The predentary is hooked dorsally and has a bevelled edge as in basal neoceratopsians. The dentary is massive and bears a small ventral flange. As in neoceratopsians, the surangular bulges laterally, but it lacks the lateral wall to the glenoid present in other members of the group. The retroarticular process is short.

Weak, incipient primary ridges are present on the cheek teeth of the holotype, and are less pronounced in the referred juvenile specimen. Where visible, the roots appear to lack lateral grooves, and the eruption pattern in the dentary is not as rigidly determinate as in neoceratopsians although more ordered than in psittacosaurs and *Chaoyangsaurus*[12]. Cingula are not developed near the crown bases, and worn teeth display oblique wear facets as in primitive ornithischians.

The referred juvenile skull is about half as long as the holotype. It differs from the holotype of *Liaoceratops* in features characteristic of juvenile ceratopsians[9,13,14], including fewer teeth, vaulted frontals, a weaker jugal horn and a proportionately shorter and narrower frill. Similar differences are observed in the growth series of other basal ceratopsians such as *Psittacosaurus*[15] and *Protoceratops*[9]. Comparison between the juvenile and holotype specimens shows that the squamosal contribution to the frill margin increases allometrically with growth and the squamosals form half the frill margin in the adult. This contrasts with *Protoceratops*, in which the squamosal contribution to the frill decreases proportionately throughout ontogeny.
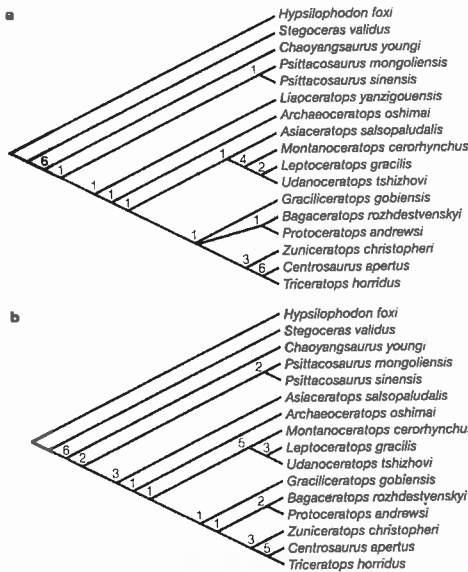

Figure 3 Phylogenetic relationships among ceratopsians. **a,** A strict consensus cladogram of two most-parsimonious trees (200 steps; consistency index, 0.69; retention index, 0.78) derived from analysis of our data set (based in part on refs 4, 17, 18) placing *Liaoceratops* as the most basal neoceratopsian. Integers above internodes are decay indices. The strict and Adam's consensus trees have identical topologies. **b,** Single most-parsimonious cladogram (190 steps; consistency index, 0.73; retention index, 0.81) based on phylogenetic analysis of the same data set with *Liaoceratops yanzigouensis* excluded. We note the different phylogenetic positions of *Archaeoceratops* and *Asiaceratops* and higher decay indices relative to a after exclusion of *Liaoceratops yanzigouensis*.

Discussion. Cladistic analysis (see Supplementary Information) posits *Liaoceratops* as the most basal neoceratopsian (Fig. 3a). Derived characters shared with other neoceratopsians include the lateral processes of the rostral, an expanded frill with squamosal participation, a spherical occipital condyle, a deep temporal bar, a triangular postorbital and laterally convex surangular. *Liaoceratops* still retains a number of primitive ceratopsian characters, however. For example, the quadratojugal is flat rather than transversely expanded, the rostral is unkeeled, an epijugal is absent, and the maxillary teeth have weakly developed primary ridges and oblique occlusion angles. Indeed, some character states in *Liaoceratops* are intermediate between those of psittacosaurids and higher neoceratopsians, documenting an incremental evolution for certain neoceratopsian diagnostic characters.

We note that *Liaoceratops* also exhibits characters traditionally used to diagnose either psittacosaurids or more exclusive clades within Neoceratopsia. For example, *Liaoceratops* bears a weak ventral flange on the dentary and has an infratemporal fenestra that is wider ventrally, as in some, but not all, *Psittacosaurus* species[16]. Analysis of the data set with *Liaoceratops* excluded results in a decrease in tree length of ten steps, and a concomitant increase in the support for nodes near the base of Ceratopsia, including Psittacosauridae, Neoceratopsia and the clade that unites them (Fig. 3b). The mosaic character distribution in *Liaoceratops* introduces homoplasy to the data, which strips away some traditional psittacosaurid synapomorphies, and repolarizes certain characters within Neoceratopsia, causing a reversal in the phylogenetic order between *Asiaceratops* and *Archaeoceratops*.

Liaoceratops is the oldest known neoceratopsian, and represents a significant stratigraphic range extension for this clade, whose other members are Albian[4] or younger. *Liaoceratops* co-occurs with specimens of *Psittacosaurus* in the lowermost part of the Yixian Formation, whereas *Chaoyangsaurus* is known from the underlying, probably Late Jurassic[12] Tuchengzi Formation. The basal ceratopsian split between psittacosaurids and neoceratopsians occurred no later than the earliest part of the Cretaceous, and both lineages appear to have acquired some of their diagnostic features rapidly within the latest part of the Jurassic and possibly the earliest part of the Cretaceous. The combination of these temporal constraints with the previously unsuspected mosaic evolution introduced by *Liaoceratops* indicates a more rapid rate of character evolution at the base of Ceratopsia and its major subclades than was hitherto recognized[4]. □

1. Dodson, P. & Currie, P. in *The Dinosauria* (eds Weishampel, D. B., Dodson, P. & Osmólska, H.) 593–618 (Univ. California Press, Berkeley, 1990).
2. Dodson, P. in *Encyclopedia of Dinosaurs* (eds Currie, P. J. & Padian, K.) 473–478 (Academic, San Diego, 1997).
3. Sereno, P. The origin and evolution of dinosaurs. *Annu. Rev. Earth Planet. Sci.* 25, 234–256 (1997).
4. Sereno, P. in *The Age of Dinosaurs in Russia and Mongolia* (eds Benton, M. J., Shishkin, M. A., Unwin, D. M. & Kurochkin, E. N.) 480–516 (Cambridge Univ. Press, New York, 2000).
5. Swisher, C. C. *et al.* Further support for a Cretaceous age for the feathered-dinosaur beds of Liaoning, China: new ⁴⁰Ar/³⁹Ar dating of the Yixian and Tuchengzi Formations. *Chinese Sci. Bull.* 46, 2009–2013 (2001).
6. Xu, X., Wang, X.-L. & You, H.-L. A primitive ornithopod form the Early Cretaceous Yixian Formation of Liaoning. *Vertebrata PalAsiatica* 38, 318–325 (2000).
7. Lo, C.-H., Chen, P.-J., Tsou, T.-Y., Sun, S.-S. & Lee, C. Y. ⁴⁰Ar/³⁹Ar laser single-grain and K–Ar dating of the Yixian Formation, NE China. *Palaeoworld* 11, 328–340 (1999).
8. Dong, Z.-M. & Azuma, Y. in *Sino-Japanese Silk Road Dinosaur Expedition* (ed. Dong, Z.-M.) 68–89 (China Ocean, Beijing, 1997).
9. Brown, B. & Schlaikjer, E. M. The structure and relationships of *Protoceratops*. *Ann. NY Acad. Sci.* 40, 133–266 (1940).
10. Sternberg, C. M. Complete skeleton of *Leptoceratops gracilis* Brown from the Upper Edmonton Member on Red Deer River, Alberta. *Nat. Mus. Can. Bull.* 123, 225–255 (1975).
11. Bohlin, B. *Fossil Reptiles from Mongolia and Kansu* (The Sino-Swedish Expedition, Statens Etnografiska Museum, Stockholm, 1953).
12. Zhao, X.-J., Cheng, Z.-W. & Xu, X. The earliest ceratopsian from the Tuchengzi Formation of Liaoning, China. *J. Vert. Paleontol.* 19, 681–691 (1999).
13. Maryanska, T. & Osmólska, H. Protoceratopsidae (Dinosauria) of Asia. *Palaeontol. Polonica* 33, 133–181 (1975).
14. Dodson, P. Quantitative aspects of relative growth and sexual dimorphism in *Protoceratops*. *J. Paleontol.* 50, 929–940 (1976).
15. Coombs, W. P. Juvenile specimens of the ornithischian dinosaur *Psittacosaurus*. *Palaeontology* 25, 89–107 (1982).
16. Sereno, P. C. in *Dinosaur Systematics, Perspectives and Approaches* (eds Carpenter, K. & Currie, P.) 203–210 (Cambridge Univ. Press, New York, 1990).
17. Chinnery, B. J. & Weishampel, D. B. *Montanoceratops cerorhynchus* (Dinosauria, Ceratopsia) and relationships among basal neoceratopsians. *J. Vert. Paleontol.* 18, 569–585 (1998).
18. Makovicky, P. J. in *Mesozoic Terrestrial Life* (eds Tanke, D. & Carpenter, K.) 243–262 (Univ. Indiana Press, Bloomington, 2001).

Remains of *Homo erectus* from Bouri, Middle Awash, Ethiopia

Berhane Asfaw*, W. Henry Gilbert†, Yonas Beyene‡, William K. Hart§, Paul R. Renne||, Giday WoldeGabriel¶, Elisabeth S. Vrba# & Tim D. White†

*Rift Valley Research Service, P.O. Box 5717, Addis Ababa, Ethiopia
†Department of Integrative Biology and Laboratory for Human Evolutionary Studies, Museum of Vertebrate Zoology, VLSB, University of California, Berkeley, California 94720, USA
‡Department of Anthropology and Archaeology ARCCH, Ministry of Youth, Sports and Culture, Addis Ababa, Ethiopia
§Department of Geology, Miami University, Oxford, Ohio 45056, USA
||Berkeley Geochronology Center, 2455 Ridge Road, Berkeley, California 94709, USA, and Department of Earth and Planetary Science, University of California, Berkeley, California 94720, USA
¶EES-6/MS D462 Los Alamos National Laboratory, Los Alamos, New Mexico 87545, USA
#Department of Geology and Geophysics, Yale University, New Haven, Connecticut 06511, USA

The genesis, evolution and fate of *Homo erectus* have been explored palaeontologically since the taxon's recognition in the nineteenth century. Current debate[1] is focused on whether early representatives from Kenya and Georgia should be classified in a separate ancestral species ('*H. ergaster*')[2–4], and whether *H. erectus* was an exclusively Asian species lineage that went extinct[5,6]. Lack of resolution of these issues has obscured the place of *H. erectus* in human evolution. A hominid calvaria and postcranial remains recently recovered from the Dakanihylo Member of the Bouri Formation, Middle Awash, Ethiopia, bear directly on these issues. These ~1.0-million-year (Myr)-old Pleistocene sediments contain abundant early Acheulean stone tools and a diverse vertebrate fauna that indicates a predominantly savannah environment. Here we report that the 'Daka' calvaria's metric and morphological attributes centre it firmly within *H. erectus*. Daka's resemblance to Asian counterparts indicates that the early African and Eurasian fossil hominids represent demes of a widespread palaeospecies. Daka's anatomical intermediacy between earlier and later African fossils provides evidence of evolutionary change. Its temporal and geographic position indicates that African *H. erectus* was the ancestor of *Homo sapiens*.

The Early Pleistocene Dakanihylo ('Daka') Member comprises 22 to ≤45 m of sediments unconformably atop the Pliocene Hatayae Member of the Bouri Formation[7] (Fig. 1). These deposits contain abundant archaeological and palaeontological remains embedded in primarily alluvial deposits relating to lakeside beaches or shallow water deposits in distributary channels[8]. Initial interpretations identified Daka sediments as postdating hominid remains and Acheulean artefacts from Bodo[9]. However, the Daka artefacts clearly antedate those at Bodo, and single-crystal ⁴⁰Ar/³⁹Ar dating of a pumiceous unit at the base of the Member gave an age of 1.042 ± 0.009 Myr (ref. 8). The entire Dakanihylo Member is of reverse magnetic polarity, so the minimum age of its palaeoanthropological contents is ~0.8 Myr.

An extensive vertebrate fauna was recovered from the Daka Member. Faunas of this age are rare in Africa. Of 713 identified specimens (see Supplementary Information for faunal list), 377 are bovids, including three new species and two new genera[10]. The bovid assemblage is dominated by alcelaphine diversity and abundance not recorded at older African sites. Widespread open grassland habitats are thereby indicated. Adjacent water-margin habitats are evidenced by three *Kobus* species and abundant hippo fossils.

Daka Member archaeological sites are abundant. Bone modifications characteristic of the butchery of large mammals by hominids scar several equid, bovid and hippo postcrania. Lithic assemblages closely conform to African early Acheulean analogues. Handaxes and cleavers are ubiquitous elements, with invasive flake scars and fewer flake removals than later Acheulean counterparts[8].

A hominid calvaria (BOU-VP-2/66) was discovered *in situ* in Daka Member silty sand by W.H.G. on 27 December 1997. The specimen was orientated base-down, without associated artefacts, encrusted by fossilized root casts. Surface detail is well preserved, with no sign of fluvial transport or surface weathering. Its vault and supraorbitals exhibit perimortem scraping damage; the frontal and parietals bear multiple sets of subparallel striae, each with internal striations. The patterning and morphology of these marks is unusual and inconsistent with cutmarks made by hominids engaged in defleshing activities. We tentatively attribute this damage to animal gnawing.

The calvaria preserves a largely intact base and is only slightly distorted (plastic deformation skews the vault slightly to the individual's left (Fig. 2)). Endocranial capacity is 995 cm³ (measured repeatedly with teff seed). The thick supraorbital tori are strongly arched, with markedly depressed glabellar and supraglabellar regions. Radiographs reveal an asymmetrical frontal sinus extending to the left midorbital level. The frontal squama is bossed at midline and there is weak sagittal keeling there and on the parietals. The mandibular fossa is deep and anteroposteriorly short. Supramineal and supramastoid crests and angular tori are weak. The small mastoids are small. There is no true occipital torus demarcated superiorly by a supratoral sulcus. Rather, the occipital squama rises vertically and curves anteriorly. Viewed posteriorly, the undistorted parietal walls would have been vertical. The cranial vault is smaller and shorter than Olduvai hominid OH-9 and is phenetically similar to the partly described Buia cranium from Eritrea[11]. Three isolated hominid femora and a proximal tibia were recovered from Daka deposits far removed from the calvaria (Fig. 1). No femur is complete, but all display the marked platymeria and extremely thick midshaft cortex characteristic of *H. erectus*.

The new 'Daka' hominid fossils afford unique insights into unresolved spatial and temporal relationships of *H. erectus*. Most fossils attributed to this taxon came to light in Java, China, Europe and Africa during the twentieth century. Additional genus and species names were proposed before the application of modern

systematics united them under *H. erectus* in the 1960s. The discovery of older Kenyan fossils in the 1970s and the application of cladistic methods in the 1980s produced a variety of phylogenetic and taxonomic assessments of Early and Middle Pleistocene *Homo*. In his 1985 distillation, Delson[1] identified two basic research problems involving *H. erectus*: whether the African fossils were conspecific with the Trinil holotype and other Asian representatives; and whether the species showed stasis or phyletic change through its 1.5-Myr span. Both problems have persisted, and at ~1.0 Myr in the Horn of Africa the new Daka fossils now bear directly on them.

It has been proposed that the name *H. erectus* be restricted to a purported Asian clade (species) exemplified by fossils of disparate antiquity from Trinil, Sangiran, Zhoukoudian and Ngandong[5,6]. We examined the hypothesis that *H. erectus* was a specifically Asian clade by metrically and cladistically analysing the Daka calvaria. Its cranial metrics (see Supplementary Information) overlap with both Asian and African sample ranges and fail to distinguish the fossil consistently from either sample.

Previous applications of cladistics to *H. erectus* have been criticized on the basis of issues of character independence and variation[12–14], as well as the potentially confounding effect of gene flow[15,16]. We agree with these and other valid cautions[17,18]. However, to examine the hypothesis that *H. erectus* was a distinct African clade, we experimented with Hennigian parsimony analyses to investigate potential clustering of relevant crania. From recent published literature we compiled the 22 characters most widely and appropriately used in the cladistic analysis of calvarial anatomy in *H. erectus* and close relatives. We divided Early and Middle Pleistocene *Homo* fossils into operational taxonomic units on the basis of the palaeo-demes defined by Howell[19] (these are sets of fossils representing spatially and temporally bounded 'communities' below the species level; specimen-by-specimen palaeo-deme content and details of our analysis are presented in Supplementary Information).

Regardless of the software parameters used, or the removal of later Asian demes, the hypothesis of a deep cladogenesis between African and Asian *H. erectus* is unsupported by our analyses (Fig. 2). Previous cladistic efforts have noted difficulty with the African OH 9 specimen because it consistently aligned with the Asian fossils,

thereby being interpreted as a sort of Tanzanian outpost of 'Asian' morphology[5] or as an evolutionary intermediate[20]. The recovery of the Buia and Daka fossils, almost certainly from the same eastern African deme, compounds such problems. Like OH 9, these new African specimens share many derived characters with Asian and European specimens. As a consequence, the cladistic method, regardless of serious questions concerning its applicability here, fails to support the division of *H. erectus* into Asian and African clades. Whether viewed metrically or morphologically, the Daka cranium confirms previous suggestions[15,16] that geographic subdivision of early *H. erectus* into separate species lineages is biologically misleading, artificially inflating early Pleistocene species diversity. Rather, the Daka calvaria is consistent with the hypothesis of a widespread, moderately polymorphic and polytypic species at ~1.0 Myr (refs 21, 22).

Because it is from a poorly sampled period[23], the newly discovered Daka calvaria is also important for assessing evolutionary mode and tempo in *H. erectus*. A key barrier to such assessment is the lack of chronological control for many Pleistocene Eurasian hominids—a persistent problem that confounds attempts to document patterns of morphological change across time. Chronometric placement is superior in eastern Africa, where the earliest fossils attributed to *H. erectus* (Nariokotome deme) date to ~1.78 Myr (ref. 2). These fossils have smaller braincases than later African species representatives, including Daka. This pattern could also characterize Eurasia, where the earliest hominid fossils from Sangiran, Java[24], and Dmanisi, Georgia[1], might be more primitive than younger regional counterparts (although the chronological placement of most Eurasian fossils is inadequate relative to what is now available for eastern Africa[25]).

Chronological and anatomical seriation of the African fossils from KNM-ER3733/3883 (Koobi Fora) to OH 9, to Daka/Buia to Bodo[26], is now available. In many features, including cranial capacity and its extensive developmental correlates, hominid crania in this eastern African succession comprise a morphocline consistent with the hypothesis that they sample a single evolving lineage. To recognize the basal fossils representing this apparently evolving lineage with the separate species name '*H. ergaster*' is therefore doubtfully necessary or useful[2]. At most, the basal members

of the *H. erectus* lineage should be recognized taxonomically as a chrono-subspecies (*H. erectus ergaster*). Suggestions that *H. ergaster* itself contains multiple species, even in a single locality[27], seem completely unsupported by the data[4].

The origins of the widespread, polymorphic, Early Pleistocene *H. erectus* lineage remain elusive. The marked contrasts between any potential ancestor (*Homo habilis* or other) and the earliest known *H. erectus* might signal an abrupt evolutionary emergence some time before its first known appearance in Africa at ~1.78 Myr. Uncertainties surrounding the taxon's appearance in Eurasia and southeast Asia make it impossible to establish accurately the time or place of origin for *H. erectus*. Available evidence is insufficient to detect the direction of its geographic dispersal. Given new perspectives afforded by the discoveries at Dmanisi in Eurasia, the assumption that the earliest *H. erectus* populations emigrated from Africa to Eurasia[14,28,28,29], rather than invading Africa from Eurasia[30], is premature. Whatever its time and place of origin, and direction of spread, this species dispersed widely, and possibly abruptly, before 1.5 Myr. The Daka calvaria indicates that by 1 Myr the taxon had colonized much of the Old World without speciating—a finding of considerable biogeographic and behavioural significance. Through time and across its eastern hemispheric range, the technologies employed by this taxon ranged from Oldowan to Acheulean.
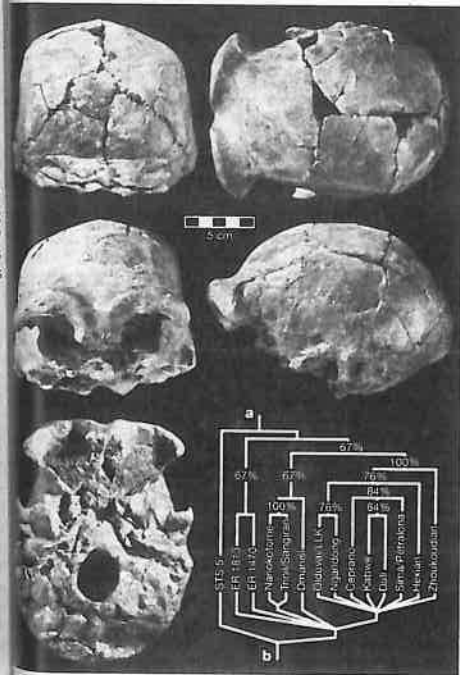
The resemblance of the Daka calvaria to Asian representatives of *H. erectus*, and its morphological intermediacy between earlier and later African specimens, provide strong evidence that it samples a widely distributed lineage that evolved during the million years after its Pliocene origin. The phylogenetic unity of *H. erectus* did not persist indefinitely. By ~0.5 Myr, very different hominid crania in Africa and Asia (Bodo versus Zhoukoudian) indicate that a hominid speciation event might have occurred in circum-Daka times[26]. Further sampling of the Daka to Bodo transition in Africa is needed to examine the rate of morphological change, as well as the hypothesis that the fractionation of *H. erectus* might have been related to the ~0.95-Myr onset of large magnitude global climatic oscillations. □

1. Delson, E. Palaeobiology and age of African *Homo erectus*. *Nature* 316, 762–763 (1985).
2. Walker, A. C. & Leakey, R. E. F. *The Nariokotome* Homo erectus *Skeleton* (Harvard Univ. Press, Cambridge, Massachusetts, 1993).
3. Wood, B. A. *Koobi Fora Research Project Vol. 4* (Clarendon Press, Oxford, 1991).
4. Gabunia, L., Vekua, A. & Lordkipanidze, D. New human fossils from Dmanisi, eastern Georgia. *Archaeol. Ethnol. Anthropol. Eurasia* 2(6), 128–139 (2001).
5. Andrews, P. J. An alternative interpretation of the characters used to define *Homo erectus. Courier Forschunginstitut Senckenberg* 69, 167–175 (1984).
6. Groves, C. P. *A Theory of Human and Primate Evolution* (Clarendon Press, Oxford, 1989).
7. DeHeinzelin, J. *et al.* Environment and behavior of 2.5-million-year-old Bouri hominids. *Science* 284, 625–629 (1999).
8. DeHeinzelin, J., Clark, J. D., Schick, K. D. & Gilbert, W. H. (eds) *The Acheulean and the Plio-Pleistocene Deposits of the Middle Awash Valley, Ethiopia* (Royal Museum of Central Africa, Tervuren, Belgium; *Ann. Sci. Geol.*, 104 (2000)).
9. Kalb, J. *et al.* Geology and stratigraphy of Neogene deposits, Middle Awash Valley, Ethiopia. *Nature* 298, 17–25 (1982).
10. Vrba, E. S. New fossils of Alcelaphini and Caprinae (Bovidae: Mammalia) from Awash, Ethiopia, and phylogenetic analysis of Alcelaphini. *Palaeont. Afr.* 34, 127–198 (1997).
11. Abbate, E. *et al.* A one-million-year-old *Homo* cranium from the Danakil (Afar) depression of Eritrea. *Nature* 393, 458–460 (1998).
12. Brauer, G. & Mbua, E. *Homo erectus* features used in cladistics and their variability in Asian and African hominids. *J. Hum. Evol.* 22, 79–108 (1992).
13. Kennedy, G. E. On the autapomorphic traits of *Homo erectus. J. Hum. Evol.* 20, 375–412 (1991).
14. Kramer, A. Human taxonomic diversity in the Pleistocene: Does *Homo erectus* represent multiple hominid species? *Am. J. Phys. Anthropol.* 91, 161–171 (1993).
15. Harrison, T. in *Species, Species Concepts, and Primate Evolution* (eds Kimbel, W. H. & Martin, L. B.) 345–371 (Plenum, New York, 1993).
16. Turner, A. & Chamberlain, A. Speciation, morphological change and the status of African *Homo erectus. J. Hum. Evol.* 18, 115–130 (1989).
17. Lovejoy, C. O., Cohn, M. J. & White, T. D. Morphological analysis of the mammalian postcranium: A developmental perspective. *Proc. Natl Acad. Sci. USA* 96, 13247–13252 (1999).
18. Trinkaus, E. Cladistics and the hominid fossil record. *Am. J. Phys. Anthropol.* 83, 1–11 (1990).
19. Howell, F. C. Paleo-demes, species clades, and extinctions in the Pleistocene hominin record. *J. Anthropol. Res.* 55, 191–243 (1999).
20. Martinez, I. & Arsuaga, J. L. The temporal bones from Sima de los Huesos Middle Pleistocene site (Sierra de Atapuerca, Spain). A phylogenetic approach. *J. Hum. Evol.* 33, 283–318 (1997).
21. Rightmire, G. P. *The Evolution of* Homo erectus: *Comparative Anatomical Studies of an Extinct Human Species* (Cambridge Univ. Press, Cambridge, 1990).
22. Rightmire, G. P. Evidence from facial morphology for similarity of Asian and African representatives of *Homo erectus. Am. J. Phys. Anthropol.* 106, 61–85 (1998).
23. Aguirre, E. Poor fossil record and major changes around 1 MaBP. *Hum. Evol.* 15, 51–62 (2000).
24. Larick, R. *et al.* Early Pleistocene ^{40}Ar/^{39}Ar ages for Bapang Formation hominins, Central Jawa, Indonesia. *Proc. Natl Acad. Sci. USA* 98, 4866–4871 (2001).
25. Olsen, J. W. New light on the earliest occupation of east Asia. *Anthropologie* 37, 89–96 (1999).
26. Rightmire, G. P. The human cranium from Bodo, Ethiopia: Evidence for speciation in the Middle Pleistocene. *J. Hum. Evol.* 31, 21–39 (1996).
27. Schwartz, J. H. Taxonomy of the Dmanisi crania. *Science* 289, 55 (2000).
28. Ambrose, S. H. Paleolithic technology and human evolution. *Science* 291, 1748–1753 (2001).
29. Bar-Yosef, O. Lower Paleolithic sites in South-western Asia: Evidence for 'Out of Africa' movements. *Anthropologie* 37, 51–69 (1999).
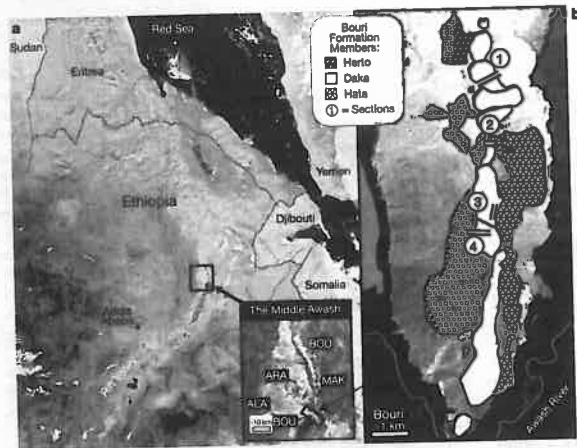30. Clarke, R. Out of Africa and back again. *Int. J. Anthropol.* 15, 185–189 (2001).

Figure 1 Maps and generalized sections. a, Landsat and aerial photographic imagery showing the location of the Middle Awash study area, its major hominid-bearing localities, and the exposure of Bouri Formation sediments. The 1.0-Myr Daka Member of this formation is shown in white. b, Measured stratigraphic sections of this Member show the placement of Acheulean artefacts, hominid fossils, radiometric dates and geomagnetic polarity determinations (normal polarity in section 3 and cap of section 4 overlie the Daka Member).

Figure 2 Views of the Daka calvaria and cladograms representing majority rule (a) and consensus (b) of the 75 most parsimonious phylogenies generated by PAUP 4.0b8 (Swofford). The Daka cranium is in the 'Olduvai/LLK' deme. See the text and Supplementary Information for analytical details. Cladogram b is more conservative, showing the nodes that are stable across all equally parsimonious phylogenies. These branching diagrams are presented only to illustrate the limitations of a cladistic approach to phylogeny among this set of fossils, and the lack of calvarial evidence for a deep cladogenetic division between the African and Asian fossils.