

## Revisiting the origin of modern humans in China and its implications for global human evolution

GAO Xing<sup>1,2\*</sup>, ZHANG XiaoLing<sup>1,2,3</sup>, YANG DongYa<sup>2,4</sup>, SHEN Chen<sup>2,5</sup> & WU XinZhi<sup>1,2</sup>

<sup>1</sup> Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China;

<sup>2</sup> Laboratory of Human Evolution, Chinese Academy of Sciences, Beijing 100044, China;

<sup>3</sup> Graduate University of Chinese Academy of Sciences, Beijing 100049, China;

<sup>4</sup> Department of Archaeology, Simon Fraser University, Vancouver V5A 1S6, Canada;

<sup>5</sup> The Royal Ontario Museum, Toronto M5S 2C6, Canada

Received August 30, 2010; accepted November 7, 2010

The debates over the origin of modern humans have long been centered on two competing theories: the “Out-of-Africa” (single-place origin) theory and the “Multi-regional Evolution” theory. China is an extremely important region where many ancient human fossils were collected along with numerous associated faunal remains and artefacts. These cultural remains, unearthed from different areas in the country and covering a long time span, will help clarify the controversy. The study of cultural materials in China is expected to shed important light on biological evolutionary patterns and social and technical developments of those early humans as well as their environmental conditions. Based on the analysis of Chinese fossils and associated materials, in conjunction with some genetic studies, this paper aims at evaluating each of the two theories in order to stimulate more discussions. Our study suggests that the evolutionary model of “Continuity with Hybridization” is most relevant in reflecting the current understanding of human evolutionary history in China. Furthermore, we propose that the concept of regional diversity of evolutionary models should be seriously considered to illustrate different evolutionary modes applied to different parts of the world.

**origin of modern humans, China, human fossils, molecular biology, palaeolithic archaeology**

**Citation:** Gao X, Zhang X L, Yang D Y, et al. Revisiting the origin of modern humans in China and its implications for global human evolution. Sci China Earth Sci, 2010, 53: 1927–1940, doi: 10.1007/s11430-010-4099-4

Paleoanthropological research, once an esoteric discipline in China, has caught great public attentions over the past two decades. In particular, the debate over the origin of modern humans has heated up between two competing theories: the “Out-of-Africa” (single-place origin) theory and the “Multi-regional Evolution” theory. Clearly, the scope of the debates has gone beyond academic discussions in anthropology and genetics, creating a hot topic of public interests as well.

Evidence from China has been a fundamental part of the debate, including many different types of human fossils,

such as *Homo erectus* and *Homo sapiens*, recovered from many parts of the country. China was once considered by many to be a regional center for the origin of modern humans; it also provides an excellent case study in support of “Multi-regional Evolution” theory. However, some new arguments have strongly challenged this theory and blurred the previously seemingly clear picture of human evolution in the region. The new debate clearly reflects the complexity of human evolutionary history, and has encouraged us to re-examine all lines of evidence and piece together a puzzle of when, where, and even how modern humans originated and evolved.

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

The main goal of this paper is to evaluate and examine the key arguments and core evidence in great detail from each of the two competing theories on the origin of modern humans. Special efforts are also made to re-examine the traditional lines of evidence for their validity and usefulness for the current study of human evolution.

## 1 Background and history of the controversy

The term “modern humans”, *Homo sapiens sapiens*, or late *Homo sapiens* refers to those early humans who share anatomical characteristics (e.g., muscle and skeletal structure, brain size and structure and even behaviour) with current living populations.

It is commonly agreed that the earliest humans originally emerged in Africa and evolved into *Homo erectus* before they emigrated out of Africa into Europe and Asia about 2 million years ago. These *Homo erectus* immigrants then evolved into archaic *Homo sapiens* and late *Homo sapiens* [1]. According to this model, the origin of modern humans should not be a special research issue; rather it concerns the last stage of a continuous evolution process. After comparing numerous human fossils recovered from all over the world, Wolpoff, Wu and others proposed a “multi-regional evolution” theory and argued that the world’s four major human groups (previously termed “races”) can be linked to much older humans in the same region [2–5]. This view gained strong support from many anthropologists and archaeologists, particularly East Asian scholars. However, it was strongly challenged when Cann and co-workers published their so-called “Eve Hypothesis”, which was based on mitochondrial DNA analyses of modern living populations [6]. This new theory argued that all modern humans could be traced back to a single female individual living in Africa some 200 kyr ago; all of other branches outside this single-origin had become extinct. The theory, also called “Out of Africa” or “Replacement Model”, is gaining more and more support from genetic studies and has become a popular theory even among paleoanthropologists.

The issue has been hotly debated in the academic world for more than 20 years. The debate is focused on whether modern humans originated from multiple regions or just one single region subsequently spreading out to other parts of the world. Other relevant questions include whether there was any interruption of the human evolution process in Eurasia, which was the driving forces for the emergence of modern humans, and how did earlier humans migrate and interact with other populations. These are the key issues that supporters of either model have to address in order to convince their opponents.

China in particular and East Asia in general has become a central battlefield for the debate. The study of human fossils from the region enabled Weidenreich to put forward the theory of continuous evolution of ancient humans more than

half a century ago [7, 8]. Wolpoff et al. [2] developed the theory further, proposing the “Multi-regional Evolution” theory as a general model to explain human evolution around the world. After carefully examining Chinese human fossils and investigating potential interactions with other contemporary humans in the other parts of the world, Wu [9] proposed the “Continuity with Hybridization” model to explain the emergence of some new features among Chinese fossils.

In China, both academics and public media did not pay much attention to the “Out-of-Africa” model and the debates it generated in the late 1980s and the early 1990s. This could be attributed simply to the fact that most Chinese academics believed strongly that China has an unbreakable stronghold for the multi-regional theory and that academic communications or exchange of ideas between West and East was insufficient during that period of time. The situation made a dramatic turn when a group of Chinese geneticists published a series of genetic papers claiming that Chinese scientists should support the “Out-of-Africa” theory [10–15]. After questioning the reliability of the dates of Chinese fossil and cultural evidence, they further pointed out that there was a significant gap in the evidence for human existence in China between 100 and 50 kyr ago. If the gap could be proven to be true, there would be a significant problem for the multi-regional hypothesis.

However, if we closely examine the debate, we realize that the two schools of thought lack true interaction, which stems from different research emphases. We believe that it is the time to integrate multiple lines of evidence from human fossil morphology, genetics of living and past human populations, archaeology, paleoenvironmental sciences, and chronometry to evaluate the strengths and weaknesses of each piece of evidence in order to achieve a more convincing model of the origin of modern humans.

## 2 “Multi-regional Evolution” and “Continuity with Hybridization”

### 2.1 Development of theories

The proposal for the “Multi-regional Evolution” theory and the more recent “Continuity with Hybridization” theory can be traced back to 1930s–1940s [5]. Weidenreich was the first to notice some common skull characteristics between Peking Man unearthed at Zhoukoudian, and modern East Asian (previously termed Mongoloid) populations, and proposed a strong ancestor-descendant lineage between the two groups. He further proposed that there should be four major ancestor-descendant lineages in East Asia, Java, Europe and Africa [7, 8]. Weidenreich’s hypothesis was later confirmed by R. Wu in the 1950s after he studied other human fossils from Ziyang, Changyang, Liujiang, and Maba. Wu believed that those human fossils provided links between Peking Man and modern East Asian populations. In 1959, Wu and his coworkers [16] published their paper

supporting the continuity of human evolution in China.

With more human fossils unearthed in China, such as those from Yuanmou, Jianshi, Lantian, Shiyu, and Lijiang, Wu further supports the continuous evolution model of ancient humans in China. Wu notes that the inherent relationship between ancient human fossils from different periods can be clearly demonstrated by shared physical characteristics [17] such as shovel-shaped incisors, location of zygomatic bone, broad nasal aperture, mandibular torus among others. Based on their detailed studies of human fossils unearthed from China, Indonesia and Australia, Wolpoff, Wu, and Thorne [2] proposed the “Multi-regional Evolution” theory in 1984 as the model for the origin of modern humans. According to the model, all living human populations in Asia, Africa and Europe are direct descendants of local archaic *Homo sapiens* and even local *Homo erectus*. The high frequency of some of the shared physical characteristics in China is often cited as strong evidence to support such a continuous regional evolutionary hypothesis. Wu and his colleagues hypothesized that the current level of genetic diversity of human populations is the balanced result of selective adaptation and gene flow, with the latter playing an extremely important role in keeping humans from becoming separate species. Based on his detailed comparative studies on Chinese and European archaic *Homo sapiens*, Wu identified several Chinese human fossils that show morphological evidence of possible gene flow from Europe, but insisted that overall, human evolution in China has followed the model of continuous evolution with hybridization, with continuous evolution playing the main role. There is no evidence to support any large-scale immigration replacing indigenous populations in China [18]. In 1990, based on a morphological study of human fossils from Dali, Jinniushan, and Hexian, Wu provides strong arguments that the mosaic nature of Chinese *Homo sapiens* can be traced back to some *Homo erectus* characteristics, thus disproving the notion that *Homo erectus* had become extinct and been replaced by later human populations. Furthermore, Wu’s work [4] identified a temporal trend of morphological features associated with Chinese human fossils. He noted many shared and lasting features as the evidence of local continuous evolution, and the emergence of some new features in Chinese human fossils as the indication of gene flow from other regions. In 1998, Wu [9] studied the characteristics of the skulls and teeth of many Late *Homo sapiens* remains unearthed from China and proposed a hypothesis of the “Continuity with Hybridization” model. Wu believed that this new hypothesis is a more accurate and precise version of the “Multi-regional Evolution” theory in East Asia. It is probably the model that best explains human evolution throughout the whole history in China. The model does not exclude the possibility of some small-scale population replacements in some regions but subsequent gene flow may have blurred or covered up such minor events. Wu stated that by no means should the “Continuity with Hy-

bridization” model be considered to be a universal model that is applicable to all parts of the world. The origin of modern humans can be a complex and diverse process, and different regions must have gone through different evolutionary processes [9].

## 2.2 The key points

Thus, the “Continuity with Hybridization” theory can be traced back to the Weidenreich’s theory but it offers a more sophisticated mechanism for interpreting human evolution histories in China and East Asia. The key points of the theory can be summarized as: 1) humans in East Asia have undergone a continuous evolution since the arrival of *Homo erectus* around 2 million years ago, without any interruption and without large-scale population replacements; 2) relative geographic isolation from outside has allowed ancient humans in China develop some regional features which became distinctive from western populations of the Old World; 3) indigenous human populations in China had exchanged genes with outside populations, and the rate of such exchanges has increased over time, keeping all human populations within the same species; 4) due to its vast geographic region and diverse ecological conditions, it is most likely that ancient humans in East Asia may have differentiated into a number of regional groups—local extinction, interregional migrations, and even population replacements could occur as well, resulting in a huge regional diversity and showing an evolutionary pattern similar to a river network; and 5) due to vast environmental diversity, ancient humans worldwide must have undergone different evolutionary modes, neither the “Continuity with Hybridization” nor “Complete Replacement” model is capable of covering all regions.

## 2.3 The main supporting evidence

The “Continuity with Hybridization” theory is supported by both fossil and archaeological evidence.

First, the human fossils that provide evidence supporting the “Continuity with Hybridization” theory mainly include human skulls and teeth, and were unearthed from more than 70 locations in China. Commonly shared morphological characteristics include: a flatter facial profile, a lower nasal saddle, a flat or slightly concave bone surface between nasal aperture and eye orbits, more rectangular eye orbits, curved edges of the zygomatic process of maxilla, higher junction locations of the zygomatic process and the body of maxilla, the maximal cranial width located at the middle third of its total length, a stronger mid-sagittal ridge on earlier human fossils, and shovel-shaped upper incisors [5]. There are also many transitional mosaic features that can be identified from *Homo erectus* to *Homo sapiens*. For example, *Homo erectus* from Hexian has a high cranial index, a weak post-orbital constriction, and a high squamal portion of temporal.

These features are rarely seen in other *Homo erectus* but commonly found in *Homo sapiens*. Conversely, the early *Homo sapiens* from Maba shows a stronger postorbital constriction, the skull from Dali shows stronger brow ridges and a sharper connection of occipital and nuchal planes of the occipital bone, skulls from Dali and Ziyang still possess angular torus, and parietal bone from Xujiayao shows a thicker skull. These features are considered by others to be distinctive features of *Homo erectus* only. Skulls from Yunxian provide another perfect example of combination of both *Homo erectus* and *Homo sapiens* characteristics. All of these observations clearly demonstrate a lack of clear-cut boundary between the two subspecies and instead provide strong evidence to support evolutionary continuity from *Homo erectus* to *Homo sapiens*.

There are several Chinese human fossils with features typical of those from the West, which may indicate gene flow: the Dali skull with a bony eminence between the eye orbit and the piriform aperture; a Nanjing skull with a protruding nasal saddle; the Maba skull with circular orbits and sharp inferolateral orbital margins; skulls from Liujiang, Ziyang and Lijiang with chignon-like structure on their occipital bones, the Lijiang skull with carabelli cusp on the first upper molar; the Upper Cave No.102 skull with more lateral oriented anterolaterial surface of frontoasphenoidal process of zygomatic bone; and the Ordos skull with higher frontonasal suture (than frontomaxillary suture) [4, 5, 9].

Palaeolithic archaeological evidence also supports the “Continuity with Hybridization” theory. From perspectives of lithic technology and typology, the Pleistocene human cultural complex has been generally divided into five technical modes: Mode I, also called the Oldowan Mode, characterized by simple pebble and flake tools; Mode II, or the Acheulian Mode, featured with bifacially-worked handaxe; Mode III, or the Mousterian Mode, associated with Levallois technique; Mode IV, or the Upper Palaeolithic Mode, characterized by blade technology and Mode V, or the Mesolithic Mode, characterized by microblade technology [19]. Mode IV is considered to be the cultural identity of early modern humans. While the five modes could be all detected from Africa and western Eurasia, only Mode I was mainly present throughout the whole Palaeolithic in China, and even continued into Neolithic, with only a very few of sites producing (partially and temporally) products from the other modes. Therefore, Chinese Palaeolithic technology also has a continuous tradition and development, with minor and occasional exchanges of technology with the West [5, 20].

## 2.4 Comments

The “Continuity with Hybridization” theory is therefore based on direct evidence of fossil materials: the continuity of morphological evolution of human fossils from East Asia as well as the continuity of Palaeolithic cultural develop-

ment from early humans to modern humans in the region. The theory not only emphasizes the continuous evolution of indigenous populations in the region, but also the interactions of those local populations with immigrants from the outside. This model can successfully explain that, since they first left Africa more than 2 million years ago, ancient *Homo erectus* did not evolve into multiple species but remained to be a single one. This theory is consistent with other lines of evidence including Palaeolithic archaeology. Of course, more studies are needed to cross-examine this theory. First, more human fossils are needed to accurately represent populations and to piece together a high-resolution picture. Next, Palaeolithic cultural remains, although relatively rich, can be still problematic in making connections between lithic industries and particular human populations. And last, the lack of precisely dated sites for critical time periods in the evolutionary process adds uncertainty to the study of some fossils and cultural remains. Some of these disadvantages have been legitimately questioned by supporters of the “Out-of-Africa” theory.

## 3 The “Out-of-Africa” or the “Replacement” theory

### 3.1 The theory and its development in China

The original version of the “Out-of-Africa” or “Replacement” theory first appeared in the middle 1970s. Based on their study of late Pleistocene human fossils in Africa, Protsch [21] and Howells [22] speculated that modern humans originated in Africa and subsequently spread to the rest of the world. But the formal statements of the theory (causing wide implications) derived from an influential publication by Cann and her colleagues [6] in 1987. The research team examined mitochondrial DNA (mtDNA) from placentas of 147 women whose ancestry came from five regions: Africa, Asia, the Caucasus region, Australia, and New Guinea. The study suggested that: 1) modern African populations have higher genetic diversity than any populations in any other continent, indicating that African populations are a relatively “old” group since it would take a longer time to accumulate mitochondrial genetic variation; 2) the phylogenetic tree built from the mtDNA sequences places Africans at the root of the tree, and reveals two major branches: one with only African populations, the other with Africans and other worldwide populations, suggesting an African origin for modern humans from the other parts of the world. The team uses the timing for the peopling of New Guinea, Australia, and New World to calculate a human mtDNA mutation rate of 2%–4% per million years. With the assumption of this constant mutation rate throughout human evolution, the team speculates that 1) all modern humans can be traced back to a common ancestor who lived in Africa 140–290 kyr ago; and 2) some descendants may have left Africa about 90–180 kyr ago and spread to the rest

of the world. Because mtDNA is only inherited maternally, public media has named this female common ancestor Eve; as a result, the “Out-of-Africa” theory is more commonly known as the “Eve Theory” [6].

Cann et al. [6] selected mtDNA as the marker for the study because mtDNA follows a special inheritance and mutates at a faster rate compared to nuclear DNA. The faster mutation rate results in higher genetic variability, which can serve as a magnifier in the examination of population histories. Its maternal inheritance without recombination makes it a simple and efficient tool for tracing phylogenetic relationships of individuals and populations. As a result, mtDNA is said to provide a new perspective for understanding when, where and how modern human originated and spread.

Following Cann et al., other geneticists conducted similar studies and reached similar conclusions. For example, Templeton’s comparison and analysis of phylogenetic trees based on mtDNA and Y chromosome data suggests an African origin for the ancestors of modern populations in other regions and detects at least two “Out of Africa” migrations [23]. Additionally, some anthropologists and archaeologists have found that their own fossils and archaeological records could be explained by this theory; therefore, “Replacement” theory soon became a mainstream theory in the West.

Since 1998, some geneticists have published papers based on analysis of modern Chinese populations to support the “Out-of-Africa” theory, challenging the notion of continuous evolution of humans in China and East Asia, and instead, proposing that modern Chinese descended from African immigrant populations who replaced the Chinese indigenous populations [10–15].

Most of the early Chinese studies use Y chromosome DNA (Y-DNA). In contrast to maternally inherited mtDNA, Y-DNA is paternally inherited. Y-DNA is believed to be the ideal DNA marker to trace migration histories of male individuals and populations [24]. Su et al. [11, 13] believe that single nucleotide polymorphism (SNP) on un-recombined region of Y chromosome is a stable DNA marker for reconstructing evolution and migration of early humans.

In 1998, Chu et al. [10] used 30 autosomal microsatellite loci (microsatellites) to study the genetic structure of 28 Chinese populations. The study found a significant genetic differentiation between Northern and Southern Chinese populations. The diversity of southern populations is greater than those from the North, which seems to be consistent with a scenario of non-local origin for modern Chinese populations. When combined with linguistic evidence, Chu et al. propose that modern humans from Africa first arrived in Southeast Asia and moved northward into China and East Asia.

Su et al.’s [11] study of 925 male Y-chromosome samples, including 739 from East Asia, show that the genetic diversity of populations in Southeast Asia is greater than that of northern populations. Considering the alleged lack of

human fossils in East Asia between 50–100 kyr ago, the authors speculate that the first modern humans arrived in southwest Asia around 60 kyr ago, and spread northward to East Asia, where indigenous populations had become extinct during or prior to the last glacial period. Ke et al. [12] studied 19 SNP loci of Han Chinese samples from 22 provinces in China and found a regional difference between the North and South, with greater diversity of haplotypes appearing in southern populations. In addition, there are several unique haplotypes (such as H7, H10, H11, and H12) that are only found in southern populations, lending further support to the notion that ancestors of modern Chinese originally arrived from the South and moved northward. The study further examines 3 Y-SNP loci shared by southern and northern populations, with some assumptions (0.18% as the mutation rate, 20 years as a generation, 750–2000 as effective population size), and calculates the arrival time of the first modern humans in China to be approximately 18–60 kyr ago.

The same research group later investigated three Y chromosome biallelic markers (YAP, M89 and M130) on 12,127 male individuals from 163 populations from Southeast Asia, Oceania, East Asia, Siberia and Central Asia [14]. The data indicate that all individuals carry a mutation of the three markers. The three mutations (YAP +, M89T, and M130T) occur simultaneously with another mutation (M168T), which is believed to have originated around 35–89 kyr ago in Africa. Thus, the paper speculates that indigenous archaic human populations in East Asia have no genetic contributions to modern living populations in the region. Zhang and his team [25–28] carried out a comprehensive population genetic study and constructed phylogenetic relationships of major East Asian mtDNA haplogroups. Their analysis also supports the “Out-of-Africa” theory, demonstrating that modern humans immigrated along the Asian coastline in the South, and points to a significant immigration into China from Southeast Asia around 60 kyr ago. They caution that more data and work are needed to validate these conclusions [25, 28].

Subsequently, a number of papers were published with similar conclusion. A new study by the Human Genome Organization (HUGO) Pan-Asian SNP Consortium initiated a large-scale regional study on Asian autosomal chromosome variation in order to obtain a genetic diversity map of Asian populations SNP [29]. The results show that the genetic structure of Asian populations has strong connections with the geographical distribution of the language: 90% of the haplotypes seen in East Asian populations can be found in Southeast Asian or Central and South Asian populations, showing a gradual decrease in variation from south to north. The study speculates that Southeast Asia should be the primary gene pool for East Asian populations. The study supports the theory that modern humans migrated to Southeast Asia first and then spread northwards to East Asia.

### 3.2 The key points

The key points of the “Out-of-Africa” theory or the “Replacement” theory can be summarized as: 1) modern humans (i.e., late *Homo sapiens*) is species that shares no common features with *Homo erectus* and archaic *Homo sapiens*; 2) modern humans probably originated in Africa 140–200 kyr ago; 3) Africa is the only origin of modern humans, and modern populations in the other parts of the world are descendants of modern human emigrant from Africa; 4) lines of human evolution in Africa are continuous whereas other regions display interruptions; 5) migration of modern humans from Africa represents a complete replacement process, that is, the indigenous ancient Eurasia humans became extinct, a lack of interbreeding with migrant African groups means that indigenous populations made no genetic contribution to the gene pool of modern living populations; 6) in East Asia, modern humans first arrived in Southeast Asia, and then spread northward; 7) in China, modern humans arrived about 60 kyr ago from the south and moved northward; 8) before the arrival of modern humans, the indigenous human populations (i.e., *Homo erectus*) in China became extinct during the last glacial period, and therefore there was no interactions between the two groups in China.

### 3.3 The main supporting evidence

As previously discussed using a number of case studies, the main evidence of the “Eve Theory” is from studies of genetic diversity and variation of living human populations around the world. These studies utilize either maternal mtDNA or paternal Y-DNA to analyze the genetic diversity of modern populations to reconstruct the origin and migration routes of early modern humans. The studies overwhelmingly favour Africa as the only origin of the modern human gene pool.

In addition, the theory is supported by evidence from other studies, including ancient human DNA studies, and fossil and archaeological evidence.

Ancient human DNA studies: ancient DNA extracted from human fossils, in comparison with modern human populations, can provide more direct evidence to establish a specific genetic relationship between ancient and modern populations. Because of DNA degradation over time, there are only a few instances of such successful analyses. Krings et al. [30] and Ovchinnikov et al. [31] successfully extracted DNA from Neanderthal fossils unearthed from a Feldhofer cave in Germany and a Mezmaiskaya cave in the North Caucasus region respectively [30, 31]. Comparison of the recovered ancient mtDNA sequences suggests that despite being located 2500 km apart, the most recent common ancestor of these two Neanderthal samples lived 151–352 kyr ago, whereas the separation time of modern human and Neanderthal mtDNA is speculated to be 365–853 kyr ago.

Therefore, Neanderthal mtDNA is significantly different from mtDNA sequences of modern humans. Caramelli et al. [32] analyzed DNA from 24 kyr-old modern human remains from Europe, proving that the recovered ancient DNA sequence is still within the range of modern humans but significantly different from contemporary Neanderthal mtDNA sequences. The results indicate that there is an unbridgeable “gap” (discontinuity) between Neanderthal and modern humans, suggesting that Neanderthals did not contribute to the gene pool of modern humans. In a more recent study, Briggs et al. [33] compared five Neanderthal mitochondrial genomes. This study revealed that the Neanderthal mtDNA variation observed 38–70 kyr ago is only 1/3 of that seen in contemporary modern humans [33]. The study further speculates that Neanderthal long-term effective population size is less than that of modern humans or extant Great Apes, and even under a constant decrease, particularly in later Neanderthals, which is likely due to the expansion of modern humans from Africa.

Human fossil evidence: relative to the genetic analysis, morphological studies of human fossils are used as supplementary evidence to support the “Replacement” theory. Cann et al. [6] in 1987 quoted some paleoanthropologists’ work to support their mtDNA analysis. Those paleoanthropologists argued that transition from archaic *Homo sapiens* to anatomically modern humans (late *Homo sapiens*) first took place in Africa 100–140 kyr ago. In 2001, Nieuwöhner [34] compared late Neanderthal fossils (100 kyr old) unearthed in West Asia with early modern human fossils of Skhul and Qafzeh of the same region and found that comparison of hand bones revealed a significant difference in terms of structure and function, indicating a significant behavioural difference between the two groups. The study further speculates the difference may reflect the manipulation improvement of hands, which may be closely related to the emergence of modern humans. Later, more direct supporting materials were recovered from Herto region in northern Ethiopia where human skulls dated to about 16 kyr ago [35]. This age is clearly earlier than those typical Neanderthal fossils and the skulls show some anatomically modern features. The human fossils bridge a gap between earlier ancient humans and later modern humans in Africa, providing key materials for the study of when, where and under what environment modern humans originated. Another supportive piece of evidence is from the reanalysis of human skulls from Omo in southern Ethiopia discovered in 1967 [36, 37]. The two human skulls, named Omo I and Omo II, were originally identified as *Homo sapiens*, with anatomical characteristics of modern humans. These fossils were previously dated to be 100 kyr ago, but the new dating result shows they are closer to 195 kyr old. The new date is consistent with the emergence of modern humans proposed by genetic data, thus, providing strong fossil evidence to support the “Out-of-Africa” theory.

Archaeological evidence: Cann et al., among others, no-

ticed the emergence of the common use of blade tools in Africa to be as early as 80–90 kyr ago, much earlier than the appearance of blade tools in Europe and Asia. This technological development in Africa is considered to be associated with the emergence of modern humans. Another important piece of archaeological evidence came from Blombos cave in the Cape Town region of South Africa. In 2002, Henshilwood et al. [38] published a paper in *Science* on their discovery of two pieces of ochre showing carved geometric patterns from strata of Middle Stone Age, dated 77 kyr old. The discovery is believed to reflect the capacity of early humans for descriptive, abstract thinking and expression, which is characteristic of modern human behaviour, thus providing evidence that modern humans originated in Africa. Subsequently, Mellars [39] identified more supporting evidence from archaeological sites in South Africa, particularly from Blombos cave, Boomplaas cave, Klasies River sites, and Diepkloof material. Although the dates of the archaeological sites were measured to be 55–75 kyr old, the cultural assemblages of the sites are very different from the early stage of the African Middle Stone Age culture. Instead, they are similar to cultural relics left by earlier modern humans around 45–50 kyr ago, such as blade technology, soft-hammer techniques, scrapers for leather processing, carving tools for processing bone and wood tools, specialized bone tools, composite tools, perforated clam shells used as decorations, and a large number of non-indigenous ochre, including the two pieces of ochre with complex geometric patterns from Blombos Cave. The emergence and development of these new cultural components can be traced back to 100–150 kyr ago, probably directly linking to the emergence and evolution of modern humans. Around 60–80 kyr ago and in association with rapid population expansion, the cultural phenomenon characterized by technical and thinking capacity of modern humans further developed and early modern humans in Africa were well equipped with the requisite technology and intelligence capacity to migrate “Out-of-Africa”.

### 3.4 The “Out-of-Africa” theory challenges the notion of continuous evolution of modern humans in China

The major challenges of the “Out-of-Africa” theory to the “Multi-regional Evolution” and the “Continuity with Hybridization” theories can be summarized as follows:

First, human populations in China possess low genetic diversity and lack ancient genetic haplotypes. As predicated by the theory, human populations outside of Africa have far less genetic variation than African populations; in China, northern populations have less genetic diversity than southern populations; all human populations in China have no Y-SNP that is older than African migrants; and almost all tested samples from China show “genetic traces” from Africa, refuting the notion that China is one of the origins of modern humans.

Second, there is no evidence from physical characteristics to prove the continuous evolution of humans from *Homo erectus* in China. Lahr [40] pointed out that the so-called physical characteristics supporting continuous evolution are not region-specific. The “flat face” appears mostly in Europe; the “flat nose” appears with the highest rate in Africa, not East Asia; East Asian populations do not have specific combinations of orbital shapes; blunt lateral margin of the orbit is seen most commonly in Australia, followed by Southeast Asia and Africa. Lieberman points out that, although human fossils and modern populations in China have shovel-shaped incisors, Neanderthals and early African *Homo erectus* also had shovel-shaped incisors despite different expressions; and the “short face” is not unique to ancient Asian humans [41]. Therefore, it is possible to refute the so-called continuous morphological evolution from *Homo erectus* to late *Homo sapiens* in China.

Third, there are no human fossils dating to 50–100 kyr ago in China. Ke et al. [13] point out that “[careful] study of the fossil evidence unearthed in China revealed a big gap between archaic humans (archaic *Homo sapiens*) and modern humans (late *Homo sapiens*), all archaic human fossils are all older than 100 kyr, and all of modern human fossils are not older than 40 kyr (mostly between 10–30 kyr), in other words, no human fossils are recovered from 50–100 kyr ago, which demonstrates no direct evidence to support the multiregional evolution theory”.

It has been suggested that the Last Glacial period produced environments unsuitable for human survival in China. Ke et al. [13] argue that “the...absence of human fossils in East Asia and the reason why modern humans originate from Africa can be well explained by the existence of Quaternary Glacial of 50–100 kyrBP, which made the vast majority of species difficult to survive in East Asia including mainland China. However, when the Last Glacial was over, the direct ancestors of modern Chinese (who originated from Africa) entered China through Southeast Asia to replace indigenous humans exited before the Last Glacial” [13].

### 3.5 Comments

The “Replacement” theory is based on molecular biology research, using modern technology to investigate the origin and evolution of modern humans. This new approach attempts to find genetic links between ancient and modern humans and then to reconstruct their connections in history. It provides a new approach to palaeoanthropology, which has heavily depended upon human fossils and cultural remnants of the past, to cross-examine and verify some outstanding research questions. The benefits of this approach are evident: it promotes multidisciplinary research, uses more reproducible test materials, and generates quantifiable data. It appears that DNA-based studies have a more solid foundation and more reliable conclusions; however, like any

methods in scientific research, DNA analysis also has its pros and cons, and its own limitations and assumptions.

(1) The methodology employed is based on a number of assumptions that still need to be verified. One essential assumption of this school is that the DNA mutation rate is constant throughout human evolutionary history. Various studies demonstrate that the genetic mutations of different genetic loci occur at very different rates [42]. The mutation rates cannot be constant at all times; in fact, different DNA fragments, different genes, and different populations experience different “histories” and “selection pressures”, which can explain why different studies have reported different average mutation rates (the presumption of effective population size is often quite different). In reality, researchers can only use a constant mutation rate to estimate the time of evolution. Determining the mutation rate is of critical importance as higher mutation rates will result in overestimations of evolutionary time. Likewise, lower mutation rates will result in underestimations. Consequently, the under/overestimation of mutation rates can have a significant impact on the study of different populations of the same species, such as humans. Unfortunately, there is no reliable and accurate method for estimating constant mutation rates. Caution should be taken when assessing research that involves mutation rates and other assumptions. In addition, DNA analyzed from living human populations only represents a small part of the genetic diversity accumulated by modern humans. Cann et al. [6] also admit that “the mtDNA analysis cannot study those men and women who fail to pass down their genetic and cultural information, missing the opportunity to study their contributions”.

There are many factors to be considered when attempting to utilize surviving genetic diversity to reconstruct ancient history of humans. For those successful ancient human DNA studies (mainly Neanderthal), analyses are currently limited to mtDNA, and can therefore only trace maternal lineages, which has an intrinsic disadvantage. Each locus of the human genome only captures a piece of human history, and different genetic loci may reveal very different phylogenetic patterns. As a result, a more comprehensive understanding of genetic history can only be made through the study of multiple loci [43]. Likewise, at present, the study of modern human origins in China is largely limited to the Y chromosome. More studies are needed to validate those conclusions as well.

(2) Uncertainty. Due to the uncertainty of many assumptions, the results of DNA studies are often associated with a certain level of ambiguity. For example, in 1987, Cann et al. [6] used genetic variation in modern mtDNA to trace a common ancestor to Africa who lived 140–280 kyr ago, a notably broad range of time. The timing for modern human ancestors to leave Africa and spread to the rest of world is also associated with uncertainty, with an estimation of 90–180 kyr ago, or even as late as 23 kyr ago. In many instances, mtDNA analysis cannot determine the exact time

of migration. From the published data, one can see there are numerous estimations of “the latest common ancestor” based on different molecular clocks ranging from 59 to 5 kyr old [44]. In addition, molecular biologists still debate how many waves (one or two) of Out-of-Africa migration may have taken place [23, 45, 46].

(3) Failure to acknowledge the impacts of ecological environments and human adaptability on human genetic variation: the “Out-of-Africa” theory is based on the notion that the more abundant the genetic variation, the longer the population evolutionary history. This interpretation is generally correct, but may not always be the case when taking into account the ecological environment of different regions and the differential survival of specific genetic variability in local populations. Schuster et al. [47] report the whole genome data of five indigenous individuals, including four Bushman hunter-gatherers who live in the Kalahari Desert. The results show the genetic differences among the Bushmen are much greater than the average variation between other populations in Europe and Asia (Bushman average nucleotide difference is 1.2/1000 bp, while the difference between a European and an Asian is only 1.0/1000 bp). Bushmen also contain many novel DNA mutations. The paper reports that about 25% of the SNPs are functionally significant, making them ideal gene markers to track human adaptations to environmental changes. The article further points out that the Bushman’s genetic diversity and variation may have resulted from their adaptation to dry climate and hunting-gathering economy. One implication of the study is that African populations are placed at the root of the modern human phylogenetic tree, not only due to their long evolutionary history, but also because of their adaption to environmental changes.

(4) Failure to fully appreciate impacts of recent human migrations and admixtures on genetic variation patterns: molecular biologists use modern DNA data to reconstruct ancient history. The analysis of modern DNA data can reveal genetic diversity and gene distribution, assisting in reconstructing the origin and migration of human populations. However, the reconstruction can be hindered or misled where migrations and admixtures have been intensified since the Neolithic period Holocene and in the historic period in particular. In China, historic documents record many large-scale migrations from North to South due to wars and famines, resulting in admixture of northern populations into southern populations. Therefore, it should not be surprising to see that southern populations show more genetic diversity than northern populations, evidence which had previously been used to support the claim of greater antiquity for southern populations, and the genetic origin of northern populations. The HUGO Pan-Asian SNP Consortium also reports that there are frequent gene exchanges between South and North Asia, in particular after the emergence of agriculture, when northern and central East Asian populations spread southward, changing the physical characteristics of southern populations [29].

Therefore, when using modern human population genetics to reconstruct ancient history, one must take into account such hidden “blending” data.

(5) The absolute and exclusive nature of the “Out-of-Africa” theory makes it difficult to reconcile with conflicting lines of evidence. The “Out-of-Africa” theory emphasizes that Africa is the sole origin of modern humans; human populations of the other regions are descendants of immigrants from Africa, and all indigenous populations outside Africa become extinct. Only in this way would the “Out of Africa” theory have “absolute” and “exclusive” power; it does not allow other parts of the world to have early modern humans. It also does not allow for any gene flow between those African modern humans and other archaic humans of the other part of the world. If such processes occurred, the theory would not stand. In China, there is strong evidence from human fossils and cultural remains to support a continuous evolution from *Homo erectus*-archaic *Homo sapiens*-late *Homo sapiens*. Nevertheless, advocates of the “Replacement” theory ignore the integrity of this evidence, instead citing the work of some scholars on individual fossil records to reject the continuous evolution of human fossils. Likewise, others accept the gap of 50–100 kyr of human existence in China by rejecting evidence dating to this period. It is clear that the absoluteness and exclusiveness of the theory has affected its ability to integrate with other alternative lines of evidence.

(6) Lack of support from related disciplines: according to the “Replacement” theory, one key issue relating to the interruption of human evolution in China is the Last Glacial which caused severe weather that may have contributed to the extinction of indigenous humans in China long before the arrival of modern humans from Africa. As a result, there would not have been any potential conflicts between local and migrant populations. Unfortunately, there is no evidence from palaeoanthropology, Palaeolithic archaeology, geology, palaeoenvironment, vertebrate palaeontology, and chronometry to support this speculation. Instead, studies from these fields show that, even in North China, there is no evidence for an extreme cold climate that could decimate humans while enabling other associated mammals like woolly rhinoceroses, mammoths, horses and cattle to survive to Holocene. The advocates of the “Out-of-Africa” theory seem to forget that humans are social and highly intelligent animals, more capable of adapting and surviving in harsh climates, or migrating to more suitable areas within the vast area of China.

#### 4 The “Continuity with Hybridization” theory and regional diversity of global human evolution

Over the past 20 years, the debate between the “Out-of-Africa” theory and the “Multi-regional Evolution” theory has pushed China and East Asia to the center of the contro-

versy, promoting the development of the “Continuity with Hybridization” theory. Compared to the “Out of Africa” theory, the “Multi-regional Evolution” theory or “Regional Diversity of Human Evolution” is more convincing, and is supported by many lines of evidence.

##### 4.1 Chinese human fossils provide systematic supporting evidence of interpretations

There are over 70 locations in China where human fossils have been unearthed. These human fossils provide strong evidence of continuous evolution, mosaic evolution of humans in China and gene flow with those outside China since the Pleistocene, as demonstrated by many scholars [4, 48–52]. The characteristics of cranial bones, facial bones and teeth that support continuous evolution are present on many Chinese fossils with high frequencies and appearance in group [49]. There are also four characteristics (strong sagittal ridge, strong mandibular torus, pinched nasal saddle, and congenital absence of third molar) that can be observed in modern Chinese populations but are absent from modern African populations. Interestingly, similar features can be observed in Chinese human fossils. This similarity demonstrates that modern East Asian populations evolved from local archaic populations, morphologically different from early modern human African populations, and with weak evolutionary linkages to African populations [40]. Comprehensive analyses of ancient human fossils in China demonstrate that the continuous evolution of a series of inherited characteristics indicates no major population replacement occurred in China. Otherwise, we would not expect the whole series of morphological characteristics of the early archaic humans to appear in the newly immigrated modern humans from Africa.

##### 4.2 Palaeolithic artefacts are robust evidence from technological and behavioural perspective

Numerous stone tools, bone tools and other material cultural remains from Pleistocene humans have been discovered in many archaeological sites in China. These artefacts are important for studying technological developments, productivities and subsistence practices of ancient humans in the region. Moreover, certain temporal or regional populations are expected to possess certain levels of lithic technologies. Therefore, archaeological materials can contribute greatly to investigations of prehistoric human evolution and population migrations, as well as determining the temporal-spatial and social relationships among human populations. Consequently, it evolved into an additional verification and line of evidence in the study of human fossils.

To date, more than 1000 Palaeolithic sites have been discovered in China. By comparing the technological modes of Palaeolithic cultures between East and West, Lin argues that there exists a significant difference between their cul-

tural traditions [53]. Palaeolithic cultures in China have their own tradition that can be traced back to the remote past and are believed to have developed independently. While Palaeolithic cultures in China might have been in contact with those from the outside, there is no evidence to support any large-scale cultural replacements in China. Zhang [54] proposes that in Palaeolithic China two continuously-developing main traditions exist: the southern tradition shows high stability whereas the northern tradition shows gradual and slow development until 30 kyr ago and then some “foreign” cultural components started to emerge at a few sites in North China, likely as a result of external cultural exchanges. And then, some sites start to reveal external cultural components which might be brought in through cultural exchanges with the outside, but the new cultural components are not strong enough to replace the old cultural traditions; rather they show some parallel and mingled developments. Pei et al. [55] employed a new dating technique to study some key Palaeolithic sites, including Jingshuiwan in the Three Gorge region. They found that there were continuous human activities in the region, including the period of 50–100 kyr referred to as the so-called ‘gap period’ by some scholars. The culture and technology demonstrate gradual change and development; no evidence supports substantial cultural replacements.

After investigating the temporal and spatial distributions, taphonomic conditions, techniques and functions of stone tools, and typology of Palaeolithic artefacts, the utilization pattern of raw materials, and characteristics and division of regional cultural tradition, Gao et al. [20] propose a “Comprehensive Behavioral Model” to account for Pleistocene human survival and adaptation in China, and to illustrate human evolution processes and formation of special cultural components. They suggest that human evolution and behavioural development in most of the Palaeolithic period in China clearly display continuity, stability, high mobility, localization, and adaptation. They further point out that cultural/technological developments in the region indicate a mixture of succession and innovations, but generally the preservation of traditions is more prevalent than innovations. No substantial cultural replacement and/or interruption are evident, rather absorption of external cultural components. From an archaeological perspective, these observations and analyses provide strong evidence to support the “Continuity with Hybridization” theory. In addition, a new elephant tusk unearthed from the Xinglong Cave of the Three Gorges region is found to bear some carving marks that are comparable to those found in Blombos Cave in South Africa [56]. With an antiquity of 120 kyr BP, it may be the oldest piece of Palaeolithic art work. If such art work represents the intellectual and behavioural characteristics of modern humans, then this piece of work can lend support for the local origin and evolution of modern humans in China. If there are missing links along the evolutionary chain built of human fossils, we believe that more abundant Palaeolithic sites and

artefacts can provide more convincing evidence to support the local origin and continuous evolution of modern humans in China.

### 4.3 There is no evidence to support the gap between 50 and 100 kyr and the interruption of evolution

The “Out-of-Africa” theory in China identifies a substantial gap in human fossils, suggesting that the interruption of human evolution in China may have been caused by extreme cold climate of the Last Glacial. In fact, this idea can be easily falsified by a survey of human fossils and archaeological artefacts. Many human activities can be identified in the region from 50 to 100 kyr with human remains from Lingjing in Henan, Dingcun and Xujiaoyao in Shanxi, Huanglong Cave and Bailong cave in Hubei, Jingshuiwan, Ranjialukou and Zaoziping in Chongqing, Yancunshan Cave in Zhejiang, Guanyindong in Guizhou, and Ganqian Cave, Liujiang and Chongzuo Mulanshan in Guangxi [57, 58]. The Lingjing skull and Chongzuo mandible are both recently recovered human fossils, supporting the possibility that more human fossils may be recovered in the future. Moreover, the Chongzuo mandible displays very early stages of modern anatomical characteristics, revealing a transition from early humans to modern humans in China and providing additional key evidence for the continuous evolution of humans in the area [59].

Frankly, at present we lack reliable dating techniques to assess some sites falling within the 50–100 kyr time period. Accelerator mass spectrometry (AMS)  $^{14}\text{C}$  dating technique cannot reliably date samples of such antiquity. Uranium-series technique, palaeomagnetic method, electronspin resonance and fission track method also lack the precision required for dating artefacts of this time period. More recently developed methods such as potassium-argon dating, thermo and optical luminescence method, and thermal ionization mass spectrometry (TIMS) require special samples in order to obtain reliable results. However, equating a total negation of human existence in China throughout that period as a consequence of the technical difficulties is equally biased. From a biostratigraphic perspective, many late Pleistocene sites can be reliably assessed to this time period. In fact, it is not necessary to depend solely upon absolute dating when archaeological contexts provide biostratigraphic formation, associated faunal and floral remains and evidence of palaeoclimatic events. Absolute dating challenges are associated with the study of human fossils and archaeological sites in the West as well. For example, one of most important fossils supporting the “Out-of-Africa” theory, the Omo skull, has been dated with differing results [36, 60–62]. Even the newest results raise concerns regarding the sample layer and its relationship with human fossils [63, 64].

The hypothesis that the Last Glacial’s extreme cold climate led to mass extinctions of ancient Chinese populations

can be rejected. The Last Glacial is generally believed to span 74–10 kyr ago, during which the world was generally cool, with substantial climate fluctuation. Based on the study of the monsoon climate of Loess Plateau of China, 130–74 kyr BP was the time of the Last Interglacial with summer monsoon covering the entire plateau. The average temperature and precipitation were higher than those of today. After entering the Last Glacial stage, dated to 59–24 kyr ago, the interglacial time extends. Once the climate warmed, the summer monsoon activities extended to cover most of the Loess Plateau in its central and southern regions. Even during the Last Glacial Maximum (about 18 kyr ago), the summer monsoon moved its northern boundary to Southeast Loess Plateau, while further South was still under the control of summer monsoon with continuous soil formation [65]. Thus, most parts of China, even those in the Last Glacial period, were not exposed to conditions sufficient to cause mass extinction; even in the coldest times there should have been many areas suitable for humans and other animals to live. In South China, there are the Panda-Stegodon fauna throughout the Pleistocene, including gorilla, saber-toothed elephant, and rhinoceros, which are all warm or hot climate species. In North China, mammoth, woolly rhino, bears, hyenas, wolves, wild horses, bison, wild boar, and other large Pleistocene mammals survived to the end of Pleistocene, with many still present today. These animals were able to survive the harsh environments of the last glacial climate conditions. In all likelihood, humans were better able to survive considering their intelligence, and their abilities to make and use tools, to control and use fire, to migrate and choose good habitant sites, and to make clothes. In addition, since *Homo erectus* arrived in China, ancient humans had experienced many glacial-interglacial cycles since the early Pleistocene, of which the Last Glacial was not the most severe [66, 67]. It would be difficult to reconcile the survival of indigenous humans in China during the worst glacial cold climates occurring earlier if they were driven to extinction later despite their stronger survivability and the relatively milder Last Glacial climate. In addition, if those local indigenous inhabitants were unable to survive the harsh climates, how could those new immigrants from the Southern warm zone adapt and survive in their new and cold land?

#### 4.4 The origin and regional diversity of evolution of modern humans in the Old World

The continuous evolution of modern humans in China and the indigenous origin of modern Chinese are solidly supported by a wide range of evidence. In fact, the “Continuity with Hybridization” theory of East Asia and China and the “African Origin of Modern Chinese” theory are not necessarily mutually exclusive. The intersection of the two theories can help better understand the origin and evolution of modern humans, but only when the “absoluteness” and “ex-

clusiveness” of the latter is weakened or removed.

Genetic evidence was once overwhelmingly supportive of the “Out of Africa” theory and rejected the “Multi-regional Evolution” theory. The evidentiary boundary between these two theories has been blurred due to numerous studies that have offered data and conclusions that support the latter [24]. Hawks et al. [68] used variance analysis and cluster analysis to examine the physical characteristics of Australians and their ancestors. Their results rejected the theory that the ancient humans of that region were completely replaced by the modern human immigrants from Africa [68]; Adcock et al.’s work on mtDNA of Australians tend to support Hawks’ conclusion [69]. Zhao et al. [70] analysed 11000 base pairs of non-coding regions on chromosome 22 to calculate that all modern human DNA sequences in this region were derived from a latest common ancestor about 1.29 million years ago, thus indicating the origin and evolution of modern humans are more complex than described by the “Out-of-Africa” theory. Yu et al. [71] also examined 10000 base pair DNA segment on chromosome 10 from African, Asian and European individuals and determined the latest common ancestor to be from more than 1 million years ago, and even, using different assumptions, no later than 0.5 million years ago. A study on a non-coding 10346 bp region on X-chromosome also suggested only a low possibility that non-African modern human lineages come from small-scale populations in Africa [43].

A recent study on ancient human DNA shed new light on the issue. Krause et al. [72] analyzed mtDNA sequence from a phalanx of human fossil excavated from the Denisova cave of southern Siberia. They demonstrated that the fossil might belong to a previously unknown human species. The ancient DNA reveals its latest common ancestor with Neanderthal and modern humans lived about 1 million years ago. However, the stratigraphic examination and the dating results of the site indicate that the individual lived 30–50 kyr ago. From the same time period, Neanderthal fossils (with mtDNA recovered) were found at another site less than 100km away. Characteristic modern human culture (the Late Palaeolithic culture) is commonly seen in the same region. It seems that three different human populations co-existed in southern Siberia, and no complete replacements occurred. Having considered Indonesian *Homo florensis* (17 kyr ago), we have good reason to speculate that during Pleistocene, several human lineages coexisted in Eurasia.

Based on data from around the world and discussions from all perspectives, we believe that the origin and evolution of modern humans is a complex process and that the important evolution centers of the Old World reveal diverse regional models.

In Africa, continuous evolution of ancient humans and continuous impacts on the other parts of the world: Africa is a major center for human evolution. Ancient human popula-

tions in that region underwent dynamic evolution: the early modern humans emerged from indigenous and more archaic local populations, and they continued to evolve and, through continuous migration, gradually spread to Eurasia, impacting earlier and regional human populations in Eurasia. However, the impact was not to replace existing human populations, but more likely to interbreed with the local indigenous populations, enhancing genetic connections of humans around the world [23]. Notably, the impact is not unidirectional. Theoretically, humans could migrate from Eurasia back to Africa. Historic record shows Arabs and Phoenicians migrated to Africa from Eurasia; there is no reason not to believe that similar activities occurred in the remote past.

In Europe and Western Asia, where ancient humans may have encountered the effects of population bottlenecks, replacements can be said to be a main mode of evolution. In western Eurasia, the archaic *Homo sapiens* is Neanderthal, which is generally believed to have been driven to extinction by their inability to effectively adapt to new environments, and/or to compete against immigrant modern humans with more advanced technology and higher intelligence. Some recent studies also propose another possibility: local Neanderthals were not completely replaced by modern humans, but rather interbreeding occurred. Researchers at Washington University found a skull that had features typical of both modern humans and Neanderthals [73, 74]. The skull dated to 35 kyr old and was unearthed from a cave in southwest Romania. The skull bears typical Neanderthal features, such as a more flat forehead, more prominent bone at post-ear portion, and larger upper molars. It also exhibits typical modern human traits, such as brow ridge and cranial index, showing a mosaic evolutionary pattern. The study shows that Neanderthals and immigrant modern humans may have co-existed and interbred; therefore, initial arrival and subsequent development of modern humans is a complex and dynamic process. Recent ancient DNA studies of Neanderthal fossils yielded some interesting observations: Neanderthal mtDNA variation is only 1/3 of that of late *Homo sapiens* of the same period, with smaller effective population sizes (smaller than those of modern humans or Great Apes) [33]. The study reduces the effective population size to account for direct and indirect pressures associated with competition against modern humans, but the study does not overtly support replacement. Most recently, an international team extracted adequate amounts of DNA from three of twenty-one recovered Neanderthal fossils [75]. The results revealed some interesting comparative data: human populations in Eurasia (e.g., French, Chinese), instead of human populations in Africa (e.g., South African people, Yoruba people), are genetically closer to Neanderthals. The research shows that modern humans in Eurasia may have interbred with Neanderthals. The analysis further identifies some Neanderthal genes or gene fragments in living human populations, estimating approximately

1%–4% of human genome might come from Neanderthals. Therefore, when all lines of evidence are combined, it appears that human evolution in Western Eurasia follows the partial replacement model: new immigrants from Africa made up most of the population and these new immigrants also interbred with local Neanderthals.

In East Asia, the “Continuity with Hybridization” should be the model for human evolution. The East Asian model should be in some degree similar to the African model, that is, indigenous archaic humans gradually evolved both physically and behaviorally into modern humans, with occasional gene exchanges with populations from South and West. The local indigenous people remain as the majority of human populations; external genes may alter the genetic pool to a certain degree, but these changes have never reached the point that would constitute a replacement.

## 5 Conclusions

In this review, we demonstrate with clear evidence that the origin and evolution of modern humans is a complex issue. While controlled by genetic forces, the progress of evolution was also affected by cultural and social factors. Researchers should consider not only common characteristics of human groups living in one area, but also variations caused by adaptations of different human populations to different environmental conditions. As a result, no single universal model can explain the diversity of human evolutions.

The “Continuity with Hybridization” theory is based on systematic studies of rich fossil materials and Pleistocene cultural relics in China and East Asia. It gains strong support from multiple lines of evidence from a range of disciplines. The theory is developed from studies of East Asia and is applicable to human evolution in that region. It does not exclude other models for other regions. It does not deny that Africa is one center of human evolution; rather, it insists that the “Out-of-Africa” immigrants interbred with, as opposed to replace, local archaic humans. In Europe and west Asia, these new immigrants became the main body of later human populations in the region, with some gene flow from Neanderthals. Overall, human migrations should be viewed as multi-directional with mutual effects on both populations. It is hoped that this observation is not overlooked when deciphering human evolutions in the Old World. Incorporating and synthesizing all arguments, we have developed a new hypothesis in which modern human evolutions in different parts of the Old World are accounted for “the Regional Diversity Model”.

The study of human evolution still faces many problems and difficulties: fossils and artefacts are not adequate to paint a refined picture of human evolution; retrieved information from the ancient remains is still associated with low accuracy and low precision; different lines of evidence have

not been well integrated and synthesized together; many disciplines have not been brought together to make a truly interdisciplinary integration; more theoretical framework is needed to help study the complexity of human evolution. Therefore, it has become essential to make scientific field exploration and laboratory research more systematic. Systematic research will enable us to obtain more critical materials and more refined information, to launch more large projects that promote multidisciplinary integration and multi-regional cooperation and to construct more systematic and comprehensive theory, all in order to fully understand the origin of modern Chinese and human evolution in the world.

*This work was supported by National Basic Research Program of China (Grant No. 2006CB806400), Specific Basic Research Program of Ministry of Sciences and Technology of China (Grant No. 2007FY110200), Knowledge Innovation Program of the Chinese Academy of Sciences (Grant No. KZCX2-YW-Q1-04), National Natural Science Foundation of China (Grant No. J0603965), CAS/SAFEA International Partnership Program for Creative Research Teams, and Royal Ontario Museum Research Grant. Our special thanks go to Dr. Camilla Speller and Ms. Antonia Rodrigues for editing and commenting on the draft of the manuscript. We also want to thank our anonymous reviewers for their constructive comments.*

- 1 Coon C. *The Origins of Races*. New York: Alfred A Knopf Inc, 1962. 1–200
- 2 Wolpoff M H, Wu X Z, Thorne A. 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*. New York: Alan R Liss Inc, 1984. 411–483
- 3 Wolpoff M H. *Human Evolution* (1996–1997 edition). New York: McGraw-Hill, 1996
- 4 Wu X Z. The evolution of humankind in China (in Chinese). *Acta Archaeol Sin*, 1990, 9: 312–321
- 5 Wu X Z. Evidence of multiregional human evolution hypothesis from China (in Chinese). *Quat Sci*, 2006, 26: 702–709
- 6 Cann R, Stoneking M, Wilson A C. Mitochondria DNA and human evolution. *Nature*, 1987, 325: 31–36
- 7 Weidenreich F. Six lectures on *Sinanthropus pekinensis* and related problems. *Bull Geol Soc China*, 1939, 19: 1–110
- 8 Weidenreich F. The skull of *Sinanthropus pekinensis*, a comparative study on a primitive homind skull. *Palaeontol Sin-New Ser D*, 1943, 10: 1–485
- 9 Wu X Z. Origin of modern humans of China viewed from cranio-dental characteristics of Late *Homo sapiens* in China (in Chinese). *Acta Archaeol Sin*, 1998, 17: 276–282
- 10 Chu J, Huang W, Kuang S, et al. Genetic relationship of populations in China. *Proc Natl Acad Sci USA*, 1998, 95: 11763–11768
- 11 Su B, Xiao J, Underhill P, et al. Y-chromosome evidence for a northward migration of modern humans into Eastern Asia during the Last Ice Age. *Amer J Hum Genet*, 1999, 65: 1718–1724
- 12 Ke Y, Su B, Xiao J, et al. The Y-SNP Polymorphism distribution in China and origin and migration of Chinese. *Sci China Ser C-Life Sci*, 2001, 44: 225–232
- 13 Ke Y, Su B, Li H, et al. Y-chromosome evidence for no independent origin of modern human in China. *Chin Sci Bull*, 2001, 46: 411–414
- 14 Ke Y, Su B, Song X, et al. African origin of modern humans in East Asia: A tale of 12,000 Y chromosomes. *Science*, 2001, 292: 1151–1153
- 15 Jin L, Su B, Reply to J. Hawks: The Y chromosome and the replacement hypothesis. *Science*, 2001, 293: 567
- 16 Wu R K, Cheboksarov N N. On the continuity of the development of physical type, economic activity and culture of humans of ancient time in the territory of China. *Soviet Ethnogr*, 1959, 4: 3–25
- 17 Wu X Z, Zhang Y Y. Comprehensive study of fossil humans in China (in Chinese). In: Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, ed. *Collected Papers of Paleoanthropology*. Beijing: Science Press, 1978. 28–41
- 18 Wu X Z. Comparative study of early *Homo sapiens* from China and Europe (in Chinese). *Acta Archaeol Sin*, 1988, 7: 287–293
- 19 Clark G. *World Prehistory*. 2nd ed. Cambridge: Cambridge University Press, 1969
- 20 Gao X, Pei S W. An archaeological interpretation of ancient human lithic technology and adaptive strategies in China (in Chinese). *Quat Sci*, 2006, 26: 506–513
- 21 Protsch R. The absolute dating of upper Pleistocene sub-Saharan fossil hominids and their place in human evolution. *J Hum Evol*, 1975, 4: 279–322
- 22 Howells W W. Explaining modern human evolutionists versus migrations. *J Hum Evol*, 1976, 5: 477–495
- 23 Templeton A R. Out of Africa again and again. *Nature*, 2002, 416: 45–51
- 24 Sheng G L, Lai X L, Wang W. Molecular anthropology and the origin of modern human (in Chinese). *Hereditas*, 2004, 26: 721–728
- 25 Yao Y G, Kong Q P, Bandelt H J, et al. Phylogeographic differentiation of mitochondrial DNA in Han Chinese. *Am J Hum Genet*, 2002, 70: 635–651
- 26 Kong Q P, Yao Y G, Sun C, et al. Phylogeny of East Asian mitochondrial DNA lineages inferred from complete sequences. *Am J Hum Genet*, 2003, 73: 671–676
- 27 Palanichamy M, Sun C, Agrawal S, et al. Phylogeny of mitochondrial DNA macrohaplogroup N in India, based on complete sequencing: Implications for the peopling of South Asia. *Am J Hum Gen*, 2004, 75: 966–978
- 28 Kong Q P, Sun C, Wang H W, et al. Large-scale mtDNA screening reveals a surprising matrilineal complexity in East Asia and its implications to the peopling of the region. *Mol Biol Evol*, 2010, doi: 10.1093/molbev/msq219
- 29 The HUGO Pan-Asian SNP Consortium. Mapping human genetic diversity in Asia. *Science*, 2009, 326: 1541–1545
- 30 Krings M, Stone A, Schmitz R W, et al. Neanderthal DNA sequences and the origin of modern humans. *Cell*, 1997, 90: 19–30
- 31 Ovchinnikov I V, GÖtherström A, Romanova G P, et al. Molecular analysis of Neanderthal DNA from the northern Caucasus. *Nature*, 2000, 404: 490–493
- 32 Caramelli D, Lalueza-Fox C, Vernesi C, et al. Evidence for a genetic discontinuity between Neanderthals and 24000 year old anatomically modern Europeans. *Proc Natl Acad Sci USA*, 2003, 100: 6593–6597
- 33 Briggs A W, Good J M, Green R E, et al. Targeted retrieval and analysis of five Neandertal mtDNA genomes. *Science*, 2009, 325: 318–321
- 34 Nieuwöhner W A. Behavioral inferences from the Skhul/Qafzeh early modern human hand remains. *Proc Natl Acad Sci USA*, 2001, 98: 2979–2984
- 35 White T D, Asfaw B, DeGusta D, et al. Pleistocene *Homo sapiens* from Middle Awash, Ethiopia. *Nature*, 2003, 423: 742–747
- 36 MacDougall I, Brown F H, Fleagle J G. Stratigraphic placement and age of modern humans from Kibish, Ethiopia. *Nature*, 2005, 433: 733–736
- 37 Fleagle J G, Assefa Z, Brown F H, et al. Paleoanthropology of the Kibish Formation, southern Ethiopia: Introduction. *J Hum Evol*, 2008, 55: 360–365
- 38 Henshilwood C S, d'Errico F, Yates R, et al. Emergence of modern human behavior: Middle Stone Age engravings from South Africa. *Science*, 2002, 295: 1278–1280
- 39 Mellars P. Going East: New genetic and archaeological perspectives on the modern human colonization of Eurasia. *Science*, 2006, 313: 796–800
- 40 Lahr M M. The multiregional model of modern human origins: A reassessment of its morphological basis. *J Hum Evol*, 1994, 26: 23–56
- 41 Lieberman D E. Testing hypotheses about recent human evolution

- from skulls. *Curr Anthropol*, 1995, 36: 159–196
- 42 Rodriguez-Trelles F, Tarrio R, Ayala F J. Erratic overdispersion of three molecular clocks: GPDH, SOD, and XDH. *Proc Natl Acad Sci USA*, 2001, 98: 11405–11410
- 43 Yu N, Fu Y X, Li W H. DNA polymorphism in a worldwide sample of human X chromosomes. *Mol Biol Evol*, 2002, 19: 2131–2141
- 44 Curnoe D, Thorne A. Number of ancestral human species: A molecular perspective. *Homo—J Comparative Hum Biol*, 2003, 53: 201–224
- 45 Forster P, Matsumura S. Did early humans go North or South? *Science*, 2005, 308: 965–966
- 46 Thangaraj K, Nandan A, Sharma V, et al. Deep rooting *in-situ* expansion of mtDNA Haplogroup R8 in South Asia. *PLoS One*, 2009, 4: e6545
- 47 Schuster S C, Miller W, Ratan A, et al. Complete Khoisan and Bantu genomes from southern Africa. *Nature*, 2010, 463: 943–947
- 48 Liu W. Mongoloids and the origin and evolution of modern human in China (in Chinese). *Acta Archaeol Sin*, 1997, 16: 55–73
- 49 Zhang Z B. Evidence for origin of Chinese populations: Time and space changes of craniometric traits (in Chinese). *Quat Sci*, 1999, 19: 113–124
- 50 Wu X Z. Discussion on the results of some molecular studies concerning the origin of modern Chinese (in Chinese). *Acta Archaeol Sin*, 2005, 24: 259–269
- 51 Wu X Z. New Arguments on continuity of human evolution in China (in Chinese). *Acta Archaeol Sin*, 2006, 25: 17–25
- 52 Liu W, He J N, Wu X J, et al. The comparisons of cranial Non2-metric features between upper cave skulls and modern North Chinese populations, and Late Pleistocene human evolution in China (in Chinese). *Acta Archaeol Sin*, 2006, 25: 26–41
- 53 Lin S L. Comparison of technological mode of Paleolithic Culture between China and the West (in Chinese). *Acta Archaeol Sin*, 1996, 15: 1–20
- 54 Zhang S S. Regional industrial gradual advance and cultural exchange of Paleolithic in North China (in Chinese). *Acta Archaeol Sin*, 1990, 9: 322–333
- 55 Pei S W, Zhang J F, Gao X, et al. Optical dating of the Jingshuiwan paleolithic site of Three Gorges, China. *Chin Sci Bull*, 2006, 51: 1334–1342
- 56 Gao X, Huang W B, Xu Z Q, et al. 120–150 ka human tooth and ivory engravings from Xinglongdong Cave, Three Gorges Region, South China. *Chin Sci Bull*, 2004, 49: 175–180
- 57 Wu R K, Wu X Z. Paleolithic Site in China (in Chinese). Shanghai: Shanghai Scientific and Technological Publishing House, 1999
- 58 Shi L, Zhang X, Shen G. New chronological evidence for the origin of modern humans in China (in Chinese). *J Nanjing University (Nat Sci)*, 2003, 26: 89–94
- 59 Jin C, Pan W, Zhang Y, et al. The Homo sapiens cave hominin site of Mulan Mountain, Jiangzhou district, Chongzuo, Guangxi with emphasis on its age. *Chin Sci Bull*, 2009, 54: 3848–3856
- 60 Howell F C. Hominidae. In: Maglio V M, Cooke H B, eds. *Evolution of African Mammals*. Cambridge: Harvard University Press, 1978. 154–248
- 61 Smith F H. Models and realities in modern human origins: The African fossil evidence. In: Aitken M J, Stringer C B, Mellars P A, eds. *The Origin of Modern Humans and the Impact of Chronometric Dating*. New Princeton: Princeton University Press, 1992. 234–248
- 62 Wolpoff M H. Multiregional evolution: The fossil alternative to Eden. In: Mellars P, Stringer C B, eds. *The Human Revolution: Behavioral and Biological Perspectives on the Origins of Modern Humans*. Princeton: Princeton University Press, 1989. 63–105
- 63 Brown F H, Fuller C. Stratigraphy and tephra of the Kibish Formation, southwestern Ethiopia. *J Hum Evol*, 2008, 55: 366–403
- 64 Feibel C S. Microstratigraphy of the Kibish hominin sites KHS and PHS, Lower Omo Valley, Ethiopia. *J Hum Evol*, 2008, 55: 404–408
- 65 Liu D S. Loess and Arid Environment (in Chinese). Hefei: Anhui Scientific and Technological Press, 2009
- 66 Bassinot F C, Labeyrie L D, Vincent E, et al. The astronomical theory of climate and the age of the Brunhes-Matuyama magnetic reversal. *Earth Planet Sci Lett*, 1994, 126: 91–108
- 67 EPICA Community Members. Eight glacial cycles from an Antarctic ice core. *Nature*, 2004, 429: 623–628
- 68 Hawks J D, Oh S, Hunley K, et al. An Australasian test of the recent African origin theory using the WLH-50 calvarium. *J Hum Evol*, 2000, 39: 1–22
- 69 Adecock G J, Dennis E S, Easteal S, et al. Mitochondrial DNA sequences in ancient Australians: Implications for modern human origins. *Proc Natl Acad Sci USA*, 2001, 98: 537–542
- 70 Zhao Z, Li J, Fu Y, et al. Worldwide DNA sequence variation in a 10-kilobase noncoding region on human chromosome 22. *Proc Natl Acad Sci USA*, 2000, 97: 11354–11358
- 71 Yu N, Zhao Z, Fu Y X, et al. Global patterns of human DNA sequence variation in a 10-kb region on human chromosome 1. *Mol Biol Evol*, 2001, 18: 214–222
- 72 Krause J, Fu Q, Good J, et al. The complete mitochondrial DNA genome of an unknown hominin from southern Siberia. *Nature*, 2010, 464: 894–897
- 73 Trinkaus E, Moldovan O, Milota Š, et al. An early modern human from the Peștera cu Oase, Romania. *Proc Natl Acad Sci USA*, 2003, 100: 11231–11236
- 74 Soficaru A, Dobos A, Trinkaus E. Early modern humans from the Peștera Muierii, Baia de Fier, Romania. *Proc Natl Acad Sci USA*, 2006, 103: 17196–17201
- 75 Green R, Krause J, Briggs A, et al. A draft sequence of the neandertal genome. *Science*, 2010, 328: 710–722