The Origin of Modern East Asians

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Abstract: With the development of paleogenetics in the past decade, it has become evident that modern humans do not have a phylogenetic origin in the appearance of a new species *Homo sapiens*; therefore, anatomical, behavioral and genetic aspects of modernity are not the consequence of the same, single event. In this paper, we examine the evidence for anatomical, behavioral and genetic modernity in East Asia. In each case, modernity can be understood as part of a multiregional evolutionary *process*, rather than as an entity. Although these three aspects of modernity are somewhat independent, each evolving at different times, they are linked through demographic changes that began in the late Pleistocene - increased survivorship and population expansions that changed the course of human evolution.

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1 The pattern of human evolution

The human lineage originated in Africa, near the end of the Pliocene. The time of origin of this lineage, the unique ancestors of recent and living human populations, is defined by when it became distinct from other australopithecine lineages. Some researchers regard the lineage as synonymous with the human species itself, *Homo sapiens*^[1, 2], using a phylogenetic definition^[3] of *Homo sapiens*, rather than an anatomical one. The time of origin may be 2.3 myr, relying on the Hadar specimen AL-666^[4], or possibly a few hundred thousand years older based on the first appearance of *Australopithecus africanus* in East Africa, at Garhi^[5]. Later, beginning slightly less than two million years ago, the human species began to grow in number and expand in range, although it remained quite small for most of the Pleistocene, totaling as little as one million or less^[6].

For most of the time *Homo* has existed, until recently, half or more of these populations

lived in Africa^[7], and the remainder dispersed unevenly across the rest of the inhabited old world. Because most people lived in Africa, most gene flow within *Homo* was from Africa to the more peripheral populations of Eurasia. The human population grew slowly throughout the Pleistocene, changes in the rate of population size increases only began to significantly accelerate just before the Neolithic, and this acceleration continued and increased during the time that humans learned to control their food resources^[8] and agriculture and domestication became common. The accelerated population size increases continued to the present, with different rates in different regions. As a result population sizes and their distribution have changed dramatically, and Africa is no longer the most populous region of the world. Those parts of the world, such as East Asia, where soils were fertile and/or animals that were suitable for domestication were found became the most populous, and today these regions are where the highest population numbers and densities are found.

From a multiregional perspective, the human species evolved as its populations increased in size, from the beginning of the Pleistocene when initial geographic dispersals from Africa led to distinct populations established around the tropics and semi-tropics of Eurasia. Subsequent dispersals, size expansions, and population movements created a network of related populations encompassing the inhabited world. This evolutionary pattern was structured by the initial and ongoing geographic dispersals of human populations [9]. Their continued interconnections through gene flow and population movements allowed adaptive genes and behaviors, under selection, to spread throughout the human range as people with them had more surviving offspring. This assured that the trends in human evolution became universal and the genes that made us human were everywhere. But the dispersals of adaptive genes and behaviors were uneven and some populations remained isolated for long periods of time. Genes dispersing when contacts were reestablished can be identified because they are much older than the time they first appear in the populations with reestablished contacts. This phenomenon, called "introgression" (10), demonstrates a human past in which there were subspecies.

Human populations have existed within this network for most of the time of *Homo sapiens*, virtually every one with both multiple ancestors and multiple descendants: an ethnogenetic pattern^[11]. Each of these populations was unique because of their individual histories and adaptations, but each of them was also part of this human network, interconnected by gene flow and population movements.

Multiregional evolution, which models the human evolutionary process as this dynamic network of populations, was first fully published in 1984^[12] by Dr. Wu Xinzhi of the IVPP, Beijing, Dr. Alan Thorne of the Department of Prehistory, Australian National University, Canberra, and one of us, Dr. Milford Wolpoff of the University of Michigan, Ann Arbor. The

key elements of the multiregional pattern begin with the global evolutionary changes under selection that were created by the dispersal of adaptive genes^[13] for language, intelligence, technical skills, and other factors that help make us modern humans. Each of these important elements began in different places, but all of them ended everywhere, and modernity is what we are today. Several lines of evidence indicate that this pattern of modernity is based on the evolutionary changes described above, and not on massive population or species replacements. The persistence of regionally dominant features in various parts of the world, specially the peripheries – "regional continuities"^[14] – demonstrates that replacement did not take place; replacement would obliterate the earlier features. Moreover, genetic data now confirm the exchange of genes between different populations of archaic humans, and between archaic and modern humans, supporting earlier anatomical observations. Therefore, it is most likely that the global changes in the history of *Homo* came from genes dispersing through a network of populations, under selection, and not successive widespread population or species replacements.

2 Complex modern human origins in East Asia

Multiregional evolution was first explained in detail^[12] in the context of the fossil evidence for human evolution in East Asia. The East Asian fossil record shows that there was a complex origin for the modern humans in the region^[15]. Modern East Asians did not begin as an intrusive species that replaced earlier hominids, as once thought. The continuity of regionally predominant features in East Asia throughout the Middle and Late Pleistocene shows that recent and modern East Asian populations are not the unique descendants of invading Africans. Their ancestry includes Africans, but also other human populations that entered East Asia at various times from both north and south, and also includes earlier East Asians. The archaeological record also indicates this pattern, in which there were a number of dispersals into Asia, not always from the same point of entry^[16]. The key anatomical observations that helped establish this complex view of East Asian origins and evolution include the many regionally predominant features found to span the time of the human habitation of East Asia, that provide evidence that earlier East Asians are part of this complex ancestry. Following Wu Xinzhi^[17] and others, today we recognize that the long-lasting regionally predominant features in East Asia are exemplified by (but are not limited to) facial characteristics such as the common presence of: a more or less horizontal line formed by the sutures between the nasal, maxilla and frontal bones; an antero-lateral forward facing surface of the frontosphenoidal process of the zygomatic bone; flat nasal root quadrangular orbit shape with the infero-lateral margin rounded; a close to vertical nasal profile, at least for the upper part of the nose; flat or slightly concave bone surface between the pyriform aperture

and the orbit; curved surface on the lower margin of the zygomatic process of the maxilla; shovel shaped incisors (all 23 Pleistocene upper central incisors from China are shovel-shaped) wherein the crown surface is flat and the marginal ridges well-developed^[18].

That regionally predominant facial features exist for East Asians has an important implication for identifying modern humans everywhere. Had modern humans evolved recently as a new species with unique, modern anatomy, behavior, and genetics, their identification would be quite simple because all of these elements would be tied together in an exclusive package that clearly identified the new species when it first appeared, and reflected its unique attributes.

But both anatomical variation and genetic analysis show a much more complex evolutionary pattern. Africans play a significant role in the evolution of all populations of *Homo*, but not the role of the sole ancestor^[19]. Moreover, Africans were not the sole purveyors of modernity. Although African population expansions were highly influential in the evolution of modernity, the Africans considered the earliest modern humans are not particularly "modern" and, conversely the remains considered to be early modern human found away from Africa are not especially similar to recent and living African populations. For instance, considering the Skhul site^[31], there has been much discussion about the modernity and affinities of the Skhul males such as Skhul 4, 5 and 9, but none of them are generally identified as African. Less well-preserved females such as Skhul 2 raise the issue of their modernity since Skhul 2 preserves a mixture of features unmatched in any recent or living woman from anywhere. These include an exceptionally great interorbital distance, and a supraorbital torus that is quite is thick and continuous across the forehead, projecting strongly from the frontal squama so that there is a deep, strongly expressed supraorbital sulcus above and posterior to the torus. The earliest modern samples from other regions across the old world are also not especially like Africans²¹, nor is there genetic evidence of an African bottleneck at this time^[20].

It is quite clear from the last decade of discoveries in paleogenetics, the study of ancient genes preserved in fossils, that *modern humans everywhere* have a complex ancestry.²¹ The pattern of descent that makes this ancestry complex is revealed by instances of numerous and significant cases of interbreeding between Neandertals, Denisovans^[22], and populations emerging from Africa^[23-26]. As we described it above, this is an ethnogenetic pattern.

Today, both Asian and European populations have Neandertal-specific genes. Recent history of dramatic population expansions and local replacements beginning in the Neolithic strongly influences the distribution of surviving Neandertal nuclear genes all over the world of Africa. In the recent past the number of Neandertal genes in Europeans was higher than at present; for instance, about 10% of the DNA recovered from "Ötzi", the 5,300-year-old Copper age Tyrolean Iceman [29] is of Neandertal origin, compared to about

4% in living Europeans.

The fact of Neandertal interbreeding with some of the ancestors of East Asians is also incontrovertible. Some of this intermixture quite likely happened in Western Asia at the beginning of the Late Pleistocene^[30], where analysis of the well-published fossil remains from Skhul and Tabun^[31,32] reveals a mixture of anatomical features^[33] from dispersing Africans and from local populations with both East Asian and European roots. From Western Asia there were continued dispersals to Europe and across the rest of Asia through the Middle and Late Pleistocene^[34]. Populations in Europe and China today have different frequencies of Neandertal-derived DNA sequences. Because most of them are quite rare, Hawks and Throckmorton argue^[35]: It is plausible that genetic drift has played a large role in differentiating these populations. ... this hypothesis predicts that the actual size of these Late Pleistocene populations was very small relative to contemporary populations within Africa, and compared to their descendants after 30,000 years ago(p. 345).

Therefore, the distribution of Neandertal-derived sequences indicates gene flow and also that population sizes in East Asia (and other peripheral regions) before 30,000 years ago were extremely small.

This was only one of many instances of gene flow from the center to the edges of the human range. Ancient populations of Asia also mixed with local Denisovans. The archaic Denisovans lived over an extraordinarily broad geographic and ecological range, from Siberia to tropical Asia^[36]. Their appearance in Asia was more recent than the populations carrying Neandertal genes, but older, in turn, than the most recent significant dispersals into the region.

These multiple dispersals and subsequent mixtures of East Asian ancestors with Neandertals and Denisovans describe the most recent part of a complex series of interactions that took place across Asia over a long time span^[37], combining gene dispersals that were mostly from the more heavily populated regions of Africa, with the more ancient East Asian populations who contributed some of the regionally predominant features that continued to recent or present times. It is a pattern that demonstrates while there were many cases of mixture and local replacements, *none of the dispersals resulted in complete replacement across Asia*. Thus Asia remains the best-documented example of multiregional evolution.

3 What does it mean to be modern?

The mixtures of human populations described above indicate that modernity in East Asia (and elsewhere) is not the result of a new human species replacing a more ancient one (or

ones). Because living populations do not uniquely descend from any single recent source, *modernity is not a single thing, or a single event*. It is therefore difficult to define. However, the fundamental common denominator underlying any meaning of modernity within our complex evolving lineage is that it describes all living human populations and their recent ancestors^[38,39]

The way we look at it is that there are anatomical, behavioral, and genetic facets of modernity, and that while related, they are not three aspects of the same thing. Each of these has different meanings that can best be understood by viewing them as processes evolving at different times in differing patterns. "Different", however, does not mean completely "independent". Both paleogenetics and a better understanding of modern genetic diversity, demonstrate how genetic, anatomical, and behavioral modernity are intricately related. They address three different aspects of humanity that are united in ways that are best expressed by the precept that *all recent and living humans are modern* and related to each other, to a large extent, through the demographic changes beginning in the Late Pleistocene and dramatically accelerating in the Neolithic.

Thus we describe modernity as a complex process which has observable manifestations in the anatomy, behavior, and genetics of recent and living humans. These aspects of modernity arose as different gradual^[40] processes over a long timespan. The past is quite different from the present, and modernity today is not a specific event but the current condition of an ongoing process of change. The process today is an evolutionary *pattern* of changes that differs from the older archaic patterns in both tempo and mode. In the modern pattern, there are increasingly rapid biological, genetic, and social changes within our worldwide, interconnected human species. These changes create three of the most unique aspects of humanity today and therefore of modernity: 1) ongoing, rapid, accelerating genetic evolution; 2) a significantly mixed ancestry for human populations^[41] associated with the absence of human races^[42] despite extensive geographic variation, because of the existence of widespread, exogamous, genetic ties between groups; and 3) the consequences of increased longevity^[43] in multigenerational relationships: grandparents, and the wider kinship/social systems that develop around them^[44].

4 The three faces of modernity in East Asia

4.1 The three faces of modernity East Asia: anatomical

Anatomical modernity has always been difficult to define^[45]; this is because modernity is a process that took place in many regions across the world, and is not the result of the dispersal of modern people from Africa^[21] with a unique, defining "package" of features. Many of the

characteristics often said to be diagnostic of modern humans actually appear independently, at different times and not always first in Africa. East Asia is generally *not* at the late end of a process wherein modernity spreads. Quite to the contrary, some widely dispersed modern features appear there first, for instance the maxillary notch^[46], present in facial remains from the Lower Cave Zhoukoudian. Most elements of a true chin appear together at just about the same time in China, the Levant, and South Africa, as described below.

The earliest *fossils* recognized as "modern" from regions away from Africa, as we noted above, are neither particularly similar to Africans in appearance, nor particularly modern in the sense of being similar to people living today^[47]. Early expressions of anatomical modernity vary by region, a result of global trends coupled with regional variations, and a consequence of mixture. Genetic evidence demonstrates that Africa plays an important role in this process as the center of the human range with the highest Pleistocene population numbers, but the process of modernity was long-term and complex, and involved the mixture of African populations with those from other regions, mixtures of extra-African populations with each other, and significant changes in selection. For instance, from Europe to East Asia, regions furthest from Africa, modern human populations are on average more gracile, with crania smaller, thinner, and more rounded than their Late Pleistocene predecessors from the same regions. One might assume this gracility to be a consequence of genetic influences from Africa, spread by dispersing gracile Africans. But it is not evident that dispersing Africans themselves were especially small or gracile.

In East Asia, human remains from the later part of the Middle Pleistocene are not anatomically modern, in that specimens like them are not found among recent or living populations from the region, and yet they share some features with penecontemporary specimens from other areas of the world that differ from earlier "*Homo erectus*" remains. These features include more globular crania with a rounding of the posterior portion of the skull, expanded frontal breadth and occipital plane elongation associated with a reduced nuchal torus and the separation of opisthocranion from its midpoint. Nevertheless, the Middle Pleistocene East Asian crania are long and relatively low with prominent supraorbital tori. Dali^[48] (Shaanxi Province) and Jinniushan^[49] (Liaoning Province) are the two best-preserved of these crania, and there is a partial skeleton associated with Jinniushan with evidence of a relatively large pelvis supporting a broad, barrel-shaped trunk similar to both Neandertals and to earlier Middle Pleistocene specimens such as the pelvic remains from Sima de los Huesos in Sierra de Atapuerca^[50]. Some of the facial features are regionally predominant throughout the Pleistocene, with characteristics as reported above.

We begin with the continuation of the regionally predominant features from pre-modern East Asians of the early Late Pleistocene as a demonstration that later arriving Africans alone cannot have been unique ancestors of early modern East Asians. Maba (Guandong Province)^[53] and Xujiayao (Shanxi Province) are early Late Pleistocene East Asians from northern China with larger crania than their Middle Pleistocene predecessors. The Xujiayao remains are incomplete and fragmentary; vault fragments are quite thick, in some cases thicker than Zhoukoudian specimens and always within their range. The parietals suggest low but curved vaults with prominent temporal lines but lacking angular tori or sagittal keels. The two partial occipitals are much less angled than the earlier specimens, with rounded posteriors, weak nuchal tori, and extrasutural bones at lambda. A mandibular ramus is short and broad, and the juvenile maxilla holds a shovel-shaped incisor with strong marginal ridges bordering



Fig.1 The most complete early modern crania from different regions

"Modern" is not the same as "African". Herto^[51] is the earliest complete near-modern human cranium from Africa, and Jebel Irhoud 1, almost as complete, is somewhat later. These crania, to the far left, have African features that might be expected to disperse if modernity was an African change. They are shown here with the (later dated) earliest complete or almost-complete modern crania from (left to right) Europe (Pestera cu Oase 2^[52]), East Asia (Liujiang)^[65], and Australia (Kow Swamp 1 and Keilor). These are the earliest specimens with sufficient preservation to reflect facial anatomy without the bias that often comes with reconstruction. The anatomical features of Herto and Jebel Irhoud 1 are not compelling as exclusive anatomical sources for the shared modern features in the other specimens. It is difficult to demonstrate that populations represented by Herto and Jebel Irhoud are *uniquely* ancestral to the later remains, but it is also difficult to disprove the broader hypothesis that they are among their ancestors. The broader hypothesis is supported by paleogenetics.

a flattened crown with a basal tubercle. It is less prognathic than its Zhoukoudian or Jinniushan counterparts.

Maba is a partial calotte with upper face with distinct laterally thinning supraorbital tori projecting from the frontal squama and arching over rounded orbits in a manner reminiscent of earlier East Asian crania. The upper face is very flat across, the orbits and cheek below are anterior-facing and (like Dali) the nasal bones are narrow compared with the broad interorbital area and meet at the midline in a narrow ridge. The nasal suture with the frontal is flattened, on the same horizontal plane as the adjoining suture between maxillary and frontal bones. The forehead has an enlarged frontal boss, which bulges centrally very much like the Zhoukoudian foreheads. A weak sagittal keel begins at its center. Maba has vault bone thinning comparable to Jinniushan, smaller central and lateral supraorbital heights, and a somewhat higher nasal angle, beginning somewhat inferior to the top of the nose.

The earliest specimen with unarguably modern human anatomy is the Zhirendong (Guangxi Zhuang Autonomous Region) mandible^[54]. The Zhiren cave layer with human remains, including a mandible with a chin, is of late Middle or earlier Late Pleistocene age, stratigraphically higher U-series dates indicate a minimum age of ~100 kyr, the same age or somewhat older than the Klasies River Mouth mandibular sample from South Africa, which it resembles where features can be compared. The Zhiren 3 mandible has a distinct triangular trigonum mentale projecting slightly from a vertical symphyseal surface whose angulation "is above those of all Middle and Late Pleistocene archaic humans, slightly above those of the sub-Saharan African and Middle Paleolithic modern human samples, and exceeded only by the interquartile range of the earlier Upper Paleolithic sample" (ref. 54, p. 19202). Above the eminence there is a concave *incurvatio mandibulae* and a crest extends along the midline of the anterior symphysis from the superior aspect of the mental trigone. This crest and the trigone below are bordered by distinct incisura mandibulae anterior. In all, this anatomy describes a thoroughly modern chin^[55]. In most respects the Zhiren 3 mandible resembles mandibles within the Klasies River Mouth sample^[56]. The Klasies mandibles have a significant range of symphyseal height, angulation, and chin development, and Zhiren 3 fits within it. Zhiren 3 is quite similar in size and symphysis verticality to one of the smaller specimens, KRM 14695, but its trigonum is more distinctly developed, similar in its anatomy to KRM 21776, with which it also shares a crest extending from the apex of its trigonum along the sagittal plane to between the I1 sockets. Insofar as it also fits within the range of variation, the Zhiren mandible also resembles mandibles from Skhul^[31], of slightly younger age, in that it fits within their anatomical range.

Younger Late Pleistocene cranial remains preserving diagnostic modern Asian characteristics come from Southeast Asia (including Indonesia) and continental East Asia. In Southeast

Asia the recently discovered ~50 kyr Laotian specimen Tam Pa Ling has cranial features such as the distinct superciliary arches and a rounded sagittal contour with parietal bossing which are the normal conditions for many recent crania, but are unlike Late Pleistocene East Asian crania such as Maba and Xujiayao. Maxillary incisors^[57] are shoveled in the Asian manner that persists throughout the Pleistocene, with marginal ridges bordering a straight crown face^[18]. As seen from above, the upper facial contour as defined by the superior orbital margins is flattened.

Moh Khiew^[58] from Thailand is a much more recent (~26 kyr) adult female burial including much of a cranium and mandible, with all teeth represented. Systematic dental and osteological comparisons are provided and a "close affinity to the Shandingdong female (103), among other things, is suggested. These affinities are not unique and close phenetic affinity is also shown with the Coobool Creek (Australia) female sample. The authors conclude: "it was a member of a population of Sundaland dwellers during the Late Pleistocene, who may share common ancestry with the present-day Australian Aborigines and Melanesians".

The human remains from Wajak, discovered in the late 19th century, have been well described^[59] but are of uncertain age. The cranial remains show what have often been described as a mixture of East Asian and Australian characteristics. Both cranial specimens lack a supraorbital torus, and only Wajak 2 has any expression of a lateral torus. These features, the shape and slope of the Wajak 1 forehead and the broad interorbital area are similar to Shandingdong 101 and the flatness across the nasal bones resembles Liujiang. The late Alan Thorne often presented Wajak 1 as an anatomical link between Liujiang from East Asia and Keilor from Australia, and writing together, Wolpoff, Wu, and Thorne [60] concluded (p. 440): "while they resemble the Australian populations in a number of features, we concur that the Wajak remains seem to reflect the effects of gene-flow from the north." Now, direct U-series dating of human bone fragments from Wajak 2 and 3 bracket the remains between 37 and 28 kyr^[61], and from our perspective Wajak represents the southern-most extent of East Asian characteristics in the later Pleistocene. Apart from demonstrating the range for East Asian features, it does not seem that these Late Pleistocene remains from Southeast Asia specifically or especially address East Asian evolution. Their importance lies in understanding Late Pleistocene population dynamics in the region more broadly, stretching from Sundaland to Sahul.

In continental East Asia, the earliest of the early modern crania from the Late Pleistocene are from Laibin (Chilinshan), Laishui, Liujiang, Shandingdong, and Ziyang^[62,63]. These crania are modern in that they are recent, have anatomical features that are not unusual for recent and living humans, and to some extent resemble recent or living East Asians. But

not all of the dates associated with these crania are certain, some are basically unknown because of uncertain stratigraphic contexts. The Ziyang (Sichuan Province) provenience is unclear and while Liujiang, Guangxi Province, is reported to have an early date, in fact it has been variously dated to ~20, 67, 111, 139, or >153 kyr^[64], and the association of the dates with the skeleton is uncertain^[65]. This is unfortunate since it is the most complete cranium of this group and there are postcranial remains as well. It is possible that the cranium and postcranial remains fell or were thrown into a fissure that opened into older deposits in the cave, in a manner that is similar to what has been suggested for Jinniushan. The Liujiang cranium retains a number of specifically East Asian features, including the facial flatness, proportions and orientation of the nose, rounding of the lower outside borders of the orbits, and the weak shoveling of the lateral incisors.

A ~60 kyr male cranium with associated skeleton from Laishui^[78], Hebei Province, resembles Jinniushan in many ways, ranging from its projecting, continuously developed supraorbitals and sloping forehead and robust cranial vault, to its relatively large innominate and vertically thin superior pubic ramus. Differences, however, are found in the larger cranial size and the face, and Laishui is described as "robust but essentially modern"^[66]. There are "pinched" nasal bones (the bones meet at so closed an angle that they almost face laterally) that are elevated and form a strong nasal angle to the face, in a manner reflecting Maba and similar to Shandingdong 101 (see below).

Laibin (Chilinshan^[62], Kwangsi Province) is dated to 39-44 kyr^[67]. It consists of a cranial base and partial face. The lower nasal border of this specimen from South China is quite wide and the palate is deep, broad and short. Alveolar prognathism is moderate. The zygomatic bones are rather flattened and are positioned forward; the orbital process is nearly horizontal and is at close to a right angle with the anterior face of the bone. Contrasting with Liujiang, there are weakly expressed canine fossae. The lower nasal border is sharp. The nuchal region is well-developed and the occiput is robust, with central nuchal torus development and a distinct external occipital protuberance, that, with other features, suggest it is male.

Somewhat later, Shandingdong (Zhoukoudian Upper Cave, Beijing District) with an AMS radiocarbon date^[68] of 24-29 kyr, is the most recent^[69] of the samples we will discuss. When Weidenreich first wrote^[70] on the Shandingdong crania, he was addressing what was then a key question about racial origins, whether there once were pure races in the Pleistocene that subsequently mixed to form today's hybridized populations. He took the Shandingdong specimens as proof that there never were, reasoning that if races had been "pure" in the past, and mixed with each other more and more over time until achieving their present state in which no pure races are left, we would expect that the variation in a past sample

should be less than today's, as there was less intermixture in the past. But he interpreted the comparative anatomy of the Shandingdong crania to show, if anything, more variation, suggesting that just within the three Shandingdong crania ancestors of Chinese, Eskimos, and Melanesians could all be found. Similar interpretations were that the crania were ancestors of Native Americans^[71,72], or just "generalized "Mongoloids" broadly ancestral to Asian and American populations ^[73,74].

One common conclusion found in all of these older studies is that the Shandingdong crania are likely ancestral to populations in both eastern Asia the Americans, but are not the same as the living populations of these regions^[75]. Weidenreich^[70] himself made this point quite clearly; questioning Shandingdong's specifically Chinese affinities. It was his contention that the three Shandingdong crania "show certain common features of an Asian sort, but typify "three different racial elements, best to be classified as primitive Mongoloid, Melanesoid and Eskimoid". In particular, he wrote "... recent North Chinese may be considered as more advanced types, but traceable to ancestors like those represented by the Upper Cave man".

Separating Shandingdong and living or recent populations is some 30 thousand years of evolution that we now recognize includes the most rapid evolutionary changes in all human history^[27]. Little wonder then, that various multivariate analyses^[76] fail to show the crania specifically cluster with modern crania from Asia; the crania from Shandingdong are *not from modern Asian populations*, they are *ancestors of them*^[77].

While anatomically modern, and related to recent/living populations, the anatomy of these Late Pleistocene Southeast and East Asians is *not* particularly like either penecontemporary or older Africans such as Jebel Irhoud, or Hero (Figure 1). Every one of these Late Pleistocene East Asian crania preserves features that have been regionally predominant in East Asia throughout the Pleistocene^[78-80], demonstrating that some of their ancestry was local. Moreover, many of the crania also retain archaic elements that were more common broadly across Eurasia earlier in time.

Yes, beginning at about 100 kyr there is a "gap" in the fossil record of some 40 kyr or a bit more without diagnostic cranial remains, with modern human populations appearing afterwards, as Jin and Su^[81] asserted. But the absence of evidence is not evidence of absence, and now, more than a decade later, there are human remains within the "gap" they identified. While not diagnostic, teeth discovered at Huanglong Cave^[82] (Hubei Province) are associated with archaeological material and dated to a narrow range of 101-81 kyr by U-series^[83]. In any event, it is not the presence of a gap in the fossil record that could demonstrate a discontinuity in populations; the necessary evidence would have to come from the comparison of the earlier and later populations. In this case the comparison of cranial remains shows that there are common features, earlier and later, that are regionally

predominant in East Asians, and as a group, predominant nowhere else. Moreover, the "gap" as it exists now, is *within* the fossil sample identified as "early modern human", not between early modern humans and an older taxon.

Examining the resultant pattern of Pleistocene evolution in East Asia, what is perhaps most interesting is how *unlike* accretion it is. Accretion^[84] is the theory that groups of Pleistocene hominids^[85] evolved in partial or complete genetic isolation from the rest of humanity through the gradual accumulation of distinctive morphological traits because of successive founder effects. As these traits became more common, they also became less variable according to this hypothesis. Genetic drift is proposed to have caused this evolution, resulting from an initial small population size at the time of first dispersal and either complete isolation or drastic reduction in gene flow between this deme and contemporary human populations elsewhere.

East Asia provides anatomical evidence of a very different process. Regionally predominant features persist through the Pleistocene and into the Holocene, while anatomical modernity increases in intensity and frequency through time, because natural selection, not drift, plays the predominant role as the agent of evolutionary change, as is normally the case^[86].

4.2 The three faces of modernity East Asia: behavioral

Behavioral modernity has proved to be difficult to define partially because of the hope to identify the *potential* for modern behavior (cognitive and symbolic) from archaeological remains. Many archaeologists have argued that behavioral modernity (this human potential) can be recognized by evidence of behaviors similar to living and recent hunter/gatherers^[87]. But without a replacement theory explaining evidence of modernity by the arrival of a new species, and linking behavioral and anatomical modernity together, we contend that behavioral modernity can most accurately be described as an ongoing process rather than a discrete "modern" package of new behavioral potentials that appeared together. We take behavioral modernity to mean the range of behavioral potentials that can be found in recent and living populations, as reflected in their culture and society, and *we expect that their expression differed from place to place*.

For historical reasons, including the early excavations of many European sites, behavioral modernity has been equated with the rapid transition from the Middle to the Upper Paleolithic in Europe^[88], or at least the European Upper Paleolithic has been used to model it. But we question whether it is reasonable to describe behavioral modernity everywhere this way. In the last decade, numerous archaeological discoveries have undermined the idea of a uniquely European "human revolution"^[89] and questioned whether a Eurocentric approach is appropriate outside of Europe. The key fact is that aspects of behavioral modernity that

include archaeological materials interpreted as evidence of human social and cognitive capacity appear outside of Europe, in several Middle Stone Age contexts in both Africa^[90,91] and at scattered Middle Paleolithic sites across Eurasia, where they do not take the form of a revolutionary "package"^[92].

In East Asia, modern behaviors are not evidenced the same way as in Europe^[93]. Divisions of Stone Age industries into a Lower, Middle, and Upper Paleolithic as in the west, or Early, Middle, and Late Stone Age as in Africa, or the description of technological changes as Mode 1, 2, and 3^[94], are not really possible^[95]. Blade technology similar to what serves as a marker for the European Upper Paleolithic is only known from penecontemporary sites in western-most China in Shuidonggou (Ningxia)^[96], Mongolia, eastern Siberia^[97], and the eastern sub-region of Jilin Province^[98]. But at the same time in northern and Central China there are mostly continuations of much older core and flake dominated assemblages, in some areas with the addition of bone tools and evidences of body decorations^[99]. Microblades subsequently spread into South China, where core choppers made from river pebbles or nodules had earlier predominated. Later changes in northern China involve the addition of hafted microblades to these assemblages, in many cases associated with flat grindstones similar to those associated with starches at Holocene sites^[100].

North and South China are also genetically different^[101], and as we discuss below they have different genetic histories, at least as great as those between Northern and Southern Europe if not more so. Cleary, the pattern and details of changes in both the genetics and the archaeological assemblages across eastern Asia are quite different than in Europe, although in both cases populations with modern anatomy are present well before the end of the Late Pleistocene. This is an unsurprising demonstration of a fact that is well known from studying humans today; there is no necessary association between human anatomy and human cultures. Different assemblages or different cultures, whether seen in the past or present, are not the behavioral markers of different human species^[102]. They cannot be treated the way (for instance) differences in gorilla and chimpanzee behaviors are treated. Obviously there are no genes for these assemblages, and the stone tools don't breed!

Yet, it is our assessment that modern behavior in East Asia, and in all regions, however it is expressed, may have similar causation in the expanding population sizes of the late Pleistocene driven by improvements in adult survivorship^[43]. While adult survivorship was very low for much of the Plio-Pleistocene, increasing gradually but slowly in the Early and Middle Pleistocene, older adult ratios increased dramatically in the Late Pleistocene, especially after (more-or-less) 40,000 years ago; for the first time many adults lived to be older, old enough to become grandparents^[44]. This marks the onset of major demographic changes at a time of evidence for greater archaeological complexity^[103].

Increased adult survivorship generates population growth, the basis of the Late Pleistocene to current population expansions that are reflected in archaeological and genetic evidence. Not only does increased survivorship create the potential for greater lifetime fertility for individuals who are living longer, but the investment of older individuals in their children's families influences their inclusive fitness both by increasing the fertility of their children and the survivorship of their grandchildren^[104]. Thus, not only does increased adult survivorship lead to population growth, but population expansions have a multiplicative factor.

These demographic changes, including the increase in adult survivorship itself, directly influence behavioral complexity^[105]. Larger populations foster innovation and behavioral diversity. Older adults expand the possibilities for behavioral complexity by promoting the intergenerational accumulation and transfer of information and resources^[106] that allowed for intricate kinship systems and other social networks that are uniquely human. Multigenerational families have more (and more knowledgeable) members to teach and reteach important lessons^[107], repetition that is important in the transmission of cumulative cultural knowledge^[108] and its rapid accumulation in a ratchet-like process^[109].

Thus, like anatomical modernity, behavioral modernity can be seen as an ongoing process. The marked increase in the number of older adults reflects a shift to a modern life history pattern, one in which three-generation relationships are important, and one that results in the large-scale population expansions that underlie the pattern of genetic modernity and the successful adaptations of modern humans.

4.3 The three faces of modernity East Asia: genetic

Genetic modernity describes the genetic diversity of the living human species, including regional patterns of variation. The complex pattern of genetic variation in the human species today did not originate at a single time or in a single place to disperse as modernity spread^[110]. It is expressed differently from place to place; as the latest appearing of all aspects of human modernity, the time and pattern of its appearance are quite different from anatomical and behavioral modernity. This is because modern genetic diversity is a consequence of the recent dramatic acceleration of genetic change, mostly postdating the end of the Pleistocene^[8, 27].

Paleogenetics and a better understanding of the origin of modern genetic diversity have created a rather different idea of genetic modernity, and further demonstrate that the concepts of anatomical, behavioral, and genetic modernity address three different aspects of humanity related through demographic changes and united in the precept that all recent and living humans are modern^[21].

Simply put, genetic modernity in East Asia (and elsewhere) is the consequence of the large

number of genetic changes that came with the exponential population expansions of the Neolithic, as human populations began to control their food resources through domestication and agriculture. With more people there were more mutations, and with them "the Neolithic and later periods would have experienced a rate of adaptive evolution >100 times higher than characterized most of human evolution" (ref. 8, pp. 20756-20757). Many recently evolved genes shared by modern populations come from these changes; domestication and agriculture were probably far more important for this process than the genetic changes thought to come from "modern human origins".

East Asian populations today are descendants of these demographic expansions, with their genetic consequences, that covered over what once may have been a wider diversity of peoples. If nothing else, the distribution of Denisovan genes shows this. Their distribution is widespread across Asia, but

"Aboriginal Australians, Near Oceanians, Polynesians, Fijians, east Indonesians, and Mamanwa (a "Negrito" group from the Philippines) have all inherited genetic material from Denisovans, but mainland East Asians, western Indonesians, Jehai (a Negrito group from Malaysia), and Onge (a Negrito group from the Andaman Islands) have not (ref. 37, p. 516).

The most parsimonious explanation for this pattern is that peoples with higher numbers of Denisovan genes were once widespread across Asia^[24], and the mainland populations^[111] with the smallest number of Denisovan genes today were either more recent immigrants to the region, or the populations that most recently numerically dominated it (or both), creating the mixtures that underlie the modern pattern of genetic diversity.

What comes before genetic modernity in East Asia?

Genetic evidence suggests that ~50–35 kya modern humans, who carried a small percentage of Neanderthal genes, were already living or arriving in East Asia. Thus, as in western Asia, where Middle Paleolithic assemblages were made by different morphotypes of humans (archaic modern humans and local Neanderthals), the human biological variability in East Asia could be even more complex (ref 95, p. 327).

The only ancient nDNA known for the region is from the Tianyaun Cave, Beijing District. Tianyaun is among the latest of the early modern sites discuss here, with an estimated age of 42-39 kyr^[112]. Tianyaun 1 is a partial adult skeleton (lacking cranium)^[113] of a skeletally robust, anatomically modern individual. In discussing the Tianyaun 1 mandible, Shang and colleagues note the specimen: "exhibits several features that place it close to the late archaic humans (represented primarily by the Neandertals) or between them and early modern *Homo sapiens*, corresponding to what is known from the nDNA of the specimen^[114]. DNA analysis reveals the unsurprising conclusion that the Tianyaun specimen was related to present day

Asians, including Native Americans, but already diverged from the ancestors' of modern Europeans. That reflects the phylogenetic relationships^[115] of at least some East Asian genotypes, but what of their phenetic relationships? Was Tianyaun genetically modern, in the sense of being similar enough to be included in any specific modern population? The answer is probably not. The specimen revealed no more Neandertal or Denisovan ancestry than present day people from East Asia do, but it lacks recently evolved genetic variation, and markers of the populations that later predominated the region, mixing with earlier inhabitants. This provides an estimate of the antiquity for admixture between the Denisovans and the ancestors of modern Asians^[115].

What genetic evidence does unequivocally show is that while all of us have significant African ancestry, the mixture of Africans with other populations was quite significant and Africans alone cannot be the unique and only ancestors of all. Because of his mixed ancestry President Obama once described himself as "a mutt". The legacy of modern human origins studies is the recognition that we all are mutts.

5 Conclusions: the origin of modern East Asians

The recognition that all across the inhabited world, modernity describes recent and living humans and is not a product of phylogeny (the appearance of a new, modern human species) permits a more nuanced view of what it means to be a modern human. Modernity has anatomical, behavioral, and genetic aspects that are consequences of biological, social, and genetic changes, linked by accelerating demographic transformations that have come to distinguish living and recent humans. Emerging from a changing life history pattern characterized by increased adult survivorship, modernity is an ongoing process, a pattern of human evolution that both reflects historic variation and gene flow, and the dispersals of newly adaptive genes under selection.

In a truly multiregional manner these continue to appear at different places and in different times and modernity has no single origin. Modern human origins in East Asia reflect this worldwide pattern but are unique because East Asia is unique. Distinctive details of the history and habitation of East Asia include its past population and the adaptations imposed on it by the cyclic ice ages, the pattern of gene flow into and within the region, and the genetic contributions of ancient humans. Regionally predominant anatomical features have as long a history in the Pleistocene of East Asia as, regionally predominant features have in any other region of the world, and evolutionary changes shared throughout the world occurred in East Asia no later than in other regions. Yet, the most significant evolutionary event in East Asia was not in the Pleistocene but in the Holocene; again as in other regions

of the world, this was the control of food resources through domestication and agriculture, with strong and significant effects on anatomical, behavioral, and genetic modernity that are still unfolding.

All human populations today are equally modern. In terms of their modernity, East Asian populations arrive at the same "finish line" of modernity as other populations across the world do, and at the same time. There is no mystery about how this can be. It is because the "finish line" is not found in the appearance of a phylogenetic entity, or a "kind" of human being, or one particular human potential; rather, modernity can be defined by the current stage of our shared journey and the processes that inform it.

It was not our origins that made us what we are, and it is not our genealogy that makes us unique. It was the steps taken along the way, along a multitude of interwoven paths from a beginning that, once cleared of taxonomic haze, we can hope to understand, to an end that is not yet in sight^[116].

References

- [1] Wolpoff MH, Thorne AG, et al. The case for sinking *Homo erectus*: 100 yeas of Pithecanthropus is enough![A]. In: Franzen JL ed. 100 Years of Pithecanthropus: The *Homo erectus* Problem. Courier Forschungsinstitut Senckenberg, 1994, 171: 341-361.
- [2] Wildman DE, Uddin M, et al. Implications of natural selection in shaping 99.4% nonsynonymous DNA identity between humans and chimpanzees: enlarging genus *Homo*[C]. Proceedings of the National Academy of Sciences USA, 2003, 100(12): 7181-7188.
- [3] We use "species" here in the sense of "evolutionary species," described by a line of descent, not a specific physical form. Evolutionary species are defined by their beginning at the time of speciation, their unique evolutionary pathway, and by their ending in extinction or speciation.
- [4] Kimbel WH, Johanson DC, Rak Y. Systematic assessment of a maxilla of Homo from Hadar, Ethiopia[J]. American Journal of Physical Anthropology, 1997, 103: 235-262.
- [5] Asfaw B, White T, Lovejoy O, et al. Australopithecus garhi: A new species of early hominid from Ethiopia[J]. Science, 1999, 284: 629-635.
- [6] Eller E, Hawks J, Relethford JH. Local extinction and recolonization, species effective population size, and modern human origins[J]. Human Biology, 2004, 76(5): 689-709.
- [7] Relethford JH. Genetics and the Search for Modern Human Origins[M]. New York: Wiley-Liss, 2001.
- [8] Hawks J, Wang ET, et al. Recent acceleration of human adaptive evolution[C]. Proceedings of the National Academy of Sciences USA, 2007, 104(52): 20753-20758.
- [9] Hawks J. Centre and edge: a foundational concept in human population dynamics. Before Farming (2011, in press).
- [10] Hawks J, Cochran G. Dynamics of adaptive introgression from archaic to modern humans[J]. PaleoAnthropology, 2006:101-115
- [11] Moore JH. Putting anthropology back together again: the ethnogenetic critique of cladistic theory[J]. American Anthropologist, 1994, 96(4): 925–948.
- [12] Wolpoff MH, Wu Xinzhi, Thorne AG. Modern Homo sapiens origins: a general theory of hominid evolution involving the fossil evidence from East Asia[A]. In: Smith FH, Spencer F eds. The Origins of Modern Humans: A World Survey of the Fossil Evidence. New York: Alan R. Liss, 1984, 411–483.
- [13] Hawks J, Wolpoff MH. The accretion model of Neandertal evolution[J]. Evolution, 2001, 55: 1474-1485.
- [14] Wolpoff MH. Multiregional Evolution: the fossil alternative to Eden[A]. In: Mellars P, Stringer CB. Eds. The Human Revolution: Behavioural and Biological Perspectives on the Origins of Modern Humans. Edinburgh: Edinburgh University Press, 1989, 62-108.
- [15] In the sense that complexity of descent differs descent from a single source, see Alves I, Šrámková Hanulová A, et al. Genomic

- data reveal a complex making of humans[J]. PLoS Genetics, 2012, 8: e1002837.
- [16] Dennell R, Petraglia MD. The dispersal of *Homo sapiens* across southern Asia: how early, how often, how complex?[J]. Quaternary Science Review, 2012, 47: 15-22.
- [17] Wu Xinzhi. Palaeoanthropological and molecular studies on the origin of modern humans in China: aspects of hominid evolution[J]. Transactions of the Royal Society of South Africa, 2005, 60(2): 115-119; Wu Xinzhi, Cui Yaming. On the origin of modern humans in China[J]. Before Farming, 2010/4, article 6: 1-6.
- [18] Crummett TL. The three dimensions of shovel-shaping[A]. In: Moggi-Cecchi J ed. Proceedings of the Ninth International Symposium on Dental Anthropology[C]. International Institute for the Study of Man. Florence: Angelo Pontecorboli Editore, 1995, 305-313
- [19] Wolpoff MH, Lee Sang-Hee. The African origin of recent humanity[A]. In: Reynolds SC, Gallagher A eds. African genesis: perspectives on hominin evolution. Cambridge Studies in Biological and Evolutionary Anthropology. Cambridge University Press, 2012, Chapter 18, 347-364.
- [20] Sjödin P, Sjöstrand AE, et al. Resequencing data provide no evidence for a human bottleneck in Africa during the penultimate glacial period[J]. Molecular Biology and Evolution, 2012, 29(7): 1851–1860.
- [21] Caspari R, Wolpoff MH. The process of modern human origins: the evolutionary and demographic changes giving rise to modern humans[J]. In: Smith FH, Ahern JCM eds. The Origins of Modern Humans: Biology Reconsidered. New York: Wiley-Liss, 2013, Chapter 11, 355-390.
- [22] No diagnostic skeletal remains of Denisovans have been found. But they were once widespread across Asia, with a larger range than any hominid group before recent humans36. The ancient skeletal groups that fit this distribution range from Dali in the North to Ngandong in the south; some have interpreted their nDNA relationships and histories to demonstrate Denisovans and Neandertals were two co-evolving lineages (Lalueza-Fox C, Gilbert MTP. Paleogenomics of archaic hominins. Current Biology, 2011, 21:R1002 R1009). If so, while there no human races (subspecies) today21, we contend Neandertals were a human race (Wolpoff MH. How Neandertals inform human variation[J]. American Journal of Physical Anthropology, 2009, 139(1):91-102) and the Denisovans, from what we know of their genetics, most probably could be interpreted as a human race as well.
- [23] Abi-Rached L, Jobin MJ, et al, The shaping of modern human immune systems by multiregional admixture with archaic humans[J]. Science, 2011, 334: 89-94.
- [24] Reich D, Green RE, et al. Genetic history of an archaic hominin group from Denisova Cave in Siberia[J]. Nature, 2010, 468(7327): 1053-1060.
- [25] Sánchez-Quinto F, Botigué LR, et al. North African populations carry the signature of admixture with Neandertals[J]. PLoS ONE, 2012, 7(10): e47765.
- [26] Mallick S, Schraiber JG, et al. A high-coverage genome sequence from an archaic Denisovan individual[J]. Science, 2012, 338: 222-226
- [27] Cochran G, Harpending HC. The 10,000 Year Explosion. How Civilization Accelerated Human Evolution[M]. New York: Basic Books, 2009.
- [28] Gignoux CR, Henn BM, Mountain JL. Rapid, global demographic expansions after the origins of agriculture[C]. Proceedings of the National Academy of Sciences USA, 2011,108: 6044-6049.
- [29] Keller A, Graefen A, et al. New insights into the Tyrolean Iceman's origin and phenotype as inferred by whole-genome sequencing[J]. Nature Communications, 2012, 3: 698.
- [30] Hodgson JA, Bergey CM, Disotell TR. Neandertal genome: the ins and outs of African genetic diversity[J]. Current Biology, 2010, 20(12): R517-R519.
- [31] McCown TD, Keith A. The Stone Age of Mount Carmel: The Fossil Human Remains from the Levalloiso-Mousterian[M]. Volume II. Oxford: Clarendon Press, 1939.
- [32] Kramer A, Crummett TL, Wolpoff MH. Out of Africa and into the Levant: Replacement or Admixture in Western Asia?[J]. Quaternary International, 2001, 75(1): 51-63.
- [33] Dobzhansky Th. On species and races of living and fossil man[J]. American Journal of Physical Anthropology, 1944, 2(3): 251-265.
- [34] Hershkovitz I, Smith P, et al. Middle Pleistocene dental remains from Qesem Cave (Israel)[J]. American Journal of Physical Anthropology, 2011,144: 575-592.
- [35] Hawks J, Throckmorton Z. The relevance of archaic genomes to modern human origins[A]. In: Smith FH, Ahern JCM eds. The Origins of Modern Humans: Biology Reconsidered. New York: Wiley-Liss, 2013, Chapter 10, 339-354.
- [36] Reich D, Patterson N, et al. Denisova admixture and the first modern human dispersals into Southeast Asia and Oceania[J]. American Journal of Human Genetics, 2011, 89: 516-528.

- [37] Rasmussen M, Guo X, et al. An Aboriginal Australian genome reveals separate human dispersals into Asia[J]. Science, 2011, 334:
- [38] Wolpoff MH. Describing anatomically modern *Homo sapiens*: A distinction without a definable difference[A]. In: Novotný VV, Mizerová A eds. Fossil man New Facts, New Ideas. Papers in Honor of Jan Jelínek's Life Anniversary. Anthropos (Brno), 1986, 23: 41-53; followed by Stringer CB. What makes a modern human. Nature, 2012, 485: 33-35.
- [39] Wolpoff MH, Caspari R. What does it mean to be modern?[A]. In: Clark GA, Willermet CM eds. Conceptual Issues in Modern Human Origins Research. New York: Aldine de Gruyter, 1997, 28-44, and combined bibliography on 437-492.
- [40] But not at a constant rate, the great majority of modern features appeared in the last 50,000 years, most of these in the last 10,000 years.
- [41] Eswaran V, Harpending H, Rogers AR. Genomics refutes an exclusively African origin of humans[J]. Journal of Human Evolution, 2005. 49:1-18.
- [42] Hunley KL, Healy ME, Long JC. The global pattern of gene identity variation reveals a history of long-range migrations, bottlenecks, and local mate exchange: Implications for biological race[J]. American Journal of Physical Anthropology, 2009, 139(1): 35-46.
- [43] Caspari R, Lee Sang-Hee. Older age becomes common late in human evolution[C]. Proceedings of the National Academy of Sciences USA, 2004,101: 10895-10900.
- [44] Caspari R. The evolution of grandparents[J]. Scientific American, 2011, 305(2): 44-49.
- [45] Schwartz JH, Tattersall I. Fossil evidence for the origin of Homo sapiens[J]. Yearbook of Physical Anthropology, 2010, 53: 94–121.
- [46] Pope GG. 1991 Evolution of the zygomaxillary region in the genus Homo, and its relevance to the origin of modern humans[J]. Journal of Human Evolution, 1991, 21(3):189-213.
- [47] Wolpoff MH, Hawks JD, et al. Modern human ancestry at the peripheries: A test of the replacement theory [J]. Science, 2001, 291: 293-297.
- [48] Wu Xinzhi, Athreya S. A description of the geological context, discrete traits, and linear morphometrics of the Middle Pleistocene hominin from Dali, Shaanxi Province, China[J]. American Journal of Physical Anthropology, 2013,150:141–157.
- [49] Lü Zuné. The Jinniushan hominid in anatomical, chronological, and cultural context[A]. In: Shen Chen, Keates SG eds. Current Research in Chinese Pleistocene Archaeology. Oxford: Archaeopress, 2003,127–136.
- [50] Rosenberg KR, Zuné Lü, Ruff CB. Body size, body proportions, and encephalization in a Middle Pleistocene archaic human from northern China[C]. Proceedings of the National Academy of Sciences USA, 2006,103(10):3552–3556.
- [51] White TD, Asfaw B, et al. Pleistocene Homo sapiens from Middle Awash, Ethiopia[J]. Nature, 2003, 423: 742-747.
- [52] Trinkaus E. Denisova cave, Peştera cu Oase, and human divergence in the Late Pleistocene[J]. PaleoAnthropology, 2010: 196-200.
- [53] Maba may be somewhat older. Neither a published uranium series Late Pleistocene age nor a Middle Pleistocene age of a flowstone can be clearly be associated with the specimen (Wu Xiu-Jie, Schepartz LA, et al. Antemortem trauma and survival in the late Middle Pleistocene human cranium from Maba, South China[C]. Proceedings of the National Academy of Sciences USA, 2011, 108 (49): 19558-19562.
- [54] Wu Liu, Jin Chang-Zhu, et al. Human remains from Zhirendong, South China, and modern human emergence in East Asia[C].
 Proceedings of the National Academy of Sciences USA, 2010,107(45): 19201-19206.
- [55] In the sense that the anatomy of the symphysis (anterior and posterior surfaces) is of a form that is commonly found in recent and living populations.
- [56] Lam YM, Pearson OM, Smith CM. Chin morphology and sexual dimorphism in the fossil hominid mandible sample from Klasies River Mouth[J]. American Journal of Physical Anthropology, 1996, 100(4): 545-557.
- [57] Demeter F, Shackelford LL, et al. Anatomically modern human in Southeast Asia (Laos) by 46 ka[C]. Proceedings of the National Academy of Sciences USA, 2012, 109(36): 14375-14380.
- [58] Matsumura H, Pookajornb S. A morphometric analysis of the Late Pleistocene human skeleton from the Moh Khiew Cave in Thailand[J]. Homo, 2005, 56: 93-118.
- [59] Dubois E. The Proto-Australian fossil man of Wadjak. Java. Koninklikje Akademie van Wetenschappen te Amsterdam B, 1922, 23:1013-1051; Jacob T. Some Problems Pertaining to the Racial History of the Indonesian Region. Utrecht: Drukkerij Neerlandia, 1967.
- [60] Wolpoff MH, Wu Xinzhi, Thorne AG. Modern Homo sapiens origins: a general theory of hominid evolution involving the fossil evidence from East Asia[A]. In: Smith FH, Spencer F eds. The Origins of Modern Humans: A World Survey of the Fossil Evidence. New York: Alan R. Liss. 1984. 411-483.
- [61] Storm P, Wood R, et al. U-series and radiocarbon analyses of human and faunal remains from Wajak, Indonesia[J]. Journal of Human Evolution, 2013, 64: 356-365.
- [62] Wu Xinzhi, Poirier FE. Human Evolution in China: A Metric Description of the Fossils and a Review of the Sites[M]. New York: Oxford University Press, 1995.
- [63] Kaifu Y, Fujita M. Fossil record of early modern humans in East Asia[J]. Quaternary International, 2012, 248: 2-11.
- [64] Keates SG. The chronology of Pleistocene modern humans in China, Korea, and Japan[J]. Radiocarbon, 2010, 52(2-3): 428-465.

- [65] Shen Guanjun, Wang Wei, et. al. U-Series dating of Liujiang hominid site in Guangxi, Southern China[J]. Journal of Human Evolution, 2002, 43(6): 817–829.
- [66] Etler D. Homo erectus in East Asia: Human ancestor or evolutionary dead-end?[J]. Athena Review, 2004, 4(1): 37-50
- [67] Shen Guanjun, Wang Wei, et al. Mass spectrometric U-series dating of Laibin hominid site in Guangxi, southern China[J]. Journal of Archaeological Science, 2007, 34(12):2109-2114.
- [68] Hedges REM, Housley RA, et al. Radiocarbon dates from the Oxford AMS system: Archaeometry Datelist 14[J]. Archaeometry, 1992, 34: 141–159.
- [69] The age of the site is not settled, It could easily be as young as Keilor. The Hedges et al. determination cited here68 is the oldest of the various estimates.
- [70] Weidenreich F. On the earliest representatives of modern mankind recovered on the soil of East Asia[J]. Peking Natural History Bulletin, 1939, 13: 161-174.
- [71] Neumann GG. The Upper cave skulls from Chou-Kou-Tien in the light of Paleo-Amerindian material (abstract)[J]. American Journal of Physical Anthropology, 1956, 14: 380.
- [72] Oschinsky L. The Most Ancient Eskimos[M]. Ottawa: Canadian Research Centre for Anthropology, University of Ottawa, 1964.
- [73] Coon CS. The Origin of Races[M]. New York: Knopf, 1962, 474-475.
- [74] Wu Xinzhi. Study on the Upper Cave man of Choukoutien[J]. Vertebrata PalAsiatica, 1961, 3: 202-211. (Wu's translation)
- [75] Wu Xinzhi. The origin and dispersal of anatomically modern humans in East and Southeast Asia[A]. In Akazawa T, Aoki K, Kimura T eds. The evolution and dispersal of modern humans in Asia. Tokyo: Hokusen-sha, 1992, 373-378.
- [76] Brown P. The first Mongoloids? Another look at Upper Cave 101, Liujiang and Minatogawa 1[J]. Acta Anthropologica Sinica, 1998,17:255–275; Kaminga J, Wright RVS. The Upper Cave at Zhoukoudian and the origins of the Mongoloids[J]. Journal of Human Evolution, 1988, 17(8): 739-767; Wright RVS. Correlation between cranial form and geography in *Homo sapiens*: A computer program for forensic and other applications[J]. Archaeology in Oceania, 1992, 27(3): 128-134; Van Vark GN, Dijkema J. Some notes on the origin of the Chinese people[J]. Zeitschrift für die Verleichende Forschung am Menschen, 1988, 39(3-4): 143-148.
- [77] a point made quite clearly by Hanihara in Hanihara T. Craniofacial continuity and discontinuity of Far Easterners in the Late Pleistocene and Holocene[J]. Journal of Human Evolution, 1994, 27(5): 417-441.
- [78] Etler DA. The fossil evidence for human evolution in Asia. Annual Review of Anthropology, 1996, 25: 275-301.
- [79] Pope GG. Replacement versus regional continuity models: the paleobehavioral and fossil evidence from East Asia[A]. In: Akazawa T, Aoki K, Kimura T eds. The Evolution and Dispersal of Modern Humans in Asia. Tokyo: Hokusen-sha, 1992, 3-14.
- [80] Weidenreich F. The skull of Sinanthropus pekinensis: A comparative study of a primitive hominid skull[J]. Palaeontologia Sinica, New Series D, Number 10 (whole series No. 127), 1943.
- [81] Jin Li, Su Bing. Natives or immigrants: modern human origin in East Asia[J]. Nature Reviews Genetics, 2000,1:126-133.
- [82] Liu Wu, Wu Xianzhu, et al. Huanglong cave: a Late Pleistocene human fossil site in Hubei province, China[J]. Quaternary International, 2010, 211: 29-41.
- [83] Shen Guanjun, Wu Xianzhu, et al. Mass spectrometric U-series dating of Huanglong Cave in Hubei Province, central China: Evidence for early presence of modern humans in eastern Asia[J]. Journal of Human Evolution, 2013 (in press).
- [84] Hublin J-J. Climatic changes, paleogeography, and the evolution of the Neandertals[A]. In: Akazawa T, Aoki K, Bar-Yosef O eds. Neandertals and Modern Humans in Western Asia. New York: Plenum, 1998, 295–310.
- [85] It was initially proposed to explain Neandertal evolution in Europe.
- [86] Thompson JN. Relentless Evolution[M]. Chicago: University of Chicago Press, 2013.
- [87] Wadley L. What is cultural modernity? A general view and a South African perspective from Rose Cottage Cave[J]. Cambridge Archaeological Journal, 2001,11(2):201–221.
- [88] Shea JJ. Homo sapiens is as Homo sapiens was. Behavioral variability versus "behavioral modernity" in Paleolithic archaeology[J]. Current Anthropology, 2011, 52(1): 1-35.
- [89] McBrearty S. Down with the revolution[A]. In: Mellars P, Boyle K, et al. eds. Rethinking the Human Revolution. Cambridge: McDonald Institute for Archaeological Research, 2007,133-151.
- [90] Henshilwood CS, Marean CW. The origin of modern human behaviour: critique of the models and their test implications[J]. Current Anthropology, 2003, 44: 627-665.
- [91] D'Errico F, Henshilwood CS, Nilssen P. An engraved bone fragment from 70,000- year-old Middle Stone Age levels at Blombos Cave, South Africa: implications for the origin of symbolism and language[J]. Antiquity, 2001, 75: 309-318.
- [92] Habgood PJ, Franklin NR. The revolution that didn't arrive: A review of Pleistocene Sahul[J]. Journal of Human Evolution, 2008, 55:187–222.

- [93] Norton CJ, Jin JJH. The evolution of modern human behavior in East Asia: current perspectives[J]. Evolutionary Anthropology, 2009, 18:247–260.
- [94] Foley R, Lahr MM. On stony ground: Lithic technology, human evolution, and the emergence of culture[J]. Evolutionary Anthropology, 2003, 12: 109-122.
- [95] Bar-Yosef O, Wang Y. Paleolithic archaeology in China[J]. Annual Review of Anthropology, 2012, 41:319–335.
- [96] Ningxia Kaogu Yanjiusuo. Shuidonggou: The Report of 1980 Excavation. Beijing: Science Press, 2003 (In Chinese).
- [97] Derevianko AP. The Upper Paleolithic in Africa and Eurasia and the Origin of Anatomically Modern Humans[J]. Novosibirsk: Institute of Archaeology and Ethnography Press, Russian Academy of Science, Siberian Branch, 2011
- [98] Chen QJ, Wang CX, et al. Palaeolithic artifacts from Shirengou site, Helong county, Yanbian city[J]. Acta Anthropologica Sinica, 2006, 25: 106–114.
- [99] Qu Tongli, Bar-Yosef O, et al. 2012. The Chinese Upper Paleolithic: geography, chronology, and techno-typology[J]. Journal of Archaeological Research, 2013, 21: 1-73
- [100] Liu Li, Ge Wei, et al. Plant exploitation of the last foragers at Shizitan in the Middle Yellow River Valley China: evidence from grinding stones[J]. Journal of Archaeological Science, 2011, 38: 3524–532.
- [101] Chu JY, Huang Wen, et. al. Genetic relationship of populations in China[C]. Proceedings of the National Academy of Sciences USA, 1998, 95(20):11763–11768,
- [102] Accepting archaeological assemblages or traditions as markers of different human taxa is an often-made assumption in studies of human evolution that, in our opinion, should never be assumed.
- [103] Zilhão J. The emergence of ornaments and art: an archaeological perspective on the origins of "behavioral modernity" [J]. Journal of Archaeological Research, 2007, 15(1): 1-54.
- [104] Hawkes K. Grandmothers and the evolution of human longevity[J]. American Journal of Human Biology, 2003, 15: 380-400,
- [105] Kaplan HS, Robson AJ. The emergence of humans: the co-evolution of intelligence and longevity with intergenerational transfer[C]. Proceedings of the National Academy of Sciences USA, 2002, 99: 10221-19226.
- [106] Lee RD. Rethinking the evolutionary theory of ageing: transfers, not births, shape senescence in social species[C]. Proceedings of the National Academy of Sciences USA, 2003, 100(16): 9637-9642.
- [107] Strimling P, Enquist M, Eriksson K. Repeated learning makes cultural evolution unique[C]. Proceedings of the National Academy of Sciences USA, 2009, 106: 13870-13874.
- [108] Hill K, Barton M, Hurtado AM. The emergence of human uniqueness: characters underlying behavioral modernity[J]. Evolutionary Anthropology, 2009, 18:187–200.
- [109] Tomasello M. The question of chimpanzee culture[A]. In: Wrangham R, McGrew W, et al. eds. Chimpanzee cultures. Cambridge MA: Harvard University Press, 1994.
- [110] Sjödin P, Sjöstrand AE, et al. Resequencing data provide no evidence for a human bottleneck in Africa during the penultimate glacial period[J]. Molecular Biology and Evolution, 2012, 29(7): 1851–1860.
- [111] Including populations once connected to the mainland when sea levels were lower, during the last Ice Age.
- [112] Shang Hong, Tong Haowen, et al. An early modern human from Tianyuan Cave, Zhoukoudian, China[C]. Proceedings of the National Academy of Sciences USA, 2007, 104: 6573–6578.
- [113] Shang H, Trinkaus E. The Early Modern Human from Tianyuan Cave, China[M]. College Station: Texas A&M University Press, 2010.
- [114] Fu Qiaomei, Meyer M, et al. DNA analysis of an early modern human from Tianyuan Cave, China[C]. Proceedings of the National Academy of Sciences USA, 2013, published ahead of print.
- [115] Skoglund P, Jakobsson M. Archaic human ancestry in East Asia[C]. Proceedings of the National Academy of Sciences USA, 2011,108(45): 18301-18306
- [116] Wolpoff MH. What do we mean by human and why does it matter?[J]. Evolutionary Anthropology, 1994, 3(4): 116-117.

东亚现代人的起源

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摘要:古遗传学过去十年的发展表明,现代人在全新物种——智人的出现过程中并没有一个系统发育学意义上的起源,因此,解剖学、行为学和遗传学方面的现代性并不是一个相同且单一事件的结果。本文研究了东亚解剖学、行为学和遗传学方面的证据,现代性在每个方面都可以被理解为多地区进化过程的一个片段,而不是一个整体。三个方面的现代性在某种程度上是相互独立的,而且各自都是在不同的时间发展出来,直到晚更新世的人口变化才使三者相互关联起来;人类存活率的提高和不断扩张改变了人类的进化行程。

关键词:亚洲:人类:进化:现代性

1 人类进化模式

人类支系在上新世末期起源于非洲。这一支系是指近期和现存人群的唯一祖先,已明显不同于其他南方古猿。有些学者不是根据解剖学上的定义,而是根据系统发育学的定义 [3] 认为,这个支系与人类物种——"智人" [1,2] 本身是同义的。根据哈达(Hadar)AL-666 号标本 [4],人类支系可能起源于 230 万年前;或者依据东非 Garhi 地区 [5] 南方古猿非洲种的首次出现时间,也许还要更早几十万年。其后在近 200 万年前,人类种群的数量开始增长,并在地域上向外扩张,但在更新世的大部分时间,人类总的数量还仍然很小,只有大约一百万或更少 [6]。

人属形成以后至最近的大部分时间里,一半甚至更多的人都生活在非洲^[7],其余则不均匀地分布在旧大陆的居住地。因为大部分人类居住在非洲,所以人属内的大多数基因流是从非洲流向欧亚大陆的边缘人群。人口数量的增长在整个更新世都很缓慢,在新石器时代前不久才出现明显地加速,并且在人类学着掌控他们的食物源^[8]以及普遍了解了农业、畜牧业之后,加速度更加提高。人口规模的加速增长持续至今,在不同的地区有着不同的速率。人口规模与分布开始出现了显著的区别,非洲不再是世界上人口最多的地区。像东亚等世界上土地肥沃和动物资源更为丰富的地区,人口变得很稠密,直到今天还仍有着最高数量和最高密度。

从多地区进化的观点来看,人类在更新世初期就随着人口规模的增加而进化,开始 从非洲扩散到欧亚大陆的热带和亚热带地区。随着扩散、扩张和迁移,人类就形成了整个 世界的居住网络。这种进化模式由人类群落最初的及持续发生的地理扩散构成^[9]。人群之 间通过基因流和迁移保持着持续的联系,允许了有选择的适应基因和行为随着更多存活下

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来的子孙后代扩散到整个人类的生存区域,确保了人类进化趋势的普遍性和人类基因扩散 到世界的每个角落。值得说明的是,适应性基因和行为的分布是不均匀的,有些人群在长 时间与外界隔离。这些人群的基因在重新与外界建立联系时能够被识别出来,因为它们是 比重建人群基因更为古老的分散基因。这种现象成为"基因渗入(introgression)^[10]", 证明人类在过去曾经存在有亚种。

人群,实际上每一个人以及他们的多个祖先和多个后代在智人阶段的大多数时间里 都存在于这个网络即种族遗传模式之中[11]。每一个人群都是独一无二的,因为他们都有 自己的历史和适应过程, 但是每一个人群也是人类网络中的一部分, 通过基因流动和人群 迁移彼此关联。

多地区进化理论主张人类进化过程是一个由人群形成的动态网络的模型,这个理论 是由北京中国科学院古脊椎动物与古人类研究所的吴新智教授、堪培拉澳大利亚国立大学 的 Alan Thorne 博士和我们密歇根大学的 Milford Wolpoff 博士于 1984 年首次明确提出的[12]。 多地区进化模式的关键是自然选择下的全球性进化变化,这种自然选择是由语言、智力、 技术等使我们成为现代人的适应性基因[13]的扩散所形成的。每一个重要的元素都开始于 不同的地区,结束时却全都无处不在,现代性就是我们今天的样子。有几项证据指示现代 性的模式是基于上述进化改变形成的,而不是人群或物种的大规模替代,因为在世界的各 个地区,特别是边缘地带,世界上不同地区的区域性主导特征具有持续性,这种"区域连 续性"[14]证明替代并未发生过,因为替代会抹去更早的特征。另外,目前遗传数据证实 在不同地区的古老人群之间以及古老人群与现代人群之间存在着基因交流,支持早期解剖 学观察所得出的结论。因此,人属历史上发生的全球性变化源自基因通过人群网络的扩散, 同时还受到选择以及不连续广泛传播的人群或物种替代的作用。

2 东亚地区复杂的现代人起源

多地区进化的理论首次得以详细地解释是由于东亚地区有关人类进化方面的化石证 据的发现[12]。东亚地区的化石记录表明当地现代人的起源是一个复杂的过程[15]。现代东 亚人的起源并非如曾经所想,始于侵入性物种对早期原始人类的取代。在东亚地区,地区 主导性特征在中更新世和晚更新世的连续性表明,近现代东亚人群不可能仅是入侵性非洲 人种的后裔。他们的祖先既包括非洲人,又包括在不同时期进入东亚南部和北部的其他人 群以及更早的东亚人。考古学记录也指示了这样的格局,即有许多扩散进入东亚的事件, 而这些扩散并不总是来自同一个地方[16]。很多关键性的解剖学特征有助于这种复杂的东 亚人类起源和进化观点的建立,包括在东亚人类的时间跨度内一直存在的地区主导性特征, 为更早的东亚人是这个复杂祖先中的一部分提供了证据。现在,根据吴新智等人的观点[17], 我们认识到东亚地区长期存在很多占主导的区域性特征,比如(但不限于)共同存在的面 部特征,例如:

- 1) 额骨与上颌骨、鼻骨之间的骨缝成一条大致水平的弧线:
- 2) 颧骨额蝶突的前外侧面比较朝向前方:
- 3) 鼻根扁平:

- 4) 眼眶略成长方形且其下外侧边缘圆钝;
- 5) 鼻梁侧面接近垂直(至少是鼻梁的上部);
- 6) 梨状孔与眼眶之间的骨面平或稍凹:
- 7) 上颌骨颧突与颧骨上颌突下缘合成曲线:
- 8) 铲形门齿(中国更新世所有的23个上门齿化石均为铲形), 其特征在于顶面平, 边缘嵴发达^[18]。

存在于东亚人种中主要的占主导的区域性面部特征对于确定各地的现代人具有重要的意义。如果现代人作为一种近期形成的,具有独特的现代解剖特征、行为模式以及遗传特点的新物种,就能很容易将他们识别出来,因为所有这些因素都会被绑定在一起作为其专属特征,所以当它首次出现并展现其独特属性时,我们便能轻易地识别出这个新物种。

解剖变异和遗传分析却显示一个复杂得多的进化格局。非洲人在所有的人类进化中扮演着重要的角色,但并非是唯一祖先的角色^[19]。并且,非洲人并非现代性的唯一承载者。虽然非洲人群的扩张在现代性的进化中有高度的影响,但是被认定为最早现代人的非洲人类化石标本并不特别的"现代",相反的,在非洲以外地区发现的被认定为早期现代人的人类化石标本与近期的或现今生活在非洲的人群相比也并没有特别的相似。例如,Skhul遗址^[31],虽然有很多有关 Skhul 男性的现代性和这个地点不同标本间相似性的讨论,例如 Skhul 4,Skhul 5 和 Skhul 男性的现代性和这个地点不同标本间相似性的讨论,例如 Skhul 4,Skhul 5 和 Skhul 9,但是他们都没有被广义地识别为非洲人。保存不完好的女性标本,例如 Skhul 2,引起了关于其现代性的问题,因为她表现出的混合特征与任何地方的近代或现存的女性的特征都并不一致。这些特征包括异常大的眶间距,以及相当粗壮并贯穿整个前额、明显突出于额鳞的眶上隆凸,这样就在眶上隆突上方和下方形成了一个深深的、显著的眶上沟。来自于旧大陆最早的早期现代人标本与非洲人并非特别相像^[21],此时也没有非洲人瓶颈的遗传证据^[20]。

在过去的几十年,从对保存于化石中古老基因进行的古遗传学研究中可以明显地发现,各地的现代人类都有一个复杂的血统^[21]。数量众多且典型的尼安德特人、丹尼索瓦人^[22]与新兴于非洲的人群之间杂交的事实解释了这种复杂血统的形成原因^[23-26]。正如前文提到的,这是一种种族遗传模式。

现今的亚洲和欧洲人类都具有尼安德特人独有的基因。始于新石器时代^[27]的大型人口扩张与当地人口替代的全新世历史强烈地影响着非洲以外地区保存下来的尼安德特人的核基因分布情况^[28]。在不久的过去,尼安德特人在欧洲人群中的基因数量比现在高,例如,与现代欧洲人携带有 4% 的尼安德特基因的情况不同,从 5300 年前铜器时代的提洛尔冰人 "Ötzi"^[29] 中复原出的 DNA 中,约 10% 属于尼安德特人。

尼安德特人与一些东亚人的祖先发生过杂交是毋庸置疑的。一部分这样的杂交很有可能于晚更新世早期发生于西亚地区^[30]。根据已详细研究并发表的分析,在这个地区发现的 Skhul 和 Tabun^[31,32] 化石遗存表现出一种混合的解剖学特征^[33],其来源既包含出自非洲的人口,又有同时具有东亚和欧洲的血统的当地居民。从中更新世到晚更新世,西亚人继续扩散至欧洲和亚洲的其他地区^[34]。现在的欧洲人和中国人有着不同程度的源自尼安德特人的 DNA 序列。大部分序列很罕见,所以 Hawks 和 Throckmorton 认为,"遗传飘变在这些人群的分化过程中起到重要的作用的说法是可信的……这个假说预测了这些晚更新世人群的实际规模与同时期的非洲人群及其三万年后的后代相比非常小"^[35](P.345)。

源自尼安德特人序列的分布指示了基因流动的存在以及东亚(和其他周边地区)的人口规模在三万年前非常小。

这只是众多人类基因流从中心到边缘的例证中的一个。亚洲的古代居民也曾经与当地丹尼索瓦人之间发生杂交。古老的丹尼索瓦人曾经居住在从西伯利亚到亚洲的热带地区,一个极为广阔的地域与生态范围^[36]。他们在亚洲的出现晚于携带着尼安德特基因的人类,早于最近显著扩散进入这一区域的人群。

亚洲祖先与尼安德特人和丹尼索瓦人的多次扩散以及随后之间杂交展现了一系列复杂的相互作用的最近部分,跨越了整个亚洲,经历了很长时间^[37],大多源自非洲人口稠密地区的基因与具有区域性、主导性、持续性特征的更加古老的东亚人群之间的基因结合。这种模式证明了大量杂交和取代发生的同时,基因扩散并未导致亚洲的古代当地人类被完全取代。亚洲仍然是具有最完善记录的多地区进化实例。

3 现代的意义是什么?

上述东亚人群(以及其他地区)的混合并不是新的人群替代了更古老的人群的结果。现存人群并不仅来源于任何单个近期起源,现代性不是一个单独的事情或单独的事件,因此很难对其下定义。在我们复杂的进化支系内,任何现代性意义之下的基本而共同的涵义是,它是对所有活着的人群及其最近的祖先的描述^[38,39]。

我们这样看待现代性,现代性表现于解剖学、行为学和遗传学方面,它们并不是同一事件的三个方面,尽管它们相互关联。每一方面有不同的意义,其最好的理解方式是将它们视为在不同事件和不同模式中发展的过程。"不同"并不完全意味着"独立"。古遗传学和对现代遗传多样性更深入的认识向我们展示,遗传学、解剖学和行为学现代性的概念是如何以错综复杂的方式相关联的。它们分别涉及到人性的三个不同方面,这三个方面被一个共同的准则联合在一起。这个准则最好的解释是,所有近代和现存的人类都是现代的,并在很大的程度上是相互关联的。这些关联从晚更新世开始,建立在新石器时代急剧加速的人口变化的基础上。

我们将现代性描述为一个复杂的过程,在近期的和活着的人类身上可以观察到这个过程的解剖学,行为学和遗传学方面的表现。这些方面现代性是在一个长的时间内随着不同而逐渐的过程而产生^[40]。过去与现在是非常不同的。今天的现代性不是一个特定的事件,而是一个正在进行的处于变化过程中的状态,这个过程是一个在节奏和模式上不同于古代的进化样式。在现代的进化样式中,世界范围内互相联系的人类经历着迅速的生物性、遗传性和社会性变化。这些变化造就了现代人性,乃至现代性的三个最独特的方面: 1)正在发生的、快速的且仍在加速的遗传学进化; 2)人类群体显著的混合祖先,与人种无关^[37],尽管存在很大的地理差异,但是在不同族群中存在广泛的、异族通婚的遗传学联系; 3)延长的寿命在多世代关系中产生的结果 ^[38]:祖父母和以他们为中心发展起来的更广泛的亲缘关系和社会系统 ^[39]。

4 东亚现代性的三个方面

4.1 解剖学的现代性

解剖学现代性一直非常难以定义^[45],这是因为现代性是一个过程,它发生在全世界的多个地区,并不是简单的从非洲来的、具有一系列独特的、标志性特征的现代人的扩散所导致的^[21]。事实上,很多被认为是现代人的标志性特征会在不同的时间独立出现,而且并不总是最早出现在非洲。东亚在现代性传播的过程中基本上不位于最末端。正相反,一些广泛分布的现代特征在东亚最早出现,例如上颌切迹^[46],在周口店下洞中发现的面部遗存中存在。真正下颌颏的大多数证据在中国,拉凡特和南非几乎同时出现,这一点在下文中还将提到。

最早被认定为"现代"的化石,发现于远离非洲的地方,其特点既不特别与非洲人相似,也不特别与现生人群有相似感的现代人相似^[47]。早期解剖学上现代性的表现在不同地区之间存在差异,这是全球趋势与地区特色结合,以及人群混合的结果。遗传学证据表明非洲在这一过程中扮演了重要角色,它是人类活动范围的中心,在更新世的时候人口数量也是最多的。但是现代性是一个长期的、复杂的进程,包括非洲人与其他来源的人种的混合,非洲以外地区的人群之间的相互混合以及自然选择下产生的显著变化。举例来说,从欧洲到离非洲最远的东亚,现代人与他们来自相同地区的晚更新世祖先相比,总体来说要更为纤弱一些,头盖骨更小、更圆。很容易假设这种纤弱是从非洲向外扩散的纤细非洲人所带来的遗传影响,但是并没有证据表明从非洲扩散的非洲人本身是特别小或者纤弱的。

在东亚,中更新世晚期的人类遗存并不是解剖学上现代的人,标本上的特征不能在当地近期或现生的人群中找到,但他们却与来自世界其他地区的、更早的直立人不同的准同时期标本具有一些相同的特征。这些特征包括更加趋于球形的脑颅、头骨后部圆隆、额骨更宽、枕平面更长,还有两个与后者有联系的特征,即项圆枕缩小和颅后点与项圆枕分开。尽管如此,东亚中更新世的颅骨长而相对低矮,眶上隆突明显。陕西大荔人和辽宁金牛山人是保存最完好的这样两个颅骨,与金牛山人颅骨相关联的还有一件颅后骨骼,是一件较大的骨盆,证明其躯干宽大,呈桶形,与尼安德特人和更早的中更新世标本相似,例如 Sierra de Atapuerca 的 Sima de los Huesos 地点发现的骨盆遗存。某些整个更新世在地区占主导的面部特征也表现出上述情况。

我们从东亚晚更新世早期的前现代人表现出的地区主导性特征的连续性开始说起,来证明后来来到东亚的非洲人不可能是东亚早期现代人的唯一祖先。广东马坝人^[53] 和山西许家窑人是发现自华北的东亚晚更新世早期的早期现代人,他们具有比他们的中更新世祖先更大的脑颅。许家窑人遗存不完整而且破碎,穹窿碎片很厚,有些比周口店的标本还要厚,并总是落在周口店标本的变异范围内。这些顶骨暗示了许家窑人具有低矮而弯曲的穹窿以及突出的颞线,但缺少角隆突和正中矢状脊。两件部分枕骨与更早的标本相比具有更加圆隆的后部,微弱的项圆枕,人字点处有缝间骨。一件短而宽的下颌支,在属于少年的上颌骨上附有一颗扁平齿冠,两边有着强烈边缘脊以及基结节的铲形门齿。其突颌程度比其周口店和金牛山的标本小。

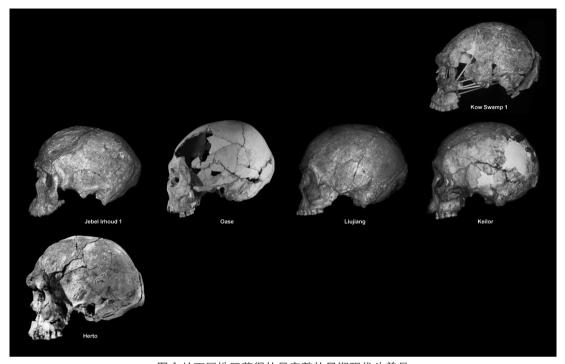


图 1 从不同地区获得的最完整的早期现代头盖骨 Fig.1 The most complete early modern crania from different regions

"现代"并不与"非洲"完全相同。Herto^[51] 是来自非洲的最早的完整近现代人类头盖骨,而 Jebel Irhoud 1,几乎同样完整,年代要稍微晚些。这些在最左边的头盖骨,具有非洲特征,如果现代性意味着所有标本都变得与非洲标本相似,这些特征应该会扩散到其他标本上。它们在这儿与来自欧洲的(Pesteta cu oase 2^[52])、东亚的(柳江)、和澳大利亚的(Kow Swamp 1 和 Keilor) 最早的完整或接近完整的现代头盖骨一起展示(从左到右)。这些是最早的具有足够面部保存的样本,反映了面部解剖学特征,没有经常存在的由重建带来的误导。Herto 和 Jebel Irhoud 1 的解剖学特征作为其他样本中的共同的现代特征的解剖学来源是并不令人信服的。很难证明 Herto 和 Jebel Irhoud 所代表的人群是否是较晚人类遗存的唯一祖先,但是同样难以证份的是一个更广泛的假说:他们与他们的祖先同时存在。这个更广泛的假说得到了古遗传学的支持。

马坝标本是一件不完整的头盖骨,上面部的眶上隆突两侧明显变薄,从额鳞突出并随着眼眶轮廓弯曲,令人想起更早的东亚颅骨形态。上面部横向非常扁平,眼眶和其下的颊骨朝向下方。与大荔一样,鼻骨相对于宽阔的眶间区域较窄,并在中线上的一个窄脊上相交。鼻额缝平坦,与相邻的额颌缝位于同一个水平面上。前额有一个增大的额骨隆突,在中心突起,与周口店标本的前额很相似。一个微弱的正中矢状脊从它的中心开始。马坝与金牛山标本相比,其穹窿骨较薄,中部和两侧的眶上高较小,以及从鼻骨顶点稍下开始的鼻角稍高。

广西智人洞下颌骨是一件最早的、带有无可辩驳的现代人解剖特征的标本。智人洞有人类遗存的层位形成于中更新世晚期或晚更新世早期,出产了带有下颌颏的下颌骨 [54],其上方地层的铀系测年结果指示其最小年龄为约 10 万年,这个年代与在南非克拉济斯河口发现的具有可与其相比特征的下颌骨的年代相同或稍早。智人洞 3 号下颌骨有明显的三角形颏三角,从正中联合的垂直表面处轻微突出,下颌联合"形成的角度比所有中更新世和晚更新世的古老人类标本都大,比撒哈拉以南非洲的和旧石器时代中期的现代人标本稍

大,并超过了较早的旧石器时代晚期的标本变化的四分间距" (ref. 54, p.19202)。在这个突出的下方有一个下凹的下颌切迹,一个脊从颏三角上方开始沿着正中联合的前中线延伸。这个脊和下方颏三角下方的界限处有一个明显的位于前方的下颌切迹。总的来说,这个解剖特征描述了一个彻底的现代的下颌 [55]。在大多数方面,智人洞 3 号下颌骨与克拉济斯河口的标本相似 [56]。克拉济斯河口的下颌骨正中联合高度和角度以及颏隆凸的发育程度具有相当大的变异范围,智人洞 3 号也在其范围内。智人洞 3 号下颌骨在大小与正中联合的垂直程度上与一个更小的标本 KRM 14695 相似,但它的颏三角更加发达;在解剖特征上与 KRM 21776 更相似,它们具有相似的从颏三角顶点沿着正中矢状面延伸至 I1 牙槽的脊。如果将落在变异范围内的情况也考虑在内的话,智人洞下颌骨也与稍年轻的 Skhul^[31]下颌骨相似,智人洞标本落在其变异范围内。

年代较晚的保存有现代亚洲标志性特征的晚更新世颅骨遗存发现于东南亚(包括印度尼西亚)和东亚。最近,在东南亚老挝 Tam Pa Ling 发现的距今约 5 万年的标本具有明显的眉弓和顶骨隆起的圆隆矢状轮廓的颅骨特征,这些特征是很多现代颅骨的正常情况,但却与东亚晚更新世颅骨,如马坝和许家窑并不相似。它的上颌门齿呈铲形^[57],这在亚洲是贯穿整个更新世的特征,平直的牙冠面两侧界限处有边缘脊^[18]。如上文所述,以眼眶上缘确定的面部轮廓上部是平扁的。

在泰国 Moh Khiew 发现的人类化石是一个年代更晚的成年女性遗存(约 2.6 万年),包括颅骨的大部分和带有全部牙齿的下颌骨^[58]。经过详细的牙齿和骨骼比较,结果显示它"与山顶洞女性(103 号标本)具有亲缘关系"。这些相似性不是单一的,该标本同样显示出与 Coobool Creek(澳大利亚)女性标本相似的表型。研究者的结论是,"它是晚更新世巽他大陆上人群中的一员,可能与今天的澳大利亚土著和美拉尼西亚人有着共同的祖先"。

Wajak 的人类遗存发现于 19 世纪晚期,已经过详细的描述 ^[59],但年代不确定。颅骨遗存的特征常被描述为东亚和澳大利亚混合性状。两个颅骨标本都缺少眶上圆枕,而且仅有 Wajak 2 有外侧圆枕。Wajak 1 前额的形状和倾斜程度以及宽阔的眶间区域这些特征,与山顶洞 101 标本相似,鼻骨横向扁平与柳江标本相似。Alan Thorne 经常将 Wajak 1 当为东亚的柳江人和澳大利亚的 Keilor 人之间的解剖联系,并同 Wolpoff 与吴新智院士一起撰文,Throne ^[60] 总结道,"它们与澳大利亚人群在很多特征上相似,我们一致认为 Wajak 遗存似乎反映了来自北方基因流的效应"。现在对 Wajak 2 和 3 的人类骨骼碎片进行的直接铀系测年结果,将这些遗存的年代框定在了 2.8-3.7 万年之间 ^[61];在我们看来,Wajak 代表了晚更新世特征在东亚最南端的变化程度。除了证明东亚特征的范围,这些晚更新世东南亚遗存似乎没有对东亚的人类进化作出特别的贡献。其重要性在于帮助我们更广泛地理解晚更新世时,从巽他大陆到萨胡尔大陆的当地人口动态。

在东亚大陆,晚更新世最早的早期现代人颅骨发现于来宾,涞水,柳江,山顶洞和 资阳 ^[62,63]。这些颅骨是现代的,因为具有在近期和现在活着的人类中常见的解剖特征,在 某些程度上与近期和现在活着的人类相似。但与这些颅骨相关联的测年结果并不都是确定 的,有些由于不明确的地层背景,其年代基本上仍然未知。资阳人(四川省)的来源不确 定,而柳江人(广西省)的年代被报道为 2 万年,6.7 万年,11.1 万年,13.9 万年,或是 大于 15.3 万年 ^[64],这些年代与骨骼遗存的关系并不明确。这非常可惜,因为柳江头骨这

个组别中最完整的一个,并且也同时发现了颅后骨骼。颅骨和颅后骨骼遗存有可能落入或被扔进了洞中有更古老沉积物的裂缝中,就像金牛山标本所暗示的那样。柳江颅骨保持了很多东亚的特异性特征,包括扁平的上面部、鼻部的比例和朝向、眼眶下外缘呈圆形以及侧门齿微弱的铲形。

一个发现于河北省涞水距今约 6 万年,并与其他骨骼相关联的男性颅骨^[78],在很多方面与金牛山标本相似,从它前突而连续的发达眶上结构,以及倾斜的前额和粗壮的颅骨穹窿,到它较大的髋骨以及垂直而薄的耻骨上支。然而,不同点也同时存在于更大的颅骨大小和面部,涞水标本被描述为"粗壮但基本上现代"^[66]。夹紧的鼻梁骨(鼻骨距离非常近,以至于他们接近平行)与面部形成了明显的鼻骨角,反映了马坝的状况并且与山顶洞 101 相似(见下文)。

广西麒麟山来宾^[62]的年代是 3.9-4.4 万年^[67]。标本包括颅底和部分面部。这个中国南方标本的鼻下边界较宽,腭部深,宽而短。齿槽突颌水平中等。颧骨较扁平而且朝向前方,眶突接近水平,与颧骨前表面构成接近于直角的角度。与柳江标本不同,犬齿窝的发育较微弱。鼻下边界尖锐。项区发达而且枕部粗壮,中心项隆突发达,有明显的枕外隆突,与其他特征一起暗示这个标本是男性。

稍晚的北京山顶洞标本是我们将要讨论的年代最晚的标本^[69],AMS 放射性碳测年结果为 2.4-2.9 万年^[68]。当魏敦瑞第一次描述山顶洞颅骨^[70]时,他提到一个当时关键性的种族起源问题,即更新世时是否存在后来与其他种族融合而形成今天的杂交人群的纯种族。他用山顶洞标本作为证据来证明这样的种族从来没有存在过,并辩论道,如果过去的种族是纯的,后来随着时间越来越多地相互混合,直到达到他们现在的状态(没有留下纯的种族),我们应该能够在过去的标本中看到比今天更少的变异,因为过去没有现在这么多的种族间融合。但是他将山顶洞颅骨的比较解剖特征来证明,作为中国人,爱斯基摩人和美拉尼西亚人祖先的山顶洞的三个颅骨标本显示出的内部变异却更大。与此相似的解读是这些颅骨是美洲原住民的的祖先^[71,72],或是亚洲和美洲人群广泛祖先的"广义蒙古人种"。

在这些较早的研究中一个常见的结论是山顶洞颅骨有可能是东亚和美洲人群的先人,但却并不是现在生活在这些地区的人群的祖先。魏敦瑞^[70]自己对关于山顶洞与中国人特别的亲缘关系这个问题说的很清楚。他的论点是三个山顶洞颅骨"表现出某些亚洲特征",但代表了"三个不同种族的元素,最好将他们归为原始蒙古人种、美拉尼西亚人和爱斯基摩人"。他还特别提到"……近期北方中国人可以被认为是一个高级的类型,但可以追溯到以山顶洞人为代表的祖先"。

将山顶洞人与近期或现在活着的人群区分开的是约三万年的进化,现在我们认识到 这段时间中包括了人类全部历史上最迅速的进化改变^[27],因此,各种多变量分析结果中 山顶洞颅骨都没有把亚洲现代人颅骨聚为一类也是不奇怪的,山顶洞的颅骨并非来自现代 亚洲人群,而是他们的祖先。

这些晚更新世东南亚和东亚人群具有现代的解剖结构,并与近期的或现在活着的人群相关联,他们的解剖特征与其准同时代的或更早的非洲人(如 Jebel Irhoud 或 Herto)不相似(图1)。每个这样的晚更新世东亚头骨都保存了整个更新世在东亚占主导的特征^[78-80],证明他们的一部分血统是来自本地的。此外,很多颅骨还保留了更早时在欧亚大陆常见的古老的元素。

从大约 10 万年前开始,化石记录中的确存在一个约四万年或更长的空白,正如金力和宿兵主张的那样,在这个空白中没有出现标志性的颅骨遗存,后来才出现现代人。但是没有证据并不等于在那段空白期间东亚大陆没有人类存在,而现在,十多年过去了,考古学家已经发现了这段空白中的人类遗存。在黄龙洞(湖北)发现的牙齿及与之相关的考古材料,年代被铀系测年法确定为 8.1-10.1 万年前 [83],但并没有表现出标志性的特征。无论如何,这个化石记录中的空白并不能证明东亚人口不连续;如果要证明这一点,证据必须从比这个空白更早的和更晚的人群的比较中得出。这样的比较显示,比这个空白更早或更晚的遗存具有共同的,在东亚占主导地位的特征,并且这些特征作为一个群体,在其他地方并不占主导地位。此外,现在存在的空白被归为早期现代人的化石标本内部,并不是早期现代人和更古老的分类单元之间的空白。

我们研究更新世东亚人类进化结果的格局,也许最有意思的是它与累积进化多么不相似。累积进化^[84] 是指更新世人类群体^[85] 在与其他地方的人类部分或完全的隔离中,随着逐渐明确的形态特征积累、通过建立者效应而进化的理论。根据假设,当这些特征变得更加常见,其多样性也会逐渐变小。遗传漂变被认为是这种进化的原因,是一个初始的人口较少的人群的第一次扩散的结果,遗传漂变或者导致完全隔离,或者导致与其他地区的同时代人类群体的基因交流剧烈减少。

东亚在一个非常不同的过程中提供了解剖学证据。区域性占主导的特征在更新世直 到全新世持续存在,然而解剖学上的现代性由于自然选择的作用,而非漂变,在表现程度 和出现频率上都扮演着进化变化中间人的主要角色,就像通常的情况那样^[86]。

4.2 行为学现代性

行为学现代性是难以定义的,一部分原因是我们希望从考古遗存中识别现代行为的可能性(认知上的和象征性的)。很多考古学家争辩行为学现代性(这种人类的潜能)可以从与现存的或近期的狩猎采集者的相似行为中识别^[87]。但并没有一个其他的理论可以解释新物种到来的现代性的证据,并将行为学和解剖学上的现代性联系起来,我们认为行为学现代性可以被准确的描述为一个持续的过程,而不是有一个特定的具有新的行为学可能性的"现代"整体。我们认为行为学现代性意味着近代或者现存的人群中能够反映他们文化和社会的行为可能性的范围,而且我们预期它们在各地的表达是不同的。

因为历史原因,包括许多欧洲地点的早期发掘,行为学现代性一直与欧洲的旧石器时代中期到晚期的迅速转变被划上等号^[88],或至少欧洲旧石器时代晚期一直被用作行为学现代性的模型。但是我们质疑用同样的方式去描述其他地方的行为学现代性的做法的合理性。在过去的几十年里,数量庞大的考古学发现削弱了仅见于欧洲"人类革命"的观点^[89],并且质疑以欧洲为中心的方式在欧洲以外是否也是合适的。一个关键的事实是行为学现代性的多个方面在欧洲以外出现的证据,包括可以被解读为与人类社交和认知能力有关的人类学材料,存在于数个中石器时代环境,即在非洲^[90,91],也在零星分布在欧亚大陆的中石器时代遗址,在这些遗址中的材料并没有采取革命性的"整体"的形式。

在东亚,现代行为留下证据的方式与欧洲不同^[93]。石器时代在欧洲被划分为旧石器时代早期、中期和晚期,在非洲被划分为石器时代早期、中期和晚期,或是根据技术变化的描述将其分为模式一、模式二和模式三的方式^[94],这在东亚不太可能^[95]。与作为欧洲旧石器时代晚期标志性工具相似的石片技术仅发现于中国最西边的准同时代地点宁夏水洞

沟 ^[96],蒙古、西伯利亚东部 ^[97] 以及吉林省的东部地区 ^[98]。但是与此同时,在中国的北部和中部有着基本连续的古老得多的以石核和石片占主导地位的石制品组合,在某些地区还有骨器和身体装饰的证据 ^[99]。在中国南部,以前占主导地位的是用鹅卵石或石结节制作的石核砍砸器,随后细石器传播到了这里。中国北方更晚的变化包括在原有的基础上增加了有柄细石叶,在很多情况下都与在全新世地点中与处理淀粉类食物有关的石器相似的扁平磨石相关联 ^[100]。

中国南方和北方在遗传上也是不同的^[101],下文将会讨论他们具有不同的遗传历史,他们之间的差异至少不比欧洲南部和北部之间的差异少。毫无疑问的,虽然这两地具有现代解剖特征的人群在晚更新世末期结束时都存在,但东亚存在的这种遗传和考古石制品组合上的变化的格局和细节与欧洲十分不同。这是对一个广为人知的现代人类研究结果的一个不太令人意外的证明:人类解剖结构和人类文化并不一定相关。不同的石制品组合或不同的文化,无论在过去或现在是否存在,都不是不同人类种族的行为标记^[102]。我们不能像对待比如大猩猩和黑猩猩之间的行为差异那样对待人类的不同文化,而且我们也清楚石器不会杂交!

然而,我们认为东亚的,事实上是所有地区的现代行为,无论它是如何表达的,可能有相似的原因,那就是晚更新世由成人生存率提高带来的人口规模增长^[43]。成人存活率在上新世至更新世的大部分时期内是非常低的,早更新世和中更新世逐渐缓慢地增长,在晚更新世老年成人的比例急剧增长,特别是 4 万年以后,历史上首次许多成年人可以活到成为爷爷奶奶的年纪^[44]。这标志着在一个考古学更复杂的时代的主要人口变化的开始^[103]。

成年人存活率的提高导致人口增长,这是晚更新世到现代人口的膨胀过程的基础,也为考古学和遗传学证据所证实。存活率的提高不仅仅导致那些活的更久的人具有更高的潜在生育率,而且老年个体对子女家庭的参与,提高了子女的生育率和孙儿女的存活率,从而提高了他们的健康水平^[59]。成年人存活率的提高导致人口增长,人口膨胀有一个倍增的因素。

这些人口学变化,包括成年人存活率本身的提升,影响了行为学的复杂性^[105]。更大的人口数量能够产生更多的创新和行为多样性。老年人通过促进知识和资源的代间积累^[106]和转移来孵育行为学多样性,其结果是形成了人类独有的复杂的亲戚系统和其他社交网络。多代家庭有更多的和更具有知识的家庭成员来教授或者重复教授重要的课程^[107],重复对于传递积累性的文化知识^[108]及其在一个棘齿轮¹⁾状过程中的迅速积累是极重要的^[109]。

这样,和解剖学现代性一样,行为学现代性可以被视为一个持续的过程。老年成人的显著增加标志着人类历史格局向现代生活的转变,在这个格局里,三个世代的关系是重要的,这个格局还导致了大规模的人口增长,也构成了遗传学现代性格局的基础,同样也是现代人的成功适应。

4.3 遗传学现代性

遗传学现代性描述了现存人类的遗传学多样性,包括变异的区域格局。人类物种今天遗传变异的复杂格局并非源自单一地点和单一时间,并随着现代性的传播而分散[110]。它在不同的地方有不同的表达方式。作为人类现代性中最晚出现的方面,它出现的时间和

¹⁾ 译者注: 棘齿轮, 一种带齿的轮子, 装有一个掣子, 用以防止轮子向回滑动, 而只允许向一个方向转动。

方式与解剖学和行为学上的现代性有很大不同。这是因为现代遗传变异是近期发生的遗传 学变化的急剧加速的结果,大多数发生在更新世结束之后^[8,27]。

"对古遗传学和对现代遗传变异起源更深刻的理解让我们对遗传学现代性有了不同的认识,并进一步证明了解剖学、行为学和遗传学上的现代性表达了人类的三个不同的方面,这三个方面通过人口变化相互关联,并在所有近期的和现在活着的人类都是现代人的事实中统一起来"^[21]。

简单地说,东亚(和其他地方)遗传学上的现代性是大量遗传变化的后果,这种遗传变化随着人类群体开始通过驯养动物和发展农业控制他们的食物来源导致新石器时代人口数量呈指数增加而带来的。人口越多,变异就越多,并且"新石器时代和更晚的阶段适应性进化的速率可能比人类进化大多数时间的 100 倍还要多。"很多最近产生的,在人类群体中共有的基因都来源于这种变化;驯养动物和农业对这个过程起到的作用可能比"现代人起源"带来的遗传变化重要得多。

今天的东亚人口就是这些人口扩张的后代,他们将同样的遗传变化,带到了也许曾被多样性更大的人群占据的地区。如果不谈其他,丹尼索瓦人基因的分布就说明了这一点。这些基因在亚洲广泛分布,但是"澳大利亚原住民,近大洋洲人,波利尼西亚人,东印度尼西亚人以及 Mamanwa 人(菲律宾的一个尼格利陀族群)都具有丹尼索瓦人的遗传物质,但在东亚,西印度尼西亚,Jehai(马来西亚的一个尼格利陀族群)和 Onge(阿曼达群岛上的一个尼格利陀族群)并没有。"

对这种格局最简单的解释是,具有更多丹尼索瓦人基因的人群曾经在亚洲广泛分布^[24],今天具有最少丹尼索瓦人基因的大陆人群^[111],要么是后来迁徙进入这个地区的移民,要么是在最近以数量优势占据了这个区域(或二者兼有),从而创造了人群混合,这是遗传学现代性现代格局的基础。

东亚的遗传学现代性出现之前是什么?

遗传证据显示携带着一小部分尼安德特基因的现代人类在距今大约 3.5-5 万年已经居住在或者到达东亚。这样,就像在西亚一样,旧石器时代中期的石制品组合是由属于不同形态型的人类(古老型现代人和当地尼安德特人)制造的,东亚人类的生物学多样性也许更加复杂 (ref 95, p. 327).。

这个地区唯一已知的古代核 DNA 来自北京地区的田园洞。田园洞是我们在这里讨论的最晚的早期现代人地点之一,年代估计为距今 4.2-3.9 万年 [112]。田园洞 1 号是一件部分成人骨骼(缺少头骨) [113],它的骨骼粗壮,是解剖学上现代的人。在讨论到田园洞 1 号下颌骨时,尚虹和同事注意到这件标本"显示出几项与晚期古老型人类(主要以尼安德特人为代表)相近,或是介于晚期古老型人类和早期现代智人之间的特征",这与来自这件标本的 nDNA 的结果相对应 [114]。 DNA 分析得到了一个并不让人震惊的结论,田园洞样本与包括美国土著人在内的今天的亚洲人相关联,但是已经与现代欧洲人的祖先分异。这反映了至少部分东亚基因型的系统发育 (phylogenetic)关系 [115],但是它们的表型关系呢?在足够相似可以被任何特定现代人群包括的意义上,田园人是否在遗传学上是现代的呢?答案很有可能是否定的。样本显示了不比今天的东亚人更多的尼安德特人或丹尼索瓦人祖先,但是它缺少近期形成的遗传变异,以及后来在当地占主导地位的人群与更早居民混合的遗传标记。这为估计丹尼索瓦人和现代东亚人祖先之间的混合的古老型提供了线索 [115]。

遗传证据能够明确显示的是尽管我们所有人都有显著的非洲血统,其他人群与非洲人的混合也是显著的^[41],非洲人自己不可能是所有人独特且唯一的祖先。因为他的混合祖先,奥巴马总统曾经描述他自己是"杂种狗"。现代人种起源研究的遗产就是意识到我们全部都是杂种狗。

5 结论:现代东亚人的起源

对于现代性描述的是,在人类居住的世界里近代和现存的人类,而不是对一个系统发育史(一种新的、现代的人种的出现)产物的认识,表达了一种关于现代人涵义更微妙的观点。现代性包含解剖学、行为学和遗传学的方面,这些侧面引发了生物、社会和遗传上的变化,并通过加速人口结构的转变相互关联,这种转变促成了近代的与现存人口的分化。现代性来自不断变化的、以增长的成年人生存率为标志的生活历史格局中,是一个持续的过程,反映了历史变异和基因流以及新适应基因在选择压力下扩散的人类进化样式。

上述这些过程在不同地点和不同时间点仍然以真正多地区的方式继续出现,现代性的起源并不是单一的。东亚现代人的起源可以反映整个世界的格局,但是却又是独特的,因为东亚是独特的。东亚的历史和人类在此居住的独特细节包括它过去的人群和循环冰期所强加在他们身上的适应,外源的和内源的基因流模式和古老型人类的基因贡献。地区占主导的解剖特征在更新世的东亚有着和其他地区主导性特征一样长的历史,而且全世界共有的进化改变发生在东亚的时间并不比其他地区晚。然而,东亚最显著的进化事件并非发生在更新世而是全新世;正如世界的其他地区,这是由于通过驯养动物和农业对食物资源的控制,对解剖学、行为学和遗传学上的现代性产生了强烈而显著的影响,这种影响现在仍在持续。

今天所有的人类群体都是现代的。根据他们的现代性,东亚人群与世界范围内的其他人群同时到达了同一个现代性"终点"。这并没有任何神秘之处。因为"终点"并不是系统发育实体的出现或是人类的一个"种类",也不是一种特别的人类潜能,相反地,现代性可以用我们共同经历的旅程的目前状态,以及表现出现代性的过程来定义。

并不是我们的起源造就了我们,也不是我们的谱系使我们特殊。而是在旅途中我们沿着从起点开始的大量交织的路线迈出的步伐,一旦我们清除了上分类学的迷雾,我们就有希望了解这个起点,并最终到达一个还没有在视野中出现的终点^[116]。

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