Why was a moving obstacle easier to miss (or perceive) than a stationary one? The answer is probably associated with the fact that carnivorous and insectivorous bats rely on moving prey for survival, and they apparently concentrate more intently on moving objects while hunting. In behavioural experiments, it is essential to present an animal with tasks which are more relevant to situations encountered in its natural environment.

'Motion detectors' have been found in a cat's inferior colliculus[10] and auditory cortex[11], and it is likely that the bat's auditory system also contains neurones that are particularly sensitive to an echo source moving in a particular direction and at a particular speed. Indeed, cortical neurones sensitive to a moving sound source have been found in the big brown bat (*Eptesicus fuscus*) by P. Wasserbach (personal communication).

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Pygmy chimpanzee as a possible prototype for the common ancestor of humans, chimpanzees and gorillas

A CONVINCING theory of human origins must clarify man's relationships with living primates and with the ancestral forms known only through fossils. Phylogenetic relationships have previously been determined mainly by anatomical similarities, but now, biochemical similarities provide independent criteria for evolutionary relationships. Albumin and transferrin immunology, immunodiffusion, DNA annealing and amino acid analysis all indicate that chimpanzees, gorillas and humans share a substantial common ancestry, and that the Asiatic apes (gibbons and orangutans) diverged earlier from this lineage[1–3]. These findings directly conflict with the more widely held view that all the great apes diverged from a common ancestor long after the 'origin' of the evolutionary line leading to modern humans[4]. The molecular data consistently suggest a much more recent origin of the man–chimpanzee–gorilla separation than was previously imagined, namely, in the range of 4–6 M yr ago[3,5]. These data show that, although the two chimpanzee species (*Pan paniscus* and *P. troglodytes*) are biochemically distinct, they are more closely related to each other than either is to humans or gorillas[6,7]. The chimpanzees speciated, then, after the initial three-way split. We therefore, here contend that, among living species, the pygmy chimpanzee (*P. paniscus*) offers us the best prototype of the prehominid ancestor. Biochemical, morphological, behavioural and palaeontological data support this proposition and argue for a relatively recent and accelerated divergence of the hominid from the pongid line.

If this cladogram is correct, then an ancestor for the earliest hominids must also be a suitable ancestor for chimpanzees and gorillas. The morphological similarities between the three groups should logically be derived from the common ancestor, rather than by evolutionary convergence, or by parallelism from distinct primate lineages. In fact, the modern African apes may be viewed as size variants in a single morphotypic series, going stepwise from the smaller *P. paniscus* to the large male gorilla. The scant hominid fossil record during the past 4–8 M yr, and the absence of any fossil chimpanzees or gorillas, forces us to work backwards from the living hominoids to reconstruct a prototype of the comnon ancestor.

Chimpanzees have generally been considered closer to this prototypic ape than gorillas, because the latter are more specialised morphologically and behaviourally. They are larger and males are twice the size of females; they have a more specialised diet, more restricted habitat and less flexible social behaviour than chimpanzees. Morphologically, pygmy chimpanzees are more 'generalised' in body size, body build and sexual dimorphism than the common species and may provide a better prototype for studying the derivation of the earliest hominids and African apes.

Pygmy chimpanzees on the average weigh less than the average common chimpanzee, but with much overlap: 25–48 kg, compared to 25–60 kg or somewhat more[8]. Pygmy chimpanzees have smaller facial and canine dimensions, smaller average cranial capacities (350 cm^3 compared with 390 cm^3), and the two species can be discriminated on mandibular length alone[9].

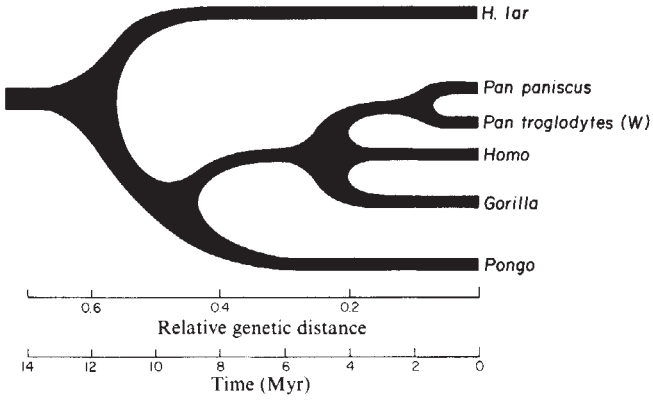


Fig. 1 Molecular cladogram showing genetic relationships of the ape and human lineages.

Pygmy chimpanzees have a narrower trunk and more gracile upper body, as reflected in significantly smaller clavicular length, scapular dimensions and iliac and sacral breadths[8]. Their upper and lower limbs are of about equal length, whereas arms of common chimpanzees are relatively longer.

As to sexual dimorphism, pygmy chimpanzees are moderately sexually dimorphic in body weight, but no dimorphism can be detected in cranial capacity, limb bone lengths or robusticity, or in anterior and posterior dentition[10]. They have relatively small and only slightly dimorphic canine teeth[11]. Overall, this is less dimorphism than occurs in common chimpanzees and no more than occurs in modern humans.

Observations on the behaviour of pygmy chimpanzees, either in their natural habitat in the Zaire River Basin or in captivity, have not been extensive. They feed high in trees, move and feed on the ground[12,13], and in captivity walk bipedally more than do common chimpanzees (S. Savage-Rumbaugh, personal communication). They therefore encompass the spectrum of locomotor behaviour of living African hominoids: arboreality, terrestriality and bipedality. Laboratory and field studies reveal pygmy chimpanzees as highly intelligent and flexible in feeding, locomotor, sexual and communicatory behaviour[14–16].

Given these morphological and behavioural data, we maintain that pygmy chimpanzees present a general pattern from

Table 1 Comparison of pygmy chimpanzee and early hominid pelvis, femur and humerus (in mm)

Measurement	Early hominids	Pygmy chimpanzees
Femur length	280*, 280†	293 (264–315)
Femoral head diameter	31†	30.5 (28–34)
Acetabular diameter	37†	36 (32–38)
Innominate length	170†	253 (232–272)
Iliac breadth	113†	97 (80–118)
Sacral breadth	76†	63 (51–70)
Humerus length	235*	285 (250–307)

* AL 288–1 from Hadar, Ethiopia[18].
† Sts 14 from Sterkfontein, South Africa. Measurements from A.L.Z. (unpublished data); femur length from Lovejoy[23].

which other African hominoids could have developed. This contention is further supported by comparing pygmy chimpanzees with the earliest hominids.

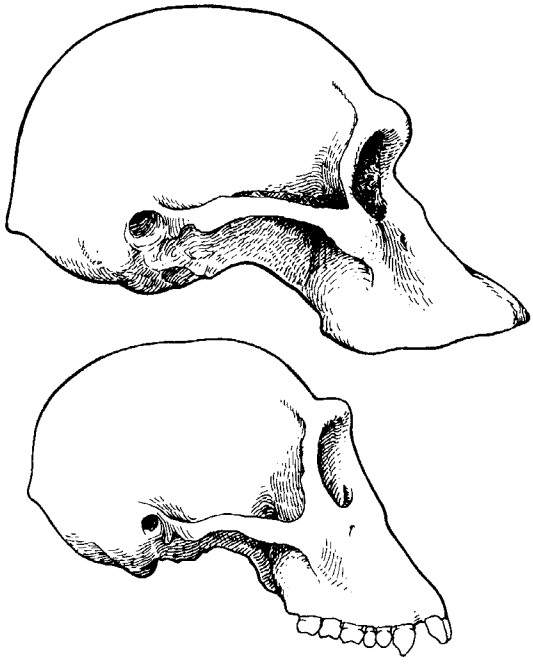
The fossil record, based on dentition, shows the occurrence of *Australopithecus* by 3.5 M yr ago in the mosaic savannas of Eastern Africa[17]. By 3 M yr ago, the hominids were distinct from apes in the broader and shorter pelvis, larger cranial capacity, larger postcanine teeth and somewhat smaller canines[18,19].

P. paniscus provides a suitable comparison for *Australopithecus*[20]; they are similar in body size, postcranial dimensions and, as Figs 2 and 3 show, even in cranial and facial features, although this *Australopithecus* has a larger cranial capacity (485 cm^3)[21] than *P. paniscus* (350 cm^3).

Postcranial dimensions are given in Table 1. Femoral length, femoral head and acetabular diameters are very similar. Humerus and innominate lengths, and breadths of sacrum and ilium are different. These findings demonstrate early hominid affinities with apes. Probably the initial acquisition of hominid upright locomotion entailed reduction of upper limb length and broadening of the ilium and sacrum.

Homo and *Pan* (both species) differ in their genomes by approximately 1%, a value characteristic of sibling species[22]. The genetic changes accounting for the morphological differences between man and chimpanzee may be only a small fraction of that amount. A few regulatory genes may have large somatic effects, whereas the remaining structural genes may be time dependent in their rate of fixation, and of little selective significance.

Fig. 2 Side view, drawn to scale, of Sterkfontein 5 (above) and adult female *P. paniscus* (below).



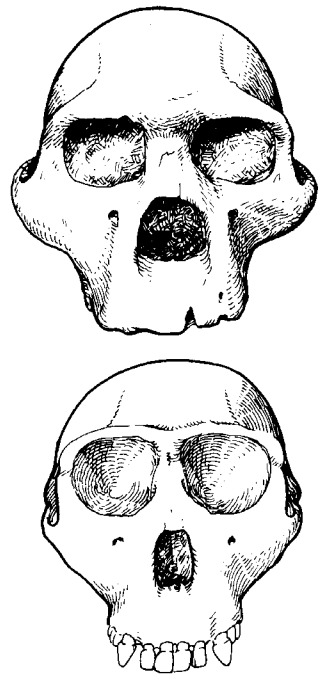


Fig. 3 Front view, drawn to scale, of Sterkfontein 5 and adult female *P. paniscus*.

The ultimate strength of any hypothesis rests on its compatibility with all lines of evidence, on its ability to withstand falsification and on its power of prediction. We hypothesise (1) that as our knowledge of the fossil record improves, hominids before 3.0 M-yr ago should continue to converge on the pygmy chimpanzee-like condition, cranially and postcranially, as they seem to do dentally, (2) that Pliocene pongids ancestral to chimpanzees and gorillas should do likewise, and (3) that at least one lineage of late Miocene ape (perhaps *Ramapithecus*) should continue to develop evolutionary trends begun in the early Miocene and evolve into a form similar to the extant pygmy chimpanzee.

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Axons from eyes grafted in *Xenopus* can grow into the spinal cord and reach the optic tectum

THE transplantation of embryonic eyes in Amphibia is a long established approach for testing the ability of nerve fibres to grow through unusual regions of the central nervous system[1,2]. As the behaviour of growing ectopic fibres may disclose the mechanisms of axonal guidance[3–7], this approach has recently attracted new interest[8–12]. We are studying the behaviour of optic fibres entering the spinal cord from a heterotopic eye grafted on to the dorsal trunk region of *Xenopus* embryos[10,11]. Here we report on the paths used by ectopic fibres to travel in the spinal cord, their possible termination in the hindbrain, and their ability to reach the optic tectum.

Eye vesicles from *Xenopus laevis* embryos at stage 25 (ref. 13) were grafted on to the dorsal region of other embryos at stage 23. Results were studied at larval stages. In 52 tadpoles, the grafts developed into morphologically normal eyes located on the back of the animal, just dorsal to the spinal cord and at different distances from the brain (Fig. 1). Twenty animals (out of the 52 mentioned above) were cut sagittally and stained by Holmes' silver method[16] for histological analysis: seven of the grafted eyes had developed an optic nerve whose fibres entered the spinal cord. These fibres seemed to grow mainly rostrally. We have confirmed this by tracing the paths of degenerating fibres in the remaining 32 tadpoles. Twelve of these animals had a considerable number of degenerating fibres in the spinal cord (Fig. 2). In each case we found most argyrophilic debris rostral to the graft; a smaller amount occurred caudally. Quantification of fibres in this type of preparation is not possible, but we estimate that approximately three-quarters of the fibres grew rostrally. No specific path seems to have been used by these optic axons; degenerating fibres were broadly distributed in the dorsal half of the white matter of the spinal cord (Fig. 2*a*). In particular, they

Fig. 1 Tadpole of *Xenopus laevis* with a third eye grafted at embryonic stage 23 (ref. 13) and now (stage 58) growing above the spinal cord. The brain and the normal eyes with their optic nerves can be seen through the transparent tissue of the tadpole head. Embryos were obtained in our laboratory by induced mating[14] of wild animals and were operated on in full-strength Niu and Twitty solution[15] containing antibiotics (10,000 U l^{-1} of penicillin G and 25 mg l^{-1} of streptomycin sulphate) and anaesthetic (0.02% MS-222, Sandoz). In the sagittal silhouette of the tadpole CNS the paths of optic fibres issuing from the normal (1) and grafted eyes (2–4) are represented. (1) Normal optic tract terminating in the anterior optic tectum; (2) ectopic fibres terminating in the medulla oblongata in triocular and in blinded (that is, binocularly enucleated) animals; (3) ectopic fibres termininating in the posterior optic tectum in blinded animals; (4) ectopic fibres growing caudally. Scale bar (applies to photograph only), 1 cm.

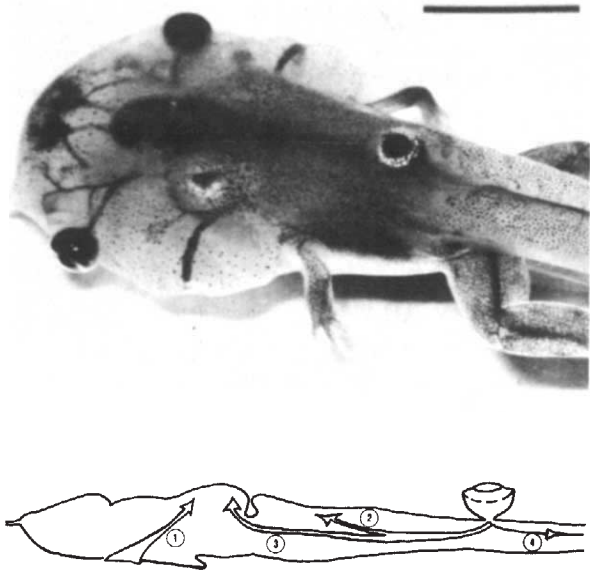
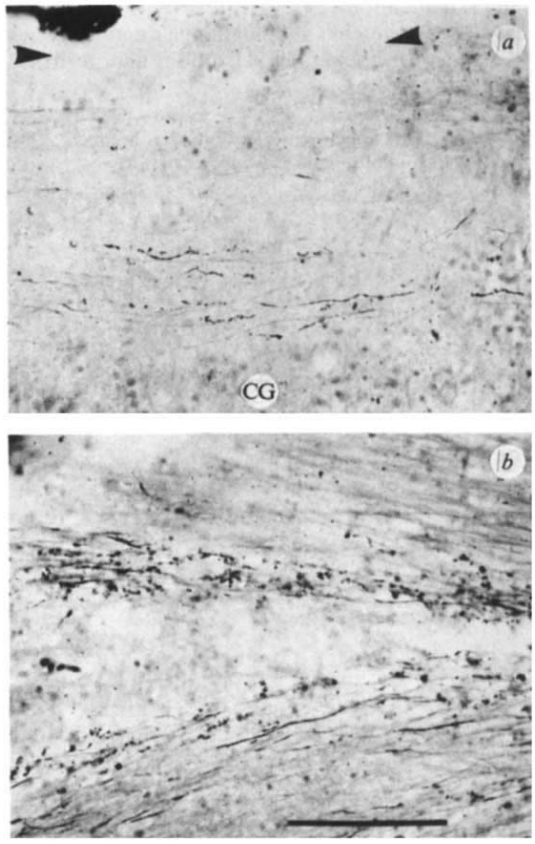


Fig. 2 Degenerating fibres in the spinal cord of experimental tadpoles. Horizontal section; rostral is left. The grafted eye was opened and the retina was gently peeled out. After 24 h the animals were fixed in neutralised 10% formalin and processed to demonstrate degenerating nerve fibres and terminals by a modification of Nauta's reduced silver method[17]. *a*, The ectopic fibres are localised near the central grey (CG); they were found bilaterally in various positions inside the dorsal white matter, but never close to the pial surface (between arrows). *b*, Degenerating fibres in the dorsal funiculi; in this region (hindbrain), they are diverging. Scale bar, 100 μm.



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