

***Orrorin tugenensis* Femoral Morphology and the Evolution of Hominin Bipedalism**

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Bipedalism is a key human adaptation and a defining feature of the hominin clade. Fossil femora excavated in Kenya and attributed to *Orrorin tugenensis*, at 6 million years ago, purportedly provide the earliest postcranial evidence of hominin bipedalism, but their functional and phylogenetic affinities are controversial. We show that the *O. tugenensis* femur differs from those of apes and *Homo* and most strongly resembles those of *Australopithecus* and *Paranthropus*, indicating that *O. tugenensis* was bipedal but is not more closely related to *Homo* than to *Australopithecus*. Femoral morphology indicates that *O. tugenensis* shared distinctive hip biomechanics with australopiths, suggesting that this complex evolved early in human evolution and persisted for almost 4 million years until modifications of the hip appeared in the late Pliocene in early *Homo*.

Bipedalism is one of very few human characteristics that appears to have evolved at the base of the hominin clade [species more closely related to modern humans than to any other living species (*1*)]. Recent fossil discoveries have apparently pushed back the origin of the hominin clade into the late Miocene, to 6 to

7 million years ago (Ma). The oldest known potential hominin fossils, attributed to *Sahelanthropus tchadensis*, come from Toros-Menalla in Chad and are biostratigraphically dated to ~7 Ma (2). Currently, *Sahelanthropus* is only known from craniodental evidence, and although the position of the foramen magnum suggests that it was bipedal (3), postcranial fossils are needed to confirm this conclusion. The next oldest potential hominin remains were discovered in 2000 by Senut, Pickford, and colleagues (4) from localities (5.7 to 6.0 Ma) in the Lukeino Formation in Kenya (5, 6) and attributed to *Orrorin tugenensis*. Of the fossils assigned to *O. tugenensis*, three fragmentary femora (BAR 1002'00, 1003'00, and 1215'00) are critical pieces of evidence be-

cause they are interpreted as having derived characteristics indicating bipedalism (7). However, some of these features are also found in non-bipedal primates and are therefore inconclusive (8). Similarly, a study of the femora based on computerized tomography (9) suffered from poor image resolution and does not provide convincing evidence of bipedality (10). The discoverers have also cited the femora in formulating hypotheses about early hominin phylogenetic relationships (4), but these have been disputed (8, 11, 12). Thus, the morphology of the *O. tugenensis* femora is critical to our understanding of the origin of bipedalism and phylogenetic relationships of the earliest hominin taxa, yet the functional and phylogenetic implications of their morphology remain highly controversial. We present here a quantitative, morphometric (shape) comparison of the most complete *O. tugenensis* femur, BAR 1002'00, of a young adult.

When compared to the proximal femora of a large and diverse sample of great apes, modern humans (including small-bodied adult individuals from African Pygmy and Andaman Island populations), as well as Plio-Pleistocene hominin femora (13), the *O. tugenensis* femur (BAR 1002'00) more closely resembles femora attributed to early hominin taxa (*Australopithecus* and *Paranthropus*) than do those of extant apes, fossil *Homo*, and modern humans. Multivariate analyses of shape (canonical variates, cluster analysis, and principal components analysis) reveal that modern human proximal femora are distinct from those of extant great apes primarily in having a relatively large head and short distance between the head and lesser trochanter. Canonical variates axis 1 (Fig. 1A) is a contrast vector driven by these distinguishing features of shape (table S1),

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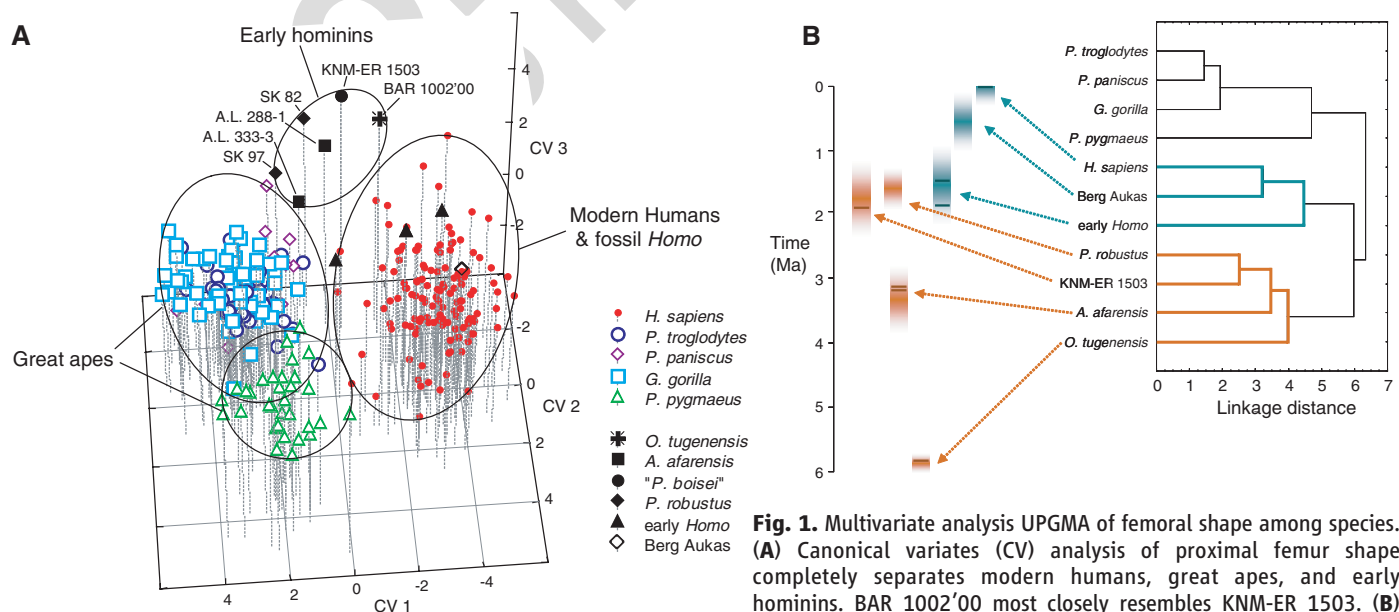


Fig. 1. Multivariate analysis UPGMA of femoral shape among species. **(A)** Canonical variates (CV) analysis of proximal femur shape completely separates modern humans, great apes, and early hominins. BAR 1002'00 most closely resembles KNM-ER 1503. **(B)** Cluster analysis (UPGMA of Mahalanobis D^2 distances) shows three and a cluster of BAR 1002'00 and early hominins. The early hominin an 4 million years, with a major change in hip structure in early *Homo*.

distinct clusters: a great ape cluster, a cluster of modern and fossil *Homo*, and a cluster of BAR 1002'00 and early hominins. The early hominin femoral morphology exhibited by BAR 1002'00 appears to persist for more than 4 million years, with a major change in hip structure in early *Homo*.

and the non-*Homo* fossil hominins (including BAR 1002'00) occupy an intermediate position in this part of multivariate space. The second axis separates orangutans from African apes, modern humans, and all the fossils. Orangutans have relatively large femoral heads (related to mobility rather than more pronounced weight support) combined with narrow femoral shafts, a combination of features not seen in modern or fossil hominin femora. The third axis, driven by neck length and breadth, and shaft breadth, serves to separate early hominin femora from those of extant apes, modern humans, and fossil *Homo* taxa. BAR 1002'00 resembles the early hominin femora, which are characterized in this and previous analyses by a combination of long and

anteroposteriorly constricted necks, mediolaterally broad shafts, and smaller heads (relative to modern humans) (14–17). This morphological complex is not merely an allometric consequence of the small size of many of the fossils (fig. S3), including A.L. 288-1 and BAR 1002'00 (18), as the small-bodied modern humans and apes in this sample do not resemble the early hominins. Three distinct clusters summarize these affinities (Fig. 1B); modern humans and fossil *Homo* form a group that is linked to a cluster of *Australopithecus*, *Paranthropus*, and *O. tugenensis*, and these two groups are joined by a more distant cluster of extant apes.

The features (long, narrow neck and broad proximal shaft) characterizing *O. tugenensis* and

australopith (19) femora are not biomechanically independent, and reflect differences in hip morphology related to gait mechanics. Modern humans gait is distinct from the kinematics of bipedalism in other primates in several ways, including very little lateral displacement and a slight drop in the contralateral hip during stance phase (20, 21). These characteristics are made possible in part by the flared, short iliac blade and by the recruitment of the lesser gluteal muscles on the ipsilateral side, which counteract the tendency of the body weight force to lower the contralateral hip (Fig. 2). The very flaring ilia and long femoral necks of australopiths improve the gluteal muscle lever arm and thus counter the torque of body weight (17), but the long necks also increase the bending moment on the proximal femoral shaft. These elevated bending moments are resisted by the greater mediolateral width of the femoral diaphysis, especially proximally where bending moments are highest (22).

O. tugenensis shares this uniquely archaic hominin morphological pattern, thus providing strong evidence that *O. tugenensis* was adapted to bipedalism 6 million years ago. This evidence is functionally consistent with other morphological features believed to be linked to bipedalism in the *O. tugenensis* femora, including a marked obturator externus groove, the presence of an intertrochanteric line, vertical gluteal tuberosity (third trochanter), and a slightly enlarged head (7). BAR 1002'00 bears distinct markings for the medial and lateral extents of the vastus musculature, but it lacks the prominent, raised linea aspera that is distinctive of modern and fossil *Homo* femora. In this manner, BAR 1002'00 resembles some australopith femora [e.g., A.L. 288-1ap (23)]. The relative femoral head size of BAR 1002'00 is intermediate between, and overlaps with, the distribution of *Pan* and *Homo* femora; the femoral head of BAR 1002'00 is large compared to *Australopithecus*, *Paranthropus*, and African ape femora, but relatively smaller than those of orangutans and fossil and modern *Homo*. Furthermore, the difference between BAR 1002'00 and *Australopithecus* and *Paranthropus* in relative femoral head size is within the expected level of intraspecific variation based on extant standards.

To investigate how proximal femur shape has changed over the course of human evolutionary history, we plotted against time the multivariate shape Mahalanobis D^2 distance between each femur and the mean shape of *Homo sapiens* femora. Distances are consistently high until the appearance in the late Pliocene and early Pleistocene of femora attributed to *Homo* (fig. S4). The early *Homo* femora retain the primitively long necks and broad shafts (16, 24–27), suggesting the retention of relatively broad ilia (28), but more closely resemble modern human femora in having larger heads and broader necks. In conjunction with significantly greater femoral length (29), these features provide evidence of a transition to a more modern humanlike bipedal

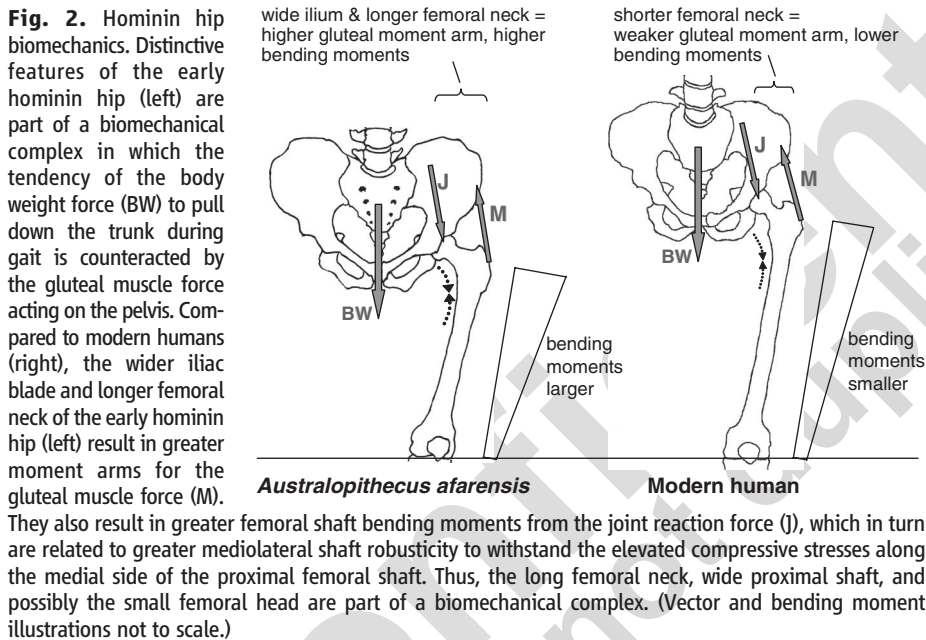


Fig. 3. Morphological comparisons among femora of or attributed to (A) *P. troglodytes*, (B) *O. tugenensis* (BAR 1002'00), (C and D) *Paranthropus robustus* (SK 97 and SK 82, reversed), (E) *A. afarensis* (A.L. 288-1ap), (F) *Paranthropus boisei* (KNM-ER 1503, reversed), (G) early *Homo* (KNM-ER 1481), and (H) modern *H. sapiens*. Like other early hominin femora (C to F), BAR 1002'00 (B) is distinct from those of modern humans (H) and great apes (A) in having a long, anteroposteriorly narrow neck and wide proximal shaft. Early *Homo* femora (G) have larger heads and broader necks compared to early hominins. In addition to these features, modern human femora (H) have short necks and mediolaterally narrow shafts. Scale bar, 2 cm.

gait including greater speed and energetic efficiency compared to earlier hominins (16, 24–27). Further changes in femoral anatomy (e.g., shorter neck, narrower shaft) occur in the genus *Homo* in the Middle Pleistocene and can be linked in part to obstetrical factors (28).

In light of the marked changes in femoral anatomy from at least 2 Ma to the present, the close morphological similarity between femora of *O. tugenensis* at 6 Ma and *Australopithecus* and *Paranthropus* in the later Pliocene is especially pronounced (Fig. 1 and table S3). Although among the early hominin taxa, *Ororin* has the smallest Mahalanobis D^2 distance from the modern human centroid, BAR 1002'00 is much closer to all early hominin taxa than to the modern human centroid in shape space (table S3). The external morphology of *O. tugenensis* provides no indications of differences in bipedal gait compared to *Australopithecus* or *Paranthropus*. This suggests that the pattern of bipedal gait characteristic of australopiths evolved very early in the human lineage, and perhaps they were also the characteristics of the first bipedal hominins. This form of bipedalism appears to have persisted as a successful locomotor strategy for as long as 4 million years (Fig. 1B). Additional lower limb fossils from the late Miocene and early Pliocene will be needed to test this hypothesis.

Similarities in femoral morphology, however, do not rule out possible differences in overall repertoires of positional behavior. Upper limb fossils of *O. tugenensis* retain morphological features related to arboreal climbing, including a pronounced humeral brachioradialis flange and a curved proximal manual phalanx (4). The included angle measured on BAR 349'00 (proximal phalanx) is 52°, significantly greater than those of modern humans and *Macaca mulatta* (t test, $P < 0.05$), and significantly lower than those of orangutans (fig. S5). In degree of curvature, BAR 349'00 most closely resembles *Pan troglodytes*. The *Pan*-like curvature of the proximal phalanx close to the *Pan-Homo* last common ancestor supports the hypothesis that bipedalism evolved from an ancestor adapted to orthograde and vertical climbing, consistent with a climbing and knuckle-walking repertoire (30), rather than

an orangutan-like arboreal specialist (31). Therefore, while *O. tugenensis* was bipedal, it most probably also climbed trees (4), presumably to forage, build nests, and seek refuge. Whether arboreality played a greater role in the locomotor repertoire of *O. tugenensis* in comparison to *Australopithecus* remains unresolved. The available evidence of internal cortical morphology of BAR 1002'00 (7, 9) leaves open the possibility that *O. tugenensis* had a pattern of neck bone cortical thickness that differed from the human-like pattern observed in *Australopithecus* (32) and would be consistent with the use of a wider range of hip joint postures like those used by great apes during climbing. The external anatomy of BAR 1002'00 indicates bipedality, but is also consistent with a locomotor repertoire involving an appreciable scansorial component (33, 34).

The similarity between *O. tugenensis* and australopith femora weakens support for scenarios in which *O. tugenensis* is ancestral to *Homo* to the exclusion of *A. afarensis* (4). Instead, the overall primitive hominin morphology of the *O. tugenensis* femur, along with primitive dental anatomy, is consistent with the more parsimonious hypothesis that it is a basal member of the hominin clade. In sum, the comparative biomechanical anatomy of *O. tugenensis* femora suggests that *O. tugenensis* is a basal hominin adapted to bipedalism, and current evidence suggests that an *Australopithecus*-like bipedal morphology evolved early in the hominin clade and persisted successfully for most of human evolutionary history.

References and Notes

1. B. A. Wood, B. G. Richmond, *J. Anat.* **196**, 19 (2000).
2. M. Brunet *et al.*, *Nature* **434**, 752 (2005).
3. C. P. Zollikofer *et al.*, *Nature* **434**, 755 (2005).
4. B. Senut *et al.*, *C. R. Acad. Sci. Paris Ser. II* **332**, 137 (2001).
5. A. L. Deino, L. Tauxe, M. Monaghan, A. Hill, *J. Hum. Evol.* **42**, 117 (2002).
6. Y. Sawada *et al.*, *C. R. Palevol* **1**, 293 (2002).
7. M. Pickford, B. Senut, D. Gommery, J. Treil, *C. R. Palevol* **1**, 191 (2002).
8. D. R. Begun, *Science* **303**, 1478 (2004).
9. K. Galik *et al.*, *Science* **305**, 1450 (2004).

10. J. C. Ohman, C. O. Lovejoy, T. D. White, *Science* **307**, 845 (2005).
11. L. C. Aiello, M. Collard, *Nature* **410**, 526 (2001).
12. C. J. Cela-Conde, F. J. Ayala, *Proc. Natl. Acad. Sci. U.S.A.* **100**, 7684 (2003).
13. Materials and methods are available as supporting material on Science Online.
14. M. H. Day, *Nature* **221**, 230 (1969).
15. A. C. Walker, *J. Hum. Evol.* **2**, 545 (1973).
16. H. M. McHenry, R. S. Corruccini, *Am. J. Phys. Anthropol.* **49**, 473 (1978).
17. C. O. Lovejoy, K. G. Heiple, A. H. Burstein, *Am. J. Phys. Anthropol.* **38**, 757 (1973).
18. M. Nakatsukasa, M. Pickford, N. Egi, B. Senut, *Primates* **48**, 171 (2007).
19. We use "australopith" as a vernacular term to refer to *Australopithecus* and *Paranthropus* species, following (1).
20. F. A. Jenkins, *Science* **178**, 877 (1972).
21. J. T. Stern Jr., R. L. Susman, *Am. J. Phys. Anthropol.* **55**, 153 (1981).
22. C. B. Ruff, in *Primate Locomotion: Recent Advances*, E. Strasser, J. G. Fleagle, A. Rosenberger, H. M. McHenry, Eds. (Plenum, New York, 1998), pp. 449–469.
23. T. D. White *et al.*, *Nature* **440**, 883 (2006).
24. D. R. Carrier, *Curr. Anthropol.* **25**, 483 (1984).
25. W. L. Jungers, *J. Hum. Evol.* **17**, 247 (1988).
26. K. L. Steudel-Numbers, *J. Hum. Evol.* **51**, 445 (2006).
27. M. D. Sockol, D. A. Raichlen, H. Pontzer, *Proc. Natl. Acad. Sci. U.S.A.* **104**, 12265 (2007).
28. C. B. Ruff, *Am. J. Phys. Anthropol.* **98**, 527 (1995).
29. B. G. Richmond, L. C. Aiello, B. A. Wood, *J. Hum. Evol.* **43**, 529 (2002).
30. B. G. Richmond, D. R. Begun, D. S. Strait, *Yrbk. Phys. Anthropol.* **116**, 70 (2001).
31. S. K. Thorpe, R. L. Holder, R. H. Crompton, *Science* **316**, 1328 (2007).
32. C. O. Lovejoy, R. S. Meindl, J. C. Ohman, K. G. Heiple, T. D. White, *Am. J. Phys. Anthropol.* **119**, 97 (2002).
33. J. T. J. Stern Jr., R. L. Susman, *Am. J. Phys. Anthropol.* **60**, 279 (1983).
34. J. T. J. Stern Jr., *Evol. Anthropol.* **9**, 113 (2000).
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Supporting Online Material

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Materials and Methods
Figs. S1 to S6
Tables S1 to S3
References

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