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Craniofacial morphological microevolution of Holocene populations in northern China

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In order to better understand microevolutionary processes in Holocene Chinese craniofacial morphology, an analysis has been done on 21 metric traits on Neolithic (*n*=161), Bronze Age (*n*=423) and modern (*n*=134) adult male skulls from northern China. The results indicate that the physical characters of these Chinese populations evolved throughout the Holocene. From the Neolithic to Bronze Age to present day, general trends include: cranial and facial sizes decrease; the nose gets narrower and longer; the orbits become narrower and higher; the head is more globular. The expression of the cranial features varies between the different time periods. The decrease in cranial size primarily occurred from the Bronze Age to present day. However, the decrease in facial size, the narrowing of the nose, and the elevation of the orbits took place throughout the Holocene. These traits are likely still evolving. This evolving pattern of the cranial features for the Holocene Chinese populations is similar to that found elsewhere in the world. The decrease in overall craniofacial size is associated with changes in climate and diet. In addition, it is possible that the craniofacial morphological microevolution is controlled by human evolutionary mechanisms.

Holocene Chinese populations, microevolution, skull, morphology

According to the fossil evidence, the origin and evolution of humans can be traced back to 6—7 Ma ago in Africa[1]. Starting from *Sahelanthropus tchadensis*, the possible earliest human found in Chad, and then following *Australopithecus*, *Homo habilis*, *Homo erectus*, archaic *Homo sapiens* and modern *Homo sapiens*, the morphological characteristics of humans changed significantly over this period of time. These changes include: increase in absolute and relative cranial capacity; increase in stature; more orthognathic face; decrease in mandibular size; the occurrence of a pronounced chin; the reduction in cranial size differences for sex; tooth size (especially for canine) decreases; the length of upper limb relative to body size decreases; skeletal robustness decreases. Human intelligence has also increased, while language and behavior have become more complex. During the Late Pleistocene, humans migrated to many regions throughout the Old World and eventually into the New World. In the subsequent Holocene (Neolithic, Bronze Age, Iron Age), after the appearance, migration, admixture and extinction of numerous ancient populations, the different modern racial groups appeared, forming the current distribution of human populations[2−4].

After the height of the Last Glacial Maximum (18 ka BP), the climate became warmer and there is an increase in humans migrations and admixture[3]. Many changes in hunter-gatherer's lifestyle, culture, technology, behavior

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and economic patterns occurred. The Holocene is the key time period for the formation and differentiation of modern human populations. Accordingly, Holocene human remains, especially some extinct human populations excavated from Neolithic and Bronze Age archaeological sites are very important to study the formation and evolution of modern human populations, and the differentiation into distinct groups. For the past few decades, a series of studies have been conducted on the Holocene human remains from different regions and time periods. These studies allow us to think of the problems on the Holocene humans more deeply[5−10].

In the past, it has been proposed that the primary cranial morphological features of Late Pleistocene humans are very similar to those of Holocene humans, thus remaining unchanged[11−13]. However, some recent studies of Holocene populations indicate that the physical characters of these humans are still evolving. Examples include: 70% of the cranial features of northern populations from Chile have distinct temporal changes[14]; the calvarium becomes longer and narrower, and the face becomes narrower and higher in certain American populations from the mid-19th century to the 1970s[15]; the cranial robustness of African northeast Nubians decreases, and the head shape becomes more brachycephalic, while the tooth and mandible sizes decrease[16,17]; the cranial capacities of Europeans decrease by 95—165 cm^3 for males and 74—106 cm^3 for females[18]; the stature and upper facial height of Japanese increase[19].

Holocene human skeleton remains are very rich in China. Archaeological, physical anthropological and genetic data indicate that nearly all of the various populations living in China for the past 10000 years are Mongoloids except for a few minority groups in northwest China, who have some European features in their genetic makeup. The studies of the Chinese Holocene human populations primarily focus on distinguishing “racial features” among the sub-populations. Due to the good preservation of skulls, most analyses concentrate on those materials. For the microevolution of physical characters of Holocene Chinese populations, some preliminary studies have been done. For instance, throughout the Holocene, the cranial and facial heights increased, accompanied by decreases in breadth and length[20,21]. In other cases, features like orbits, nasal and facial shapes were shown to have undergone minor changes for the people living in the Yellow River region[22]. Nevertheless, these studies were preliminary in nature. The above presents a comprehensive analysis of microevolution in northern China during the Holocene.

1 Materials and methods

1.1 Materials

To avoid the influence of age, sex and geographic region, we chose 718 adult male skulls from northern Chinese collections, which are housed in the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, and the Research Center for Chinese Frontier Archaeology of Jilin University. Three hundred and thirty-eight skulls were measured by us, while data for the remaining 380 skulls were culled from published works (Table 1, Figure 1).

Table 1 Skull materials used in this study

Age	Population	*N*	Geographic origin
Neolithic Age	Qinghai	26	Yanshan[23]; Liuwan[24]
(7000—4000 a BP)	Shannxi	32	Banpo[25]; Huaxian[26]
	Hebei	41	Jiangjialiang (this work)
	Henan	27	Xishan (this work)
	Shandong	35	Dawenkou[27]; Xixiahou[28]; Chengzi[29]; Wangyin[30]
Bronze Age	Henan	111	Yinxu[31]
(4000—2500 a BP)	Qinghai	153	Lijiashan[32]; Shangsunjiazai[33]; Xiaohandi; Mapai (this work)
	Gansu	60	Donghuishan (this work); Huoshaogou[33]
	Shannxi	43	Zaimao; Longxian; Wayaogou (this work)
	Shanxi	27	Youyao (this work)
	Jilin	29	Shaodagou[34]; Xingjiadian[35]; Wanfabozi[36]; Jiutai (this work)
Present day (100 a BP)	North China	134	Hebei; Shanxi; Shandong; Henan (this work)

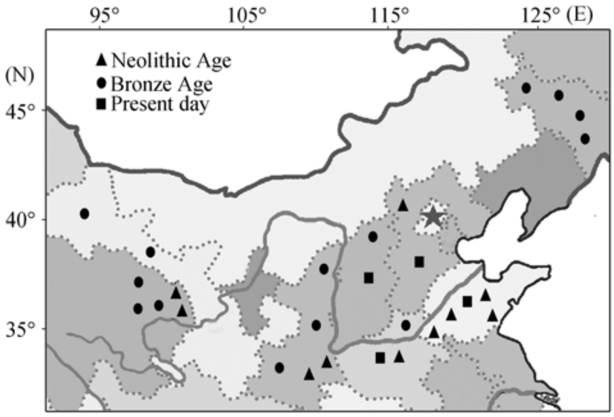

Figure 1 The distribution of the populations used in this study.

1.2 Methods

We chose 21 cranial traits (12 linear measures and 9 indices) for this analysis (Table 2). The means of the 21 measurements were derived for the different populations. Statistical analyses were performed using SPSS and were considered significantly different if $P \leqslant 0.05$. Non-parametric independent-sample tests were used to test for statistically significant differences for Neolithic, Bronze Age and modern populations. We calculated percentages of the temporal craniometrical changes for these traits, using a formula derived by Zhang[21]. The formula is as follows:

Percentages of the temporal craniometrical changes (%) = 100 × (X_1–X_2) / X_1, where X_1 and X_2 are average cranial measures of one population divided into different cultural periods.

Figure 2 describes the methodology to collect the craniofacial measurements. The cranial and facial dimensions are cubage (Figure 2 (a), (b)), the nasal dimension is triangle (Figure 2(c)), and the orbital dimension is rectangle (Figure 2 (d)). The formulas are: cranial cubage = cranial length × cranial breadth × cranial height; facial cubage = bizygomatic breadth × upper facial height × profile length; nasal area = 1/2 × nasal breadth × nasal height; orbital area = orbital breadth × orbital height.

2 Results

2.1 Morphological variation in the craniofacial complex between the Neolithic and Bronze Age human populations

Thirteen measures and indices are statistically significantly different. From the Neolithic to Bronze Age, two

Table 2 Comparison of the cranial morphometric data of the different time periods in Holocene Chinese populations

Matin	Measurement	Neolithic Age		Bronze Age		Present day		Significant test		
		N	Mean	*N*	Mean	*N*	Mean	Neolithic-Bronze Age	Bronze Age-present day	Neolithic Age-present day
1	Cranial length a)	113	178.8	407	182.1	131	176.9	0.000*	0.000*	0.038*
8	Cranial breadth a)	100	139.9	398	141.3	129	137.1	0.119	0.000*	0.003*
17	Cranial height a)	88	140.9	297	138.4	98	136.3	0.000*	0.001*	0.000*
1: 8	Cranial index	95	78.5	389	77.7	129	77.6	0.109	0.745	0.201
1:17	Cranial length-height index	85	78.7	290	75.7	98	76.9	0.000*	0.001	0.005*
17:8	Cranial breadth-height index	79	101.0	282	98.3	98	99.6	0.000*	0.026*	0.080
5	Basis length a)	94	104.1	289	101.7	98	98.7	0.000*	0.000*	0.000*
40	Profile length a)	85	100.1	261	97.1	98	94.0	0.000*	0.000*	0.000*
40:5	Gnathic index	85	96.1	259	95.6	98	95.3	0.321	0.586	0.204
48	Upper facial height a)	120	73.2	356	71.9	130	72.2	0.006*	0.533	0.057
45	Bizygomatic breadth a)	80	137.0	331	137.0	121	132.6	0.968	0.000*	0.000*
48:45	Upper facial index	76	53.9	300	52.6	120	54.4	0.003*	0.000*	0.264
45:8	Transverse cranial facial index	66	98.7	319	97.2	119	96.9	0.002*	0.396	0.003*
48:17	Vertical crania-facial index	77	52.1	262	52.3	95	53.2	0.675	0.024*	0.027*
51	Orbital breadth a)	111	43.4	388	42.1	130	40.6	0.000*	0.000*	0.000*
52	Orbital height a)	113	34.1	384	34.3	130	35.4	0.317	0.000*	0.000*
52:51	Orbital index	108	78.5	382	81.5	130	87.1	0.000*	0.000*	0.000*
45	Nasal breadth a)	131	27.3	396	26.8	132	25.2	0.035*	0.000*	0.000*
55	Nasal height a)	121	54.8	397	54.9	132	55.3	0.901	0.237	0.270
45:55	Nasal index	114	49.8	393	49.1	132	45.7	0.112	0.000*	0.000*
77	Nasion-frontal angle b)	105	146.4	277	146.1	97	145.9	0.692	0.739	0.563

* $P \leqslant 0.05$; a) in mm; b) in (°).

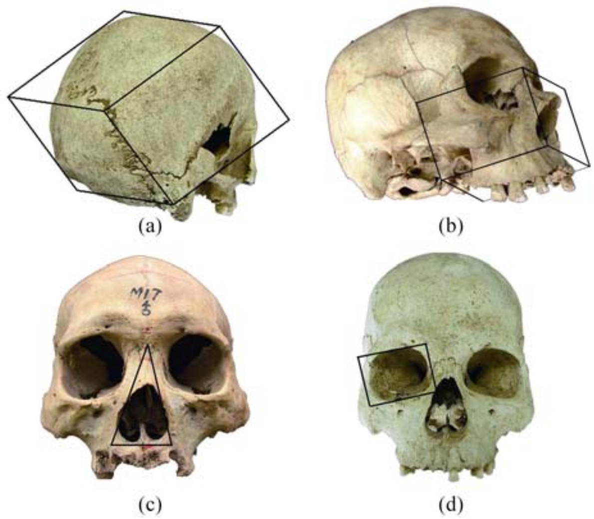

Figure 2 The methods to measure the craniofacial size. (a) Cranial cubage ; (b) facial cubage; (c) nasal area; (d) orbital area.

traits (cranial length and orbital index) increased significantly. Eleven measurements decreased significantly, including cranial height, cranial length-height index, cranial breadth–height index, basis length, profile length, upper facial height, upper facial index, transverse cranial facial index, orbital breadth, nasal breadth and nasal index (Table 2, Figure 3). The orbital index (up 3.8 %) and cranial length–height index (up 3.8 %) changed the most.

Eight traits have no statistically significant difference, including cranial breadth, cranial index, gnathic index, cranial breadth, vertical crania-facial index, orbital height, nasal height, and nasion-frontal angle (Table 2).

2.2 Morphological variation in the craniofacial complex between the Bronze Age and modern human populations

Fourteen measures and indices have statistically significant differences. From the Bronze Age to present day, five traits increased significantly, including cranial breadth-height index, upper facial index, vertical crania-facial index, orbital height and orbital index. Nine traits decreased significantly, including cranial length,

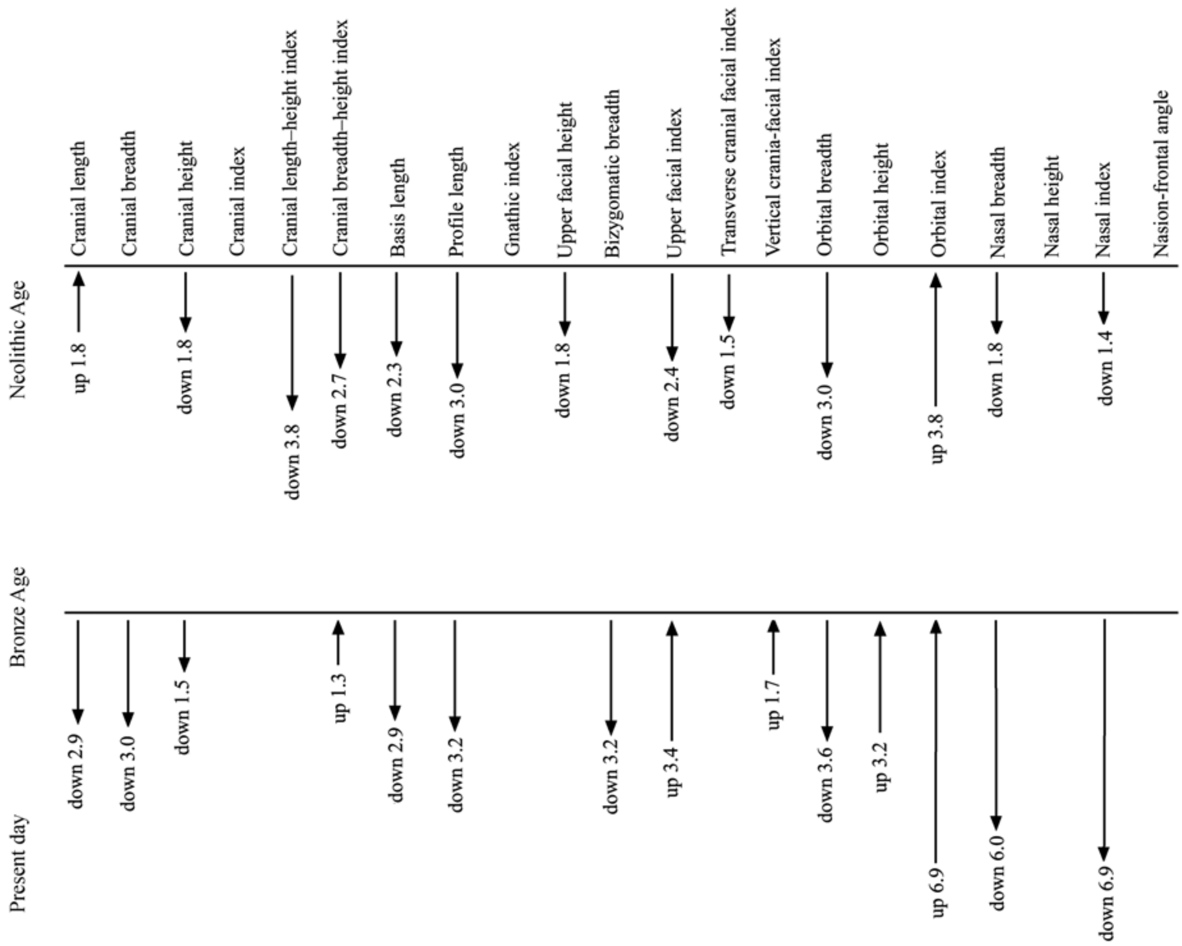

Figure 3 The changes of the cranial metric traits in Holocene Chinese Populations from the Neolithic, Bronze Age to present day (%).

cranial breadth, cranial height, basis length, profile length, bizygomatic breadth, orbital breadth, nasal breadth and nasal index (Table 2, Figure 3). The orbital (down 6.9 %) and nasal indices (up 6.9 %) changed the most.

Seven traits have no statistically significant differences, including cranial index, cranial length-height index, gnathic index, upper facial height, transverse cranial facial index, nasal height and nasion-frontal angle (Table 2).

2.3 Morphological variation in the craniofacial complex between the Neolithic and modern human populations

Fourteen measures and indices have statistically significant differences. From the Neolithic Age to present day, three traits increased significantly, including vertical cranial facial index, orbital height and orbital index. Nine traits decreased significantly, including cranial length, cranial breadth, cranial height, cranial length-height index, basis length, profile length, bizygomatic breadth, transverse cranial facial index, nasal breadth, nasal index and orbital breadth (Table 2, Figure 3). The nasal index (down 8.2%), orbital index (up 6.9 %) and nasal breadth (down 6.0 %) displayed the most significant variation.

Seven traits have no statistically significant differences, including cranial index, cranial breadth–height index, gnathic index, upper facial height, upper facial index, nasal height and nasion-frontal angle (Table 2).

2.4 Microevolution of cranial dimensions of Holocene Chinese populations

In the Neolithic Age, cranial cubage = 178.8 mm×139.9 mm×140.9 mm = 3524.5 cm^3. In the Bronze Age, cranial cubage = 182.1 mm×141.3 mm×138.4 mm = 3561.1cm^3. In the modern sample, cranial cubage = 176.9 mm×137.1 mm×136.3 mm = 3305.7 cm^3.

The change of the cranial size between the Neolithic and Bronze Age samples is very small, only 36.6 cm^3 (1.0 %) difference. From the Bronze Age to present day, the cranial size decreased by 255.4 cm^3 (down 7.2 %). From the Neolithic to Bronze Age to present day, the cranial size decreased by 218.8 cm^3 (6.2 %). The decreases in cranial size occurred primarily from the Bronze Age to present day (Table 3).

2.5 Microevolution of facial dimensions of Holocene Chinese populations

In the Neolithic Age, facial cubage = 73.2 mm×137.0 mm × 100.1 mm = 1003.8 cm^3. In the Bronze Age, facial cubage = 71.9 mm × 137.0 mm × 97.1 mm = 956.5 cm^3. In the present day, facial cubage = 72.2 mm × 132.6 mm × 94.0 mm = 899.9 cm^3.

From the Neolithic to Bronze Age, the facial size decreased by 47.3 cm^3 (down 4.7 %). From the Bronze Age to present day, the facial size decreased by 56.6 cm^3 (down 5.9 %). From the Neolithic to Bronze Age to present day, the facial size decreased by 56.6 cm^3 (down 10.4 %). The decreases in facial size occurred continually during the Holocene (Table 3).

2.6 Microevolution of the nasal dimensions of Holocene Chinese populations

In the Neolithic Age, nasal area = 1/2 × 27.3 mm × 54.8 mm = 748.0 mm^2. In the Bronze Age, nasal area = 1/2 × 26.8 mm × 54.9 mm = 735.7 mm^2. In the present day, nasal area = 1/2 × 25.2 mm × 55.3 mm = 696.8 mm^2.

From the Neolithic to Bronze Age, the nasal area decreased by 12.3 mm^2 (down 1.6 %). From the Bronze Age to present day, the nasal size decreased by 38.9 mm^2 (down 5.3 %). From the Neolithic to Bronze Age to present day, the nasal size decreased by 51.2 mm^2 (6.9 %). The decrease in the nasal size happened continually during the Holocene. The most distinct variation is from the Bronze Age to present day (Table 3).

2.7 Microevolution of the orbital dimensions of Holocene Chinese populations

In the Neolithic Age, orbital area = 43.4 mm × 34.1 mm = 1479.9 mm^2. In the Bronze Age, orbital area = 42.1 mm × 34.3 mm = 1444.0 mm^2. In the present day, orbital area = 40.6 mm × 35.4 mm = 1437.2 mm^2.

Table 3 The change in craniofacial size in Holocene Chinese populations from the Neolithic, Bronze Age and present day

	Neolithic-Bronze Age		Bronze Age-present day		Neolithic Age-present day	
	Change	Percentage	Change	Percentage	Change	Percentage
Cranial cubage	36.6 cm^3	up 1.0%	255.4 cm^3	down 7.2%	218.8 cm^3	down 6.2%
Facial cubage	47.3 cm^3	down 4.7%	56.6 cm^3	down 5.9%	56.6 cm^3	down 10.4%
Nasal area	12.3 mm^2	down 1.6%	38.9 mm^2	down 5.3%	51.2 mm^2	down 6.9%
Orbital area	35.9 mm^2	down 2.4%	6.8 mm^2	down 0.5%	42.7 mm^2	down 2.9%

From the Neolithic to Bronze Age, the orbital size decreased by 35.9 mm^2 (down 2.4 %). From the Bronze Age to present day, the orbital size decreased by 6.8 mm^2 (down 0.5 %). From the Neolithic to Bronze Age to present day, the orbital size decreased by 42.7 mm^2 (down 2.9 %). The most distinct change for orbital size is from the Neolithic to Bronze Age (Table 3).

3 Discussion and conclusions

3.1 The evolutionary trends of craniofacial morphology in Holocene Chinese populations

Analysis of the 21 cranial metric traits indicates that the physical characters of Chinese populations have evolved significantly over the course of the past 10000 years. From the Neolithic to Bronze Age to present day, cranial and facial sizes of Holocene Chinese populations decreased. The nose becomes narrower and longer, while the orbits become narrower and higher. The head becomes more globular (Figure 4). From the Neolithic to Bronze Age, and from the Bronze Age to present day, the expression of the cranial features varies between the different time periods.

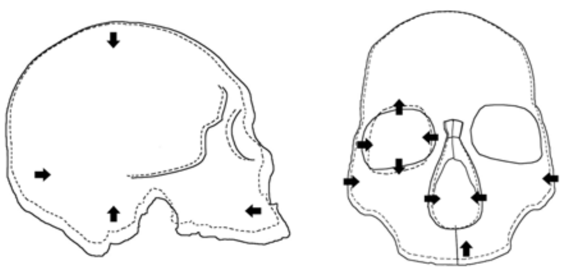

Figure 4 The sketch showing the evolutionary trends of craniofacial morphology in Holocene Chinese populations.

Based on the results of six primary cranial measurements, namely, cranial length, cranial breadth, cranial height, cranial index, cranial length-height index, cranial breadth-height index, the most pronounced difference is a decrease in cranial size between the Bronze Age and present day. The reduction in cranial size is associated with the decrease of cranial breadth and cranial height. There have been no statistically significant differences for cranial length, cranial index, and cranial breadth-height index from the Neolithic to present day. The decrease in the cranial length-height index is associated with the decrease in cranial height.

Based on the results of six facial measurements, namely, basis length, profile length, gnathic index, upper facial height, bizygomatic breadth, upper facial index, the basis length and profile length continually reduced from the Neolithic to Bronze Age to present day, while the gnathic index did not change. The decrease in facial size is associated with the decrease of the cranial breadth and profile length. The upper facial height and upper facial index did not change significantly from the Neolithic to present day.

Through time, the transverse cranial facial index decreased, which suggests that the narrowing of the bizygomatic breadth evolved faster than the cranial breadth.

Based on the results of the orbital measurements (orbital breadth, orbital height, orbital index), the orbital index decreased through time. From Neolithic to Bronze Age, the orbital index increased, and orbital breadth decreased, while orbital height did not change significantly. From the Bronze Age to present day, the orbital breadth continually decreased, while the orbital height and orbital index increased.

Based on the results of the nasal areas (nasal breadth, nasal height, nasal index, nasion-frontal angle), the nasal index continually decreased, while the nasion-frontal angle had no significant change. The decrease of the nasal index is associated with the reduction of the nasal breadth, while the nasal height did not change significantly.

3.2 Reasons for the cranial morphological microevolution in Holocene populations

There are two primary reasons which may cause the variation in physical characters among Holocene human populations. One is the human migration and admixture, and the other is that the differences are controlled by human evolution. Based on the study of Holocene human skeletons from China, the populations are all classified as Mongoloids, except for the groups from the Xinjiang region. According to the physical characters, the Neolithic humans can be divided into two main groups roughly following the border of the Yangtze River[37]. This two types' division continued to the Bronze Age[38−40]. The physical characters of modern Chinese are also divided into north and south types. The studies of haematology[41], dermatology[42] and molecular biology[43−44] also support this division. All the specimens utilized in this study are adult males and originate from north of the Yangtze River, which means the impacts from geographic regions, sex and ages can be excluded.

The Neolithic (7000－4000 a BP) human skulls used in the present study were collected from 5 provinces of Qinghai, Shaanxi, Hebei, Henan and Shandong. The Bronze Age (4000－2500 a BP) cranial specimens came from Henan, Qinghai, Gansu, Shaanxi, Shanxi and Jilin provinces. All the modern human skulls are from North China. Based on this analysis, the reason for the variation in cranial features cannot be simply attributed to human migration and admixture.

During the Holocene, global climates gradually became warmer and more geographic regions were available for human habitation. Exceptions do exist for this pattern. For instance, according to some historic records[45,46], during the period of 2200－2000 BC, there was a 3℃ decrease in temperature in the mid-latitude regions, causing drought in some areas (e.g. Yellow River region). These types of climate changes would have impacted the overall physical characters of humans and other members of the biotic community. In addition, the subsistence change from hunting and gathering to plant and animal domestication influenced human morphological features[47]. The transition to softer foods would have led to a degeneration of the muscles related to mastication, which would have resulted in less prognathic facial bones. Currently, these explanations are tentative and further studies are necessary.

Previous studies on the microevolution of cranial morphological features in Holocene humans indicate that many human populations around the world follow the trend towards decreasing cranial size[14－16,18]. Our study suggests the differences and changes of physical characters are influenced by variation in environment and diet. Overall, the physical characters of Holocene human populations in China have some microevolutionary trends, suggesting that modern humans are still evolving. This microevolution is related to the environment, climate and diet, and in addition to human evolutionary mechanisms.

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