

Palaeoanthropology

Evolution and palaeobiology of robust *Australopithecus*

Eric Delson

THE evolutionary lineage that ends with living humans can now be traced more accurately back towards 4 Myr (million years) ago, partly because of studies of a second major early hominid clade (evolutionary radiation or sub-lineage), the 'robust' species of *Australopithecus*. New fossils relevant to this group were presented at a recent symposium*, but more important than these were re-analyses of known data which led researchers closer to a general agreement on the early phases of human phylogeny. Several previously suggested evolutionary trees were widely rejected in favour of a new interpretation which followed from the description by R. Leakey and colleagues last year (see my News and Views article, *Nature* 322, 496-497; 1986) of an ancient robust skull.

As many as six African species that lived ± 1 Myr ago are now placed into the broadly defined genus *Australopithecus*, presumably including the ancestry of *Homo* as well as the distinctive robust group. It is the relationships among these species (especially the latter clade) and their palaeobiology which the meeting was designed to clarify.

A carefully defined chronological framework is required to answer questions about the number of contemporaneous species and to help to allocate fossils to these species. Frank Brown (University of Utah) presented such a framework for the Lake Turkana Basin site units that have yielded most early hominids from East Africa. The find-spot of each major specimen was relocated and tied into a revised stratigraphical column, resulting in temporal placements with narrow error of margins only ± 0.05 - 0.1 Myr. In addition, Brown's palaeogeographical studies demonstrate the

presence of a lake in the basin before about 3.5 and after 2.0 Myr ago, but not certainly in between. The lack of deposition in the Koobi Fora region from 2.5-2.0 Myr ago was probably caused by volcanic uplift in the south-east segment of the basin, rather than caused by any climatically linked phenomena.

Recently published data indicate that *Australopithecus afarensis* ranged between 3.5 (Laetoli) and 3.1 Myr ago (Hadar); biochronology in southern Africa cannot decipher the relative age of the *A. robustus* sites Swartkrans (member 1) and Kromdraai B, but both appear to be roughly 1.9-1.6 Myr old (Elizabeth Vrba, Yale University; my own work). Swartkrans can be divided into five members, of which the lower three each yield specimens of robust *Australopithecus* and *Homo*, as well as stone and bone artefacts. These accumulations may have each taken only 10-20,000 yr to form if the Holocene, warm-climate member 5 is a valid guide, but whether they together span 0.1 Myr or over 1 Myr was debated (Bob Brain, Transvaal Museum, Pretoria). New dental specimens reveal no trends across this time interval (Frederick Grine, State University of New York at Stony Brook), but the postcrania suggest that *Australopithecus robustus* was physically capable of making the tools recovered (Randall Susman, Stony Brook).

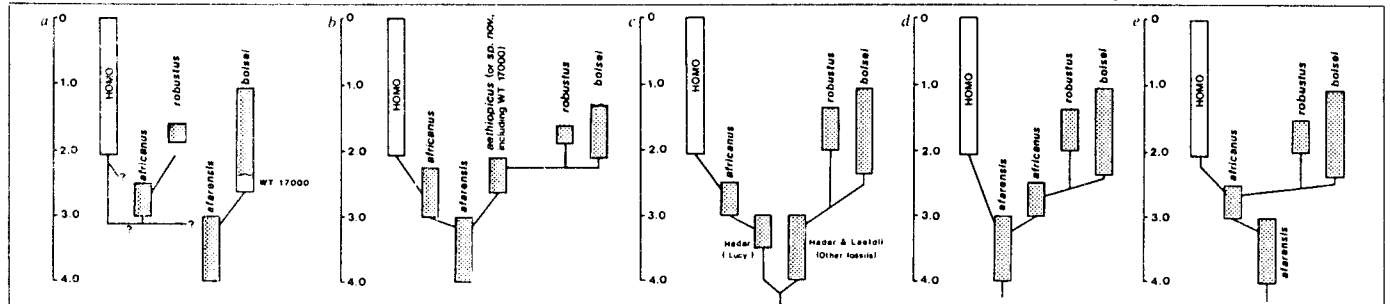
New fossils from the West Turkana region of Kenya support last year's find of WT 17000, a distinctive robust cranium slightly younger than tuff D (2.5 Myr ago). Alan Walker (Johns Hopkins University, with Richard Leakey, National Museums of Kenya) continued to argue that these fossils graded into the younger *A. boisei* known from 2.1-1.5 Myr ago and that such an evolving lineage should not arbitrarily be divided into species. He also presented fossils that convincingly

supported the allocation of WT 17000 and allies to a population previously known from the fragmentary toothless mandible Omo 18-1967-18 (2.6 Myr ago). He rejected the inference of large anterior teeth in WT 17000 as a functional correlate of the posterior placement of the sagittal crest and posterior temporalis muscles, but most participants disagreed with his interpretation. Donald Johanson, William Kimbel (Institute of Human Origins, Berkeley) and Tim White (University of California, Berkeley) argued for recognition of this early robust group as *A. aethiopicus*, a name given formally to the Omo mandible in 1978 by Arambourg and Coppens. I tentatively accept this view and will use the name here, although others might object.

Kimbel and White discussed variation in *Australopithecus* samples, suggesting that the Sterkfontein collection of *A. africanus* is among the most variable, whereas that from Hadar and Laetoli combined is more homogeneous. A new face, palate and partial vault from Sterkfontein presented by Ronald Clarke (Wokingham, United Kingdom) strikingly supports that view, but there was little acceptance of Clarke's claim that his Stw 252 (and STS 71, among others) represents a new species tending towards the robusts. East African dental evidence does reveal that lower premolars older than about 2.1 Myr ago (*A. aethiopicus*?) shared conservative features with Swartkrans fossils and could be distinguished from more derived younger specimens of *A. boisei*, while a third dental morph occurs at Omo between about 2.8-2.2 Myr ago, possibly a 'gracile' taxon leading into *H. habilis* (Gen Suwa, University of California, Berkeley).

A. boisei was also shown to be distinct in the ultrastructure of the molar enamel, which was both much thicker and somewhat differently built up than that of other hominoids: more secretory cells were active at one time, to lay down a thick enamel layer rapidly, with less emphasis on stress resistance (Lawrence Martin and Grine, Stony Brook; Bernard Wood, University of Liverpool). In terms of body-size estimates for these species, there was surprising uniformity both

*The Evolutionary History of the Robust *Australopithecines*. State University of New York at Stony Brook, 27 March-1 April 1987.



Phylogenetic schemes for *Australopithecus* species preferred by: a, Walker and Johanson; b, Delson, Grine, Howell, Olson; c, Olson's 1981-85 scheme, no longer adopted by him; d, Johanson and White's 1979-85 scheme, no longer supported by them; e, Skelton, McHenry and Drawhorn, 1985. Scheme b is now the most generally accepted. (Courtesy of F. Grine.)

across taxa and between workers (William Jungers, Stony Brook; Henry McHenry, University of California, Davis). Using an ape model based on limb joint size (but excluding modern humans), Jungers estimated average sample weights as follows: *A. afarensis*, 58 kg; *A. africanus*, 53 kg; *A. robustus*, 62 kg; and *A. boisei*, 63 kg. The Hadar range of 30–81 kg included all but the largest (88 kg) robust individuals.

There are now only two main hypotheses about the phylogenetic relationships among the early hominid species, both of which seem to agree that *A. afarensis* was a conservative species near the common ancestry of all later forms. The first hypothesis (*a* in the figure) is that *A. boisei* includes *A. aethiopicus*, *A. africanus* led only to *A. robustus* and the ancestry of *Homo* is unclear (Walker, Johanson). The second (*b* in the figure) is that *A. aethiopicus* is the sister-taxon (or perhaps common ancestor) of the later robusts, whereas *A. africanus* may be the sister of *Homo* (Delson; Grine; F. C. Howell, University of California, Berkeley; Kimbel; Todd Olson, City University of New York Medical School). The previous hypotheses that *A. afarensis* actually included two species, a robust taxon leading to later forms (effectively via *A. aethiopicus*) and a 'gracile' form including 'Lucy' which with *A. africanus* was on the *Homo* line (*c* in the figure); or that *A. africanus* was on the robust clade with *A. afarensis* leading directly to *Homo* by way of an unknown intermediate (*d* in the figure); or that *A. africanus* was a (post-

afarensis) common ancestor of the robusts and *Homo* (*e* in the figure), were generally rejected by their original proponents because of the conservative features shared by *A. aethiopicus* and *A. afarensis* to the exclusion of *A. africanus*.

Participants broadly rejected the first hypothesis, implying polyphyly of the robust species, because of the many derived features shared by *A. robustus* and *A. boisei*. Only one or two derived features are shared by *A. aethiopicus* and either *A. robustus* or *A. boisei*, although the three species do share a group of character complexes uniting them in the robust clade.

Thus, the second hypothesis is the least contested, but is by no means universally accepted. If a strictly cladistic classificatory scheme were to be followed, as argued by Grine and Olson, among others, *A. africanus* could be included in *Homo*, with the robust species termed *Paranthropus* and the genus *Praeanthropus* resuscitated for *A. afarensis*. However, most workers prefer to retain a more broadly defined *Australopithecus* pending detailed analysis of the new fossils and clearer determination of the phyletic role of *A. africanus*, which remains pivotal after more than 60 years of controversy. □

Eric Delson is Professor of Anthropology at Lehman College and the Graduate School, City University of New York and is in the Department of Vertebrate Paleontology, American Museum of Natural History, New York, New York 10024, USA.