Palaeoanthropology

Palaeobiology and age of African *Homo erectus*

from Eric Delson

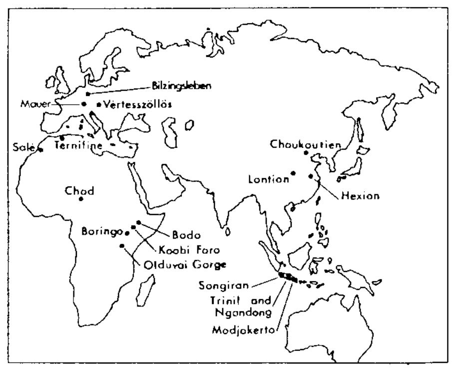
FINDS of ever-older human relatives and potential ancestors have caught the public's imagination in recent years. Kenyan fossils newly described on page 788 of this issue by Brown *et al.*[1] could help to swing the pendulum of public interest back toward younger fossils belonging to species of our own genus, *Homo*. Since 1969, Richard Leakey and his colleagues have recovered human and other fossils from deposits along the eastern shore of Lake Turkana in northern Kenya. Now, a group has crossed to the west side of the lake; early work has yielded a fossil already touted in the press as a "strapping youth" whose bones will shed yet more light on human ancestry[2].

The new fossil has been identified as a representative of *Homo erectus*, the extinct species first named *Pithecanthropus erectus* or "Java Man" by Dubois in 1894. Skulls of many individuals of this form are now known from Java and China, mainly estimated to date between 1·2 and 0·25 Myr old[3,4]. It is widely accepted that populations similar to *H. erectus* were directly ancestral to the earliest members of the living species *H. sapiens*, although the exact timing, geography and mode of transformation are still controversial. Unfortunately, limb bones are scarce in the Asian sites, and some of the most complete have been questioned as to their specific identification[5].

That is the main value of the new Kenya fossil — it preserves almost all of the skeleton of a 1·6-Myr-old individual who can be sexed (as male, by pelvis shape) and aged (12 years, from tooth eruption timing). Fossils identified as *H. erectus* have been known in eastern Africa since 1960, when Louis Leakey reported a skull cap from Olduvai which matched those from Asia. Moreover, Olduvai and other sites have yielded partial limbs and pelves attributed to *H. erectus*, but none has been associated with a well-preserved cranium, always rendering precise taxonomic identification doubtful. The West Turkana fossil (catalogued as KNM-WT 15000) preserves most of the skull and lacks only the extremities and forelimbs (the right humerus remains). The team expects to find additional portions of the skeleton with further excavation, but this degree of preservation is otherwise unknown before the Neanderthals of 40,000–100,000 years ago. By comparison, 'Lucy', the 3-Myr-old partial adult female skeleton of *Australopithecus afarensis* recovered by Johanson[6], has a lower jaw but only bits of the skull; many fewer ribs and vertebrae; the upper and lower leg bones of only one side of the body; but does preserve most of the two forearms and left humerus missing in WT 15000.

What will this new information tell us about how *H. erectus* lived? That is still hard to say, but one point much emphasized is the apparently great height of the individual: 1·6 m (5 ft 5 in) at death, perhaps 1·8 m (6ft) if adult[2]. Brown *et al.*[1] have moderated this claim, especially because the skull of *H. erectus* was lower than that of the modern *H. sapiens* whose bones were used to develop the height regressions; the regression estimates should consequently be reduced.

Previous estimates for the height of *H. erectus* ranged between 1·55 and nearly 1·8 m[7,8]. They were usually based only on the length of the femur (thigh bone) and did not consider skull height differences. Thus, the WT fossil might not have been especially large for this species to begin with. Moreover, additional cavils need to be evaluated. Modern humans show an adolescent growth spurt, especially in males. If such a spurt existed in *H. erectus*, it might have led to a height greater than the estimated 1·6 m, had the specimen lived longer.



Locations of major *Homo erectus* sites. There is controversy over whether the European and Baringo fossils should be allocated to *H. erectus* or *H. sapiens*[12]!

Similarly, it is unclear that dental eruption timing then was the same as it is today; T. Bromage and C. Dean have questioned the equivalence of such timing in *Homo* and *Austalopithecus* species based on counts of perikymata (developmental lines in tooth enamel)[9]. On the other hand, if most *H. erectus* individuals were rather shorter than WT 15000 (which is less likely), it is possible that this individual was atypically tall or died young because selection acted against his continued growth.

Palaeoanthropologists will probably be more interested, however, in the insights that this fossil will provide into the patterns of growth and inter-individual differences among earlier humans. As evidenced by both dental eruption and epiphyseal fusion stages, WT 15000 was clearly juvenile. Yet Brown *et al.*[1] note that the face is larger and more massive than that of an adult *H. erectus* skull from the east side of Lake Turkana they have just described[10]. That skull, ER 3733, is widely accepted as female, so that its relative gracility compared with WT 15000 is not surprising (except for the age of the latter). It would be interesting to compare WT 15000 with ER 3883 (ref. 10). Some authors think the latter was a male (ref. 8) but I consider it another female and the large but stratigraphically younger Olduvai OH9 to be the male in this sexually dimorphic species.

This question leads inexorably to the two main recent foci of attention on *H. erectus*: does the species illustrate stasis or phyletic change through its 1·5 Myr span; and are the African forms really the same species as the Asian? One of the most important types of information that bear on both these questions is accurate ages for the fossils. Although Pope[3] and other workers have recently argued that the oldest Asian *H. erectus* are often significantly younger than previously thought (1–1·2 Myr at most), careful re-analysis of several East African geological sequences has clarified the age of the earliest supposed members of the taxon there. Also in this issue, McDougall *et al.*[11] on page 792 present new data on the age of one major Turkana Basin marker horizon, the Okote Tuff complex. They report that the basal levels of this 10–15-m-thick unit date to no more than 1·64 Myr. The pumice fragments dated have a composition different from that of the enclosing tuff, suggesting reworking upwards of older pumice into the slightly younger tuff. Brown and Feibel[12] on page 794 offer further local correlations and review other dates which indicate that it is not much younger (>1·52, probably >1·6 Myr). In addition, they determined that a tuff slightly below the horizon of WT 15000 is equivalent to one of two newly defined tuffs on either side of the Lower Okote, yielding the age of 1·55–1·65 Myr for the skeleton.

These dates and others in the Early Pleistocene (through to perhaps 1·0 Myr) make it simple to begin the study of temporal variation in *H. erectus*. But as noted by Pope[3], dates in Asia are still highly uncertain and younger African fossils (especially in the Maghreb) are also of questionable age. Thus, although studies such as those of Howells[13] and Rightmire[14] have suggested that variation through time is not continuous or even directional in *H. erectus*, Wolpoff[15] has recently argued strongly for a gradualistic view of temporal variation and change in this species. His comparisons of 13 cranial characters across specimens grouped into three time ranges are superficially persuasive, but there are too many potential problems for his analysis to be convincing. Several individual fossils are of questionable identification, sexual variation is not considered and the raw data are not available to see the precise effects of these factors. Equivocal age determinations and the use of time bands rather than age estimates that would permit regression analysis also disturb me. As Wolpoff notes, it has been "excruciatingly difficult to test the punctuated equilibrium model in the fossil record", not least because of methodological disagreements among researchers.

An examination of Wolpoff's list of specimens reveals that whereas East African and Indonesian fossils dominated the 'early' and 'middle' *H. erectus* time groups, the sample from Zhoukoudian, China dominates the 'late'. Some authors have recently questioned whether such comparisons are as meaningful as we might like—are the African fossils indeed members of a palaeobiological species *H. erectus* as defined from the unique characteristics of the Asian specimens defining this taxon? Howell[16] reviewed the concensus position of geographical identity some years ago, providing a detailed descriptive definition without specific regard for the derived versus the conservative nature of the characters discussed. Rightmire[17,18] has been the most vocal recent proponent of this view, arguing that several uniquely derived characters define *H. erectus* in Asia and Africa without recourse to the arbitrary use of temporal gaps or rubicons.

On the other hand, Wood[19] and Andrews[20] argue strongly that African fossils assigned to *H. erectus* share only conservatively retained features with Asian members of that species, not any of their derived characters. Thus, they imply the need for recognition of a new species to receive African fossils possibly intermediate between *H. habilis* and *H. sapiens*. Stringer[21] is more cautious, but agrees with the lack of shared derived features in specimens from the two regions; he notes further that if *H. erectus* were to be defined broadly enough to include all of these fossils, most derived conditions seen in the younger Asian specimens (especially those found in China) would reject the concept of stasis in favour of definite change over time.

Palaeoanthropologists continually make the claim that more fossils will help answer pressing questions, and field workers who find them reap well-deserved rewards. If WT 15000 is any example of the quality of material to be expected in future years from the West Turkana sequence, there will certainly be much grist for our mills. But the milling process must include careful and probing analyses of all the available fossils, matched with a willingness to test both revisionist and entrenched hypotheses and to embrace new interpretations, if we are to take full advantage of the hard-won fossils. □

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