

Fossil Humankind and Other Anthropoid Primates of China

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*More than 70 sites have yielded human fossils in China. They are attributed to *Homo sapiens erectus* and *Homo sapiens sapiens*. The earliest one is possibly about 1.7 Ma. A series of common morphological features, including shovel-shaped incisors and flatness of the face, characterize them. There is a morphological mosaic between *H. s. erectus* and *H. s. sapiens* in China. The existence of common features and the morphological mosaic suggest continuity of human evolution in China. That there are a few features which are more commonly seen in the Neanderthal lineage, occurring in a few Chinese fossil skulls, probably suggests gene flow between China and the West. Based on them, in 1998 I proposed an hypothesis—continuity with hybridization—for human evolution in China. The hypothesis is supported by paleolithic archeology, and it supports the multiregional evolution hypothesis of modern human origins. The anatomically modern humans of East Asia originated most probably in China. Although some nonhuman anthropoid primates of China—*Gigantopithecus*, *Sivapithecus*, *Ramapithecus* and *Lufengpithecus*—have been suggested as the direct ancestors of human beings, the discovery of more specimens and further studies do not support these suggestions. Therefore, it is most probable that the transition between apes and humans did not occur in China.*

KEY WORDS: humans; nonhuman primates; evolution; China.

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IMPORTANT HUMAN FOSSILS FOUND IN CHINA

Paleoanthropology has been studied in China for >80 years, and >70 sites have yielded human fossils. (Wu and Poirier, 1995). More than 1000 sites with Paleolithic cultural remains have been found in China. The human fossils of China can be attributed to 2 subspecies: *Homo sapiens erectus* and *Homo sapiens sapiens* (Wu *et al.*, 1989; Wu and Shang, 2002).

Two upper human incisors unearthed in 1965 from Yuanmou County, Yunnan Province, are probably the earliest human fossils of China (Wu and Dong, 1985, Figure 5.1; Wu and Poirier, 1995, Figure 2.1). They are associated with an Early Pleistocene fauna and the stratum is *ca.* 1.7 Ma per 3 paleomagnetic laboratories in China. Wu and Poirier (1995, pp. 13–14) presented a different explanation of the magnetic profile, according to which the date of the site is probably 0.5–0.6 Ma. An Electron Spin Resonance date of 1.1–1.6 Ma has been given for the mammalian fossils from the site (Huang, and Grun, 1998)

A fossil skull composed of fragments of cranial and facial bones and teeth was found at Gongwangling, Lantian County, Shaanxi Province in 1964 (Wu and Dong, 1985, Figure 5.2; Wu and Poirier, 1995, Figures 2.2 and 2.3). It is associated with an Early Pleistocene fauna. The stratum was dated by paleomagnetism to 1.15 Ma (Wu and Poirier, 1995, p. 22) Two almost complete but heavily distorted skulls were found at Quyuan River Mouth, Yunxian County, Hubei Province in 1989 and 1990 (Wu and Poirier, 1995, Figures 2.19 and 2.20). The associated fauna is from the Early Pleistocene and the paleomagnetic date is 0.87–0.83 Ma. But its electron spin resonance date is 0.565 Ma (Wu *et al.*, 1999, p. 58).

The most famous specimens of *Homo sapiens erectus* are those from Locality 1 of Zhoukoudian (Wu and Dong 1985, Figures 5.4–5.6; Wu and Poirier, 1995, Figures 2.6—2.16) The site is Middle Pleistocene in age and had been estimated to be 0.5 Ma for a long time before the 1970s. In the late 1970s and early 1980s a series of new dates were obtained for different geological layers of the Zhoukoudian, deposits, with new techniques such as fission track, uranium series, paleomagnetism, and thermoluminescence. There are some minor differences among the various dates, but all of them indicate a general idea that the ancient humans lived in the cave for long time, probably as long as 300,000 years. They appeared there about 570,000 years ago according to electron spin resonance dating and left about 230,000 years ago based on Uranium series and electron spin resonance (Wu *et al.*, 1999, p. 46).

Skulls of *Homo sapiens erectus* have been found also centrally in China. A skullcap is from Longtandong Cave, Hexian, Anhui Province in 1980 (Wu and Dong 1985, Figure 5.7; Wu and Poirier, 1995, Figure 2.17). Three other cranial and facial fragments of a skull and a skullcap are from Huludong

Cave, Tangshan, Nanjing in 1993 (Wu *et al.*, 2002, Plate 5–7). They show geographical diversity of morphology and morphological changes through time.

Skulls of archaic or early *Homo sapiens sapiens* been found at Dali, Shaanxi Province, Jinniushan, Liaoning Province and Maba, Guangdong Province. Penecontemporaneous cranial fragments have been found at Xujiayao and Dingcun of Shanxi Province, Chaoxian County, Anhui Province and Changyang County, Hubei Province (Wu and Poirier, 1995, Figures 3.2, 3.3, 3.8, 3.4 3.6, 3.11–3.12, 3.9 for Dali, Jinniushan, Maba, Xujiayao, Dingcun, Changyang).

Fossil skulls of late or anatomically modern *Homo sapiens sapiens* have been found at Upper Cave near Peking Man Cave, Liujiang County of Guangxi Zhuang Autonomous Region, Ziyang County, Sichuan Province, Lijiang and Chenggong Counties, Yunnan Province etc (Wu and Poirier, 1995, Figures 4.1–4.3, 4.6–4.7, 4.9–4.10, 4.12 for Upper Cave, Liujiang, Ziyang and Lijiang).

In addition, there are fossil cranial and postcranial fragments and many teeth of both subspecies of *Homo sapiens* unearthed from many other sites (Wu and Poirier, 1995).

FEATURES INDICATING CONTINUITY OF EVOLUTION

Among the fossils there are some common features. All of the upper incisors from Pleistocene China are shovel-shaped. The suture between the frontal bone above and the nasal and maxillary bones below form a more or less horizontal curve; the upper faces of all of the skulls are low and flat; the nasomalar angle is large (*ca.* 140°); the nasal saddle is flat; the orbits are quadrangular; the inferolateral orbital margin is rounded instead of sharp; the anterolateral surface of the frontosphenoidal process of the zygomatic bone faces more forward; the lower margin of the cheek bones is curved instead of straight; the juncture 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 mid-sagittal ridge (Wu and Poirier, 1995, pp. 234–235). Although all of these characters are not uniquely present in China, they occur at higher frequencies in Pleistocene China and combinations of them are much more frequent in Pleistocene China than elsewhere.

In addition to the common features supporting continuity, there is a morphological mosaic between *Homo sapiens erectus* and *Homo sapiens sapiens* in China, which indicates a gradual transition between the subspecies. For example, the skull of *Homo sapiens erectus* from Hexian has a postorbital constriction index, length-height index of the temporal squama, and posterior

surface of the pyramid as high as those of *Homo sapiens sapiens*. The skullcap of early *Homo sapiens sapiens* from Maba is as constricted in the postorbital region as that of *Homo sapiens erectus*. In general the anterior branch of the middle meningeal artery is thicker than the posterior branch in *Homo sapiens sapiens* and the ratio of the diameter of anterior branch to posterior branch is the reverse in most skulls of *H. s. erectus*, but the branching patterns of the artery in skull No. 5 of *H.s. erectus* from Zhoukoudian (Qiu *et al.*, 1973) and skull No. 2 from Nanjing are similar to that in *Homo sapiens sapiens*. The connection between the occipital and nuchal planes of the occipital bone in the skull of *Homo sapiens sapiens* is generally a rounded turn while in *Homo sapiens erectus* there is an angular turn, which also occurs in the skulls of early *H. s. sapiens* from Dali and Jinniushan. The angular torus has been described as one of the unique features of *Homo sapiens erectus*, while it also exists in skulls of *Homo sapiens sapiens* from Dali and Ziyang. In addition, there is debate on whether the Yunxian skulls should be attributed to *Homo sapiens erectus* or *Homo sapiens sapiens* because they have characteristic features of both subspecies (Li *et al.*, 1994; Zhang, 1995). Accordingly, the specimens are good examples of morphological mosaic no matter to which subspecies of *Homo sapiens* they belong. The mosaic between *Homo sapiens erectus* and *Homo sapiens sapiens* of China implies that no clear-cut demarcation line can be drawn to separate the taxa. *Homo sapiens erectus* does not deserve the rank of a species in the sense of biological taxonomy; it is probably a chronological subspecies of *Homo sapiens sapiens*. (Wolpoff *et al.*, 1993).

The existence of common features and the morphological mosaic between the 2 subspecies of *Homo sapiens* suggests that the human evolution in China is continuous.

FEATURES INDICATING GENE FLOW

A few extraordinary features are exhibited in a few human fossils of China: the protruding nasal saddle of skull No.2 from Yunxian (Wu and Poirier, 1995, Figure 2.20) and skull No.1 from Nanjing (Wu *et al.*, 2002, Plate 5), the circular orbit and sharp inferolateral orbital margin of the skull from Maba (Wu and Poirier, 1995, Figure 3.8), the surface bulge between the piriform aperture and orbit in the skull from Dali (Wu and Poirier, 1995, Figure 3.2) and skull No.1 of Nanjing (Wu *et al.*, 2002, Plate 5), the chignon-like structure of the occipital region of skulls from Ziyang (Wu and Poirier, 1995, Figure 4.9), Liujiang (Wu and Poirier, 1995, Figure 4.6) and Lijiang, and the more lateral orientation of the anterolateral surface of the frontosphenoidal process of the zygomatic bone in the skull of Upper Cave No. 102

(Wu and Poirier, 1995, Figure 4.2). In the Pleistocene epoch these features are rare in China, but they are more frequent in Africa and Europe, especially in the Neanderthal lineage. A most reasonable explanation for their occurrence in Pleistocene China is that they are due to small amounts of intermittent gene flow from the West.

HYPOTHESIS: CONTINUITY WITH HYBRIDIZATION

Based on the continuity and gene flow between China and the West, human evolution in China could be summarized as continuity with hybridization (Wu, 1998). The continuous evolution gave the ancient human populations in China and adjacent regions a higher frequency of occurrence of certain morphological features and their combination than in the West and made their descendants, the modern Mongolians, easily identified and differentiated from other people on the basis of morphology. Hybridization or interbreeding reduced the degree of isolation between different populations and kept the unity of humankind as one species without speciation after going through a rather long process of evolution. Gene flow became stronger in later periods including the Late Pleistocene and Holocene, so the differences between the human populations of China and the West became smaller through time. The frequencies of occurrence of regionally common features became lower in modern population of China.

Continuity with hybridization is also supported by abundant archaeological evidence in China. Paleolithic artifacts occur at >1000 Pleistocene sites in China. Almost all of them are Oldowan or Mode I (Jia, 1985; Jia and Huang, 1985; Qiu, 1985; Zhang, 1985). Only a few sites have yielded artifacts of other Modes. Baise Basin of Guangxi Zhuang Autonomous Region has yielded many Acheulean handaxes (Hou *et al.*, 2000). Artifacts representing the transition between Mousterian and Aurignacian techniques have been unearthed at Shuidonggou in Ningxia Hui Autonomous Region (Licent and de Chartin, 1928). The context indicates that the Mode I technique persisted for a long time in China, and the human population at only a few sites introduced cultural elements from the West. So the Paleolithic history of China is also a process of continuous development with a small amount of cultural exchange with the West (Zhang, 1990).

The hypothesis of continuity with hybridization in China implies that the anatomically modern *Homo sapiens* of China originated from the indigenous people—early *Homo sapiens* of China—which supports the multiregional evolution hypothesis of the origin of modern humans.

The Neolithic population of China can be lumped into 3 groups: Southern, Northeastern and Northwestern (Shang, 2002) The geographical

differences among the populations are lower than those in the Paleolithic period. Some of the morphological features such as the quadrangular shape of orbit, rounded orbital margin and others commonly seen in Paleolithic populations are no longer common in the Neolithic period, which indicates that gene flow within China and with other regions became much stronger then.

But other common features such as shovel-shaped incisors, flatness of the face and nasal saddle are still continuously present in the Neolithic period.

Human evolution in China is like a network, neither ladder-like nor bush-like. Continuity is the main process; gene exchange within China and with other regions, extinction and replacement of local populations are supplementary. Gene exchange became more frequent through time.

IMPORTANT FOSSILS OF NONHUMAN ANTHROPOID PRIMATES OF CHINA

In addition to human fossils there are many fossils of nonhuman anthropoids in China. Some of them have been considered to be direct ancestors of hominids.

Weidenreich (1946) proposed *Gigantopithecus blacki* as the forerunner of *Homo* through *Pithecanthropus* of Java, who was the forerunner of the Peking Man. His specimens of *Gigantanthropus* were collected from drug stores in Hong Kong. In the mid-1950s, Wenzhong Pei and his team went to Guangxi Zhuang Autonomous Region to search for the sites whence the fossils came. They found two caves with *Gigantanthropus*. The excavation of one of the sites—the Giant Ape Cave of Liucheng—yielded 3 mandibles and >1,000 isolated teeth (Zhang, 1985). No crania or postcranial skeletons have been found. The specimens indicate that *Gigantopithecus blacki* is not one of the direct forerunners of hominids (Wu, 1962a,b). Studies of more isolated teeth from other sites in Guangxi, Hubei and Chongqing are concordant with this conclusion. The associated fauna of various sites yielding *Gigantopithecus* indicate that they lived in Early and Middle Pleistocene.

In the mid-1970s 2 anthropoid mandibles were found in Lufeng County, Yunnan Province at a Miocene site, Shihuiba (Wu and Xu, 1985). They were attributed to *Ramapithecus* and *Sivapithecus*. After excavations of several seasons the specimens totaled 5 skulls, 10 mandibles, 6 cranial fragments, 41 maxillary and mandibular fragments, 29 lower dentitions, 650 isolated teeth, 1 scapula, 1 clavicle, 2 phalanges, apromaximal femoral fragment, and 1 metatarsal bone. In 1985, Rukang Wu and Qinghua Xu indicated that *Ramapithecus* of Lufeng may be more closely related to the common

ancestor of humans and the African great apes than *Sivapithecus* of the same site is (Wu and Xu, 1985) In 1987, Rukang Wu restudied the fossils and proposed for the Lufeng specimens a new name, *Lufengpithecus lufengensis* for all of the specimens (Wu, 1987). The specimens attributed to *Sivapithecus* and *Ramapithecus* previously are males and females, respectively. The skull has some characteristic features such as the glabellar region and frontal triangle are very depressed, the supraorbital ridge is thin and protruding, presence of a transverse ridge in the glabellar region, and a concave midsagittal line of the face. In addition, the supraorbital ridges are medianly discontinuous. The orbit of the male individual is ovoid with the transverse diameter slightly longer than the vertical one; that of female is probably quadrangular. The interorbital region is rather broad and depressed. The naso-alveolar clivus is sloping. The piriform aperture is narrow and long. The palate is relatively wider and shallower than those of modern great apes. The dental arch slightly diverges at the posterior end. The distance between the tips of the crowns of the upper canines of that two sides is greater than that between their roots. The buccal and lingual cusps of first premolar of the female individual are nearly equal in size. The cusps are higher and the wrinkles are more than those of *Sivapithecus* in Pakistan. The enamel is thick. Sexual dimorphism is quite obvious. *Lufengpithecus* is an aberrant branch in primate evolution. It is on the lineage of neither hominids nor orangutans.

Crown formation time of *Lufengpithecus lufengensis* is closer to that of *Australopithecus afarensis* and *A. africanus*, and is longer than that of *A. robustus* and *A. boisei*. The pattern of compactness of perikymata is similar to that of modern humans, and different from that of apes. (Zhao *et al.*, 1999).

Zhao and Lu (2002) found that the eruption sequence of the lower permanent dentition of *Lufengpithecus lufengensis* is determined as M₁ I₁ I₂ M₂ P₃ P₄ C M₃. This pattern is ape-like rather than human-like. The age of emergence of the first molar is similar to that of extant apes, other Miocene hominoids, australopithecines, and early *Homo*, rather than that of modern humans, which indicates the life history pattern of *Lufengpithecus* is ape-like, not human-like (Zhao personal communication). Kelly (2003) considered that *Lufengpithecus lufengensis* shares several cranial and dental synapomorphies with *Pongo*, most of which are different features from those shared by *Sivapithecus* and *Pongo*. However, in the cranial features that most clearly distinguish *Pongo* from other apes, *Lufengpithecus lufengensis* does not closely resemble *Pongo*, or the morphology is too distorted to permit a definite character assessment. *Lufengpithecus lufengensis* also possesses a suite of apomorphic features that could preclude them from direct orangutan ancestry.

A juvenile skull, 8 fragments of maxilla, 9 fragments of mandible and >1000 teeth of a hominoid were recovered from a few Miocene sites in

Yuanmou County, Yunnan Province in 1980s and 1990s. Zheng and Zhang, (1997, with Plate 13–22) proposed that the Yuanmou specimens represent a new species: *Lufengpithecus yuanmouensis*. The facial bones of the left and right sides are nearly completely preserved. The face is short and broad, the interorbital region is broad, but without depression, the orbit is rounded, the anterior nasal aperture is broad, and the width of the posterior part of the dental arch is longer than that of the anterior part. The lower first premolar possesses one cusp instead of two, the molars are short, wide and without cingula, and the lower second molar tends to have only 4 cusps. Zheng and Zhang (2003) suggested that *Lufengpithecus* spp. from Lufeng and Yuanmou were on the evolutionary line toward hominids.

Kelly (2003) compared the infant cranium with equivalently aged cranium of extant great apes and found an overall morphological pattern that is broadly similar to that of *Pan*, with few if any features that can be viewed as plausible synapomorphies with *Pongo*.

Harrison and coauthors (2002) considered the Lufeng, Kaiyuan and Yuanmou samples to belong to 2 separate species within a single genus: *Lufengpithecus lufengensis* and *L. keiyuanensis*. From a phylogenetic perspective, the current available evidence suggests that *Lufengpithecus* is either a primitive hominid that represents the sister taxon of the Ponginae + Homininae or a primitive sister taxon to the Ponginae. Harrison *et al.* (2002) favor the second alternative, but acknowledge that a more comprehensive comparative analysis is needed to substantiate the phylogenetic and taxonomic affinities of *Lufengpithecus*.

Delson (2003) agreed to lump the Miocene ape samples from Lufeng, Yuanmou (including Zhupeng, Xiaohe, and Leilao) and Kaiyuan into a single genus, *Lufengpithecus*. He considered them to be an eastern representative of the conservative hominid stock that existed before the split between Ponginae and Homininae (the African ape-human clade) and they were most closely related with *Oreopithecus* (Delson, 2003).

Huang *et al.* (1995) proposed a fragment of mandible and lateral upper incisor from Longgupo, Wushan, Chongqing Municipality as the earliest hominid in China. It is estimated to be *ca.* 2 Ma by paleomagnetism and faunal correlation. But restudy of the mandibular fragment showed that the position of the anterior contact facet of the first premolar is situated lingually rather than centrally on the mesial surface of the tooth, the ratio of talonid length to the crown width of the second premolar is much larger than that of early *Homo* of East Africa, the size of the mandible and teeth are much smaller than those of early *Homo* of East Africa and Dmanisi, and they are concordant with counterparts in Yuanmou *Lufengpithecus*. Most of the characters which have been used by some scholars to attribute

Longgupo mandible mandible to *Homo* are shared by hominids and apes, including bifurcation of the root of the premolar which is a character of *Lufengpithecus* that seldom occurs in hominids. Accordingly, the Longgupo mandible belongs to an ape instead of a hominid. Among the ape fossils available in China, *Lufengpithecus* is the closest relative of the Longgupo ape. Whether they have an ancestor-descendant relation depends on further findings. (Wu, 2000). Restudy of the incisor indicates that the morphology is very similar to that of modern humans and quite different from that of early Pleistocene hominids elsewhere. (Wang, 1996). The geological profile shows that the incisor was probably intrusive.

Therefore, none of the anthropoid primates in China are direct ancestors of humans. Humans in China most probably originated from Africa. But the paleo-environments of southern China in the Miocene and Pliocene were suitable for human life and various kinds of apes lived there, so the possibility to discover forerunners of humans in southern China after making great efforts to explore the Neogene deposits should not be ignored.

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