

THE EVIDENCE FOR HUMAN EVOLUTION (A REVIEW)

ANDREW T. CHAMBERLAIN

(Department of Archaeology and Prehistory, The University of Sheffield,
Sheffield S10 2TN, England)

Vingnanam — Journal of Science 5: 30 — 42 (1990)

ABSTRACT: The main sources of evidence for human evolution are reviewed. The pattern of diversification of primates from their origins at the beginning of the Cenozoic era has been reconstructed using a combination of morphological evidence from fossil and living species together with measures of biomolecular similarity. Hominids evolved from a common ancestor shared with the living African apes, and throughout the Pliocene and much of the lower Pleistocene hominids were confined to their continent of origin. The earliest identifiable fossil hominids are less than 6 million years old and the origin of our own species ('anatomically modern' *Homo sapiens*) probably occurred with the last few hundred thousand years. Recent hypotheses concerning the evolution of the unique hominid adaptation of bipedalism are discussed.

Introduction

During the second half of the 19th century following the publication of Charles Darwin's "The Origin of Species" (Darwin 1859) the theory of evolution by natural selection became widely accepted among natural scientists. Interest and speculation about human ancestry was stimulated by Darwin's work, although Darwin himself was initially cautious about discussing human evolution. In his later book "The Descent of Man" (Darwin 1871) he was more forthcoming on the issue and assembled "three great classes of facts" which he held to demonstrate conclusively that humans had evolved from 'lower' animals. Darwin's evidence consisted of the homologous anatomical structures and physiological processes in humans and other animals; the similarities between humans and animals in patterns of growth and mode of development; and the presence in humans of rudimentary structures and organs that were best explained by gradual evolution from animals in which the same structures were fully functional. This body of indirect evidence was considered by Darwin to demonstrate that humans had evolved under the same constraints and mechanisms of natural selection as had other organisms, despite the absence (at the time he was writing) of any evidence for intermediate forms, either fossil or living, that could bridge the gap between humans and their closest relatives among the primates.

The evidence available today to students of human evolution is augmented by two major sources of data that were undiscovered in Darwin's lifetime. There are now a large number of fossil hominids, dating from about 6 million years ago (6 Ma) up to the end of the Pleistocene, which allow some of the intermediate stages of human evolution to be identified

and investigated. Secondly there is a new source of comparative data generated by the recently developed methods of molecular biology which provides an objective means of comparing the biological affinities of living species of primates, thus allowing independent corroboration of phylogenies derived from morphological evidence. This article summarises the position of the hominids within the phylogeny of the primates; reviews the fossil remains *Australopithecus* and early *Homo*; and discusses the origins of the uniquely human adaptation of bipedalism. The term 'hominid' is used throughout in its cladistic sense of referring to the monophyletic group that includes all taxa more closely related to *Homo sapiens* than to any other living primate.

Primate Evolution and the Molecular Clock

Modern primates occupy forest, woodland and grassland biomes that broadly fall within the tropical region. Their present day distribution is also constrained by their historical biogeography (Hoffstetter 1974), and by the pressures of human predation and modern changes in land-use (Harcourt 1990; Box 1991). Together with other modern orders of mammals, primate origins can be traced back to the beginning of the Cenozoic (Tertiary) era, to about 65 Ma (Szalay and Delson 1979; Martin 1990). Recent discoveries in Algeria have shown that anthropoid primates, the group that includes modern monkeys and apes, had evolved by at least 45 Ma (Godinot and Mohboubi 1992). The divergence of the anthropoids into their two major existing infraorders, the New World (Platyrrhine) and Old World (Catarrhine) faunas, is now estimated to have occurred before 40 Ma, after which the widening of the Atlantic Ocean in the late Eocene would have rendered faunal interchange between Africa and South America improbable (Martin 1990).

The pattern of diversification of the Old World monkeys and apes (including humans) has been established by combining the evidence from well dated fossils with the results of morphological and biomolecular comparisons between living representatives of the different catarrhine lineages (Martin 1990). After two lineages become separated the DNA and protein sequences of species diverge as random genetic mutations steadily accumulate in each lineage. In nuclear DNA, over 90 percent of which appears to be non-functional, most of this evolutionary change is selectively neutral since it neither benefits nor disadvantages the organism. Most mutations in mitochondrial DNA are also either in non-coding regions or are 'silent' substitutions that do not cause changes in the amino acid sequences coded by the molecule. Thus the rate of DNA evolution is largely determined by internal factors that are remote from environmental influence, such as the efficiency of DNA repair mechanisms and the time between germline replications.

Protein and DNA comparisons have yielded a highly corroborated sequence of branching among the extant catarrhine primate lineages (Goldman *et al.* 1987; Jeffreys 1989; Miyamoto and Goodman 1990). This branching pattern (Figure 1) can be converted into a 'clock' for determining the time of individual branching events by calibrating at least one speciation event against reliably dated fossil evidence. The molecular phylogeny for hominoids

is usually calibrated at two points, by the fossil evidence for the emergence of the cercopithecoid (Old World monkey) lineage at 25 - 35 Ma, coupled with a date for the origin of the lineage leading to the orang-utan which diverged from the African ape and human lineage before 13 Ma (see below). Interpolation of the dates of the other branching points shown on Figure 1

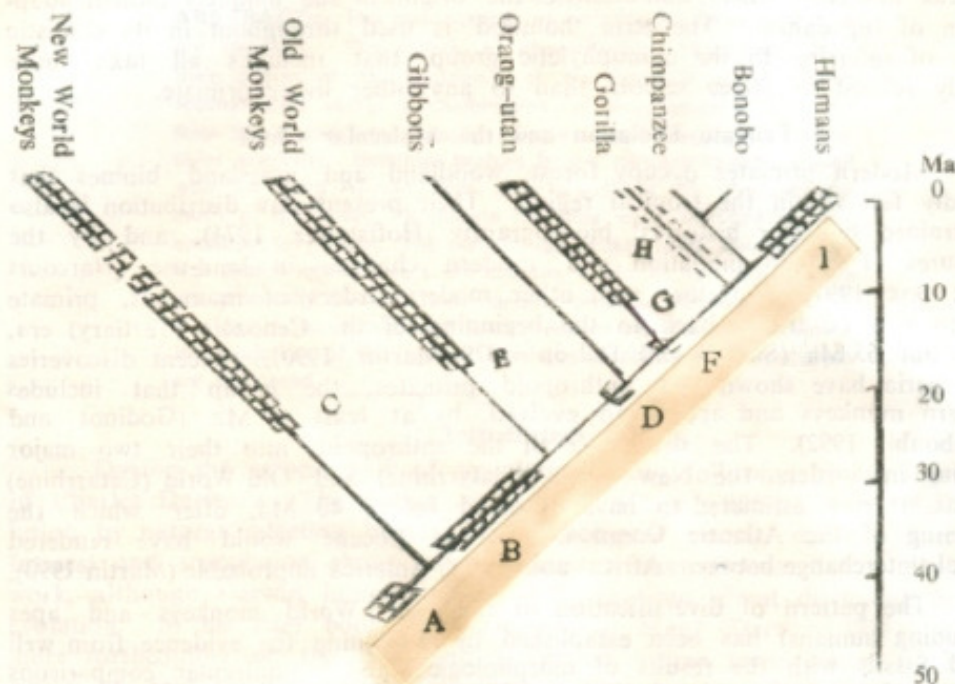


Fig 1. Phylogenetic tree for living anthropoid primates, based on the branching sequence established from biomolecular and morphological evidence. The hatched regions indicate the extent of the fossil record for each of the groups of living primates. Fossil evidence for the first appearance of these lineages is as follows: A. Anthropoids (*Algeripithecus*); B. Catarrhines (*Aegyptopithecus*, *Propliopithecus*); C. Platyrrhines (*Branisella*); D. Hominoidea (*Proconsul*); E. Cercopithecoids (*Victoriapithecus*); F. Great Apes (*Afropithecus*); G. Pongines (*Sivapithecus*); H. ?Gorillines (Samburu Hills); I. Hominids (*Australopithecus*).

might conceivably be affected by changes in the rate of molecular evolution, which may have slowed down as generation lengths have increased during primate evolution (Li and Tanimura 1987). In fact generation length is relatively stable among the living apes, ranging from about 11 years in gibbons to between 12 and 14 years in great apes, and developmental timing in early hominids appears to resemble that of living apes, rather than modern

humans (Beynon and Dean 1988). It is probable therefore that generation length in apes, and by inference the rate of neutral molecular evolution, has changed significantly only in the terminal phase of the evolutionary history of modern *Homo sapiens*.

One prediction of the 'molecular clock' is that humans diverged from the African apes in the late Miocene, less than 10 Ma and perhaps as recently as 7 Ma. The Asian middle Miocene genus *Ramapithecus* was formerly classified as a close relative of the hominids (Pilbeam 1972; Szalay and Delson 1979), but following the synonymy of *Ramapithecus* with *Sivapithecus* (Greenfield 1979), and the identification of derived characters linking *Sivapithecus* to the living orang-utan (Andrews and Cronin 1982; Ward and Pilbeam 1983), the origins of the hominid clade are now thought to lie outside the Asian continent. The divergence of the human and chimpanzee lineages must have predated the earliest known fossil hominids, which occur in Africa later than 6 Ma (Table 1). An estimated date of 8 Ma for hominid origins can be obtained from the molecular phylogeny by interpolation from a date of 16 Ma for the origin of the orangutan clade, which in turn is bracketed by the appearance of the earliest known fossil great ape *Afropithecus*, dated to 17 Ma (Leakey and Leakey 1986) and the occurrence of *Sivapithecus* (a fossil relative of the orang-utan) in Asia at about 13 Ma (Kappelman *et al.* 1991).

Genetic investigations of living human populations using a range of different gene frequency and nucleotide sequence data offer strong support for an African origin of modern *Homo sapiens* within the last 400 thousand years (Cann *et al.* 1987; Cavalli-Sforza *et al.* 1988; Vigilant *et al.* 1989; Long *et al.* 1990; Bowcock *et al.* 1991). Some biologists, however, have criticised their colleagues' interpretations of the mitochondrial DNA data (Spuhler 1988; Excoffier and Langaney 1989; Maddison 1991), and palaeoanthropologists are divided over the implications of the DNA results for theories of human evolution (Mellars and Stringer 1989; Brauer and Smith 1992). Some anthropologists continue to advocate in situ evolution of *Homo sapiens* in every area of Africa, Asia and Europe rather than in Africa alone (Thorne and Wolpof 1992).

The Earliest Hominids

The late Miocene primate fossil record in Africa is exceedingly sparse (Pickford 1986), and the period of hominid evolution from 8 to 4 Ma is thus poorly known. The earliest fossils that can be assigned with confidence to the human lineage are attributed to the primitive hominid genus *Australopithecus*, which is present in East Africa from about 6 Ma (Hill and Ward 1988: see also Tables 1 & 2). The oldest fossil hominid yet discovered is a mandible from Lothagam in Kenya. This fossil was found in sedimentary

Table 1: Earliest fossil evidence for hominids in Africa

Date (Ma)	Site	Specimen	Taxonomic Attribution
3.0	Hadar, Ethiopia	AL 288-1 'Lucy' skeleton	<i>A. afarensis</i>
3.35	Koobi Fora, Kenya	ER 2602 cranial fragments	<i>A. afarensis</i>
3.4	Omo, Ethiopia	Omo 20-1886 tooth	<i>Australopithecus</i>
3.5	Laetoli, Tanzania	LH 4 mandible	<i>A. afarensis</i>
<4.0	Maka, Ethiopia	MAK VP 1.1 femur	<i>A. afarensis</i>
4.0	Belohdelie, Ethiopia	BEL VP 1.1 cranial fragments	<i>A. afarensis</i>
c. 4.0	Fejej, Ethiopia	FJ 4 SB 1,2 teeth	<i>A. afarensis</i>
4.0	Kanapoi, Kenya	KP 271 humerus	<i>A. afarensis</i>
>4.2	Chemeron, Kenya	BC 1745 humerus	<i>Australopithecus</i>
4.9	Tabarin, Kenya	TH 13150 mandible	<i>cf. A. afarensis</i>
>5.5	Lothagam, Kenya	LT 329 mandible	<i>cf. A. afarensis</i>
c. 8.0	Samburu Hills, Kenya	SH 8531 maxilla	Hominoid (<i>cf. Gorilla</i>)

deposits between volcanic layers with radiometric dates of 3.8 and 8.5 Ma; faunal correlations suggest that the specimen is older than 5.5 Ma. Although White (1986) expressed reservations about the attribution of the Lothagam mandible to *Australopithecus*, Hill and Ward (1988) present a convincing case

Table 2: First and Last Appearances of Hominid Taxa in Africa

Taxon	First Appearance (Ma)	Last Appearance (Ma)	Maximum Geographical Range
<i>A. aethiopicus</i>	2.6	2.3	E. Africa
<i>A. afarensis</i>	> 5.0	2.8	E. Africa
<i>A. africanus</i>	3.1	2.3	S. Africa
<i>A. boisei</i>	2.3	1.4	E. Africa
<i>A. robustus</i>	1.9	1.2	S. Africa
<i>H. habilis</i>	2.4	1.5	Africa
<i>H. erectus</i>	1.75	0.4	Africa, Asia
<i>H. heidelbergensis</i>	0.4	0.1	Africa, Asia & Europe
<i>H. sapiens</i>	0.1	—	Worldwide

The taxonomic classification adopted in this Table follows Delson (1987) for species in the genus *Australopithecus* and Stringer (1984) for species of *Homo*. The species '*Homo heidelbergensis*' has been substituted in place of Stringer's informal taxon 'archaic *Homo sapiens*'.

for its assignment to that taxon. An earlier fossil jaw from late Miocene deposits at Samburu Hills in Kenya is non-hominid, having closest affinities with the extant great ape *Gorilla* (Hill and Ward 1988). Confirmation of this taxonomic attribution for the Samburu Hills fossil, which is dated to around 8 Ma, would provide a minimum date for the divergence of the gorilla lineage and would therefore further constrain the timing of the origin of the human lineage.

Hominids are better represented in the early Pliocene with at least ten African fossil hominid sites now identified in the interval from 5 to 3 Ma (Table 1; Figure 2). Most of the fossils from these sites have been attributed to *Australopithecus afarensis*, a species which is best known from the samples recovered at Laetoli in Tanzania and Hadar in Ethiopia. The postcranial fossils at Hadar and the fossilised hominid footprints at Laetoli provide clear evidence of bipedalism in *Australopithecus afarensis*, although this species also retained some anatomical adaptations for arboreal locomotion (Susman *et al.* 1984).



Fig 2. Map of early hominid sites in Africa.

The earliest fossil skeletal evidence for the genus *Homo* appears in East Africa before 2.0 Ma. Three isolated teeth from Member E of the Shungura formation at Omo, Ethiopia, dated to about 2.4 Ma have been attributed to the genus *Homo* (Howell *et al.* 1987). At Koobi Fora in Kenya the genus *Homo* first appears in the upper part of the Burgi Member, dated to 1.9 Ma (Wood 1991). The type series of *Homo habilis* from Olduvai Gorge in Tanzania includes specimens from Bed I, dated to 1.85 Ma, and from the lower part of Bed II, dated to 1.7 Ma (Tobias 1991). Specimens that have been attributed to *Homo habilis*, particularly the cranial remains of early *Homo* from Koobi Fora, are heterogeneous in their morphology (Chamberlain

and Wood 1987; Lieberman *et al.* 1988; Chamberlain 1989) and there is currently no clear consensus on the taxonomic status of this species (Tobias 1991; Wood 1991). The species *Homo erectus* which first appears at 1.75 Ma in the KBS member at Koobi Fora, Kenya, subsequently occupied a wide region of the Old World, persisting until 0.4 Ma in North Africa and 0.25 Ma in China (Rightmire 1990). A summary of the first and last appearances of conventional fossil hominid species in Africa is given in Table 2.

The earliest stone tools have been found in deposits dated to 2.7 Ma at Kada Gona in the Hadar region of Ethiopia (Harris 1986). All sites in Africa yielding the remains of *Homo habilis* have also produced evidence of stone tool manufacture or use, and many anthropologists view the manufacture of stone tools as the exclusive prerogative of *Homo*. This assumption has been challenged by Susman (1988) who argues that the fossil hand bones of *Australopithecus robustus* show that this species may have possessed a precision grip as sophisticated as that of *Homo habilis*. The fossil remains of 'robust' australopithecines are frequently found at the same sites as *Homo habilis*, and it is thus impossible to exclude *Australopithecus* as a potential maker or user of stone tools.

The evolution of bipedalism

Although a variety of modes of locomotion have been adopted by primates (Martin 1990), the immediate ancestors of hominids were large bodied hominoids that were probably adapted to climbing and suspensory postures (Susman *et al.* 1984). Several theories have been advanced to explain the evolution of upright posture and bipedal gait, a form of locomotion that among primates is unique to hominids (Day 1986). Hominoids have been considered to be preadapted to develop bipedalism, but a large number of anatomical and physiological changes are implicated in the change from habitual quadrupedal to bipedal locomotion (Aiello and Dean 1990). This suggests that considerable advantages in energy saving or in enhanced reproductive success must have accrued when hominids adopted this form of locomotion. Skeletal modification for bipedalism are found in the earliest fossil hominids, and the occurrence of fossilised footprints of hominids at Laetoli in Tanzania shows that the australopithecines were capable of walking fully bipedally.

Rodman and McHenry (1980) showed that when a bipedal animal walks it consumes less energy than a quadruped of the same body size, although this advantage is reversed at higher speeds. Adaptive advantages in long distance bipedal walking might have included scavenging opportunities (from being able to follow migrating animals; Sinclair *et al.* 1986), or the ability

to carry food in order to provision mothers who had dependent infants (Lovejoy 1981). However, recent models of early hominid social structure (Foley and Lee 1989) exclude the monogamous group structure on which Lovejoy's provisioning hypothesis is founded, and there is no evidence of the widespread adoption of hunting or substantial meat eating by hominids prior to the appearance of *Homo*.

Wheeler (1984, 1991a, 1991b) has shown that by adopting a bipedal posture early hominids would have been able to reduce the heat load from incident solar radiation in the middle of the day. Further efficiency in thermoregulation would have stemmed from the loss of body hair in hominids, which would have allowed effective heat removal through convective cooling augmented by sweating. Since windspeeds are higher and air temperatures and humidity are lower away from the ground surface, the bipedal posture also enhances evaporative cooling. Wheeler (1991b) argues that the combination of bipedalism with loss of body hair enabled early hominids to maximise the time spent on foraging for low density or scattered resources in equatorial grassland habitats.

Alternative scenarios in which there might have been a selective advantage for bipeds include the need to detect and defend against predators (Kortlandt 1980), enhancement of the efficiency of tool use (Marzke 1986, or the ability to move across steep and sparsely vegetated terrain (Jaanusson 1991). The process by which adaptations end up serving a useful function additional to the function for which they were originally selected has been characterised by Gould and Vrba (1982) as 'exaptation'. It is likely that regardless of the initial impetus for bipedalism in early hominids, other benefits and opportunities emerged to contribute to the success of this radical change.

Acknowledgements

An earlier version of this paper was presented at a seminar held in the Science Faculty of the University of Jaffna in January 1989. It is dedicated to the memory of Rajani Thiranagama who arranged my visit to the University of Jaffna, and whose intelligence, generosity and courage greatly enhanced the lives of all who had the pleasure of working with her.

References

- Aiello, L. and Dean, C. (1990) *An introduction to human evolutionary anatomy*. Academic Press, London. 596 pp.
- Andrews, P. J. and Cronin, J. E. (1982) The relationships of *Sivapithecus* and *Ramapithecus* and the evolution of the orang-utan, *Nature* 297, 541-546.

- Beynon, A. D. and Dean, M. C. (1988) Distinct dental development patterns in early fossil hominids. *American Journal of Physical Anthropology* 63, 23-27.
- Bowcock, A. M., Kidd, J. R. and Mountain, J. L. (1991) Drift, admixture, and selection in human evolution: a study with DNA polymorphisms. *Proceedings of the National Academy of Sciences of the U.S.A.* 88, 839-843.
- Box, H. O. (1991) *Primate responses to environmental change*. Chapman and Hall, London. 442 pp.
- Brauer, G. and Smith, F. H. (1992) *Continuity or replacement? Controversies in: Homo sapiens evolution*. Balkema, Rotterdam. 315 pp.
- Cann, R. L., Stoneking, M. and Wilson, A. C. (1987) Mitochondrial DNA and human evolution. *Nature* 325, 31-36.
- Cavalli-Sforza, L. L., Piazza, A., Menozzi, P. and Mountain, J. (1988) Reconstruction of human evolution: bringing together genetic, archeological, and linguistic data. *Proceedings of the National Academy of Sciences of the U.S.A.* 85, 6002-6006.
- Chamberlain, A. T. (1989) Variations within *Homo habilis*. pp. 175-181. In: *Hominidae*. Jaca, Milan.
- Chamberlain, A. T. and Wood, B. A. (1987) Early hominid phylogeny. *Journal of Human Evolution* 16, 119-133.
- Darwin, C. R. (1859) *On the origin of species by means of natural selection or the preservation of favoured races in the struggle for life*. Murray, London. 490 pp.
- Darwin, C. R. (1871) *The descent of man and selection in relation to sex*. Murray, London.
- Day, M. H. (1986) Bipedalism: pressures, origins and modes. pp. 188-202. In: *Major topics in primate and human evolution*. Cambridge University Press, Cambridge.
- Delson, E. (1987) Evolution and palaeobiology of robust *Australopithecus*. *Nature* 327, 654-655.
- Excoffier, L. and Langaney, A. (1989) Origin and differentiation of human mitochondrial DNA. *American Journal of Genetics* 44, 73-85.
- Foley, R. A. and Lee, P. C. (1989) Finite social space, evolutionary pathways, and reconstructing hominid behaviour. *Science* 243, 901-906.
- Godinot, M. and Mahboubi, M. (1992) Earliest known simian primate found in Algeria. *Nature* 357, 324-326.
- Goldman, D., Giri, P. R. and O'Brien, S. J. (1987) A molecular phylogeny of the hominoid primates as indicated by two-dimensional protein electrophoresis. *Proceedings of the National Academy of Sciences of the U.S.A.* 84, 3307-3311.

- Gould, S.J. and Vrba, E. S. (1982) Exaptation - a missing term in the science of form. *Paleobiology* 8, 4 - 15.
- Greenfield, L. O. (1979) On the adaptive pattern of "Ramapithecus". *American Journal of physical Anthropology* 50, 527 - 548.
- Harcourt, C. (1990) *Lemurs of Madagascar and the Comoros*. International Union for the Conservation of Nature, Cambridge. 240 pp.
- Harris, J. W. K. (1986) Decouverte de materiel archeologique Oldowayen dans le rift de l'Afar. *L'Anthropologie* 90, 339 - 357.
- Hill, A. and Ward, S. (1988) Origin of the Hominidae: the record of African large hominoid evolution between 14 My and 4 My. *Yearbook of Physical Anthropology* 31, 49 - 83.
- Hoffstetter, R. (1974) Phylogeny and geographical deployment of the primates. *Journal of Human Evolution* 3, 327 - 350.
- Howell, F. C., Haesaerts, P. and de Heinzelin, J. (1987) Depositional environments, archeological occurrences and hominids from Members E and F of the Shungura Formation (Omo basin, Ethiopia). *Journal of Human Evolution* 16, 665 - 700.
- Jaanusson, V. (1991) Morphological changes leading to bipedalism. *Lethata* 24, 443 - 457.
- Jeffreys, A. J. (1989) Molecular biology and human evolution pp. 27 - 52. In: *Human Origins*. Clarendon Press, Oxford.
- Kappelman, J., Kelley, J. and Pilbeam, D., (1991) The earliest occurrence of Sivapithecus from the middle Miocene Chinji Formation of Pakistan. *Journal of Human Evolution* 21, 61 - 73.
- Kortlandt, A. (1980) How might hominids have defended themselves against large predators and food competitors? *Journal of Human Evolution* 9, 79 - 112.
- Leakey, R. E. and Leakey, M. G. (1986) A new Miocene hominoid from Kenya. *Nature* 324, 143 - 148.
- Li, W - H. and Tanimura, M. (1987) The molecular clock runs more slowly in man than in apes and monkeys. *Nature* 326, 93 - 96.
- Lieberman, D. E., Pilbeam, D. R. and Wood, B. A. (1988) A probabilistic approach to the problem of sexual dimorphism in *Homo habilis*: a comparison of KNM - ER 1470 and KNM - ER 1813. *Journal of Human Evolution* 17, 503 - 511.
- Long, J. C., Chakravarti, A. and Boehm, C. D. (1990) Phylogeny of human beta - globin haplotypes and its implications for recent human evolution. *American Journal of Physical Anthropology* 81, 113 - 130.

- Lovejoy, C. O. (1981) The origin of man. *Science* 211, 341 - 350.
- Maddison, D. R. (1991) African origin of human mitochondrial DNA re-examined. *Systematic Zoology* 40, 355 - 363.
- Martin, R. D. (1990) *Primate origins and evolution: a phylogenetic reconstruction*. Chapman and Hall, London. 804 pp.
- Marzke, M. W. (1986) Tool use and the evolution of hominid hands and bipedality pp. 203 - 209. In: *Primate evolution*. Cambridge University Press, Cambridge.
- Mellars, P. and Stringer, C. (1989) *The human revolution*. Edinburgh University Press, Edinburgh. 800 pp.
- Miyamoto, M. M. and Goodman, M. (1990) DNA systematics and evolution of primates. *Annual Review of Ecology and Systematics* 21, 197 - 220.
- Pickford, M. (1986) Geochronology of the Hominoidea: a summary. pp. 123 - 128. In: *Primate evolution*. Cambridge University Press, Cambridge.
- Pilbeam, D. R. (1972) *The ascent of man: an introduction to human evolution*. Macmillan, New York. 207 pp.
- Rightmire, G. P. (1990) *The evolution of Homo erectus*. Cambridge University Press, Cambridge. 260 pp.
- Rodman, P. S. and McHenry, H. M. (1980) Bioenergetics and the origin of hominid bipedalism. *American Journal of Physical Anthropology* 52, 103 - 106.
- Sinclair, A. R. E., Leakey, M. D. & Norton-Griffiths, M. (1986) Migration and hominid bipedalism. *Nature* 324, 307 - 308.
- Spuhler, J. N. (1988) Evolution of mitochondrial DNA in monkeys, apes, and humans. *Yearbook of Physical Anthropology* 31, 15 - 48.
- Stringer, C. (1984) Human evolution and biological adaptation in the Pleistocene. pp. 55 - 83. In *Hominid evolution and community ecology*. Academic Press, London.
- Susman, R. L. (1988) Hand of Paranthropus. *Science* 240, 781 - 784.
- Susman, R. L., Stern, J. T. and Jungers, W. L. (1984) Arboreality and bipedality in the Hadar hominids. *Folia Primatologica* 43, 113 - 156.
- Szalay, F. S. and Delson, E. (1979) *Evolutionary history of the primates*. Academic Press, New York. 580 pp.
- Thorne, A. G. and Wolpoff, M. H. (1992) The multiregional evolution of humans. *Scientific American*, April, 28 - 33.

- Tobias, P. V. (1991) *Olduvai Gorge, Volume 4. The skulls, endocasts and teeth of Homo habilis*. Cambridge University Press, Cambridge. 921 pp.
- Vigilant, L., Pennington, R., Harpending, H., Kocher, T. D. and Wilson, A. C. (1989) Mitochondrial DNA sequences in single hairs from a southern African population. *Proceedings of the National Academy of Sciences of the U.S.A.*, 86, 9350 - 9354.
- Ward, S. C. and Pilbeam, D. R. (1983) Maxillofacial morphology of Miocene hominoids from Africa and Pakistan. pp. 211 - 238. In: *New interpretations in ape and human ancestry*, Plenum, New York.
- Wheeler, P. E. (1984) The evolution of bipedality and the loss of functional body hair in hominids. *Journal of Human Evolution* 13, 91 - 98.
- Wheeler, P. E. (1991a) The thermoregulatory advantages of hominid bipedalism in open equatorial environments: the contribution of increased convective heat loss and cutaneous evaporative cooling. *Journal of Human Evolution* 21, 107 - 115.
- Wheeler, P. E. (1991b) The influence of bipedalism on the energy and water budgets of early hominids. *Journal of Human Evolution* 21, 117 - 136.
- White, T.D. (1986) *Australopithecus afarensis* and the Lothagam mandible. *Anthropos (Brno)*, 23, 79 - 90.
- Wood, B. A. (1991) *Koobi Fora Research Project, Volume 4. Hominid cranial remains*. Clarendon Press, Oxford. 466 pp.

Received for publication May 1989.