

# Homo erectus in East Asia: Human Ancestor or Evolutionary Dead-End?

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In order to better understand the nature of *Homo erectus*, the significance of its evolutionary history in East Asia, and the role it played in human evolution, it is first necessary to come to grips with what is meant by the term itself, as *H. erectus* has come to mean different things to different people. For some, *H. erectus* represents the first truly pandemic human species and the direct progenitor of archaic and modern *H. sapiens*. For others, *H. erectus* is an interesting footnote to the saga of human evolution, a distinct species that emerged in the East, only to go extinct without issue when modern humans expanded their range out of Africa to encompass the far reaches of the Old World. From this latter perspective *H. erectus* serves as the eastern analog of what is thought, by some, to be another failed experiment in humanity - the Neanderthals. The very manner in which *H. erectus* is conceived is thus held captive to two competing views of human

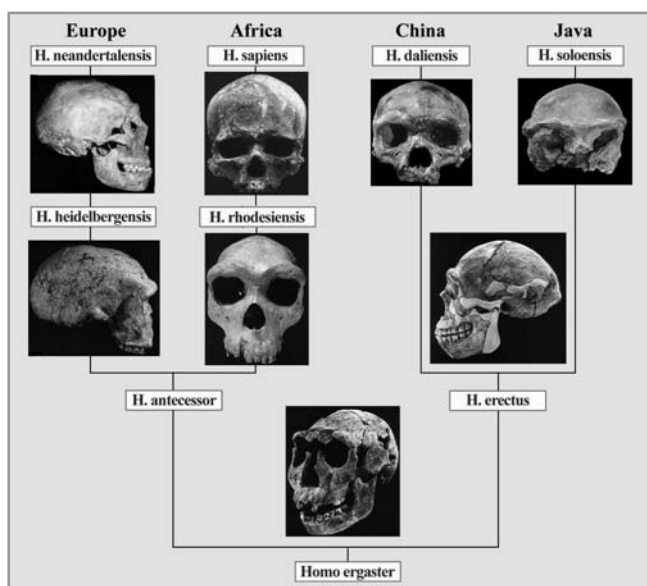
evolution, part of an intractable debate that continues to swirl over the origins of anatomically modern people.

Many readers are assuredly familiar with the contours of this debate, between those who advocate a recent, uniregional origin for modern *Homo sapiens* in Africa (henceforth termed the “recent out of Africa,” or ROA, hypothesis) versus those who support a more deeply rooted, multiregional origin for our species (termed MRE for “multiregional evolution”). The implications of these two differing interpretations of modern human origins for understanding the course of human evolution and the status of *H. erectus* during the last 1.8 million years of earth history are manifold.

One major premise of the uniregional ROA hypothesis is that modern humans originated in sub-Saharan Africa between 100-200,000 years ago by evolving a set of unique physical features and cultural innovations that allowed them to disperse throughout the world, replacing older, more archaic human lineages that had established themselves in various regional settings. Most advocates of this hypothesis view the genus *Homo* as subject to the same evolutionary processes of divergence and differentiation as any other biological entity. ROA supporters are thus prone to use cladistic analysis, which attempts to partition fossil specimens into distinct evolutionary lineages by documenting uniquely derived features (autapomorphies) that separate one from another (Harrison 1993; see box 1).

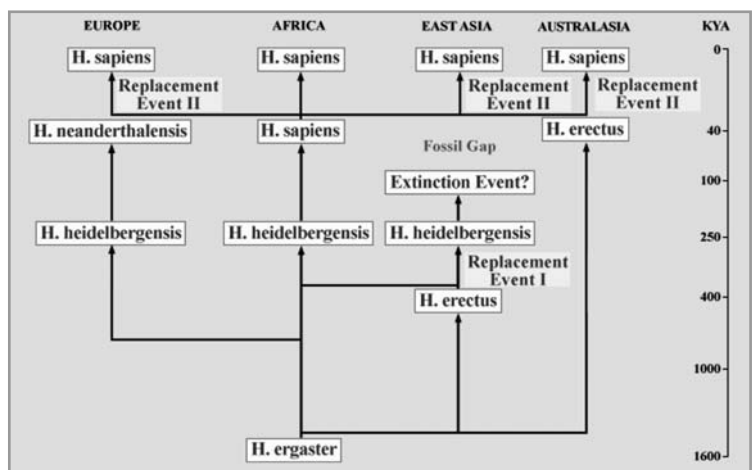
## Box 1: Pleistocene hominid phylogenies: multilinear and recent out of Africa theories

The phylogeny in figure 1 is consistent with Tattersall’s (1999) multilinear paradigm that envisions multiple species of *Homo* throughout the Pleistocene. In this rendition Asian descendants of *H. erectus* are viewed as possessing derived features that distinguish them from their common ancestor and each other. Post-erectine Chinese hominids (*H. daliensis*) are derived in having larger cranial capacities in association with changes in the structure of the braincase and cranial base. Australasian descendants of *H. erectus* (*H. soloensis*) likewise show significant increases in cranial capacity, but retain ancestral erectine-like features of the cranium (Swisher et al. 1997). The establishment of separate species to accommodate this diversity is in keeping with the multilinear interpretation of hominid phylogeny.



**Fig.1:** Proposed full extension of multilinear hominid phylogeny during the Pleistocene. The author presents this phylogeny as a logical extension of the multilinear paradigm, but does not subscribe to it.

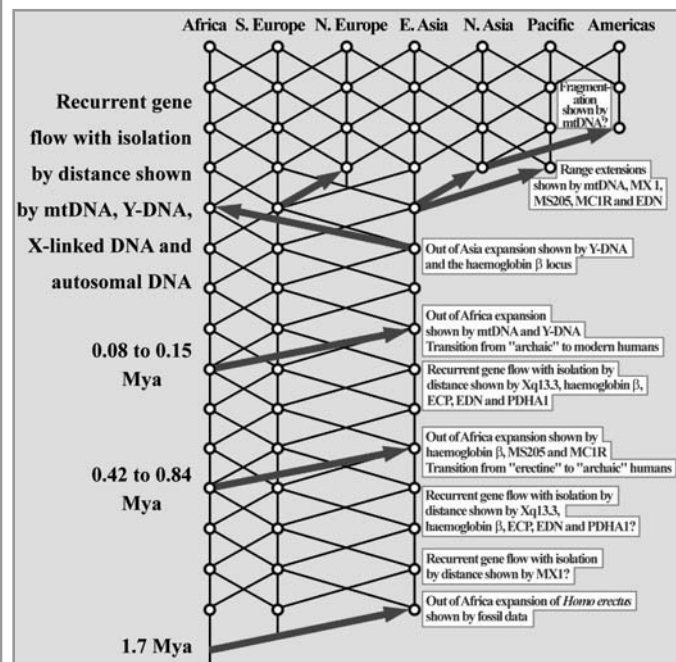
Figure 2 attempts to summarize current views of hominid phylogeny held by the majority of ROA advocates. In this scheme *H. ergaster* serves as the Last Common Ancestor (LCA) of all later Pleistocene hominids. It is now thought to have dispersed out of Africa to western Eurasia (Dmanisi, Georgia) as early as 1.8 mya (Gabunia et al. 2000, 2001). It is hypothesized that this eastern dispersal led to a speciation event with the establishment of *H. erectus* in East Asia (China) (Huang et al. 1995) and Australasia (Java) (Swisher et al. 1994). Further west *H. ergaster* is thought to have evolved into *H. heidelbergensis* in Europe and Africa, the European branch leading to the late Pleistocene Neanderthals (*H. neanderthalensis*) and the African branch to *H. sapiens*. Many proponents of ROA interpret post-erectine, pre-modern hominids of China as part of an eastern range expansion of *H. heidelbergensis* that led to cohabitation with, or the replacement of, *H. erectus*. A fossil gap between pre-modern and modern humans in East Asia is thought by some advocates of ROA to represent a true lacuna attributable to an extinction event that led to a depopulation of East Asia prior to the arrival of modern *H. sapiens* (Jin and Su 2000). *H. erectus* is thought to have survived in Australasia as a distinct taxon well into the late Pleistocene (Swisher et al. 1997).



**Fig.2:** Summation of Pleistocene hominid phylogeny as conceptualized by ROA. The author presents this as a logical interpretation of ROA, but disagrees with its basic premises.

**Box 2: Pleistocene hominid evolution according to MRE**

The diagram in figure 3, adapted from Templeton (2002), reflects the underlying premise of multi-regional evolution (MRE), that human evolution during the Pleistocene is characterized by discrete dispersal events intercalated with recurrent gene flow with isolation by distance.



**Fig.3:** Reticular interpretation of hominid evolution during the Pleistocene based on recent genetic research.

The two latest “out of Africa” dispersals may be associated with major transitions in the fossil record, from erectines to archaics and archaics to modern humans. The genetic signals of other dispersals may have been lost through selective sweeps associated with major transitions in the human fossil record. In this scheme human evolution (i.e. the evolution of the genus *Homo*) from the beginning of the Pleistocene on is characterized by one evolving lineage with no speciation.

Notwithstanding the pitfalls of identifying true autapomorphies (Nowaczewska 2000), the cladistic mindset has led some anthropologists to suggest that there was a proliferation of human species throughout the Pleistocene (see Tattersall 1999). In this cladogenetic, multilineal scheme there are ancestral species that occupy nodes of divergence, terminal species that represent the end products of lineages diverging from one another, and intermediate or transitional species that serve as links between the nodes and terminations. If the multilineal paradigm is strictly adhered to an elaborate genealogy of Pleistocene hominids can be created (fig.1). Most multilinealists, however, do not subscribe to as species rich a phylogeny as so depicted. A favored interpretation of Pleistocene hominid phylogeny for many multilinealists is presented in fig.2. No matter how many Pleistocene species of *Homo* are recognized, the crux of human evolutionary studies for multilinealists is to try to understand their defining features and in particular what factors led to the emergence of modern humans, *sui generis*, from their not quite fully formed forebears (see Foley and Lahr 1997).

As one may suspect, the opponents of the uniregional multilinealists are the multiregional unilinealists. Rather than seeing modern humans

as the result of a relatively recent, unique speciation event, the unilinealists see our species as the end product of a continuously evolving lineage that has been arbitrarily divided into time successive chronospecies, generally speaking *H. erectus* and *H. sapiens*. These species are seen as part of an evolutionary continuum so, as logic dictates, many proponents of MRE recognize but one species of human during the Pleistocene, i.e. the ever-evolving *H. sapiens*, of which we are the latest incarnation (Wolpoff et al. 1994a) (see box 2). Human evolution during the last 1.8 million years has hence been both anagenetic and incremental. For proponents of MRE, the task of human paleontology is to better understand the transitions that have catapulted early *H. sapiens* (i.e. *H. erectus*) from a marginal player on the world’s stage to our present role as producer and director of not only our own future but that of the world-at-large (Hawks and Wolpoff 2001a, 2001b).

**Refinements of ROA and MRE:** Although many ROA supporters reject the idea that there were meaningful interactions between archaic and modern humans subsequent to the latter’s extra-African dispersal, some of its advocates are more amenable to compromise regarding the role that regionally distributed archaic humans

played in the origins of modern people. From Bräuer’s standpoint, proponents of ROA can be sorted into two camps, those who support “hard” or “soft” replacement. The hard ROA position emphasizes the near total replacement of Eurasian and Australasian archaics by dispersing African moderns (Stringer 1984, 1988), while soft ROA (the Afro-European model of Bräuer, 1984, 1992, 2001) allows for varying degrees of gene flow and hybridization between various regional groups and advancing moderns, as well as the persistence of some regional traits across the archaic/modern boundary. This “hybridization and replacement” model, while more malleable than the “total replacement” model, nonetheless still emphasizes replacement versus *in situ* evolution, and unidirectional extra-African versus multidirectional pandemic dispersals, as the predominant mode by which the modern human phenotype spread throughout the world.

Although proponents of MRE continue to document regional continuity in Europe (Frayer 1993), Western Asia (Kramer et al. 2001), Eastern Asia (Wolpoff et al. 1984; Wolpoff 1985; Etlar and Li 1994; Etlar 1996), and Australasia (Hawks et al. 2000), its basic, underlying premise is that modern humans do not share an exclusively African origin. Instead, MRE contends that all human populations of the past made differential contributions to all populations of the present. In this context there is no need to assert that Pleistocene humans from different regions of the world were necessarily the lineal antecedents of their present day inhabitants. MRE does not deny the possibility that various local evolutionary histories, some entailing the replacement of one population by another, may have unfolded in different regions of the world at different times in the past. In this sense MRE is not necessarily contingent on regional continuity, i.e. the direct linkage of predecessor with successor populations, in any given region of the world, although this may well be the case. While the focus of MRE has generally been on regional continuity, a greater emphasis on the pandemic nature of the human species throughout the Pleistocene and the trans-regional timing of major transitions in the fossil record may better help elucidate factors that led to the emergence of modern humans.

**Debating the evidence:** Advocates of ROA and MRE have been very aggressive in challenging each other on a number of fronts, including genetics, phylogenetics, archaeology, and the

fossil record. The genetic evidence in favor of ROA rests primarily on studies of mitochondrial DNA (mtDNA) and the Y-chromosome. Advocates of ROA claim that these studies prove a late Middle Pleistocene to early Late Pleistocene exclusive African origin for all living people (Cann et al. 1987; Hammer 1995; Jin et al. 2000; Brookfield 2001; Harpending 2001; Jorde et al. 1998; 2000; Ke et al. 2001; Vigilant et al. 1991). Proponents of MRE, however, have countered with studies of autosomal genes of the nuclear genome, and the X-chromosome, that show evidence of deep population structure within our species that greatly predates the appearance of modern *H. sapiens* (Harding et al. 1997; Harris and Hey 1999).

Phylogenetic studies have been used by advocates of ROA to negate the reality of regional traits while attempting to validate the existence of derived, species defining features (autapomorphies) of Asian *H. erectus* (Andrews 1984; Bilsborough 2000). On the other hand advocates of MRE use similar studies to demonstrate regional continuity in Europe, Asia, and Australasia (Wolpoff et al. 1994b, 2001).

Certain aspects of the archaeological record have been cited by supporters of ROA to show a clear divide between the cognitive powers of archaics and moderns (Foley and Lahr 1997), while supporters of MRE have used other aspects of the archaeological record to demonstrate continuity between archaic and modern technology (Kramer et al. 2001).

Finally, the fossil evidence of human evolution during the Pleistocene has been used by partisans of ROA to show that the earliest record of modern humans is in Africa and the Levant to the exclusion of other regions (Stringer and Andrews 1988), while supporters of MRE use the human fossil record to demonstrate the transitional nature of pre-modern forms of *H. sapiens* in various regions of the Old World. Below an attempt is made to review some of these issues.

**Genetic evidence:** Over the last two decades the sequencing of various segments of the human genome has resulted in the accumulation of increasingly refined datasets relevant to deciphering the relationships of extant human populations to one another and to extrapolating human population histories (Harpending 2001; Harpending and Rogers 2000; Harpending and Eller in press; Relethford 1998; Relethford and Harding 2001). The analysis of these datasets has generally supported ROA's contention that the

modern human genome emerged as the result of a population bottleneck in sub-Saharan Africa during the last 100,000 years. The primary datasets that have been employed are the mtDNA genome, non-coding and/or non-recombining segments of the Y-chromosome and various genes or non-coding segments of the nuclear DNA genome.

These datasets, however, do not necessarily reflect the same population histories, as there is no intrinsic relationship between the lineages they represent. Matrilineal mtDNA lineages and patrilineal Y-chromosome lineages, for instance, track different demographic components of our shared genetic heritage, while the nuclear genome, which is subject to recombination, follows a different set of rules entirely. It is not surprising, therefore, that the nuclear genome reflects deep population structure within modern human populations that predate the emergence of anatomically modern humans (Ayala 1996; Harding et al. 1997; Harris and Hey 1999; Hawks et al. 2000; Relethford and Harding 2001). What therefore seem to be contradictory indicators of coalescence in our genetic past may in reality be different facets of our shared heritage reflected through the prism of modern genomics (see Hawks et al. 2000b; Hawks and Wolpoff 2001b).

Another concern that needs to be addressed is the underlying premise employed in the analyses of various genomic datasets. Since the 1970s the neutral hypothesis, which posits that much of the human genome is selectively neutral and hence evolves at a statistically calculable rate (i.e. the molecular clock), has been the prevailing paradigm used to interpret haplotype trees demonstrating branching orders in the sequestration of extant populations. The rooting of these genealogical trees in Africa has been used as evidence in support of ROA, while the neutral hypothesis supports the idea that a population bottleneck was the only effective means by which genetic variation in modern human populations has been constricted.

Recent studies, however, are showing that various non-coding segments of the genome play a significant role in gene regulation (Chu 1998; Demitzakis et al. 2002). In addition, mtDNA has been implicated in various metabolic diseases of the nervous system, such as Parkinson's syndrome, etc. (Wallace 1999), and in apoptosis (programmed cell death) associated with the aging process (Green and Reed 1998). These studies highlight a new appreciation of the

role played by the mitochondrial genome in the regulation of neurological and other basic life processes that have certainly been altered in the evolution of modern humans. Changes in the function and expression of mitochondrial genes may therefore have been of decisive importance in the evolution of modern neurochemistry and, concomitantly, various parameters of modern human physiology and behavior (Ruiz-Pesini et al. 2004). If this is the case, the entire mitochondrial genome may be subject to positive directional selection, in effect neutralizing the neutral hypothesis (Wise et al. 1998).

The remaking of the human genome in the transition from pre-modern to modern *H. sapiens* may thus have been the result of multiple selective sweeps rather than a single population bottleneck. Reinterpreting the genetic data based on a different set of premises than those held by advocates of ROA results in an entirely different set of conclusions that favor a more multifaceted interpretation of recent human evolution that emphasizes multiple dispersals and recurrent gene flow with isolation, all of which redound in favor of MRE (Templeton 2002; Hawks et al. 2001b). Other factors such as "cultural hitchhiking" in which cultural evolution is hypothesized to have "reduced the diversity of genes which have similar transmission characteristics to selective cultural traits" (Whitehead et al. in press) may also help to explain the process by which genetic homogenization of modern human populations has taken place.

**Regional traits vs. species defining autapomorphies:** It is interesting to note the similarities in how another dataset relating to MRE and ROA has been evaluated and disposed of. This dataset consists of morphological features, mentioned above, that on the one hand are used to support the existence of Asian regional traits championed by supporters of MRE, while on the other hand are used to support the existence of uniquely derived, species defining features (autapomorphies) of *H. erectus*, championed by supporters of ROA.

Regional traits have been used, ever since Weidenreich's classic studies of "Peking Man" (Weidenreich 1936, 1937, 1943), as a lodestone pointing towards continuity in the evolution of regional populations in Europe, East Asia, and Australasia. Supposed autapomorphies of *H. erectus* in Asia, have been used by supporters of ROA to buttress their position that archaic populations throughout Eurasia were distinct at the species level and uninvolved in the origins of

modern humans. What is interesting to note is that many of these traits are virtually identical. Moreover, both interpretations have been challenged by a variety of studies and shown to be wanting to varying degrees.

The basic problem with utilizing morphological features as determinants of evolutionary relationships is the polytypic nature of the human species, the polymorphic character of the traits under consideration, and the peripatetic amblings of human beings during the Pleistocene. There is, moreover, an epistemological difference between the two approaches. Regional traits, no matter how misconstrued by their critics, need not be unique to any given region, nor must they necessarily be derived relative to the ancestral condition; i.e. a regional trait can be a primitive retention that is maintained at a high frequency in one part of the world while lost in another. Thus,

if it is shown that a particular regional trait occurs in other regions of the world or that the trait is plesiomorphic (i.e. an ancestral retention) for the taxon under consideration, its value as a regional marker is not necessarily diminished if it can be shown to occur in greater frequency and for a greater length of time in the region under study. Species defining autapomorphies are, on the other hand, by definition both unique and derived. If it can be shown that the trait is neither, its value as a species defining character is totally compromised.

In his monograph, *A Theory of Human and Primate Evolution*, Groves' (1989) critique of regional traits falls victim to the first error. He dismisses most of them by demonstrating that they are not unique to the region they are supposed to characterize or that they are plesiomorphic for humans as a whole. This sort of analysis would

obviate the usefulness of a character said to be autapomorphic, but does little in the way of negating a character said to be regional. Lahr's (1994) critique, published in the *Journal of Human Evolution*, is more substantive as she demonstrates that a number of supposedly East Asian regional traits are redundant, not genetically controlled or do not follow the expected regional frequency pattern. On the other hand, her study re-substantiates the well-known, empirically obvious fact that the East Asian face is characterized by transversal flatness and high, laterally flaring cheek bones, a suite of features seen in nearly all East Asian hominids, both living and fossil (Wang and Tobias 2000, 2001). Unfortunately, Lahr's analysis includes only one dental feature, third molar agenesis. By not including upper incisor shoveling the impact of her study is diminished. Her research does, how-

### Box 3: The earliest Chinese hominid: truth or consequences?

Since the "recent out of Africa" (ROA) hypothesis of modern human origins gained popularity in the 1990s, vigorous attempts have been made to isolate Asian *H. erectus* from the mainstream of human evolution. One such attempt has been the recognition of an early species of *Homo* at the Longgupo cave site in Wushan, Sichuan province, China. In 1995, fragmentary fossil remains from Longgupo Cave, consisting of a mandibular fragment containing a well worn P4 and M1 (fig.4) and an unassociated, isolated upper incisor, all dated to approximately 1.9 mya, were attributed to an early form of the genus *Homo*, said to be ancestral to an exclusively Asian *H. erectus* that eventually went extinct without issue (Huang et al. 1995; Ciochon 1995). This identification of the Longgupo remains, however, as belonging to a possible ancestor of an Asian delimited *H. erectus*, is controversial. In point of fact, the Longgupo mandibular specimen has been shown to favorably compare with Asian apes from late Miocene through early Pliocene sites in Yunnan, while lacking features commonly seen in early specimens of

*Homo* (Wu 2000; Etlar et al. 2001). The Wushan mandibular P4 (fig.4) is characterized by a slit-like anterior fovea; anteriorly placed, twinned protoconid and metaconid; and a broad, recessed talonid basin. The Wushan mandibular M1 is characterized by 5 cusps arrayed around the periphery of a broad, deep talonid basin, a buccally placed hypoconulid and differential wear on the buccal (cheek-side) cusps. Comparing the Wushan mandible to the fossil hominoid specimen from Yuanmou, Yunnan, dated to 6-5 mya (fig.5), note the overall similarity of lower P4 morphology, in particular the constricted anterior fovea; the anteriorly positioned twinned protoconid and metaconid; the broad, deep talonid basin; and the sub-oval shape of the crown. M1 morphology does not differ in any discernable way from that seen in the Wushan specimen. Compared to the Wushan specimen, the P4 of the Dmanisi jaw (fig.6), dated to 1.8 mya, has centrally rather than anteriorly placed bulbous protoconid and metaconid, and a delimited talonid basin constricted into a distally placed posterior fovea, analogous to the mesially positioned anterior fovea. The

Dmanisi M1 is distinguished by bulbous cusps that fill in the talonid basin, and has a distally rather than buccally placed hypoconulid. The Dmanisi M1 occlusal wear is evenly distributed over the tooth crown.

In addition, the isolated upper incisor found at Longgupo is indistinguishable from that of a modern human (Wang 1996; Wu 2000; Etlar et al. 2001) and was most probably "brought in by flowing water or other forces into the fissure of the comparatively old Longgupo Cave deposits . . . and mixed with the Longgupo fauna" (Wang 1996; Etlar et al. 2001). Hence, there is a strong possibility that the Longgupo specimens are a palimpsest and do not represent a valid hominid taxon (see also Schwartz and Tattersall 1996). It is, therefore, extremely unlikely that the Longgupo remains are an early hominid ancestor of an exclusively Asian delimited *H. erectus*.

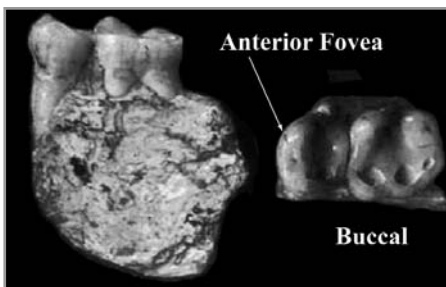


Fig.4: Two views of the Wushan (Longgupo) dentition, with mandible and associated fourth premolar (P4) and first molar (M1) (photo: H Lanpo).

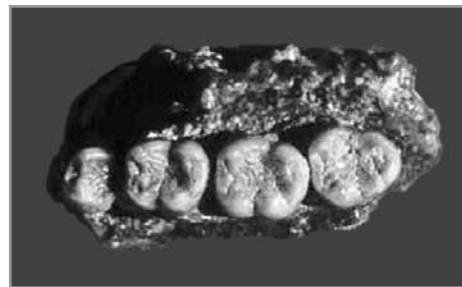


Fig.5: Mandibular dentition, with fourth premolar (P4) and three molars, of hominoid fossil from Yuanmou, Yunnan, dated 6-5 mya (photo: Li Kunsheng).



Fig.6: Mandibular dentition of the Dmanisi hominid, dated to 1.8 mya (photo: L. Gabunia).



**Fig.7:** Map of China showing hominid sites discussed in the text. Yuanmou, Yunnan has a diverse late Miocene/early Pliocene mammalian fauna that includes a large number of hominoid fossils akin to late Miocene *Lufengpithecus* from the nearby site of Lufeng. The late Pliocene Wushan mandibular fragment, thought by some to have hominid affinities (Huang et al. 1995), actually compares favorably to fossil ape specimens from Yuanmou and Lufeng. Relatively complete material of *H. erectus* in China is known from Zhoukoudian, Lantian, Yunxian, Hexian, and Nanjing. Relatively complete material of a pre-modern form of *H. sapiens* is known Dali and Jinniushan. Recent re-dating of Chinese hominid sites raises the distinct possibility that there is no overlap between *H. erectus* and pre-modern *H. sapiens* in China (contra Chen and Zhang 1991; Chen et al. 1994), with all *H. erectus* specimens being older than 400,000 years and all pre-modern specimens being younger than 250,000 years (Shen 2001).

ever, confirm the expected regional patterning of M3 agenesis (see also Liu and Zeng 1996), and it can be assumed it would have likewise confirmed the prevalence of upper incisor shoveling in East Asia as well. Others have done significant research in respect to upper incisor morphology to document the distinctive pattern of East Asian shoveling and its higher incidence in East Asia than anywhere else (Crummett 1994; Liu 1995, 1999a, 1999b). Nevertheless, Lahr's study actually lends support to the recognition of two major phenetic complexes that characterize East Asian people both now and in the past, one facial and one dental. It suffices at present to say that attempts to negate the reality of regional traits in East Asia are less than devastating and, in fact, more often than not can be interpreted to support the very thing they are intended to criticize.

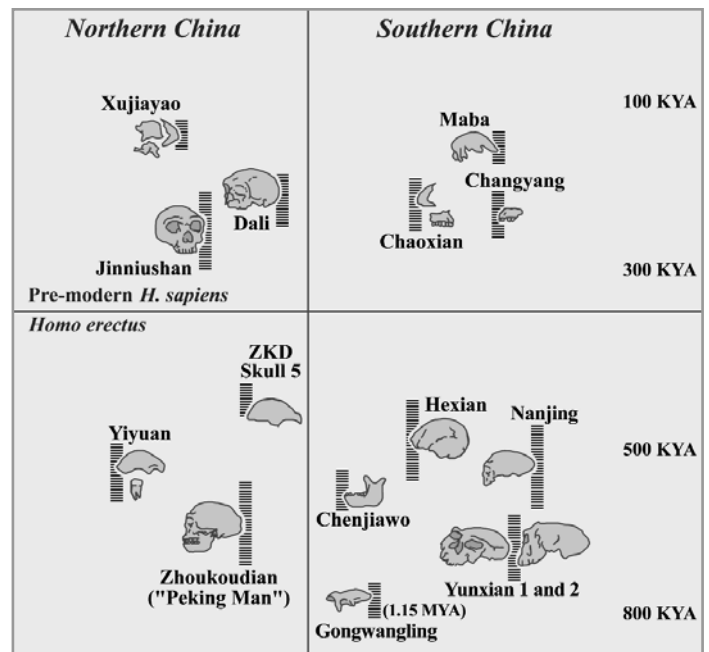
Although many East Asian traits once considered to provide evidence for continuity have been challenged, the reality of autapomorphies that define an exclusively Asian *H. erectus* has been effectively shown to be entirely wanting (Bräuer and Mbua 1992; Asfaw et al. 2002). In point of fact, multilinealists have been hard pressed to present a case for species defining autapomorphies for any Middle through Late Pleistocene hominids other than the Neanderthals. The abandonment of autapomorphies of an Asian delimited *H. erectus* by many

supporters of ROA has not, however, left them nonplused in their advocacy of ROA. In like manner, the abandonment of many traits linked to regional continuity should not be misconstrued as a vindication of ROA. If, for the sake of argument, the Neanderthal and Ngandong (i.e. late Javan occurrence of "*H. erectus*") questions are set aside, there remains a swath of archaic humans, distributed throughout much of the Old World, from Africa through the Middle East to South and East Asia, that could have gradually evolved into modern *H. sapiens* without any major replacement event. This position does not deny that some important local replacements, in such peripheral areas as Europe or insular Southeast Asia, may have taken place. In this regard it would be foolish to suggest that populations have not frequently been supplanted throughout recorded history. The history of the last few millennia, or the past few centuries for that matter, gives stark testimony to this rather self-evident fact. Is it so surprising then that certain marginal populations in western Europe (e.g. Neanderthals) or Java (e.g. the Solo/Ngandong population) may have met a similar fate?

The intermittent movement of both genes and people, due to changing paleoclimatic or other paleogeographical and paleoecological factors, throughout the central "zone of sapienization" identified above, could account for

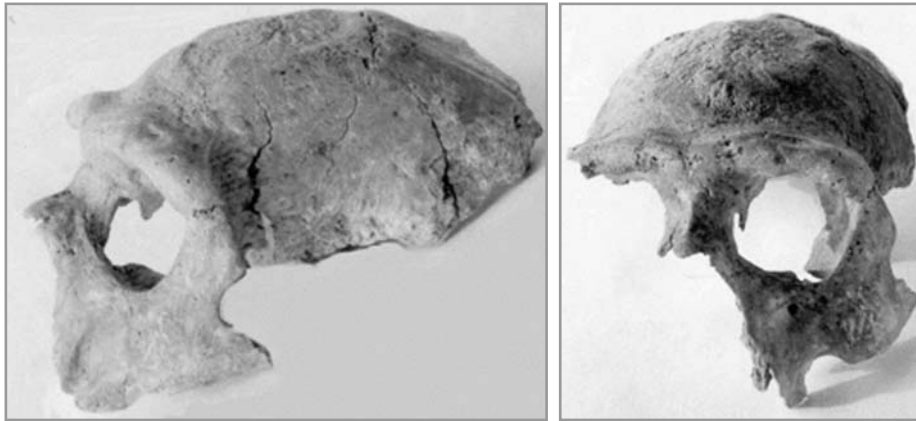
apparent disparities in both the tempo and mode of human evolution in various regions of the Old World. It is unlikely that this process took place in the same, exact manner or at the same, exact time in, for instance, Africa and East Asia. There could very well have been staggered transitions towards a more modern morphology, various regions at times leading the way and at other times lagging behind. This position is consistent with Bräuer's soft replacement model, that suggests the emergence of modern humans was "multi-causal, different in various regions and hardly rapid . . ." or for that matter uniform. At this point, however, MRE and "soft" ROA part ways. "Soft" ROA still emphasizes extra-African dispersal and replacement, while accommodating limited amounts of hybridization and continuity. MRE, on the other hand, hypothesizes that there was a continuous human presence in central regions of the Old World uninterrupted by any major replacement event. To the contrary, the introduction of exogenous genes into local gene pools may have played a significant role in initiating major transitions in the fossil record rather than near or total replacement of one population by another.

**Fossil evidence:** If the Longgupo remains are discounted (see box 3), the earliest human remains in East Asia belong to the partial cranium from Gongwangling in Lantian county,



**Fig.8:** Distribution of erectine and archaic Chinese fossil hominids during the Pleistocene. Recent reinterpretations of the dating of East Asian hominid fossils strongly suggests that all specimens of *H. erectus* in China are older than 400,000 years, while pre-modern archaics are younger than 250,000 years. Hence there was no overlap between the two groups as once thought.

**Box 4: The Nanjing fossils and dating of Chinese hominids**



**Fig.9:** This partial cranium of *H. erectus* from Nanjing (shown at left in profile, and at right in frontal view) is in all details nearly identical to the reconstruction of “Peking Woman” affected by Weidenreich nearly six decades ago. The Nanjing *H. erectus* site contains a fauna that correlates with layers 6-7 at Zhoukoudian and documents a southern deployment of the Zhoukoudian deme half a million or more years ago (photo:Lu Zume).

New dates obtained for fossil hominids from Nanjing, Hexian, Zhoukoudian, and Yunxian indicate that all known specimens of *H. erectus* in China are older than 400,000 years. These dates mitigate against the likelihood that *H. erectus* and pre-modern forms of *H. sapiens* coexisted in China as had been previously suggested.

The Nanjing fossil hominids (fig.9) were discovered in 1993-1994 at Hulu Cave, Tangshan Hill (N32°, E119°), on the outskirts of Nanjing (old Nanking). Based on the detailed description and metric data supplied in the monographic treatment of the hominid remains by the Tangshan Archaeological Team (1997) there can be no doubt regarding their great similarity to *Homo erectus* as known from the “Peking Man” site at Zhoukoudian (see also Wang and Tobias 2000). Interestingly, the associated fauna at Hulu Cave is so similar to that found at Zhoukoudian that direct correspondences can be made to layers 6-7 of Zhoukoudian Locality 1. These layers have produced only a scanty amount of hominid material and have been previously dated between 400-350,000 ya. Mass spectrometric U-series dating of speleothems from Tangshan Cave, combined with ecological and paleoclimatic evidence, however, indicates that the Nanjing hominids should be dated to at least 580,000 ya, or more likely 620,000 ya (Zhao et al. 2001). This age is 270,000 years older than previous estimates. Other Chinese sites yielding *H. erectus*, such as the upper layers at Locality 1 at Zhoukoudian and the Hexian site in Anhui, have recently been redated in excess of 400,000 ya (Shen 2001; Shen et al.1996; Grun et al. 1998), while the Yunxian hominids from Quyuankou in Hubei have recently been dated in excess of 580,000 ya (Yan 1993; Chen et al. 1996). The main sequence at Zhoukoudian that has yielded the majority of *H. erectus* specimens is now thought by some to be approximately 800,000 years old or older (Shen 2001). These dates indicate that all Chinese *H. erectus* specimens are older than previously thought and do not overlap with later more advanced archaic specimens known from Dali, Maba, and Jinniushan dated to approximately 250,000 - 120,000 ya. (Shen 2001). The conjectured contemporaneity of *H. erectus* and *H. sapiens* in China (Chen et al. 1991, 1994) is thus most likely a chimera.

The resolution of dating incongruities such as those discussed above goes a long way to resolving various conundrums associated with the Chinese human fossil record. If the above temporal ordering is accepted, the trajectory of human evolution in China becomes more lineal and straightforward. What becomes most relevant are 1) the relative heterogeneity of *H. erectus* in China at the demic level and 2) the transformation of human populations in China from the erectine to the archaic bauplan between 400,000 and 250,000 ya. Given the worldwide dearth of human fossils remains between 750,000 and 400,000 ya and the margin of error associated with employed dating techniques, it can be argued that there is no discrepancy between the course of human evolution in the East and West during the Middle Pleistocene. In its broad outlines the transformation of the human lineage from *H. erectus* to archaic and later pre-modern forms of *H. sapiens* should be viewed as simultaneous throughout the then inhabited world.

Saanxi province, China dated in excess of 1 mya (Etler 1996) (fig.7). Recent re-dating of other hominid fossils in China has helped to clarify their temporal sequence (fig.8; see box 4). As in Africa, there is clear evidence of transitional human fossils in East Asia. Advocates of ROA have a difficult time evaluating this material. If these specimens are seen as descendants of an Asian delimited *H. erectus*, they have evolved in parallel to western archaics. If they are placed in *H. heidelbergensis*, there must have been a replacement event in East Asia preceding the advent of modern *H. sapiens*. This would then entail two major replacement events having taken place in this part of the world. MRE suggests that there were transitional forms between *H. erectus* and modern *H. sapiens* in Asia just as there were in Africa. The new dates show that *H. erectus* in China is older than previously thought and does not overlap with more advanced archaic Chinese.

The major issue in Chinese paleoanthropology thus becomes a question of the relationship of time-successive hominids to one another? Are the archaic Chinese fossils transitional between earlier erectines and later moderns? Do the Chinese archaics represent a continuation of the erectine lineage in East Asia that eventually goes extinct? Or, are the archaics representative of an incursion from the West, distinct from their erectine predecessors? To address these issues a null hypothesis, that Chinese archaics dating from approximately 250,000 - 100,000 ya, are transitional forms between Chinese erectines and early moderns, can be proposed. In order to demonstrate replacement as the mode by which modern humans became established in East Asia the above stated null hypothesis must first be falsified.

As mentioned previously, one means used to discredit the transitional nature of Chinese archaics has been to deny the existence of regional characters in East Asia. But is it necessary to document regional characters in order to demonstrate continuity? It is interesting to note that supporters of ROA have never been very much concerned with the presence of regional traits in the one region of the world they are most interested in, i.e. Africa. They, nevertheless, believe that continuity in human evolution occurred there, if nowhere else. In point of fact the underpinning of ROA is a soft interpretation of continuity theory in Africa.

As summarized by Lahr (1994), citing Stringer and Andrews (1988), the ROA model is

predicated on the following three assumptions: “first, the presence of archaic-modern transitional fossils in the African late Middle Pleistocene, represented by the group of Ngeloba, Irhoud, Omo 2, Florisbad, Eliye Springs; second, the appearance of early upper Pleistocene fossils in Africa and the Middle East, like Klasies River Mouth, Border Cave, Singa, Mumba, Qafzeh and Skhul; and third, the morphological discontinuity between Neanderthals and moderns observed in Europe.” Nowhere to be found is any mention of “regional traits” that characterize both fossils and modern Africans, reflecting an ancestor-descendant relationship. That is to say, supporters of ROA do not bother trying to demonstrate “regional continuity” in Africa. It is left to multiregionalists to try to demonstrate such a relationship in other regions of the world, and if they encounter difficulties in doing so that is supposed to redound in favor of the ROA position.

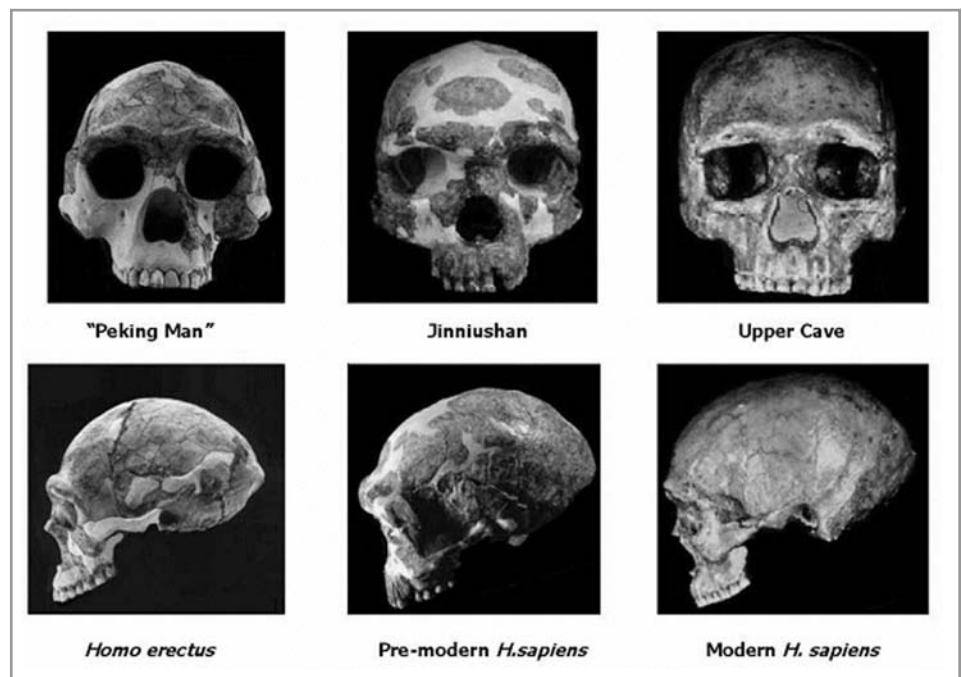
MRE, however, does not necessarily rely on documenting regional traits to demonstrate continuity in human evolution in particular regions of the world, nor does MRE dismiss them. Rather, advocates of MRE can apply the same criteria that supporters of ROA apply to the African fossil record; i.e. first, there should be fossils of a transitional nature in East Asia during the late Middle Pleistocene; second, the appearance of modern-looking fossils should occur during the early Upper Pleistocene; and third, there should be the lack of any major discontinuity in the fossil record of the region under study. If the above conditions are demonstrated in East Asia or any other region of the world outside of Africa, then the null hypothesis of continuity in the region under study will remain unfalsified, and the whole foundation of ROA itself begins to founder. An analysis of these conditions in East Asia follows.

*Condition 1:* There should be archaic-to-modern transitional fossils during the late Middle Pleistocene of East Asia. This is readily demonstrated in China where a group of transitional fossils from the same broad time range as that in Africa is well documented (fig.10). These include partial or complete crania from Maba, Dali, and Jinniushan, more fragmentary cranial remains from Xujiayao and Chaoxian, and a significant dental sample from Tongzi (Wu and Poirier 1995; Etlar 1996) (figs.7,8). Whatever doubts one may have about the exact ages of these specimens, there is no question that they can all be dated to the late Middle Pleistocene or

very early Upper Pleistocene, i.e. between 250 and 100 kya, broadly contemporaneous with similar fossils from Africa. Some ardent supporters of “hard” ROA have expressed doubts about the relationship between these archaic Chinese fossils and earlier local *H. erectus* populations and suggest that post-erectus/pre-modern humans in China show closer affinities to European archaics (i.e. *H. heidelbergensis*) (Stringer 1988; Rightmire 1998) than they do to predecessor populations of *H. erectus*. Very few, if any, researchers who have worked with the Chinese material have, however, made similar assessments. In addition, the same could be said about specimens considered precursorial to modern humans in Africa, i.e. they are more similar to archaics from other regions than they are to the populations that preceded them in Africa. Verdict: An unbiased, objective evaluation of the data from China confirms Condition 1, that there are late Middle Pleistocene transitional fossils in China.

*Condition 2:* There should be modern looking fossils during the early Late Pleistocene in East Asia. Until recently, this was somewhat problematic and it is still controversial. There is admittedly a significant gap in the human fossil record in China from approximately 30-100,000 years ago (Etlar 1996). This is when the

European Neanderthals flourished, so it is puzzling as to why there is such a dearth of fossil human remains in China from this period of time. Nevertheless, recent redating of the fully modern Liujiang material from the southern Chinese region of Guangxi, consisting of a well-preserved cranium and partial skeleton discovered in the 1950s, indicates an antiquity in excess of 100,000 years and perhaps as old as 150,000 years before present (Shen et al. 2002). Although the original provenience of the Liujiang remains within the cave deposits from whence they were retrieved is still debated, corroborating evidence from the immediate vicinity is supportive of the early age assignment. This would place fully modern *Homo sapiens* in southern China in a time frame identical to that of the earliest representatives of modern humans known from anywhere in Africa. There are, moreover, other remains that bear on this issue. The Xujiayao material, dated to approximately 100 kya, is a case in point. Bräuer (1992) states that “the remains from Xujiayao . . . are too fragmentary and morphologically quite heterogeneous to be of much help in clarifying what happened (in China)” during the transition to modern humans. The Xujiayao remains, however, consist of two fairly complete parietals, a number of parietal fragments, a nearly complete temporal, two rela-



**Fig.10:** As in Africa, there is clear evidence of transitional human fossils in East Asia. Advocates of ROA have a difficult time evaluating this material. If these specimens are seen as descendants of an Asian delimited *H. erectus*, they have evolved in parallel to western archaics. If they are placed in *H. heidelbergensis*, then there must have been a replacement event in East Asia preceding the advent of modern *H. sapiens* in East Asia. This would then entail two major replacement events having taken place in this part of the world. MRE suggests that there were transitional forms between *H. erectus* and modern *H. sapiens* in Asia just as there were in Africa.

### Box 5: Chinese fossils throw light on phylogenetic affinities of Atapuerca-Gran Dolina hominids

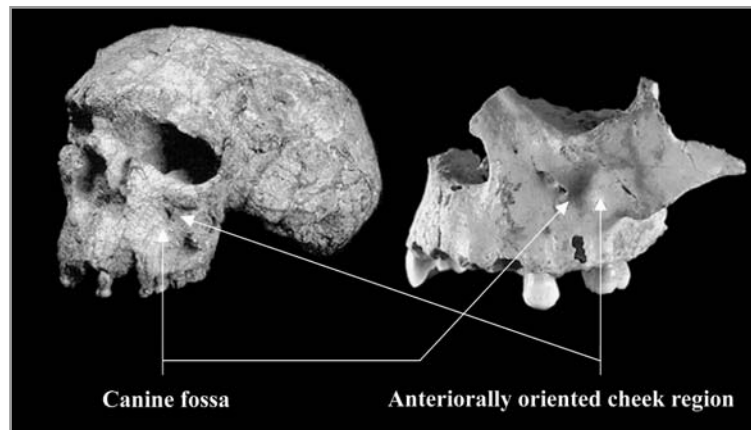
The hominid species, *Homo antecessor*, founded on a number of craniofacial specimens from Lower Pleistocene deposits at Atapuerca, Spain, was described as the common ancestor of Neanderthals (“*H. neanderthalensis*”) and modern humans (*H. sapiens*) (Bermúdez de Castro et al. 1997). In this context, fossil hominids from Asia attributed to *H. erectus* were said to represent a side branch of the human family tree, unrelated in any lineal sense to modern Asian or non-Asian people (Gibbons 1997). The new taxon of *H. antecessor*, however, does not differ in any substantial way from previously known Asian fossils attributed to *H. erectus*. In fact, the material from Atapuerca-Gran Dolina is further evidence that *H. erectus* was a widespread, pandemic, polytypic human species (Asfaw et al. 2002), in the same fashion that its inheritor, *H. sapiens*, has been and still is.

The diagnosis of *H. antecessor* as a distinct hominid species rests primarily on a number of craniofacial features, identified as “fully modern” in character, seen in the juvenile upper partial face (ATD6-69) and associated cranial remains (Bermúdez de Castro et al. 1997). These traits include midfacial characters such as a coronally oriented infraorbital surface associated with a well-developed canine fossa, and a horizontal, high rooted, inferior zygomaxillary border, as well as cranial vault features such as a double arched supra-orbital torus and a convex superior border of the temporal squama (Bermúdez de Castro et al. 1997). A number of non-diagnostic dental and mandibular traits are also included in the definition of the new species, some of which will be discussed below.

The craniofacial features of so-called *H. antecessor*, which are said to represent a unique combination of traits derived in the direction of later Eurasian hominids, are, however, seen in the very same combination in at least one Chinese fossil hominid attributed to *H. erectus* (i.e. Yunxian 2; fig. 11) (Li and Etlér 1992), while the specifically midfacial features said to distinguish *H. antecessor* from previously known Lower and Middle Pleistocene hominids are seen in all Chinese *H. erectus* fossils in which the relevant area is preserved (Etlér 1996; Wang and Tobias 2000). Cranial vault features said to distinguish *H. antecessor* are differentially seen in a number of *H. erectus* fossils from China (Etlér 1996; Wu and Poirier 1995).

The Yunxian hominids consist of two virtually complete crania initially dated to the Middle Pleistocene based on their stratigraphic position and faunal associations (Li and Etlér 1992). Later research, including the recovery of typical Lower Pleistocene mammalian taxa from the hominid bearing stratum (Etlér and Li 1994; Li 1997), paleomagnetic studies (Yan 1993), and ESR dating of associated mammalian dental remains (Chen et al. 1996), however, indicate a late Lower or early Middle Pleistocene provenance for the Yunxian hominids, making them more or less contemporaneous with the new Atapuerca finds. Although the two Yunxian crania have been subject to various degrees of plastic deformation, substantial portions of the midface, supra-orbital region, and basicranium are preserved intact and can serve as a basis of comparison with ATD6-69 and other Atapuerca-Gran Dolina specimens.

The midfacial morphology of the Yunxian crania has been described as follows: “The Yunxian crania show features of the mid-face common to non-neandertal late archaic and early modern *H. sapiens* (for example, the face is flattened and orthognathic with moderate alveolar prognathism; the maxilla has a distinct canine fossa; the lateral part of the maxilla is oriented coronally and highly angled to the zygomatic; there is a high origin of the zygomatic root; a horizontal inferior zygomaxillary border and a pronounced malar incisure, and so on)” (Li and Etlér 1992). This description, in all its particulars, is identical to that of ATD6-69. Thus, the midfacial morphology identified by Bermúdez de Castro et al. (1997) as “fully modern” and which they suggest “antedates other evidence of this feature by 650,000 years” was described in a penecontemporary human specimen from China five years prior to their description of the Atapuerca juvenile! Other features mentioned by Bermúdez de Castro et al. (1997) as being in unique combination in the Atapuerca



**Fig. 11:** Yunxian vs. Atapuerca-Gran Dolina mid-facial anatomy. Features of the ATD6-69 juvenile mid-face from Atapuerca (right) are said to have a fully modern facial topography including “a prognathic (nonflat) mid-face, a well-developed canine fossa, a horizontal zygomaxillary border and a sharp lower nasal margin” (Bermúdez de Castro et al. 1997). These very same features can be seen in the Yunxian 2 face (left) and in material of *H. erectus* from Zhoukoudian and Nanjing. (photo: Li Tianyuan, J.M. Bermudez de Castro).

remains, such as a double arched supraorbital torus and a convex superior margin of the temporal squama are also seen in the Yunxian 2 cranium, as well as other specimens from China attributed to *H. erectus*, including Lantian (double arched supra-orbital torus); and Hexian, Nanjing, and Skull V from Zhoukoudian Locality 1 (convex superior margin of the temporal squama) (Wu and Poirier 1995; Etlér 1996). There is, therefore, nothing unique about the morphological pattern of the Atapuerca remains that warrants creation of a new human species.

When the Yunxian remains were initially described great emphasis was placed on the

modern character of their facial topography, as facial remains of *H. erectus* were, and still are, relatively rare. It was stressed that modern human facial anatomy seemed to occur earliest in Asia, while the more obliquely set ancestral hominid pattern persisted in the West, eventually giving rise to the derived Neanderthal pattern seen in the Late Pleistocene. This conclusion must now be re-evaluated in light of the new Atapuerca-Gran Dolina specimens. Modern human facial topography should be recognized as a polymorphic condition of *H. erectus* throughout its range.

Equal weight in assessing the phylogenetic affinities of the Yunxian crania was also given to their basicranial morphology, a portion of the human cranial anatomy not sampled at Atapuerca-Gran Dolina. In this regard it was observed that both Yunxian crania preserve a morphology identical to that seen in other specimens of Asian *H. erectus*. Li and Etlér (1992), therefore, while noting the “modern” features of the Yunxian face and certain similarities with archaic western hominids in cranial vault morphology, attributed the Yunxian specimens to a local variant of *H. erectus* and stressed the polytypic nature of that taxon.

The Atapuerca-Gran Dolina remains show that populations similar to Yunxian and Lantian in mid-facial and cranial vault morphology were widespread throughout the northern hemisphere during the Lower and early Middle Pleistocene. In addition, a comparison of the Atapuerca-Gran Dolina mandibu-



lar morphology as described by Bermúdez de Castro et al. (1997), with the penecontemporary *H. erectus* mandible from Lantian, Chenjiawo, shows complete identity in all salient features. Personal observation of the Chenjiawo mandible at the IVPP in Beijing, China confirms that it has a mylohyoid groove that “extends anteriorly nearly horizontal and courses into the mandibular body as far as the level of M2/M3” and other features identified by Bermúdez de Castro et al. (1997) as mandibular traits defining *H. antecessor* as distinct from their conception of *H. erectus*. The fact that the Atapuerca-Gran Dolina remains also show evidence of shovel-shaped upper incisors and reduced mandibular M3s, common features of Asian *H. erectus* and all later fossil and living Asians (Liu and Zeng 1996; Etlér 1996), is further evidence that there is, in fact, no such thing as so-called Asian *H. erectus* in contradistinction to other purported late Lower - early Middle Pleistocene species of *Homo*. On the contrary, the Atapuerca specimens more than adequately demonstrate that *H. erectus* was a wide-ranging, polytypic human species ancestral to all later forms of humanity. *H. erectus* was therefore not a side branch of the human family tree but part and parcel of its main trunk.

In conclusion, as the Yunxian and Lantian specimens are, in broad terms, contemporaneous with the Atapuerca remains, and as they cannot be adequately differentiated from one another morphologically, they can best be evaluated phylogenetically as representative of a broadly defined *H. erectus*, which served as the base for local evolutionary developments in Europe, Africa, continental East Asia, and insular Southeast Asia. Furthermore, neither Atapuerca-Gran Dolina nor Yunxian have any direct bearing on the question of modern human origins, other than to demonstrate that late Lower Pleistocene - Middle Pleistocene *Homo* had not yet differentiated to any considerable extent into regional or species specific variants. Moreover, the similarities between the Atapuerca specimens, Yunxian, and Lantian (both at Gongwangling and Chenjiawo) suggest that specimens of *H. erectus* as known from Zhoukoudian should not be misconstrued as displaying the “typical” or most widespread combination of *H. erectus* traits. In fact, these former specimens probably represent the nominal, generalized morphology of *H. erectus* better than the more specialized specimens from Zhoukoudian, the description of which has served as the *de facto* basis for the definition of *H. erectus* ever since Weidenreich’s classic monographs on “Peking Man” in the 1930s and 40s (Weidenreich 1936, 1937, 1943).

tively complete occipitals, the ramus and posterior body of a lower jaw, and a juvenile maxilla with intact dentition, all associated with a prolific archaeological assemblage that includes proto-prismatic cores (Wu and Poirier; Etlér and Li 1994). If this material was found in Africa it would surely not be so easily dismissed. In fact, Bräuer’s characterization of the Xujiayao remains would appear to be equally applicable to material such as that from Klasies River Mouth (which consists of a lower jaw, a fragmentary frontal bone, pieces of parietal, a zygomatic bone, and some isolated teeth), if not for the fact that the latter is so central to the argument for modern human origins in Africa.

Rather than dismissing the Xujiayao material, which has generally been attributed to late pre-modern *H. sapiens* in China, it needs to be re-evaluated in the light of new Chinese discoveries, particularly the as yet undescribed skull from Laishui dated between 60-30 kya. The Laishui cranium, a cast of which is on public display at Peking University’s Sackler Museum of Archaeology, has extremely robust supraorbital tori that preserve an archaic morphology, a relatively sloping forehead, along with a robust but essentially modern cranial vault, cranial base, and face (Etlér 1996; Bräuer 2001). This specimen, as well as others from the late Upper Pleistocene in China, such as a calva from Huanglong in Shanxi and an occipital from Shiyu in Shanxi, shows features highly reminiscent of those seen in homologous material from Xujiayao (Etlér 1996). How modern specimens from Salawusu in Inner Mongolia, dated to between 65-35 kya, fit into the emerging picture of Upper Pleistocene human evolution in China also requires further study. It can be argued, however, that the earliest modern Chinese fossils show a higher retention of archaic features than analogous material from further west.

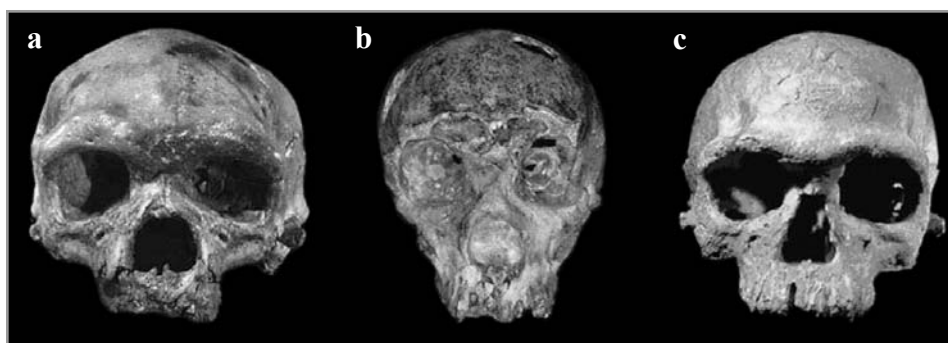
While data are still limited, there is every reason to believe that more fossils representing this crucial period of human evolution in China will eventually be found (*contra* Jin and Su 2000). It is therefore very premature to dismiss the possibility of early modern humans in East Asia having an antiquity equivalent to that seen in Africa and the Middle East. Verdict: The final disposition of Condition 2 is still pending, but all indications are it will be verified sooner rather than later.

*Condition 3:* There should be a lack of any major discontinuity in the human fossil record of China. Here we are on firmer ground. Advocates

of ROA originally held that Asian *H. erectus* and its late Middle Pleistocene descendants shared autapomorphies that set them apart from western archaics and early moderns as an evolutionary dead-end, implicitly recognizing continuity between earlier more “primitive” and later more “advanced” pre-modern human populations in China. (This assessment of the evolutionary relationship between Asian *H. erectus* and later archaic humans in China such as Dali and Jinniushan also flies in the face of the proposition, mentioned above, that the latter specimens show greater affinities to western archaics than *H. erectus*.) Supporters of MRE, of course, have long documented many features shared by these two groups of fossils (Wu and Poirier 1995; Etlér 1996; Etlér and Li 1994). It seems fair to state that continuity between *H. erectus* and “archaic” *H. sapiens* in China has been generally accepted. Those features that differ between the two groups are equivalent to the differences that ROA supporters would claim separate *H. ergaster* from *H. heidelbergensis* in Africa; i.e. they are transitional in nature.

The question then arises as to whether there is any discontinuity between late pre-modern Chinese and early moderns. The answer to this question revolves around whether one accepts or rejects the validity of the trait complexes relating to East Asian facial and dental morphology mentioned earlier as local evolutionary markers in East Asia. I would argue that their presence in erectine, pre-modern, and early modern specimens in China speaks to a definite degree of morphological continuity, and certainly gives no indication of discontinuity, between antecedent pre-modern and subsequent early modern populations in East Asia. Verdict: It can be concluded that there is no evidence for derived traits in Chinese archaics that would preclude them from being ancestral to later moderns.

In conclusion, of the three conditions used by advocates of ROA to demonstrate continuity, two are as demonstrable in East Asia as in Africa: there are transitional fossils during the late Middle Pleistocene in China, and there is no evidence of discontinuity between Chinese archaics and early Chinese moderns. The third prediction, the presence of early moderns during the early Upper Pleistocene, while not yet well documented, has not been disproved. Moreover, the continuity of at least two significant trait complexes between late archaics and early moderns in China gives weight to the third prediction’s eventual verification. It can therefore be argued



**Fig.12:** *a.* (Asia): Dali, China; *b.* (Europe): Saccopastore, Italy; *c.* (Africa): Jebel Irhoud 1, Morocco. The three examples show regional variation in human cranial form and structure 120,000 years ago. Note the overall similarity between the Dali (*a*) and Irhoud (*c*) crania, in particular the flat and broad mid-face, squared eye sockets, and keeled braincase. This differs significantly from the Neanderthal (*b*) cranium from Europe, which has a narrow projecting mid-face, rounded eye sockets, and globular braincase. In other features, the Dali cranium is similar to Saccopastore, in particular the broad shape of the nose and guttering of the lower border of the nasal opening. The Dali cranium also retains many *H. erectus*-like features seen in earlier human fossils from China.

that based on the fossil record continuity between archaic and modern humans in East Asia is a very viable option. There is, in addition, other non-fossil evidence that supports MRE, both genetic (see above) and archaeological (see below).

**Archaeological evidence:** Lahr (1994), as a spokesperson for the hard ROA position, argues that archaeological data can be used to buttress the case for replacement of archaics by moderns in Europe, although it is conceded that the evidence is more equivocal in Africa and the Middle East. As regards East Asia she states, “the lack of material and objective information about East Asian and Javanese technologies does not allow the inclusion of these important regions in the discussion, although the appearance of Upper Palaeolithic in Siberia at approximately 35 kya suggests population movement into this area.”

This statement by Lahr is characteristic of the selective vision of many supporters of ROA. Rather than confront an issue that is not in accord with their *a priori* assumptions about modern human origins in Africa, they dismiss it out of hand. To say there is a lack of material and objective information about Paleolithic industries and technologies in East Asia is to negate over 70 years of archaeological research in China and, in particular, the last 50 years of intensive work by Chinese archaeologists not only at the IVPP in Beijing, a world-reknowned paleontological and paleoanthropological institution, but also the work of countless archaeologists at provincial and local levels throughout China, who have accumulated a wealth of data pertaining to the Chinese Paleolithic. Many summaries of these finds and researches are available in English, written by both Chinese and foreign scholars

(Aigner 1981; Wu and Olsen 1985; Clark and Schick 1988; Ling 1996; Zhang 1999; Hou et al. 2000; Keates 2000; Leng 2001).

What the Chinese Paleolithic shows is that it developed, to a large extent, independently from outside influences. There is no evidence of Paleolithic industries associated with the West to be found in China, and attempts to identify certain assemblages as “Acheulian,” “Mousterian,” or “Solutrean,” etc. were abandoned decades ago (Aigner 1981). This is not to say that various technological modes identified in the West were non-existent in China (see Hou et al. 2000). It is clear, however, that the Chinese Paleolithic, up to and including the Upper Paleolithic, must be seen in its own context (Clark and Schick 1988), a fact which does not meet the expectations of a “replacement” model for the origins of modern East Asians, but is fully in accord with MRE.

There is one final point to be made regarding the assertion by many advocates of ROA that “a number of early modern specimens from China and Australasia exhibit basic similarities with early modern humans from Europe and

even Africa” (Bräuer 1992; see also Kamminga 1992; Brown 2002), the implication being that this points to an external source of origin for early moderns in the East. This observation is, however, totally in accord with the core concept of MRE presented in this paper. If there was a “central zone of sapienization” extending from Africa through the Middle East to East and Southeast Asia during the late Middle Pleistocene/early Late Pleistocene transition, with heightened contact due to increased multilateral dispersals and concomitant genetic communication, it should be expected that all early moderns, be they from Africa, Europe, or Asia, would share in certain “grade” features that would tend to unite them phenetically to the exclusion of present-day populations in their respective regions of habitation.

**Conclusion:** In conclusion, evidence is mounting that the emergence of modern humans during the Late Pleistocene was characterized by a “multi-causal and complex demographic process” and “a complex migration and mixing process, variable degrees of continuity in various regions of the world, and strong ties between eastern and western parts of the Old World” (Brauer 1992). A similar conclusion was reached from a study of the Yunxian crania, from Hubei province, China (Li and Etlar 1992), in which it was noted that, “the differential distribution of character states associated with *H. sapiens* in regionally disparate Middle Pleistocene human populations suggests that the events leading to the emergence of modern humans were not restricted to one region of the world alone. In addition, the mix of characters in the Yunxian crania demonstrates that the taxon *H. erectus* is founded on a set of ancestral hominid traits and regional polymorphisms. It hence has no meaning in a cladistic framework. In light of the above considerations we feel it is best to view all



**Fig.13:** Comparison of Yunxian 2 with archaic and modern human crania. Two hominid crania from Yunxian, Hubei province, China that have a mix of erectine and archaic features have recently been dated to the early Middle Pleistocene between 800,000 - 560,000 ya. (Chen et al. 1996, 1997; Yan 1993). This scan of the second Yunxian cranium shows its overall similarity to the archaic Petrolona specimen from Greece (center). Yunxian 2 nevertheless retains ancestral features of the cranial vault and base not seen in the later more derived Petrolona specimen. Cranial capacity of Yunxian 2 is estimated at no more than 1100 cc.

Middle Pleistocene hominids in a broad perspective as an essential part of one evolving lineage in direct ancestry to modern humans" (figs.11-13; see box 5).

From a genetic perspective, the significant role of African dispersals cannot be denied, but as Templeton (2002) has recently stated, "A coherent picture of recent human evolution emerges with two major themes. First is the dominant role that Africa has played in shaping the modern human gene pool through at least two - not one - major expansions after the original range extension of *Homo erectus* out of Africa. Second is the ubiquity of genetic interchange between human populations, both in terms of recurrent gene flow constrained by geographical distance and of major population expansion events resulting in interbreeding, not replacement." It must be acknowledged, moreover, that evidence for ancient multilateral dispersal events could very well have been obscured by the recent population history of our species. The resources of the human genome are, however, just now being fully accessed. Much new information will surely come to light that will better document the course of human genetic evolution. The fossil record of human evolution will also continue to accumulate, likewise shedding new light on our origins and the role of *H. erectus* in human evolution.

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Dennis Etlar has spent the past two decades conducting paleoanthropological research in China, working in collaboration with Chinese paleoanthropologists and Paleolithic archaeologists. He has been involved in a number of projects that helped open the door to foreign participation in paleoanthropological and archaeological research in China, including the description and analysis of early Middle Pleistocene human crania from Yunxian, Hubei; the joint Chinese-American study and excavation of early Paleolithic sites in the Nihewan basin of Hubei; the joint Chinese-American study of fossil hominoid remains from the Yuanmou basin, Yunnan and the re-interpretation of fossil hominoid specimens from the Longgupo site in Sichuan. He has published numerous scientific articles that have helped bring the rich fossil record of Chinese hominids to the attention of the world-at-large.



Presently Dennis teaches Physical Anthropology at Cabrillo and Gavilan colleges on the central coast of California, where he makes his home in Santa Cruz. He continues his interest in Asian paleoanthropology and hosts a website on the "Fossil Evidence for Human Evolution in China," that can be accessed at [www.chineseprehistory.org](http://www.chineseprehistory.org).

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**Glossary:**

*agenesis*: failure of a biological structure to develop.

*alveolar*: tooth-bearing portion of the upper jaw.

*alveolar prognathism*: forward projection of the maxilla, or upper jaw.

*anagenesis*: one form of speciation in which a species evolves through time into a new species. Anagenesis is contrasted with cladogenesis (single, continuous line vs. distinctive branching, respectively).

*anterior fovea*: depression in forward part of tooth.

*autapomorphy*: new morphological trait unique to a group in an evolutionary lineage; uniquely derived feature.

*autosome*: any chromosome except a sex chromosome.

*basicranium*: part of the occipital bone at the bottom of the skull.

*bauplan*: The generalized, idealized archetypical bodyplan of a major taxon.

*buccal*: relating to the cheek.

*calva*: uppermost portion of the braincase (equivalent to calotte).

*canine fossa*: a depression above the canine tooth on the cheek of modern humans resulting from the reduction in the size of the face.

*cladistics*: the school of evolutionary biology that seeks to make evolutionary hypotheses through interpreting patterns of primitive and derived characteristics; a method for determining the evolutionary relationships among animal groups by comparing shared morphological features. These relationships are usually depicted in a cladogram.

*cladogenesis*: one form of speciation in which one species evolves through time into two or more descendant species. Cladogenesis is contrasted with anagenesis.

*coronally oriented infraorbital surface*: The surface of the face below the eye orbits is on a flat plane horizontal to the midline of the skull.

*cranial vault*: combination of bones that encase the skull.

*cultural hitchhiking*: co-evolution of culture and genes; reduction in genetic diversity when neutral or nearly-neutral genes (such as mtDNA) and selectively advantageous cultural traits are transmitted in parallel.

*cusps*: pointed or rounded bumps on the occlusal or chewing surface of a tooth.

*deme*: a population, or cluster of individuals,

with a high probability of mating with each other compared with their probability of mating with a member of some other population, and therefore having a substantial amount of genetic exchange.

*electron spin resonance (ESR) dating*: dating method that measures the concentration of electron traps in a material, which accumulate through natural radiation; method yields a minimum, rather than actual, age.

*exogenous*: originating from outside the organism or system.

*gene flow*: the movement of genes into or through a population by interbreeding, or migration and interbreeding, with another population.

*grade*: a level of organization based on the presence of common biological features and used in assessing different evolutionary lines of animals.

*haplotype*: combination of genetic markers or polymorphisms present in a gene or genome, such as the mtDNA, that are inherited together as a unit.

*hypoconulid*: one of several cusps on a lower tooth.

*malar incisure*: notch on the cheekbone (malar is equivalent to zygomatic).

*mandible*: lower jaw.

*maxilla*: upper jaw.

*metaconid*: one of several cusps on a lower tooth.

*mitochondrial DNA (mtDNA)*: DNA in mitochondria of cells, rather than nuclei. Because mitochondria occur outside the cell of the nucleus, mtDNA is typically only passed on through the female, and hence reveals matrilineal relationships. Rate change for mtDNA is much faster than DNA of the nucleus, making it suitable for analyses of recent evolutionary developments.

*mylohyoid groove*: longitudinally running groove on the internal surface of the mandible (lower jaw), where the mylohyoid muscle (flat, triangular muscle forming the floor of the mouth) attaches.

*non-coding*: DNA sequence not involved in coding for a protein end-product.

*non-recombining*: those portions of the human genome that do not combine, including mtDNA and the Y-chromosome. Because they are non-recombining, the mutations that occur in these segments of DNA are not reshuffled or mixed into new combinations, and hence, accumulate in a linear or chronological fashion.

*nuclear genome*: full set of chromosomes, and corresponding inheritable traits, from the nucleus of a cell.

*occlusal wear*: wear on the chewing surface of a tooth.

*orthognathic*: without forward projection of the upper or lower jaw; strait-jawed.

*paleomagnetism*: dating method based on the periodic reversals of the earth's magnetic polarity, often employed in dating of early hominine sites.

*phylogeny*: the study of evolutionary development of a species, often expressed with a family tree.

*plesiomorphic*: said of a trait that is an ancestral retention.

*polymorphism*: genetic variability for a trait.

*polytypic*: comprising several subspecies or geographical variants.

*population bottleneck*: reduction in population size that may cause changes in gene frequency within a population.

*protoconid*: one of several cusps on a lower tooth.

*proto-prismatic cores*: blocks of lithic material prepared in such a fashion as to produce an elongated flake when struck ancestral to Upper Paleolithic cores from which blade-like flakes were struck.

*shoveling*: characterized by upper incisor teeth reinforced with extra enamel at their edges of the tongue side.

*speleothem*: a mineral deposit formed in a cave by the action of water.

*supraorbital torus*: ridge above the orbits on a skull, very pronounced in *H. erectus*, Neanderthals, and some australopithecines (from supra: above; orbital: eye; torus: ridge).

*talonid basin*: feature on a lower tooth.

*temporal squama*: a portion of the temporal bone, which is located at the side of the skull near the ear, the squama is flat or fanlike in modern humans and projects upward and forward.

*trait complexes*: group of attributes or characters within a species for which heritable differences can be defined.

*uranium series (U-series) dating*: dating method based on the decay of a number of isotopes of uranium.

*Y-chromosome*: a chromosome unique to males, on which sex-determination genes are located, consisting largely of non-recombining sequence. Genetic variation on the Y-chromosome can show inheritance of specific genes or mutations through the paternal line, and also track male migrations through time and space.

*zygomaxillary border*: meeting place (or suture) where the zygomatic (cheekbone) meets the maxilla (upper jawbone).