Geometric morphometric analysis of the early Pleistocene hominin teeth from Jianshi, Hubei Province, China

LIU Wu[1]*, Ronald CLARKE[2] & XING Song[1,3]

[1] *Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China;*
[2] *University of the Witwatersrand, Johannesburg, South Africa;*
[3] *Graduate University of Chinese Academy of Sciences, Beijing 100049, China*

Although the early Pleistocene hominin fossils found in East Asia continent are widely recognized as the earliest hominins migrated from Africa, debates remain on the morphology and taxonomy of these fossils. In this study, dental crown shape of the three early Pleistocene hominin teeth (P^3, M^1, and M_1) found in Jianshi, Hubei Province of China was analyzed by means of geometric morphometrics. The comparative samples of fossil hominins from Africa, Asia, and Europe as well as those of modern humans (N=257) were used. The results indicate that the contour, asymmetry, and cusp patterns of these three types of teeth differ obviously between the fossil hominins and modern humans. The crown shape of P^3 in most fossil hominins including *Australopithecus*, African early *Homo,* and Asian Pleistocene hominins are asymmetric with their crown occlusal contours long and curving elliptic-shaped. The occlusal contour of the fossil hominin M^1 is symmetric and rectangle-shaped with no marked cusp protrusion. The crown shape of fossil M_1 is characterized by asymmetric contour with slightly projected metaconid and hypoconid. On the contrary, in modern Chinese and some European late Pleistocene hominins, the crowns of P^3s show symmetric contours with buccal side wider than lingual side; the crown shape of M^1 is asymmetric with lingual cusp distal-placed, especially for hypoconid; the M_1 has symmetric and round crown contour. Our study reveals that *Australopithecus* has wide variations in its crown shape, whereas these dental morphospaces of Asian hominins are closely placed. The crown contour, symmetry, and cusp patterns of these three teeth of Jianshi hominin resemble those of Asian early and middle Pleistocene hominins. No marked difference in dental crown shape is shown between the Jianshi hominin and other Chinese *Homo erectus*, and there is also no evidence in support of the Jianshi hominin's closeness to *Australopithecus* and African early *Homo* members.

human evolution, tooth, shape, geometric morphometric, Jianshi, Hubei, China

The size, morphology, and internal structure of human teeth show obvious evolutionary changes and differences between species. Besides, the human teeth sometimes preserve the information of environment, diet, and living activities of humans [1–3]. For many years, studies of human teeth rely

mainly on the observed feature, linear measurement, angle, and indices. Because human teeth are not regular-shaped and the occlusal morphology of premolar and molars are especially complicated, the traditional method for tooth study cannot capture and quantify some detailed morphological features on the tooth surface. For the past decade, geometric morphometric has developed as a new means of biological shape analysis [4, 5]. With the digital photogra-

*Corresponding author (email: liuwu@ivpp.ac.cn)

phy and computer-assisted image technique, this method can obtain information of tooth shape, contour symmetry, size-related proportion, and cusp patterns, which makes it possible to analyze complicated dental morphology, and has played more and more important roles in paleoanthropological studies [6–8].

For many years, there have been debates on the origin and evolutionary taxonomy of East Asian *Homo erectus* [9, 10]. In the past three decades, some early Pleistocene hominin fossil and activity sites were found in China. The possibility of existence of early hominins different from *Homo erectus* has been proposed [11–13]. Among the discovered fossils, the mandible and teeth found in Longgupo, Wushan of Chongqing and Jianshi of Hubei Province are most important. Some colleagues believe that they show many differences in dental morphology compared with Chinese *Homo erectus*, but they resemble *Homo habilis, Australopithecus*, and *Meganthropopus* found in Indonesia. These early Pleistocene fossils may represent taxa of early hominins rather than *Homo erectus* [11–13]. These studies caused the controversies on the identification of dental morphology and classification for the early Pleistocene hominin teeth [14, 15]. The study of the three hominin teeth found in Jianshi shows that the morphology of the Jianshi upper molar is similar to that of S-6 of mandible from Indonesia and *Australopithecus robustus*; upper premolar and molar resemble those of S-4 from Indonesia. Based on these analyses, the classification of the Jianshi teeth into *Meganthropopus* was proposed [13]. The biostratigraphic analysis and paleomagnetic dating of the deposit yielding the Jianshi hominin teeth give an age range of 1.95–2.15 Ma [13]. Therefore, classifying the Jianshi hominin teeth as *Meganthropopus* has raised the possibility of another kind of hominins rather than *Homo erectus* existing in early Pleistocene of China. The previous description and comparison of the Jianshi hominin teeth was carried out with traditional method, which can only get limited morphological information. Besides, the comparative samples are not enough in the study. Therefore, further geometric morphometric analysis of the Jianshi teeth will reveal additional morphological information, which may demonstrate the morphological variation and evolution of early Pleistocene hominins in China.

In this study, geometric morphometric and image-analyzing technique were used to describe and compare the crown shape of the Jianshi hominin teeth and the comparative samples of fossil hominins representing different period and taxa from around the world. Special attentions are paid to the dental morphological differences with African *Australopithecus* and early *Homo*, as well as the middle and late Pleistocene hominins from Asia and Europe. Based on these analyses, some problems related to the evolution of the early Pleistocene hominins in China are discussed.

1 Geometric morphometric and its application in paleoanthropological studies

For many years, the studies of human teeth have been carried out through morphological description and linear measurement. The drawbacks of the traditional method are obvious including the limited and disperse information obtained, and sometimes subjective judgment cannot be avoided. To overcome these drawbacks, tooth shape has received more attentions. Shape is the geometric properties of an object invariant to position, orientation, and isometric size differences [4, 5]. The resulted morphometric is a multivariate statistic method examining central tendencies of shape, shape variation, group differences in shape, and associations of shape with extrinsic factors [4, 5]. This method analyzes and compares the morphological differences between specimens by means of linear distance, angle, and relative areas. Although morphometirc can obtain some shape information, and further deals with two-dimensional and three-dimensional shape analysis [16–20], the morphological variations it gets are still limited, and especially it cannot capture the information of specimens' contour and symmetry.

Recently, with the advances in multi-statistics and digital image techniques, the emphasis of morphometric studies turns to the detailed analysis of landmarks of biological specimens [21]. By analyzing the data from the biological landmarks, geometric shape information can be maximally captured, which created a new method for biological shape analysis—geometric morphometrics [4, 5, 22, 23]. The advantage of geometric morphometrics is overcoming the limitation of the previous morphometrics, which only rely on linear distance, index, angle, and relative areas, and integrative interspace information of biological landmarks cannot be captured. By integrating landmark information, geometric morphometrics put the whole shape information of the contour, symmetry, and ranging patterns of different parts of the specimens together and display graphically [22–24]. In the field of hominin tooth studies, this method has been applied to the premolar and molar crown shape analysis of European middle Pleistocene hominins [6–8].

2 Materials and methods

2.1 Materials

The dental specimens used in the present study include the three Jianshi hominin teeth found in 2000 and some comparative specimens. The three Jianshi teeth are lower first molar (PA1277), upper third premolar (PA1278) and upper first molar (PA1279) (Figure 1). The comparative specimens were chosen from *Australopithecus*, African early *Homo* (including *Homo habilis* and *Homo ergaster*), European middle and late Pleistocene hominins (including Ne-

anderthals), Asian *Homo erectus*, Asian archaic *Homo sapiens*, Asian late *Homo sapiens*, and modern Chinese. Among them, the seven teeth of S-1, S-4, and S-6 from Sangiran, and W-H-2 and W-H-23 from Wajak, Indonesia were classified Aisan *Homo erectus* and Aisan late *Homo sapiens* respectively. The specimens include both fossils and casts. All the specimens used in the present study are housed in Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, and University of Witwatersrand, South Africa respectively. Table 1 lists detailed information of the specimens.

2.2 Photographing and defining landmarks and semi-landmarks

(1) Photographing specimens. High resolution pictures of occlusal surfaces of each tooth were taken with Cannon EOS-5D digital camera fitted with a 100 mm Macro-Cannon lens. The teeth were fixed on the baseboard with its cemento-enamel junction (CEJ) parallel to the camera lens. An aperture of f/32 was used for the maximum depth of field. Teeth of the same side with those of Jianshi were used in this analysis; to maximize the sample size, ACDsee was employed to mirror teeth of the opposite side. A millimeter scale was placed parallel to occlusal surface of every tooth when photographing.

(2) Landmarks. Landmarks are biologically and geometrically homologous points [21–23], such as the protuberances, sutures, intersection points on bone or teeth, and other prominent anatomical points on bone or tooth surfaces [21–23]. Therefore, landmarks bear geometric information of biological structures, which make them useful in analyzing shape similarities and disparities of certain organs of intra- or inter-groups. The shape variations can be acquired through analyzing the ordination data of landmarks [23, 24].

(3) Semilandmarks. As mentioned above, landmarks correspond to the well-defined anatomical points, which are always absent on the surfaces of many biological structures, for instance, the irregular external outline of tooth. To solve this problem, Bookstein [24] introduced the concept of semilandmarks, which means numerous spots dispersed on the object outline. To reduce the randomness of semilandmarks,

Table 1 Specimens used in this study

	P^3	M^1	M$_1$
Jianshi	PA 1278	PA 1279	PA 1277
N=3	*N*=1	*N*=1	*N*=1
Australopithecus	STW1, STW183, STW498 SK-55, SK-65, KNM-CH1 MG_2613	Taung, STW1, STW183, STS8, SK-55, LH-3, LH-6, LH-21, AL-33, AL-200, KNM-CH1, OH-5	Taung, STW11, STS-24, STS52B, STS MEMBER 4 SK6, SK1588, LH-2, LH -3t, MLD-2, AL-333w, AL-333w-12, AL-333w-60, AL-128, AL-145, AL-200, AL-266, AL-288, AL-400
N=38	*N*=7	*N*=12	*N*=19
African early *Homo*		OH-13	SK-15, KNM-ER-992A, KNM-ER-1502, KNM-ER-1506, KNM-ER-1507, KNM-ER-1802
N=7		*N*=1	*N* =6
European Pleistocene Hominins	Arago 7, Arago 21, Krapina 48, Krapina 49 Le Moustier 1, Heidelberg Neanderthal (AN514), Neanderthal (AN1657)	Arago 21, Le Moustier 1 Krapina 48, Steinhem Mladec 1, Heidelberg Neanderthal (AN1657)	Maucer 1, Arago-13, Hortus 4, Regourdou 1, Vindijia206, Gibraltar, Ehr.1010-69, Krapina Md. H, Krapina Md. E (Krapina 57), Krapina Md. G, Krapina Md. D, Istritz
N=27	*N*=8	*N*=7	*N*=12
Asian *Homo erectus*	Sangiran(S-4), Zhoukoudian (PA 67, ZKD 19), Xichuan (PA 524)	Sangiran (S-4), Zhoukoudian (ZKD105, ZKD33 ZKD 140'), Xichuan (PA 529), Meipu (PA637)	Sangiran (S-1, S-6), Zhoukoudian (PA 69, AN105, AN 112 ZKD36, ZKD137', ZKD34), Xichuan (PA 532)
N=19	*N*=4	*N*=6	*N*=9
Asian archaic *Homo sapiens*	Chaoxian, Changyang (PA 76)	Chaoxian, Changyang (PA 76)	
N=4	*N*=2	*N*=2	
Aisan late *Homo sapiens*	Qafzeh, Wajak (W-H-2) UC110, Liujiang	Qafzeh, Wajak (W-H-2) Liujiang, UC110, UC102	Qafzeh, Wajak(W-H-23) UC101, UC104, UC108
N=14	*N*=4	*N*=5	*N*=5
Modern Chinese	*N*=54	*N*=47	*N*=47

a sliding technique [21] is introduced to make semiland-marks sliding along the curve to minimize either the bend-ing energy or the Procrustes distance. The later criterion was used in this study. After the sliding, semilandmarks are also called sliding-semilandmarks, which are granted statis-tically the functions of the real landmarks in exhibiting pre-cisely the shape information of objects [22, 23]. We here follow Gómez-Robles et al. [7, 8] to define 30 semiland-marks on the surface of each tooth.
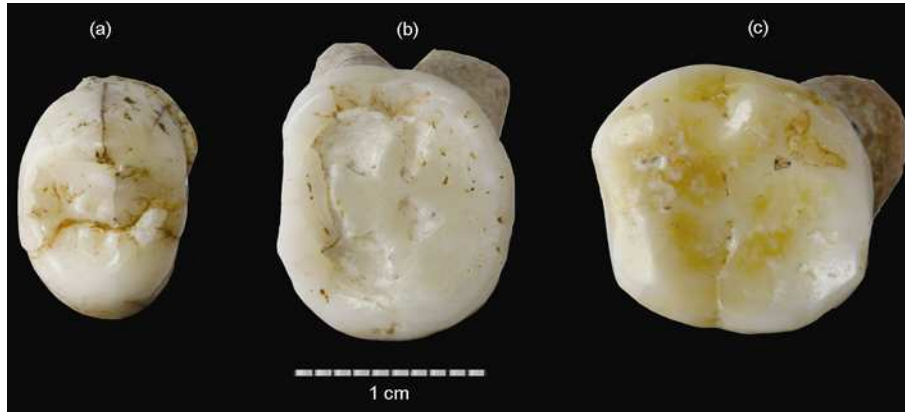
(4) Defining landmarks and semilandmarks. The four

Figure 1   Hominin teeth found in Jianshi. (a) Upper third premolar (PA1278); (b) upper first molar (PA1279); (c) lower first molar (PA1277).
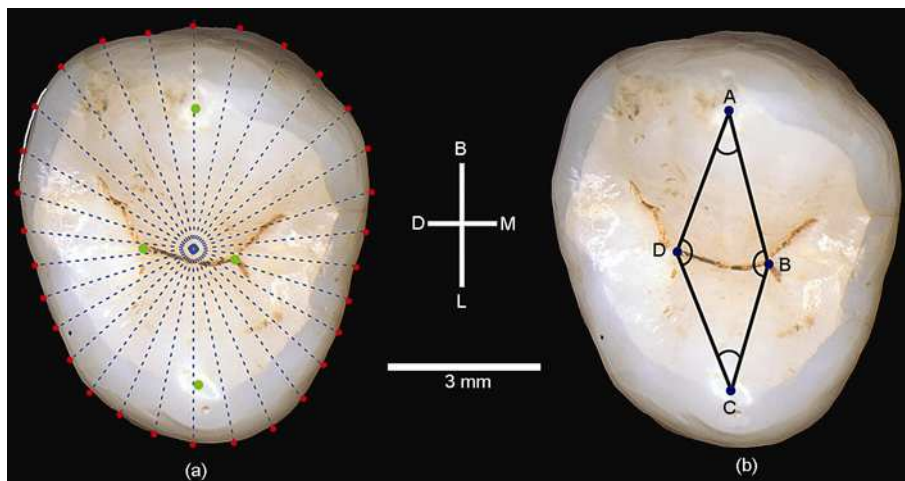

Figure 2   Occlusal surface of upper third premolar showing. (a) Landmarks and semilandmarks; (b) polygon and cusp angles. In the cross, B: buccal; L: lingual; M: mesial; D: distal. The same below.
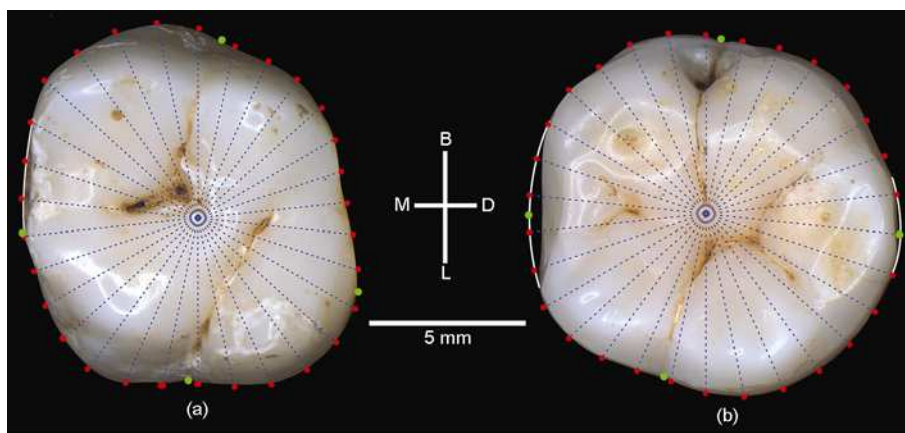

Figure 3   Occlusal surface of upper first molar (a) and lower first molar (b). Both surfaces show landmarks and semilandmarks.

landmarks on the occlusal surface of P^3 are: landmark 1, tip of the buccal cusp; landmark 2, the intersection of mesiobuccal groove with the central groove; landmark 3, tip of the lingual cusp; landmark 4, the intersection of distolingual groove with the central groove. The four landmarks on the occlusal surfaces of M^1 and M_1 were defined as the most buccal, the most mesial, the most lingual, and the most distal points of the crown. Cusp tips were marked in the center of the wear facet when the specimen showed little wear. The landmarks defined above were used to locate the gravity center, from which 30 equiangular fan lines were drawn, and semilandmarks were corresponded to the intersection points of the fan lines with the crown external outlines (Figures 2 and 3). MakeFan6 was used to draw the fan lines [25].

2.3   Geometric morphometric analysis

After the occlusal surfaces of teeth had been photographed and the landmarks and semilandmarks on the surfaces marked, a series of TPS [26–28] software were employed to analyze the coordinate data to acquire the shape information of studies objects.

(1) GPA (Generalized Procrustes Analysis). The primitive landmarks or semilandmarks data contained some non-shape elements, mainly including size, location, orientation, which would leave the subsequent shape analysis imprecise. To avoid this problem, GPA was employed aiming at excluding non-shape information through minimizing the Procrustes distance among the corresponding landmarks or semilandmarks of specimens. After GPA, the differences reflected by coordinate data could represent objectively the real shape differences among specimens. Therefore, GPA could be regarded as a tool from which raw data could be obtained to conduct the subsequent shape analysis. GPA also produces a consensus or average configuration of object sample and scatters of corresponding landmarks or semilandmarks around their mean points [21–23].

(2) TPS (Thin Plate Spline). TPS could visualize the detailed process of how certain landmark configuration deformed into another one through the transformed TPS grids [22]. The transformation between two different landmark configuration could be broken into uniform component and non-uniform component, with the former leaving the grid lines parallel, while the later deforming particular region of TPS grid to reflect the disproportionate lengthening or shortening of one portion to another [22]. Therefore, non-uniform transformation needs energy, which could be used to derive a set of powerful shape descriptors, the partial warps scores. Principle component analysis of these scores is equal to relative warp analysis, which could reduce the total variations to a smaller number of independent dimensions to illustrate the main patterns of morphological variations. TpsRelw was used here to conduct the relative warps analysis.

Because of the crown size differences among hominins of various ages and species, allometric analysis is essential to be conducted. We have to make sure whether or not the tooth crown shape is impacted by its size and how large this impaction might be [29–34]. GPA mentioned before could produce a useful score called centroid size, which was defined as the squared root of the sum of squared distances of a set of landmarks from their centroid. Therefore, it is useful in representing the real crown size. Multivariate regression analysis of shape data on the centroid size was performed to see if there is any allometry.

Beyond geometric morphometrics (the analysis of crown outline, cusp pattern, allometry, and so on), the relative cusp basal area, relative polygon area (polygon: the area drawn by connecting the cusp apices of four landmarks mentioned above), and cusp angles (the four angles of polygon) were also measured precisely to explore the differences among samples.

3   Results

3.1   Upper third premolar (P^3)

Relative warp analysis shows that the first two factors of PCA (PC-1 and PC-2) account for 45.91% of the total variations. Morphological variation along PC-1 is clearly illustrated by the TPSgrids of the relative warps in the extremes of the *x*-axis (Figure 4). Specimens with positive PC-1 values tend to display an asymmetric crown contour with distal side bulging and mesial side flat. Because the crown BL dimension is markedly bigger than MD dimension, the crown occlusal outline is slightly narrow and bending ellipse-shaped. Besides, the specimens with positive PC-1 values have their landmarks on the buccal cusps placed more centrally; the distance between mesial and distal landmarks is relatively big; polygon extends in MD direction and contracts in BL direction. The specimens plotted in the negative area of PC-1 have symmetric occlusal shape with buccal cusp bulging to both mesial and distal directions, and lingual cusp only projects to lingual direction, which forms a symmetric occlusal contour with buccal portion wider than the lingual portion. The specimens with negative PC-1 values have their four landmarks placed in symmetric pattern with the two landmarks in buccal cusp and lingual cusp closer to the border of occlusal outline, and the two landmarks in mesial and distal portions close to each other. This landmark pattern makes polygon narrowly rhombus-shaped in the center of the occlusal surface. The specimens along the PC-2 have a similar crown shape with few variations. The specimens in the positive region of PC-2 have slightly asymmetric crown contours with buccal cusps mesially bulging slightly and polygon closer to buccal portion. The specimens distributed in the negative region of PC-2 have approximately symmetric crown contours with their buccal cusps bulging mesiodistally and lingual cusps
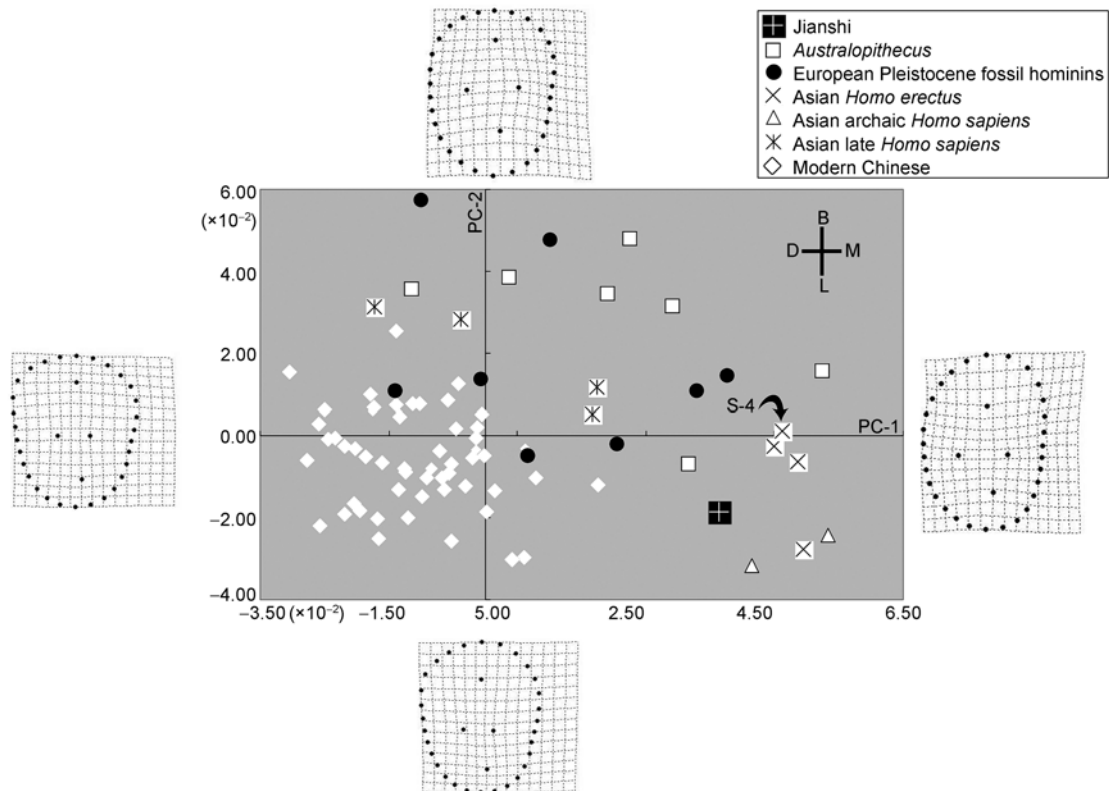
Figure 4 Distributions of individual P³ crowns on PC-1 and PC-2. TPS-grids illustrate the morphological variation trends of the specimens along each principal component.

flat in the lateral sides. This cusp pattern makes the crown wider in buccal portion. The polygons are small and narrow rhombus-shaped situated slightly close to lingual portion.

The specimens of modern Chinese are mainly on the left side of lower portion of Figure 4 characterized with symmetric polygon and crown outlines. Most of the fossil hominins are placed on the right portion of Figure 4 with asymmetric crown shape. Six of the seven *Australopithecus* P³ stay loosely in the positive region of PC-1 indicating great morphological variations. The East Asian fossil hominins stay in the lower-right region of Figure 4 close to each other. East Asian late Pleistocene hominins are closer to modern Chinese than to other fossil hominins. In Figure 4, Jianshi P³ stays near other East Asian fossil hominins. It is worth noting that nearly all the European fossil hominins are in the positive region of PC-2 but spread around along the PC-1 with some specimens in the modern humans area. Further analyzing the distribution of the European specimens shows that the specimens in the left region close to modern humans are European late Pleistocene Neanderthals, whereas the specimens in the right region are European middle Pleistocene hominins (Krapina and Arago). Chinese *Homo erectus* and archaic *Homo sapiens* are all in the lower-right region of Figure 4 with typical asymmetric crown shape, which also occurs in Jianshi P³ (Figures 1 and 4). The relative cusp area, relative area of polygon and cusp

angles listed in Table 2 also indicate that the patterns of these features of Jianshi P³ are closer to those of Asian *Homo erectus*.

3.2 Upper first molar (M¹)

Relative warp analysis shows that the first two factors (PC-1 and PC-2) represent 45.91% of the total variations. Along the PC-1 axis of Figure 5, the specimens plotted in the positive region have approximately symmetric crown contours with their BL dimensions greater than MD dimensions. Besides, the crown mesial side is flat and distal side is slightly bulging. The specimens in the negative region of PC-1 show obviously asymmetric crown contours. The lingual cusp is placed more distally; paracone and hypocone bulge markedly; and metacone and protocone contract. These cusp patterns cause the paracone-hypocone distance obviously larger than the metacone-protocone distance, which also make the skewed and asymmetric occlusal shape. Compared with the obvious shape variations revealed in PC-1, the shape variations caused by PC-2 are relatively small. The specimens distributed in the positive region of PC-2 have obviously bulging paracones and contrasted metacones. The crown lingual profiles are gentle and symmetric. These patterns make the crown occlusal profile shaped as BL dimension slightly bigger than MD dimension,

Table 2 The relative cusp area, relative polygon area and cusp angles of P³

Specimen/samples	Relative cusp area (%)		Relative polygon area (%)	Cusp angles (°)			
	Buccal cusp	Lingual cusp		Angle-A	Angle-B	Angle-C	Angle-D
Jianshi	63.1	36.9	12.2	40	147	56	117
Australopithecus	53.7	46.3	13.1	53.9	136.6	59.3	110.3
European Pleistocene Hominins	55.7	44.3	13.6	50.8	134.0	60.4	115.0
Asian *Homo erectus*	62.1	37.9	11.3	47.3	141	61.5	110.3
Asian archaic *Homo sapiens*	64.0	36.0	10.4	43.5	154.5	53	109
Asian late *Homo sapiens*	57.0	43.1	12.0	48.7	136.0	56	119.3
Modern Chinese	59.2	40.8	10.6	36.9	154.3	42.7	126.1
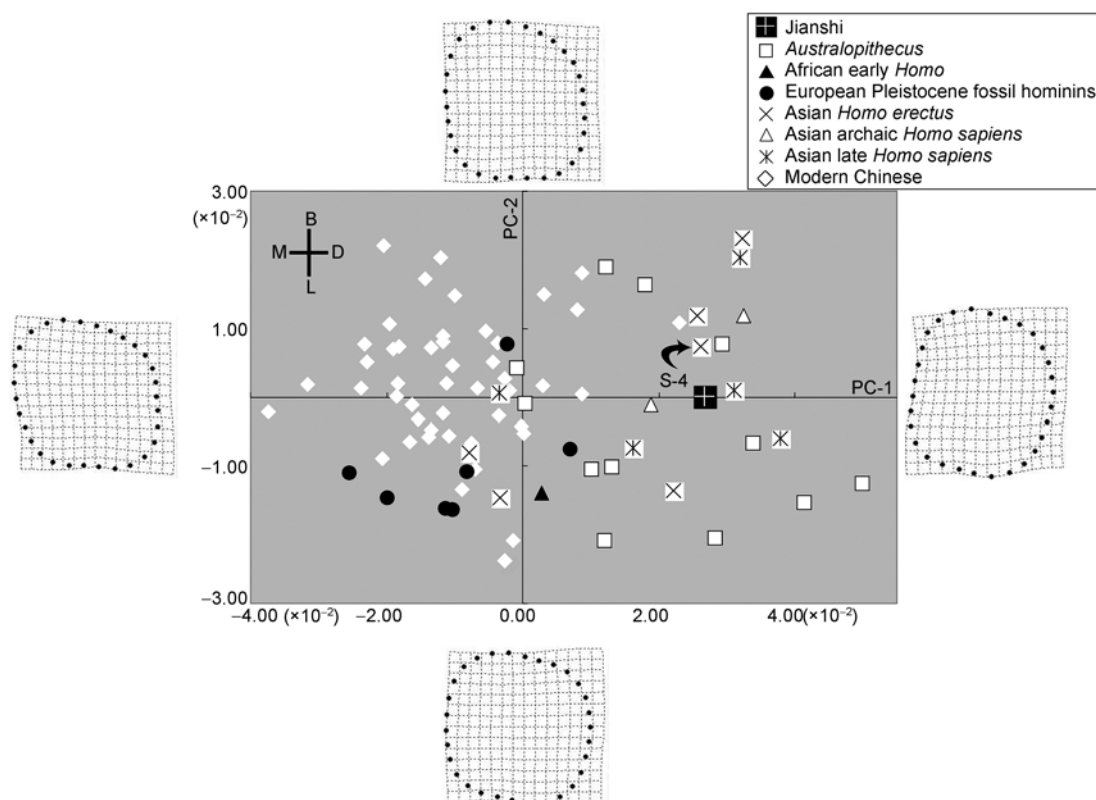
Figure 5 Distributions of individual M¹ crowns on PC-1 and PC-2. TPS-grids illustrate the morphological variation trends of the specimens along each principal component.

buccal portion narrower and inclining mesially, and lingual portion wider and symmetric. The teeth in the negative region of PC-2 have approximately symmetric crown with only hypocones slightly bulging lingually. The crown BL dimensions are closer to those of MD, which makes the occlusal surface round-shaped.

Nearly all the specimens of modern Chinese are distributed in the left region of Figure 5 with negative PC-1 values. Besides, most of the modern specimens are in the positive region of PC-2. Among the 49 modern specimens, only 6 teeth are in the positive region of PC-1. Even so, they are still very close to other modern specimens. Most specimens of fossil hominin are in the right region of Figure 5 with positive values of PC-1, but teeth of European middle and late Pleistocene hominins are placed in the lower-left region

of Figure 5, which have the negative values for both PC-1 and PC-2. Such a distribution indicates that M¹ crowns of modern Chinese have asymmetric shape with lingual cusps displaced distally. The M¹ crown shape of European Pleistocene hominins resembles that of modern Chinese also having asymmetric crown shape. But except for distal displacement, the lingual cusp of European fossil hominin's M¹ also bulges lingually. All the fossil hominins, except the European specimens, are in the right region of Figure 5 clearly separating from modern human and European fossil hominins. These fossil hominins share their symmetric crown occlusal shape. The distributions of *Australopithecus* and African *Homo* in Figure 5 are widespread, occupying the whole right half region. The Chinese Pleistocene hominins are also within this region but the Chinese speci-

mens group together closely. Jianshi M^1 stays close to other Chinese fossil hominins. The Indonesian specimen S-4 is close to Jianshi and other Chinese fossil hominins. The morphospace of these fossil specimens suggests that symmetric crown shape is a primitive feature, whereas modern or derived feature for M^1 crown shape is asymmetric profile. Taking all the findings of geometric morphometric analysis of M^1 crown shape of world-wide fossil hominins and modern humans into consideration (see Figures 1 and 5), we find that the crown occlusal shape of Jianshi M^1 resembles those of other fossil hominins of China, all having symmetric crown shape.

3.3   Lower first molar (M_1)

Relative warp analysis indicates that the first two factors (PC-1 and PC-2) account for 45.22% of the total variations. The specimens with positive values of PC-1 in the right region of Figure 6 have symmetric-shaped crowns with their MD dimensions obviously bigger than BL dimensions. The teeth in the negative region of PC-1 have their crowns contrasting mesiodistally and bulging buccolingually, which makes the occlusal profile round-shaped. The joining region of hypoconid and hypoconulid looks flat, which reduces the whole symmetry. The specimens distributed in the positive region of PC-2 have approximately symmetric occlusal shape with MD dimensions greater than BL dimensions. Endoconids of these teeth bulge pronouncedly. The specimens with negative values of PC-2 have obviously asymmetric crown shape characterized by bulged hypoconulid and metaconulid.

Although the specimen distribution in Figure 6 overlaps to some extent, the general trend clearly shows modern humans staying in the left region with symmetric and round crown shape and fossil hominids in the right having asymmetric crown shape with MD dimension greater than BL dimension. Much more variations can be found in the fossil hominins. Five of the eight specimens of Chinese *Homo erectus* stay close to each other with Jianshi tooth nearby. S-1 and S-6 from Indonesia are slightly far from Jianshi specimen. Specimen W-H-23 of late Pleistocene hominin from Indonesia is in the modern human group. Compared with P^3 and M^1, the crown shape variations of M_1 and differences among samples are much smaller than those of other teeth.

3.4   Allometry

The regression analysis of the CS values with uniform component and non-uniform component, which represents total shape variation and partial variation respectively, shows that the influences of tooth size to the crown shape
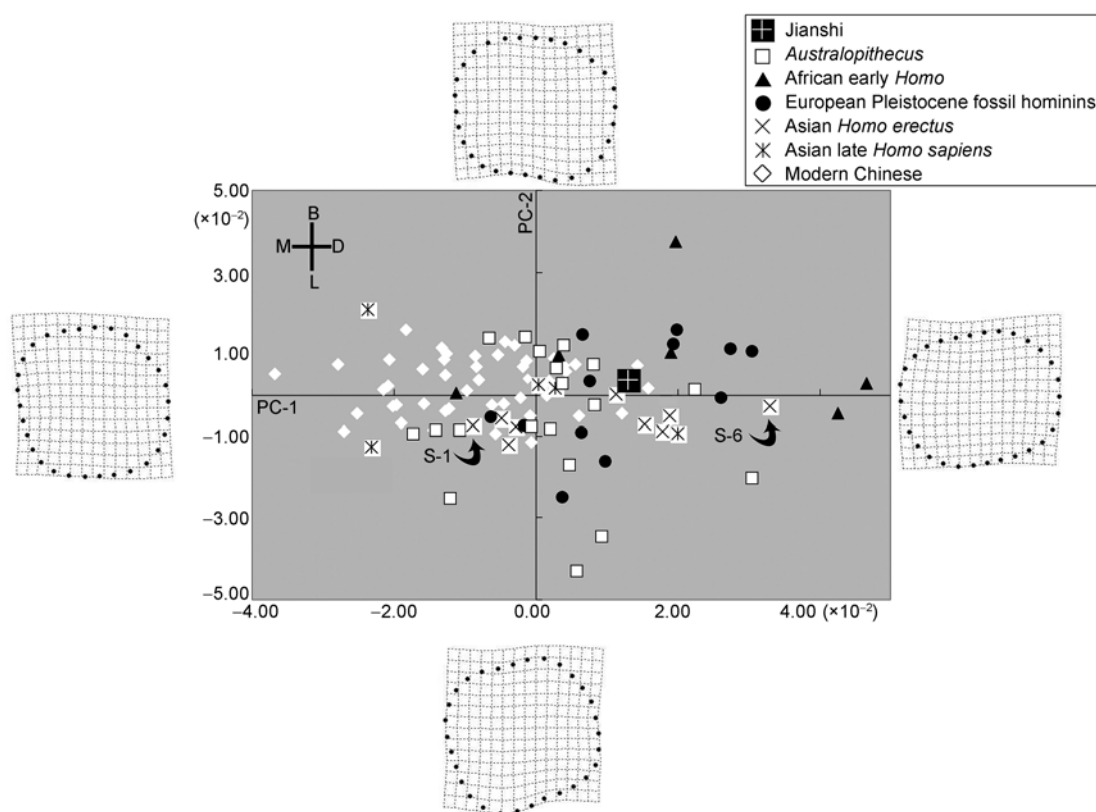

Figure 6   Distributions of individual M_1 crowns on PC-1 and PC-2. TPS-grids illustrate the morphological variation trends of the specimens along each principal component.

vary in the three types of teeth ranging 12.5%, 20.3%, and 3.15% respectively. The allometirc influence is more obvious in M^1 and P^3, and weaker in M_1 (see Figure 7 and Table 3 for details). In P^3, the general trend of allometry is that with the increase of tooth size (CS value), the crown shape tends to be asymmetric. So, the small-sized P^3 has more symmetric external crown profile and polygon more centralized. However, because lingual cusp slightly declines mesially, the polygon profile is not symmetric as the external profile of the crown. As the tooth size increases, the mesial side of the crown becomes flat and distal side bulges. Polygon extends along the BL direction and contracts buccolingually, which makes the P^3 crown obviously asymmetric. The allometric trend of M^1 is that the increase of tooth size causes the change from asymmetric to symmetric direction. When the tooth size of M^1 increases, crown BL dimension increases, but paracone contracts centrally. Among the three types of teeth studied here, the expression of allometry is weakest. With the increase of tooth size, only metaconid and entoconid slightly bulge, but the symmetric pattern of external contour does not change obviously.
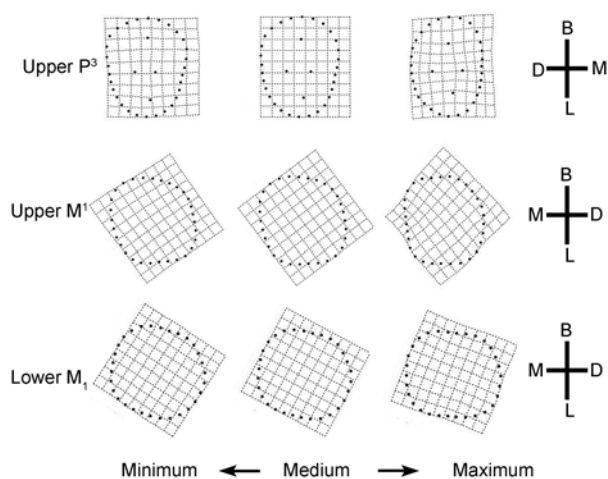

Figure 7   The crown shape of three types of teeth related to variation in Centroid Size (CS). The TPS-grid shows the transformation of the mean shape into a small individual (left), as estimated by the regression model, and into a large specimen (right).

Table 3   Centroid Size (CS) of Jianshi and comparative samples

	P^3	M^1	M_1
Jianshi	2.97	3.78	4.04
Australopithecus	3.11	3.83	3.74
African early *Homo*		3.43	3.45
European Pleistocene hominins	2.61	3.46	3.33
Asian *Homo erectus*	2.92	3.67	3.60
Asian archaic *Homo sapiens*	2.76	3.48	
Asian late *Homo sapiens*	2.62	3.56	3.28
Modern Chinese	2.36	3.17	3.22

4   Discussions and conclusions

4.1   Evolutionary change and inter-species difference of crown shape

The geometric morphometric analysis of crown shape of 260 teeth including Jianshi, and comparative samples of *Australopithecus*, African early *Homo*, Asian and European Pleistocene hominins, and modern Chinese indicates that even though some overlapping of tooth shape exists between different species, there are still obvious differences of crown shape and cusp pattern between fossil hominins and modern humans. The P^3 crown shape of *Australopithecus* and Asian Pleistocene hominins is long oval-shaped and very asymmetric with distal side bulging, mesial side flat, and occusal profile curving The P^3 crown shape of modern Chinese is symmetric with buccal portion wider than lingual portion, and the slender and rhombus polygon is placed centrally on the occlusal surface. The European fossil hominins of Arago and Krapina have their crown shape similar to that of African and Asian fossil hominins, whereas Neanderthals living more recently tend to have more symmetric crown profile, which also occurs in modern Chinese. These findings suggest that asymmetric crown shape is a primitive feature. In contrast, symmetric crown shape and polygon are relatively derived features. The crown shapes of Chinese fossil hominins including Jianshi are similar to each other (Figures 3 and 8). The two Indonesian specimens S-4 and W-H-2 from the early Pleistocene site of Sangiran and late Pleistocene site Wajak resemble Chinese *Homo erectus* and archaic *Homo sapiens*, and Chinese late *Homo sapiens* respectively.

The present study reveals that African and Asian fossil hominins share some M^1 crown shape patters, including symmetric and rectangular-shaped occlusal profile with no obvious cusp bulging. In contrast, the M^1 crown shape of modern Chinese and European Pleistocene hominins is obviously asymmetric with lingual cusp displaced distally especially for hypocone. The present study also shows that the variations of M^1 crown shape are great, whereas the M^1 crown shape of Chinese fossil hominins is similar to each other. The two Indonesian specimens of S-4 and W-H-2 are also close to Chinese fossil specimens. A recent study by Gomez-Robles et al. [6] shows that *Australopithecus* has symmetric M^1 crown shape with polygon squared-shaped and no obvious cusp bulging; the M^1 crown shape of European Pleistocene is very asymmetric with polygon oblique rectangle-shaped and lingual cusp inclined distally especially for hypocene. These findings are consistent with the present study. But Gómez-Robles et al.'s study also shows that modern Europeans have their M^1 crown shape similar to *Australopithecus*, and different from European Pleistocene hominins. Based on their findings, Gómez-Robles et al. [7] proposed that modern Europeans still preserve the primitive feature of symmetric M^1 crown shape, whereas skewed

skewed M_1 crown shape occurred in European Pleistocene hominins is a derived feature. However, the present study shows that M^1 crown shape of modern Chinese is similar to European Neanderthals, and different from African and Asian fossil hominins (Figures 4 and 9). The different findings from the two studies may suggest that tooth shape differences exist among modern human populations. Further studies are needed to confirm this possibility.

The present study indicates that the M_1 crown occlusal surface is symmetric-round shaped in modern humans. The M_1 crown shape of fossil hominins is asymmetric-shaped with metaconid and hypoconid slightly bulging, and protoconid and endoconid not well developed. But compared with P^3 and M^1, the M_1 crown shape does not differ significantly among various fossil hominins, and between fossil hominin and modern humans.

A worth-noting phenomenon revealed from the present study is that the evolutionary trend and inter-species differences of the crown shape for the three types of teeth are not the same. For example, the P^3 crown shape is very asymmetric in *Australopithecus* and Asian Pleistocene hominins, whereas the P^3 crown shape tends to be symmetric in Neanderthals and modern Chinese; the African and Asian fossil hominins have symmetric-shaped M^1 crown, but the M^1 crown shape is asymmetric in Neanderthals and modern Chinese. Currently, the reason for this phenomenon is unknown. We believe that the different evolutionary rates of various features in the three types of teeth may cause this, but the possibility of errors caused by the small sample size

cannot be excluded. Despite that, the crown shape of each tooth still shows certain evolutionary trend. The Asian Pleistocene hominins are placed between earlier fossil hominins and modern humans, but are more close to modern humans.

4.2 The influence of allometry on tooth crown shape

The regression analysis of CS values with uniform component and non-uniform component shows that some influence of tooth size on crown shape exists for the three types of teeth in the present study. Previous studies [1, 2, 6, 8] have confirmed that early hominins, like *Australopithecus*, have bigger teeth than later hominins. Therefore, the tooth shape changes of humans through time should be related to the allometry. The present study indicates that among the three types of teeth, size has more obvious influence on the crown shape in P^3 and M^1 than M_1. But in general, the influence does have significant affect on crown shape and has no proportionate relationship between tooth and shape, because the tooth shape variations are mainly related to the cusp patterns [6–8, 35].

4.3 Geometric shape of Jianshi hominin teeth

The dental features of human are characterized by their great inter-species and intra-species variations [1, 2, 36]. Because most dental features vary in the pattern of quasi-continuous variation [36, 37], it is difficult to set a
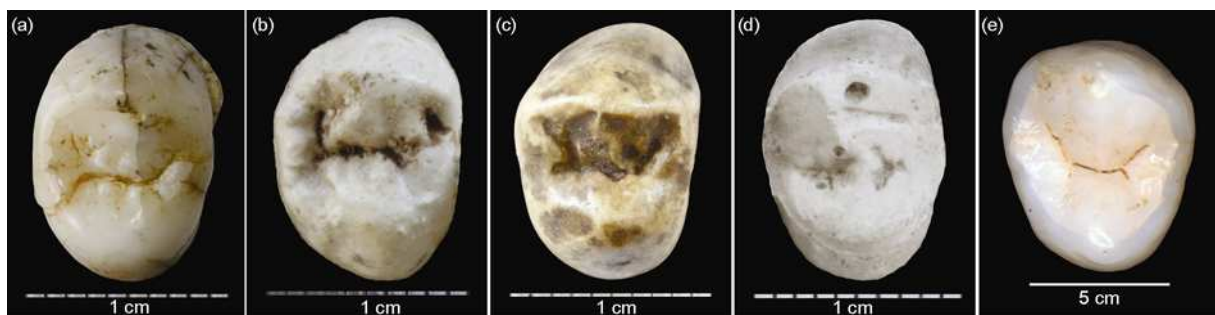

Figure 8 The occlusal views of P^3s. (a) Jianshi (PA1278); (b) *Australopithecus* (SK55); (c) Zhoukoudian *Homo erectus* (ZKD19); (d) Indonesian *Homo erectus* (S-4); (e) modern Chinese.
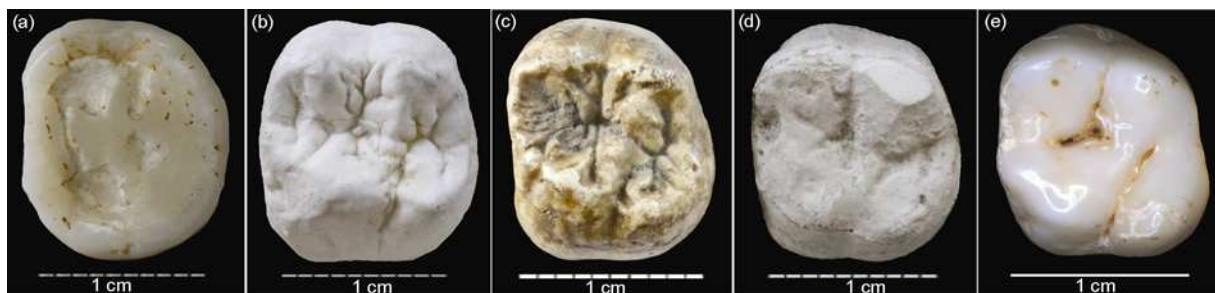

Figure 9 The occlusal views of M^1s. (a) Jianshi (PA1279); (b) *Australopithecus* (LH-3h); (c) Zhoukoudian *Homo erectus* (ZKD140'); (d) Indonesian *Homo erectus* (S-4); (e) modern Chinese.

clear-cut point for distinguishing species or populations. Besides, it is impossible to find the dental features shared by all the members of a specific species, and they occurred only in some species. Even so, if in some morphospace, only individuals of some specific species occupy it, the specimens falling in the morphospace should be treated as belonging to this species. For the past two decades, several studies have proved that tooth crown area, relative cusp area, cusp pattern and local shape of crown, and occlusal surface have obvious differences among different species of *Australopithecus*, early *Homo* and Pleistocene hominins [38–44]. Recently, geometric morphometric studies further confirmed the evolutionary and taxonomic values of tooth shape features [38–44].

The present study of crown shape of three types of teeth for worldwide fossil hominin and modern humans indicates that most fossil hominins (including *Australopithecus*, African early *Homo*, and most Asian and European Pleistocene hominins) are distributed in two separate morphospace regions (Figures 4–6). In general, all three teeth of *Australopithecus* show great variations in crown shape, which occupy nearly the whole morphospace of fossil hominins. Some recent studies also support these variations [6–8]. The African early *Homo* specimens used in the present study include *Homo habilis* and *Homo ergaster*, but they are few in number with only M^1 and M_1 included in analysis. The crown shape of the African early *Homo* specimens resembles that of *Australopithecus*. Among the European fossil hominins used in the present study, Arago and Krapina are close to African and Asian fossil hominins in crown shape distribution, whereas Neanderthals with younger ages resemble modern humans. The Chinese fossil hominins are distributed closely to each other in morphospace, especially for *Homo erectus* and archaic *Homo sapiens*, suggesting the Chinese hominins resemble each other more than to other specimens in crown shape. Previous study [9] indicates that the morphological features of early Pleistocene hominins from Sangiran of Indonesia resemble those of *Australopithecus* and *Homo habilis*, and differ from other East Asian *Homo erectus*. With this finding, the Sangiran specimens were classified into *Meganthropopus*. However, among the four Sangiran teeth analyzed in present study, P^3 and M^1 all numbered as S-4 are close to the grouped morphospace of Chinese fossil hominins; for the two teeth of M_1, S-1 are distributed close to modern humans, and S-6 stays in the region of Chinese fossil hominins, *Homo habilis*, and European fossil hominins. These analyses suggest that Asian early and middle Pleistocene hominins have similar crown shape. The analyses of three Jianshi hominin teeth indicate that the crown shape of the three teeth resemble that of other Asian *Homo erectus* with their morphospace within the Asian *Homo erectus* area. Our study did not find the evidence to support the tooth crown shape of Jianshi hominin differing from Zhoukoudian *Homo erectus*, and showing special resemblance to African early hominins.

Geometric morphometric has just been used to study hominin fossils for a few years. So far the collected dental data are only analyzed in two-dimensional space revealing the information of dental symmetry, cusp pattern, and size-related proportion. All information cannot be collected by traditional method. Therefore, geometric morphometric is a supplement to the traditional method. We notice that the findings from present study differ from previous studies with traditional method. It should be pointed out that two of the three Jianshi hominin teeth were severely worn, which caused some morphological features to be lost. Until now, just limited studies of hominin teeth with geometric morphometric have been conducted. The evolutionary and taxonomic values of various findings revealed from the studies are not conclusive. The explanations based on the related analysis are preliminary and need to be further studied. However, all the studies so far conducted reveal the evolutionary and taxonomic significance of the tooth shape from the geometric morphometric analysis [4–8, 21–24]. With these in mind, it is necessary to reconsider the morphology and taxonomy of the Jianshi hominin teeth.

1   Hillson S. Teeth. Cambridge: Cambridge University Press, 1986. 1–368

2   Alt K W, Rosing F W, Teschler-Nicola M. Dental Anthropology Fundamentals, Limits and Prospect. New York: Springer-Verlag/ Wien, 1998. 1–367

3   Martinón-Torres M, Bermúdez de Castro J M, Gómez-Robles A, et al. Dental evidence on the hominin dispersals during the Pleistocene. Proc Natl Acad Sci USA, 2007, 104: 13279–13282

4   Slice D E. Geometric morphometrics. Ann Rev Anthropol, 2007, 36: 261–281

5   Adams D C, Rohlf F J, Slice D E. Geometric morphometrics: Ten years of progress following the 'Revolution'. Ital J Zool, 2004, 71: 5–16

6   Martinón-Torres M, Bastir M, Bermúdez de Castro J M, et al. Hominin lower second Premolar morphology: Evolutionary inferences through geometric morphometric analysis. J Human Evol, 2006, 50: 523–533

7   Gómez-Robles A, Martinón-Torres M, Bermúdez de Castro J M, et al. A geometric morphometric analysis of hominin upper first molar shape. J Human Evol, 2007, 53: 272–285

8   Gómez-Robles A, Martinón-Torres M, Bermúdez de Castro J M, et al. Geometric morphometric analysis of the crown morphology of the lower first premolar of hominins, with special attention to Pleistocene Homo. J Human Evol, 2008, 55: 627–638

9   Anton S. Natural history of *Homo erectus*. Yearbook Phys Anthropol, 2003, 46:126–170

10 Liu W. The advances in the studies of *Homo erectus* and some problems of the origin and evolution of Chinese *Homo erectus*. Acta Anthropol Sin, 2004, 23(Suppl): 1–11

11 Gao J. Australopithecine teeth associated with *Gigantopithecus*. Ver-

tebrata PalAsiatica, 1975, 13: 81–88

12 Huang W P, Ciochon R, Gu Y M, et al. Early *Homo* and associated artifacts from Asia. Nature, 1995, 378: 275-278

13 Zheng S H. Jianshi Hominid Site. Beijing: Science Press, 2004. 1–412

14 Zhang Y Y. The "*Australopithecus*" of west Hubei some early Pleistocene hominids of Indonesia. Acta Anthropol Sin, 1984, 3: 85–92

15 Wu X Z. Longgupo hominoid mandible belongs to ape. Acta Anthropol Sin, 2000, 19: 1–10

16 Ashraf M T. Morphometric—Applications in Biology and Paleontology. Heidelberg: Springer-Verlag Publishers, 2004. 1–263

17 Liu W, Hlusko L, Zheng L. Morphometric analysis of hominoid lower molars found in Yuanmou of Yunnan Province, China. Primates, 2001, 42: 123–134

18 Liu W, Zheng L, Alan W. Three-dimensional morphometric analyses of hominoid lower molars from Yuanmou of Yunnan Province, China. Acta Anthropol Sin, 2002, 21(suppl): 1–13

19 Bailey S E. A morphometric analysis of maxillary molar crowns of Middle-Late Pleistocene hominins. J Human Evol, 2004, 47: 183–198

20 Xing S, Liu W. Morphometric analysis of Chinese teeth: Molar crown and cusp areas of a recent North Chinese Population. Acta Anthrpol Sin, 2009, 28: 179–191

21 Bookstein F L. Landmark methods for forms without landmarks: Morphometrics of group differences in outline shape. Med Image Anal, 1997, 1: 225–243

22 Zelditch M L, Swiderski, D L, Sheets H D, et al. Geometric Morphometrics for Biologists: A Primer. San Diego: Elsevier Academic Press, 2004. 1–443

23 Slice D E. Modern Morphometrics in Physical Anthropology. New York: Kluwer Academic, 2005. 1–383

24 Bookstein F L. Applying landmark methods to biological outline data. In: Mardia K V, Gill C A, Dryden I L, eds. Image Fusion and Shape Variability Techniques. Leeds: Leeds University Press, 1996. 79–87

25 Sheets H D. Imp, integrated morphometric package. 2001, http://www.canisius.edu/~sheets/morphsoft.html

26 Rohlf F J. TpsDig. Ecology and Evolution, SUNY. New York: Stony Brook, 1998, http://life.bio.sunysb.edu/morph/

27 Rohlf F J. TpsRelw. Ecology and Evolution, SUNY. Stony Brook, New York.   1998, http://life.bio.sunysb.edu/morph/

28 Rohlf F J. TpsRegr. Ecology and Evolution, SUNY. Stony Brook, New York. 1998, http://life.bio.sunysb.edu/morph/

29 Klingenberg C P. Heterochrony and allometry: The analysis of evolutionary change in ontogeny. Biol Rev, 1998, 73: 79–123

30 Mosimann J E. Size allometry: Size and shape variables with characterizations of the lognormal and generalized gamma distributions. J Am Stat Assoc, 1970, 65: 930–945

31 Bailey S E, Lynch J M. Diagnostic differences in mandibular P4 shape between Neandertals and anatomically modern humans. Am J Phys Anthropol, 2005, 126: 268–277

32 Hills M, Graham S H, Wood B A. The allometry of relative cusp size in hominoid mandibular molars. Am J Phys Anthropol, 1983, 62: 311–316

33 Wood B A, Uytterschaut H. Analysis of the dental morphology of Plio-Pleistocene hominids III. Mandibular premolar crowns. J Anat, 1987, 154: 121–156

34 Leonard W R, Hegmon M. Evolution of P3 morphology in Australopithecus afarensis. Am J Phys Anthropol, 1987, 73: 41–63

35 Bailey S E. A morphometric analysis of maxillary molar crowns of Middle-Late Pleistocene hominins. J Human Evol, 2004, 47: 183–198

36 Scott G R, Turner C G. The Anthropology of Modern Human Teeth: Dental Morphology and its Variation in Recent Human Populations. Cambridge: Cambridge University Press, 1997. 1–320

37 Gruneberg H. Genetical studies on the skeleton of the mouse. IV. Quasi-continuous variations. J Genet, 1952, 51: 95–114

38 Wood B A, Abbott S A. Analysis of the dental morphology of Plio-Pleistocene hominids: I. Mandibular molars: Crown area measurements and morphological traits. J Anat, 1983, 136: 179–219

39 Wood B A, Abbott S A, Graham S H. Analysis of the dental morphology of Plio-Pleistocene hominids: II. Mandibular molars-study of cusp areas, fissure pattern and cross sectional shape of the crown. J Anat, 1983, 137: 287–314

40 Wood B A, Uytterschaut H. Analysis of the dental morphology of Plio-Pleistocene hominids: III. Mandibular premolar crowns. J Anat, 1987, 154: 121–156

41 Wood B A, Engleman C A. Analysis of the dental morphology of Plio-Pleistocene hominids: V. Maxillary postcanine tooth morphology. J Anat, 1988, 161: 1–35

42 Suwa G, Wood B A, White T D. Further analysis of mandibular molar crown and cusp areas in Pliocene and Early Pleistocene hominids. Am J Phys Anthropol, 1994, 93: 407–426

43 Suwa G, White T D, Howell F C. Mandibular postcanine dentition from the Shungura formation, Ethiopia: Crown morphology, taxonomic allocations, and Plio-Pleistocene hominid evolution. Am J Phys Anthropol, 1996, 101: 247–282

44 Suwa G. Serial allocation of isolated mandibular molars of unknown taxonomic affinities from the Shungura and Unso formations, Ethiopia, a combined method approach. J Human Evol, 1996, 11: 269–282