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New progress in understanding the origins of modern humans in China

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Abstract Hypotheses concerning the origins of modern humans have been intensively debated, and two competing models, the recent "Out-of-Africa" and "Multiregional Evolution" paradigms, have dominated research and discussions for decades. Evidence from China has played a fundamental role in this debate: regional continuity and replacement by populations in-migrated from Africa have both been suggested and supported mainly by paleoanthropologists and geneticists, respectively. As more evidence has accumulated, new results obtained, and more scholars from various disciplines become involved, supporters of the recent "Out-of-Africa" model agree more or less with the "Multiregional Evolution" model regarding the complex history of modern humans and their interbreeding with other archaic populations (e.g., Neandertals). Recent discoveries of new human fossils, Paleolithic archaeological materials, and ancient DNA evidence in China have yielded a large body of information regarding the formation and development of modern humans in this region. However, controversies continue, including that most molecular biologists insist on the replacement of archaic populations by modern humans dispersed from Africa, while most paleoanthropologists and archaeologists propose an enhanced "Continuity with Hybridization" model. In this paper, we compile new results and progress in China and present the current debates and issues on the origins of modern humans. Finally, we offer several suggestions for future studies.

Keywords China, Origins of modern humans, Modern behavior, Recent out-of-Africa, Continuity with hybridization, Interdisciplinary research

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1. Introduction

Since the recent "Out-of-Africa" model was proposed by three geneticists (Cann et al., 1987), research on the origins and evolution of modern humans (*Homo sapiens sapiens*) has become a critical issue in the scientific community and one of the major focuses of popular media as well. In particular, the debate over the origins of modern humans has intensified between two competing theories: the "Out-of-Africa" (single-place origin or Total Replacement) theory and the "Multiregional Evolution" paradigm (Stringer, 1992, 2002, 2014; Stringer and Andrews, 1988; Wolpoff et al., 1984, 2000; Wolpoff, 1999; Ke et al., 2001a, 2001b; Templeton, 2002; Wu, 1998, 2006; Gao et al., 2010). Recently, as more evidence has accumulated, a deeper understanding of these issues has been achieved and models of the origins of modern humans have been revised accordingly. Research on human fossils from Eurasia has demonstrated that various morphological hominid taxa were present in the Upper Pleistocene. Combining fossil evidence of the mosaic characteristics of

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Neanderthals and early modern humans, some scholars have proposed an assimilation model for modern human origins (Smith et al., 1989). Recent ancient DNA analyses detected the interbreeding of early modern humans and Neanderthals which generated various genetic taxa during the formation of early modern humans (Green et al., 2010; Fu et al., 2014, 2015; Vernot and Akey, 2014). As a result, some of the supporters of the total replacement model have shifted to an assimilation model. From an archaeological point of view, modern behavior documented in material culture appeared in various regions at different times which are not always synchronous with the fossil and genetic records. Thus, behavioral modernity is not exclusively associated with anatomically modern humans, consequently some scholars have shifted their research focus increasingly toward behavioral variability (Shea, 2011).

Meanwhile, new achievements in modern human origins research in China have been made in paleoanthropology, archaeology and molecular biology. Recent studies have demonstrated that modern human morphological characteristics appeared quite early, as documented in fossils from the late Middle Pleistocene at the Dali site in Shaanxi (Wu, 2014) and the Panxian Dadong site in Guizhou (Liu et al., 2013), and in the early Upper Pleistocene in Zhiren Cave in Guangxi (Liu et al., 2010; Jin et al., 2009) and the Lingjing site in Henan (Li et al., 2017). New fossils found in Huanglong Cave in Hubei (Liu W et al., 2009) and Fuyan Cave in Hunan (Liu et al., 2015) as well as other key sites indicate that fossil hominids with fully early modern human morphology were present in South and Central China as early as 100 ka (see Liu et al., 2016 for a recent review). The DNA sequences reconstructed for an early modern human from Tianyuan Cave in North China revealed that individual derived from a population that was ancestral to many present-day Asians and Native Americans but postdated the divergence of Asians from Europeans (Fu et al., 2013). Evidence from Paleolithic archaeology indicates a continuous development of lithic technology in China and greater East Asia since the Early Paleolithic, and no obvious gap existed from 50–100 ka as has been proposed by some geneticists examining the Chinese fossil and archaeological records in support of the "Out-of-Africa" hypothesis (Ke et al., 2001b), which may imply that no total population replacement occurred during this period in the region (Gao, 2014). These new finds and research progress, especially achievements gained through carefully coordinated interdisciplinary studies, have made the origins and evolution of modern humans in the region much clearer as more details are revealed. However, controversies and some missing links remain, and interpretations of the same evidence are variable. The main goal of this paper is to summarize new progress in research on the origins of modern humans, especially in China, and invoke an interdisciplinary and integrative research strategy to further pursue this complex subject.

2. Current research on the origin of modern humans in Western academic circles

2.1 New progress in molecular biology and a revision of the recent "Out-of-Africa" model

One of the most important recent discoveries in human evolution is evidence of interbreeding between Neanderthals and modern humans brought to light by molecular biologists. This find has confirmed that Neanderthals contributed a certain number of genomes to the gene pool of present-day populations instead of simply going extinct, which had been the prevailing paradigm previously. A draft sequence of the Neanderthal genome derived from individuals found in Vindija Cave, Croatia was published in 2010 (Green et al., 2010). Comparison with present-day humans suggests that between 1% and 4% of the genomes of Eurasian populations today are derived from Neanderthals (Green et al., 2010). In 2014, a high-resolution genome sequence of a 45000-year-old modern human male from the Ust'-Ishim site in Siberia indicated that this individual shares roughly 2.3% of his genome with Neanderthals, and places the time window for the admixture between the ancestors of this individual and Neanderthals at approximately 60–50 ka (Fu et al., 2014). The analysis of the Ust'-Ishim individual has also demonstrated that there was a northern dispersal route of modern humans which implies a complex evolutionary history of modern humans (Fu et al., 2014). At Peştera cu Oase in Romania, 6–9% of the genome of a 42–37 ka-old modern human is derived from Neanderthals, and the Neanderthal admixture occurred through only four to six generations, dating to less than 200 years before the time the Oase modern human lived (Fu et al., 2015). Although there is only a small proportion of the Neanderthal genome present in the present-day population of Eurasia, the exact amount varies among individuals. Researchers uncovered different areas containing Neanderthal genetic markers from a larger sample of present-day Eurasians which occupies 20% of the whole genome. Moreover, the admixture of the Neanderthal genome in that of modern humans allowed populations dispersing out of Africa to obtain the ability to cope with the harsh environmental conditions and endemic diseases in the new habitats they encountered (Krings et al., 2000; Sankararaman et al., 2012, 2014; Vernot and Akey, 2014). Genetic research on Neanderthal and Denisovan fossils in the Siberian Altai region indicates the ancestors of Neanderthals interbred with early modern humans from Africa around 100 ka, which is much earlier than has been previously suggested (Kuhlwilm et al., 2016). The above-mentioned evidence demonstrates that the Total Replacement Model that modern humans emerged from Africa around 200 ka, dispersed into

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other regions, and replaced all other local archaic populations cannot stand further because of the considerable interbreeding of Neanderthals and early modern humans in West Asia, Europe, and the Altai region of Siberia.

Recent research also suggests that several hominid lineages appeared simultaneously during the formation of modern humans and they shared certain genetic relationships with those modern populations. As an archaic population, the Denisovans of the Siberian Altai who lived simultaneously with early modern humans around 50–30 ka were identified on a genetic basis (Krause et al., 2010; Reich et al., 2010, 2011; Meyer et al., 2012). Their genome is nearly absent in present-day populations and exists only in low proportions among some groups in Asia (~5%) and Oceania (~1–2%) (Reich et al., 2010, 2011; Vernot et al., 2016). Molecular biologists have reconstructed a complex story and relationships among different ancient populations. Ancient DNA analysis of a female individual from Siberia shows that there were genetic exchanges among Neanderthals, Denisovans, and early modern humans, and an unknown source in the Denisovan genome was detected as well (Prüfer et al., 2014). These data argue against a simple model that suggests a single modern human population emerged in Africa and replaced all other indigenous archaic hominid groups in the rest of the world.

As genetic analyses made the recent "Out-of-Africa" model widely popular in the past 30 years, current progress in the techniques and methods of molecular biology constantly bring new data and views to the table, allowing us to rethink modern human origins. Some of the supporters of the "Out-of-Africa" model have revised the original model: the assumption of total replacement by in-migrated modern humans from Africa has been eliminated; the importance of hybridization in human evolution has been acknowledged, especially in the origins of modern humans; continuous and mosaic evolution has been more-or-less accepted (Stringer, 2002, 2014). However, the revised "Out-of-Africa" model, or partial replacement model, insists that Africa-originated modern humans are the main stream in modern human evolution which has borne the major contribution to the present-day populations, and the dispersed modern humans from Africa assimilated other archaic populations instead of integrating into the indigenous groups of other regions (Smith et al., 2005). It should be noted that the revision of the recent "Out-of-Africa" model was based on the assumption that a small number of Neanderthal and Denisovan genomes contributed to the genetic makeup of present-day humans, however, no genome sequences of the archaic population in East Asia have yet been obtained.

A small number of scholars note that the recent "Out-of-Arica" model adopted some unproven suppositions and data, and, as a result, they seriously doubt or fundamentally deny this hypothesis on the basis of methodology and logicality (Templeton, 2007; Huang, 2015).

2.2 New discoveries and research results on the human fossil record

New discoveries of and research on human fossils in Africa and surrounding regions, have pushed back the timing of the origin of modern humans to a point earlier than that suggested by genetic analysis on one hand, and unveiled more evidence of the interbreeding of early modern humans and other hominid groups on the other. Thirteen 400–200 ka-old teeth found in Qesem Cave, Israel exhibit morphological features similar to the early modern human fossils discovered at Qafzeh and Skhul instead of Neanderthals (Hershkovitz et al., 2011, 2016). Furthermore, hominid fossils discovered recently at Jebel Irhoud in Morocco have expanded the emergence of early modern humans in this region to around 300 ka. These fossils exhibit archaic features, but some key modern features are present in the facial morphology which indicates a complex history of early modern human evolution in Africa (Hublin et al., 2017). Actually, hypothetical interbreeding between modern humans and Neanderthals was initially proposed based on morphological studies (Smith, 1984; Trinkaus et al., 1999; Wolpoff, 1999). A 35 ka-old cranium from Romania exhibits a mosaic of modern human morphology, such as reduced maxillae with pronounced canine fossae, a narrow nasal aperture, small super-ciliary arches, etc., and Neanderthal morphology, such as a moderately low frontal arc, a large occipital bun, and a high coronoid process, etc. This indicates considerable Neanderthal/modern human admixture (Soficaru et al., 2006).

Another example of the complexity of human evolution and the origin of modern humans was the discovery of and debate about *Homo floresiensis* discovered on Flores Island in Indonesia. These fossil hominids living simultaneously with modern humans exhibit strong morphological similarity with *Homo erectus*. They were initially dated to around 19–11 ka (Tocheri et al., 2007; Morwood et al., 2004), but new analyses push back their age to 50 ka (Sutikna et al., 2016). Research on hominid fossils found in caves in Guangxi and Yunnan provinces in South China suggests possibly a new human taxon colloquially called the Maludong Hominid. Such fossils exhibit obvious archaic morphological features but derive from individuals who lived in this region only 14.5–11.5 ka. It has been suggested that they could be the descendants of *Homo erectus* migrating out of Africa (Ji et al., 2014; Curnoe et al., 2012). These finds, together with the Denisovans identified by genetic studies in the late Upper Pleistocene, demonstrate the complexity and variability of human evolution and disprove the hypersimplistic scenario of Total Replacement proposed by the recent "Out-of-Africa" hypothesis.

Research on newly discovered fossils from the Lower Pleistocene and some synthetic studies provide insights for better

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understanding the origins of modern humans. Comparison of five craniums dated to ca. 1.85 Ma found at the Dmanisi site in Georgia demonstrates larger inter-group variations in morphology, and researchers have proposed that they would be considered different species had they been found in Africa. They further argued that different hominid taxa named after Lower Pleistocene fossils found in Africa might not be valid considering the potential inter-group variability, and suggest rethinking the methodology of classification of fossil hominids (Lordkipanidze et al., 2013). Antón et al. (2014) summed up the early hominid fossils and proposed that the derived features of modern humans did not simultaneously appear as a package but, instead, emerged successively during the long course of human evolution. Although those analyses focused on early hominid fossils, they also shed light on how to define modern humans and interpret morphological variations apparent in various hominid groups.

Meanwhile, supporters of the multiregional evolution model have strengthened their argument based on new finds and analytical research. For many years, this model has been misunderstood as suggesting independent origins of modern humans in Africa, Europe, and Asia. In fact, the multiregional evolution model explores the formation of morphological modernity and emphasizes the admixture of morphology and genome in human evolution instead of the origins of hominids, although this model is rooted in the ancestor-descendant lineage model of Weidenreich (Wu, 2006; Wolpoff et al., 1984). With respect to morphological modernity, supporters of the "Multiregional Evolution" model and the recent "Out-of-Africa" model are coming closer together: Stringer (2014) notes that the formation of morphological modernity was not a single event but a process characterized by various patterns at different times; while Wolpoff and colleagues (Caspari and Wolpoff, 2013) consider modernity as a continuous on-going process involving anatomy, behavior and genes, and this process created phenotypic and genetic variations due to changes in demography and adaptation to different environments.

2.3 New progress in Paleolithic archaeology and rethinking "modern human behaviour"

Besides researchers in the field of physical morphology and molecular biology, archaeologists are also active contributors to research on the origins of modern humans. While paleoanthropologists and geneticists are seeking answers to when, where and how modern humans evolved, archaeologists try to identify and explain the nature of modern human behavior and its origins and evolution based on material culture (Mellars, 2005; Klein, 2009).

2.3.1 Defining "modern human behaviour"

As the only living hominid species, modern *Homo sapiens* has often been viewed as the winner of a de facto competition with other ancestral human groups, leading many to assume that they should have had more advanced material culture relative to those other groups (Mellars, 1989). Based on the development and changes within the western European Middle-Upper Paleolithic sequence, that is, the Mousterian techno-complex presumably created by Neanderthals was replaced by the Aurignacian techno-complex, apparently produced by modern humans, the latter was regarded as the material symbol of early modern humans. As a result, a list of modern human behavioral criteria was proposed by some scholars based on Aurignacian cultural components including blade technology, the use of pigments, long distance transportation of raw material, art, ornamentation and other factors (Mellars, 1989, 2006a, 2007). However, this list became longer and longer as new archaeological finds in different regions of the world accumulated, and the capacity for distinguishing the cultural uniqueness of modern humans correspondingly became weaker and weaker. Henshilwood and Marean (2003) noted that the list of modern human behaviors has a distinct Eurocentric bias and is not applicable universally. More importantly, the logic used to select a list of cultural materials is obviously empirical: distinguishing modern behavioral traits depended on materials recovered from archaeological sites, but this approach usually ignored the nature of those sites and their formation processes which could profoundly affect what archaeologists actually recovered from those sites. Instead, Henshilwood and Marean (2003) proposed that only those cultural materials bearing symbolic content can be considered signals of modern behavior. This model has found support among more scholars recently (Nowell, 2010). Thus, the majority of work on modern human behavior has focused on non-utilitarian objects such as ornaments, engraving on artifacts, and pigments (Bouzouggar et al., 2007; d'Errico et al., 2009; Peng et al., 2012; Henshilwood et al., 2009; Rodríguez-Vidal et al., 2014). Meanwhile, research on the evolution of human cognition and intellectual capacity (Henshilwood et al., 2002; Wadley et al., 2009), consciousness (Tattersall, 2004), brain evolution (Coward and Gamble, 2008; Coolidge and Wynn, 2005), and the emergence of language (Schepartz, 1993; d'Errico et al., 2003) revealed by symbolic materials has drawn a great deal of attention from scientists of various disciplines such as linguistics, cognitive science, brain neurology, and the social sciences.

2.3.2 The origin and evolution of modern human behavior

Modern behaviors were once considered to have emerged abruptly and replaced the cultures of the Neanderthals after modern humans migrated into Europe (Mellars, 1992). As more evidence was uncovered in Africa and, under the influence of the recent "Out-of-Africa" hypothesis, some

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scholars have proposed that modern behavior first evolved in Africa (Klein, 1995). The reason for the emergence of complex modern behavior has been linked to the appearance of language which was caused by genetic mutation of the human brain. These two hypotheses favor a single revolution model of modern behavioral origins (Bar-Yosef, 2002). However, McBrearty and Brooks (2000) note that so-called modern behaviors, including blade technology, the use of pigments, long-distance transportation of raw material, art, and ornamentation, among others, appeared as early as 300–250 ka and evolved cumulatively and continuously after synthesizing Middle Stone Age materials from Africa. Similar to research on the origin of modern humans, two competing paradigms appeared for the origins of modern behavior: the revolution and evolution models. In addition to these two models, a saltation model has been proposed referring to the 100–70 ka evidence of ornamentation and pigment use discovered in North and South Africa (d'Errico and Stringer, 2011). After correlating population size and genetic data, scholars found the population size in Europe prior to 40 ka characterized by prolific symbolic behavior and complex technologies was similar to that in Africa 100 ka ago. Therefore, proponents of the saltation model suggested that the package of modern behaviors was not stabilized until 40 ka after its emergence at 100 ka, the reason for this apparent saltation being the size of the population and human groups (d'Errico and Stringer, 2011).

2.3.3 The proprietor of modern behavior and the issue of cultural exchange

Modern behaviors were once considered linked to modern humans exclusively. However, d'Errico (2003) and Zilhão (2006) noted that artifacts generally associated with the Aurignacian, such as ornaments and engraved symbols, were also found in Mousterian sites. More specifically, during the Middle-Upper Paleolithic transition, the association of typical Neanderthal fossils and bone tools, ornaments, and Upper Paleolithic stone tools demonstrated that the long-standing proposed exclusive relationship between modern humans and so-called modern behavior is unsupportable. As a result, some scholars suggested abandoning the term modern human behavior, and proposed new descriptors including modern behavior and behavioral modernity instead. Scholars still debate the appearance of modern behavior among Neanderthals; whether they evolved independently or resulted from the acculturation of modern humans' culture (d'Errico et al., 1998; Bar-Yosef and Bordes, 2010; Hublin et al., 2012). Surprisingly, reinvestigation of archaeological materials from the Trinil *Homo erectus* site in Java identified a number of intentionally engraved symbols on shells which are dated to as early as 540–430 ka by $^{40}Ar/^{39}Ar$ and OSL techniques (Joordens et al., 2015). The 150–120 ka-old marks found on ivory in Xinglong Cave in Chongqing in central China also suggest the possibility that archaic humans engaged in symbolic behavior (Gao et al., 2004). These new discoveries have amassed a large body of information critical to understanding the cognitive ability of *Homo erectus* as well as both archaic and modern *Homo sapiens*. These finds have reminded scholars that hominid groups expressing so-called modern behaviors are much more complex than we have generally supposed.

Increasingly, researchers have realized that the evolution of culture was more rapid and more variable than changes in phenotypic morphology and the genome, therefore there is no simple one-to-one correlation possible between certain cultural complexes and a particular hominid taxon. In fact, so-called modern human behavior appeared at different times in different regions and among various human groups, and it is not exclusively associated with modern humans; some modern behaviors were clearly expressed by our Neanderthal cousins. Consequently, archaeologists are not obsessed with modern behavior or behavioral modernity, but seek to trace the behavioral diversity of different hominid groups (Shea, 2011). Nevertheless, some scholars insist on a strict recent "Out-of-Africa" model using archaeological data as supporting evidence (Mellars, 2006b). They propose that only modern humans migrating out of Africa ca. 50 ka survived the evolutionary competition but received no genetic contributions from archaic hominid groups from other regions. They subsequently dispersed to other continents such as South Asia and Australia following coastal routes (Mellars, 2006b).

3. New progress in research on the origin of modern humans in China

3.1 Persistence of the "Out-of-Africa" model in molecular biology

China, a key area in debates over the origins of modern humans (Gao et al., 2010), has yielded a large amount of fossil and archaeological evidence post-*Homo erectus* for which the region was once considered one of the originating centers of East Asian present-day humans. During the current discussions of modern human origins, this long-established model has been challenged which makes the story of modern human origins in this area unclear. Scholars must rethink and relocate the ancestors of East Asians accordingly. The major points of the "Out-of-Africa" model include: (1) present-day humans are a different species from *Homo erectus* and a different subspecies from archaic *Homo sapiens*; (2) modern humans emerged in Africa between 200–100 ka and dispersed out of that continent following a southern route via Southeast Asia and then north into East Asia; (3) in China, modern humans first arrived in South China around 60–50 ka and then moved further north; (4) prior to the arrival of modern

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humans 100–50 ka, a harsh environment made China an unfavorable area which caused the extinction of the local human population; (5) in-migrated modern human groups never met indigenous archaic hominids in China (Ke et al., 2001a, 2001b; Jin and Su, 2000; Su et al., 1999; Chu et al., 1998).

Not much progress has been made in molecular biology recently on the study of early modern human origins in China and greater East Asia, and earlier published evidence has been repeatedly cited. More research now focuses on tracing the origins of certain ethnic groups based on the presupposition of an African origin of modern humans (Zhang X M et al., 2013, 2015). From this perspective, the views outlined by Yan Shi are representative: 95% of the present-day human genome originated in Africa and modern humans in other continents migrated from Africa after 100 ka, therefore the rest of the debate centers on whether there was a single dispersal or multiple dispersals out of Africa; although hominid lineages represented by fossil finds at Zhoukoudian (0.7 Ma), Yuanmou (1.7 Ma), and Wushan (2 Ma) once existed, they all ultimately became extinct (Yang, 2014).

3.2 Enhanced arguments concerning the "continuity with hybridization" model in paleoanthropology

Based on the Multiregional Evolution model, a "continuity with hybridization" scenario was proposed by Wu (1998, 2006) aimed at exploring the origins of modern humans and human evolution in East Asia. The key points of this model can be summarized as: (1) humans in East Asia have undergone continuous evolution since the arrival of *Homo erectus* without any interruption and without large-scale population replacements; (2) relative geographic isolation allowed ancient humans in China to develop distinctive regional features different from western populations in the Old World; (3) indigenous human populations in China exchanged genes with allochthonous populations and the rate of such exchanges increased over time, keeping all human populations within a single species; (4) the exchange of genes with outside groups was secondary compared to regional continuity; integration rather than replacement occurred between local populations and small-scale newcomers (see Gao et al., 2010 for a recent review).

Modern human origins in East Asia have been hotly debated. Progress has been made in the past decade in this area and fossils have been found or reinvestigated at several sites including Huanglong Cave in Hubei, Zhiren Cave in Guangxi, Panxian Dadong in Guizhou, and the Lingjing site in Henan. New chronometric results and morphological analyses of those fossils demonstrate a complex evolutionary history of hominids which does not agree with the recent "Out-of-Africa" model (Liu et al., 2016).

The Dali cranium (Wu, 2014) is a mosaic combining common features of late Middle Pleistocene hominids and some characteristics of early modern humans. It also exhibits features of East Asian *Homo erectus* and west Eurasian Middle Pleistocene hominids. This cranium belongs to neither *Homo erectus*, nor *Homo heidelbergensis*, and the population represented by the Dali cranium made a greater contribution to the formation of early modern humans in China than did Chinese *Homo erectus* or Middle Pleistocene hominids from Africa. Analysis of the newly discovered Xuchang crania dated to 125–105 ka from the Lingjing site in Henan exhibit a mosaic pattern of archaic and modern morphological features: although they share pan-Old World trends with Neanderthals, they also reflect eastern Eurasian ancestry in having low, sagittally flat, and inferiorly broad neurocrania which indicates a pattern of substantial regional continuity in eastern Eurasia into the early Late Pleistocene and for some level of east-west population interaction across Eurasia (Li et al., 2017).

Fossils found in late Middle and early Upper Pleistocene contexts in South China show early modern human morphological features as well. The Panxian Dadong teeth, dated to 300–130 ka, exhibit a combination of archaic and derived features, although those derived features are not diagnostic enough to specifically attribute the Panxian Dadong teeth to *Homo sapiens* (Liu et al., 2013). The Zhiren mandible, around 100 ka old, exhibits derived modern human anterior symphyseal morphology, with a projecting tuber symphysis, distinct mental fossae, modest lateral tubercles, and a vertical symphysis, and exhibits a lingual symphyseal morphology and robustness that place it close to later Pleistocene archaic humans (Liu et al., 2010). Those fossils bearing a mixture of primitive and derived morphological features imply that there were some populations in transitional states in South China from archaic to modern *Homo sapiens* which are also generally considered early modern humans in the late Middle and early Upper Pleistocene. Fuyan Cave in Hunan has yielded 47 human teeth dating to more than 80 ka, and with an inferred maximum age of 120 ka. The morphological and metric assessment of those teeth supports their unequivocal assignment to *Homo sapiens* (Liu et al., 2015). Additional discoveries of modern human fossils include Huanglong Cave in Hubei (Liu W et al., 2009), Lunan and Tubo caves in Guangxi (Bae et al., 2014; Li et al., 1984; Shen et al., 2001), Mawokou Cave in Guizhou (Zhao et al., 2016) and others, which commonly date to the late Middle and early Upper Pleistocene (ca. 120–80 ka).

Important new information has been obtained through reinvestigation of previously-found fossils applying new methodology. Specimens from the Xujiayao site in the Nihewan Basin have been reanalyzed, and the osseous labyrinths were reconstructed using CT scanned data (Wu et al., 2014). Xujiayao 15 falls in the middle of Neanderthal variation and is distinct from the other Xujiayao samples. This eastern Eurasian labyrinthine dichotomy occurs in the context of none of the

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distinctive Neanderthal external temporal or other cranial features. As such, it raises questions regarding possible cranial and postcranial morphological correlates of *Homo* osseous labyrinthine variation, and the use of individual "Neanderthal" features for documenting population affinities (Wu et al., 2014). On the contrary, it could also be evidence of possible admixture of late archaic hominids across Eurasia.

3.3 Evidence and perspectives from archaeology

Archaeologists in China were silent early in the debate over modern human origins. As an evolutionary gap between 100–50 ka in China was proposed by geneticists to support the replacement model, some paleoanthropologists began to seek evidence from the Paleolithic archaeological record to invalidate such a claim (Wu, 2005; Wu and Xu, 2016). As a result, some archaeologists joined the battle (Gao, 2014; Gao and Pei, 2006). Archaeological materials contribute to discussions of modern human origins in two ways: (1) the continuity with hybridization model is supported by the Paleolithic sequence of China; (2) Paleolithic remains from China enrich the discussion of modern behavior and supply a regional perspective to behavioral variability.

After systematic synthesis of cultural materials in Paleolithic China, Gao (2012, 2014) noted that the development of Paleolithic industries in the region occurred in one uninterrupted trajectory indicating that Pleistocene hominids survived and evolved continuously in the region. Through the study of the emergence of some so-called "western cultural elements" such as Levallois technological products, Acheulean-like assemblages, and blade tools in the Chinese Paleolithic, it is apparent they never became the mainstream in stone tool production, let alone replaced local techniques of tool manufacture, but were assimilated into the local material culture. Such archaeological evidence has provided strong support for evolutionary continuity of Pleistocene hominids in China and greater East Asia and the continuity with hybridization hypothesis instead of the recent "Out-of-Africa" model. The occupation hiatus between 100 ka and 50 ka proposed by molecular biologists has received little support from archaeology because a certain number of sites have now been dated to this temporal window as a result of improved chronometric techniques, especially the Optically Stimulated Luminescence (OSL) method. Moreover, paleoenvironmental reconstruction in China shows that the region was not as harsh as what supporters of the recent "Out-of-Africa" model have suggested, especially South China. The "Comprehensive Behavioral Model" (Gao, 2013, 2014) strengthens the argument in favor of aboriginal populations' capability for survival and evolution into modern humans. Observations and analyses of the unique behavioral patterns and social attributes of human beings also provide useful insights into issues such as the nature of geographic isolations for different human groups and the possibility of maintaining a single biological species of human groups living in different regions through time.

Numerous archaeological materials discovered at the Shuidonggou site cluster provide a large body of information to fuel discussions of behavioral variability and the influence of in-migrated populations in certain areas. In addition to various technological complexes, this site cluster has yielded abundant material culture and behavioral characteristics including bone tools, ornaments, fireplaces, complex spatial organization, heat treatment of raw material, and plant food gathering. This aggregated information yields a complex story of the adaptation, migration, cultural exchange, and technological evolution of hominids in East Asia since ca. 40 ka (Gao et al., 2008; Liu D C et al., 2009; Gao et al., 2013; Li et al., 2016). Beginning roughly 40 ka, blade technology with Levallois features appeared in this area. Technological comparisons with similar finds in Siberia and Central Asia indicate population dispersals from the west or north of the site (Li et al., 2013, 2014; Peng et al., 2014). However, this techno-complex did not persist in the area, played little role in shaping the local lithic technology, and was eventually replaced by a local core-flake technology instead. Meanwhile, advanced cultural materials which are generally attributed to modern behaviors appeared in the local techno-complex including finely-retouched tools, ornaments and heat treatment of raw material (Wang et al., 2009; Guan et al., 2011; Peng et al., 2012; Zhou et al., 2013), implying that no replacement occurred in this area. Instead, local populations evolving toward modern humans remains the mainstream interpretation.

Excavation and research in the Qinling Mountains have uncovered a much longer sequence of continuous evolution of material culture and human behavior. Mode 1 technology with pebble choppers, simple cores and flakes, and flake-based retouched tools first appeared in this area around 1 Ma. This industry was followed by assemblages characterized by cores, flakes, and small retouched tools such as side-scrapers, points, and atypical burins. Although Acheulian assemblages typified by large-cutting tools such as handaxes, picks, and cleavers are present in this area, this industry shows some characteristics of the local pebble-tool industry as well. In addition, the age of the Acheulian assemblages in the Qinling Mountains is generally later than similar industries in the West. These data demonstrate both the continuity and complexity of these lithic industries and the possibility of cultural and/or population interactions in the region (Wang and Lu, 2016).

Other research reveals similar patterns in the adaptation of late Upper Pleistocene populations, such as the intensification of animal resource use and evidence of a broad spectrum revolution which highlights the complex, variable, and regional features of modern behaviors in particular ways (Zhang Y et

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al., 2009a, 2009b; Zhang S Q et al., 2009; Zhang et al., 2012; Zhang Y et al., 2013; Wang et al., 2016; Zhang et al., 2016).

4. Problems and challenges in current research

Every discipline engaged in the study of human evolution is characterized by its own inherent strengths and weaknesses (Gao, 2017). Modern molecular biology is typified by large data returns and replication of experiments and analyses. This approach has greater potential to uncover the mechanism of human evolution in a microscopic perspective. With much faster progress, it would be the cutting edge, and even the leading method, of human evolution research if the time limits of ancient DNA extraction can be expanded. However, there are some uncertain and untested presuppositions in this field which result in some doubt and uncertainty. Numerous hypotheses are obtained by tracing the genetic variabilities of present-day populations instead of fossil humans. Therefore, it is premature to regard this indirect evidence of modern human origins as conclusive and factual. Fossil remains provide direct morphological descriptions of individuals, the evolutionary stage of the source population, and definition of human taxa which must be recorded and interpreted by researchers. Generally, the evolutionary framework reconstructed based on the fossil record is reliable, however, problems with some specimens remain in certain regions and preservation environments. More specifically, issues of dating can impact the evolutionary interpretation of human fossils and some could be misleading with respect to our understanding of human evolution. Furthermore, gaps in the fossil record commonly remain due to the scarceness of fossil evidence and the limited number of fossils also introduces the possibility of misinterpretation of the evolutionary stage of certain specimens and the characteristics of certain populations. Archaeological material supplies direct evidence of the spatial and temporal distribution of hominids, technological evolution, and cognitive development, while it is simultaneously indirect evidence of human taxa individuals and groups, the evolutionary stage of hominids, and migrations of human groups. Archaeological material is abundant, which can help reconstruct the evolutionary framework of material culture. It also provides a large body of information which can help answer questions such as when hominids first appeared in a certain region, where they dispersed to, whether the evolution of a certain region was continuous or not, what ecosystems and adaptation strategies were exploited, and whether or not interaction among ancient human groups occurred. However, this data-set's weakness is its association with particular human ancestral groups or evolutionary stage of hominids. Moreover, cultural behavior can be shaped by the environment and availability of raw materials, showing great variability in the mechanisms of change, and are very weakly correlated with anatomical and genetic evolution.

Consequently, strengthening communication and interaction among traditional paleoanthropological and archaeological fields and the burgeoning molecular biological fields, understanding each discipline's specialties and demands, and carrying out inter-disciplinary and integrative research, is the right direction and strategy to employ in pursuing research on human origins and evolution in the future.

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