian *H. sapiens* from China. LYC1 exhibits a combination of dental traits (no hypoconu-

lid, C6, C7, and 'X' groove pattern) that could only be identified in three recent Chinese *H. sapiens* individuals. No comparative specimens matched the LYC1 scores for all five non-metric traits. Additionally, no comparative specimen from any taxa was found to lack a hypoconulid, but express an MTC, demonstrating LYC1's uniqueness.

Compared to other Late Pleistocene East Asian fossil *H. sapiens*, the Laoya Cave M₃ is distinctive. The talonids of the fossil *H. sapiens* from Daoxian Fuyan Cave, Tianyuan Cave, Huanglong Cave, and Maludong are enlarged, and in some cases the talonid is even larger than the trigonid, whereas the LYC1 has a narrowed talonid. M₃, with a buccolingually narrowed talonid, and a resultant triangle crown outline shape, could have been a typical feature in East Asian Early and Middle Pleistocene and other earlier hominins. M₃s of some recent *Homo* groups (Neanderthals, fossil *H. sapiens*, and recent *H. sapiens*) tend to have an enlarged talonid relative to the trigonid, though M₃ crown outlines are quite variable. The M₃s of other East Asian fossil *H. sapiens* are characterized by multiple cusps, and all include a hypoconulid, unlike LYC1 for which the hypoconulid is absent.

Mtg 1 and Mtg C of Minatogawa hominins also develop a hypoconulid in their M_3 s (see Figure 2 and Figure 4 in Kaifu et al. (2011)). Additionally, extra cusps like C6 and/or C7 are present in the M_3 s of the Daoxian Fuyan and Huanglong caves (Liu et al., 2010b, 2015). The MTC, which is highly rare in East Asian Middle Pleistocene fossil hominins (see Xing et al., 2014; Liu et al., 2017) and absent from all the specimens of East Asian fossil *H. sapiens*, appears in LYC1. A high and continuous MTC of the lower molar is frequently found in specimens of Neanderthal lineage (Bailey et al., 2011; Martínez de Pinillos et al., 2014). However, a continuous MTC also exists in *Australopithecus* and Sangiran Early Pleistocene hominins (Kaifu et al., 2005; Moggi-Cecchi et al., 2006). Finally, the linear type of extreme enamel extension detected in East Asian fossil *H. sapiens* from Daoxian Fuyan Cave and Huanglong Cave (Liu et al., 2010b, 2015), is not present in the LYC1 M_3 .

The AMS dating of mammalian bones extracted from consecutive layers of the Laoya Cave deposits have provided a very continuous dispositional sequence and reliable chronology. The reliability of the dating at this site is especially important compared to the absence of stratigraphic backgrounds and/or reliable dating results for the majority of East Asian fossil *H. sapiens* (Wu and Poirier, 1995). The LYC1 permanent M_3 includes morphological characteristics that are common in other East Asian Late Pleistocene hominins, but its distinctive suite of traits expands the known morphological diversity among the East Asian Late Pleistocene hominins (Liu et al., 2010a, 2010b, 2015; Curnoe et al., 2012; Wu et al., 2012, 2014; Wu and Trinkaus, 2014; Xing et al., 2015). However, we should be cautious not to overstate LYC1's exceptionality because it is not unusual for a particular combination of traits to only appear in one individual (SI Table 4). Although rare, the dental morphology of LYC1, combined with other findings from the Zhiren, Huanglong, and Fuyan caves, suggests a more expanded morphological diversity in East Asia, including some archaic characteristics, than previously recognized (Liu et al., 2010a; present study). Similarly, recent DNA studies of southeastern Islanders have revealed a more archaic signature unknown previously and have expanded further the genetic diversity of recent *H. sapiens* (Skoglund et al., 2015; Pagani et al., 2016; Vernot et al., 2016). New findings of fossil hominins with secure dates and stratigraphic contexts such as the Laoya Cave site, and molecular studies of more specimens of modern humans, either fossilized or extant, may reveal more unique or surprising phenotypes. All these will certainly contribute to a better understanding of modern human evolution in East or Southeast Asian.

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