nature

Palaeoanthropology

The earliest *Sivapithecus*?

from Eric Delson

THE search for a fossil ancestor (or even an extinct close relative) of the human lineage has met with mixed success over the past few decades. During the 1960s, the view that *Ramapithecus* was an ancestor of humans as contrasted with the great apes became dogma in anthropology[1], questioned by few workers and those usually on invalid grounds. Sharper attacks on this position characterized the 1970s, as details of molar enamel thickness, dental proportions and wear patterns revealed little difference between this taxon and *Sivapithecus*, its contemporary in 9 – 13 million year old rocks in India and Pakistan[2,3]. Finds of more complete specimens attributable to *Sivapithecus* confirmed the similarity of these taxa and moreover permitted the inference that this expanded *Sivapithecus* group shared derived facial and dental features with *Pongo*, the living orangutan[4,5]. This left the fossil ancestry of human and African apes, joined phyletically by numerous generic and biomolecular studies[6], open to question. Minority alternative views have arisen which suggest that *Sivapithecus* is ancestral (or at least closely related) either to all great apes and humans[7] or to orangutans and humans alone[8].

New evidence on the morphology and temporo-spatial distribution of *Sivapithecus* is therefore of great interest in this discussion. On page 173 of this issue, Leakey and Walker[9] report and briefly describe new fossils from Buluk, Kenya, which they assign to an indeterminate species of *Sivapithecus*. This information is potentially exciting because the fossils are found in sediments that are more than 17 million years (Myr) old, as documented on page 175 by McDougall and Watkins[10], far older than the earliest Eurasian fossils assigned to *Sivapithecus*. Based on this

age, Leakey and Walker now accept that *Sivapithecus* could well be the common ancestor of all later large apes, but realize that it tells little about the divergence of either the African lineage (Homininae: chimp, gorilla, human) or Asian (Ponginae: orangutan) lineage implied by molecular studies. But how accurate is their "unequivocal" identification and subsequent phyletic assessment, and what more (or less) can be inferred from these fossils?

Before these questions can be approached, it is useful to review the Buluk primates and other known occurrences of Miocene large apes. The fossil primate material from Buluk is rather scrappy, but four species are said to be present: three 'apes' of varying size and a more common species of Old World monkey. Although not cited by Leakey and Walker, the monkey has recently been described in detail by Meave Leakey[11], who assigned it to *Prohylobates*, a genus otherwise known only from slightly younger deposits in Egypt and Libya[12], rather than to *Victoriapithecus* of the Kenyan ? Early to Middle Miocene (or about 17–15 Myr)[13,14]. This apparent affinity with northern rather than eastern African taxa is mirrored in the remainder of the Buluk faunal list, which suggests either that the environment was more open than other Early Miocene sites nearby (perhaps akin to that of the Kenyan Middle Miocene sites Maboko and Fort Ternan) or that there was an influx of immigrant species.

Of the Buluk hominoid primates, a few specimens are referred to a small species, most to the new *Sivapithecus*, and an isolated tooth and dentulous mandible fragment to *Kenyapithecus wickeri*. The last taxon, intermediate in size, is best known from Fort Ternan but has also been reported from Maboko and nearby Majiwa[15] and from Emuruilem (Nachola)[16]. There is still some controversy over the name and number of species of *Kenyapithecus* to be recognized but, despite previous synonymization with *Ramapithecus*, most authors now accept that *Kenyapithecus* is a distinct African mid-Miocene genus. While Pickford[15] has grouped *Kenyapithecus* with the *Sivapithecus–Pongo* clade, Andrews[17] places it on a separate lineage predating the Ponginae–Homininae divergence, because of its lack of derived *Pongo*-like features.

A number of other fossil 'populations' may also be relevant to understanding the Buluk specimens. In Asia, *Sivapithecus* is well documented in the Indo-Pakistan Siwaliks at about 12.5 Myr from remains with the distinctive facial characteristics seen in more complete younger specimens but, on dental evidence[18], may extend back to over 14 Myr; recently, remains as young as 5.5 Myr have been assigned to this genus[19]. In Pakistan, the most complete fossils date to about 8 Myr. A large sample (probably representing a single species with high sexual dimorphism, contra Wu and Oxnard[20]), of similar age from China has also been placed in *Sivapithecus* and/or *Ramapithecus*[21] but may require reassessment. The wide interorbital spacing and distinctive high-crowned incisors are not comparable to Siwalik *Sivapithecus*, although dental morphology is similar.

Sivapithecus has also been identified in Turkey and eastern Europe as old as 15 Myr, mainly on the basis of thick molar enamel, which Martin has shown to be a more complex character than previously thought[22]. The identification of *Sivapithecus* in Greece (see ref. 23) has been more widely accepted[24]. De Bonis and Melentis[23] have now reported that the maxillary morphology of the Greek fossils, which they term *Ouranopithecus*, is more similar to that of hominines than *Sivapithecus* (see ref. 5). Kelley and Pilbeam[25] have suggested that the morphology thus revealed was derived and they have linked *Ouranopithecus* to hominine ancestry, but I prefer the de Bonis and Melentis interpretation that hominies share the ancestral morphology of this region, with the pongines like *Sivapithecus* being derived. Given that *Ouranopithecus* does share other derived features with *Sivapithecus*[24], it seems best to retain all the Eurasian thick-enamelled Miocene apes in a single clade.

In the light of this diverse assemblage of African and Eurasian Miocene larger hominoids, it is somewhat surprising that Leakey and Walker[9] only compare the Buluk fossils to *Proconsul* and the Siwalik *Sivapithecus*. The novel faunal elements would suggest a wider search for comparative samples. Based upon the description and a brief examination of casts (courtesy of Walker), it seems to me that at least one alternative interpretation of the Buluk material is possible, if not more likely — that it represents a large *Kenyapithecus*. Pickford[15] has presented new metrical data on *Kenyapithecus* which support the idea that the Buluk *Sivapithecus* is the male of a species whose female is identified there as *Kenyapithecus*. For example, his estimate of the length of a male upper canine of *Kenyapithecus* is slightly greater than that given for the Buluk male, while molar lengths are comparable to, or slightly smaller than, those estimated for Buluk from roots; Leakey and Walker[9] do not give the direct measurements of the few relatively complete molars they have.

More to the point is the comparison of maxillofacial and mandibular morphology and enamel ultrastructure. The Buluk mandible is stated to be "remarkably similar" to an edentulous one from the Pakistani Siwaliks, but while this is so by comparison with *Proconsul*, there is little to differentiate among the Eurasian forms, all of which share superior and inferior transverse mandibular tori as well as a deep and thick corpus. The Buluk maxilla is not specifically compared with any Siwalik specimen, but the described morphology does read like that seen in several Asian *Sivapithecus* faces. It is not clear, however, that the described pattern is unique to *Sivapithecus* or is as well developed in Buluk as in the Eurasian fossils. An enamel thickness of 1.5 mm is given for the cuspal region of one broken, but little worn, upper molar, somewhat less than the 2–2.5 mm recorded for Pakistani *Sivapithecus*[26]. Martin[22] has shown that ultrastructural detail (unknown in this case) as well as size normalization, is needed to make an accurate estimate, of the enamel pattern, but the Buluk fossils may present the "intermediate-thin" pattern, predicted by Martin but not yet observed. (Neither *Kenyapithecus* nor *Dryopithecus* has yet been analysed.)

The essence of Leakey and Walker's comparative analysis is that since the Buluk fossils are not *Proconsul*, they must be *Sivapithecus*. While the first part of this syllogism is unquestioned, their conclusion is by no means inescapable. The lack of even superficial comparisons with *Kenyapithecus*, with the Moroto maxilla (which has long been assigned to a large species of *Proconsul*[27], but may be of Middle Miocene age[5] and thus rather younger than most of that taxon) or with *Dryopithecus* is surprising. It would seem, in fact, that an allocation to *Kenyapithecus* would be both more biogically parsimonious and reasonably supported by the morphological evidence. That *Kenyapithecus* is positioned close to the divergence of Ponginae and Hominae is thus reaffirmed, but the implications for the broader phylogeny of large hominoids in terms of palaeontology or molecular-clock calibrations are uncertain. □

1. Simons, E.L. & Pilbeam, D.R. *Folia primatol.* **3**, 81 (1965).
2. Simons, E.L. & Pilbeam, D.R., in *The Functional and Evolutionary Biology of Primates* (ed. Tuttle, R.L.) 36 (Aldine, Chicago, 1972).
3. Greenfield, L. *Am. J. phys. Anthrop.* **50**, 527 (1979).
4. Andrews, P. & Tekkaya, I. *Palaeontology* **23**, 85 (1980).
5. Ward, S.C. & Pilbeam, D.R. in *New Interpretations of Ape and Human Ancestry* (eds Ciochon, R.L. & Corruccini, R.S.) 211 (Plenum, New York, 1983).
6. Andrews, P. *Nature News and Views* **314**, 498 (1985).
7. Kay, R.F. & Simons, E.L. in *New Interpretations of Ape and Human Ancestry* (eds Ciochon, R.L. & Corruccini, R.S.) 577 (Plenum, New York, 1983).
8. Schwartz, J.H. *Nature* **308**, 501 (1984).
9. Leakey, R.E.F. & Walker, A. *Nature* **318**, 173 (1985).
10. McDougall, I. & Watkins R.T. *Nature* **318**, 175 (1985).
11. Leakey, M.G., *Folia primatol.* **44**, 1 (1985).
12. Delson, E. *Geobios* **12**, 725 (1979).
13. von Koenigswald, G.H.R. *Foss. Vertebrates Afr.* **1**, 39 (1969).
14. Szalay, F.S. & Delson, E. *Evolutionary History of the Primates* (Academic, New York, 1979).
15. Pickford, M. *J. hum. Evol.* **14**, 113 (1984).
16. Ishida, H., Pickford, M., Nakaya, N. & Nakaya, Y., *Afr. Study Monogr., Kyoto Univ.* Suppl. 2, 73 (1984).
17. Andrews, P. in *Ancestors: The Hard Evidence* (ed. Delson, E.) 14 (Alan R. Liss, New York, 1985).
18. Raza, S.M. *et al. Nature* **306**, 52 (1983).
19. Sankhyan, A.R. *J. hum. Evol.* **14**, 573 (1985).
20. Wu Rukang & Oxnard, C.E. *Nature* **306**, 258 (1983).
21. Wu Rukang, Lu Quigwu & Xu Qinghua, *Acta Anthropol. Sin.* **3**, 1 (1984).
22. Martin, L. *Nature* **314**, 260 (1985).
23. DeBonis, L. & Melentis, J. *C. r. Hebd. Séanc. Acad. Sci., Paris, Ser. II* **300**, 429 (1985).
24. Martin, L. & Andrews, P. *Cour. Forschungsinst. Senckenberg* **69**, 25 (1984).
25. Kelley, J. & Pilbeam, D.R. (abstract) *Am. J. phys. Anthrop.* **66**, 188 (1985).
26. Pilbeam, D.R., Rose, M.D., Badgley, C. & Lipschutz, B. *Postilla* **181**, 1 (1980).
27. Pilbeam, D.R. *Bull. Yale Peabody Mus. Nat. Hist.* **31**, 1 (1969).

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