

Palaeoanthropology

Human phylogeny revised again

from Eric Delson

A newly recovered cranium of one of the early human species called robust australopithecines may well force palaeo-anthropologists to reconsider the evolutionary relationships among all *Australopithecus* forms. On page 517 of this issue¹, Walker and colleagues describe two specimens (a partial lower jaw and a skull lacking most of the teeth and part of the skull roof) found in sediments on the west side of Lake Turkana, Kenya, dated about 2.5 million years (Myr) old. Many of those who have had the opportunity to study a replica of the skull feel that it is the most exciting fossil hominid found since 'Lucy' in 1974 (ref. 2).

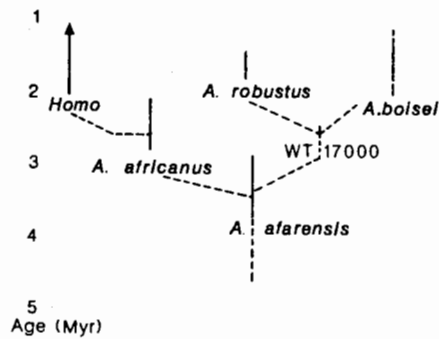
The record of early humans (upright bipeds with small canines and apparently already partly expanded brains in comparison to body size) begins about 4–5 Myr ago in eastern Africa. The first well-preserved remains are those from Laetoli (about 3.7 Myr) and Hadar (3.3–3.0 Myr) generally termed *A. afarensis*. This species is often thought to be close to the base of the radiation of Plio–Pleistocene humans, but opinions differ widely on details. Later australopithecine species include the 'gracile' *A. africanus* of South Africa, 3.0–2.3 Myr in age; 'robust' *A. robustus* (and perhaps a distinct *A. crassidens*) from 1.9–1.6-Myr-old caves in South Africa; and the hyper-robust *A. boisei* from eastern Africa, well known

between about 2 and 1.3 Myr ago. Based on his identification of isolated teeth and the revision of Omo chronology by Brown *et al.*³, Grine⁴ has argued that *A. boisei* may occur as early as 2.5 Myr ago in Lake Turkana basin. The earliest *Homo* fossils appear about 2 Myr ago in both eastern and southern Africa.

Although there is no consensus, most probably agree with the interpretation of Rak⁵ and of Kimbel and colleagues⁶ that *A. afarensis* is close to the common ancestor of two main lineages of early humans, one leading to *Homo* but unknown in the 2–3 Myr interval, the other passing through a 'gracile' stage to terminate in several robust species (of which the South African form is most like the common ancestor).

Others, especially Olson⁷, have suggested that *A. afarensis* is a mixture of two species, with most of the cranial and dental material being an early robust form based on shared features that are considered derived for the robust lineage, whereas Lucy and other less complete remains are like gracile forms and later *Homo*. Skelton *et al.*⁸ conclude that a third option is best: deriving both *Homo* and robust forms from *A. africanus*, with *A. afarensis* as an earlier ancestral stage.

The new robust fossils add to this already confusing picture. Walker *et al.*¹ make two main points in their analysis,



Possible evolutionary relationships among Plio-Pleistocene hominids. Solid lines, known ranges of taxa; dashed lines, probable range extensions and hypothesized relationships.

They argue first, that the new specimens can be included within the known species *A. boisei*; and second, that their antiquity now makes it impossible for South African *A. robustus* to have been ancestral to *A. boisei*.

In their Table 2, Walker *et al.* summarize the distribution among australopithecine taxa of 22 craniodental character states but their data do not, in my opinion, support allocation of KNM-WT 17000 to *A. boisei*. Of the 22 features, the new skull is apparently phylogenetically conservative in 11 and reasonably conservative in two more; in one (orbital height), it is similarly conservative in that only *A. boisei* is derived. In having the I² roots medial to the nasal margin, all post-*afarensis* forms are linked indeterminately. Thus, 15 of 22 features are phylogenetically neutral. In four characters, WT 17000 is grouped squarely with the other robust forms by derived features, but then only three remain to place the skull within the robust group. Of these, the shape of the orbital margins links it to *A. robustus*, whereas foramen magnum shape is shared with *A. boisei*; in neither character, however, is the state known in *A. afarensis* nor can an ancestral condition be readily determined.

The absence of a maxillary fossula appears to be a second link to *A. boisei*, but only if Rak's interpretation of development of the fossula in the *africanus-robustus* lineage and loss by *boisei* is accepted. If the fossula and related anterior pillars are functionally linked to canine root size, the fossula could even be independently derived in the two South African species — I consider this character as yet of indeterminate polarity. Walker *et al.* add to these tabulated features the supposedly *boisei*-like nature of the infraorbital, nasal and zygomatic root regions, but interpretations of those similarities differ among observers. We are thus left with only large overall size (and geography) as reasons for including WT 17000 within *A. boisei* and in the light of the quite distinctive mosaic of characters seen in WT 17000 (for example, prog-

nathic lower face and lack of a bare area where the muscle crests join), I would have assigned it to *A. boisei* only hesitantly at best. Further analysis (including study of Olson's⁷ characters of the mastoid and nasal region) could well show WT 17000 to be a rare case in which a new hominid merits description as a new species.

On the question of phylogeny, Walker *et al.* have argued that the great age of the new material falsifies the hypothesis that *A. robustus* or a similar taxon was ancestral to *A. boisei*. But it is possible (although undemonstrated) that a form resembling *A. robustus* inhabited southern (or eastern) Africa between 3 and 2.5 Myr ago, giving rise to all of the post-2.5 Myr robust species including WT 17000. As the new skull (and Lucy before it) showed, predicting fossil morphology in barren time periods is a risky pursuit.

But it is morphology and not time that reveals which taxa (or samples) are most closely related, and in this case, it seems best to interpret the new West Turkana robust forms as representing a population near the divergence of the southern and eastern variants. Although retaining

many character states seen in *A. afarensis* (and perhaps *A. africanus* as well), the form represented by WT 17000 presents several features characterizing all robust forms but few specific to either *boisei* or *robustus*. Its discovery leads paleoanthropologists to reassess the trends suggested by Rak for relating the gracile and robust species and the relationship of *A. afarensis* to all later species. The figure illustrates one such view. □

1. Walker, A., Leakey, R.E., Harris, J.M. & Brown, F.H. *Nature*, 322, 517 (1986).
2. Johanson, D.C. & Edey, M. *Lucy* (Simon & Schuster, New York, 1981).
3. Brown, F.H., McDougall, I., Davis, T. & Maier, R. in *Ancestors: The Hard Evidence* (ed. Delson, E.) 82 (Liss, New York, 1985).
4. Grine, F.E. in *Ancestors: The Hard Evidence* (ed. Delson, E.) 153 (Liss, New York, 1985).
5. Rak, Y. *The Australopithecine Face* (Academic, New York, 1983).
6. Kimbel, W.H., White, T.D. & Johanson, D.C. in *Ancestors: The Hard Evidence* (ed. Delson, E.) 120 (Liss, New York, 1985).
7. Olson, T.R. in *Ancestors: The Hard Evidence* (ed. Delson, E.) 102 (Liss, New York, 1985).
8. Skelton, R.R., McHenry, H.M. & Drawhorn, G.M. *Curr. Anthropol.* 27, 21 (1986).

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