S. J. Edelstein

Department of Biochemistry,
Sciences II,
30 Quai Ernest Ansermet,
University of Geneva,
CH-1211 Geneva 4, Switzerland

An Alternative Paradigm for Hominoid Evolution

Biological clock data from protein sequences indicate times for the divergence of humans and African apes that are only 2-3 million years before the present and hence inconsistent with the generally accepted view of *Australopithecus* on the evolutionary line to *Homo*. This inconsistency has been reconciled for most investigators by postulating a slowing of the biological clock among higher primates. However, there is no independent evidence for such a slowing, and for a number of reasons a specific slowing is unlikely. Therefore, an alternative paradigm is considered here based on the hypothesis that the molecular clock data are correct. The main consequence of this hypothesis is the placement of *A. afarensis* in a position ancestral to African apes. An argument in support of this alternative paradigm is formulated concerning the evolution of knuckle-walking in African apes from ancestors whose bipedalism was already well developed. Published data are cited, particularly concerning the structure of the wrist, which accommodate poorly the evolution of African apes from palmigrad-walking or brachiating ancestors resembling *Proconsul africanus* or *Pongo*. These arguments suggest that an alternative paradigm of hominoid evolution placing *A. afarensis* ancestral to *Homo*, *Gorilla*, and *Pan* warrants further consideration.

Introduction

In recent years, reconstructions of hominoid evolution have advanced the estimated divergence of humans and African apes from about 20 million years before the present (Myr BP) to 4-10 Myr BP, principally on the basis of biomolecular data (GOODMAN, 1963; SARICH & WILSON, 1967; SARICH & CRONIN, 1976; CORRUCCINI, et al., GOODMAN, et al., 1983b; SIBLEY & AHLQUIST, 1984), with the line of evolution leading to *Homo* defined by *Australopithecus afarensis* fossils at 3-4 Myr BP (JOHANSON et al., 1982). An inconsistency in this conceptualization concerns biological clock calculations from protein sequence changes which give much more recent divergence times, e.g. only 1.3-2.2 Myr BP for *Homo* and *Pan* (chimpanzee), and led GOODMAN et al. (1983b) to postulate a slowing down of the clock in hominoids due to «prior selection» of «perfected adapatations». However, this interpretation is open to challenge (EDELSTEIN, 1986), in part from considerations of hemoglobin topology (EDELSTEIN, 1981). Arguments suggesting a general slowing of the biological clock in higher primates have also been proposed (BRITTEN, 1986; KOOP et al., 1986), based on improved DNA repair mechanisms or lengthening generation times. Whereas such arguments remain highly speculative, there has been effectively no evaluation of the alternative that the clock data are correct and a bipedal species such as *A. afarensis* was ancestral to African apes. Indeed, certain anatomical data reexamined here, involving principally the appearance of knuckle-walking uniquely among African apes, favor such an alternative paradigm.

Anatomical Evidence

Morphological affinities between *A. afarensis* and *Pan* have been previously emphasized, including similarities in cranial features and postcranial dimensions (ZIHLMAN *et al.*, 1978; WHITE, *et al.*, 1983), but *Pan* has always been assumed to be closer to the ancestral form. However, knuckle-walking derived from bipedalism could have occurred in response, for example, to selective pressures associated with inhabiting dense forests. In such environments locomotion in a stooped posture aided by the forelimbs may well have provided a major selective advantage, both for maneuvering under branches and for added speed. The ability of the fingers in the knuckle-walking position to penetrate for added traction may also have provided advantages in negotiating slippery hills or muddy terrain in wet habitats. The attribution of more ancestorlike features to *Pan* compared to *A. afarensis*, apart from preconceptions derived from the existing paradigm, is based on the larger pelvis, slightly smaller cranial capacity, smaller postcanine teeth, and somewhat larger canines, but these features could have accompanied the evolutionary reversal associated with the habitats involved in the selection of knuckle-walking.

Identification of possible hominoid ancestors from the Miocene include species such as *Proconsul africanus*, a simian quadruped with postcranial morphology that some investigators have interpreted as indicative of brachiation (LEWIS, 1971) or knuckle-walking (CORNROY & FLEAGLE, 1972). However, new insights were obtained by McHENRY & CORRUCCINI (1983) in studies of the wrist joint of *Proconsul, Homo, Pan, Gorilla, Pongo, Hylobates*, and *Macaca* involving 30 parameters for the lunate (4), scaphoid (5), capitate (5), hamate (3), radius (8), and ulna (5), with the measurements converted to dimensionless shape variables and analyzed by multivariate procedures. The first canonical variate accounts for 65% of the total discrimination and their mean projections are presented in *Table 1*. These results place *Proconsul* at an intermediate position near the center of the distribution, with *Pan* and *Gorilla* at one extreme and *Pongo* (orangutan), with its negative value, at the other extreme.

Since there is general support of a cladogram with the divergence of *Pongo* at the node to *Homo-Pan-Gorilla*, the knuckle-walking mode of locomotion could reasonably be expected to have prevailed for the ancestor to this node, with residual traces of knuckle walking in *Pongo*. However, the opposite situation appears to prevail, with *Homo* intermediate between *Proconsul* and *Pan-Gorilla*, suggesting that knuckle-walking had a distinct origin independent of a brachiating ancestor resembling *Pongo*. It should also be noted that in *Pongo* use of forelimbs for locomotion is either palmigrade or fist-walking, as distinct from knuckle-walking, with locomotion resembling knuckle-walking reported only rarely, as in the case involving an orangutan in captivity crossing a slippery floor (TUTTLE & BASMAJIAN, 1975). Another argument against knuckle-walking as an ancestral condition is that human infants are not known to use any form of locomotion resembling knuckle-walking that might be recapitulative of an ancestral pattern. The extensive differences in the wrist of *Pongo* versus *Pan* summarized by McHENRY & CORRUCCINI (1983) also suggest that the transition from palmigrade forelimb locomotion to knuckle-walking is too complex to have been achieved in a concerted step, supporting the idea of an intermediate stage involving bipedalism.

Indications of bipedal ancestors for African apes might also be sought in the morphology of the foot. Data from LESSERTISSEUR & JOUFFROY (1975) summarized in *Table 1* are suggestive in this regard, since for three indices, length of the tarsus, the lever index, and the relative shortness of the toes, the chimpanzee and especially the gorilla (notably for the lever index) show affinities with the human foot, while values for *Pongo*

TABLE 1 - *Summary of morphological parameters.*

	Proconsul africanus	Homo sapiens	Gorilla	Pan	Pongo
Wrist data:	− 0.17	3.93	8.35	8.81	− 9.49
Foot indices:					
T/P		53.3	39.2	34.9	27.9
W/R		39.4	46.1	28.2	19.6
o_m/P		22.1	34.4	35.5	42.5

Wrist data are mean projections along first canonical variate from *Table 1* of McHENRY & CORRUCCINI (1983); the original data also includes values for *Hylobates*, − 6.61, and *Macaca*, − 3.18. Foot indices are from *Table 1* of LESSERTISSEUR & JOUFFROY (1975), where T/P is the length of the tarsus as a percentage of the length of the foot; W/R is the lever index; o_m/P is the length of the longest free toe (o_2 in humans, o_3 in other genera) as a percentage of the lengh of the foot.

are more removed. Several other studies also support the idea of knuckle-walking derived from bipedalism (AIELLO, 1981; STERN & SUSMAN, 1981; TUTTLE, 1981).

Discussion

On the basis of the data presented here, it is reasonable to conclude that the fossil record cannot be used to dismiss *a priori* the clock data indicating a recent divergence of *Homo* and *Pan*. Since the biological clock for hemoglobin indicates one nucleotide replacement per *alpha* or *beta* chain every 2.5 Myr, the presence of one difference per chain between humans and gorillas indicates a divergence at about 2.5 Myr BP and the absence of any hemoglobin differences between *Pan* and *Homo* places their divergence at considerably more recent times (GOODMAN *et al.*, 1983b). Similar estimates are obtained from the average of 10 polypeptide chains, specifically *Homo-Pan* divergence at 1.3-2.2 Myr BP, with gorilla divergence 0.5-0.9 Myr earlier (GOODMAN *et al.*, 1983b). Nucleotide replacements that do not alter protein sequence due to coding degeneracy could alter the estimates, but no differences were observed between the human sequence of the *beta*-globin gene and 361 nucleotides from exon I, exon II, and part of exon III of the corresponding chimpanzee gene (SAVATIER *et al.*, 1985). With respect to other biomolecular data, recent DNA hybridization results have been interpreted in terms of *Homo-Pan* divergence 6.3-7.8 Myr BP, but the dating hinges on an estimate of the *Pongo* clade branching at 16 Myr BP (SIBLEY & AHLQUIST, 1984), whereas considerably more recent estimates have also been proposed (ANDREWS & CRONIN, 1982; GOODMAN *et al.*, 1983a). Other complications concerning the DNA hybridization data may arise from the assumption of linearity of *delta* $T_{50}H$ values with divergence times over a range of organisms that probably differ widely in their distribution of single nucleotide replacements and more extensive chromosomal alterations.

Conclusions

Issues raised here are supportive of a bipedal ancestor for African apes. While extensive further evaluation of morphological data will clearly be required, questions of
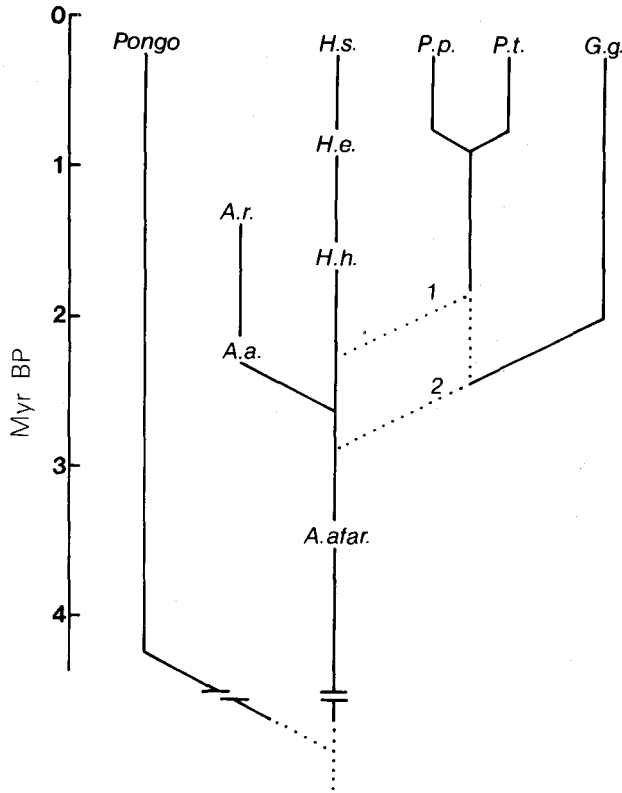
Figure 1. - A possible scheme for the cladogenesis corresponding to the alternate paradigm for hominoid evolution. The abbreviations used are: *A. r.*, *A. a.*, and *A. afar.* for *Australopithecus robustus, africanus*, and *afarensis*, respectively; *H. s.*, *H. e.*, and *H. h.* for *Homo sapiens, erectus*, and *habilis*, respectively; *P. p.* and *P. t.* for *Pan paniscus* and *troglodytes*, respectively; and *G. g.* for *Gorilla gorilla*. Sloping lines at the branching points may include transient species and are therefore not inconsistent with the estimated limit of 100,000 years for speciation in a punctated evolutionary process (GOULD, 1982). Dotted lines 1 and 2 refer to the two major cladistic possibilities linking *Pan* with either *Homo* or *Gorilla*. Divergence of *A. africanus* prior to the evolutionary line to *H. habilis* follows the arguments based on fossil analysis (JOHANSON & WHITE, 1979; WHITE *et al.*, 1983).

cladogenesis must also be considered. Cladistic data from protein sequence changes place *Gorilla* divergence before the *Homo-Pan* clade (GOODMAN *et al.*, 1983b). Although the mtDNA analysis is not definitive on this point (FERRIS *et al.*, 1981; BROWN *et al.*, 1982), there is weak support for a *Gorilla-Pan* clade (SIBLEY & AHLQUIST, 1984). Ambiguities thus remain in hominoid cladogenesis, but were divergence of *Gorilla* to have occurred before the *Homo-Pan* clade, the paradigm of ancestral bipedalism would require parallel evolution of knuckle-walking in separate radiations to *Pan* and *Gorilla* from early *Australopithecus*, in what would have been a period of high activity within the framework of punctuated equilibrium (GOULD, 1982). A possible formulation of the evolutionary branching implied by the alternative paradigm is presented in *Figure 1*.

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