

On the origin of modern humans in China

Xinzhi Wu

Institute of Vertebrate, Paleontology and Paleoanthropology, Beijing 100044, China

Abstract

The Multiregional Evolution Hypothesis (MEH) and the Recent Out of Africa Hypothesis (ROAH) are two main hypotheses bearing on the origin of modern humans. In China, there are many common morphological features among Pleistocene human fossil skulls. These features and the morphological mosaic between *Homo sapiens erectus* and *Homo sapiens sapiens* of China indicate the continuity of human evolution in this region. There are a few skulls possessing one or two features that suggest gene flow from the West to China. Based on the evidence of continuity and gene flow, a new hypothesis, *Continuity with Hybridization*, was proposed in 1998 for characterizing human evolution in China. This hypothesis is also supported by the Paleolithic archaeological record of China. There are serious problems with the ROAH. For example, the dates of the last common ancestor of anatomically modern humans obtained, determined by different investigators using molecular clock estimates, vary considerably. Further, the important assumptions of the ROAH—a constant mutation rate and no loss of gene variants during human evolution—cannot be verified. The results of recent studies on ancient DNA could be interpreted in different ways, and could also be interpreted as supporting the MEH. Also, the Paleolithic artifacts from the Near East and China do not support the ROAH.

© 2003 Elsevier Ltd and INQUA. All rights reserved.

1. Introduction

The origin of modern humans is a focus of intense debate in paleoanthropology. For several years, discussion in this area has involved the exploration of two main hypotheses. The Recent Out of Africa (ROAH) or Total Replacement Hypothesis is the prevalent one currently, while the Multiregional Evolution Hypothesis (MEH) is less known and less accepted, especially among Western scientists, but is supported by evidence provided by the human fossil assemblages of China, as well as by archaeological and other evidence.

2. Continuity in human evolution of China

The notion of the continuity of human evolution of China was proposed by Weidenreich more than half a century ago (Weidenreich, 1943). In his monograph on the study of the skulls of Peking Man from Zhoukoudian (then called *Sinanthropus pekinensis*), he suggested no fewer than 12 morphological features that he believed to indicate continuity of human evolution of east Asia. These features were: a midsagittal crest and parasagittal depression; presence of the Inca bone (Os Incae); certain “Mongolian features” of the nasal bridge and cheek region of the maxilla and zygomatic

bone; exostoses of the maxilla, temporal bone, and mandible; a high degree of platymerism of the femur combined with a strong deltoid tuberosity of the humerus; and finally, shovel-shaped upper lateral incisors. These common features were derived from comparisons of the Peking Man remains and modern Mongoloids. Some of the characters suggested by Weidenreich have been shown not to indicate a unique close relationship between Peking Man and modern Mongoloids, but rather to be primitive characteristics shared by members of the genus *Homo*.

Since Weidenreich’s time, many more Pleistocene human fossils have been found in China (Table 1, Fig. 1). New evidence indicating the continuity of human evolution of China has been derived from comparisons among these fossils instead of simply between Peking Man and modern humans.

Among the human fossils of China are some common features. All of the upper incisors found in Pleistocene China are shovel-shaped. The sutures between the frontal bone above and the nasal and maxillary bones below form a more or less horizontal curve; the upper face of all of the skulls is low and flat; the nasomalar angle is large; the nasal saddle is flat; the orbits are quadrangular in shape; the inferolateral orbital margin is rounded instead of sharp; the anterolateral surface of the frontosphenoidal process of the zygomatic bone

Table 1
Main human fossils found in China

Taxonomic assignment	Site	Primary specimen(s)	Geological epoch	Chronometric date
<i>Homo sapiens erectus</i>	Yuanmou	2 incisors	Early Pleistocene	1.7 Ma (PM) ^a
<i>H. s. e.</i>	Gongwangling	1 incomplete skull	Early Pleistocene	1.15 Ma (PM) ^b
<i>H. s. e.</i>	Yunxian	2 skulls	Early Pleistocene	565,000 yr BP (ESR) ^b ; 870,000–830,000 yr BP (PM) ^b
<i>H. s. e.</i>	Chenjiawo	1 mandible	Middle Pleistocene	650,000–500,000 yr BP (PM) ^a
<i>H. s. e.</i>	Tangshan	1 incomplete skull	Middle Pleistocene	350,000 yr BP (U) ^c ; > 500,000 yr BP (TIMS) ^c
<i>H. s. e.</i>	Tangshan	1 skull-cap	Middle Pleistocene	> 239,000 yr BP (TIMS) ^c
<i>H. s. e.</i>	Zhoukoudian	6 skull-caps; 35 skull fragments; 13 limb bone fragments; 157 teeth	Middle Pleistocene	578,000–230,000 yr BP (U); ESR; TL; FT ^{a,b}
<i>H. s. e.</i>	Hexian	1 skull-cap	Middle Pleistocene	270,000–150,000 yr BP (U) ^a
Early <i>Homo sapiens sapiens</i>	Dali	1 skull	Middle Pleistocene	209,000 yr BP (U) ^a
Early <i>H. s. s.</i>	Jinniushan	1 skull fragment	Middle Pleistocene	280,000 yr BP (U) ^a
Early <i>H. s. s.</i>	Maba	1 skull-cap	Middle Pleistocene	135,000–129,000 yr BP (U) ^a
Early <i>H. s. s.</i>	Xujiayao	16 cranial fragments	Late Pleistocene	125,000–104,000 yr BP (U) ^a
Early <i>H. s. s.</i>	Dingcun	3 teeth; 1 parietal	Late Pleistocene	210,000–160,000 yr BP (U) ^a
Early <i>H. s. s.</i>	Tongzi	6 teeth	Late Pleistocene	181,000–113,000 yr BP (U) ^a
Late <i>Homo sapiens sapiens</i>	Liujiang	1 skull; 4 bone fragments	Late Pleistocene	7000? yr BP (U) ^a
Late <i>H. s. s.</i>	Upper cave	3 complete skulls and bone fragments	Late Pleistocene	34,000–29,000 yr BP (AMS) ^a
Late <i>H. s. s.</i>	Lijiang	1 skull	Late Pleistocene	None
Late <i>H. s. s.</i>	Chuangdong	2 skulls	Late Pleistocene	None

Geological dates are based on faunal correlation; AMS, accelerator radiocarbon; PM, Paleomagnetism, U; uranium series; ESR; electron spin resonance; TL; thermoluminescence; FT; fission track.

^aWu and Poirier (1995).

^bWu et al. (1999).

^cWu et al. (2002).

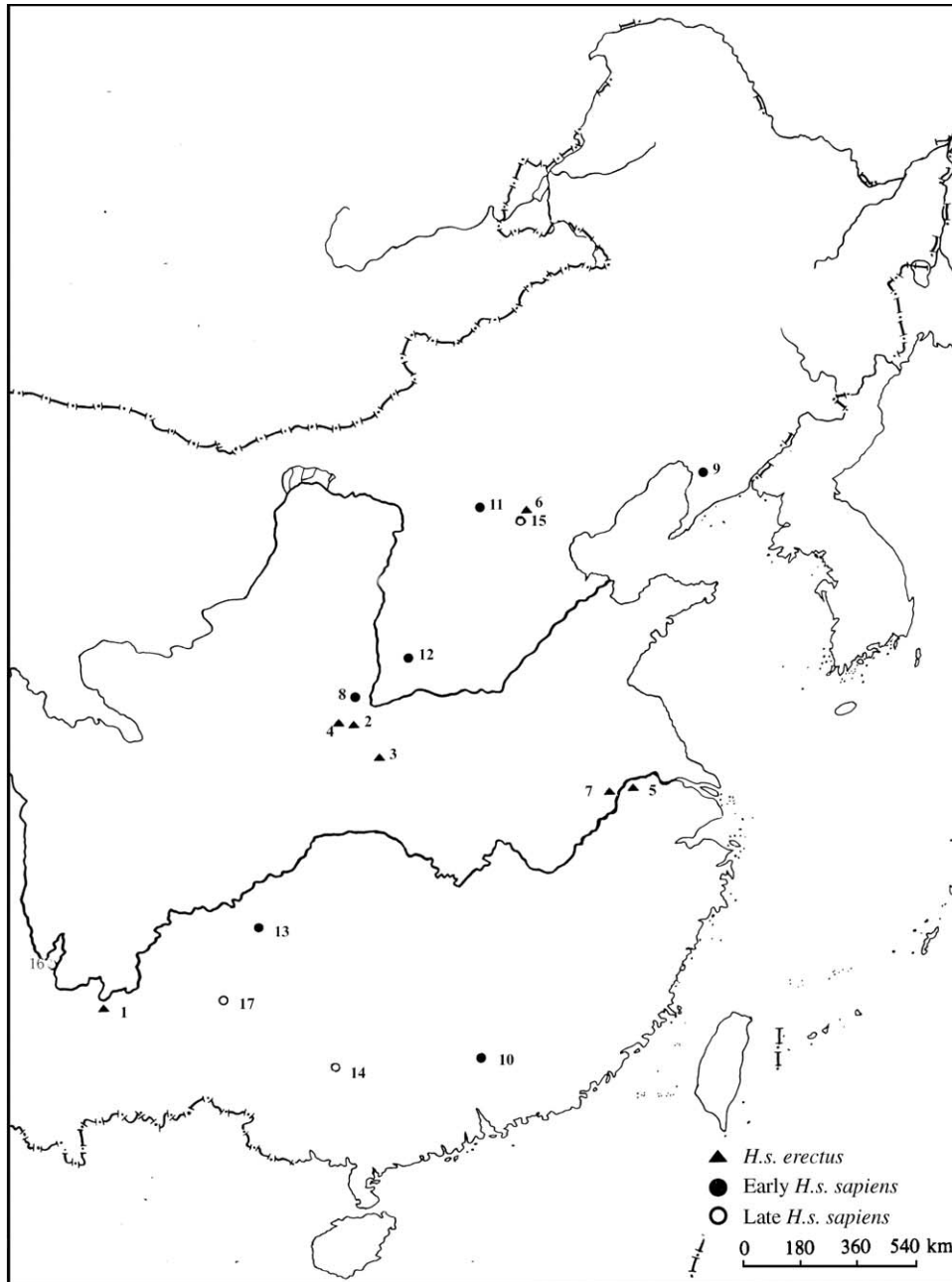


Fig. 1. Important hominid paleontological localities in China. (1) Yuanmou; (2) Gongwangling; (3) Yunxian; (4) Chenjiawo; (5) Tangshan; (6) Zhoukoudian; (7) Hexian; (8) Dali; (9) Jinniushan; (10) Maba; (11) Xujiayao; (12) Dingcun; (13) Tongzi; (14) Liujiang; (15) Upper Cave; (16) Lijiang; and (17) Chuandong Cave.

faces more forward; the lower margin of the cheek bones is curved instead of straight; the junction between this margin and the maxillary body is close to the alveolar margin; the maximum width of the cranial vault is at the middle third of its length; and earlier skulls possess a midsagittal ridge (Wu and Poirier, 1995). It is especially noteworthy that even if each of these features could be found in the fossils of other regions, the morphological complex comprising all these features is not.

In addition to the common morphological features supporting continuity, a morphological mosaic between *Homo sapiens erectus* and *Homo sapiens sapiens* can be observed in the Chinese human fossil evidence. This mosaic indicates a gradual transition between these subspecies. For example, the *H. s. erectus* skull from Hexian has as high a postorbital constriction index, as high a temporal squama, and as high a posterior surface of the pyramid, as does *H. s. sapiens*.

The early *H. s. sapiens* skull-cap from Maba is as constricted in the postorbital region as *H. s. erectus*. In general, the anterior branch of middle meningeal artery is thicker than the posterior branch in *H. s. sapiens* and the ratio is reversed in most of the *H. s. erectus* crania, but the branching patterns of this artery in the *H. s. erectus* cranium No. 5 from Zhoukoudian and No. 2 from Tangshan, Nanjing are similar to that in *H. s. sapiens*. The connection between the occipital and nuchal planes of the occipital bone in *H. s. sapiens* crania is generally rounded while in *H. s. erectus* there is an angular turn; yet the latter feature is also shown in the early *H. s. sapiens* skulls from Dali and Jinniushan. The angular torus has been described as one of the unique features of *H. s. erectus*; however, it is shown also in *H. s. sapiens* skulls from Dali and Ziyang. In addition, there is debate on whether the Yunxian skulls should be attributed to *H. s. erectus* or *H. s. sapiens* because these skulls have characteristic features of both these subspecies. So these specimens are good examples of a morphological mosaic no matter, regardless of the subspecies assignment they may be given. The mosaic between *H. s. erectus* and *H. s. sapiens* in China implies that no clear-cut demarcation can be drawn to separate these taxa. *Homo s. erectus* does not warrant the rank of a species in the practice of biological taxonomy; it is better viewed as a chronological subspecies of *H. s. sapiens* (Wolpoff et al., 1993). The existence of common characters and morphological mosaic between these two sub-species of *H. sapiens* suggests that human evolution in China was continuous.

3. Gene flow between ancient human populations of China and westward

The hypothesis of continuity proposed by Weidenreich, and especially that developed by Coon (1962) and others, had a fatal shortcoming. These hypotheses imply a total isolation between populations on different continents, and make it difficult to explain why the similarities between modern populations of different continents are much less evident than those between populations of Pleistocene humans. Wolpoff et al. (1984) suggested we envision the polytypic species, *Homo sapiens*, as a dynamic system, externally bound and protected by the limits to gene flow, and internally diversified by evolutionary forces sustaining clinal relations between differentiated populations.

Evidence of gene flow is presented on the basis of morphology in the following. In addition to the above-mentioned features, there are a few “extraordinary” features shown in a few human fossils of China. For example, the protruding nasal saddle of skull No. 2 from Yunxian and skull No. 1 from Tangshan, Nanjing (Wu et al., 2002), the circular orbit and sharp

inferolateral orbital margin of the skull from Maba, the surface bulge between the piriform aperture and orbit in the skull from Dali and skull No. 1 of Nanjing, the chignon-like structure in the occipital region of skulls from Ziyang, Liujiang and Lijiang, and the more lateralward orientation of the anterolateral surface of the frontosphenoidal process of the zygomatic bone in the skull of Upper Cave No. 102. In the Pleistocene, all of these features were rarely seen in China, but were more often shown in Africa and Europe, especially in the Neanderthal lineage. The chignon and bulge between the anterior nasal aperture and the orbit are present in higher frequencies in modern Africans than in modern Chinese (Liu Wu, personal communication). The most reasonable explanation for the fortuitous occurrence of these features in Pleistocene China is that they are attributable to small amounts of intermittent gene flow from the West.

4. Continuity with hybridization

Based on the continuity and gene flow between China and the West, human evolution in China can best be characterized as *Continuity with Hybridization* (Wu, 1998). Continuous evolution led to a situation in which ancient human populations in China and adjacent regions possessed a higher frequency of certain morphological features and the aforementioned morphological complex than in the West. This created a situation in which their descendants, the modern Mongoloid people of Asia, can be easily identified and differentiated from other populations when, for example, people of diverse genetic backgrounds gather in a big room. Hybridization or interbreeding reduced the degree of isolation between different populations and maintained the unity of humankind in one species without speciation after going through a rather long process of evolution. Gene flow became a more potent force in later periods such as the Late Pleistocene and Holocene, thus diminishing the differences between the human populations of China and those westward. The frequency of occurrence of the above-mentioned common regional morphological features thus became lower in China.

5. Arguments based on Paleolithic cultural remains

Movius (1948) had proposed that the eastern Asian stone tool cultures differed profoundly from the stone tool industries elsewhere in the Old World. Although Movius has been since criticized by many archeologists for some aspects of his analysis, the truth of his basic observations has been unchallenged. Discoveries of many new Paleolithic sites in China have made clear

that the technological differences between China and the West are evident not only in the Early Paleolithic as Movius noted, but also in the Middle and Late Paleolithic. In other words, the technological traditions in China were distinct from those of the Western World during most of the Paleolithic age.

The Paleolithic culture started in Africa about 2.5 Ma. The earliest stage is designated as Mode I or the Oldowan tradition. The tools made in this stage were very rough. About 1.7 million years ago Mode II appeared in Africa, typified by the Acheulean hand axe. The hand axe is made in a more sophisticated manner than Oldowan chopping tools and bears a special, symmetrical design. Mode III is represented by the Mousterian culture, which was widely distributed in Europe from about 200,000 through 35,000 yr BP. It is more sophisticated than Mode II, in terms of number of tool types and mode of manufacture. The emergence of Mode IV occurred in Europe and accompanied the habitation of anatomically modern humans. Cave drawings, sculptures, and ornaments are characteristic products of this stage and had not been seen before.

In China, the scenario was quite different (Table 2, Fig. 2). Artifacts in China may predate the earliest known human fossils. Artifacts have been reportedly found in deposits of around 2 Ma in limestone fissures at Longgupo, Chongqing, and Fanchang (Anhui), respectively, but these materials are awaiting detailed study and are still not broadly accepted. According to the available evidence, early humans existed in China no earlier than 1.15 Ma. Most of the Paleolithic sites have been dated only by faunal correlation and have not been dated chronometrically. Table 2 and Fig. 2 show the sites, which have chronometric dates or have yielded large numbers of artifacts. In China, the Mode I technique persisted for almost the whole of the Paleolithic age except for the last 40,000 yr. Even in last 40,000 yr, the Paleolithic artifacts made using the Mode I technique were still dominant, and only a few sites yielding artifacts made by other modes are known in China. Significantly, there was no succession of stages from Mode I through Mode V in China.

In addition, there are a few sites, which have yielded stone artifacts of uncertain age. These artifacts appear to have been made with techniques other than Mode I. For example, a biface has been collected from the ground surface not far from Gongwangling, a handaxe has been collected from the ground surface near Dingcun, and many “Acheulean-like handaxes” have been collected as surface finds at several sites in the Baise (Bose) Basin (Guangxi Zhuang Autonomous Region). From this Basin, tektite fragments associated with Mode I artifacts have been dated to 803,000 yr BP (Huang Weiwen, personal communication).

Thus, there have been different Paleolithic traditions in China and the West. In addition, Western Paleolithic

techniques appear to have been intermittently introduced to China. The difference in the tradition of Paleolithic cultures between China and the West and the fortuitous appearance of techniques other than Mode I in China were probably associated with the relationship between human populations and with their migrations. Therefore, the Paleolithic data provide support to the *Continuity with Hybridization* of human evolution in China (Wu, 1998) and thereby support the MEH.

According to a recent molecular study on modern Chinese populations, it is estimated that the anatomically modern immigrants from Africa arrived in China around 60,000 yr BP (Su et al., 1999). If the Recent Out of Africa Hypothesis (ROAH) is true, the immigrants most probably passed through Near East around 100,000 yr ago. In fact, some sites that have yielded artifacts of that time period have been found in this region. The artifacts from these sites are of Mousterian type made by Mode III techniques. If the ROAH was true, it would be reasonable to expect that after the arrival of the immigrants in China (ca. 60,000 yr ago) the Paleolithic culture of China should have suddenly changed from Mode I to Mode III. The situation was quite different from this, however. There was no interruption of the continuity of Chinese Paleolithic techniques during this period. This observations runs counter to the prediction of the ROAH. Other molecular studies have suggested different ages for the arrival of the African immigrants into east Asia. But the facts indicate there was no sudden change of technology at any time in the Paleolithic history of China.

6. Arguments based on molecular anthropology

Since 1987 when Cann et al. (1987) asserted that the most recent common ancestor (MRCA) of modern humans existed about 200,000 yr ago, the “fact” of the recent evolution of modern humans has been widely accepted in the West by many scholars and the public. In recent years many new estimates of the date of MRCA have been obtained, for example, 800,000 yr ago by Harding et al. (1998) based on study of the gene trees for β -globin, and 1.86 million years by Harris and Hey (1999) based on gene sequences on the X chromosome. The timing of the onset of the split between African and non-African populations has been variously estimated at about 137 kyr BP through a study of segregating Alu insertions, at about 100 kyr BP by mitochondrial mismatch distributions; 110 kyr BP by a study of protein polymorphisms, 156 kyr BP by a study of microsatellite loci, and 200 kyr BP from a haplotype analysis of β -globin and X-linked PDHAI (Harris and Hey, 1999). This considerable spread of estimated divergence times militates for the seriously scrutiny of the various sources of data.

Table 2
Important Paleolithic sites in China

Site	Mode	Stone artifacts	Geological age	Chronometric age (years)
Yuanmou (Yunnan)	I	22 pieces including scrapers and points	Early Pleistocene	Around 1.7 Ma (PM) ¹
Xiaochangliang (Hebei)	I	4000 pieces including scrapers, borers and points ³	Early Pleistocene	1.36 Ma (PM) ²
Donggutuo (Hebei)	I	Many pieces including scrapers and points ³	Early Pleistocene	Around 1 Ma (PM) ³
Gongwangling (Shaanxi)	I	26 pieces including choppers and scrapers ³	Early Pleistocene	1.15 Ma (PM) ¹
Yunxian (Hubei)	I	207 pieces including choppers, scrapers and bifaces ³	Early Pleistocene	565,000 yr BP (ESR) ³ ; 870,000–830,000 yr BP (PM) ³
Xihoudu (Shanxi)	I	Some pieces including choppers and scrapers ³	Early Pleistocene	1.8 Ma (PM)
Chenjiawo (Shaanxi)	I	9 pieces including choppers ³	Middle Pleistocene	650,000–530,000 yr BP (PM) ¹
Loc. 1 Zhoukoudian (Beijing)	I	About 10,000 artifacts ³	Middle Pleistocene	578,000–230,000 yr BP (U, T, ESR, FT) ^{1,3}
Loc. 15 Zhoukoudian (Beijing)	I	Over 10,000 pieces including scrapers, points, and spheroids	Middle Pleistocene	160,000–140,000 yr BP (U, ESR)
Shilongtuo (Hubei)	I	88 pieces including choppers and scrapers ⁵	Middle Pleistocene	312,000–256,000 yr BP (PM) ⁵
Miaohoushan (Liaoning)	I	76 pieces including scrapers, choppers and spheroids ³	Late Pleistocene	About 400,000–140,000 yr BP (U) ³
Dingcun (Shanxi)	I	2000 pieces including points and scrapers ³	Late Pleistocene	210,000–160,000 yr BP (U) ¹ ; 114,000–75,000 yr BP (ESR) ³
Tongzi (Guizhou)	I	12 pieces including scrapers ³	Late Pleistocene	181,000–113,000 yr BP (U) ¹
Xujiayao (Shanxi)	I	13650 pieces including scrapers, points, spheroids and burins ¹	Late Pleistocene ¹	125,000–104,000 yr BP (U)
Guanyindong Cave (Guizhou)	I	2323 pieces including scrapers and points ³	Late Pleistocene	Group A: ³ 57,000 yr BP (U) ³ ; Group B: 76,000–11,900 yr BP (U) ³
Xiaogushan (Liaoning)	IV	More than 10,000 pieces including scrapers, borers, spheroids, bone needles and harpoons ³	Late Pleistocene	40,000 yr BP (C) ³
Ziyang B (Sichuan)	I	172 pieces including choppers scrapers and points ³	Late Pleistocene	39,300–37,400 yr BP (C) ¹
Upper Cave Zhoukoudian (Beijing)	I and IV	25 pieces of stone artifacts including scrapers and ornaments ³	Late Pleistocene	34,000–29,000 yr BP (AMS) ³
Salawusu (Inner Mongolia)	I	400 pieces including scrapers burins and points ³	Late Pleistocene	35340 (C) ¹
Longtanshan (Yunnan) Loc. 2	I and III	107 pieces including choppers, scrapers and 2 pieces resembling European Mousterian scrapers ³	Late Pleistocene	30,500 yr BP (C) ¹
Shiyu (Shanxi)	I	15000 pieces including scrapers and denticulates ³	Late Pleistocene	28,945 yr BP (C) ¹
Xiaonanhai (Henan)	I	7078 pieces including scrapers	Late Pleistocene	24,100–18,900 yr BP (C) ⁵
Xiachuan (Shanxi)	V	4000 pieces including scrapers, points, borers and microblades ⁵	Late Pleistocene	362,000–16,400 yr BP (C) ⁵
Tongliang (Chongqing, Sichuan)	I	300 pieces including choppers scrapers and points	Late Pleistocene	25,450 (C); 21550 (C) ⁵
Shuidonggou Loc. 1 (Ningxia)	III and IV	Scrapers points and borers ⁵	Late Pleistocene	25,450 yr BP (C) ³ ; 38,000–16,700 yr BP (C) ⁵
Baiyanjiaodong Cave (Guangxi)	I	1000 pieces including scrapers and points	Late Pleistocene	14,630 yr BP; 12,080 yr BP (C) ⁵
Maomaodong (Guizhou)	I	1121 pieces including scrapers and choppers ³	Late Pleistocene	14,600 yr BP (C) ¹
Xueguan (Shanxi)	V	4777 pieces including scrapers, points, burins, and microblades ⁵	Late Pleistocene	13,550 yr BP (C) ⁵
Zhangnaodong Cave (Hubei)	I	2000 pieces including choppers, scrapers and points ⁵	Late Pleistocene	13,490 yr BP (C) ⁵
Fulin (Sichuan)	I	5000 pieces including scrapers points and burins ⁵	Late Pleistocene	None

Notes: (1) “Mode” indicates the tool-making technique (I–V).

(2) Source of information: ¹Wu and Poirier (1995), ²Zhu et al. (2001), ³Wu et al. (1999), ⁴Gao, X. personal communication, ⁵Wu et al. (1989).

(3) Abbreviations of dating methods: AMS: accelerator radiocarbon; C: radiocarbon; PM: paleomagnetism; U: uranium series; ESR: electron spin resonance; TL: thermoluminescence; FT: fission track.

(4) “Geological dates” are based on faunal correlation and were provided in the articles describing the Paleolithic assemblages.

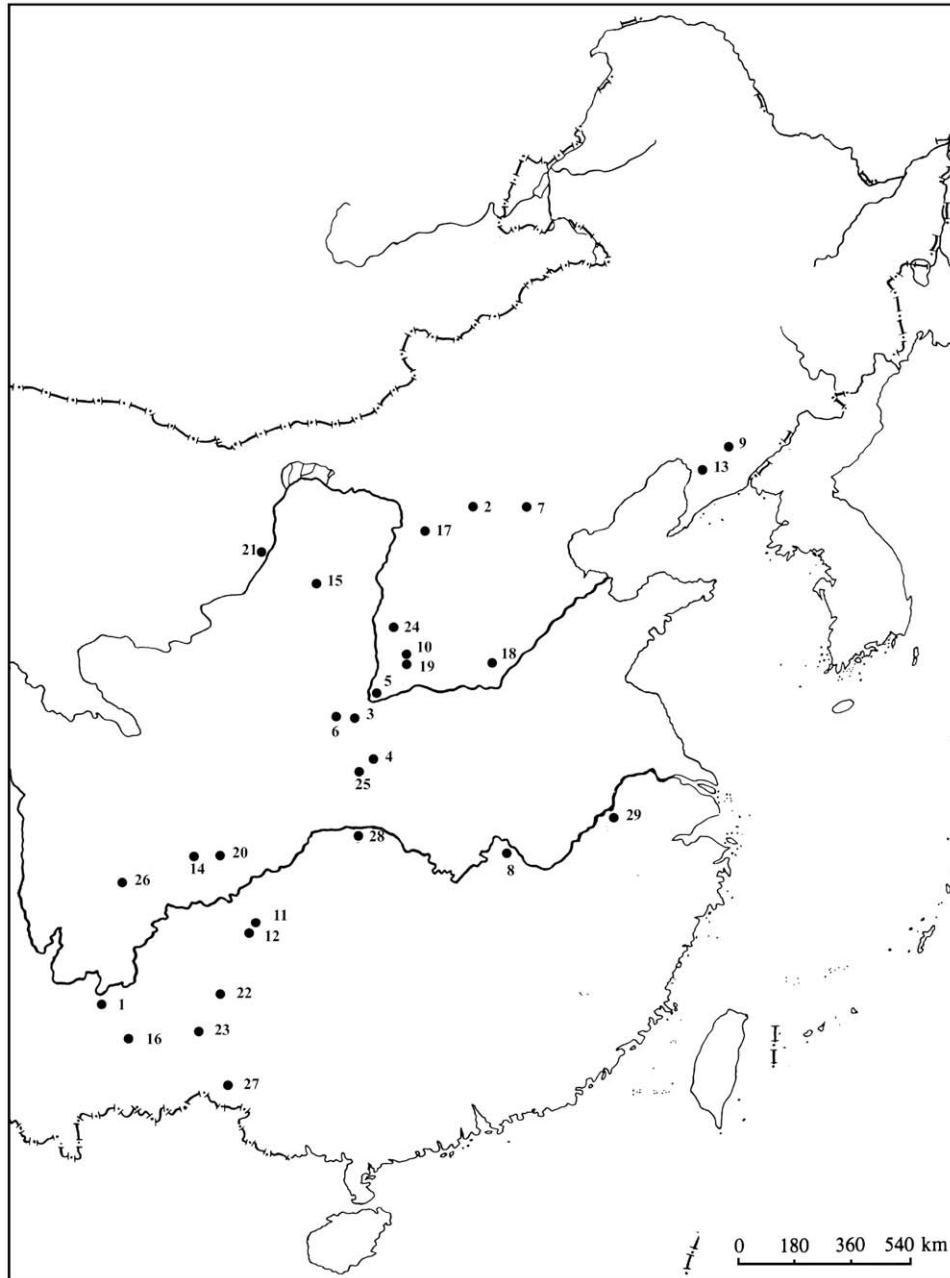


Fig. 2. Important Paleolithic archaeological localities in China. (1) Yuanmou; (2) Xiaochangliang, Donggutuo, Xujiayao; (3) Gongwangling; (4) Yunxian; (5) Xihoudu; (6) Chenjiawo; (7) Zhoukoudian; (8) Shilongtou; (9) Miaohoushan; (10) Dingcun; (11) Tongzi; (12) Guanyindong Cave; (13) Xiaogushan; (14) Ziyang; (15) Salawusu; (16) Loc. 2, Longtanshan; (17) Shiyu; (18) Xiaonanhai; (19) Xiachuan; (20) Tongliang; (21) Shuidonggou; (22) Baiyanjiao; Cave; (23) Maomaodong Cave; (24) Xueguan; (25) Zhangnaodong Cave; (26) Fulin; (27) Baise; (28) Longgupo; and (29) Fanchang.

The calculations for the dates of human population divergence are based on data of genetic variation in living humans and are grounded on three assumptions: (1) the genetic variations measured in living humans represent the total variation derived from the common ancestor; (2) there have been a constant mutation rate, thus an evenly ticking molecular clock; and (3) no interbreeding has occurred between the immigrants and the indigenous populations.

In connection with measurement of genetic variation, gene loss during human evolution has been shown by genetic studies such as the study of ancient DNA of the Australian fossil hominid of Lake Mungo ([Adcock et al., 2001](#)). Concerning the regularity of the molecular clock, [Rodríguez-Trelles et al. \(2001\)](#) have carried out an extensive investigation of three proteins and “have observed that (i) the three proteins evolve erratically through time and across lineages and (ii) the erratic

patterns of acceleration and deceleration differ from locus to locus, so that one locus may evolve faster in one than another lineage, whereas the opposite may be the case for another locus” (p. 11,405). They continued, “If we use the average rate of evolution of *Drosophila* over the last 60 Myr for estimating the time of divergence for other organisms, the divergence of the three multicellular kingdoms is estimated at 7045 Myr by GPDH, a gross overestimate, but at 451 and 398 Myr, which are blatant underestimates, by SOD and XDH, respectively” (p. 11,410). Their “observations are inconsistent with the predictions made by various subsidiary hypotheses proposed to account for the overdispersion of the molecular clock” (p. 11,405). Finally, in connection with the absence of interbreeding, this is quite unbelievable if we consider the nature of the fossil and Paleolithic evidence mentioned and the large amount of interbreeding that has occurred between colonizers and indigenous peoples throughout the world in the last several hundred years.

If the calculation of the date of the common ancestry could account for lost genetic variation and the influences of hybridization between immigrants and indigenous people, the resulting divergence date would be older. If the date of the common ancestor could be moved up to about 2 Ma, the results from both human paleontological and molecular studies could be reconciled.

Krings et al. (1999) studied the ancient DNA of a Neanderthal from the Feldhofer cave and estimated that the divergence of modern humans from Neanderthal occurred 320,000–740,000 yr ago based on 333 base pairs, but indicated that this was a preliminary, not conclusive, result. They also analysed 312 base pairs of the mitochondrial hypervariable region I and determined that the genetic distance between the subspecies of central chimpanzee and eastern chimpanzee; that between the subspecies of western and eastern chimpanzees; and that between subspecies of western and central chimpanzees were 19.7 ± 2.9 , 33.0 ± 4.5 , and 36.2 ± 6.1 , respectively. The divergence estimate between Neanderthals and modern humans is 25.6 ± 2.2 is lower than the difference between two of the three pairs of chimpanzees. If the difference between Neanderthals and anatomically modern humans corresponds to subspecies level difference, or to the level of variation within a species, interbreeding between the two groups could not be excluded. Another study of the ancient DNA of the hominids from Mezmaiskaya Cave in the northern Caucasus also has been considered as supporting for the theory that the mtDNA of Neanderthals have not contributed to that of modern humans (Ovchinnikov et al., 2000). According to Hawks and Wolpoff (2001), “The geologic, archaeological, and dating evidence shows the Mezmaiskaya cave infant to be a burial from a level even more recent than the Upper

Paleolithic preserved at the site, and its anatomy does not contradict the assessment that the Mezmaiskaya cave infant is not a Neanderthal” (p. 269).

The skeleton of a child found recently in the Lapeda Valley of Portugal may provide good evidence of interbreeding between Neanderthals and anatomically modern humans. This child lived about 25,000 yr BP “The cranium, mandible, dentition, and postcrania present a mosaic of European early modern human and Neanderthal features... This morphological mosaic indicates admixture between regional Neanderthals and early modern humans dispersing into southern Iberia. It establishes the complexities of the Late Pleistocene emergence of modern humans and refutes strict replacement models of modern human origins” (Duarte et al., 1999, p. 7604). Tattersall and Schwartz (1999) concluded that the Lapeda child was simply a chunky Gravettian child, a descendant of the modern invaders who had evicted the Neanderthals from Iberia several millennia earlier. Recently, Trinkaus and Zilhao (2002) published an article indicating that, in addition to the polarities of various traits towards early modern humans or the Neanderthals on the Largar Velho 1 child’s skeleton, “the nature of the mosaic for several complexes suggests an unusual combination of its ancestry. For example, the mastoid process is distinctly modern in its size and shape, but the juxtamastoid eminence is close to those of the Neanderthals. The general supraorbital configuration is distinctly modern, but the degree of hypertrophy of the superior orbital margin and the frontal process of the zygomatic bones is archaic. The crural index aligns it with the Neanderthals, but the indications of body breadth place it among the early modern humans. And the mentum osseum is derived in a modern human form, yet the symphyseal retreat aligns it with archaic humans” (p. 515).

7. Discussion

Studies on human fossil skulls provide direct evidence for investigating the modern human origins, but their numbers are not sufficient to provide unequivocal clarification of the details of the process of human evolution in China. Fossils of humans who lived in the period between 100,000 and 30,000 yr BP are urgently needed in order to make the conclusion more convincing.

Although evidence provided by archeological data is indirect, great weight of Paleolithic archaeological remains from in China and the Near East provide convincing arguments that disprove the strict replacement of indigenous people of China by the immigrants from Africa. The long-term distinction of the Paleolithic tradition of China from that of Europe and Africa also supports the hypothesis of continuity with hybridization

of human evolution in China. Although human fossils of China are not numerous, artifacts from more than 1000 Paleolithic sites in China that support this hypothesis. This abundance of evidence should be convincing and the trends derived from these data should not be considered as coincidental.

Most of the molecular studies relevant to the problem of modern human origins are based on the studies of the DNA of living humans. The materials studied are mainly mitochondrial DNA and the nuclear DNA of the sex chromosomes. As mentioned above, the conclusions of these studies have been based on unproven assumptions. The few DNA studies carried out on human fossils have been based on only a small number of base pairs; the conclusions have been ambiguous and the results could be explained in other ways. The causes of differences between the estimated dates of population divergence from the MRCA may be attributable to different amount of gene loss, to the different mutation rates of different loci, or possibly other factors. The different dates of the MRCA represent only “locus-specific conclusion[s]” instead of a “genome-wide conclusion” and may imply different times of migration from Africa. Thus, the conclusions derived from the available molecular data concerning the origin of modern humans are premature.

A recent survey of the complete mtDNA genome variation in humans showed that “the ubiquity of genetic exchange between human populations, both in terms of recurrent gene flow constrained by geographical distance and of major expansion events resulted in interbreeding, not replacement” (Templeton, 2002, p. 45). This conclusion, based on a comprehensive study of the mtDNA genome approaches the conclusion of the MEH instead of the strict Replacement theory.

In general, any hypothesis of modern human origins should fit the evidence obtained from all related disciplines. Efforts should be made toward the reconciliation of research results from different disciplines because ultimately they must be telling one story.

Acknowledgements

This paper was presented at the 5th Conference on the Evolution of East Asian Paleoenvironment. I am grateful to the National Natural Science Foundation of China for its financial support that allowed me to participate in the meeting. Thanks also to the Organizing Committee of the conference for inviting me to attend. This research has been supported by the Basic Research Project of Ministry of Science and Technology of China (No. 2001CCA01700). I thank Professor P.V. Tobias for his generous help in English writing during his short stay in Beijing. Thanks also to Dr. N. Jablonski for her helpful suggestions on improving

this article. I am also grateful to Professor Senshui Zhang and Dr. Xing Gao for checking the Table of important Paleolithic sites in China and to Dr. Hong Shang for drafting the maps.

References

- Adcock, G.J., Dennis, E.S., Eastal, S., Huttley, G.A., Jermin, L.S., Peacock, W.J., Thorne, A., 2001. Mitochondrial DNA sequences in ancient Australians: implications for modern human origins. *Proceedings of National Academy of Sciences* 98, 537–542.
- Cann, R.L., Stoneking, M., Wilson, A.C., 1987. Mitochondria DNA and human evolution. *Nature* 325, 31–36.
- Coon, C.S., 1962. *The Origin of Races*. Knopf, New York, 742pp.
- Duarte, C., Mauricio, J., Pettitt, P.B., Souto, P., Trinkaus, E., Plicht, H., van der, Zilhao, J., 1999. The early Upper Paleolithic human skeleton from the Abrigo do Lago Velho (Portugal) and modern human emergence in Iberia. *Proceeding of National Academy of Sciences* 96, 7604–7609.
- Harding, R.M., Fullerton, S.M., Clegg, J.B., Griffiths, R.C., 1998. Gene trees for β -globin: inferences on the origins of modern humans. In: Omoto, K., Tobias, P.V. (Eds.), *The Origins and Past of Modern Humans—Towards Reconciliation*. World Scientific Publishing Co., Singapore, pp. 23–35.
- Harris, E.E., Hey, J., 1999. X chromosome evidence for ancient human histories. *Proceedings of National Academy of Sciences* 96, 3320–3324.
- Hawks, J., Wolpoff, M.H., 2001. Brief communication: paleoanthropology and the population genetics of ancient genes. *American Journal of Physical Anthropology* 114, 269–272.
- Krings, M., Geisert, H., Schmitz, R., Krainitzki, H., Paabo, B., 1999. NNA sequence of the mitochondrial hypervariable region II from the Neanderthal type specimen. *Proceedings of National Academy of Sciences* 96, 5581–5585.
- Movius, H.L., 1948. The Lower Paleolithic cultures of southern and eastern Asia. *Transactions of the American Philosophical Society (New Series)* 38, 329–420.
- Ovchinnikov, I.V., Götherström, A., Romanova, G.P., Kharitonov, V.M., Lindeén, K., Goodwin, W., 2000. Molecular analysis of Neanderthal DNA from northern Caucasus. *Nature* 404, 490–493.
- Rodriguez-Trelles, F., Tarrío, R., Ayala, F.J., 2001. Erratic overdispersion of three molecular clocks: GPDH, SOD, and XDH. *Proceedings of National Academy of Sciences* 98, 11405–11410.
- Su, B., Xiao, J., Underhill, P., Deka, R., Zhang, W., Akey, J., Huang, W., Shen, D., Lu, D., Luo, J., Chu, J., Tan, J., Shen, P., Davis, R., Cavalli-Sforza, L., Chakraborty, R., Xiong, M., Du, R., Oefner, P., Chen, Z., Jin, L., 1999. Y-chromosome evidence for a northward migration of modern humans into Eastern Asia during the Last Ice Age. *American Journal of Human Genetics* 65, 1718–1724.
- Tattersall, I., Schwartz, J.H., 1999. Hominids and hybrids. *Proceeding of National Academy of Sciences* 96, 7117–7119.
- Templeton, A.R., 2002. Out of Africa again and again. *Nature* 416, 45–51.
- Trinkaus, E., Zilhao, J., 2002. Phylogenetic implications. In: Zilhao, J., Trinkaus, E. (Eds.), *Portrait of the Artist as a Child. The Gravettian Human Skeleton from the Abrigo do Lago Velho and its Archeological Context*. *Trabalhos de Arqueologia* 22, 497–518.
- Weidenreich, F., 1943. The skull of *Sinanthropus pekinensis*: a comparative study of a primitive hominid skull. *Palaeontologia Sinica (New Series D)* (10), 1–298.
- Wolpoff, M.H., Wu, X.Z., Thorne, A.G., 1984. Modern *Homo sapiens* origins: a general theory of hominid evolution involving the fossil

- evidence from East Asia. In: Smith, F.H., Spencer, F. (Eds.), *The Origins of Modern Humans. A World Survey of the Fossil Evidence*. Alan R Liss, New York, pp. 411–483.
- Wolpoff, M.H., Thorne, A.G., Jelinek, J., Zhang, Y., 1993. The case for thinking *Homo erectus*: 100 years of *Pithecanthropus* is enough! In: Franzen, J.L. (Ed.), *100 years of Pithecanthropus: The Homo erectus Problem*. Courier Forshungsinstitut Senkenberg, 171, 341–361.
- Wu, X.Z., 1998. Origin of modern humans of China viewed from cranio-dental characteristics of late *Homo sapiens*. *Acta Anthropologica Sinica* 17, 276–282.
- Wu, X.Z., Poirier, F.E., 1995. *Human Evolution in China. A Metric Description of the Fossils and a Review of the Sites*. Oxford University Press, New York, 317pp.
- Wu, R., Wu, X., Zhang, S. (Eds.), 1989. *Early Humankind in China*. Science Press, Beijing, 437pp (in Chinese).
- Wu, R.K., Zhang, Y.Y., Wu, X.Z., 1999. Nanjing skull No. 1. In: Wu, R.K., Li, X.X. (Eds.), *Homo erectus from Nanjing*. Jiangsu Science and Technology Publishing House, Nanjing, pp. 261–273 (in English), pp. 34–67 (in Chinese).
- Wu, X., Huang, W., Qi, G., 2002. *Zhongguo Gu Renlei Yizhi (Paleolithic Sites in China)*. Shanghai Scientific and Technological Education Publishing House, Shanghai, 307pp.
- Zhu, R.X., Hoffman, K.A., Potts, R., Deng, C.L., Pan, Y.X., Guo, B., Shi, C.D., Guo, Z.T., Yuan, B.Y., Hou, Y.M., Huang, W.W., 2001. Earliest presence of humans in northeast Asia. *Nature* 413, 413–417.