

**100 YEARS OF  
PITHECANTHROPUS  
THE *HOMO ERECTUS*  
PROBLEM**

Edited by

**JENS LORENZ FRANZEN**

**Forschungsinstitut Senckenberg  
Frankfurt am Main**

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## The Case for Sinking *Homo erectus*. 100 Years of *Pithecanthropus* is Enough!

Milford H. Wolpoff, Ann Arbor (U.S.A.)

Alan G. Thorne, Canberra (Australia)

Jan Jelínek, Brno (Czech Republic)

Zhang Yinyun, Beijing (Peoples Republic of China)

### Abstract

Some half-century ago, *Homo erectus* came to replace a variety of geographically distinguished genera, including "*Pithecanthropus*", "*Sinanthropus*", "*Meganthropus*", "*Atlanthropus*", in order to clarify the evolutionary process by burying a nomenclature that was obscuring it. With the discoveries and theoretical advances of recent decades, the continued use of *Homo erectus* has now become a major impediment to understanding the Pleistocene evolution of humans. Moreover, there is good reason to regard the taxon itself as invalid.

We propose here to merge *Homo erectus* within the evolutionary species *Homo sapiens*. The origin of *Homo erectus* lies in a cladogenic event at least 2.0 myr ago. We view the subsequent lineage as culturally and physically adapted to an increasingly broad range of ecologies, ultimately leading to its spread across the old world prior to the beginning of the Middle Pleistocene. *Homo erectus* differs from *Homo habilis* in a number of ways. The vast majority of these distinctions also characterize *Homo sapiens*. The few distinctions of *Homo sapiens* that are not shared with *Homo erectus* appear to be responses to, or reflections of, continuing evolutionary trends of increasing cultural complexity, increasing brain size, and the progressive substitution of technology for biology.

*Homo erectus* is a polytypic species, divided into several distinct geographic variants which each show at least some genetic continuity with the geographic variants of the polytypic species *Homo sapiens* that is reflected in shared unique combinations of morphological features. There is no distinct boundary between *Homo erectus* and *Homo sapiens* in time or space, and cladogenesis does not seem to mark the origin of *Homo sapiens*. Instead, the characteristics of *Homo erectus* and *Homo sapiens* are found to be mixed in seemingly transitional samples from the later Middle Pleistocene of every region where there are human remains. The regional ancestry of *Homo sapiens* populations makes monophyly impossible for the species if the earlier populations are in a different species. We interpret this to mean that there is no speciation involved in the emergence of *Homo sapiens* from *Homo erectus*. These reasons combine to require that the lineage be regarded as a single evolutionary species.

### Kurzfassung

Vor ungefähr einem halben Jahrhundert ist der Begriff *Homo erectus* an die Stelle einer ganzen Reihe geographisch unterschiedener Gattungen, wie "*Pithecanthropus*", "*Sinanthropus*", "*Meganthropus*", "*Atlanthropus*", getreten, um eine Nomenklatur zu ersetzen, welche die stattgefundenen Evolutionsprozesse bis dahin eher verbarg. Infolge der Entdeckungen und theoretischen Fortschritte der letzten Jahrzehnte ist der fortgesetzte Gebrauch des Begriffes *Homo erectus* nunmehr selber zu einem Hindernis geworden, wenn es darum geht, die Evolution des Menschen im Pleistozän zu verstehen. Mehr noch, es gibt mittlerweile gute Gründe, dieses Taxon überhaupt als ungültig zu betrachten.

Daher schlagen wir vor, *Homo erectus* in der evolvierenden Art *Homo sapiens* aufgehen zu lassen. Der Ursprung des *Homo erectus* liegt in einem Abspaltungsprozeß, der mindestens 2 Millionen Jahre zurückliegt. Wir betrachten die daraus hervorgegangene Entwicklungslinie als kulturell wie physisch an eine zunehmend breite Spanne von Umweltbedingungen angepaßt, was schon vor Beginn des Mittel-Pleistozäns zu ihrer Ausbreitung über die Alte Welt führte. *Homo erectus* unterscheidet sich von *Homo habilis* in vielfältiger Weise. Die Mehrzahl dieser Unterschiede charakterisiert auch den *Homo sapiens*. Die wenigen Unterschiede, die der *Homo sapiens* nicht mit dem *Homo erectus* teilt, erscheinen wie Reaktionen auf Entwicklungstendenzen in Richtung auf zunehmende kulturelle Vielfalt, zunehmende Größe des Gehirns und fortschreitenden Ersatz von Biologie durch Technologie.

*Homo erectus* ist eine polytypische Art, aufgesplittert in mehrere geographische Varianten, von denen jede zumindest einige genetische Kontinuität mit entsprechenden geographischen Varianten des ebenfalls polytypischen *Homo sapiens* aufweist. Dies drückt sich in einzigartigen gemeinsamen Merkmalskombinationen aus. Es gibt keine deutliche Grenze, weder zeitlich noch räumlich, zwischen *Homo erectus* und *Homo sapiens*. Der Ursprung des *Homo sapiens* scheint nicht auf einen Abspaltungsprozeß zurückzugehen. Statt dessen stellt man in jeder Region mit Funden aus der Zeit des vermutlichen Übergangs im späten Mittelpleistozän fest, daß sich charakteristische Züge des *Homo erectus* mit solchen des *Homo sapiens* vermischen.

Die regionale Abstammung des *Homo sapiens* stünde im Widerspruch zur Annahme seiner monophyletischen Entstehung, würde man die früheren Populationen einer anderen Art zuordnen. Wir interpretieren dies in dem Sinne, daß die Entstehung des *Homo sapiens* aus dem *Homo erectus* mit keiner Speziation verbunden war. Das führt zu der Forderung, diese Entwicklungslinie als eine einzige evolvierende Art anzusehen.

### Introduction

More than 50 years after DUBOIS discovered the first true "missing link", and 40 years after SCHWALBE (1899) provided the first comparative analysis of the Trinil skullcap, workers such as LEGROS CLARK (1940) argued that a variety of similar forms be subsumed in "*Pithecanthropus*". Ten years later the variation was described at an even lower taxonomic level as *Homo erectus* replaced "*Pithecanthropus*" in order to clarify the evolutionary process by burying a taxonomic no-

menclature that was obscuring it (MAYR, 1950). Perhaps ironically, with the discoveries and theoretical advances of the decades since, the continued use of *Homo erectus* may now have become the major impediment to understanding the Pleistocene evolution of humans. There are good reasons to consider the taxon invalid. We propose here to merge *Homo erectus* within the evolutionary species *Homo sapiens*.

### Understanding Polytypism

Perhaps the most important impetus for examining the question of whether *Homo erectus* and *Homo sapiens* should be regarded as different species, derives from an appreciation of the problems involved in interpreting the evolution of polytypic species. With regard to the evolution of Pleistocene *Homo*, there are two historic sources for these problems. First, there is a series of questions that have been raised by criticism of WEIDENREICH's (1943, 1946) polycentric theory; actually, questions of HOWELLS' misrendering of the theory. Second, there are problems involved in understanding the evolution of polytypic species that stem from the acceptance of species definitions that simply do not allow past polytypic species to have existed.

Because of his (at that time) unique experience with the human evolutionary record for three continents, WEIDENREICH had a prescient view of the pattern of human evolution. He contended that human evolution was best understood as a network of interconnected populations that retained regional continuity within at least some geographic areas, which he called centers (hence "polycentrism"). Each of the four major evolutionary centers he proposed retained differences at the racial level (1947), and could be directly related to the races of today. At the same time there was significant gene flow between regions and the evolving species maintained its unity as a whole. For instance, in summarizing his understanding of Australasian evolution, he wrote (1943: 249-250): "at least one line leads from *Pithecanthropus* and *Homo soloensis* to the Australian aborigines of today. This does not mean, of course, that I believe all the Australians of today can be traced back to *Pithecanthropus* or that they are the sole descendants of the *Pithecanthropus* - *Homo soloensis* line."

In other words, while WEIDENREICH believed that significant aspects of the skeletal morphology of Aboriginal Australians were to be found in their regional antecedents, the Javan *Homo erectus* people, he never regarded this as a unique ancestral-descendant relation. He posited that some of the ancestry of the

Australians is to be found elsewhere, and not all of the descendants of the Javans live in Australia.

WEIDENREICH illustrated this evolutionary pattern as a trellis, with main vertical lines representing the centers of evolution, and diagonal connections between them reflecting the patterns of genetic interchange. This would seem quite straightforward, but after his death the theory was misinterpreted in an illustration that reproduced the vertical lines of descent but did not retain the diagonal lines of gene exchange - HOWELLS' (1959: 236) "Candelabra" theory. This was attributed to WEIDENREICH and characterized as the theory in which: "Human evolution progressed in each corner of the world, (essentially apart) from what was happening in the other corners" (p. 234).

HOWELLS asked of this theory, how one could explain the independent evolution of four major races: "WEIDENREICH has at least four different evolving human varieties, living far apart, moving ahead by fits and starts, producing their own special peculiarities of form ... Yet these four careers at last converged to produce the same kind of man everywhere. And all, miraculously enough, breasted the tape at the same time" (p. 235).

HOWELLS discounted and discredited the theory because he could provide no answer as to how this could have happened. This is not surprising, in view of the fact that the "four independent converging lines" were actually a consequence of HOWELLS' misinterpretation of WEIDENREICH's theory. Yet, in spite of its origin in a misrepresentation, the assumption that there must be parallel independent lines in a regional continuity view of human evolution has taken on a life of its own. For instance, it has become a centerpiece of similar criticisms of the Multiregional Evolution concept (THORNE and WOLPOFF, 1981; WOLPOFF, WU, and THORNE, 1984) that builds on WEIDENREICH's publications - see KLEIN (1990), STRINGER and ANDREWS (1988), BRACE (1991), ROUHANI (1989), FAGAN (1991), and LEWIN (1991b). This misrepresentation has

its own intellectual history, independent of the evolutionary model it misquotes, and has become one of the important sources of criticisms raised about explanations of Multiregional Evolution.

Even given the correct interpretation of WEIDENREICH's polycentric trellis model, the question remains as to how the geographic demes he envisioned for *Homo erectus* could have remained distinct across a species boundary, if *Homo sapiens* evolved out of this ancestral species. WEIDENREICH himself, as discussed below, never regarded this as a serious problem since in his "Single Species Hypothesis" he regarded all Pleistocene *Homo* (as known then) as *Homo sapiens*.

However, WEIDENREICH's hypothesis was not widely accepted, which brings us to a more general

consideration, the lack of evolutionary modeling for polytypic species. This is surprising, in view of the significant number of living polytypic vertebrate species most of us are familiar with (MAYR, 1969: 38-50), such as bears, dogs, baboons, and other mammals including e. g. *Homo sapiens*. Other polytypic species include birds of paradise and pigeons, kingsnakes and pythons, varanid and scincid lizards, Salamanders and tree frogs. In contrast, polytypic fossil species are virtually unknown (VAN VALEN, 1966), and the question we find interesting is why this is so. In particular, we are concerned that this might be an artifact of how species are defined in the fossil record, theoretically as well as operationally [LEVINTON and SIMON, 1980; and see KIMBEL and RAK (1992)].

### Species Definitions

It has been suggested that the virtual absence of descriptions of polytypic species in the fossil record could be an artifact of applying the criteria of morphospecies (i.e. phylogenetic species) (WOLPOFF, WU, and THORNE, 1984: 448; TURNER and CHAMBERLAIN, 1989). A number of authors have equated these, including most recently BOCK (1989: 54-55) who dismisses both because "they fail to distinguish between the species and the phyletic lineage". Current usage of morphospecies, or phylogenetic species, continue to define polytypism out of existence on the species level. However, we believe that the evolutionary species concept of SIMPSON (1961), especially as developed by WILEY (1978, 1981) provides a very productive alternative approach for examining the problems posed by polytypism in the fossil record. WILEY (1978) defines an evolutionary species as: "a single lineage [one or more demes that share a common history of descent not shared by other demes] of ancestor-descendent populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate."

We find this a useful definition, and one which corresponds closely to the species concept we have developed over the last decade to deal with the special problems engendered by the existence of evolving polytypic species within *Homo*.

The evolutionary species concept by implication retains the essence of MAYR's (1963) biological species - reproductive isolation - while avoiding many of its deficiencies: lack of time-depth, absence of operational criteria, and perhaps most importantly emphasis on reproductive ties (gene flow) as a major cohesive force (LEWONTIN, 1974). The biological species concept does not provide for an explanation of cohesion with species that is fundamental to the evolutionary species concept; that is, the observation that reproductive boundaries are a critical aspect of the main characteristic shared across the populations of a species - its evolutionary pattern (WILEY, 1981; WOLPOFF, WU, and THORNE, 1984). Evolutionary species can be seen as biological species

extended over time. The concept provides a clear link between the biological species and chronospecies. Indeed, BOCK (1986) regards the biological species as a paradigm that encompasses the evolutionary species concept, and we have little disagreement with this since the difference between a focus on gene flow vs. breeding boundaries is one of emphasis. Both mechanisms play a significant role in partitioning and controlling genetic variation within internally subdivided species.

One weakness of the biological species concept that is of particular concern to paleontologists is the difficulty of translating the main criterion of the biological species - lack of actual or potential interbreeding - into useful morphological criteria. In contrast, the evolutionary species emphasizes a behavioral aspect of a species that is readily translated into morphological criteria: the evolutionary importance of behavioral mechanisms that promote species recognition (PATTERSON, 1985): Concerning species, one aspect of estimating whether two forms have different identities is to examine various mechanisms that promote identity. The most important aspects for many species include recognition systems permitting individuals to discriminate between other members of their species and members of other species (WILEY 1981: 25).

A corollary of this definition is that the identification of successive species along a single evolutionary lineage, i.e. phyletic speciation, is unnecessary (WILEY, 1978; BONDE, 1981; BOCK, 1986). The basis for this assertion is of some interest in our considerations of the *Homo erectus* problem. We accept two of the reasons proposed for setting this widely accepted precept aside (WILEY, 1981: 39-41) as being particularly valid. These are: (1) the arbitrariness of phyletic species recognition (see SIMPSON, 1961: 165), and (2) the arbitrary mechanisms consequentially thought to promote phyletic speciation. Dismissal of the phyletic speciation concept, of course, does not imply rejection of phyletic evolution, or of gradualism as an explanation of it (contra GINGERICH, 1985). Quite the opposite, as BOCK (1986, 1989) has pointed out, speciation (the

of phyletic lineages) results from the normal processes of phyletic evolution, under "the special boundary conditions of an external isolating barrier". RIGHTMIRE (1990: 181-186) provides a very balanced discussion of this problem. Yet, he defends the phyletic speciation concept. He criticizes evolutionary species (p. 185) for encompassing too much variation ("individuals assigned to one 'species' differ substantially more in size and form than do representatives of living groups") while ironically it is WEIDENREICH's (1943) observation of just the opposite, that the normal range of variation in living humans encompasses most of the variation found in the hominid Pleistocene fossil

record, that led him to propose a single species hypothesis for all Pleistocene humans (except australopithecines).

With many systematists, we accept the precept that cladogenesis is the only way new species are formed, whether or not one of the daughter species can be separated from the parental one, as discussed by WILEY (1981: 34-35). In the fossil record, the absence of evidence reflecting cladogenesis in the origin of *Homo sapiens* from some or many populations of *Homo erectus* would support the hypothesis that only one evolutionary species is represented.

### Polytypic Species: Defined out of Existence?

As noted above, we have been concerned with the possibility that past polytypic species may have been "defined out of existence" and suspect that their perceived absence from the evolutionary record might better reflect the species definition used than paleobiological reality (see also TURNER and CHAMBERLAIN, 1989: 121). In response to this contention, it has been asserted that the absence of past polytypic species is not an artifact of definitions, but instead that "a poor fossil record of polytypic species ... may ... reveal something important about the lack of stability of geographical populations across geological time" (KIMBEL, 1991: 362).

The explanation offered for this supposition is in the form of a comment that is neither specific nor documented. According to (KIMBEL 1991: 362-363): "intraspecific geographic differentiation ... is largely ephemeral. The vast majority of local populations of polytypic species either become extinct or merge with parent populations as environments change and shift geographically over time and, as such, certainly could not be expected to leave behind much of a fossil record, let alone one with substantial time depth. Since significant morphological diversification among early hominids could hardly have proceeded without the geographic isolation and subsequent expansion of differentiated local populations, it is far more likely that the fossil record of this diversity reflects the successful establishment of new species."

Two consequences of this extraordinary assertion are: (1) that it should not be possible to recognize antecedent forms leading to existing human subgroups (i.e. today's races have no discernible ancestors), and (2) that either the majority of the living human subgroups will soon disappear, or that they will all merge into one single panmictic morph.

It follows that past polytypic species cannot be uncovered. If they existed at all they were ephemeral, and one does not expect a fossil record of ephemeral organisms. When there "seems" to be evidence of a polytypic species persisting over time, it must be a consequence of misinterpreting the fossils. We believe that this mainly demonstrates the validity of our initial concern. If past polytypic species are not defined out of existence, they are argued out of existence.

What we understand of this argument is that since polytypic species cannot be recognized in the past, we are to assume that they don't exist (or didn't exist for any significant length of time.). As KIMBEL (1991: 363) puts it: "To treat morphologically diverse clusters in the fossil record as subspecies confuses an arbitrary tool of taxonomy with evolutionary units."

But we contend instead that this stricture confuses evolutionary units by use of an arbitrary taxonomy. We, in contrast, believe that it is the present that should be a guide for interpreting the past and not visa versa.

### Species Recognition - Its Role in Polytypic Species

A species mate recognition system may be critical in maintaining reproductive boundaries between species, especially at the time of speciation (PATTERSON, 1985). Mate recognition is of particular importance among sibling species, or when an adaptive radiation brings closely related species into competition (MAYR, 1963). By maintaining reproductive boundaries, it is widely regarded as a mechanism that helps maintain species cohesion.

An understanding of the role of the mate recognition in internally subdivided species, however, has

been less well developed. In internally subdivided social species with gene flow between demes, there are multiple levels of cohesiveness. In these cases there is some level of cohesiveness within the demes themselves. This localized pattern within species may reflect WRIGHT's (1967) plateaus of stable adaptations, but there are other factors which also act to maintain cohesiveness in such demes. One of these which we believe is important in humans and other social species is the problem of differential interactions oriented by kin recognition, an aspect of behavior that is a necessary

requirement for any inclusive fitness considerations. We propose that certain mechanisms of mate recognition, balancing learned behavior and genetic predisposition to recognize certain resemblances, have evolved to meet this problem in polytypic species where migrations and mate exchanges provide a special opportunity for interactions with unrelated individuals.

When taking the problem out of the human arena, where kinship and alliance are of significant importance in mate choice, phenetic similarities play a role for other species. The complex nature of this role derives from the fact that simple similarity would enhance mating with sibs, or other close kin. How a balance is reached is suggested by a study of Japanese quail (BATESON, 1982). These birds show a clear preference for first cousins, remaining in their proximity significantly more often than in proximity with birds with other degrees of relationship (including sibs) and unrelated birds. In fact, the quails spent the least time in the proximity of their sibs. Time spent in proximity is directly related to mate choice in this species (BATESON, 1978).

The most strongly preferred mates are slightly different from individuals that are familiar from early life (BATESON, 1982). Recognition, in the quails, is based on the plumage. In humans recognition of individuals is mainly based on features of the face and we do not believe it is a coincidence that the face is where

most of the externally visible features showing regional continuity are found.

Despite the demic differences described above, no human geographic deme, today or in the past, shows a set of unique evolutionary changes that would be expected to characterize a distinct evolutionary species. These demes are not ancestral-descendent populations, each with their own distinct evolutionary tendencies and historical fates. Unique evolutionary tendencies and a historic fate characterize the species as a whole, and not any subdivision of it. The unique evolutionary tendencies in all Pleistocene *Homo* populations, widely recognized for a number of decades, involve (among other things) expansion of cranial capacity, reductions in the posterior dentition, and in skeletal robusticity. These characterize the species as a whole and involve documented changes in every geographic region with a fossil record since the beginning of the Middle Pleistocene. They are unique to no region.

We believe that some of the unique features within each local region, are important in kin identification. On the other hand, other skeletal features that show regional continuity clearly have no expression that is readily observable during life (incisor shoveling, foramen ovale form, mylohyoid foramen form, nasal sill morphology). These probably better reflect genetic continuities that are fully non-adaptive.

### Geographic Species in *Homo*: Implications for Modern Variation

Several authors have proposed that *Homo erectus* is a composite taxon that, in reality, includes a number of different genetically distinct lines, or species (ANDREWS, 1984; CLARKE, 1990; KENNEDY, 1991; STRINGER, 1984; TATTERSALL, 1986; WOOD, 1984). These proposals certainly support our assessment of persistent regional differences in *Homo*, but we do not concur with the species level of taxonomic difference central to the proposals, as detailed below. In many cases the basis for this interpretation lies in the "phylogenetic species concept" (ELDRIDGE and CRACRAFT, 1980), which defines species as "a diagnosable cluster of individuals within which there is a parental pattern of ancestry and descent, and beyond which there is not" (p. 92).

Phylogenetic species are distinguished by the presence of one or more uniquely derived features (autapomorphies) according to this view (ELDRIDGE and CRACRAFT, 1980: 107; TATTERSALL, 1986, 1991; KENNEDY, 1991). This definition means that species are, as BOCK (1989: 55) perhaps best puts it, "what(ever) a taxonomist recognizes as such".

The phylogenetic view of species has no basis in the biological species concept. As TATTERSALL admits (1991: 80): "the Phylogenetic Species Concept, which defines the species as the minimal diagnosable unit, is

clearly not applicable to the living biota since it fails to admit the crucial distinction between differentiated populations where the irreversible genetic event of speciation has and has not intervened." Moreover, the concept addresses none of the issues important in the biological species concept, such as the question of how cohesiveness is established (for instance whether through a common adaptive plateau, homeostatic mechanisms, or external boundaries to gene flow). In general phylogenetic species do not conform to the genetic notion of a species as protected gene pools. The concept, in all, places paleontologists between the jaws of a dilemma. To ignore it is to dismiss the most unambiguous and easily reproducible means of defining something called a past species, while to employ it is to make comparisons of past with living species into comparisons between apples and oranges, and to dismiss the answers that many studies of living species provide for questions about how the evolutionary process works.

Support for the interpretation of multiple geographic species in Middle and Upper Pleistocene *Homo* mainly rests on the assumption of validity for the phylogenetic species concept, since it relies on establishing the presence of long lasting morphological differences between demes (especially in ANDREWS (1984), although see TURNER and CHAMBERLAIN (1989) and

BRÄUER (1990) for contrary views on whether the differences actually occur). However, if there actually were multiple geographic species of *Homo* in the Middle and Upper Pleistocene, evolution within this adaptive radiation would involve a heretofore unknown magnitude of homoplasy. The parallel trends in these species, involving brain size expansion, posterior dental reduction, postcranial gracilization, toral degeneration, among other changes, would provide an unprecedented opportunity to develop innovative explanations.

Moreover, if the geographic variants of *Homo erectus* are to be regarded as valid species, several of the living races of *Homo sapiens* would have to be regarded as valid species as well. This is because in many cases the same unique combination of skeletal features that differentiate the geographic variants of *Homo erectus* have been found to differentiate geographic variants of living people (WEIDENREICH, 1943, 1946;

COON, 1962; THORNE and WOLPOFF, 1981; WOLPOFF, WU, and THORNE, 1984; HUBLIN, 1986; JELÍNEK, 1980a, 1981, 1982; WU, 1987, 1988b; VAN VALEN, 1986; POPE, 1988, 1991; ECKHARDT, 1987, 1989; ETLER, 1991). However, the fact that there is only one polytypic species of living humans, the evidence linking some of the geographic variants of that species to the geographic variants of the Middle Pleistocene, and the precept that the present should be used to interpret the past, combine to provide a convincing reason to set contentions of speciation within *Homo erectus* aside.

The view that *Homo erectus* is a single polytypic species continues to receive wide support from a number of scholars, many of whom do not agree on other aspects of the human evolutionary pattern (cf. BRÄUER, 1990; BILSBOROUGH and WOOD, 1986; DELSON, 1990; ECKHARDT, 1987; HOWELLS, 1980; TURNER and CHAMBERLAIN, 1989; WOLPOFF, WU, and THORNE, 1984).

### The "Transition" Problem

Where is the boundary between *Homo erectus* and *Homo sapiens*? There are four areas of the world where the fossil records are sufficient to examine this question. In Indonesia, the Ngandong sample has defied taxonomic assessment. It is not that workers lack opinions, but rather that the opinions do not appear reconcilable. In Africa, Europe, and Asia, samples variously allocated to *Homo erectus* and *Homo sapiens* appear to overlap in time during the later Middle Pleistocene (approximately 200-400 kyr). In all three regions, the overlaps may simply be the result of poor dating. If the dating is accurate, however, do we have evidence of one species replacing another with populations that are contemporaneous for a period of time, or do we have evidence of the inability to draw a distinct boundary between the two taxa because there is no boundary? Can the seeming chronological and anatomical overlap of different morphs be taken as evidence that a transition is taking place at this time, perhaps more noticeable because the rate of change may be faster than that earlier or later?

In the African fossil record this period is very well represented. The latest crania show clear continuity with recent and modern African populations (JELÍNEK, 1980b). Earlier, Lake Ndotu, Kabwe, Elandsfontein, Bodo, Salé, and Thomas Quarry crania seem to date to this general span (HUBLIN, 1986). RIGHTMIRE (1990) regards the former four as *Homo sapiens* and the later as *Homo erectus*, while admitting to some *sapiens*-like features in Salé, and some *erectus*-like features in Broken Hill and Ndotu. HOWELLS (1980) regards Kabwe and Elandsfontein as *Homo erectus* specimens (Bodo was not well known in 1980). CLARKE (1976) first regarded Ndotu as a new subspecies of *Homo erectus*, largely based on the unexpected conclusion that the occipital contours and "thickened"

nuchal torus were like the Zhoukoudian remains. He has more recently come to agree with most others in classifying the specimen as *Homo sapiens* (1990).

The entirety of this sample might, in fact, be allocated to early *Homo sapiens* (WOLPOFF, 1980a). The three earliest of the crania are of special interest, since they best reflect a mix of characteristics. Salé seems to be the most ancient of the crania (HUBLIN, 1986; CLARKE, 1989). It is a very small vault that lacks supraorbitals and face. Salé is at the low end of the *Homo erectus* range, approximating 880 cc. in endocranial volume and has other *erectus* features such as thick cranial vault bones. However, it lacks a superior nuchal line and the nuchal musculature is clearly developed pathologically. The cranium is rounded, almost globular, as seen from above, and it is quite gracile in the *Homo erectus* context. Seemingly modern features of the occiput are probably attributable to this condition (HUBLIN, 1985), and the specimen is as difficult to classify as it is to date. The Thomas Quarry frontal, which may not be fully adult, is small. The supraorbitals are moderately thick and projecting, and by itself this region resembles *Homo erectus*. The remaining portion of the vault, however, suggests a shorter and more rounded cranium, and in this respect it resembles Salé. The other of the older crania in this sample is Bodo, a very large specimen with an extraordinary facial size (its nasal breadth is the largest known in *Homo*). The size and robustness of the facial region, including supraorbitals, provide an anatomical link with African *Homo erectus*, but it is clearly a much larger cranium than any vault traditionally allocated to this taxon. The later crania are also characterized by a morphological mix of features, and it would be difficult to establish a clear boundary, morphologically or temporally, between African *Homo erectus* and *Homo sapiens* based on these crania. As CLARK (1989: 565) put



it, there is a "variable degree of mixing of *Homo erectus* and modern characteristics."

Crania from the later Middle Pleistocene of Europe include Steinheim, Swanscombe, Biache, Arago, and Petralona that are usually considered to be early *Homo sapiens* (WOLPOFF, 1980b and references therein - although not by STRINGER (1981) who interprets the differences among them differently). In fact there is a tendency to consider all of the European finds as *Homo sapiens* (c.f. HOWELL, 1960), although some find this problematic for the more robust specimens. Bilzingsleben is sometimes regarded as *Homo erectus* (VLCEK, 1978), and Vértesszölös has been described as a *Homo erectus/sapiens* specimen by THOMA (1966). In fact, it is likely that the main source of variation between these specimens is not phylogenetic at all, but rather combines time and sexual dimorphism. This variability is exacerbated by the likelihood that the males (Petralona, Bilzingsleben, and Vértesszölös) appear to be earlier than the females, but its presence in a single population is confirmed at Atapuerca.

Bilzingsleben is the only specimen consistently regarded as *Homo erectus*. Yet, when the fragments of this specimen are compared with the much more complete cranium from Petralona, numerous similarities emerge. The frontals share a high nasion position with a flat, projecting glabellar region above it. The central supraorbital region projects markedly anterior to the base of the low-angled frontal squama, and the anterior margins of the supraorbitals preserved in Bilzingsleben suggest that both specimens also share a low upper facial angle. There is also significant similarity in the occiputs, where comparisons are possible, although the occipital plane of Petralona is somewhat longer, mainly due to the presence of a very large extra-sutural bone at lambda. The angle between the nuchal plane and the vertical face at the back of the occiput is virtually identical, as is the form of the low, vertically thick and horizontally extensive nuchal torus, lacking any supratoral sulcus or resorbed area above it. Both crania are very thick, especially posteriorly. The third male, represented by the occipital from Vértesszölös, shares some of these similarities although the eroded torus is more medially restricted while the nuchal plane is much longer than the occipital plane (WOLPOFF, 1977) - a feature particularly reminiscent of *Homo erectus*.

None of the females have been regarded as *Homo erectus*, and these specimens differ especially in the occipital regions, preserved in Steinheim, Swanscombe, and Biache. Yet, the (low) parietal height/(high) occipital breadth relation of the three is very archaic. The size of the crania, especially Steinheim that may be only slightly larger than 900 cc (WOLPOFF, 1980b), and the thickness and projection of the Steinheim supraorbital tori, combine to reveal features that are more archaic than often perceived. The greatest differences between the more and less archaic specimens in this sample are occipital differences that

very conceivably could be attributed to sexual dimorphism although the temporal difference may play a role as well. It is most reasonable to conclude that this is a sample with mixed morphology, partitioned into two distinct subsets because of the marked sexual dimorphism and earlier dates for the males.

This period in China is rich with crania, including the Zhoukoudian H3 (CHIU et al., 1973; WU and LIN, 1983) and Hexian (WU, 1983; WU and DONG, 1985) crania which are often regarded as *Homo erectus* (WU and DONG, 1985; WU and LIN, 1983). Moreover, there are specimens from Jinniushan (LŠ, 1989), Dali (WU, 1981; WU and WU, 1985), and Chouhu (ZHANG, 1984, 1986) that have been allocated to *Homo sapiens*. Of these, the Zhoukoudian specimen is clearly the most *erectus*-like, and is the oldest. When it was described, CHIU et al. (1973) pointed to a number of progressive trends the specimen suggests, when compared with the earlier locality 1 materials, including brain size expansion and supraorbital reduction (also see WU and LIN, 1983). Progressive trends in the dental remains from Zhoukoudian were more recently established by ZHANG (1991). He was able to show that a pattern of reduction characterized the later to earlier teeth from the site that was very similar to other cases of Middle Pleistocene hominid dental reduction.

Hexian would appear to be later, and in many respects is unlike the Zhoukoudian remains and instead resembles the Indonesian humans (WOLPOFF, 1985). This suggests that there may have been a gradient in morphology running from the north to the south of East Asia, and that some of Hexian's features may better reflect this gradient than its taxonomic affiliation. The more southerly specimens have proven extremely difficult to classify, as is discussed below. Chouhu (ZHANG, 1984; ETLER, 1990), the most fragmentary of the specimens, is quite unlike former two in occipital morphology but in our view could easily represent a step as the local *Homo erectus* condition evolves into a more modern morphology. It is much like the European female described above. Jinniushan and Dali both mix *erectus* and *sapiens* characteristics. Jinniushan, which may be considerable later (POPE, 1992), combines a large and thin cranium with a gracilized posterior (LU 1989), and an anterior frontal and face that is reminiscent of the L2 Zhoukoudian female. As a whole the sample shows a mix of features that characterize *Homo erectus* and *Homo sapiens* locally (JELINEK, 1982). Each specimen has a different combination of these features.

In Java, the only hominids that can be related in any way to the transition question are represented by the Ngandong cranial population. Instead of two morphologies in this case, there has simply been a long term disagreement about how to classify these people. Some include them in *Homo erectus* or its equivalent (cf. LE GROS CLARK, 1955) "*Pithecanthropus*" (JACOB, 1967, 1981; SANTA LUCA, 1980; HOWELLS, 1980; RIGHTMIRE, 1990, 1991), while others include them in



*Homo sapiens* (THORNE, 1971; WOLPOFF, 1980a), which can be seen yet again as indicating the difficulty in placing individuals in a transition period. Those who have hitherto considered the Ngandong people to be *Homo erectus* (cf. RIGHTMIRE, 1991) may now have to reconsider their position in the light of new dates that indicate this site may be as recent as 100,000 years (BARTSTRA, 1988). If maintenance of a *Homo erectus* status continues to be preferred for Ngandong, on anatomical grounds, it would have to be seen as evidence that there is an overlap of *Homo erectus* and *Homo sapiens* of at least 200,000 years duration. If true, this would also make the taxonomy of certain Pleistocene Australians very problematic, as many of them show the most detailed anatomical similarities with the late Pleistocene Indonesians (THORNE, 1984; WOLPOFF, 1991).

In sum, for those regions where appropriate fossils can be found, there are difficulties in clearly establishing where the *Homo erectus* - *Homo sapiens* boundary lies. We interpret this to indicate that there is

no clear boundary. The important point is that there appears to be a transition over similar time spans in four different places. There does not appear to have been a single origin of an anatomically distinct species in one region. In our view the taxonomic affiliations of the specimens discussed above are problems of classification and not of the perception of the evolutionary process. In some cases features attributable to the two species are mixed throughout the sample, while in others the sample as a whole has proved difficult to classify. For this reason we regard the solution to the taxonomic problem as arbitrary, and a matter of taste, rather than as a matter of systematics. What is more interesting, from our perspective, is the fact that there are any problems of classification at this boundary at all. Should there have been cladogenesis at about this time, we would expect taxonomic clarity rather than taxonomic confusion. There is a real contrast between the pattern of hominid variation during this period and the pattern of variation at the end of the Pliocene, when *Homo erectus* first appeared.

### Problem of Defining Modern *Homo sapiens* - What can be defined?

Another aspect of the lack of a clear boundary between *Homo erectus* and *Homo sapiens* is the absence of an operational definition for *Homo sapiens*. It is always possible that this absence reflects the validity of KIMBEL and RAK's (1992) remark that "there cannot be any definition of a species taxon because species are individuals, not classes". Yet they do admit that a species has diagnostic characters and in defense of their own favored species concept, the phylogenetic one, they assert: "The phylogenetic species concept ... does not require that characters of organismal clusters in a species be autapomorphic [but see KENNEDY, 1991], only that the organismal clusters themselves be diagnosable as representing a distinct reproductively cohesive lineage. ... species may be diagnosable by any unique set of character states."

But what if the species is not diagnosable by any set of character states? It is difficult to avoid the implications of the fact that there is great difficulty in diagnosing *Homo sapiens* skeletally in a manner that can be consistently applied across the geographic range of the living species.

Two definitions for *Homo sapiens* have been offered in recent years (HOWELL, 1978; DAY and STRINGER, 1982). Both of these equate *Homo sapiens* with modern *Homo sapiens*. The HOWELL definition was never operationalized, and in any event involves far too many criteria to be applied to most fossil remains. The DAY and STRINGER (1982) definition with or without the slight modifications provided by STRINGER and ANDREWS (1988), was found to exclude a large number of recent and living Aboriginal Australians from the human species (WOLPOFF, 1986; BROWN, 1990), and the authors accept that it is not valid (personal communication). This is not simply a

problem of trying to define instead of diagnose, as some would lead us to believe (cf. KIMBEL and RAK, 1992). If diagnostic features are a consequence of species, their absence has powerful implications for species recognition. KIMBEL and RAK (1992) note: "the diagnosis of a species taxon is a list of 'symptoms' of genealogical cohesion; diagnostic characters are those that are held to distinguish one genealogically cohesive system of parental ancestry and descent from other similar and/or closely related systems."

The inability to diagnose this particular species implies, then, the inability to show it is actually a distinct genealogically cohesive system.

In our opinion, the reason for this state of affairs is a consequence of both the pattern of evolution and the 'hidden agenda' in the definitions that have been proposed. The unsuccessful attempts to uniquely define *Homo sapiens* began with the assumption that the European Neandertals were not *Homo sapiens*, and developed criteria to identify *Homo sapiens* that showed this to be the case. These criteria do not work because they began with the wrong assumption. The underlying assumption for any definition of *Homo sapiens* must be about who is in it, and not who is not (WOLPOFF and THORNE, 1991). We must begin with the precept that all recent and living people are *Homo sapiens* (THORNE and WOLPOFF, 1991). A definition that begins here includes many, if not all, Neandertals in our species, as well as numerous individuals from other regions presently excluded. But such a definition would have its own problems, not the least of which is the exclusion of some Middle or Late Pleistocene individuals from *Homo sapiens* while other contemporaries are included (ZHANG, 1986). Does this mean that there were two contemporary species of *Homo*, coexisting at

different times in different places, or is it an artifact of the definition?

We believe the latter is the case. The underlying problem is that there does not seem to be a single unique recent origin for all living populations, and therefore it is understandable that we cannot find a single set of features that uniquely identifies them (such a unique set of characters is an expected conse-

quence of the single recent origin theory). Instead what we find is that different features show distributions that vary across both time and space, which irrevocably confuses clade and grade variation; that is, variation across demes and variation within demes over time. KIMBEL and RAK (1992) quite correctly say that "diagnostic characters do not make the species", but we believe that the absence of diagnostic characters goes a long way towards unmaking it.

### Does a Definition of *Homo erectus* include *Homo sapiens*?

LE GROS CLARK (1955) argued persuasively that the differing geographic variants of pre-*Homo sapiens* populations ("*Pithecanthropus*", "*Sinanthropus*", "*Meganthropus*", "*Atlanthropus*", and so on) should be lumped in a single taxon *Homo erectus*. He provided a definition for the species which, following his "present to past" approach to human evolution, served to distinguish *Homo erectus* from *Homo sapiens*. This distinction became the focus of other definitions of *Homo erectus*. For instance, HOWELLS (1980: 1) introduces his review with the observation "we should begin consideration of *Homo erectus* by considering *Homo sapiens*". The idea that *Homo erectus* should be defined in relation to *Homo sapiens* has become almost ubiquitous (see HUBLIN, 1986; HOWELL, 1978; RIGHTMIRE, 1988). But this is the opposite direction from that taken by the evolutionary process. It is, after all, *Homo sapiens* that evolved from *Homo erectus*. The more useful and informative question is what separates *Homo erectus* from its australopithecine ancestors. To our knowledge only three workers have addressed this issue, WOOD (1984), RIGHTMIRE (1990) and WOLPOFF (1991).

RIGHTMIRE (1990: 189) provided a short list of nine *Homo erectus* cranial features "that seem to be derived ... relative to earlier *Homo*". This list included almost all of features that WOOD (1984: 102) found to be derived in the species, relative to a last common ancestor of all *Homo* species. RIGHTMIRE pointed out that "there is variation, and not all characters are expressed in each of the individuals assigned to *Homo erectus*". In fact, we find that three of the nine features he discussed do not characterize enough *Homo erectus* specimens to be accurate in a diagnosis. Omitting these, the characters remaining are italicized in the list below (note, however, that while referring to the same character states, they are often defined somewhat differently).

WOLPOFF'S (1991) description of *Homo erectus* uniquenesses is also in relation to *Homo habilis*, its contemporary and possible ancestor. This is summarized and expanded below. Characters that vary in magnitude or expression are included, as long as the variation does not include expressions that are common in *Homo habilis*. Many of the comparisons involve features that are sexually dimorphic in both species, and the comparisons take sex into account. In all cases the adult morphology is described:

- large body size;
- *large cranial vaults* (virtually all of the specimens lie above the maximum *Homo habilis* brain size thus far reported, of 750 cc);
- *anteriorly projecting, vertically thick and continuous supraorbital tori*, separated from the frontal squama by *supratoral sulci*;
- flattening of the frontal squama broken by a meiotic eminence;
- presence of a *sagittal keel*;
- reduced facial prognathism;
- broadening and lowering of the face (specifically, expansion of the midface, zygomaxillary region, nasal breadth, and orbital size, with reduction of the lower face and mandible);
- lateral nasal aperture eversion;
- angulation of the nasal bones in the sagittal plane, and
- expansion of their breadth relative to the breadth of the nasal aperture (while the breadth of the nasal aperture itself expands);
- low temporal squama with a posterior border that is unarched;
- maximum parietal breadth at the mastoid (or asterionic) notch;
- *thickening of the cranial wall*, involving both cortices and diplotæ;
- kyphosis (flexion) of the cranial base;
- marked angulation between the tympanic and the petrous;
- presence of an occipitomastoid crest and digastric sulcus;
- a distinct *nuchal torus*, overhanging the superior nuchal line and marking a strong angulation between occipital and nuchal planes;
- *transversely wide occiput* with expanded nuchal muscle attachment area;
- dominance of sagittal length of the nuchal plane over the occipital plane length;
- coincidence of inion and opistocranium;
- relative size reduction in the later erupting premolars and molars, in the context of general reductions in the posterior teeth;

- lateral maxillary incisor expansion relative to the central incisors;
- reduction in the magnitude of sexual dimorphism, as expressed metrically and morphologically, especially sexual dimorphism in the canines;
- reduction in relative forearm length;
- appearance of transverse thickening of the femoral neck;
- weakened femoral pilaster and
- low pilastric index.

Taking into account the uneven preservation of cranial, mandibular, and body parts between regions, these features in combination describe normal variation in all of the taxon. With *Homo sapiens* excluded from the analysis, these are the autapomorphies that can be demonstrated for *Homo erectus*.

But *Homo sapiens* should now be considered, as the question asked here is to what extent *Homo sapiens* can be characterized, as a whole or in part, by these features. This question is not as simple as it might seem, as we envisage three different forms that shared unique features linking *Homo erectus* and *Homo sapiens* take. First, there are features that characterize earlier populations of the species, but become rare, attenuated or extinct later (for instance in living populations). Second, there are features which in *Homo sapiens* are further developed or more prominently expressed than in *Homo erectus*. Third, there are features whose expression changes, in some cases considerably. Variation in this pattern can occur once, or a number of times (cranial thickness, supraorbital development, and some of the facial changes exemplify this). These three possibilities delimit the question of how *Homo sapiens* relates to *Homo erectus*. The fact that they follow different patterns of variation reflects the evolutionary process, but the fact that they express a similarity in derived characters reflects a phylogenetic relationship.

Given these provisos, in the listing below, we indicate those apomorphic features of *Homo erectus* that also characterize some *Homo sapiens*. To weigh this comparison in the direction of maximizing difference, we restrict our *Homo sapiens* sample to the last 30,000 years, a period during which it is universally accepted that the only humans are unquestionably modern *Homo sapiens*. Moreover, we want to make it clear that presence in *Homo sapiens* means commonly present and does not mean that we were only able to

find a feature as a rare variant in a large number of crania. Nonetheless, it is evident that the great majority of features that distinguish *Homo erectus* from *Homo habilis*, are preserved in a significant number of *Homo sapiens* specimens:

- large body size;
- large cranial vaults
- vertically thick continuous supraorbital tori, which when present are separated from the frontal squama by supratatorial sulci;
- flattening of the frontal squama broken by ametopic eminence and presence of a sagittal keel;
- low facial prognathism;
- broad short faces (with broad noses and large orbits, and continuing reduction of the lower face and mandible);
- lateral nasal aperture eversion;
- paracoronary angulation of the nasal bones, and maintenance of nasal bone breadth relative to the breadth of the nasal aperture;
- low temporal squama with a posterior border that is unarched;
- maximum parietal breadth at the mastoid (or asterionic) notch;
- kyphosis (flexion) of the cranial base; petrotympanic angulation;
- presence of an occipitomastoid crest and digastric sulcus;
- a distinct nuchal torus, overhanging the superior nuchal line;
- relative size reduction in the later erupting premolars and molars, in the context of general reductions in the posterior teeth;
- lateral maxillary incisors remain substantially expanded relative to the central incisors;
- reduced sexual dimorphism, as expressed metrically and morphologically, including that of canines;
- short forearms;
- long legs;
- thick femoral necks.

#### **Do *Homo erectus* Autapomorphies Preclude a *Homo sapiens* Ancestry ?**

ANDREWS (1984) identified several autapomorphies in *Homo erectus*, and attempted to use them to show that *Homo erectus*, by any definition, was not a probable ancestor of *Homo sapiens*. The underlying assumption can be stated: "If it can be demonstrated that either *H. erectus* or *H. sapiens* ... possessed de-

rived traits not shared with the other group, then the hypothesis that they are conspecific can be rejected" (KENNEDY, 1991: 376). ANDREWS' study is widely cited as one of the more detailed of the recent cladistic analysis of the three species of *Homo*: *habilis*, *erectus*, and *sapiens*. The analysis, however, was based on se-

lected data from the literature (unfortunately not emphasizing facial characters). From it he recognized a short list of *Homo erectus* autapomorphies (with which we do not particularly concur): frontal and parietal keels, thickened cranial vault bone, angular torus, inion well separated from endinion, mastoid fissure separating the anterior face of the process from the petrosal crest, and a recess present between the entoglenoid process and the tympanic plate.

Using this list he developed two far-reaching proposals: (1) most *Homo erectus* specimens that are derived for these character states are from east Asia, and the African specimens are only linked to the Asian ones through plesiomorphic characters; (2) the existence of the autapomorphies indicates that *Homo erectus* could not be the direct ancestor of *Homo sapiens*. He concluded that the African and east Asian *Homo erectus* specimens were in different species and that the direct ancestor of *Homo sapiens* was *Homo habilis*.

We have great difficulty with the contention that autapomorphies can provide the basis for positing that one species cannot be the ancestor of another. We would prefer to believe that these species were capable of evolution and that features can change over time. Furthermore, HUBLIN (1989) makes quite the opposite case with regard to *Homo erectus* autapomorphies. He argues that most of these uniquely derived features can be related to the unusual skeletal mass that especially characterizes the later *Homo erectus* remains. As these are aspects of a single morphological complex, a reversal would not be unexpected and an ancestry for *Homo sapiens* could not be excluded. For reasons discussed above, we also do not accept the phylogenetic species concept as valid. Subsequently we too reject the associated notion that a single or a few autapomorphic features can define distinct species, because this would mean the breakup of polytypic species, past and present, and in particular would require the interpretation that living humans consist of several distinct species. Instead we contend that for a phylogenetic analysis to provide support for a hypothesis of ancestry, it must be through sister group analysis showing closeness of relationship, and not from the assumption that the evolutionary process does not operate in creating significant diversity within species.

### *Homo erectus* as a Stage of Human Evolution

SCHWALBE (1904), and much later ARAMBOURG (1958), outlined a model of human evolution emphasizing a progression through universal stages of organization. In this evolutionary model *Homo erectus* is seen as the ancestor of *Homo sapiens*, clearly not a point of contention among most paleoanthropologists, except for those who accept both the "Eve Theory" for the recent African appearance of modern humans and a definition of *Homo erectus* which restricts this species to east and southeast Asia. If *Homo erectus*, in its entirety or only one geographic portion of it, is regarded

Even more troublesome is the fact that the particular autapomorphies ANDREWS claims for *Homo erectus* are virtually all invalid. In particular the keeling, thickened vault bone character state (especially if the details of thickening are left unspecified as in the ANDREWS presentation), angular torus, and separation of inion from endinion characterize numerous late Pleistocene, Holocene, and living humans. This brings focus to another difficulty we have with the ANDREWS analysis (as well as those by STRINGER (1984) and WOOD (1984)). Most of these so-called autapomorphies they use are particularly common in the Australian variant of *Homo sapiens*, and regularly occur elsewhere. Are we to conclude that this makes Australians a different species, just as the Australasian *Homo erectus* variant is said to be a different species? Of course not, but it is for just this reason that the precept of using the present as a guide to understanding the past forces one to reject the contention of geographic speciation in *Homo erectus*.

In our analysis of the features distinguishing *Homo erectus* from *Homo sapiens*, we were able to identify only a few *Homo erectus* characters that we can conclude are not also shared by *Homo sapiens*:

- Anteriorly projecting supraorbital tori;
- thickening of the cranial wall, involving both cortices and diplöe;
- strong angulation between occipital and nuchal planes;
- dominance of sagittal length of the nuchal plane over the occipital plane length;
- coincidence of inion and opistocranium;
- weakened femoral pilaster and a low pilastric index.

Of these, some actually are present in recent *Homo sapiens*, albeit rarely, and many are common in earlier (or so-called "archaic") *Homo sapiens*. Moreover, all of these differences can be linked to the evolutionary trends that span both species, of increasing cultural complexity, increasing brain size (and therefore cranial vault size), and the morphological consequences of the progressive substitution of technology for biology. We contend that this short list does not provide a justifiable or valid foundation for suggestions that *Homo erectus* is not ancestral to *Homo sapiens*.

as the ancestor of *Homo sapiens*, the question remains whether the appearance of *Homo sapiens* involved a gradual (although perhaps accelerated) transition, or cladogenesis. The nature of the transition, and the absence of clear boundaries provides convincing evidence, in our view, that no species split occurred in these Middle Pleistocene hominids.

Evolutionary trends within the *Homo erectus* sample support this interpretation. Whether the sample is considered in its entirety (WOLPOFF, 1984; RIGHTMIRE, 1990), or regional sub-samples are de-

scribed (for instance, see ZHANG's 1991 analysis of the Zhoukoudian teeth or RIGHTMIRE's 1990 discussion of brain size change in Indonesia), numerous characteristics of *Homo erectus* show significant evolutionary change in the direction of *Homo sapiens* throughout the Early and Middle Pleistocene. These evolutionary trends are not all in the same direction. Thus, as brain size and many of the cranial dimensions increase, posterior tooth size and the dimensions of the mandibular corpus decrease.

Therefore, no single underlying cause, such as a change in body size, could account for these trends. *Homo sapiens* would appear to be their consequence.

Given the absence of cladogenesis between them, the question remains whether the specimens presently assigned to *Homo erectus* can validly be considered both a stage in human evolution and part of the species *Homo sapiens*. There are four ways of approaching this issue.

First, if the demes of the polytypic species *Homo erectus* are by in large related to the demes of *Homo sapiens*, as THOMA (1973) points out, the two taxa must be merged for the principle of monophyly to apply, even though there might be consistent differences that characterize all of the *Homo sapiens* demes. Otherwise, *Homo sapiens* would not consist of a group of geographic demes, their last common ancestor, and all the descendants of that ancestor.

Of course, this argument is weakened somewhat by the fact that genetic continuity reflected in some features is not the continuity of populations.

Second, species need not be regarded as static, and contrary to the assessments of some authors a phylogenetic approach does not rest on the assumption that punctuated equilibrium is the only mode of evolutionary change (WILEY, 1981). As discussed above, the evolutionary species concept allows for evolutionary change. In fact, the degree of variability is irrelevant to the issue since the species question is one of phylogenetics and not of phenetics. Without cladogenesis it seems quite unjustified to arbitrarily divide this lineage into species, whether or not there is significant evolutionary change within it. And in fact, within a broader primate context there is not that much difference between *Homo erectus* and *Homo sapiens*. The former can largely be subsumed within the range of the later.

Third, we can examine the question of whether subsuming *Homo erectus* within *Homo sapiens* results in an *unrealistically small* amount of phylogenetic diversity in the hominids. STANLEY (1979) argues that rates of speciation differ through the span of a taxon, and are highest early on (a pattern that well-fits the Hominidae). This would suggest that the longer a taxon exists, the lower the average rate of speciation within it. Summarizing a large body of data about speciation rates, FOLEY (1991: 416-417) predicts that the number

of species in the Hominidae is expected to range between 3 and 11, with a mean expectation of under 6. Without *Homo erectus* the minimum possible number of hominid species covering the approximately 7 myr of the Hominidae's existence would appear to be 5, in our view: *Australopithecus afarensis*, *A. boisei*, *A. africanus*, *Homo habilis*, *H. sapiens*. Virtually all workers believe there are more species than this, and we conclude that compared with expectations based on other primates, the problem with hominid taxonomy is clearly not that there are too few species!

Fourth, we can ask whether subsuming *Homo erectus* within *Homo sapiens* results in an *unrealistically large* amount of phenetic diversity within the resulting species. That this is an important question is suggested by the fact that at least one worker believes that, even as presently defined, *Homo sapiens* encompasses too much variation: "Most human fossils of the last half-million years are conventionally referred to the species *Homo sapiens*, which is thereby stretched to limits which would strain the average mammalian genus" (TATTERSALL, 1991: 80). But, is this actually true?

WEIDENREICH reported quite the opposite conclusion as a result of systematic comparison of fossil and living human variation with *Canis familiaris*. Of course one might argue that the variation in dogs is an invalid comparison because of their domestication and breeding into distinct types. Yet, domestication is a process often used to describe the later stages of human evolution, and the recognized dog breeds have been created by diversifying varieties and establishing high frequencies of different allele combinations, and not by different genes. They therefore remain as a valid model of the amount of genetic variation encompassed within a polytypic species, even though their phenotypic variation is packaged in an unusual way.

Moreover, the magnitude of variation within living humans is often underestimated. The impetus of WEIDENREICH's "single species hypothesis" was, after all, his experience from comparative anatomy, that the individual details of human fossils could be largely incorporated within the range of variation of living peoples. We concur, as it is our experience that the range of variation in recent *Homo sapiens*, whether in a single fossil sample (for instance the Klasies River Mouth Cave mandibles 16424 and 13400) or in a single living population of the species, often encompasses what others have regarded as multiple taxa (WOLPOFF, 1992). If this range is taken as "normal" for hominids of the Pleistocene, TATTERSALL's concern is clearly unwarranted.

Finally, we can ask whether the amount of variation within a species is a valid concern. TATTERSALL himself uses a species definition that relies on a distinct beginning (cladogenesis) and a distinct end (extinction or a second cladogenesis) to delimit the boundaries, as

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we do. Unlike us, he further accepts the criterion of a single unique link, establishing a unique ancestral-descendant pattern of relationship among the members. Nowhere within the phylogenetic definition he uses does the question of amount of variation appear, and we agree with this. The evolutionary species is also not delimited by the amount of variation it encompasses, for if it were, this would place an arbitrary limit on the amount of evolution that could occur in a species, an

#### Precedents for Sinking *Homo erectus*

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Our contention that *Homo erectus* cannot be validly distinguished as a different species from *Homo sapiens* has been embraced by a number of workers before us, spanning the last half-century. The first to address this issue, from the perspective of the modern conception of what constitutes *Homo erectus*, was WEIDENREICH. In discussing the nomenclature of the Zhoukoudian remains (1943: 246), he admitted that his use of "*Sinanthropus pekinensis*" was a convenience" ... without any "generic" or "specific" meaning or, in other words, as a "latinization" of Peking Man".

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His view of the Zhoukoudian taxonomy was quite explicit, and one with which we concur: "... it would not be correct to call our fossil "*Homo pekinensis*" or "*Homo erectus pekinensis*"; it would be best to call it "*Homo sapiens erectus pekinensis*". Otherwise it would appear as a proper "species", different from "*Homo sapiens*", which remains doubtful, to say the least." WEIDENREICH's primary reasons for this approach were threefold. First, as mentioned above much of the range of variation in *Homo erectus* can be subsumed within the normal range of variation of recent and living *Homo sapiens*. Second, the fossil races of *Homo erectus* correspond to the living races of *Homo sapiens*. Third, the total amount of variation in *Homo sapiens*, including fossil and living, is not especially great, in his comparative view. For instance, he found the differences among dog varieties to be at the level of subfamily variation in the higher primates - he held that the variation among dog varieties made a reasonable comparison for the human/gorilla differences - far exceeding the variation within *Homo sapiens*.

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THOMA (1962, 1973) presented an evolutionary model for Pleistocene hominids that was very similar to COON's (1962), in that he envisioned (1973: 532) "at least three collateral phyla [that] passed through three evolutionary phases, within the framework of a species.... Because the recent end points of [each] phylon is not separated from the others at a specific level, the taxonomic limits of *Homo sapiens* must be necessarily extended in the past back to the point of ramification" in order for it to be monophyletic.

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In this later precept, he differed from COON, who chose to retain the two species, *erectus* and *sapiens*, and then stumbled badly in trying to explain how different populations evolved from the one to the other. THOMA's analysis was based on a combination of two

unacceptable and unnecessary stipulation. The fact is that for species to be validly related in a phylogenetic scheme, their definition must allow for the pattern of descent to be established and for this the sizes of the entities are not important. This is the very sort of phenetic concern that the change in paradigms from species-groups-as-similar-entities to species-groups-as-related-entities is supposed to have avoided.

assumptions; he accepted the most important element of the biological species concept, that a species defines the limits to gene flow, and accepted the phylogenetic view that taxa are monophyletic. He concluded that given its geographic differentiation and ancestral position, *Homo erectus* could not exist as a valid separate taxon but must be regarded as an earlier portion of the polytypic species *Homo sapiens*.

On the basis of his allometric studies, HEMMER (1967, 1969) concluded that the ground-plan ("Anlage") of the cranium "is the same from the earliest definite members of the *erectus* group (e.g., "*Pithecanthropus IV*" from Sangiran, Java) to the modern races of *H. sapiens*.... Since these features vary among the recent races no less significantly than between different fossil groups, or between fossil and recent populations, it is impossible to draw a line anywhere for species delimitation unless one intends also to split up recent man into several species. Therefore it seems necessary to include all of these fossil and recent groups in the single species *H. sapiens*" (1969: 179).

The problem of consistency has plagued all of those who have tried to equate fossil and modern geographic variation in the same taxonomic scheme. The idea of separate species for living populations is unacceptable, and clearly incorrect, [although some have regarded the notion as valid, even in this century (HILL, 1940)]. The precept of using the present to interpret the past is clearly the acceptable approach for HEMMER, as well as for ourselves.

Although primarily concerned with early hominid evolution, ROBINSON (1967: 98) addressed the *Homo erectus* question as part of his general revision of hominid taxonomy. He argued that in the broad view of human evolution, "most of the obvious physical change had already occurred" at the time of the appearance of *Homo erectus*. All subsequent human populations were mainly characterized by a single evolutionary trend, in his view, "the realization of the cultural potential". He believed *Homo erectus* and *Homo sapiens* should therefore be subsumed in the single species *Homo sapiens*, because it has priority. It is ironic that if this viewpoint now becomes known as the "single species hypothesis", as WOOD (quoted in LEWIN 1991b) and KIMBEL (1991) propose, ROBINSON would have to be considered one of its earlier adherents.



JELÍNEK (1978, 1980a, 1981) considered *Homo erectus* as a subspecies of *Homo sapiens*, because there are no clear boundaries between them - morphological, chronological, behavioral, or environmental. He concludes from this that there is no genetic barrier between them. Focusing on the transitional specimens spanning the *erectus-sapiens* boundary, he concluded that the African, European, north Asian, and Indonesian samples can each be described as normal variations within the limits of a single species. Moreover, he raised the issue of criteria for species definitions, questioning whether global morphology, regional morphology, chronology, or cultural traditions provide the more valid means of separating the species. In his view, the anatomical links between Middle and Late Pleistocene populations from different regions make it impossible to regard some, such as Ngandong, as *Homo erectus* while other contemporaries are *Homo sapiens*. "Have we any solid scientific grounds on which to consider Middle Pleistocene European finds, with earlier morphological cranial changes, as *Homo sapiens* and the extra-European finds evolving in the same direction but in somewhat different degree and time sequence of adaptation into different conditions as *Homo erectus*? The whole mode and the process of the hominid evolutionary process shows that there are not, and that in the past [there] could not have been differences at the species level, but only at the subspecies level, whether the cerebralisation process - as only one part of the mosaic of evolutionary changes - started earlier or later. The logical consequence of such a situation is to lead us to consider the different African, European, and Asian finds of *H. erectus* type as *Homo sapiens erectus*" (JELÍNEK, 1978: 427-428).

He argued further that *Homo sapiens* is a polytypic species and its evolution is mosaic. "The anatomical links between Middle and Late Pleistocene populations are important for another reason - these links are strongly regional. If the differential diagnosis between *Homo erectus* and *Homo sapiens* cannot be other than by convention, and ... this convention must be different for different geographical regions, then the value of such a difference should be critically considered. ... It is time to replace the paleontological species with a biological one. ... Paleontological taxonomy cannot be in contradiction with ... biological facts"

### The Origin of *Homo erectus*

The phylogenetic relationships and taxonomy of the hominid populations immediately ancestral to *Homo erectus* are in a state of flux (STRINGER, 1986; TOBIAS, 1989, 1991; WOOD, 1987). Despite this, we believe that at the moment, the following tentative conclusions can be drawn. *Homo erectus* appears in east Africa, certainly at Lake Turkana, as a distinct definable cranial morphology (WALKER and LEAKEY, 1978) by at least 1.9 million years ago (raising the possibility that it may have evolved somewhere else in Africa). The earliest complete definitive cranium, ER 3733, just postdates this figure, while more problematic

(JELÍNEK, 1981: 88). HUBLIN (1986) took the position that cladistically, *Homo erectus* does not exist as a taxon separate from *Homo sapiens*. But he was not fully comfortable with his conclusion, and subsequently tied his interpretation of the species to the punctuational approach. HUBLIN was willing to accept *Homo erectus* as a pre-*sapiens* grade if it could be demonstrated that it exhibited evolutionary stasis. On the other hand, if significant evolution could be shown "*Homo erectus* should be included in *Homo sapiens*" (p. 184). In his 1986 paper he did not clearly define his position, but since we are convinced that there is indeed a record of significant evolutionary changes in *Homo erectus*, we take HUBLIN's position to be in support of our own.

R.E.F. LEAKEY (1989: 55) recognizes the pattern of Pleistocene human evolution we have described: "I do not favour the idea that the modern form of our species had a single geographical origin. The fossil evidence from widely separated parts of the world indicates to me that *Homo sapiens* in the modern form arose from populations of the more archaic form wherever it was established; and that similarly, these archaic forms arose from established populations of so-called *Homo erectus*. There are specific examples that cannot be brushed aside."

He proposed to use the beginning of encephalization, surely one of the unique hominid trends in both morphological and metric change, to define the beginning of a single evolving lineage, and argued (p. 57) that: "the enlarged and more complex brain arose only once, in the lineage embracing both *Homo erectus* and *Homo sapiens*." He added: "I am increasingly of the view that all of the material currently referred to as *Homo erectus* should in fact be placed within the species *sapiens* [which would] project *Homo sapiens* as a species that can be traced from the present, back to a little over two million years."

This would employ evolutionary species criteria for justifying the process of merging *Homo erectus* with *Homo sapiens*, since it establishes species identity through the persistence of a long term, clearly important, evolutionary trend.

crania such as ER 1590 and 1805 are very slightly earlier (FEIBEL et al., 1989) but still after the earliest cranium ER 2598. The putative ancestor of *Homo erectus*, *Homo habilis* (sensu lato), does not only predate the *Homo erectus* occurrences at Lake Turkana and survives this emergence by at least several hundred thousand years in a seemingly unaltered form in Bed II, Olduvai Gorge (cf. OH 13, in comparison with ER 1813). The most reasonable interpretation of these facts is that *Homo erectus* arises as a cladogenic event.

Characters that diagnose *Homo erectus* commonly appear together in virtually all *Homo erectus*



specimens, subject to the vagrancies of preservation. Many of these features can also be found, albeit rarely and in isolation, in others attributed to *Homo*. A combination of body size variation (midget to basketball player height) and the marked sexual dimorphism of these earlier hominids confuses the meaning of this earlier distribution, but what is most important, we believe, is the isolated nature of the occurrences. Thus, we find *Homo erectus* features in the lower border of the nasal aperture and inferior maxilla of STS 52, the cranial base of STS 19/58, the cranial rear of STW 53, the midface and temporo-mastoid region of SK 80/847, the endocranial size of ER 1470, and the frontal and occipitomastoid morphology of ER 1813. That several Plio-Pleistocene specimens each have a few different *Homo erectus* features does not make them *Homo erectus*, but also does not negate the validity of those features in diagnosing *Homo erectus*, when found in combination. The coalescence of these and other fea-

tures into a pattern thereafter commonly found in all humans of the Lower Pleistocene, and later, strongly suggests that there had been the type of adaptive and morphological reorganization that characterizes new species. This supports the implications drawn from the existence of *Homo habilis* specimens that postdate the earliest *Homo erectus* remains - *Homo erectus* arose in a distinct cladogenic event and thereby has a definable beginning.

Our interpretation of hominid systematics at the time of the earliest *Homo erectus* in East Africa, prior to the beginning of the Pleistocene, is that there are a minimum of three hominid species, as WALKER and LEAKEY (1978) suggested more than a decade ago. We hope this will reassure those who are concerned that our hidden agenda is to "bring the single species hypothesis back" (cf. WOOD, quoted in LEWIN (1991b); KIMBEL, 1991).

### Summary: Why Merge the Taxa?

To review, for the reasons summarized below we propose here to merge the *Homo erectus* sample in the expanded evolutionary species *Homo sapiens*. Its origin is in a cladogenic event that is at least 2.0 myr. We view the subsequent lineage as culturally adapted to an increasingly broad range of ecologies, ultimately leading to its spread across the world some half or more million years later. *Homo erectus*, the name generally accepted for our lineage in the Early Pleistocene, differs from contemporary *Homo habilis* in a number of ways. The vast majority of these distinctions also characterize *Homo sapiens*; that is, the diagnosis of *Homo erectus* relative to *Homo habilis* largely characterizes *Homo sapiens* as well. Every one of the few characters that are not shared appear to change in response to the evolutionary trends of increasing cultural complexity, increasing brain size, and the progressive substitution of technology for biology. *Homo erectus*, thus, is not a static species. It shows a number of evolutionary trends in the direction of *Homo sapiens*.

Moreover, *Homo erectus* is a polytypic species, divided into several distinct geographic variants which show continuity with the geographic variants of the polytypic species *Homo sapiens* through the sharing of unique combinations of morphological features. There is no distinct boundary between *Homo erectus* and *Homo sapiens* in time or space.

### Behavioral Evolution in a Single Species

While the fusion of *Homo erectus* and *Homo sapiens* as proposed here is a purely biological concept that removes much of the confusion and misconception inherent in the present taxonomic dichotomy, this action also has a clear message for perceptions of our behavioral evolution. We believe the notion of *Homo sapiens* as a single evolving species throughout the Pleistocene makes clear the central distinguishing fea-

That is, there is no evidence of an appearance of a new combination of features separating earlier and later populations in one area (which contrasts with the events at the origin of *Homo erectus*). The characteristics of *Homo erectus* and *Homo sapiens* are mixed in transitional samples that are found in the later Middle Pleistocene of every region where there are hominid remains. We interpret these data to mean that there is no speciation involved in the emergence of *Homo sapiens* from *Homo erectus*. The absence of a cladogenic event creating a distinct boundary at the "origin" of *Homo sapiens*, together with the related patterns of polytypism in both "species", provides an explanation for the inability to develop a valid morphological definition of *Homo sapiens*. These reasons combine to require that the lineage be regarded as a single evolutionary species.

We view this evolutionary species as spanning the entire Pleistocene. The species is geographically polytypic once human populations begin to migrate out of Africa, 1.4-1.2 myr. This polytypism is characterized in morphological combinations which include (but are not restricted to) a number of features we believe are used in kin recognition. The main evolutionary tendencies in the species are linked to the evolving cultural system and its role as both a cause and an effect in what we regard as the human biocultural evolutionary process.

ture of human behavior - the unique nature of biocultural feedback as the mechanism driving our learning, adaptation, and social organization. The idea that a set of cultural and morphological traits can be interrelated stems from DARWIN (1871) and forms the basis of much anthropological thinking about the human evolutionary process, beginning with WASHBURN (1960). The cultural evidence associated with Early Pleistocene

*Homo sapiens*, as defined here, represents a major change in complexity. The dramatic expansion of the brain case is a clear reflection of major changes in our capacity to learn and develop vastly expanded cultural systems.

For many years, interpretations of the biological aspects of human evolution have been driven by the divisions made by prehistorians (BROSE and WOLPOFF, 1971). In Europe, for example, the Late Pleistocene skeletal morphology has been broadly divided on the basis of Mousterian and Upper Paleolithic stone industries. However, the late date for the St. Césaire Nean-

dertal (MERCIER et al., 1991) makes it clear that changes in behavior through time are by no means well correlated with concurrent biological developments, if the juxtaposition of industries and hominids in the Levant had not already done so. More broadly, prehistorians devising frameworks with artifactual or adaptive changes linked to alleged speciation events can now focus on an interpretation of the archaeological record that is essentially independent of phylogenetic changes. The present global and regional variants of modern humanity must continue to be a warning of the dangers of drawing simple links between the complexities of biological and behavioral sequences.

#### Subdivisions for *Homo sapiens*

One final immediate question that stems from a dramatically enlarged *Homo sapiens* is: how do we refer to all the various time and space segments of this evolving complex of morphologies and cultures? As our merging of *Homo erectus* into *Homo sapiens* suggests, we feel strongly that the difficulties in examining the lineage have been exacerbated by excessive taxonomizing (e.g. HOWELL, 1978; GRO-VES, 1989; CLARKE, 1990). We do not wish to see temporal subspecies (cf. STRINGER, HOWELL, and MELENTIS, 1979) take the place of temporal species, as this would recreate the very problems we hope to solve.

The fossil record of *Homo sapiens* can be most validly discussed in a manner that is totally outside of a taxonomic context, since geographic subdivision at the subspecies level in the past would require a subspecies interpretation of distinctions between the races of today, and the division of the lineage into temporal subspecies would recreate all of the difficulties solved with the merger of the species. We would prefer to see the comparisons that are the requisite of any evolutionary study be made on the basis of the familiar, simple, and generalized divisions of early, middle, and late *Homo sapiens*. We would follow this with a fourth division of recent, or living. Such a course would allow the continuing assessment of the establishment of our species within Africa as early *sapiens*. The period would cover the cladogenic event that separated *sapiens* from its parent and sister species sometime before the beginning of the Pleistocene, up until the beginning of the Middle Pleistocene, some 780,000 years ago. This arrangement would also make clear that *Homo sapiens* is the only hominid ever to live outside of Africa.

Middle *Homo sapiens* would cover the period of anatomical and cultural establishment of humans outside of Africa up until approximately 130,000 years ago, when it is clear that there are the beginnings of major changes developing in some areas. This period is the subject of current debate about "modern human"

origins. Clearly, we do not envision this process as involving a speciation event.

The division of early, middle, and late as here proposed follows the same divisions used for the Pleistocene Period. Tying our definitions of the *sapiens* divisions to the geochronological divisions of the Pleistocene confers the advantage of having faunal, geologic, and paleoenvironmental data directly associated with our scheme for referring to the segments of *Homo sapiens*. Therefore, we propose the use of the geologic divisions for *Homo sapiens*. Further subdivisions are, of course, consistent for both time and space. Thus, the Zhoukoudian sample of Locality 1, spanning 400-600 kyr, would be an example of Chinese *Homo sapiens* from the Middle to late Middle Pleistocene. The European Neandertals would be an example of European *Homo sapiens* from the earlier part of the Late Pleistocene.

Finally, we recognize that not all specimens are well dated, and that for some the provenances and/or dates may never be accurate. One could potentially criticize our scheme with the argument that without information about age, it is unclear what *Homo sapiens* group to put a specimen in, while taxonomic categories based on anatomy can be defined regardless of a specimen's age. But, in fact, the taxonomic categories based on anatomy within Pleistocene *Homo* have also not proven to be particularly unambiguous to define and the confusion of grade and clade characters makes these categories inherently inaccurate; we would say, on the whole more inaccurate than the geochronological scheme we propose here. Moreover, without information about age, the importance of a specimen in any evolutionary scheme is minimized in any event, no matter how evident its taxonomy appears to be. In all, we contend that systematics based on morphology alone within the species *Homo sapiens* provides no advantage over the non-taxonomic (or perhaps, better, ataxonomic) approach we suggest.

#### Conclusions

A major objection to the merger of *Homo erectus* into *Homo sapiens* is the difficulty that some will have in conceiving of and accepting a single evolving

species spanning the last two million years. We believe, however, that we have reached the point in thinking about the later phases of our evolution when the con-

cept of *Homo erectus* - as a stage, a named ancestor, and as a time and morphological segment of our developing lineage - has clearly begun to obscure a clear understanding of the dynamic processes that have taken place. The complexity of the physical and cultural events of the last two million years are not made clearer by a proliferation of taxa - the stamp collector approach that is central to the phylogenetic species concept.

For the last thirty-odd years we have recognized

that only a single genus, *Homo*, should be used to describe our past two million years of evolution. We think that similarly, the time has come to recognize that only a single polytypic evolutionary species should be used for this period. For us it is not so much a "sinking" of *Homo erectus*, as a more basic recognition that *Homo sapiens* has priority. This taxonomic adjustment will help make clear what many workers have come to realize, that we have been wise for much longer than has been thought.

#### Acknowledgments

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**The authors' addresses:** Prof. Dr. Milford H. Wolpoff, Paleoanthropology Laboratory, Department of Anthropology, University of Michigan, Ann Arbor, MI 48109-1382, USA; Prof. Dr. Alan G. Thorne, Department of Prehistory, Research School of Pacific Studies, Australian National University, Canberra 2601, Australia; Prof. Dr. Jan Jelinek, Anthropos Institute, Moravian Museum, Brno, Czech Republic; Dr. Zhang Yinyun, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing 100044, People's Republic of China.