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

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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. 1*A*) 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 dorsodistoradial 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*.
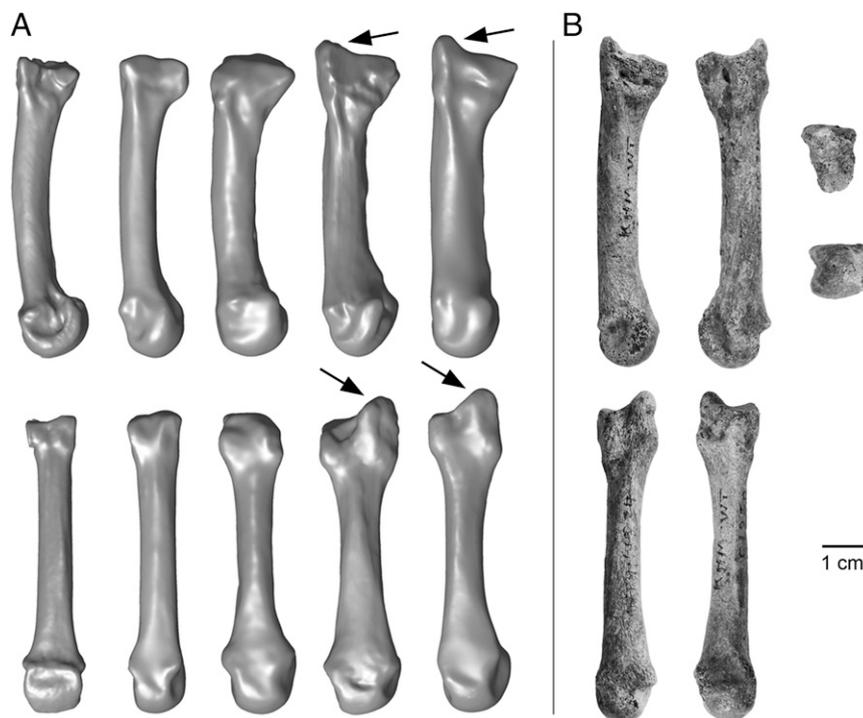
ANTHROPOLOGY

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. 1*B*). 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. 1*B* 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. 2*A*). 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. 1*B*). 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. 2*B*). 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. 2*C*, 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. 2*C*, 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
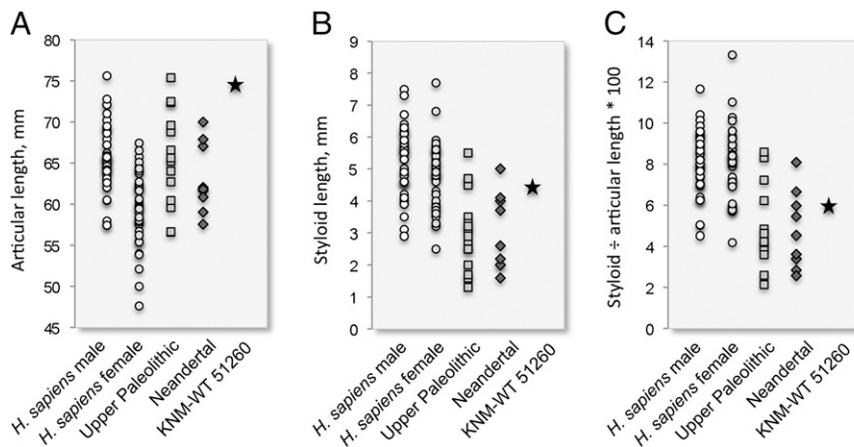
Fig. 2. Third metacarpal dimensions in modern human males (*n* = 41) and females (*n* = 38), Late Pleistocene *H. sapiens* (*n* = 18), Neandertals (*n* = 10), and KNM-WT 51260. (*A*) Articular length measured between center of proximal and distal joint surfaces. (*B*) Styloid process length measured 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 Bernadino, 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).

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