

This copy is for your personal, non-commercial use only.

If you wish to distribute this article to others, you can order high-quality copies for your colleagues, clients, or customers by [clicking here](#).

Permission to republish or repurpose articles or portions of articles can be obtained by following the guidelines [here](#).

The following resources related to this article are available online at www.sciencemag.org (this information is current as of September 9, 2011):

Updated information and services, including high-resolution figures, can be found in the online version of this article at:

<http://www.sciencemag.org/content/333/6048/1411.full.html>

Supporting Online Material can be found at:

<http://www.sciencemag.org/content/suppl/2011/09/07/333.6048.1411.DC1.html>

This article **cites 61 articles**, 6 of which can be accessed free:

<http://www.sciencemag.org/content/333/6048/1411.full.html#ref-list-1>

This article has been **cited by** 4 articles hosted by HighWire Press; see:

<http://www.sciencemag.org/content/333/6048/1411.full.html#related-urls>

This article appears in the following **subject collections**:

Anthropology

<http://www.sciencemag.org/cgi/collection/anthro>

arboreal habitats, see (30, 31)], perhaps associated with an expansion of grassland ecosystems in the South African Plio-Pleistocene (32, 33). Although there is no doubt that the eventual expansion of brain size in the genus *Homo* had a substantial impact on the functional morphology of the pelvis (and on the establishment of human pelvic sexual dimorphism), evidence from *Au. sediba* suggests that locomotor rather than obstetric demands drove the emergence of the basic *Homo* pelvic bauplan.

References and Notes

1. S. W. Simpson *et al.*, *Science* **322**, 1089 (2008).
2. C. B. Ruff, *J. Hum. Evol.* **58**, 166 (2010).
3. M. D. Rose, *Am. J. Phys. Anthropol.* **63**, 371 (1984).
4. C. V. Ward *et al.*, *Am J Phys Anthropol.* **52** (suppl.), 305 (2011).
5. M. H. Day, *Nature* **232**, 383 (1971).
6. A. C. Walker, R. E. Leakey, in *The Nariokotome Skeleton*, A. C. Walker, R. E. Leakey, Eds. (Harvard Univ. Press, Cambridge, MA, 1993), pp. 95–160.
7. C. B. Ruff, *Am. J. Phys. Anthropol.* **98**, 527 (1995).
8. L. R. Berger *et al.*, *Science* **328**, 195 (2010).
9. C. O. Lovejoy, *Gait Posture* **21**, 95 (2005).
10. J. H. Prost, *Am. J. Phys. Anthropol.* **52**, 175 (1980).
11. R. L. Susman, J. T. Stern Jr., W. L. Jungers, *Folia Primatol.* **43**, 113 (1984).
12. J. T. Stern Jr., R. L. Susman, *Am. J. Phys. Anthropol.* **60**, 279 (1983).
13. J. T. Stern, *Evol. Anthropol.* **9**, 113 (2000).
14. D. Schmitt, *J. Exp. Biol.* **206**, 1437 (2003).
15. K. L. Steudel-Numbers, M. J. Tilkens, *J. Hum. Evol.* **47**, 95 (2004).
16. K. L. Steudel-Numbers, *J. Hum. Evol.* **51**, 445 (2006).
17. C. O. Lovejoy, K. G. Heiple, A. H. Burstein, *Am. J. Phys. Anthropol.* **38**, 757 (1973).
18. J. M. DeSilva, J. J. Lesnik, *J. Hum. Evol.* **55**, 1064 (2008).
19. K. J. Carlson *et al.*, *Science* **333**, 1402 (2011).
20. It is not possible from the material currently available to determine whether the ischium is also downwardly rotated relative to its position in other australopiths.
21. R. G. Tague, *J. Hum. Evol.* **21**, 153 (1991).
22. M. LaVelle, *Am. J. Phys. Anthropol.* **98**, 59 (1995).
23. M. Haeusler, *Evol. Anthropol.* **1** (suppl.), 53 (2002).
24. H. M. McHenry, R. S. Corruccini, *Am. J. Phys. Anthropol.* **43**, 263 (1975).
25. M. Dalstra, R. Huiskes, *J. Biomech.* **28**, 715 (1995).
26. All of these features can be observed and quantified in the unreconstructed fossils. Our assessment of pelvic inlet shape and the orientation of the pubic corpora are dependent on our reconstruction, but these determinations are certain to be reasonable given the nature of the contacting surfaces and the constraints that guided the reconstruction (SOM text S1).
27. C. Berge, J.-B. Kazmierczak, *Folia Primatol.* **46**, 185 (1986).
28. B. Wood, T. Harrison, *Nature* **470**, 347 (2011).
29. C. V. Ward, *Yearb. Phys. Anthropol.* **119** (suppl. 35), 185 (2002).
30. T. L. Kivell, J. M. Kibii, S. E. Churchill, P. Schmid, L. R. Berger, *Science* **333**, 1411 (2011).
31. B. Zipfel *et al.*, *Science* **333**, 1417 (2011).
32. M. Sponheimer, J. A. Lee-Thorp, "Biogeochemical evidence for the environments of early *Homo* in South Africa," in *The First Humans: Origin and Early Evolution of the Genus Homo.*, F. E. Grine, J. G. Fleagle, R. E. Leakey, Eds. (Springer, Dordrecht, Netherlands, 2009), pp. 185–194.
33. A. I. R. Herries, P. J. Hopley, J. W. Adams, D. Curnoe, M. A. Maslin, *Am. J. Phys. Anthropol.* **143**, 640 (2010).
34. J. L. de Arsuaga, *J. Hum. Evol.* **10**, 293 (1981).
35. Y. Haile-Selassie *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **107**, 12121 (2010).
36. L. C. Aiello, M. C. Dean, *An Introduction to Human Evolutionary Anatomy* (Academic Press, London, 1990).
37. C. Berge, R. Orban-Segebarth, P. Schmid, *J. Hum. Evol.* **13**, 573 (1984).
38. L. Bondioli *et al.*, *J. Hum. Evol.* **50**, 479 (2006).
39. M. M. Abitbol, *Am. J. Phys. Anthropol.* **72**, 361 (1987).
40. R. G. Tague, C. O. Lovejoy, *J. Hum. Evol.* **15**, 237 (1986).
41. C. Berge, D. Goularas, *J. Hum. Evol.* **58**, 262 (2010).
42. R. G. Tague, *Am. J. Phys. Anthropol.* **80**, 59 (1989).
43. P. Schmid, *Folia Primatol.* **40**, 283 (1983).

Acknowledgments: We thank the South African Heritage Resource Agency for the permits to work at the Malapa site; the Nash family for granting access to the Malapa site and continued support of research on their reserve; the South African Department of Science and Technology, the South African National Research Foundation, the Institute for Human Evolution, University of the Witwatersrand, the University of the Witwatersrand's Vice Chancellor's Discretionary Fund, the National

Geographic Society, the Palaeontological Scientific Trust, the Andrew W. Mellon Foundation, the Ford Foundation, the U.S. Diplomatic Mission to South Africa, the French Embassy of South Africa, the A. H. Schultz Foundation, a Ray A. Rothrock '77 fellowship and an International Research Travel Assistance grant of Texas A&M University, the Oppenheimer and Ackerman families, and R. Branson for funding; the University of the Witwatersrand's Schools of Geosciences and Anatomical Sciences and the Bernard Price Institute for Palaeontology for support and facilities; the Gauteng Government, Gauteng Department of Agriculture, Conservation and Environment and the Cradle of Humankind Management Authority; and our respective universities for ongoing support. For access to comparative specimens, we thank E. Mbuu, P. Kiura, V. Iminjili, and the National Museums of Kenya; B. Billings, B. Zipfel, and the School of Anatomical Sciences at the University of the Witwatersrand; and S. Potze, L.C. Kgasi, and the Ditsong Museum. For comparative data, we thank T. Holliday. For technical and material support, we thank Duke University and the University of Zurich 2009 and 2010 Field Schools. Numerous individuals have been involved in the ongoing preparation and excavation of these fossils, including C. Dube, C. Kemp, M. Kgasi, M. Languzza, J. Malaza, G. Mokoma, P. Mukanela, T. Nembhundi, M. Ngcamphalala, S. Jirah, S. Tshabalala, and C. Yates. Other individuals who have given significant support to this project include B. de Klerk, W. Lawrence, C. Steininger, B. Kuhn, L. Pollarolo, B. Zipfel, J. Kretzen, D. Conforti, J. McCaffery, C. Dlamini, H. Visser, R. McCrae-Samuel, B. Nkosi, B. Louw, L. Backwell, F. Thackeray, and M. Peltier. J. Smilg facilitated computed tomography scanning of the specimens. J. DeSilva, T. Kivell, and three anonymous reviewers gave useful comments on drafts of the manuscript. The *Au. sediba* specimens are archived at the Institute of Human Evolution at the University of the Witwatersrand.

Supporting Online Material

www.sciencemag.org/cgi/content/full/333/6048/1407/DC1
SOM Text S1 and S2
Figs. S1 to S17
Tables S1 to S7
References (44–52)

5 January 2011; accepted 29 July 2011
10.1126/science.1202521

Australopithecus sediba Hand Demonstrates Mosaic Evolution of Locomotor and Manipulative Abilities

Tracy L. Kivell,¹ Job M. Kibii,^{2*} Steven E. Churchill,^{3,2} Peter Schmid,^{4,2} Lee R. Berger^{2,5}

Hand bones from a single individual with a clear taxonomic affiliation are scarce in the hominin fossil record, which has hampered understanding the evolution of manipulative abilities in hominins. Here we describe and analyze a nearly complete wrist and hand of an adult female [Malapa Hominin 2 (MH2)] *Australopithecus sediba* from Malapa, South Africa (1.977 million years ago). The hand presents a suite of *Australopithecus*-like features, such as a strong flexor apparatus associated with arboreal locomotion, and *Homo*-like features, such as a long thumb and short fingers associated with precision gripping and possibly stone tool production. Comparisons to other fossil hominins suggest that there were at least two distinct hand morphotypes around the Plio-Pleistocene transition. The MH2 fossils suggest that *Au. sediba* may represent a basal condition associated with early stone tool use and production.

The extraordinary manipulative skills of the human hand are viewed as a hallmark of humanity (1). Over the course of hu-

man evolution, the hand was freed from the constraints of locomotion and has evolved primarily for manipulation, including tool use and even-

tually tool production (2–5). Understanding this functional evolution has been hindered by the rarity of relatively complete hand skeletons that can be reliably assigned to a given taxon, based on a clear association with craniodental fossils. Only one fossil—the Olduvai Hominin 7 (OH 7) hand attributed to *Homo habilis* (6, 7)—had met these criteria during the interval between the first appearance of stone tools at 2.6 million years ago (Ma) (8) and the appearance of derived, essentially human-like morphology by 0.8 Ma (9). Here we describe an almost complete hand of *Australopithecus sediba* at 1.977 Ma (10) from

¹Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, Leipzig 04103, Germany. ²Institute for Human Evolution, University of the Witwatersrand, Private Bag 3, Wits 2050, South Africa. ³Department of Evolutionary Anthropology, Duke University, Box 90383, Durham, NC 27708, USA. ⁴Anthropological Institute and Museum, University of Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland. ⁵School of Geosciences, University of the Witwatersrand, Private Bag 3, Wits 2050, South Africa.

*To whom correspondence should be addressed. E-mail: job.kibii@wits.ac.za

Malapa, South Africa, and discuss, through comparisons with other fossils [supporting online material (SOM) text S1], its implications for understanding the evolution of human locomotion and tool use (SOM text S2).

The *Au. sediba* Malapa Hominin 2 (MH2) adult female includes an almost complete right hand in association with the right forelimb bones, in addition to several bones from the left hand (Fig. 1 and fig. S1 and tables S1 and S2). All bones of the MH2 right hand, except the trapezium, trapezoid, pisiform, and the four distal nonpollical phalanges, are present and undistorted, and most are complete. A third metacarpal was also recovered from a juvenile, presumably male individual (MH1) (11). Although in situ stone tools have not yet been recovered at Malapa, tools are documented at several South African hominin sites from the late Pliocene and early Pleistocene (12).

The anatomy of the thumb. The MH2 pollical distal phalanx is small both in breadth and length, but has a mediolaterally expanded apical tuft like that of contemporary and later hominins (Fig. 2 and table S3). The overall shape is similar to that of StW 294, a fossil that has been attributed to both *Au. africanus* (13) and *Homo* (2). However, the MH2 phalanx has a shaft that is mediolaterally narrower and dorsopalmarly taller than those of all other hominins and modern humans. In this way, it is distinctly different from the flat broad shape of the distal pollical phalanges of *Orrorin* (14), SKX 5016, attributed to *Au. robustus* (15), or OH 7 (6, 16) (Fig. 2 and table S3). MH2 has a clear ungual fossa, a well-developed ridge distal to a deeply excavated proximal palmar fossa, and a distinct proximal border to the apical tuberosity. Together, these features indicate that the MH2 thumb had a well-developed flexor pollicis longus (FPL) muscle [(17), but see (3) and SOM text S3] and a human-like palmar pad with a mobile proximal pulp, all features that have been associated with stone tool production (2, 3, 5). Such a palmar pad could have helped the thumb accommodate objects during firm precision grips (2, 17) (SOM text S3). The combination of a broad apical tuft, well-developed FPL, and a narrow, tall shaft in MH2 suggests that the tip of the thumb could incur forceful loading in flexion, but perhaps not in the same way as in other hominins. Some or all of this morphology is also present in *Orrorin* (14) and *Ardipithecus ramidus* (18). Thus, the expanded apical tufts and a well-developed FPL are either the primitive hominin condition or were convergently developed in multiple hominin taxa for tool-making and non-tool-making behaviors (SOM text S3). However, most of these features are absent in the distal pollical phalanx of *H. habilis* OH 7 (6, 14, 16).

The morphology of the MH2 proximal pollical phalanx and first metacarpal (Mc1) suggest that some key intrinsic pollical muscles necessary for forceful thumb flexion and adduction were enhanced, whereas other muscles were poor-

ly developed (19). Centrally placed on the palmar surface of the Mc1 head is a prominent “beak” flanked by depressions for large sesamoid bones (Fig. 3). Similar beaked projections have been identified in SK 84, which has been tentatively attributed to *H. erectus* [(20), but see (15)], and in juvenile first metacarpals possibly belonging to the *H. erectus* specimen KNM-WT 15000 (21). These sesamoid bones are thought to increase the moment arm during flexion and abduction for adductor pollicis oblique and flexor pollicis brevis muscles that insert on the medial and lateral sesamoids, respectively (2). The base of the MH2 proximal phalanx is robust (table S4), indicating that these muscles, as well as the abductor pollicis brevis, were enhanced. The relatively tall height of the Mc2 and Mc3 bases is also thought to alter the moment arm of the adductor pollicis muscles relative to the trapeziometacarpal joint and to enhance flexion of the thumb (22) (table S5). All of these muscles are important in modern humans for forceful precision pinch grips during stone tool production (19, 22). In contrast, chimpanzees have shorter moment arms and different planes of movement that make the thumb musculature function differently during grasping (19, 22).

The insertion for the dorsal interosseous tendon, a muscle strongly recruited during gripping of a hammerstone (19), is distally extended as in *Au. africanus*, specimens from Swartkrans, and modern humans, increasing the moment arm for thumb adduction (5, 23) (Fig. 3). However, the minimal muscle scarring in MH2 is similar to that of *Au. africanus*, indicating that this muscle was poorly developed (23) and provided less stability at the trapeziometacarpal joint than is inferred from the rugose scarring of the Swartkrans specimens (22). Similarly, the insertion site for

the opponens pollicis tendon is minimally expressed, as in *Au. afarensis* (24), suggesting that this muscle, which is important for opposition of the thumb to the fingers as well as holding and manipulating large objects (19), was also poorly developed in MH2 (Fig. 3).

The poor development of some of the pollical intrinsic musculature in MH2 may also be reflected in the gracility of the thumb bones (Figs. 1 and 3). The shaft of the MH2 first proximal phalanx and the base and shaft of the Mc1 are generally less robust than those in *Au. africanus* and later hominins and most similar to that of *Au. afarensis* (tables S4, S6, and S7 and fig. S2). Experimental research on modern humans making Oldowan tools has shown that the thumb incurs large loads during stone tool production [(19, 22, 25); but see SOM text S2]. If so, the gracility of the external morphology in the MH2 pollical bones suggests that the *Au. sediba* thumb was not subject to the same type or frequency of loading as that of other contemporary or later hominins.

The medial metacarpus and comparison to MH1. As with the first metacarpal, MH2 also appears to be primitive in the remarkable gracility of the medial metacarpals (Figs. 1 and 4). Relative to length, the mediolateral breadths of the Mc2-Mc5 shafts are narrower than even in *Au. afarensis* (tables S5, S7, and S8). However, the proximal bases and distal heads of the metacarpals are generally more robust than those of other australopiths and many later hominins (tables S5 and S8). The robust base of Mc5 suggests that the extrinsic and intrinsic musculature to the fifth finger were well developed. A powerful flexor carpi ulnaris (FCU) is consistent with the robust attachment sites on the proximal ulna (11) and is an important muscle for climbing in

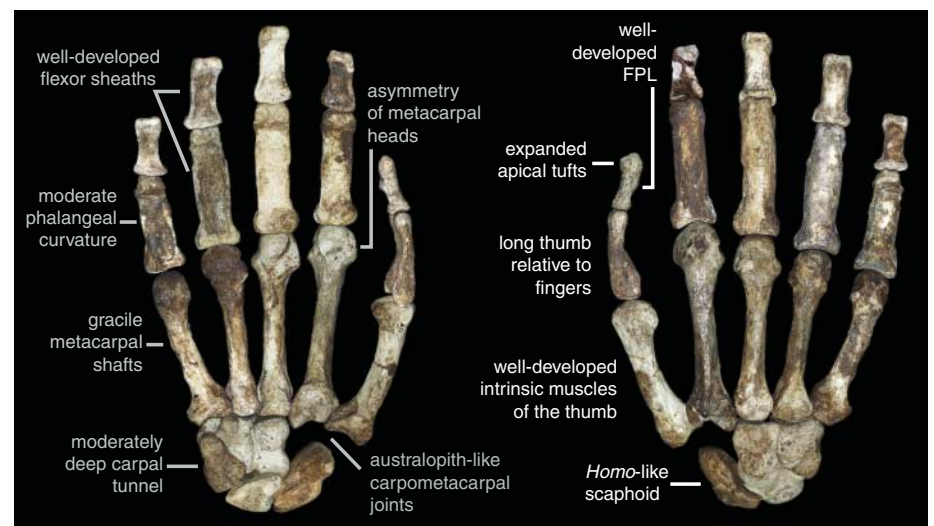


Fig. 1. *Au. sediba* MH2 right hand. Palmar (left) and dorsal (right) views of all MH2 right hand bones found in association with the right upper limb. Features of the MH2 hand traditionally considered primitive or australopith-like are labeled in gray (palmar view), and features considered derived are labeled in white (dorsal view) [(2, 3, 5), but see (14)]. The thumb is pictured in opposition, overlapping with the second metacarpal.

apes. The FCU is also strongly active in both hands during tool-making, when accelerating the wrist before strike and when stabilizing the pisiform for effective use of the abductor digiti minimi (ADM) (19). The base of the fifth proximal phalanx is similar in robusticity to that of later *Homo* (table S9), suggesting that the ADM, which is important for stabilizing the core during hammerstone strike (19), was also well developed in MH2. MH2 shares with other australopiths and *Homo* (13, 24, 26, 27) asymmetry of the metacarpal heads that is associated with the human-like ability of the fingers to accommodate to an object via the metacarpal phalangeal joints (2, 3) (Fig. 1).

The preservation of a Mc3 associated with the male MH1 individual (11) provides a rare opportunity to look at variation in hand morphology between sexes in an early hominin. Though MH1 is juvenile, the development of its Mc3 is nearing completion and is demonstrably more robust than that of the female MH2 hand (Fig. 4 and table S10). This variation in the *Au. sediba* hand bones suggests that metacarpal robusticity may at least partly reflect sexual dimorphism (28), as with other aspects of the postcranial skeleton (11), rather than variation in loading and tool-making ability in either sex in

early hominins (2). If this is the case, sexual dimorphism in metacarpal robusticity would have profound implications for the functional interpretation and species attributions of several isolated hominin hand fossils (13, 15, 20, 28).

The radial carpus. MH2 presents a mosaic of primitive and derived features in the radial carpal bones. The scaphoid is dorsopalmarly short and mediolaterally broad, its capitate facet is small, and its trapezium facet extends palmar-laterally onto the tubercle, which is less palmarly oriented than in African apes (Fig. 5). Together, these features give the MH2 scaphoid a generally human-like appearance that is clearly distinct from those of *Ar. ramidus* (18) and the African ape-like scaphoids of the OH 7 hand (6, 16) and *H. floresiensis* (29) (Fig. 5 and figs. S3 and S4). Thus, *Au. sediba* documents the only appearance of a derived scaphoid before *H. neanderthalensis* (27). However, the *Au. sediba* scaphoid tubercle is more robust and the trapezoid facet more extensive than those of modern humans. The trapezium articulation at the base of Mc1 remains dorsopalmarly curved like those in other australopiths (13, 24) and SK 84 [variously attributed to *Au. robustus* and *H. cf. erectus* (15, 20, 28)] and unlike the flatter, broader facet of SKX 5020 [attributed to

Au. robustus (15)] and the inferred morphology of OH 7 (6, 16) (Fig. 5).

The MH2 capitate is similar to that of *Au. afarensis* and *Au. africanus* (24, 30, 31) in overall morphology and unlike those of *Ar. ramidus* (18), *Au. anamensis* (31), or the cf. *Au. afarensis* specimen KNM-WT 22944 (32). However, its combination of primitive and derived features is distinct (Fig. 5 and figs. S5 and S6). The broad head is dominated by a relatively large scaphoid articulation as compared with that for the lunate (Fig. 5 and fig. S7), which is considered derived as compared with those of other australopiths (32). The capitate body shows reduced “waisting” of the neck, similar to that of modern humans, and there is both a palmar and a dorsal facet for the trapezoid (Fig. 5 and fig. S6), which is a pattern found in *H. antecessor* (9) and some modern humans (33). In contrast, the angle between the Mc2 and Mc3 facets of the capitate is similar to those of *Au. afarensis* and *Au. africanus*, being intermediate between the laterally oriented facets of *Au. anamensis* (31) and *H. floresiensis* (29) and the more distally oriented facets of *H. antecessor* and modern humans (9) (Fig. 5, fig. S8, and table S11). The more lateral orientation of the Mc2-trapezium articulation is also similar to that seen in other australopiths (5, 26, 30, 31) but is derived as compared with that of OH 7 (5, 33, 34) (fig. S9).

The reorientation of the radial carpal and carpometacarpal region typical of later *Homo* is considered advantageous for metacarpal rotation and withstanding large radioulnarly directed forces across the wrist during tool-making (2, 30, 33, 34). In comparison with other hominins, MH2 demonstrates that this morphology evolved in a mosaic fashion and in multiple ways (5, 33). In MH2, the intercarpal articulations of the scaphoid and capitate appear better suited to withstand compression across the wrist than those of other earlier and contemporary hominins (33, 34). However, the carpometacarpal articulations are australopith-like, suggesting that the MH2 thumb and index finger did not experience the same type or frequency of loading as those of later *Homo*. As a whole, the radial carpal and carpometacarpal complex probably functioned differently in MH2 as compared with the functional implications of the suite of mostly primitive features in other australopiths (33) or the suite of derived features found in later *Homo* (9, 27, 33). This mosaic morphology in MH2, especially when compared with the reverse combination of a primitive scaphoid and presumably derived Mc1-trapezium articulation in OH 7, adds to the range of morphological variation previously documented in the hominin carpometacarpal joints (5, 24, 29, 30) and to the ambiguity surrounding the polarity and functional significance of some of these features (5).

The medial phalanges and flexor apparatus. The finger phalanges similarly show a combination of primitive and derived features related to both powerful hand flexion and manipulation.



Fig. 2. Pollical distal phalanx of *Au. sediba* MH2 hand. (A) Right distal pollical phalanx of MH2 (UH 88-124) shown (from left to right) in medial, dorsal, lateral, and palmar views, compared to (B) StW 294 in medial and palmar views, (C) cast of FLK NN-A of the OH 7 hand in lateral and palmar views, and (D) SKX 5016 in medial and palmar views. Although portions of the MH2 phalanx are missing, the apical tuft at the distal end of the bone is expanded (white outline estimated by mirror-imaging preserved fossil morphology). The presence of an unguis fossa (gray highlighted area in palmar view of MH2) and a well-developed distal ridge (white arrows) to the proximal palmar fossa imply a well-developed FPL (17). The overall shape of the bone is most similar to StW 294 (table S3), which has been attributed to both *Au. africanus* (13) and early *Homo* (3), and unlike the flat, broad morphology of OH 7 (6, 16) or SKX 5016, which is attributed to *Au. robustus* (15). The distal ridge is less pronounced in SKX 5016, and all of the morphological features associated with a well-developed FPL are absent in OH 7 (14). All fossils are to scale.

The distal phalanx from the MH2 left hand, probably from ray four or five, has an apical tuft that is more mediolaterally expanded relative to its length than that of other australopiths and OH 7 (table S12). Like the broad tip of the MH2 thumb, this expansion is associated with the human-like presence of palmar pads on the fingers to distribute pressure during forceful gripping and fine manipulation of objects [(2), but see (3)]. The proximal phalanges (PPs) and intermediate phalanges (IPs) are proportionally much shorter in length as compared with those of *Au. afarensis* and OH 7 (fig. S10; table S13). The mean dorsal curvature of the PPs is less than that of *Au. afarensis*, OH 7, and a specimen tentatively attributed to *H. cf. erectus* (15) (figs. S11 and S12). The IPs lack well-developed attachment sites for the flexor digitorum superficialis tendons, bilateral depressions, and a palmar median bar that is typical of those of other australopiths (13, 24) and *Homo* (6, 9, 16, 21, 27).

In contrast, both the MH2 PPs and the IPs of rays 2 to 5 have prominent, bilateral flexor sheath ridges that appear equally or more developed than those of other australopiths (13, 15, 24) (Fig. 1). The IPs are smaller, gracile versions of the PPs and thus unlike those seen in other hominins. This morphology allows strong flexion of the fingertips. The gracility of the phalangeal shafts suggests that the MH2 fingers would be poorly suited for resisting strong dorsopalmar bending loads generated during the powerful flexion involved in arboreal locomotion. In comparison, the OH 7 IPs are robust and consistent with a hand well suited for climbing (6, 16, 35). However, with relatively shorter phalangeal length and reduced curvature, the flexor muscles in MH2 may have compensated to retain the forceful flexion of the fingers that is necessary for either grasping branches or the jaw-chuck and cradle precision grips used during stone tool production (SOM text S2).

The MH2 carpal tunnel was probably moderately deep (Fig. 5). If so, MH2 would have retained stronger wrist and hand flexion than most species of later *Homo*. The length of the scaphoid tubercle is shorter than in *H. neanderthalensis* and in the upper range of variation in modern humans, and less palmarly extended than that of African apes (fig. S13). The hamate hamulus is less distally extended than in earlier australopiths, whereas its palmar extension is intermediate between those of *Au. afarensis* and *H. neanderthalensis* (but falling within the range of modern humans) (figs. S14 and S15). The ape-like long, oval pisiform facet on the triquetrum (Fig. 5) suggests that the pisiform was rod-like, which would enhance the flexor moment arm of the FCU (30). However, the correlation between the shape of the pisiform articulation and the pisiform itself is not known. The remainder of the MH2 upper limb retains primitive, australopith-like morphology (11), suggesting that *Au. sediba* still engaged regularly in arboreal locomotion (11, 36). Taken together, the flexor apparatus of *Au.*



Fig. 3. First metacarpal (Mc1) of *Au. sediba* MH2 hand. (A) MH2 right Mc1 (UW 88-119) in (from left to right) dorsal, mediopalmar, lateral, and medial views compared to palmar (left) and medial (right) views of (B) SK 84 and (C) SKX 5020, both of which are possibly *Au. robustus* or *Homo* (15, 20, 28). (D) *Au. africanus* StW 418 and (E) a female modern human. The projecting sesamoid beak (white asterisks) is found on the palmar surface of the Mc1 head in MH2 and SK 84 (2, 20). Like the other fossil hominin Mc1s depicted here, MH2 displays a human-like, distally extended muscle marking for the insertion of the dorsal interosseous tendon on the medial shaft (white brackets), but the muscle scarring is less prominent. The insertion area for the opponens pollicis tendon on the lateral shaft (gray brackets) is poorly developed in MH2 as compared to the other hominins. SK 84 and StW 418 are from the left side and have been mirror-imaged for easier comparisons. All bones are to scale.

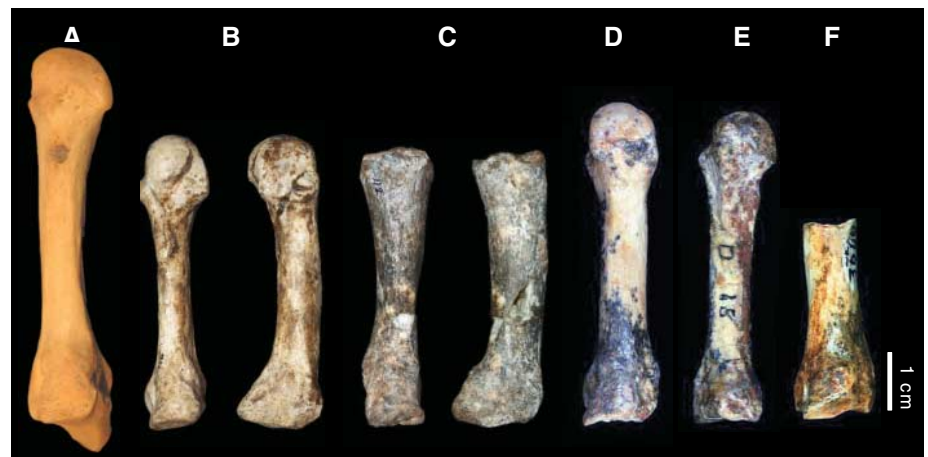


Fig. 4. Relative size of third metacarpals in *Au. sediba*. Third metacarpals of (A) a female modern human in palmar view; (B) *Au. sediba* adult female MH2 (UW 88-116) and (C) the juvenile male MH1 (UW 88-112) (11) in palmar (left) and lateral (right) views; palmar views of (D) *Au. africanus* StW 68, (E) *Au. africanus* StW 64, and (F) proximal portion of SKX 3646 of an unidentified taxon from Swartkrans. Although the juvenile MH1 metacarpal is missing its epiphyseal head, the estimated age of the skeleton [12 to 13 human years (11)] suggests that its development is close to completion (metacarpal fusion in chimpanzees occurs at 9 to 10 years of age and in humans at 14 to 16 years of age; table S10). Compared to MH2, the MH1 Mc3 is only slightly shorter in length despite missing the epiphyseal head, and the proximal base and shaft are substantially more robust (table S10). The MH1 metacarpal robusticity is comparable to StW 68 and SKX 3646, whereas MH2 is similar to StW 64. All bones are to scale.

sediba is best described as being reduced as compared with that of *Au. afarensis* and the OH 7 hand, but one that remained well suited for arboreal behaviors.

Intrinsic hand proportions. Modern humans differ from other apes in having a relatively long thumb as compared to their fingers (1, 30), which facilitates our pad-to-pad precision grip ability

(1, 2). Inferring the relative length of the thumb in fossil hominins has been challenging because it requires the preservation of several elements from the same individual (3, 37). Estimates of the intrinsic hand proportions based on the un-associated bones from multiple individuals suggest that the hands of *Au. afarensis* (30, 38) and *Au. africanus* (39) were generally human-like, but perhaps with less precision or efficiency (30). The MH2 thumb is long (length of $Mc1 + PP1 = 6.4$ cm), whereas its fingers are short (length of $Mc3 + PP3 + IP3 = 10.5$ cm), so that its relative thumb-to-finger length is greater than those in earlier or later hominins and is even greater than the upper range of variation in modern humans (Fig. 6, fig. S16, and tables S7 and S14). Relative to hand size and bi-condylar breadth of the distal humerus, MH2 also has a long thumb and short fingers as compared to other hominins (figs. S17 and S18 and table S15). Relatively short fingers might suggest that *Au. sediba* was less adept at arboreal locomotion than earlier hominins; however, the long thumb would compensate somewhat during grasping. A long thumb also enhances opposability to the fingers, facilitating the manipulation of objects.

Discussion. Although stone tools appear in the archaeological record at 2.6 Ma (8), and there is possible evidence of tool use by 3.4 Ma (40), we have a poor understanding of when and how tool-making evolved, which hominins were able to make tools, and how posited tool-making morphology may coexist within the same hand with features functionally advantageous for locomotion. Based on current evidence, the hominin fossil record can be generally divided into three stages of hand evolution, based on the retention of morphological features related to arboreal locomotion and the appearance of morphology thought to be associated with human-like tool-making ability (2, 5) (table S16). The first stage reflects morphological features that culminated in *Au. afarensis* by ~3.0 Ma and are commonly considered to be driven primarily by a reduction in the use of the hand in arboreal activities as compared with the last common ancestor (26). Though these early hominins retained curved fingers, gracile digits, and generally primitive carpal and carpometacarpal articulations, the finger lengths were reduced and consequently the thumb was relatively longer (24, 30, 26, 38). Because *Au. afarensis* and earlier hominins are not associated with stone tool technology, other features posited to be related to modern human tool-making ability, such as a well-developed FPL, probably evolved for other behaviors, manipulative or otherwise, and were exapted by later tool-making hominins or convergently evolved (14, 38). MH2 shares with these early hominins primitive carpometacarpal joint orientations, including the trapezium-Mc1 joint, gracility of the metacarpal shafts (but see MH1), and asymmetric metacarpal heads.

The second stage is represented between ~3.0 and 1.5 Ma in *Au. africanus*, isolated specimens attributed to either robust australopiths or early

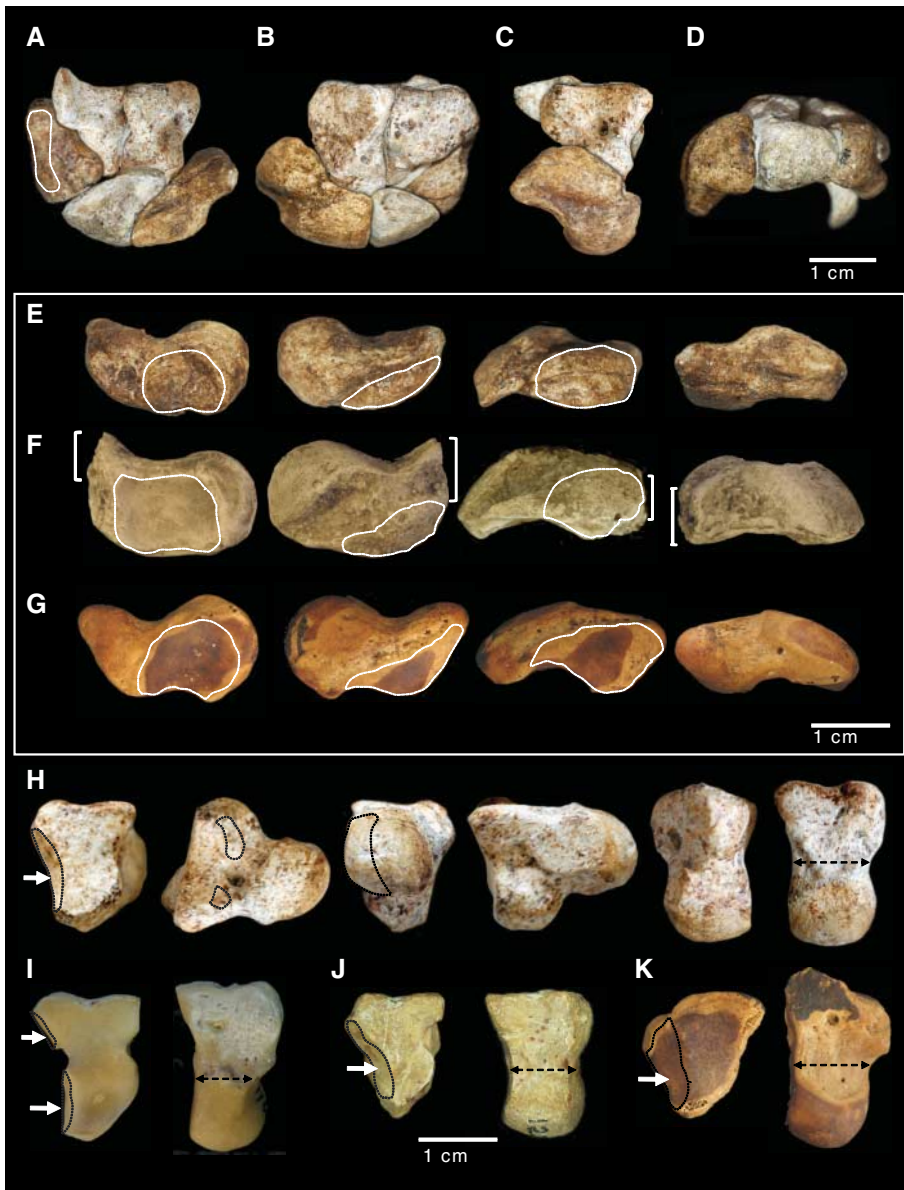
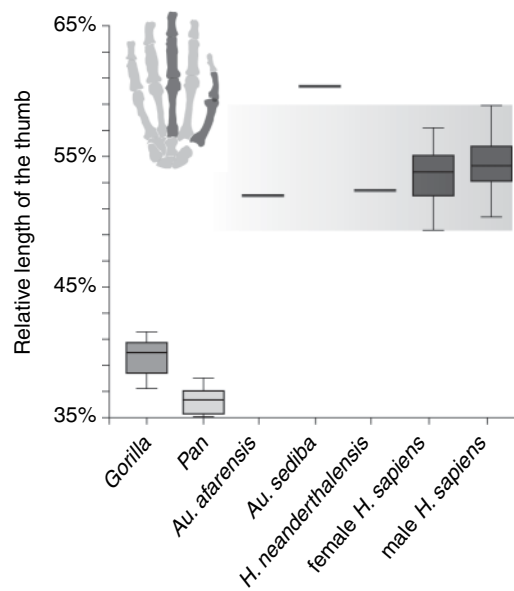


Fig. 5. *Au. sediba* MH2 wrist bones. Top, the *Au. sediba* MH2 articulated right wrist in (A) palmar (with the triquetrum's pisiform facet outline in white), (B) dorsal, (C) lateral, and (D) proximal views. Middle, (E) the MH2 right scaphoid (UW 88-158) in (from left to right) medial, proximalateral, distal, and palmar views compared with (F) a cast of FLK NN-P of the OH 7 hand attributed to *H. habilis* (6, 7) and (G) a female modern human. MH2 represents the earliest appearance of a derived scaphoid in the hominin fossil record, with a trapezium-trapezoid facet (outlined in white) that extends onto the tubercle as in humans and a slightly reduced capitate facet. MH2 is distinctly unlike the African ape-like scaphoid of the OH 7, which has trapezium facet restricted the scaphoid body and an expansive capitate facet. The OH 7 scaphoid tubercle is not preserved (missing portion is highlighted with a white bracket). Bottom, (H) the MH2 left capitate (UW 88-105, which is more complete than the right) in (from left to right) distal, lateral, proximal, medial, palmar, and dorsal views compared to distal (left) and dorsal (right) views of (I) *P. troglodytes*, (J) *Au. africanus* TM 1526 (with right capitate mirror-imaged), and (K) a female modern human. MH2 displays a primitive, more laterally facing Mc2 facet (white arrows) than the distally oriented facet of modern humans. However, *Au. sediba* is derived in having a palmar (in addition to the primitive dorsal) trapezoid facet (outlined in black on the lateral view; palmar is at the top), minimal "waisting" of the capitate body (black dotted line in dorsal views) like that of modern humans, and a relatively large scaphoid articulation as compared to that of the lunate (lunate facet outlined in proximal view). All bones are to scale.

Fig. 6. Relative length of the thumb in the *Au. sediba* MH2 hand. Shown is a box-and-whisker plot of the relative length of the thumb calculated as a ratio of the total length of the Mc1 and first proximal phalanx to the total length of the Mc3 and third proximal and intermediate phalanges within the same individual (bones highlighted in dark gray in outline of MH2 hand) in all taxa apart from *Au. afarensis*, for which that ratio is derived from multiple individuals from different sites (30, 38). MH2 has a relatively longer thumb than that of other hominins and falls outside the range of variation in modern humans (highlighted by shaded box). See table S14 for sample and methods.



Homo from Swartkans, and the OH 7 hand attributed to *H. habilis* (5). Features of the hand include more human-like thumb-to-finger proportions, a more mobile trapezium-Mc1 articulation, and increased robusticity of the metacarpals, which are thought to reflect better and more forceful manipulation of objects than in earlier hominins (2, 3, 5, 13). Although the tool-making ability of early hominins has been debated (2, 3, 20, 28), few have questioned this ability in OH 7 since its discovery in the early 1960s in direct association with Oldowan tools [(2, 3, 7, 16); but see (6, 14, 34, 35)]. Yet OH 7 also preserves a well-developed flexor apparatus for arboreal climbing and several primitive australopith-like features (6, 16). MH2 shares with many of these hominins well-developed thumb and fifth-digit flexor and abductor musculature, expanded apical tufts, and a well-developed flexor pollicis longus, all of which are associated with tool-making ability. The MH2 hand also shares with some of these hominins poor development of other aspects of the thumb musculature, moderate phalangeal curvature, and at least a moderately well-developed flexor apparatus.

The third stage is represented by the absence of arboreal features and the appearance of essentially modern human-like morphology by 0.8 Ma in *H. antecessor* (9) and later hominins (27), which together reflect committed stone tool production and a lack of arboreal locomotion (5, 33). *Au. sediba* demonstrates that some of the derived stage-three features of the radial carpals had appeared by 1.977 Ma (10). The MH2 hand has a derived reorientation of the scaphoid and capitate intercarpal articulations as compared with earlier hominins, which is considered well suited for resisting compressive loads from the thumb during tool-making (5, 33, 34). In addition, the high thumb-to-finger length proportions and strong sexual dimorphism in the hand robusticity of *Au. sediba* may broaden the range of morphologies associated with tool-making

and may complicate associating stone tool production in early hominins with specific morphological features. Although arboreal features do not necessarily preclude the ability to make stone tools (6, 16), the retention of arboreal features in MH2, together with its primitive australopith-like upper limb, suggest that *Au. sediba* still regularly engaged in arboreal behavior. Thus, *Au. sediba* does not have all of the morphological features commonly considered necessary to demonstrate a clear commitment to stone tool production (table S16). However, the direct association of the primitive African ape-like wrist of *H. floresiensis* (29) with a well-established sequence of Oldowan-like stone tools (41) suggests that the morphological criteria used to define stone tool production in hominins may need to be reevaluated.

The association of the OH 7 fossils with Oldowan stone tools (6, 7) has led many researchers to accept that the hand is that of *H. habilis* (7), and the morphology is that of a tool-making hominin (2, 3, 6, 7). *Au. sediba*, with an overall more derived morphology than OH 7, although older, should therefore also be considered a tool-maker. If so, *Au. sediba* and OH 7 demonstrate that there may have been at least two distinct morphotypes of the hominin tool-making hand during the Plio-Pleistocene transition. The OH 7 hand is derived in some morphologies in which *Au. sediba* may be comparatively primitive (such as the extremely broad and flat trapezium-Mc1 joint), and conversely, OH 7 is primitive in morphologies for which *Au. sediba* is derived (such as strongly curved and robust phalanges, an African ape-like scaphoid and carpal-Mc2 articulations, and poorly developed FPL) (6, 16) (table S16). In this view, the OH 7 hand was adapted to tool-making in a distinctly different way than *Au. sediba* and later hominins.

Alternatively, other researchers have questioned the taxonomic affiliation of the OH 7 hand fossils [(5, 14, 33, 34), see review in (35)]

and the tool-making implications of its morphology (14, 34, 35). The primitive morphology of OH 7 suggests both that these fossils might be better attributed to *Au. boisei* (14, 35) and that hominin tool-making ability should be based on the functional morphology of the hand and not solely on direct association with stone tools (6, 20, 35). *Au. sediba* reveals that many of the manual morphological features commonly associated with stone tool production—even if *Au. sediba* itself was not a tool-maker—were present by 1.977 Ma (10), and most of these features are not present in OH 7. In this light, *Au. sediba* may provide a better potential morphotype for basal *Homo* hand morphology than the hand fossils originally used to define the species *H. habilis* (7).

References and Notes

1. J. R. Napier, *Hands* (Princeton Univ. Press, Princeton, NJ, 1993).
2. M. W. Marzke, *Am. J. Phys. Anthropol.* **102**, 91 (1997).
3. R. L. Susman, *J. Hum. Evol.* **35**, 23 (1998).
4. C. V. Ward, *Yearb. Phys. Anthropol.* **119**, 185 (2002).
5. M. W. Tocheri, C. M. Orr, M. C. Jacofsky, M. W. Marzke, *J. Anat.* **212**, 544 (2008).
6. J. Napier, *Nature* **196**, 409 (1962).
7. L. S. B. Leakey, P. V. Tobias, J. R. Napier, *Nature* **202**, 7 (1964).
8. S. Semaw et al., *J. Hum. Evol.* **45**, 169 (2003).
9. C. Lorenzo, J. L. Arsuaga, J. M. Carretero, *J. Hum. Evol.* **37**, 501 (1999).
10. R. Pickering et al., *Science* **333**, 1421 (2011).
11. L. R. Berger et al., *Science* **328**, 195 (2010).
12. K. Kuman, R. J. Clarke, *J. Hum. Evol.* **38**, 827 (2000).
13. D. E. Ricklan, *J. Hum. Evol.* **16**, 643 (1987).
14. S. Almécija, S. Moyà-Solà, D. Alba, *PLoS ONE* **5**, e11727 (2010).
15. R. L. Susman, D. de Ruiter, C. K. Brain, *J. Hum. Evol.* **41**, 607 (2001).
16. R. L. Susman, N. Creel, *Am. J. Phys. Anthropol.* **51**, 311 (1979).
17. M. M. Shrewsbury, M. W. Marzke, R. L. Linscheid, S. P. Reece, *Am. J. Phys. Anthropol.* **121**, 30 (2003).
18. C. O. Lovejoy et al., *Science* **326**, 70e1 (2009).
19. M. W. Marzke et al., *Am. J. Phys. Anthropol.* **105**, 315 (1998).
20. R. L. Susman, *Science* **265**, 1570 (1994).
21. A. Walker, R. Leakey, *The Nariokotome Homo erectus Skeleton* (Harvard Univ. Press, Cambridge, MA, 1993).
22. M. W. Marzke et al., *Am. J. Phys. Anthropol.* **110**, 163 (1999).
23. M. C. Jacofsky, thesis, Arizona State University, Tempe, AZ (2009).
24. M. E. Bush, C. O. Lovejoy, D. C. Johanson, Y. Coppens, *Am. J. Phys. Anthropol.* **57**, 651 (1982).
25. C. Rolian, D. E. Lieberman, J. P. Zermeno, *J. Hum. Evol.* **61**, 26 (2011).
26. M. S. M. Drapeau, C. V. Ward, W. H. Kimbel, D. C. Johanson, Y. Rak, *J. Hum. Evol.* **48**, 593 (2005).
27. E. Trinkaus, *The Shanidar Neandertals* (Academic Press, London, 1983).
28. E. Trinkaus, J. C. Long, *Am. J. Phys. Anthropol.* **83**, 419 (1990).
29. M. W. Tocheri et al., *Science* **317**, 1743 (2007).
30. M. W. Marzke, *J. Hum. Evol.* **12**, 197 (1983).
31. M. G. Leakey, C. S. Feibel, I. McDougall, C. Ward, A. Walker, *Nature* **393**, 62 (1998).
32. C. V. Ward et al., *J. Hum. Evol.* **36**, 69 (1999).
33. M. W. Tocheri, thesis, Arizona State University, Tempe, AZ (2007).
34. M. W. Tocheri et al., *Am. J. Phys. Anthropol.* **122**, 101 (2003).
35. S. Moyà-Solà, M. Kohler, D. M. Alba, S. Almécija, *Folia Primatol. (Basel)* **79**, 215 (2008).

36. B. Zipfel *et al.*, *Science* **333**, 1417 (2011).
 37. R. J. Clarke, *S. Afr. J. Sci.* **95**, 477 (1999).
 38. D. M. Alba, S. Moyà-Solà, M. Köhler, *J. Hum. Evol.* **44**, 225 (2003).
 39. D. J. Green, A. D. Gordon, *J. Hum. Evol.* **54**, 705 (2008).
 40. S. P. McPherron *et al.*, *Nature* **466**, 857 (2010).
 41. M. W. Moore, T. Sutikna, Jatmiko, M. J. Morwood, A. Brumm, *J. Hum. Evol.* **57**, 503 (2009).

Acknowledgments: We thank the South African Heritage Resources Agency for the permits to work at the Malapa site; the Nash family for granting access to the Malapa site and continued support of research on the Malapa and John Nash nature reserves; the South African Department of Science and Technology, the South African National Research Foundation, the Institute for Human Evolution, University of the Witwatersrand, the University of the Witwatersrand's Vice Chancellor's Discretionary Fund, the National Geographic Society, the Palaeontological Scientific Trust, the Andrew W. Mellon Foundation, the Ford Foundation, the U.S. Diplomatic Mission to South Africa, the French embassy of South Africa, the Oppenheimer and Ackerman families, and Sir Richard Branson for funding; the University of

the Witwatersrand's Schools of Geosciences and Anatomical Sciences and the Bernard Price Institute for Palaeontology for support and facilities; the Gauteng Government, Gauteng Department of Agriculture, Conservation and Environment and the Cradle of Humankind Management Authority; our respective universities for ongoing support; E. Mbua, P. Kiura, V. Iminjili, and the National Museums of Kenya, B. Billings, B. Zipfel, and the School of Anatomical Sciences at the University of the Witwatersrand, and S. Potze, L. C. Kgasi and the Ditsong Museum for access to comparative fossil specimens; the staff at the Musée royal de l'Afrique centrale, Museum für Naturkunde Berlin, Max-Planck-Institute für evolutionäre Anthropologie, Powell-Cotton Museum, Universität Wien, Naturhistorisches Museum Wien, Cleveland Museum of Natural History, Harvard Museum of Comparative Zoology, and Royal Ontario Museum for access to extant comparative material; and the University of Zurich 2010 Field School. Numerous individuals have been involved in the ongoing preparation and excavation of these fossils, including C. Dube, C. Kemp, M. Kgasi, M. Languza, J. Malaza, G. Mokoma, P. Mukanela, T. Nemvhundi,

M. Ngcamphalala, S. Jirah, S. Tshabalala, and C. Yates. Other individuals who have given significant support to this project include B. de Klerk, W. Lawrence, C. Steininger, B. Kuhn, L. Pollarolo, J. Kretzen, D. Conforti, C. Dlamini, H. Visser, B. Nkosi, B. Louw, L. Backwell, F. Thackeray, and M. Peltier. J. Smilg facilitated computed tomography scanning of some of the specimens. We thank A. Deane for analysis of phalangeal curvature; and M. Skinner, D. Schmitt, D. Begun, and two anonymous reviewers for their constructive comments. This work was supported in part by the Natural Sciences Research Council of Canada and the Max Planck Society. Data are presented in the SOM.

Supporting Online Material

www.sciencemag.org/cgi/content/full/333/6048/1411/DC1
 SOM Text S1 to S3
 Figs. S1 to S18
 Tables S1 to S13
 References (42–75)

7 January 2011; accepted 29 July 2011
 10.1126/science.1202625

The Foot and Ankle of *Australopithecus sediba*

Bernhard Zipfel,^{1,2*} Jeremy M. DeSilva,^{1,3} Robert S. Kidd,^{1,4} Kristian J. Carlson,^{1,5} Steven E. Churchill,^{1,6} Lee R. Berger^{1,7}

A well-preserved and articulated partial foot and ankle of *Australopithecus sediba*, including an associated complete adult distal tibia, talus, and calcaneus, have been discovered at the Malapa site, South Africa, and reported in direct association with the female paratype Malapa Hominin 2. These fossils reveal a mosaic of primitive and derived features that are distinct from those seen in other hominins. The ankle (talocrural) joint is mostly humanlike in form and inferred function, and there is some evidence for a humanlike arch and Achilles tendon. However, *Au. sediba* is apelike in possessing a more gracile calcaneal body and a more robust medial malleolus than expected. These observations suggest, if present models of foot function are correct, that *Au. sediba* may have practiced a unique form of bipedalism and some degree of arboreality. Given the combination of features in the *Au. sediba* foot, as well as comparisons between *Au. sediba* and older hominins, homoplasy is implied in the acquisition of bipedal adaptations in the hominin foot.

The human foot is thought to be one of the critical evolutionary specializations that define our species, being central to the evolution of arguably the most critical defining character of the Hominini: bipedalism (1–5). The increasing number of pedal elements in the hominin fossil record and the morphological diversity that they display have led some to conclude that there may have been greater diversity in early human bipedalism than previously thought (6). Foot and ankle elements of *Australopithecus*

sediba shed light on the evolution of foot structure, giving a surprising look at a foot configuration with both primitive and derived characters that together have implications for our understanding of hominin bipedal diversity.

Well-preserved foot and ankle elements recovered from the Malapa site, South Africa (7, 8), include an articulated distal tibia, talus, and calcaneus directly associated with the female paratype skeleton, Malapa Hominin 2 (MH2); two fragmentary metatarsals; and a calcaneal apophysis associated with the holotype juvenile male (MH1), as well as a distal tibia provisionally associated with MH1 (7) but now thought to probably originate from another individual (Fig. 1) (9).

Tibia, talus, and calcaneus. University of the Witwatersrand (U.W.) 88-97, 98, and 99 is the only associated complete adult partial (distal) tibia, talus, and calcaneus known in the early hominin fossil record (Fig. 2). The fossils were found in articulation and remain imprisoned in matrix (7). An attempt to physically separate the three elements in contact with one another would almost certainly result in damage to the speci-

mens, risking destruction of delicate articular morphology (i.e., subchondral bone). Therefore, we sought an alternative preparation strategy: We used medical computed tomography (CT) to scan the specimen, removed the matrix digitally, and produced renderings of each element (7). Descriptions of U.W. 88-97, 98, and 99 are based on both the conjoined fossils and casts produced from high-resolution three-dimensional (3D) print-outs of the digitally separated elements (Figs. 1A and 2) (10).

The U.W. 88-97 right tibia has an anteroposteriorly expanded metaphysis relative to the anteroposterior dimensions of the articular surface, a feature typical of bipedal hominins (fig. S1). In the coronal plane, the tibial plafond is perpendicular to the shaft, similar to that found in modern humans and fossil hominins (fig. S2), indirectly suggesting a valgus knee (11, 12). In the sagittal plane, the posterior rim of the tibial plafond projects more inferiorly than the anterior rim, producing an anteriorly directed set of 6.7° to the ankle joint, suggesting arching of the foot (fig. S3) (13). The articular facet for the talus is slightly wedged in the inferior view and deeply curved in the lateral view, unlike the trapezoid-shaped and flat joint surface often found in apes (figs. S4 and S5). Discriminant function analysis clusters the MH2 tibia, as well as that originally associated with the MH1 skeleton, with humans and other fossil hominin tibiae [Fig. 3, supporting online material (SOM) text S1 and S2, and table S1]. However, both tibiae are dominated by an extremely robust medial malleolus, unlike the more gracile medial malleolus in modern humans and other fossil hominins, including *Au. africanus* (figs. S4 and S6).

U.W. 88-98 is a right talus with a humanlike moderately wedged trochlea. The trochlear body is ungrooved mediolaterally, similar to the condition in modern humans and some hominins such as A.L. 288-1 (*Au. afarensis*) and unlike many deeply grooved tali from other Plio-Pleistocene hominins such as that of OH 8 (*Homo habilis*)

¹Institute for Human Evolution, University of the Witwatersrand, Post Office Wits, 2050 Wits, South Africa. ²Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Post Office Wits, 2050 Wits, South Africa. ³Department of Anthropology, Boston University, 232 Bay State Road, Boston, MA 02215, USA. ⁴School of Biomedical and Health Sciences, University of Western Sydney, Campbelltown, New South Wales 2560, Australia. ⁵Department of Anthropology, Indiana University, Bloomington, IN 47405, USA. ⁶Department of Evolutionary Anthropology, Box 90383, Duke University, Durham, NC 27708, USA. ⁷School of Geosciences, University of the Witwatersrand, Post Office Wits, 2050 Wits, South Africa.

*To whom correspondence should be addressed. E-mail: bernhard.zipfel@wits.ac.za