

Palaeoanthropology

One skull does not a species make

Eric Delson

The palaeoanthropology community must look quite Pavlovian to outsiders — we all drool predictably every time a new fossil is discovered. In fact, such new specimens may be important not only in their own right, but in terms of wider implications for the field. Such a fossil from Konso in Ethiopia is described on page 489 of this issue by Suwa and colleagues¹, almost 40 years after Mary Leakey found, and Louis Leakey described², the first known member of its species.

Australopithecus (or *Paranthropus*) *boisei* is the morphologically most specialized member of an extinct early human clade (branch), which separated from the lineage that eventually led to living people some 3–2.5 million years ago (Myr). These so-called robust australopiths were characterized by extremely large and thickly enamelled molar teeth and jaws, which were moved by massive chewing muscles attached

to a sagittal crest (fore-and-aft ridge of bone) on top of the relatively small-brained cranium. In the two later species of this group — East African *P. boisei* and South African *P. robustus* — the incisors and canines were strongly reduced, and were even smaller than our own.

As with many early human species, *P. boisei* occurs at only a few sites: Olduvai Gorge and Peninj (Tanzania), Chesowanja (Kenya) and, especially, in the Lake Turkana Basin (in the Shungura, Koobi Fora and Nachukui/West Turkana zones on the Kenya–Ethiopia border), mainly between 2.2–1.6 Myr^{3,4}. A partial upper jaw has also been recovered from the Chiwondo Formation in Malawi, by Tim Bromage, Friedemann Schrenck and colleagues.

The discovery of a *P. boisei* skull by Suwa *et al.*¹ now extends the geographical range to the northeast (Fig. 1). Temporally, with a firm date of 1.4 Myr, it is near the previously

extrapolated latest occurrence of the species. Most of the other finds are associated with relatively moist and wooded habitats, but the Konso deposits yielding the new specimens indicate a more open, drier palaeoenvironment (although nearby subsites were also moist and wooded). In the same bed at Konso⁵ are a mandible of *Homo erectus* and an assemblage of artefacts referred to the earliest Acheulean (hand-axe) industry. In fact, revised calibration of the Olduvai Gorge sequence^{4,6} indicates that the oldest Acheulean sites there (EF-HR and MNK; see ref. 7) probably date to 1.6–1.5 Myr.

The new specimen KGA10-525 is one of the most complete skulls of *P. boisei* yet known, comprising much of the cranium and part of the lower jaw — the first association of these two elements in a single, well-preserved individual of this species. Future studies may provide new insight into the biomechanics of mastication in *P. boisei*, given the potential to look at the opposing upper and lower jaws. But perhaps the greatest importance of this specimen is its implication for the study of variation in this, and other, human populations and species.

During the 1960s there was much discussion as to whether *P. robustus* and *P. boisei* were distinct species or merely geographical variants of a single form. After Tobias' monographic treatment of the original Olduvai material⁸ and the recovery of many specimens from the Turkana Basin, recognition of two species was common. Rak's delineation⁹ of facial differences between the known samples supported this view, and increasing use of the generic name *Paranthropus* reflects a growing acceptance of Robinson's arguments¹⁰ that these two species (and their conservative relative *P. aethiopicus*) formed a distinct clade in human evolution. Nonetheless, it has been clear that the Olduvai type specimen¹ is the most 'extreme' example of *P. boisei*, whereas some of the crania from Turkana are — in certain features — morphologically intermediate between this specimen and the generally smaller and less robust South African population.

The cranium discovered by Suwa *et al.*¹ is large, even for *P. boisei*, and it has many features that place it within that species. But it also lacks some of the diagnostic features, such as the 'visor-like' cheekbones, the forward surface of which projects obliquely out and down — like a knight's faceplate — perhaps to take up chewing strain. Moreover, the sagittal crest is emphasized posteriorly, almost as in *P. aethiopicus*, and the palate is broad and short, similar to the shape seen in *Homo* (see Table 2 of the paper, page 491). Finding these atypical character states in *P. boisei* from a new population complements the



Figure 1 Map showing some of the East African localities that have yielded fossils of *Paranthropus*. All have *P. boisei*; *P. aethiopicus* also occurs at Nachukui, Omo and Koobi Fora. The skull described by Suwa *et al.*¹ comes from Konso — the most northeasterly and probably the youngest of these occurrences.

observations of Brown *et al.*¹¹ on variability in crania of this species within the Turkana Basin.

Some researchers might 'solve' the inconsistency by naming a new species for the Konso population, but both the authors and I would caution against such an oversimplified approach. Neighbouring species of living animals are generally distinguished by a lack of gene exchange (interbreeding and mate-recognition). But this biological species concept (BSC) cannot be directly applied to modern animals that are separated in space or to fossils. In both of these cases, some specialists try to draw analogies with the BSC by studying the degree of variation and overlap among well-studied neighbour species. Others argue that any discernible difference in morphology implies that interbreeding would have been unlikely, thus according full species rank more readily (the phylogenetic species concept; PSC).

The sister taxa *P. boisei* and *P. robustus* are probably the most similar species pair within the Hominini (post-ape human lineage). The new sample from Konso opens, once again, the question of their taxonomic distinction — if the diagnostic features of both species co-occur in a single population sample, are they really different species? Only by re-evaluating character-state distributions across the robust australopiths can we hope to answer this question.

Looking at an even broader scale, the number of widely accepted species in our genus, *Homo*, has increased steadily, stemming in part from the PSC philosophy presented in a seminal essay by Tattersall¹². Populations spanning the last 1 Myr were, for many decades, considered varieties of our own species *H. sapiens*. But the Neanderthals of western Eurasia (dating roughly from 200,000–30,000 yr) are now thought by many to represent a distinct species *H. neanderthalensis*, which had its roots in earlier European populations genetically isolated from African contemporaries.

The PSC advocates have recognized as many as three additional species in the interval between 1 Myr and 200,000 yr: *H. rhodesiensis* for the African populations, which are younger and more derived than *H. erectus*; *H. heidelbergensis* for European groups in the 500,000–200,000-yr range; and, most recently, *H. antecessor* for a European sample dating around 800,000 yr. *Homo antecessor* is said to show facial features that are reminiscent of *H. erectus* and some later populations, leading to the suggestion¹³ that it is the common ancestor of all of the younger species. But that interpretation is based mainly on the face of a single subadult individual, with no idea of the variation (adult or juvenile) in that sample or in juveniles of either *H. heidelbergensis* or *H. rhodesiensis*.

As Suwa *et al.*¹ note, the Konso specimens underline the importance of understanding

intraspecific variation before erecting new species based on single specimens or populations. Alternative taxonomies must be carefully considered against comparisons of modern and fossil variation. For example, it is still reasonable to include all Middle and Late Pleistocene *Homo* in *H. sapiens*, perhaps differentiated as spatio-temporal subspecies. Alternatively, the Neanderthal lineage in Europe and southwest Asia might be classed as a single species *H. neanderthalensis* (including *H. heidelbergensis* and, perhaps, *H. antecessor* as temporal stages). In such a model, the role of '*H. rhodesiensis*' is unclear, in part depending on whether it includes populations that were, ultimately, ancestral to modern *H. sapiens*, as the 'Out of Africa' hypothesis implies.

Even with the discovery of Neanderthal genetic material¹⁴, we still cannot decide whether the Neanderthals were one of several related species in an extinct radiation, a single species close to our own, or a 'race' of *H. sapiens* (with that species redefined to include 2-Myr-old *H. erectus*). How are we to choose among these or other alternatives? One approach might be to compare variation within and among the several named samples to that found in modern humans (either quantitatively or in terms of character distribution), under the hypothesis that geographical variation today is broadly comparable to past spatio-temporal variation¹⁵.

The Konso sequence has been carefully prospected for the past six years by a truly international team, with primary researchers from Japan, Ethiopia and the United States. It is perhaps fitting that a group which is so representative of modern human diversity should discover a fossil that helps us to understand the origins of that diversity. □

Eric Delson is at the American Museum of Natural History, New York, New York 10024, and in the Department of Anthropology, Lehman College, Bronx, New York 10468, USA.

1. Suwa, G. *et al.* *Nature* **389**, 489–492 (1997).
2. Leakey, L. S. B. *Nature* **184**, 491–493 (1959).
3. Suwa, G., White, T. D. & Howell, F. C. *Am. J. Phys. Anthropol.* **101**, 247–282 (1996).
4. Kimbel, W. H. in *Paleoclimate and Evolution, with Emphasis on Human Origins* (eds Vrba, E. S., Denton, G. H., Partridge, T. C. & Burckle, L. H.) 425–437 (Yale Univ. Press, New Haven, 1995).
5. Asfaw, B. *et al.* *Nature* **360**, 732–735 (1992).
6. Tamrat, E., Thouveny, N., Taieb, M. & Opdyke, N. D. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **114**, 273–283 (1995).
7. Leakey, M. D. *Olduvai Gorge Vol. 3: Excavations in Beds I and II 1960–1963* (Cambridge Univ. Press, 1971).
8. Tobias, P. V. *Olduvai Gorge Vol. 2: The Cranium and Maxillary Dentition of Australopithecus (Zinjanthropus) boisei* (Cambridge Univ. Press, 1967).
9. Rak, Y. *The Australopithecine Face* (Academic, New York, 1983).
10. Robinson, J. T. in *Evolutionary Biology Vol. 1* (eds Dobzhansky, T., Hecht, M. K. & Steere, W. C.) 69–100 (Appleton-Century-Crofts, New York, 1967).
11. Brown, B., Walker, A., Ward, C. V. & Leakey, R. E. *Am. J. Phys. Anthropol.* **91**, 137–159 (1993).
12. Tattersall, I. *J. Hum. Evol.* **15**, 165–175 (1986).
13. Bermúdez de Castro, J. M. *et al.* *Science* **276**, 1392–1395 (1997).
14. Krings, M. *et al.* *Cell* **90**, 19–30 (1997).
15. Delson, E. in *Evolutionary Biology at the Crossroads* (ed. Hecht, M. K.) 141–145 (Queens College Press, New York, 1990).

Daedalus

The ears have it

What makes an animal an appealing pet? One requirement is a face that seems 'human'. Cats, dogs and other popular pets have faces reminiscent of human infants, and trigger protective emotions in us. They also convey emotions by signals which we ourselves recognize. Daedalus now points out that the converse is also true. Good pets must be able to react to us, and to interpret our expressions and behaviour correctly. This is a severe restriction. A grasshopper (say), even one with human intelligence, could never tame a cat; the cat could never interpret the grasshopper's signals as those of a fellow creature.

So DREADCO technicians have devised a set of radio-controlled 'pet-loving robots' with various facial, ocular and vocal abilities. Each robot, guided by its unseen controller, attempts to feed, stroke, talk to and exchange friendly behaviour with an initially naive cat, dog or other animal. Those robots which succeed in making a pet of their animal will reveal the emotional signals recognized by that animal. In particular, they may prove a thesis Daedalus has held for some time. Our animal-taming abilities are severely limited by the immobility of our ears.

Cats, dogs, horses, rodents and many other creatures can swivel or shape their ears in different ways. We interpret these movements, instinctively and correctly, in emotional terms. Flattened or backwards-pointing ears suggest aggression or distress; upright and forward-pointing ones show interest and friendliness. Pet animals must be greatly discouraged by the absence of such signals from ourselves.

So Daedalus is also experimenting with a special skull-cap equipped with large electromagnetically adjustable 'ears'. A handset allows the wearer to switch them to whatever emotion he wishes to convey. With luck, the cap will enable its wearer to reach an emotional closeness with any animal that also uses ear signals.

DREADCO's ear-cap, together with any further prostheses indicated by the robot program, will transform our relations with ear-signalling animals. The most unruly dogs, aloof cats, treacherous goats and indifferent gerbils will at last respond to human affection. The acid test will be the utterly untameable Highland wild cat, reputed to hate everything and everybody on sight. If the cap can reduce this furious beast to a purring fireside moggy, a new lawn in the Garden of Eden will indeed have been opened.

David Jones