

Early Pleistocene third metacarpal from Kenya and the evolution of modern human-like hand morphology

Carol V. Ward^{a,1}, Matthew W. Tocheri^{b,c}, J. Michael Plavcan^d, Francis H. Brown^e, and Fredrick Kyalo Manthi^f

^aIntegrative Anatomy Program, Department of Pathology and Anatomical Sciences, University of Missouri, Columbia, MO 65212; ^bHuman Origins Program, Department of Anthropology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560; ^cCenter for the Advanced Study of Hominid Paleobiology, Department of Anthropology, The George Washington University, Washington, DC 20052; ^dDepartment of Anthropology, University of Arkansas, Fayetteville, AR 72701; ^eDepartment of Geology and Geophysics, University of Utah, Salt Lake City, UT 84112; and ^fDepartment of Earth Sciences, National Museums of Kenya, Nairobi, Kenya

Edited* by Erik Trinkaus, Washington University, St. Louis, MO, and approved November 13, 2013 (received for review August 23, 2013)

Despite discoveries of relatively complete hands from two early hominin species (*Ardipithecus ramidus* and *Australopithecus sediba*) and partial hands from another (*Australopithecus afarensis*), fundamental questions remain about the evolution of human-like hand anatomy and function. These questions are driven by the paucity of hand fossils in the hominin fossil record between 800,000 and 1.8 My old, a time interval well documented for the emergence and subsequent proliferation of Acheulian technology (shaped bifacial stone tools). Modern and Middle to Late Pleistocene humans share a suite of derived features in the thumb, wrist, and radial carpometacarpal joints that is noticeably absent in early hominins. Here we show that one of the most distinctive features of this suite in the Middle Pleistocene to recent human hand, the third metacarpal styloid process, was present ~1.42 Mya in an East African hominin from Kaitio, West Turkana, Kenya. This fossil thus provides the earliest unambiguous evidence for the evolution of a key shared derived characteristic of modern human and Neandertal hand morphology and suggests that the distinctive complex of radial carpometacarpal joint features in the human hand arose early in the evolution of the genus *Homo* and probably in *Homo erectus sensu lato*.

The fossil record suggests that early hominins were using and making stone tools long before the hand acquired the distinctive derived anatomy that is shared between modern humans and Neandertals (1–3). The earliest-known stone tools are 2.58 My old from Gona, Ethiopia (4), and contested stone tool cutmarks are present on 3.39 My-old bones from Dikika, Ethiopia (5); yet a complex of shared derived features that characterize the hands of modern humans and Neandertals is absent in Plio-Pleistocene hominins and not observed in the fossil record until around 800,000 y ago or later (1, 6–9).

Modern humans and Neandertals, and the 500,000-y-old hominins from Sima de los Huesos (Sierra de Atapuerca, Spain), attributed to *Homo heidelbergensis* (7, 8, 10), share a complex of derived morphological features of the hand that is reasonably linked to increased reliance on hand use for complex manipulatory tasks in comparison with earlier hominins and to extant and fossil great apes (1, 9). Most noticeable are the short fingers (relative to thumb length) and a robust thumb metacarpal (1). *Australopithecus afarensis*, *Australopithecus africanus*, and *Australopithecus sediba* also have short fingers (9, 11–14) (see ref. 15 for alternative view regarding *A. afarensis*), but with a conspicuously gracile pollical metacarpal (13–16). Robust thumb metacarpals are associated with relatively large and less-curved first carpometacarpal joint surfaces, facilitating the accommodation of large axial loads generated during strong precision and precision-pinch grasps (9, 17–20). This pattern continues through the radial carpal region with an enlarged scaphoid-trapezium joint that extends onto the scaphoid tubercle and a palmarly expanded trapezoid accompanied by a large and more palmarly placed trapezoid-capitate joint (2, 20). During forceful precision and power grips, the trapezium-trapezoid and trapezoid-capitate joints are maintained in maximum contact by the more prox-

imodistally oriented second metacarpal joints with the trapezium and capitate (20). The overall configuration of this derived joint complex is reasonably flexible in distributing compressive stresses while minimizing shear regardless of whether the thumb is compressed into the trapezium in an abducted, adducted, flexed, extended, or neutral posture (20).

The styloid process of the third metacarpal (Fig. 1A) is another distinctive feature of the modern human/Neandertal hand that is absent in all apes and other nonhuman primates, as well as Pliocene and Early Pleistocene hominins (11, 14, 16, 21–27). The dorsal extension of bone seen in a single specimen of *Au. africanus* (Stw 64) (28) is minimal and morphologically distinct from the styloid process of modern humans/Neandertals. It develops from a separate ossification center located on the dorsoradial corner of the third metacarpal base (22). In more than 90% of modern humans (29), all Neandertals (30), and *H. heidelbergensis* (7, 8), the fusion of this ossification center to the third metacarpal results in a projecting process of bone that articulates with a reciprocally beveled surface on the dorsodistal capitate proximally, with the second metacarpal radially, and sometimes with a small portion of the trapezoid (22). Alternatively, this cluster of cartilaginous precursor cells may occasionally fuse to the capitate (3.5% of cases) or trapezoid (0.5%) or present as a separate ossicle (2%) (29). However, in such cases, the resulting bony morphology indicates the presence of the styloid process (developmentally, at least).

The styloid process appears to be slightly smaller and the capitate-second metacarpal joint slightly less oblique than average in the Middle Pleistocene Atapuerca and the Neandertal

Significance

A newly discovered metacarpal from Kaitio, Kenya, dates to 1.42 Mya and provides evidence for the evolution of the modern human hand more than 600,000 y earlier than previously documented. This bone displays a styloid process, which is part of a distinctively human rearrangement of the wrist associated with enhanced hand function when making and using tools. Prior to this discovery, the first evidence of this anatomy was found only in post-*Homo erectus* archaic humans. This new find documents its appearance much earlier in time and suggests that an increased reliance on manipulatory behaviors indicated by the archeological record early in the Pleistocene selected for the modern human hand early in the evolution of the genus *Homo*.

Author contributions: C.V.W., M.W.T., J.M.P., F.H.B., and F.K.M. performed research; C.V.W., M.W.T., J.M.P., F.H.B., and F.K.M. analyzed data; and C.V.W., M.W.T., J.M.P., F.H.B., and F.K.M. wrote the paper.

The authors declare no conflict of interest.

*This Direct Submission article had a prearranged editor.

¹To whom correspondence should be addressed. E-mail: WardCV@missouri.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1316014110/-DCSupplemental.

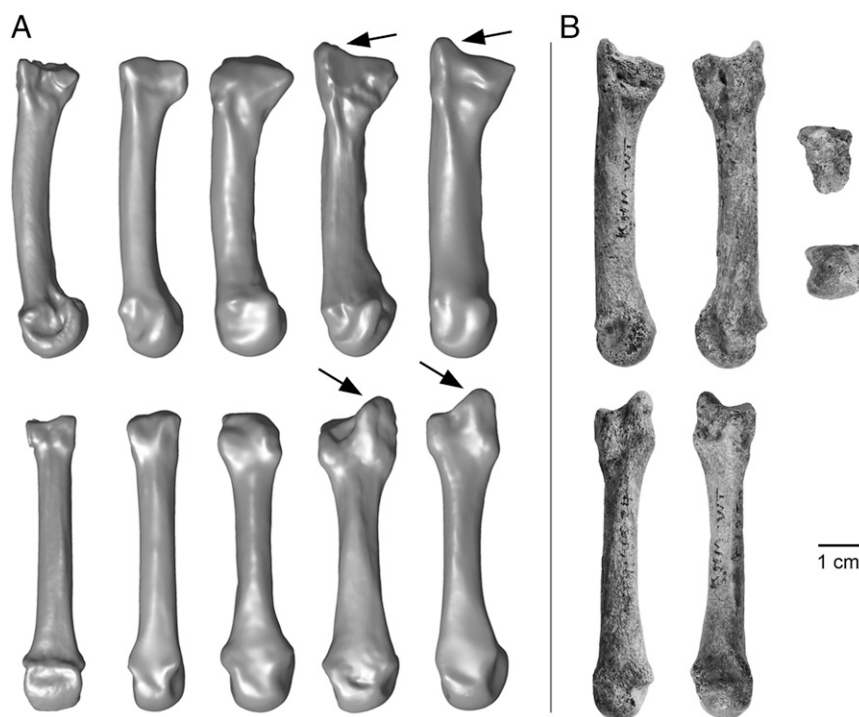


Fig. 1. (A) 3D scan images, from left to right, in radial (*Upper*) and dorsal view (*Lower*) of third metacarpals of a common chimpanzee, *Australopithecus afarensis* (A.L. 438-1d), *Australopithecus sediba* (MH 2), a Neandertal (Shanidar 4), and a modern human (USNM 380447). All are shown as from the right hand and scaled to approximately the same articular length. Note the distinctive styloid process (black arrows) is present only in the modern human and Neandertal specimens. (B) Photograph of KNM-WT 51260 in radial, ulnar, dorsal, and volar views (*Left*) and proximal and distal views (*Right*). Note the presence of a distinctly human-like styloid process.

samples compared with modern humans, but even so, the morphologies in these groups show substantial overlap with the modern human condition (7, 20, 30, 31). Moreover, the association between the developmental shift leading to a styloid process and the complex of derived radial wrist morphology documented in modern humans and Neandertals (1) suggests a reasonable functionally adaptive link with increased reliance on hand use for complex manipulatory tasks (9, 22). The third metacarpal styloid process probably also plays a role in stabilizing the intercarpal joints as well.

Thus, the third metacarpal styloid process along with these other features likely evolved together in response to selection for using the hand with strong grips involving the thumb in opposition to the other digits. When, where, in what order, and in what behavioral context these distinctive hand features evolved are key questions in the study of human evolution. Although a lack of a styloid process in an isolated hominin fossil is not evidence of a lack of an otherwise modern human/Neandertal-like wrist overall, the documentation of a third metacarpal styloid process in an early hominin would signify a major evolutionary modification to the hand relative to other known early hominins.

Results

In 2011, a team from the West Turkana Paleontology Project of the National Museums of Kenya recovered a well-preserved hominin right third metacarpal (KNM-WT 51260) from the site of Kaitio, located in northern Kenya west of Lake Turkana (Fig. 1B). Collected from a sequence of fine sandstones and siltstones in a small northern branch of Kaitio, KNM-WT 51260 lies at the level of the Lokapetamoi Tuff (Fig. S1 and Table S1) and dates to between 1.43 and 1.41 Ma or ~1.42 Mya (*SI Discussion*). KNM-WT 51260 is nearly complete, and its surface is only mildly weathered (Fig. 1B and Table S2). There are small amounts of abrasion along the margins of the articular surfaces, but they do

not obscure the contours of the bone. In all ways, this bone resembles that of a modern human in overall proportions and morphology.

The bone is long, falling within the upper range of modern human European and African American males (Fig. 2A). Most likely, KNM-WT 51260 belonged to a relatively tall individual, as metacarpal length correlates reasonably with arm length and thus with stature (32, 33). Applying stature regression equations developed for modern human males (32, 33) yields stature estimates of more than 167 cm. The presence of large individuals at this time period in the East African fossil record is not unprecedented, as comparably large individuals are known from Koobi Fora, Kenya, and Olduvai Gorge, Tanzania.

Most notable about KNM-WT 51260 is its prominent styloid process (Fig. 1B). The length of the KNM-WT 51260 styloid is close to the mean value of modern humans and among the longest of all known Late Pleistocene human specimens (Fig. 2B). The KNM-WT 51260 styloid process is unequivocally similar to that of modern humans and Neandertals and not intermediate between that of earlier hominins and later *Homo*. Relative to its length, the KNM-WT 51260 styloid is short compared with modern humans, as are those of Late Pleistocene humans (Fig. 2C, Fig. S2, and Table S3) (30). However, KNM-WT 51260 falls within the observed ranges for modern humans and Neandertals, both of which overlap considerably (Fig. 2C, Fig. S2, and Table S3), suggesting minimal functional differences among them (30, 34).

Discussion

Functionally, the human styloid process likely prevents hyperextension and subluxation of the third metacarpal base when large forces are directed from the palm toward the third metacarpal head (22). It also prevents the second metacarpal base from articulating with the capitate dorsally (22) and is associated

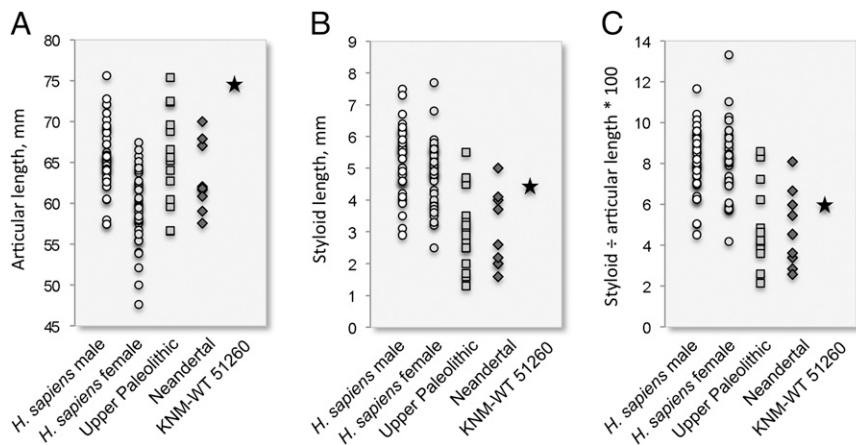


Fig. 2. Third metacarpal dimensions in modern human males ($n = 41$) and females ($n = 38$), Late Pleistocene *H. sapiens* ($n = 18$), Neandertals ($n = 10$), and KNM-WT 51260. (A) Articular length measured between center of proximal and distal joint surfaces. (B) Styloid process length measured as proximal projection from center of proximal articular surface. (C) Styloid process length expressed as a ratio of articular length. Neandertal and Upper Paleolithic *H. sapiens* have relatively shorter styloid processes than modern humans, although their ranges overlap. KNM-WT 51260 falls within the ranges of both modern and fossil specimens (Fig. S2, Table S3 and Table S4).

with derived features of the second metacarpal base and trapezoid (1, 9, 20). Thus, the styloid process most likely stabilizes the third carpometacarpal joint against mechanical loads generated when making and using tools (22, 28). It may also help stabilize the capitate (and possibly the second metacarpal base) from slipping dorsally while the second metacarpal base simultaneously stabilizes the palmar capitate-trapezoid-trapezium joints as the wrist experiences radioulnar compression during strong contraction of the thumb musculature (3, 20).

The earliest evidence of Acheulian tool technology (i.e., shaped bifacial stone tools) occurs at ~ 1.75 Mya at the nearby site of Kokiselei 4, West Turkana (35), and at Konso, Ethiopia (36). After this time, Acheulian sites become increasingly common in East Africa and elsewhere (37). The production of Acheulian tools themselves likely required considerable manual dexterity, and the emergence and subsequent proliferation of this technology may signal overall more complex manual manipulatory behaviors and/or cognitive function compared with those of other early hominins (35). No stone tools are directly associated with KNM-WT 51260, and a single morphological feature or even a set of features may not be tightly linked with a particular tool technology. However, the unambiguous presence of a third metacarpal styloid process in KNM-WT 51260 places a known derived reorganization of the wrist within a behavioral context of increased reliance on manual manipulation. For instance, the increasing regularity and abundance of Acheulian relative to Oldowan tools (37) likely signals that manual manipulation of not only stone tools, but a variety of objects, was an increasingly regular and important behavior for some hominins.

The taxonomy of KNM-WT 51260 must remain tentative, as species diagnoses of postcranial elements are typically based on direct associations with craniodental and/or mandibular remains (38, 39). However, given that the third metacarpal styloid process, a shared derived feature of modern humans, Neandertals, and *H. heidelbergensis*, is yet to be observed in the Pliocene or Early Pleistocene (6–9, 11, 14, 16, 21–27), KNM-WT 51260 most likely represents a species within the modern human-Neandertal clade and can be reasonably assigned to the genus *Homo*. At ~ 1.42 Mya in Kenya, the only species of *Homo* identified to date is *Homo erectus sensu lato* (39, 40), and KNM-WT 51260 probably represents this taxon. The only other hominin known from East Africa at this time is *Australopithecus (Paranthropus) boisei* (39). No comparable hand remains have been described for this taxon, but given that no other early hominin species shows

evidence of a styloid process or substantial reorganization of the radial portion of the wrist, it is unlikely that it would have been present in *A. (P.) boisei*.

KNM-WT 51260 provides the earliest unambiguous evidence for the evolution of a key shared derived characteristic of modern human and Neandertal hand morphology and suggests that the distinctive complex of radial carpometacarpal joint features in the human hand arose early in the evolution of the genus *Homo* and probably in *H. erectus sensu lato*. It also provides evidence that a major structural rearrangement of the hand occurred before the increased sophistication of Acheulian tools seen after 1.2 Mya (36). If indeed the production of early Acheulian tools signals an increased importance of and reliance on technology and manipulatory behaviors compared with those of earlier and other contemporary hominins, it is possible that some hominin populations of this geological age were in the process of evolving more modern human/Neandertal-like hand features. Therefore, this new third metacarpal provides an important basis with which to compare other fossils as they are discovered from comparable time periods to assess morphological diversity within the hominin hand and wrist in the early and middle Pleistocene.

Materials and Methods

The KNM-WT 51260 metacarpal was compared with a sample of modern human third metacarpals of known sex from the Terry Collection at the Smithsonian Institution's National Museum of Natural History ($n = 38$ females, $n = 41$ males) (Table S4), as well as a dataset from modern humans of unknown sex provided by E. Trinkaus (Washington University, St. Louis) ($n = 70$; Table S3). Data from 10 Neandertal and 18 Late Pleistocene *Homo sapiens* specimens also were provided by E. Trinkaus and W. A. Niewoehner (California State University, San Bernardino, CA) (Table S3). All specimens were measured with standard digital calipers to the nearest 0.1 mm (Tables S2 and S3). Allometry of bone and styloid lengths was evaluated using reduced major axis and standard least squares regression on natural logarithm-adjusted data. Groups were compared using ANOVA with the least-squares residuals with Bonferroni-adjusted post hoc contrasts (Fig. S2).

ACKNOWLEDGMENTS. We thank the crew of the West Turkana Paleontology Project for their hard work and dedication and the National Museums of Kenya and the Government of Kenya for permission to conduct research and support. We also thank Wesley A. Niewoehner and Erik Trinkaus for sharing data; the Smithsonian's National Museum of Natural History, the National Museums of Kenya, the University of the Witwatersrand, and the National Museum of Ethiopia for access to comparative collections; and Erik Trinkaus, Wes Niewoehner, Kristina Aldridge, and Casey Holliday for helpful discussions. We thank Lee Berger and Job Kibii for permission to include the scan

of MH2 in Fig. 1. This work was supported by the Leakey Foundation, the Palaeontological Scientific Trust of South Africa, the Wenner-Gren Foundation, the University of Missouri Research Council, the Smithsonian Scholarly

Studies Grant Program, and National Science Foundation Grant BCS06-21542 (to F.H.B., T. Cerling, and R. Bruhn). KNM-WT 51260 is housed at the National Museums of Kenya.

- Tocheri MW, Orr CM, Jacofsky MC, Marzke MW (2008) The evolutionary history of the hominin hand since the last common ancestor of *Pan* and *Homo*. *J Anat* 212(4): 544–562.
- Tocheri MW, et al. (2007) The primitive wrist of *Homo floresiensis* and its implications for hominin evolution. *Science* 317(5845):1743–1745.
- Orr CM, et al. (2013) New wrist bones of *Homo floresiensis* from Liang Bua (Flores, Indonesia). *J Hum Evol* 64(2):109–129.
- Semaw S, et al. (1997) 2.5-million-year-old stone tools from Gona, Ethiopia. *Nature* 385(6614):333–336.
- McPherron SP, et al. (2010) Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature* 466(7308):857–860.
- Lorenzo C, Arsuaga JL, Carretero JM (1999) Hand and foot remains from the Gran Dolina Early Pleistocene site (Sierra de Atapuerca, Spain). *J Hum Evol* 37(3–4):501–522.
- Lorenzo CM (2007) Evolución de la mano en los homínidos. Análisis morfológico de los fósiles de la Sierra de Atapuerca [Evolution of the hominid hand. Morphological analysis of the fossils from Sierra de Atapuerca]. PhD thesis (Univ Computense de Madrid, Madrid).
- Lorenzo CM, et al. (2012) Hands, laterality and language: Hand morphology in the Sima de los Huesos site (Sierra de Atapuerca, Spain). *Am J Phys Anthropol* 147(554): 195–196.
- Marzke MW (2013) Tool making, hand morphology and fossil hominins. *Philos Trans R Soc Lond B Biol Sci* 368(1630):20120414.
- Stringer C (2012) The status of *Homo heidelbergensis* (Schoetensack 1908). *Evol Anthropol* 21(3):101–107.
- Marzke MW (1983) Joint functions and grips of the *Australopithecus afarensis* hand, with special reference to the region of the capitate. *J Hum Evol* 12(2):197–211.
- Alba DM, Moyà-Solà S, Köhler M (2003) Morphological affinities of the *Australopithecus afarensis* hand on the basis of manual proportions and relative thumb length. *J Hum Evol* 44(2):225–254.
- Green DJ, Gordon AD (2008) Metacarpal proportions in *Australopithecus africanus*. *J Hum Evol* 54(5):705–719.
- Kivell TL, Kibii JM, Churchill SE, Schmid P, Berger LR (2011) *Australopithecus sediba* hand demonstrates mosaic evolution of locomotor and manipulative abilities. *Science* 333(6048):1411–1417.
- Rolian C, Gordon AD (2013) Reassessing manual proportions in *Australopithecus afarensis*. *Am J Phys Anthropol* 152(3):393–406.
- Bush ME, Lovejoy CO, Johanson DC, Coppens Y (1982) Hominid carpal, metacarpal and phalangeal bones recovered from the Hadar formation: 1974–1977 collections. *Am J Phys Anthropol* 57(4):651–678.
- Marzke MW (1997) Precision grips, hand morphology, and tools. *Am J Phys Anthropol* 102(1):91–110.
- Marzke MW, et al. (2010) Comparative 3D quantitative analyses of trapeziometacarpal joint surface curvatures among living catarrhines and fossil hominins. *Am J Phys Anthropol* 141(1):38–51.
- Trinkaus E (1989) Olduvai Hominid 7 trapezium metacarpal 1 articular morphology: contrasts with recent humans. *Am J Phys Anthropol* 80(4):411–416.
- Tocheri M (2007) Three-dimensional riddles of the radial wrist: Derived carpal and carpometacarpal joint morphology in the genus *Homo* and the implications for understanding the evolution of stone tool-related behaviors in hominins. PhD thesis (Arizona State Univ, Tempe, AZ).
- McHenry HM (1983) The capitate of *Australopithecus afarensis* and *A. africanus*. *Am J Phys Anthropol* 62(2):187–198.
- Marzke MW, Marzke RF (1987) The third metacarpal styloid process in humans: Origin and functions. *Am J Phys Anthropol* 73(4):415–431.
- Drapeau MS, Ward CV, Kimbel WH, Johanson DC, Rak Y (2005) Associated cranial and forelimb remains attributed to *Australopithecus afarensis* from Hadar, Ethiopia. *J Hum Evol* 48(6):593–642.
- Susman RL (1988) Hand of *Paranthropus robustus* from Member 1, Swartkrans: Fossil evidence for tool behavior. *Science* 240(4853):781–784.
- Ward CV, et al. (1999) South Turkwel: A new Pliocene hominid site in Kenya. *J Hum Evol* 36(1):69–95.
- Lovejoy CO, Simpson SW, White TD, Asfaw B, Suwa G (2009) Careful climbing in the Miocene: The forelimbs of *Ardipithecus ramidus* and humans are primitive. *Science* 326(5949):e1–e8, e78.
- Ward CV, Kimbel WH, Harmon EH, Johanson DC (2012) New postcranial fossils of *Australopithecus afarensis* from Hadar, Ethiopia (1990–2007). *J Hum Evol* 63(1):1–51.
- Ricklan DE (1987) Functional anatomy of the hand of *Australopithecus africanus*. *J Hum Evol* 16(7–8):643–664.
- O’Rahilly R (1953) A survey of carpal and tarsal anomalies. *J Bone Joint Surg Am* 35-A(3):626–642.
- Niewoehner WA (2006) Neanderthal hands in their proper perspective. *Neanderthals Revisited: New Approaches and Perspectives*, eds Hublin J-J, Harvati K, Harrison T (Springer, Dordrecht, The Netherlands), pp 157–190.
- Niewoehner WA, Weaver AH, Trinkaus E (1997) Neanderthal capitate-metacarpal articular morphology. *Am J Phys Anthropol* 103(2):219–233.
- Meadows L, Jantz RL (1992) Estimation of stature from metacarpal lengths. *J Forensic Sci* 37(1):147–154.
- Musgrave JH, Harneja NK (1978) The estimation of adult stature from metacarpal bone length. *Am J Phys Anthropol* 48(1):113–119.
- Trinkaus E, et al. (2010) Human remains from the Moravian Gravettian: Morphology and taphonomy of additional elements from Dolni Vestonice II and Pavlov I. *Int J Osteoarchaeol* 20(6):645–669.
- Lepre CJ, et al. (2011) An earlier origin for the Acheulian. *Nature* 477(7362):82–85.
- Beyene Y, et al. (2013) The characteristics and chronology of the earliest Acheulean at Konso, Ethiopia. *Proc Natl Acad Sci USA* 110(5):1584–1591.
- Klein RG (1999) *The Human Career* (Univ of Chicago Press, Chicago).
- Leakey LSB, Tobias PV, Napier JR (1964) A new species of the genus *Homo* from Olduvai Gorge. *Nature* 202:7–9.
- Wood B (1991) *Koobi Fora Research Project Volume 4: Hominid Cranial Remains* (Clarendon Press, Oxford, UK).
- Simpson SW, et al. (2008) A female *Homo erectus* pelvis from Gona, Ethiopia. *Science* 322(5904):1089–1092.