

New fossils from Koobi Fora in northern Kenya confirm taxonomic diversity in early *Homo*

Meave G. Leakey^{1,2}, Fred Spoor^{3,4}, M. Christopher Dean⁴, Craig S. Feibel⁵, Susan C. Antón⁶, Christopher Kiarie¹ & Louise N. Leakey^{1,2}

Since its discovery in 1972 (ref. 1), the cranium KNM-ER 1470 has been at the centre of the debate over the number of species of early *Homo* present in the early Pleistocene epoch² of eastern Africa. KNM-ER 1470 stands out among other specimens attributed to early *Homo* because of its larger size, and its flat and subnasally orthognathic face with anteriorly placed maxillary zygomatic roots³. This singular morphology and the incomplete preservation of the fossil have led to different views as to whether KNM-ER 1470 can be accommodated within a single species of early *Homo* that is highly variable because of sexual, geographical and temporal factors^{4–9}, or whether it provides evidence of species diversity marked by differences in cranial size and facial or masticatory adaptation^{3,10–20}. Here we report on three newly discovered fossils, aged between 1.78 and 1.95 million years (Myr) old, that clarify the anatomy and taxonomic status of KNM-ER 1470. KNM-ER 62000, a well-preserved face of a late juvenile hominin, closely resembles KNM-ER 1470 but is notably smaller. It preserves previously unknown morphology, including moderately sized, mesiodistally long postcanine teeth. The nearly complete mandible KNM-ER 60000 and mandibular fragment KNM-ER 62003 have a dental arcade that is short anteroposteriorly and flat across the front, with small incisors; these features are consistent with the arcade morphology of KNM-ER 1470 and KNM-ER 62000. The new fossils confirm the presence of two contemporary species of early *Homo*, in addition to *Homo erectus*, in the early Pleistocene of eastern Africa.

KNM-ER 62000, with an estimated geological age of 1.91 to 1.95 Myr old (Fig. 1; metrics in Supplementary Note 1), consists of the maxillae, the palatine bones and the right zygomatic bone of a late juvenile. On the left, the lateral half of the maxillary body, the vertical plate of the palatine bone and the temporal process of the zygomatic bone are

missing. The lateral half of the right infra-orbital area is weathered, and the left alveolar process shows some medial displacement and damage to the lateral surface. The preserved teeth include the right P⁴, both M¹s and M²s, and the unerupted crown of the right M³, exposed in its crypt above the M². The occlusal surface of the right M¹ is missing, whereas the left M¹ has a partially damaged cervical margin. In its dental development, KNM-ER 62000 most closely resembles a 13- or 14-year-old modern human. But in the hominin fossil record, at a time when development was quicker, a close match is KNM-WT 15000, whose chronological age has been estimated at approximately 8 years (ref. 21; Supplementary Note 2).

In facial size, KNM-ER 62000 is similar to smaller specimens attributed to early *Homo* and *H. erectus* (for example, KNM-ER 1813 and D2700). The preserved tooth crowns are much smaller than in *Paranthropus boisei*, larger than in eastern African *H. erectus* and most similar in size to early *Homo* (Supplementary Notes 1 and 3). In shape they stand out by being relatively long mesiodistally, with the molars being rhomboidal in outline. The P⁴ is two-rooted with an incompletely divided buccal root; the P³ alveoli indicate a similar morphology. The predicted adult palate shape is relatively shorter than in australopiths (Supplementary Note 4). The alveolar process has parallel postcanine rows, showing the greatest breadth lingually at P⁴ and buccally at M¹.

The facial morphology of KNM-ER 62000 is derived compared with *Australopithecus* and *Paranthropus*, and its affinities are with the genus *Homo*. It shows striking similarity to KNM-ER 1470 (Supplementary Note 5), sharing many of the features that single out the latter as unique among specimens of early *Homo*³. A well-defined P³ jugum marks the 'corner' between the lateral and anterior surfaces of the maxillary alveolar process, so that the canine alveoli are fully part of the anterior row. The incisor alveoli are narrow mesiodistally for early



Figure 1 | The KNM-ER 62000 face. **a–d**, Anterior (**a**), right lateral (**b**), inferior (**c**) and superior views (**d**) of the KNM-ER 62000 face. Scale bar, 3 cm.

¹Turkana Basin Institute, PO Box 24926, Nairobi 00502, Kenya. ²Department of Anthropology, Stony Brook University, Stony Brook, New York 11794, USA. ³Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig 04103, Germany. ⁴Department of Cell and Developmental Biology, University College London, London WC1E 6BT, UK. ⁵Department of Earth and Planetary Sciences, and Department of Anthropology, Rutgers University, Piscataway, New Jersey 08854-8066, USA. ⁶Department of Anthropology, New York University, New York, New York 10003, USA.

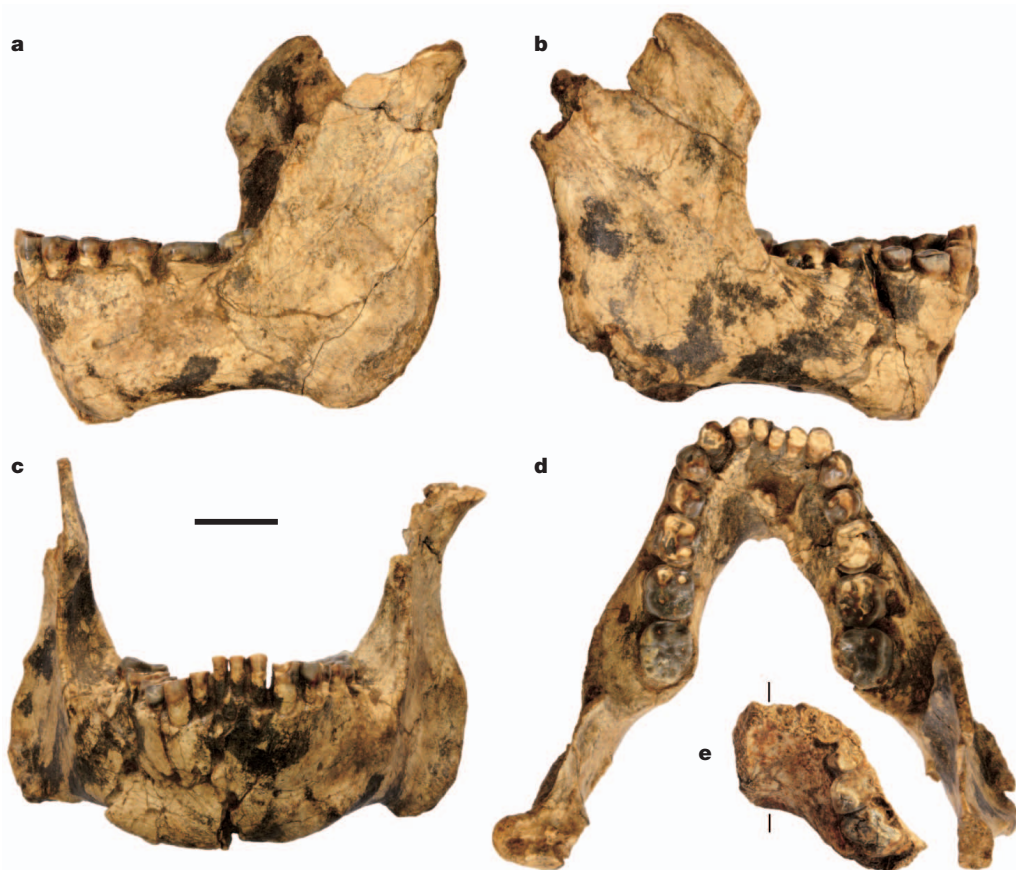


Figure 2 | The KNM-ER 60000 mandible and KNM-ER 62003 mandible fragment. a–d, Left lateral (a), right lateral (b), anterior (c) and occlusal (d) views of KNM-ER 60000. e, Occlusal view of KNM-ER 62003, with lines marking the mid-sagittal plane aligned to that of KNM-ER 60000. Scale bar, 3 cm.

Homo, show little anterior projection beyond the bicanine line, and the overlying subnasal area is transversely flat (Fig. 1c–d). In lateral view, a particularly straight facial profile is marked by a highly orthognathic nasoalveolar clivus (Fig. 1b; Supplementary Notes 5e and 6b, e). There is a distinct nasal sill, and the lateral nasal margins are rounded inferiorly, but mildly everted superiorly, implying some projection of the nasal bridge. The anterior surface of the zygomatic process is positioned between P^3 and P^4 . The midface is transversely flat with an infra-orbital area that slopes antero-inferiorly. The infraorbital foramen is placed medially and close to the orbital margin. The preserved inter-orbital morphology indicates that the nasal cavity was tall. Bi-orbital to maxillo-alveolar breadth proportions indicate that the upper face is distinctly narrow (Supplementary Note 1).

KNM-ER 60000 is a nearly complete adult mandible with an estimated geological age of 1.78 to 1.87 Myr old (Fig. 2; metrics in Supplementary Note 7). The well-preserved left side lacks only the anterior part of the ramus, including the coronoid process, but this area is well-preserved on the right side, facilitating full reconstruction (Supplementary Note 8). The right side of the corpus shows post-mortem deformation. The well-worn dentition with fully formed roots is complete through M_3 . The anterior arcade is flat across the front because narrow and short-rooted incisors sit medial, but barely anterior to the canines. The labiolingual incisor crown dimensions fall below the range observed for most eastern African *Homo* and *Paranthropus*. The P_3 to M_2 crowns are small for *Paranthropus*, and their sizes are below or at the low end of the size range for early *Homo*,

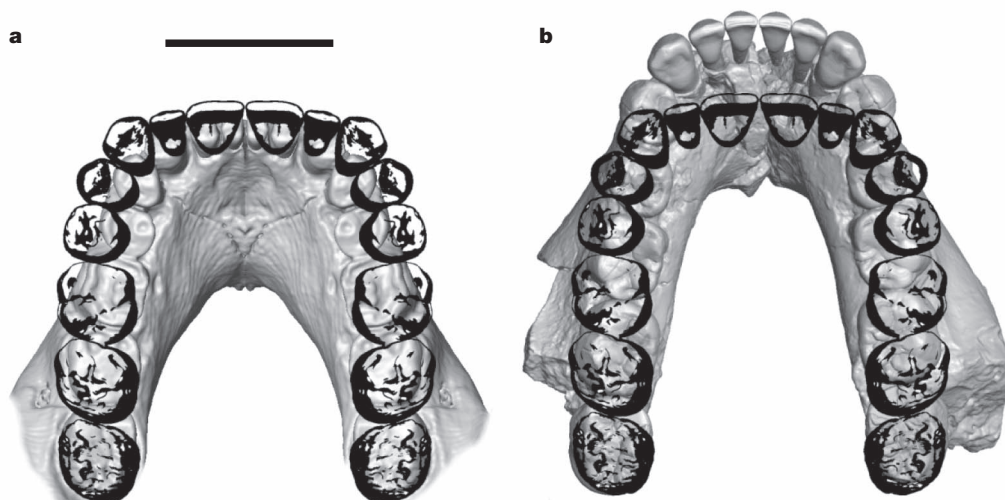
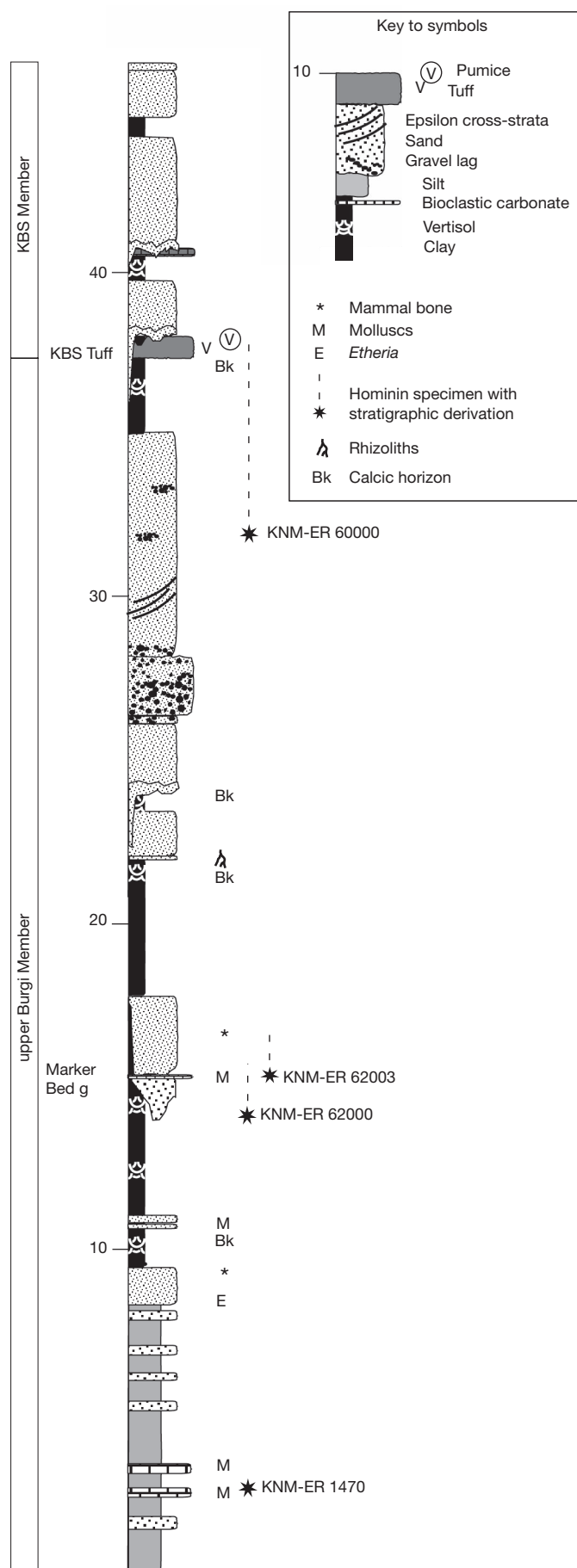


Figure 3 | Dental arcades compared. The reconstructed upper arcade of KNM-ER 62000 (outlined in black) occluded with the reconstructed lower arcades of KNM-ER 60000 (a) and KNM-ER 1802 (b), showing a good match with KNM-ER 60000 but not with KNM-ER 1802. Scale bar, 3 cm. See Supplementary Note 10 for details.



particularly their small mesiodistal dimensions (Supplementary Note 9). However, the M_3 dimensions are well within the range of early *Homo*, and the molars increase in size from M_1 to M_3 . Both M_2 and M_3 show a C7 cusp. Both premolars have distal and mesial roots that are compressed mesiodistally and incompletely separated by a deep lingual groove. The tall anterior corpus has a mandibular incisure and a labially positioned symphyseal tuber. The anterior symphyseal surface makes an angle of 70° with the alveolar margin. Lingually, an obliquely oriented post-incisive plane precedes a roughened genioglossus attachment, but there are no separate superior and inferior transverse tori. The tall but relatively narrow corpus has a single mental foramen below P_4 , and a strongly marked marginal torus with striae platysmatica that join distinct tubercles at C/P_3 and M_1/M_2 . The broad, tall ramus rises perpendicular to the occlusal plane and its root at M_2 defines a wide extramolar sulcus (10 mm). The notch between the condyle and the taller coronoid process is shallow; the latter markedly projects anteriorly (above M_2/M_3). The gonial angle is 100° ; this region is everted and extends below the corpus base causing a 'notched' appearance in lateral view. Muscle attachments are distinct: the masseter formed a thick everted flange infero-posteriorly and a clear fossa for its deep head; the marked medial pterygoid insertions extend to the mylohyoid line, which is partially bridged on the left. The mandibular foramen sits high above the occlusal plane.

KNM-ER 62003, with an estimated geological age of 1.90 to 1.95 Myr old, is a mandible fragment from just left of the midline to the distal right M_1 (Fig. 2; metrics in Supplementary Note 7). The midline inferior border is missing. The roots of the left I_1 to right M_1 are present, and the right P_3 to M_1 retain parts of their crown. Complete roots, thick cortical bone and substantial occlusal wear indicate that it is an adult or late sub-adult. KNM-ER 62003 shares the following features with KNM-ER 60000: a flat anterior arcade with short and narrow incisor roots, small premolars, similar symphysis orientation (the angle of the anterior surface is approximately 70°), an oblique post-incisive plane, and similar mental foramen and marginal torus positions. The marginal torus is less strongly developed in KNM-ER 62003 than in KNM-ER 60000, and a well-developed genial fossa delineates a superior transverse torus.

We attribute these mandibles to *Homo* rather than *Paranthropus* based on their small molars and premolars, and tall but mediolaterally narrow corpora. Despite similarities in P_3 – M_2 size, KNM-ER 60000 differs from *H. erectus* as it has a combination of smaller anterior teeth, a larger M_3 , a broader extramolar sulcus and, compared with the few known relatively complete adult and late juvenile mandibles (KNM-ER 992, KNM-WT 15000, D2735 and D2600), larger bigonial and bicondylar breadths for dental arcade size.

The discovery of a fossil (KNM-ER 62000) that is broadly contemporary with and very similar in shape to KNM-ER 1470, makes it likely that the two specimens do indeed represent a distinct taxon, separate from morphologically more generalized craniofacial specimens, such as KNM-ER 1813 and OH 65 (Supplementary Note 5). Importantly, although KNM-ER 1470 and KNM-ER 62000 span the full known size-range of early *Homo*, they share the same distinctive facial morphology, suggesting that allometry or sexual dimorphism^{5,6,8} are unlikely to be factors that underlie the differences in early *Homo* facial architecture.

The palate and teeth of KNM-ER 62000 make it possible to infer aspects of the mandible that occluded with the distinctive upper dental arcade of this specimen and KNM-ER 1470 (Fig. 3; Supplementary Note 10). KNM-ER 1802 is the mandible invariably grouped with KNM-ER 1470 (refs 3, 10, 12, 14–16), and is key to making associations with other specimens^{7,22}. However, when reconstructed it seems to be an unlikely match for KNM-ER 1470 and KNM-ER 62000, as it has a long dental arcade and an anteriorly arched incisor row. Instead, the new specimens

Figure 4 | A composite section of the Karari Ridge strata. The stratigraphic context of the three hominin fossils are shown (detailed individual sections are provided in Supplementary Note 13). The thickness of strata is given in metres.

KNM-ER 60000 and KNM-ER 62003, as well as mandibles KNM-ER 1482 and KNM-ER 1801, are a better match for KNM-ER 1470 and KNM-ER 62000 because of their shorter arcade, including a short pre-molar row, and a short, non-projecting incisor row (Supplementary Notes 10 and 11). Moreover, the pronounced anterior projection of the ramus of KNM-ER 60000 can be comfortably accommodated by the anteriorly placed zygomatic processes seen in the two crania. The species name of KNM-ER 1470, and of its associated specimens, depends on whether OH 7, the type specimen of *H. habilis*, is part of this group (see, for example, refs 15, 16, 19 for opposing views). If OH 7 is not part of this group, as suggested here by mandibular tooth shape (Supplementary Note 9) and perhaps by a photographic reconstruction of the mandible⁶, the name *H. rudolfensis* is available²³. However, we urge caution with respect to decisions on nomenclature until OH 7, which has extensive and complex taphonomic distortion, is studied further and its association with other fossils can be evaluated better.

KNM-ER 1470 provides the key evidence in studies recognizing two species of eastern African early *Homo*^{3,10–20}. Specimens have been grouped with KNM-ER 1470 mostly on the basis of a relatively large cranial size or inferred masticatory specialization^{3,12,15,16,19,20}, because it has no tooth crowns preserved, and because before the discovery of KNM-ER 62000 no other fossil shared its distinctive facial morphology. The new evidence presented here is not only consistent with two distinct craniofacial morphs but also with two mandibular morphs. One of these, best represented by KNM-ER 60000, seems to be associated with the species to which KNM-ER 1470 and KNM-ER 62000 belong. The three new specimens will greatly aid the reassessment of the systematics and early radiation of the genus *Homo*.

METHODS SUMMARY

Details of the new fossils are given in Supplementary Note 12. Their stratigraphic context within the Koobi Fora Formation²⁴ is well constrained (Fig. 4; Supplementary Notes 13), and their age derives from two temporal markers, the KBS Tuff and the Olduvai Subchron. The KBS Tuff has been isotopically dated to 1.87 Myr ago (ref. 25) and it outcrops within each of the stratigraphic sequences discussed here (Fig. 4). The base of the Olduvai Subchron, dated to 1.95 Myr ago (ref. 26), has recently been documented just to the north²⁷ and south²⁸ of these sections. KNM-ER 62003 was recovered from the lowermost upper Burgi Member in Area 130, just above a prominent intra-formational conglomerate (marker bed g), 14 m below the KBS Tuff, and very close to the projected level of the base of the Olduvai Subchron. Estimates of its age, based on stratigraphic scaling, give an age of 1.90 to 1.95 Myr old. KNM-ER 62000 was discovered in Area 131, in a comparable stratigraphic position 17 m below the KBS Tuff, deriving from a channel sand body that locally erodes through the same marker bed g. Its estimated age is 1.91 to 1.95 Myr old. KNM-ER 60000 was recovered in Area 105 from a broken sandstone block that derives from just above the KBS Tuff, and is therefore younger than 1.87 Myr old. On the basis of the local sections in Area 105, it is difficult to put a minimum age on the fossil, but magnetic polarity stratigraphy for that section²⁹ indicates that the fossil must lie within the Olduvai Subchron, and therefore cannot be younger than 1.78 Myr old²⁶. Finally, KNM-ER 1470, recovered from Area 131 and derived from 36 m below the KBS Tuff, now has an estimated age of 2.03 Myr old³⁰.

Received 25 March; accepted 12 June 2012.

1. Leakey, R. E. F. Evidence of an advanced Plio-Pleistocene hominid from East Rudolf, Kenya. *Nature* **242**, 447–450 (1973).
2. Gibbard, P. L. *et al.* Formal ratification of the quaternary system/period and the Pleistocene series/epoch with a base at 2.58 Ma. *J. Quaternary Sci.* **25**, 96–102 (2010).
3. Wood, B. *Koobi Fora Research Project Vol. 4: Hominid Cranial Remains* (Clarendon, 1991).
4. Howell, F. C. in *Evolution of African Mammals* (eds Maglio, V. J. & Cooke, H. B. S.) 154–248 (Harvard Univ. Press, 1978).
5. Johanson, D. C. *et al.* New partial skeleton of *Homo habilis* from Olduvai Gorge. *Nature* **327**, 205–209 (1987).
6. Tobias, P. V. *Olduvai Gorge Volume 4: The Skulls and Endocasts of Homo habilis*. (Cambridge Univ. Press, 1991).
7. Suwa, G., White, T. D. & Howell, F. C. Mandibular post-canine dentition from the Shungura Formation, Ethiopia: c row morphology, taxonomic allocation, and Plio-Pleistocene hominid evolution. *Am. J. Phys. Anthropol.* **101**, 247–282 (1996).
8. Miller, J. M. Craniofacial variation in *Homo habilis*: an analysis of the evidence for multiple species. *Am. J. Phys. Anthropol.* **112**, 103–128 (2000).

9. Suwa, G. *et al.* Early Pleistocene *Homo erectus* fossils from Konso, southern Ethiopia. *Anthropol. Sci.* **115**, 133–151 (2007).
10. Leakey, R. E. F. Further evidence of Lower Pleistocene hominids from East Rudolf, North Kenya, 1973. *Nature* **248**, 653–656 (1974).
11. Wood, B. A. in *Ancestors: The Hard Evidence* (ed. Delson, E.) 206–214 (Alan R. Liss, 1985).
12. Stringer, C. B. in *Major Topics in Primate and Human Evolution* (eds Wood, B., Martin, L. & Andrews, P.) 266–294 (Cambridge Univ. Press, 1986).
13. Lieberman, D. E., Pilbeam, D. R. & Wood, B. A. A probabilistic approach to the problem of sexual dimorphism in *Homo habilis*: A comparison of KNM-ER 1470 and KNM-ER 1813. *J. Hum. Evol.* **17**, 503–511 (1988).
14. Groves, C. P. *A Theory of Human and Primate Evolution* (Clarendon, 1989).
15. Wood, B. Origin and evolution of the genus *Homo*. *Nature* **355**, 783–790 (1992).
16. Rightmire, G. P. Variation among early *Homo* crania from Olduvai Gorge and the Koobi Fora region. *Am. J. Phys. Anthropol.* **90**, 1–33 (1993).
17. Kramer, A., Donnelly, S. M., Kidder, J. H., Ousley, S. D. & Olah, S. M. Craniometric variation in large-bodied hominids: testing the single-species hypothesis for *Homo habilis*. *J. Hum. Evol.* **29**, 443–462 (1995).
18. Kimbel, W. H., Johanson, D. C. & Rak, Y. Systematic assessment of a maxilla of *Homo* from Hadar, Ethiopia. *Am. J. Phys. Anthropol.* **103**, 235–262 (1997).
19. Blumenshine, R. J. *et al.* Late Pliocene *Homo* and hominid land use from western Olduvai Gorge, Tanzania. *Science* **299**, 1217–1221 (2003).
20. Clarke, R. J. A *Homo habilis* maxilla and other newly-discovered hominid fossils from Olduvai Gorge, Tanzania. *J. Hum. Evol.* <http://dx.doi.org/10.1016/j.jhevol.2011.11.007> (4 May 2012).
21. Dean, M. C. & Smith, B. H. in *The First Humans: Origin of the Genus Homo* (eds Grine, F. E., Fleagle, J. G. & Leakey, R. E.) 101–120 (Springer, 2009).
22. Bromage, T. G., Schrenk, F. & Zonneveld, F. W. Paleoanthropology of the Malawi Rift: An early hominid mandible from the Chiwondo Beds, northern Malawi. *J. Hum. Evol.* **28**, 71–108 (1995).
23. Wood, B. '*Homo rudolfensis*' Alexeev, 1986 – fact or phantom? *J. Hum. Evol.* **36**, 115–118 (1999).
24. Brown, F. H. & Feibel, C. S. Revision of lithostratigraphic nomenclature in the Koobi Fora region, Kenya. *J. Geol. Soc. Lond.* **143**, 297–310 (1986).
25. McDougall, I. & Brown, F. H. Precise ⁴⁰Ar/³⁹Ar geochronology for the upper Koobi Fora Formation, Turkana Basin, northern Kenya. *J. Geol. Soc. Lond.* **163**, 205–220 (2006).
26. Lourens, L., Hilgen, F., Shackleton, N. J., Laskar, J. & Wilson, D. in *A Geologic Time Scale* (eds Gradstein, F., Ogg, J. & Smith, A.) 409–440 (Cambridge Univ. Press, 2004).
27. Braun, D. R. *et al.* Early hominid diet included diverse terrestrial and aquatic animals 1.95 Ma in East Turkana, Kenya. *Proc. Natl Acad. Sci. USA* **107**, 10002–10007 (2010).
28. Joordens, J. C. A. *et al.* An astronomically-tuned climate framework for hominids in the Turkana Basin. *Earth Planet. Sci. Lett.* **307**, 1–8 (2011).
29. Brock, A., Isaac, G. & L.L. Paleomagnetic stratigraphy and chronology of hominid-bearing sediments east of Lake Rudolf, Kenya. *Nature* **247**, 344–348 (1974).
30. McDougall, I. *et al.* New single crystal ⁴⁰Ar/³⁹Ar ages improve time scale for deposition of the Omo Group, Omo–Turkana Basin, East Africa. *J. Geol. Soc. Lond.* **169**, 213–226 (2012).

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

Acknowledgements We thank the Governments of Kenya and Tanzania for permission to carry out this research, the Kenya Wildlife Service for permission to work in the Sibiloi National Park, the National Museums of Kenya and the National Museum of Tanzania for access to specimens in their care, and the Turkana Basin Institute for support. The National Geographic Society, the Leakey Foundation and the Max Planck Society funded fieldwork or laboratory studies. Many people helped us with this research, including N. Adamali, R. Blumenshine, C. Boesch, F. Brown, P. Gunz, J. J. Hublin, W. Kimbel, K. Kupczik, R. Leakey, C. Lepre, D. Lieberman, P. Mserwa, R. Odoyo, R. Quinn, P. Rightmire, L. Schroeder, U. Schwarz, M. Skinner, H. Temming, A. Winzer and B. Wood. Curatorial assistance was given by A. Kweka, F. Manthi, E. Mbua, M. Muungu and J. Thiringi. KNM-ER 60000 was discovered by C. Nyete, KNM-ER 62000 by D. Elgite and KNM-ER 2003 by R. Moru. We particularly thank the Koobi Fora Research Project field crew: A. Aike, S. Aila, D. Elgite, M. Kirinya, D. Gidole, O. Kyalo, A. Longaye, A. Lawri, E. Linga, J. Lonyericho, S. Lomeiku, D. Muema, A. Moru, R. Moru, S. Muge, C. Nyete, L. Nzuve, H. Sale and A. Sharamo whose fieldwork led to the discovery of these specimens, and camp managers J. Mutuku and T. Ngundo. H. Churcher, J. Coreth, A. Hammond, J. LaCarrubba, F. Kirera, C. Lepre, M. Noback, R. Quinn, M. Skinner, I. Wallace and S. Wright participated in one or more of the 2007, 2008 or 2009 field expeditions when these specimens were discovered. We are grateful to F. and J. Pinto, W. Phillips, M. Hettwer, P. Sylvester, H. Buchi, N. Seligman, E. von Simpson, J. Doerr and B. and J. Chelberg for their financial support of this fieldwork.

Author Contributions M.G.L. and L.N.L. directed the field research, in which C.S.F. and F.S. participated. C.K. and F.S. prepared the hominid fossils, F.S. and M.C.D. made the virtual reconstructions, and C.S.F. studied the geological context. M.G.L., F.S., M.C.D., S.C.A. and L.N.L. made comparative observations and carried out analyses. F.S. took the lead in writing the paper, and S.C.A., M.C.D. and C.S.F. contributed.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of this article at www.nature.com/nature. Correspondence and requests for materials should be addressed to M.G.L. (meaveleakey@gmail.com) or F.S. (f.spoor@eva.mpg.de).