PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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R. H. Tuttle

Phil. Trans. R. Soc. Lond. B 1981 **292**, 89-94
doi: 10.1098/rstb.1981.0016

Phil. Trans. R. Soc. Lond. B **292,** 89–94 (1981) [89]
Printed in Great Britain

Evolution of hominid bipedalism and prehensile capabilities

By R. H. Tuttle
Department of Anthropology and Evolutionary Biology, The University of Chicago,
1126 *East* 59*th Street, Chicago, Illinois* 60637, *U.S.A.*

In this paper, I present an updated version of the hylobatian model for the proximate ancestors of the Hominidae. The hylobatians are hypothesized to have been relatively small creatures that were especially adapted for vertical climbing on tree trunks and vines and for bipedalism on horizontal boughs. They were no more disposed toward suspensory behaviours than are modern chimpanzees and bonobos. According to this evolutionary scenario, bipedalism preceded the emergence of the Hominidae. The earliest hominids would be recognized as diurnally terrestrial bipeds that stood with full extension of the knee joints and walked with greater extension of the lower limbs than is common in non-human primates that are induced to walk bipedally on the ground.

The wealth of hominid fossils from the Hadar Formation, Ethiopia, and the Laetolil Formation, Tanzania, are generally compatible with the hylobatian model. They show that by *ca.* 4 Ma b.p. habitually terrestrial, bipedal hominids had evolved from arboreal ancestors. The Hadar hominids had curved fingers and toes, strong great toes and thumbs, and other features that suggest that they were rather recently derived from arboreal hominids and that they probably continued to enter trees, perhaps for night rest and some foraging.

The hominid hand bones from Hadar evince no features that are distinctly related to knuckle-walking. They relate neatly to counterparts in the hand of O.H. 7, a specimen that was found with stone tools. However, there is no evidence that the Hadar hominids of 3 Ma ago engaged in tool behaviour.

Introduction

During the century since Darwin published his revolutionary trilogy, virtually every major type of extant ape has served as a model for the physical and behavioural attributes of our early hominoid ancestors. Throughout this period, the common chimpanzee had a remarkable series of champions (Gregory 1927; Weinert 1932; Washburn 1967, 1968). Whereas the once popular gorilla (Smith 1924) has dropped out of candidacy, the bonobo (*Pan pansicus*) is gathering a notable lobby (Zihlman *et al.* 1978). Scaled-down orang-utans (Stern 1976) and certain characteristics of the lesser apes (Tuttle 1974, 1975, 1977) also have appeared in recent evolutionary models.

The field has been rife with speculation about the evolution of bipedalism because postcranial fossils are generally sparse and fragmentary, and are not always clearly associated with diagnostic cranial remains.

The Hominidae probably emerged from stem Hominoidea during the Miocene (22.5–5.0 Ma b.p.) or Pliocene (5.0–2.0 Ma b.p.) period. The best Miocene hominoid postcranial specimens are assigned to species in lineages that are collateral to the Hominidae. The forelimb and hindlimb remains of *Proconsul* and *Dendropithecus* from Kenyan Early Miocene localities are probably too early to be proximately ancestral to modern forms, and they exhibit few features that would link them clearly to the modern forms (McHenry & Temerin 1979). Kenyan and

European middle Miocene specimens (most notably *Pliopithecus vindobonensis*) are practically irrelevant to the evolutionary problem of hominid bipedalism. Late Miocene localities have also yielded little information. *Oreopithecus bambolii* is a peripheral anthropoid species (Simons 1972). The recently discovered postcranial bits from Potwar, Pakistan, are tentatively associated with craniodental specimens from the region (Pilbeam *et al.* 1977). These authors have sorted them into three groups on the basis of general size. These groupings parallel their assortment of the Potwar craniodental specimens. It is possible that some or all of the four small hominoid postcranial bits, i.e. a partial femoral head (GSP 9894), a partial talus (GSP 10785), a partial calcaneus (GSP 4664) and a juvenile radial diaphysis (GSP 7611), belong to *Ramapithecus punjabicus*, a species that has been championed as the most likely candidate for earliest Hominidae. But the specimens are too few and too incomplete for reliable functional inferences. For instance, if one presented functional morphologists with counterpart bits from a living hylobatid ape, I doubt that they could document that the beast was a part-time arboreal biped.

Thus, the earliest unequivocal evidence for hominid bipedalism comes from the Pliocene localities of Laetoli, Tanzania, and Hadar, Ethiopia. There, terrestrial bipedalism was well developed and presumably frequently practised. We can only speculate about how bipedalism was established among the ancestors of the Laetoli and Hadar hominids. Modern scenarios should be compatible with the new information from these important sites. Henceforth I will focus on one speculative model and its compatibility with the new Pliocene fossils and our experimental studies on living apes.

The hylobatian model today

After rejecting the theory that humans had evolved from knuckle-walking troglodytian apes, which were closely similar to the common chimpanzee, I proferred an alternative, termed the hylobatian model (Tuttle 1969, 1974, 1975). The hypothetical hylobatians weighed between 20 and 30 lb (*ca.* 9 and 13.5 kg) and were somewhat stockier than modern hylobatid apes. Vertical climbing on tree trunks and vines and bipedalism on horizontal boughs were conspicuous components of their locomotor repertoire. They commonly stood bipedally while foraging in trees and employed bipedalism during intraspecific displays. Short bursts of bipedal running and hindlimb-propelled leaps may have been important for the manual capture of insects and small vertebrates with which they supplemented their vegetable fare.

Like the lesser apes, the hylobatians had relatively long, extensible hindlimbs powered by well developed gluteal, anterior thigh and calf muscles. The centre of gravity was low in the abdominal cavity. The lumbar spine was not foreshortened and it was capable of notable lateral flexion and rotation. The hip bones were not exceptionally elongate. They were rather wide and projected laterally. The sacrum was also wide.

The hylobatians did not have a pelvic tilt mechanism of a human sort. The deep gluteal muscles were positioned to act as extensors instead of abductors of the hip joints during bipedal locomotion. However, the tendency for the hylobatian pelvis to tilt downward on the unsupported side during the swing phases of bipedal steps could be countered somewhat by rotation and lateral flexion of the spine toward the opposite side. This was effected by special portions of the erector spinae muscles, which originated on the medial surface of the hip bone and adjacent area of the sacrum (Filler 1980), and perhaps by the quadratus lumborum and lateral abdominal muscles. Lateral flexion of the spine was also important during vertical ascents and descents on vines and tree trunks and during other climbing activities of the hylobatians. The lateral flexing mechanism and low centre of gravity were important features that enabled emergent terrestrial Hominidae to walk with more extension of the hip and knee joints than their arboreally bipedal ancestors had done.

Suspensory behaviours were probably no more common in the hylobatians than in common chimpanzees or bonobos. Arm-swinging along branches was quite rare and ricochetal arm-swinging was not practised at all. The hylobatians moved between springy supports in the peripheries of trees by hoisting, bridging, and occasionally jumping. They rarely executed long vertical drops or fed in suspensory postures.

The hylobatians' thumbs and great toes were well developed, strongly muscled, and capable of wide divergence. The chest was broader transversely than anteroposteriorly, the shoulder blades lay on the back of the chest wall, and the elongate collar bones held the shoulder joints out to the sides of the body. Mobility of the shoulder and wrist joints and extensibility and rotatory capacities of the elbow complex underpinned the hylobatians' versatile climbing, reaching and suspensory behaviour.

Compatability with fossils from Laetoli and Hadar

At Laetoli the chief evidence for hominid bipedalism is the footprints of three individuals, preserved in volcanic ash that has been dated radiometrically at *ca.* 3.6 Ma B.P. The shapes of the prints are indistinguishable from those of striding, habitually barefoot humans. They indicate that the Laetoli hominids were smaller than average *Homo sapiens* (Leakey 1979; Leakey & Hay 1979).

Several localities at Hadar (*ca.* 3.0 Ma B.P.), which are younger than the Laetolil Formation, have yielded approximately forty foot bones. One of the most informative specimens is A.L. 333–115 A–M. The 13 bones were extracted from a single lump of matrix in the Denan Dora member of the Hadar Formation. The distal ends of the left metatarsal bones and the proximal phalanges of digits I–V, the middle phalanges of digits IV and V, and the basal epiphysis of a distal phalanx are well preserved. The shafts of the proximal phalanges are markedly curved ventrally. This feature is characteristic of certain full-time and part-time arboreal apes and monkeys. The basal articular surfaces of the proximal phalanges extend dorsally as shallowly excavated and lipped structures. The heads of the metatarsal bones also have dorsal articular areas. These features would facilitate extension of the metatarsophalangeal joints. This would allow the foot to be used in plantigrade postures despite the ventral curvature of the digits. Other Hadar proximal phalanges II–V, including one from 'Lucy' (A.L. 288-ly), are like A.L. 333–115. It is difficult to imagine a foot with such markedly curved phalanges fitting neatly into the footprints at Laetoli.

In A.L. 333–115, the hallucal bones are more robust than their counterparts from the lateral toes. The base of a left hallucal matatarsal (A.L. 333–54) appears to have contacted the second metatarsal bone. In these features, the Hadar foot recalls the human condition. The broad shallow grooves on the posterior surfaces of several distal fibulae indicate that the Hadar hominids had well developed peroneal muscles. In apes, the peroneus longus muscle is a powerful flexor of the hallux; and in man, it is an evertor of the foot.

The knee joint, represented by seven distal femoral and six proximal tibial specimens, is more similar to the human condition than is the Hadar foot. The femoral condyles, popliteal groove, lateral patellar ridge and fossae for the cruciate ligaments all testify to the capacity for full extension of the knee joint during bipedal stance.

The Hadar pelvis, represented by A.L. 288–1an and 288–1ao, is a potpourri of human and non-human features. The sacrum is short and broad like human sacra. The blades of the hip bones are also broad and short. But they exhibit a greater lateral flare and orientation than do their human counterparts. Despite this resemblance to non-human anthropoid primates, the broad-beamed Hadar beast was bipedal, as attested by development of the anterior iliac and ischial spines, femoral intertrochanteric lines and other features that are hallmarks of human bipedalism.

In brief, the curved pedal phalanges, robust hallux, strongly developed peroneal muscles, broad sacrum, and the shortness and lateral orientation of the iliac blades are quite compatible with the idea that the Hadar hominids were derived rather recently from arboreal bipeds. Indeed, they too may have engaged in notable tree climbing, perhaps for night rest. Whether a human pelvic tilt mechanism or lateral flexion and rotation of the spine was predominant during their bipedal walking remains to be established.

Experimental perspectives

Electromyographic, cineradiographic and other sophisticated kinesiological techniques have not been applied extensively enough to non-human primates to provide a full basis for interspecific comparisons of their bipedalism. However, they have underscored the uniqueness of habitual human bipedalism compared with the facultative bipedalism of monkeys and apes. *Hylobates*, the second most accomplished anthropoid biped, has not shown remarkably great similarities to *Homo* in the electromyographic pattern of their hindlimb muscles, forces applied to the ground, or details of the locomotor cycle (Tuttle & Cortright 1980). Less complete kinesiological results on pongid apes and monkeys indicate that during bipedalism their hindlimbs continue to function basically as if the subjects were moving quadrupedally. The gibbons resemble the pongid apes and monkeys more closely than the humans in this regard (Tuttle *et al.* 1979).

It is probably safe to assume that the early hylobatians shared a similar non-human kinesiological pattern. Because of the fully extended knee joints and other humanoid osteological features, many muscles in the lower limbs of the Hadar hominids probably would not have acted electromyographically like those of facultatively bipedal hominoid primates. A great challenge for evolutionary kinesiologists is to detail this novel pattern on the basis of sound biomechanical principles instead of analogies with the condition in extant forms.

Comment on tool behaviour

Locality FLK NN in bed I of Olduvai Gorge (dated *ca.* 1.75 Ma B.P.) and several localities in the Hadar Formation have provided considerable empirical evidence pertaining to the hands and tool behaviour of early Hominidae. It may be parsimoniously concluded that the cranial bones and 13 hand bones (Day 1976) assigned to O.H. 7 and the 12 foot bones assigned to O.H. 8 are from a single juvenile individual. Apparently, a group of hominids had come to the lake margin to forage for small vertebrates, plants and perhaps larger prey. They left behind them a number of crude stone Oldowan tools, a perhaps modified equid rib (Leakey 1971) and the body of a companion, which had fallen victim to a predator, an accident or disease.

The hand of O.H. 7 shows that its youthful possessor had a powerful grip, second to fifth fingers that were well adapted for arboreal climbing and perhaps suspensory behaviour, and fingertips and a basal thumb joint that facilitated fine manipulatory behaviour (Susman & Creel 1979). The pongid features of the fingers would not have prevented O.H. 7 from making and using Oldowan tools. Modern great apes are quite dexterous despite the locomotor specializations of their hands (Tuttle 1970). The breadth of the fingertips in O.H. 7, particularly that of the thumb, could have been adapted not only for precision grips but also for power grips on sizeable, rounded objects, wherein the thumb was widely opposed to the other fingers.

The Hadar Formation has yielded no artefacts that are contemporaneous with the numerous fossils that are assigned to *Australopithecus afarensis* (Johanson *et al.* 1978; Johanson & White 1979). About 50 hand bones are included in the hypodigm. In that there are counterparts of O.H. 7, the Hadar hands could be lineally ancestral to it.

The proximal phalanges ($N = 15$) from adult and immature digits II–V are curved ventrally and sport well developed lateral ridges for the fibrous flexor sheaths. Prominent tubercles and facets on their bases document the past presence of strong palmar and collateral ligaments. The single pollical proximal phalanx (A.L. 333–69) is quite similar to that of gracile humans.

The ventral surfaces of the middle phalanges ($N = 9$) exhibit a prominent midline ridge, flanked by fossae for the tendons of the flexor digitorum superficialis muscle and ridges for the fibrous flexor sheaths. There are only two distal phalanges from Hadar that are tentatively identified as manual. They suggest a strong hand with well developed fingertips.

The Hadar Formation has produced a wealth ($N = 19$) of metacarpal specimens. Three of them are pollical. The only complete mature pollical metacarpal bone (A.L. 333w–39) is rather chimpanzee-like. It has a well excavated basal articular surface and a small, rounded head. The medial metacarpal bones resemble human ones, except that the heads and bases are relatively narrow, giving them a gracile configuration compared with human metacarpal bones of similar length. The third metacarpal bones lack the basal styloid process. Some of the metacarpal heads evince conspicuous markings for collateral ligaments. In some instances, the articular surface extends dorsally onto the metacarpal heads. There are no features that suggest knuckle-walking.

The Hadar carpal bones include two capitates, one hamate, one pisiform and one trapezium. The pollical articular surface of the trapezium (A.L. 333–80) is rather deep, as in the chimpanzee. The gracile pisiform bone (A.L. 333–91) is elongate and rod-like, thus resembling that of a chimpanzee. This and the robust hook on the hamate bone (A.L. 333–50) indicate that the Hadar hominids had strong pisohamate and pisometacarpal ligaments and flexor retinacula.

The Hadar hands probably served primarily as manipulatory and climbing organs. The generally gracile construction of the metacarpal bones and the absence of features suggesting knuckle-walking conform well with evidence from the lower limb, which establishes that the Hadar hominids were fundamentally terrestrial bipeds. Many features of their fingers, which foreshadow the hand of O.H. 7, indicate that the Hadar hominids had strong power grips in which the thumb acted conspicuously. Strong development of the ulnar wrist may be related to climbing and other pulling actions.

I thank D. C. Johanson and D. R. Pilbeam for permission to study fossils in their keeping. The visits to Yale University and the Cleveland Museum of National History were made pleasant and productive by J. Barry, M. Bush, L. Dmytryk, H. French, D. Johanson, W. Kimbel, O. Lovejoy, M. Rose and T. White. The paper was read through by D. C. Johanson, R. G. Klein & B. Latimer. The research was supported by the Social Sciences Divisional Research Fund and the Marian and Adolph Lichstern Fund of the University of Chicago.

REFERENCES

Day, M. H. 1976 Hominid postcranial material from bed I, Olduvai Gorge. In *Human origins* (ed. G. Ll. Isaac & E. R. McCown), pp. 363–374. Menlo Park, California: W. A. Benjamin.

Filler, A. G. 1980 Anatomical evidence for the 'hylobatian' model of hominid evolution. *Am. J. phys. Anthrop.* **52**, 226.

Gregory, W. K. 1927 How near is the relationship of man to the chimpanzee-gorilla stock? *Q. Rev. Biol.* **2**, 549–560.

Johanson, D. C. & White, T. D. 1979 A systematic assessment of early African hominids. *Science, N.Y.* **203**, 321–330.

Johanson, D. C., White, T. D. & Coppens, Y. 1978 A new species of the genus *Australopithecus* (Primates, Hominidae) from the Pliocene of eastern Africa. *Kirtlandia*, no. 28, pp. 1–14.

Leakey, M. D. 1971 *Olduvai Gorge*, vol. 3. Cambridge University Press.

Leakey, M. D. 1979 Footprints in the ashes of time. *Nat. geogr. Mag.* **155**, 446–457.

Leakey, M. D. & Hay, R. L. 1979 Pliocene footprints in the Laetolil Beds at Laetoli, northern Tanzania. *Nature, Lond.* **278**, 317–323.

McHenry, H. M. & Temerin, L. A. 1979 The evolution of hominid bipedalism: evidence from the fossil record. *Yeab. phys. Anthrop.* **22**, 105–131.

Pilbeam, D., Meyer, G. E., Badgley, C., Rose, M. D., Pickford, M. H. L., Behrensmeyer, A. K. & Shah, S. M. I. 1977 New hominoid primates from the Siwaliks of Pakistan and their bearing on hominoid evolution. *Nature, Lond.* **229**, 689–695.

Simons, E. L. 1972 *Primate evolution*. New York: Macmillan.

Smith, G. E. 1924 *The evolution of man*. London: Oxford University Press.

Stern Jr, J. T. 1976 Before bipedality. *Yearb. Phys. Anthrop.* **19**, 59–68.

Susman, R. L. & Creel, N. 1979 Functional and morphological affinities of the subadult hand (O.H. 7) from Olduvai Gorge. *Am. J. phys. Anthrop.* **51**, 311–332.

Tuttle, R. H. 1969 Knuckle-walking and the problem of human origins. *Science, N.Y.* **166**, 953–961.

Tuttle, R. H. 1970 Postural, propulsive and prehensile capabilities in the cheiridia of chimpanzees and other great apes. In *The chimpanzee*, vol. 2 (ed. G. H. Bourne), pp. 167–253. Basel: Karger.

Tuttle, R. H. 1974 Darwin's apes, dental apes and the descent of man. *Curr. Anthrop.* **15**, 389–426.

Tuttle, R. H. 1975 Parallelism, brachiation and hominoid phylogeny. In *Phylogeny of the primates* (ed. W. P. Luckett & F. S. Szalay), pp. 447–480. New York: Plenum.

Tuttle, R. H. 1977 Naturalistic positional behavior of apes and models of hominid evolution, 1929–1976. In *Progress in ape research* (ed. G. H. Bourne), pp. 277–296. New York: Academic Press.

Tuttle, R. H. & Cortright, G. W. 1980 The problem of bipedalism: what do we need in order to proceed? In *Perspectives in primate biology* (ed. P. K. Seth). (In the press.)

Tuttle, R. H., Cortright, G. W. & Buxhoeveden, D. P. 1979 Anthropology on the move: progress in experimental studies of nonhuman primate positional behavior. *Yearb. phys. Anthrop.* **22**, 187–214.

Washburn, S. L. 1967 Behaviour and the origin of man. *Proc. R. Anthropol. Inst.*, pp. 21–27.

Washburn, S. L. 1968 The study of human evolution. *Condon Lectures*. Eugene: Oregon State System of Higher Education.

Weinert, H. 1932 *Ursprung der Menschheit*. Stuttgart: Enke.

Zihlman, A. L., Cronin, J. E., Cramer, D. L. & Sarich, V. M. 1978 Pygmy chimpanzee as a possible prototype for the common ancestor of humans, chimpanzees and gorillas. *Nature, Lond.*, **275**, 744–746.