of β-galactosidase (β-Gal) internal control plasmid (driven by baculovirus immediate-early gene, *ie*-1 promoter). Total DNA for each transfection was normalized with pAC5.1-V5. Cells were harvested 48 hours after transfection. Luciferase activity was normalized by determining luciferase:β-Gal activity ratios and averaging the values from triplicate wells.
48. M. F. Ceriani *et al.*, *Science* **285**, 553 (1999).
49. MOP4 is a basic helix-loop-helix, PAS-containing transcription factor that is closely related to CLOCK. It can also heterodimerize with BMAL1 to activate transcription through E box enhancers (*10*, *13*).
50. DNA binding constructs were made as LexA (1-202) fusions. VP-16 transactivator hybrids were generated in pVP-16. Two-hybrid assays were performed as described [N. Gekakis *et al.*, *Science* **270**, 811 (1995)].
51. E. A. Griffin, D. Staknis, C. J. Weitz, *Science* **286**, 768 (1999).
52. Luciferase reporter gene assays were performed in COS-7 cells as described (*12*).
53. G. A. Keesler *et al.*, *Neuroreport* **11**, 951 (2000).
54. P. L. Lowrey *et al.*, *Science* **288**, 483 (2000).
55. We thank S. Kay and C. Weitz for expression and reporter constructs and A. Chavda and C. Capodice for technical support. Supported by R37 HD14427 and RO1 NS39303, BBSRC 8/S09882, and a Spinoza Premium of the Netherlands Organization for Scientific Research. L.P.S. was supported in part by NIH Training Grant HL07901, K.K. by the University of Tokyo, and C.C.L. by the NIH.

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Earliest Pleistocene Hominid Cranial Remains from Dmanisi, Republic of Georgia: Taxonomy, Geological Setting, and Age

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Archaeological excavations at the site of Dmanisi in the Republic of Georgia have uncovered two partial early Pleistocene hominid crania. The new fossils consist of a relatively complete cranium and a second relatively complete calvaria from the same site and stratigraphic unit that yielded a hominid mandible in 1991. In contrast with the uncertain taxonomic affinity of the mandible, the new fossils are comparable in size and morphology with *Homo ergaster* from Koobi Fora, Kenya. Paleontological, archaeological, geochronological, and paleomagnetic data from Dmanisi all indicate an earliest Pleistocene age of about 1.7 million years ago, supporting correlation of the new specimens with the Koobi Fora fossils. The Dmanisi fossils, in contrast with Pleistocene hominids from Western Europe and Eastern Asia, show clear African affinity and may represent the species that first migrated out of Africa.

The identity of the first hominid species to disperse out of Africa and the timing of this dispersal remain highly controversial. The earliest known hominid fossils in Europe and Asia have either exhibited morphological characteristics specific to the region in which they were found (*1*, *2*) or were too incomplete to be identified reliably as to species (*3*, *4*). Thus, it is debatable whether any of these earliest ex-African hominids are conspecific with those from Africa. Equally debatable are the timing and cause of the first hominid dispersal outside of Africa. Few sites of critical age have yielded both significant hominid remains and artifacts from geological contexts that are amenable to reliable dating. Thus, it remains debated whether hominids dispersed from Africa in the late Pliocene to early Pleistocene, before the development of Acheulean tool technologies, or much later in the middle Pleistocene at or after 1 million years ago (Ma), well after the development of these technologies (*5*). Advocates of a post–1.0 Ma dispersal time have suggested that technological innovation, as witnessed by the Acheulean tradition, enabled hominid dispersal from Africa (*6*), whereas an earlier, pre-Acheulean dispersal supports a more ecomorphological web of factors as the cause of hominid dispersal (*7*, *8*).

Recent discoveries at Dmanisi in the Republic of Georgia (Fig. 1) provide us with a data set with which to evaluate these scenarios. Archaeological excavations at Dmanisi during the summer of 1999 produced two hominid crania, D2280 (Fig. 2) and D2282 (Fig. 3) from the same stratigraphic level and excavation pit as a hominid mandible discovered in 1991 (*3*, *9*), for which the taxonomic affinity is debated (*3*, *6*, *10*, *11*). Here we describe the new hominid fossils; their taxonomic affinity; and age, geological context, associated artifacts, and vertebrate fauna.

The new fossils. The first fossil specimen, D2280 (Fig. 2), is an almost complete calvaria, including a partial cranial base retaining slightly damaged nuchal and basilar portions of the occipital, parts of the greater wings of the sphenoid, and most of the left mandibular fossa of the temporal. The second and more complete is cranium D2282 (Fig. 3), which retains much of the face and cranial vault but has undergone lateral and dorsoventral postmortem deformation. The occipital and temporal regions are crushed on the left side, as are the zygomatic bones. The base is largely absent. Much of the median upper facial skeleton is missing, including the supraorbital torus at glabella, nasal bones, and frontal processes of the maxillae. However, the maxillae are well preserved laterally and inferiorly and retain the slightly worn right P^4-M^2, the left M^1 and M^2, and the alveoli of all other adult teeth, including those of M^3, which are visible on radiograph. D2282 is the smaller of the two, and based on gracile muscle attachments, less well-developed cranial superstructures, light dental wear, and well-demarcated cranial sutures, may be either an older subadult or young adult and possibly a female.

Both specimens are small with endocranial volumes below 800 cm^3 (Tables 1 and 2). A direct measurement using seed yielded an endocranial volume of 775 cm^3 for D2280. The cranial capacity estimate calculated from the length, breadth, and cranial index of D2282 is about 650 cm^3.

Cranial shape is similar in both specimens: spheroidal in superior view and relatively low and angular in lateral view (Figs. 2 and 3). The greatest cranial breadth is at the level of the well-pneumatized mastoid processes. The occipitals are relatively narrow and angular. The occipital angle in D2280 is 108°. A continuous occipital torus is present in each specimen, and D2280 exhibits a larger torus and more rugose nuchal muscle markings than does D2282. A pronounced occipital crest extends from the external occipital protuberance to the foramen magnum in D2280. The frontal sinus and ethmoid pneumatization are visible in D2280. A

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wide supratoral sulcus is present in D2282 and is less developed in D2280. Postorbital constriction is marked. Cranial bones are moderately thick, and no cranial cresting is present (the temporal lines are separated by at least 23 mm in D2280). Traces of an angular torus are present in both specimens, and a small sagittal keel is present in D2282. An apparent metopic eminence and sagittal keel on D2280 are probably pathological. The mandibular fossae of the temporal are mediolaterally and anteroposteriorly long and relatively deep. The entoarticular process in D2282 is projecting and formed by both temporal and sphenoidal contributions, as is the foramen spinosum. Temporal squamae are moderately long and low, although somewhat taller in D2282 than in D2280.

The D2282 facial skeleton is well preserved [Table 1 and tables 1 through 3 in Web appendix 1 (available at *Science* Online at www.sciencemag.org/feature/data/1051481.shl)]. Estimates of the facial, orbital, and zygomatic heights and orbital breadths are comparable to those of the Koobi Fora specimens assigned to *H. ergaster*. The pyriform aperture is comparatively narrow and blunt-sided and has a small prenasal fossa. The nasoalveolar clivus is wide and somewhat flattened, forming an angle close to 45° to the alveolar plane. The jugum alveolare canini is well developed, forming a distinctly flattened convexity, rising over the lower edge of the pyriform aperture. The palate is moderately long, narrow, and deep (Table 2 and Web appendix 1). The tooth rows diverge minimally from one another. The anterior zygomatic is positioned at M^1.

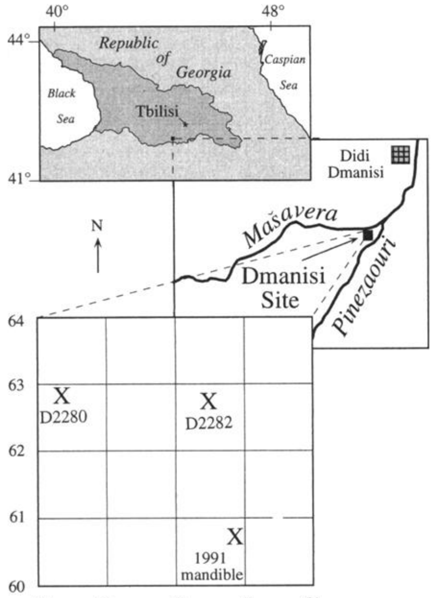

Fig. 1. General location map of the Dmanisi site, Republic of Georgia. The locations of the hominid calvaria described here and of the 1991 hominid mandible are plotted on the Site I excavation map. Excavation units are 1-m squares.

The maxillary dentition of D2282 is similar in size and morphology to that of KNM-ER 3733 and KNM-WT 15000 (Table 1 and Web appendix 1). P^4 is single-rooted and narrow-crowned. Molar crown area is larger in M^1 than in M^2 (Table 2).

Taxonomic affinity. Despite their relatively small cranial capacities, both Dmanisi fossils differ from *H. rudolfensis* and *H. habilis* and display a number of essential similarities with the crania of *H. erectus sensu lato* and particularly with its early African forms, attributed by some to *H. ergaster* (Table 2). In particular, the Dmanisi hominids are distinguished from *H. rudolfensis* and *H. habilis* by having well-developed supraorbital tori, angulation of the cranial vault, absence of cresting (variably present in earlier *Homo*), large orbital areas, and single-rooted maxillary premolars. Likewise, they share the following with early African *H. ergaster*: similar frontal and occipital inclination relative to the Frankfurt Horizontal; angular sagittal profiles; relative narrowness of the postorbital region and moderate height of the cranial vault; relief of the occipital area (particularly apparent in D2280); comparable appearance of the temporal crests and disposition of the foramina on the cranial base; thickness of the cranial vault bones; substantial pneumatization of the mastoid area; similar morphology of the temporomandibular articulation; and proportions of the facial skeleton, including the narrowness of the alveolar arch; and the presence and morphology of the supraorbital tori.

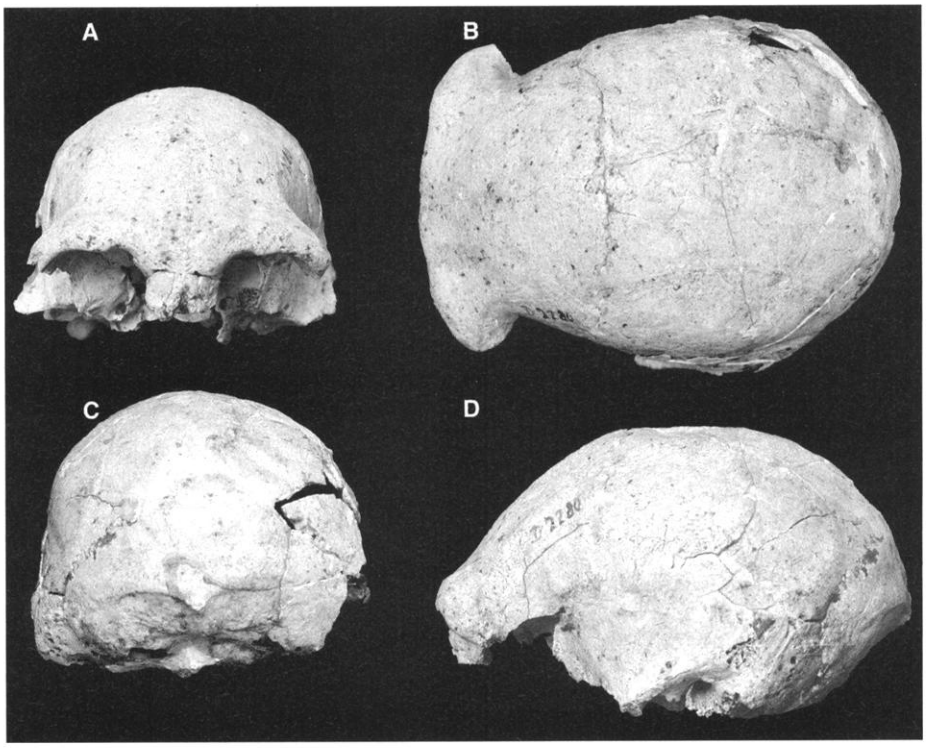

Fig. 2. The D2280 calvaria. (**A**) Frontal view, (**B**) superior view, (**C**) posterior view, and (**D**) lateral view. All views are scaled from image (B) at approximately 35% of actual size. See Table 1 for measurements.

The Dmanisi specimens differ from Asian *H. erectus* specimens of similar size, such as Trinil and Sangiran 2 from Indonesia, in essentially the same features that differentiate *H. erectus sensu stricto* and *H. ergaster*. These differences include the more moderate development of the Dmanisi supraorbital and nuchal tori, relatively taller cranial vaults, relatively thinner cranial vault bone, lesser breadths of the calvaria, somewhat smaller cranial capacities, and possibly narrower alveolar arches, although the latter cannot be assessed in the smallest of the Indonesian hominids. The only characteristic shared by the Dmanisi cranial specimen and Asian *H. erectus* and not by *H. ergaster* is the presence of an angular torus. Because this feature is evident in other non-Asian hominids, including Olduvai hominids 9 and 12 and is variably expressed in the Dmanisi fossils, we do not give it any special phylogenetic significance. Similarly, we consider the presence of sagittal keeling of the cranium, extrasutural bones, and other '*H. erectus*–like' features of the Dmanisi calvaria, which are also variably present in *H. ergaster* and possibly other early African *Homo*, to be phylogenetically insignificant.

A number of features of the Dmanisi specimens, such as the narrowness of the vault in its postorbital and occipital parts; the comparatively narrow pyriform aperture; a somewhat bulging distolingual edge of M^1 and particularly M^2; the presence of some features of a Carabelli complex on those teeth; the shortness of the anterior region of both the upper and lower jaws; the development of the mandibular symphysis (*3*, *11*), as well as features of the mandibular dentition, including small premolars, especially P_4, the mesial crest on the molars, and somewhat narrowed distal border of the crown of M_1 and M_2; and other features may indicate some degree of population isolation or clinal variation.

The combination of the features of the Dmanisi hominids appears more similar to *H. ergaster* than to *H. erectus sensu stricto* (or to earlier *Homo*). This conclusion is consistent with some studies of the Dmanisi mandible (*3*, *11*, *12*). We thus assign the Dmanisi hominids to *Homo ex gr. ergaster*.

The Dmanisi site. The Dmanisi site is located about 85 km southwest of Tbilisi, about 1 km above the confluence of the Masavera and Pinezaouri Rivers (Fig. 1) on top of an erosional spur of the Masavera Basalt, 80 m above present-day water levels. The location provided a defensible position during medieval times and today is littered with collapsed masonry structures and thick midden deposits. During archaeological excavations of a medieval bell-shaped storage pit in 1984, the underlying Plio-Pleistocene archaeological and paleontological materials at Dmanisi were discovered. This juxtaposition led to the erroneous initial report that the 1991 hominid mandible was found in a medieval storage pit (*13*), rather than in situ from the underlying Plio-Pleistocene deposits.

The canyons of the Masavera and Pinezaouri Rivers and archaeological excavation pits in the overlying sediments expose about 80 m of Masavera Basalt, which fills a paleovalley overlain by about 2.5 m of fossiliferous, volcaniclastic alluvium (*9*, *14*). Natural surface exposures through the alluvium are minimal, and details of the stratigraphy must be pieced together from the limited exposures revealed by the archaeological excavations. These excavations consist of 1-m-gridded sites and test pits excavated down to the surface of the underlying Masavera Basalt. The excavations total approximately 150 m^2. So far, over 2000 identifiable vertebrate fossils, a hominid mandible (*3*) and metatarsal (*15*), the two new fossils described here, and over 1000 stone artifacts have been recovered. The new fossils were found in the

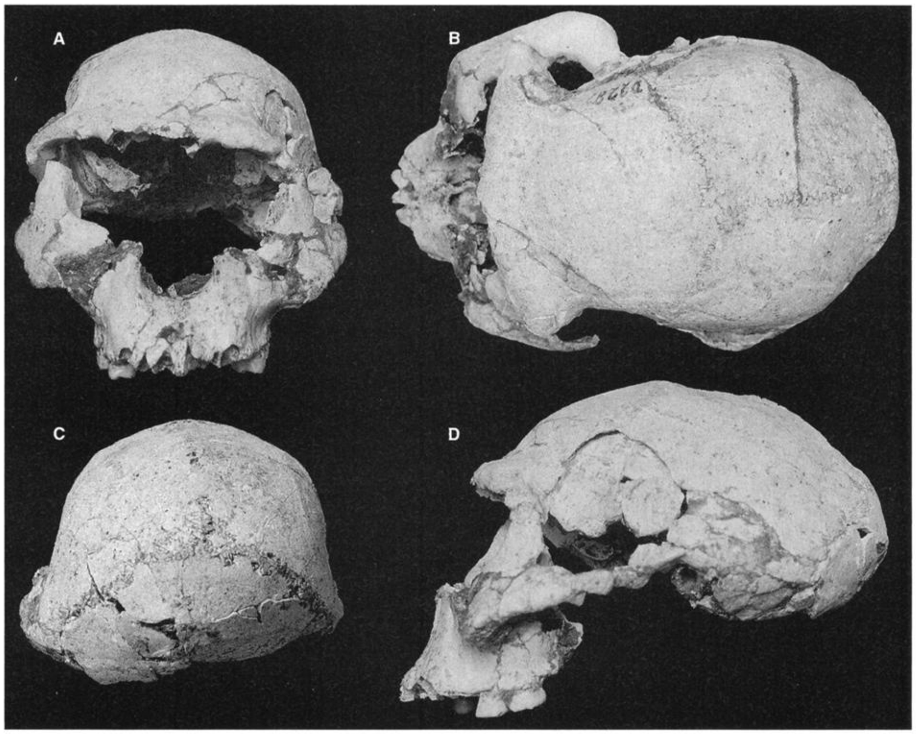

Fig. 3. The D2282 calvaria at similar scale as D2280. (**A**) Frontal view, (**B**) superior view, (**C**) posterior view, and (**D**) lateral view. In (B), note the presence of some reconstructive materials on the right zygomatic arch and superorbital; note also that the projection of the face is distorted because of postmortem deformation. In (D), note extensive postmortem crushing. All views are scaled from image (B) at approximately 35% of actual size. See Table 1 for measurements.

Table 1. Cranial and dental measurements of new hominids (in mm). Numbers in parentheses indicate approximate values; dashes indicate unavailable data. RP, right premolar; MD, mesiodistal; BL, buccolingual; LM, left molar.

Measurements	Georgia		African *H. ergaster*			Asian *H. erectus*		
	D2280*	D2282*	ER3733‡	ER3833‡	WT15000§	Sangiran 2‖	Java‡	China‡,‖
Basion-bregma height	(105)	92	108	100	102	(105)	106	–
Glabella-inion length	176†	166†	182	182	175	177	189	194
Minimum frontal breadth	75	66	91	88	90.5	(79)	88	86
Maximum cranial breadth (supramastoid)	(135)	(135)	142	139	141	140	145	147
Biorbital breadth	(103)	(93)	(104)	108	83.5	–	(115)¶	111
Bizygomatic breadth	–	(130)	(138)	(150)	121.6	–	(150)¶	148
Nasion-prosthion length	–	(81)	83	–	–	–	(82)¶	77
Orbit height	–	(37)	36	36	–	–	36¶	36
Orbit breadth	–	(40)	42	41		–	43¶	44
Maximum nasal aperture width	–	28	36	–	34.7	–	(30)¶	30
Maxillo-alveolar length	–	(61.7)	63	–	–	–	67¶	64
Alveolar width at M^2-external	–	66	66	–	66.8	–	–	71
RP^4 MD/BL	–	8.0/10.0	–	–	8.1/11.7	–	8.0/11.6	8.0/11.4
LM^1 MD/BL	–	12.5/13.0	12.6/–	–	11.3/12.1	–	11.8/13.2	11.2/12.5
LM^2 MD/BL	–	12.9/12.1	12.0/13.7	–	11.8/11.3	–	12.3/14.0	10.9/12.7

*Measurements made by L. Gabunia and A. Vekua. †Inion and opisthocranion are coincident. ‡From Wood (*34*). §From Walker and Leakey (*35*). ‖From Weidenreich (*36*). ¶Sangiran 17 only.

same 16-m^2 excavation site (Site I) and at almost the same stratigraphic level in which the 1991 hominid mandible was discovered. D2280 (grid quadrant 50/62) and D2282 (grid quadrant 52/62) were found approximately 2 m apart and approximately 2 m north of the location of the 1991 mandible (grid quadrant 52/60).

The Dmanisi deposits have been considered to be latest Pliocene in age (*3*, *9*, *15–17*) on the basis of (i) K-Ar (*14*) and ^{40}Ar/^{39}Ar dating (*18*) on the Masavera Basalt that underlies the fossil-bearing sediments; (ii) paleomagnetic correlation with the Olduvai Geomagnetic Subchron (*19*); (iii) a late middle or late Villafranchian (late Pliocene-Pleistocene) age of the associated vertebrate fauna as compared with Western Europe (*3*, *20*); (iv) comparison of the Dmanisi hominid mandible with early African *H. erectus (H. ergaster)* from Koobi Fora, Kenya (*3*, *11*, *16*); and (v) the Oldowan or Mode 1 lithic assemblage (*17*, *21*).

Although the Masavera Basalt was first dated at 0.530 ± 0.02 Ma (*22*), subsequent studies gave a K-Ar date of 1.8 ± 0.1 Ma (*14*) and a ^{40}Ar/^{39}Ar isochron date of 2.0 ± 0.1 Ma (*18*). In a paleomagnetic study of the Dmanisi site, Sologasvili *et al.* (*19*) reported an average declination (Dec) of 009°, and inclination (Inc) of 69° for the Masavera Basalt, whereas the overlying fossil-bearing sediments (Layers VI through II) gave an average of Dec = 005°, Inc = 58°. Both directions indicate normal geomagnetic polarity. As a result of these data, earlier workers (*3*, *17–19*) concluded that the normal Masavera Basalt; the fossil vertebrates, including the hominid fossils; and the stone artifacts correlate with the Olduvai Subchron, dated 1.77 to 1.95 Ma (*23*).

This late Pliocene to earliest Pleistocene age for Dmanisi was challenged by Bräuer and colleagues (*10*) and Dean and Delson (*13*), who considered that the 1991 hominid mandible was more similar to late (younger than 1 Ma) *H. erectus*, and by Klein (*6*), who suggested similarities between the mandible and Neandertal ancestors from Spain. These authors argued that the Dmanisi site must be about 1 million years old or younger.

Stratigraphy and context of the Dmanisi hominids. We divide the 2.5 m of fossiliferous, volcaniclastic alluvium that overlie the Masavera Basalt into two major stratigraphic units (designated A and B) and their subdivisions (designated numerically) (Fig. 4). These units are defined on the basis of observed differences in lithology and erosional and pedologic boundaries, and accommodate known variations in architecture and in soils' diagenetic fabrics and geomagnetic polarity (Fig. 4). This twofold scheme differs somewhat from that of Dzaparidze *et al.* (*9*), who recognized six relatively horizontally bedded layers (Layers I through VI) but did not distinguish a series of cross-cutting sedimentary structures that contain much of the fauna and artifacts.

The stratigraphically lowest unit, A1, is a black (10YR2/1), basaltic, tuffaceous loamy sand, composed primarily of pumiceous glass, plagioclase, and associated mafics. A1 is up to 50 cm thick and variably fills crevasses and low areas on the irregular surface of the Masavera Basalt. The surface of the underlying basalt as exposed in the excavation pits at Dmanisi is relatively unweathered, preserving primary flow and cooling features that indicate little or no erosion of the basalt surface before the deposition of unit A1. Unit A1 corresponds with Layer VI of Dzaparidze *et al.* (*9*).

Unit A1 is conformably overlain by unit A2, a massive-to-thinly bedded, very dark grayish-brown (10YR3/2), tuffaceous loamy sand that grades upward to a calcareous, dark yellowish-brown (10YR3/6), tuffaceous fine loamy sand; this unit has weak angular blocky structure and many carbonate veins and cavity linings and is weakly indurated by 5 to 13% secondary carbonate. The unit has uniform textures of ~70 to 75% sand, 23 to 25% silt, and 0 to 3% clay, and similar soil morphology. Unit A2 corresponds largely with Layers V and IV of Dzaparidze *et al.* (*9*), except that the upper boundary of our unit A2 is an erosional surface not previously recognized, below the carbonate cemented zone previously termed Layer III or "Kerki."

Table 2. Anatomical features of the Dmanisi hominids compared with those of other Pleistocene hominids. Characters are as defined by Lieberman *et al.* (*37*), except "mandibular," which follows Rosas and Bermudez de Castro (*11*). Hominid groups are as defined by Lieberman *et al.* (*37*), except Asian *H. erectus*, which includes the Chinese (Zhoukoudian) and Indonesian hominids exclusive of Ngandong. $\bar{x}$, mean; dashes indicate unscoreable characters.

Character	Africa			Asia	Georgia		
	1470 group	1813 group	*H. ergaster*	*H. erectus*	D2280	D2282	Mandible
			Cranial vault				
Cranial capacity	$\bar{x} = 751$	$\bar{x} = 610$	$\bar{x} = 800$	Range 750–1225	780	650?	–
Supraorbital torus	Small to absent	Moderate	Moderate	Large	Moderate/large	Moderate	–
Supratoral sulcus	Sight to absent	Present	Present	Present	Present-slight	Present	–
Glabellar prominence	Prominent	Small	Small	Small	Small	–	–
Vault thickness	Thick	Thin	Thick	Very thick	Thick	Thick	–
Compound TN crest	Variable/absent	Variable/absent	Absent	Absent	Absent	Absent	–
Nuchal plane inclination	Moderate	Horizontal	Horizontal	Horizontal	Horizontal	Horizontal	–
			Face				
Position anterior zygomatic	P4/M1	M1	M1	M1	–	M1	–
Subnasal prognathism	Moderate	Low	Low	Low	–	Low?	–
			Dental				
M_3/M_2 crown area ratio	>1	1	1	~1-<1	–	–	<1
M^1 crown area	2060*	$\bar{x} = 1617$	1440–1310	$\bar{x} = 1555$ (Java) $\bar{x} = 1365$ (China)	–	1574	–
M_1 crown area	$\bar{x} = 1840$	$\bar{x} = 1628$	$\bar{x} = 1479$	$\bar{x} = 1670$ (Java) $\bar{x} = 1480$ (China)	–	–	1651
P^4 root number	Triple	Double	Single	Single	–	Single	–
P_4 root number	Double	Usually single	Single	Single	–	–	Single
			Mandibular and maxillary				
Arcade shape	–	Long/narrow	Long/narrow	Parabola (China)	–	Long/narrow	Long/narrow
Position: anterior marginal tubercle	Absent/C/P_4	Absent/C/P_3	Absent/P_3	Usually P_3-P_4	–	–	C-P_3
Position: lateral prominence	M_2	M_2	M_1-M_3	M_1-M_3	–	–	M_1-M_2

*Value for KNM-ER-1590 only. Dental data are from Wood (*34*).

The A-B contact is an abrupt erosional surface along the base of at least two sets of broad shallow channels or rills that have cut down into unit A2 sediments. These carried surface runoff from the higher ground west-southwest of the excavation areas and become deeper and broader toward the east. Here, one deeper channel is exposed in the southern part of excavation pit XI (*9*). The more extensive shallow features are filled with brown (10YR5/3) tuffaceous loamy sand colluvium; units B1a through B1b have locally concentrated pebble to small cobble colluvial gravel.

Unit B2 is a massive, dark yellowish brown (10YR4/4) tuffaceous loamy sand, ~1.2 m thick. The upper 50 cm of this unit is a yellowish brown (10YR5/6) pedogenic calcrete with laminar, massive, and nodular fabrics (*24*). This soil, roughly the equivalent of Layer I of Dzaparidze *et al.* (*9*), formed during a long period of surface stability after deposition of unit B sediments. Below the soil in unit B2 are numerous small-to-medium irregularly shaped features, possibly krotovina, ~5 cm in diameter, which have indurated loam fill and 2- to 4-mm diagenetic carbonate linings. These are not found elsewhere in the section.

A 30-cm-thick zone within the unit B1a-b sands is cemented by ~35 to 58% $CaCO_3$ that occurred before and probably during soil formation in the upper B2 deposits. The calcite cement follows bedding planes and foresets in the sandy matrix and envelops many artifacts and bones in units B1a-b. This is the "Kerki" or Layer III of Dzaparidze *et al.* (*9*). This indurated zone is laterally continuous across the excavation areas but dips to the east, between and roughly parallel with the B2 soil and the subjacent unit A-B erosional surface.

Stable isotopes from the B2 calcrete and B1 carbonate cements have narrow ranges of $\delta^{18}O$ [−5.87 to −6.25 per mil (‰)] and $\delta^{13}C$ (−8.72 to −9.42‰) (*25*). These compositions and the fabrics of the unit B1 carbonates indicate that they are vadose zone calcite cements. The resistance of these cements may have protected the underlying sediments from weathering, a factor contributing to the excellent preservation of the fossils. We have discovered no evidence to suggest that the B1 carbonate zone was penetrated before medieval times.

In unit A, particularly the lower part of unit A2, there are numerous irregularly shaped sedimentary structures varying in size from 0.2 to 1.2 m in diameter and up to a few meters in exposed length. These structures appear lens- to tunnel-shaped in overall morphology; they cross-cut horizontally bedded strata and are bounded by sharp marginal contacts. Two or more generations of carbonate veins extend from the base of the B1 calcrete into the underlying unit A2 and connect with the thin carbonate linings of many of the large cavities but were not observed to penetrate into the sediment within these structures. For the most part, the sediment enclosed within the structures is poorly lithified and distinctively different in color, texture, and primary structures from the surrounding unit A sediment.

In the southeast corner of excavation Site I, a vertical extension of one of the larger structures was found rising upward to the A-B unit contact. This vertical extension immediately overlies the dense accumulation of fossil vertebrates from which the hominid mandible was recovered in 1991. Archaeological records and field observations indicate that most of the fossils recovered from the archaeological excavations (including the hominid jaw and two crania described here) and the artifacts come almost entirely from these irregularly shaped structures. A smaller number of lithic artifacts, fossil vertebrates, and cobble manuports have also been recovered from the overlying unit B1; the highest concentrations are in B1c. In contrast, the overlying B2 deposits are archaeologically sterile.

On the basis of the morphology, cross-cutting relationships, characteristics of the sediment within the structures, and their geomagnetic polarity (discussed below), the structures from which the bulk of the fossil remains were recovered must be intrusive fills within unit A strata that formed at the time of erosion of unit A deposits but before deposition of unit B and the subsequent precipitation of the unit B1 calcrete. These structures probably formed by underground water movement or soil piping, which eroded subsurface tunnels and cavities, during the time of erosion of unit A. Their formation was facilitated if not enhanced by the high porosity of the unit A sediments, the caliche-rich soil, and rodent burrowing.

The subsequent infill of these voids and cavities consists of a heterogeneous mixture of unit A sediments with granules and a few pebbles similar to those in unit B1. Sediment, vertebrate remains, and artifacts were apparently washed into the voids. The general preservation of the fossil vertebrates and the occurrence of articulated skeletal elements indicate little if any surficial weathering or transport of the vertebrate remains before their accumulation within the voids. The abundance of carnivore fossils in the fauna suggests that carnivores may have played a role in the accumulation of the fossils; however, clear carnivore modification of the bone is lacking. Although the contemporaneous vertebrate fossils, hominids, and artifacts are found together in the infills, there is no clear evidence such as tool marks or other bone modification to suggest that the hominids played a role in the accumulation of the assemblage. We consider the occurrence of vertebrate fossils within these structures to represent a relatively uncommon taphonomic occurrence. The closest approximation may be that reported at a fossil vertebrate site in Pakistan (*26*).

All of the geologic evidence indicates that A1 and A2 sediments were deposited by low-energy flow. Slight weathering of the A2 sediments ensued, then erosion by surface runoff from the west-southwest, which left colluvial sand and gravel in the B1 sediments. Subse-

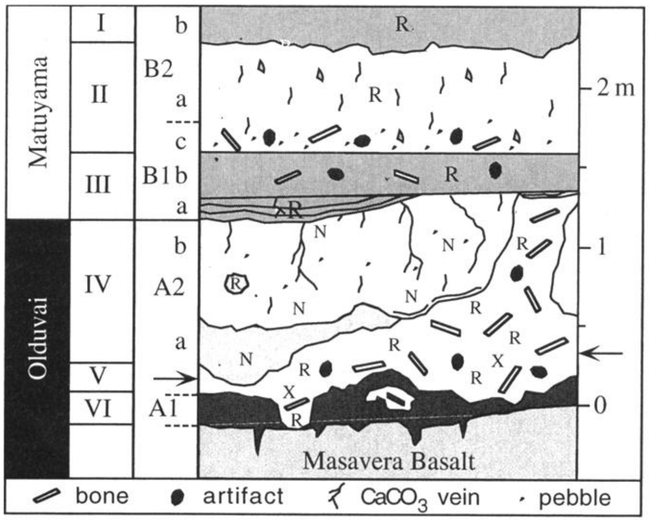

Fig. 4. General stratigraphic profile based on the eastern wall of the archaeological excavation site from which the hominid mandible and the crania reported in this study were recovered. The first column on the left is the geomagnetic polarity interval represented at the site. Black, the normal geomagnetic polarity of the Olduvai Subchron; white, Matuyama reverse chron. The age of the boundary is that of Berggren *et al.* (*23*). The second column shows the stratigraphic subdivisions from Dzaparidze *et al.* (*9*). Column three shows the stratigraphic subdivisions for the same interval reported in this study. Paleomagnetic samples taken from various levels within unit A, as well as samples from the underlying Masavera Basalt, gave normal geomagnetic polarity directions, whereas those from unit B gave reverse polarity directions. In contrast, the sediment infilling the feature (marked by arrows) gave reverse geomagnetic polarity directions, indicating the younger age relationship with the overlying unit B sediments (fig. 2 in Web appendix 2). The majority of vertebrate fossils in this excavation site, were recovered from within the feature marked by the arrows or within other sedimentary features in the excavation site sharing similar characteristics. X indicates relative stratigraphic levels from which the hominid fossils were recovered. The R (reverse polarity) and N (normal polarity) sites are representative sample sites from various stratigraphic levels.

quent to erosion, the unit B2 volcaniclastic sediments were deposited, probably by low-energy overbank flooding. These sediments were stabilized, then weathered, forming the caliche soil in upper B2. There is no gravel lag or any other evidence suggesting erosion of either the upper B2 sediments or the caliche soil that formed in them. Likewise, as indicated above, the surface of the basalt as exposed in the archaeological excavation pits shows no evidence of erosion, indicating that the main river channels of the Masavera and Pinezaouri Rivers must have been contained lateral to the excavated areas. Although the Masavera and Pinezaouri Rivers occur only 200 m to the northwest and southeast of the site, there is no evidence that the rivers ever migrated across the excavation area. This suggests that after infilling of the Masavera and Pinezaouri paleo–river valleys by the Masavera Basalt, the two rivers rapidly incised themselves into the canyons that constrain the rivers today. As the Masavera and Pinezaouri Rivers became incised into the Masavera Basalt, the Dmanisi site was spared further erosion or sediment accumulation, resting well above the floodwater levels of the adjacent rivers.

Age of the Dmanisi site. The age of the Dmanisi site is constrained by the isotopic dating of the Masavera Basalt, paleomagnetic data providing placement of the Olduvai-Matuyama boundary, the relative age of the associated vertebrate fauna, and the geomorphology of the site. A maximum age for Dmanisi is based on new laser and furnace ^{40}Ar/^{39}Ar incremental heating of samples from the base, middle, and upper surface of the Masavera Basalt. These analyses yielded well-behaved spectra with a mean plateau age of 1.85 ± 0.01 Ma [fig. 1 in Web appendix 2 (www.sciencemag.org/feature/data/1051481.shl)]. This age is similar to that reported by Majsuradze *et al.* (*14*) and Schmincke and van den Bogaard (*18*), although our analyses are accompanied by much smaller analytical uncertainty. Paleomagnetic analyses of the Masavera Basalt from the dated horizons yielded well-clustered directions indicating normal geomagnetic polarity (fig. 2 in Web appendix 2). Combined, our data support correlation of the Masavera Basalt with the Olduvai Subchron.

However, our paleomagnetic study of the overlying sediments at Dmanisi yielded significantly different results than those presented previously (*19*). Thermal and alternating-field demagnetization of 23 oriented samples taken from various horizons throughout undisturbed unit A sediments gave normal geomagnetic polarity, whereas 18 samples taken from unit B sediments consistently gave reverse directions (fig. 2 in Web appendix 2). The paleomagnetic data, in conjunction with the age and polarity of the underlying Masavera Basalt and the absence of any observable unconformity between the basalt and unit A sediment, indicate that unit A was deposited during the later part of the Olduvai Subchron. The transition at the unit A-B contact from normal to reverse polarity then correlates with the upper Olduvai-Matuyama boundary and an age of 1.77 Ma (*23*).

Additional support for an Olduvai age for the undisturbed unit A comes from dates on a thin basalt flow from near Zemo Orozmani, about 15 km along the Masavera River west of Dmanisi. This flow overlies fossil vertebrate–bearing volcaniclastic sediments that include a grayish-black vitric tuff that may be correlative with the unit A1 tuff at Dmanisi. ^{40}Ar/^{39}Ar dating of the basalt gave an age of 1.76 ± 0.01 Ma, whereas paleomagnetic analysis of the basalt yielded a direction somewhat west of the expected reverse direction (Dec = 206°, Inc = 42°), suggesting either a transition or secular variation (figs. 1 and 2 in Web appendix 2). The age of the Zemo Orozmani basalt is close in age to that expected for the upper Olduvai-Matuyama boundary (1.77 Ma), which supports our interpretation of an Olduvai (rather than Jaramillo) age for the unit A sediments at Dmanisi.

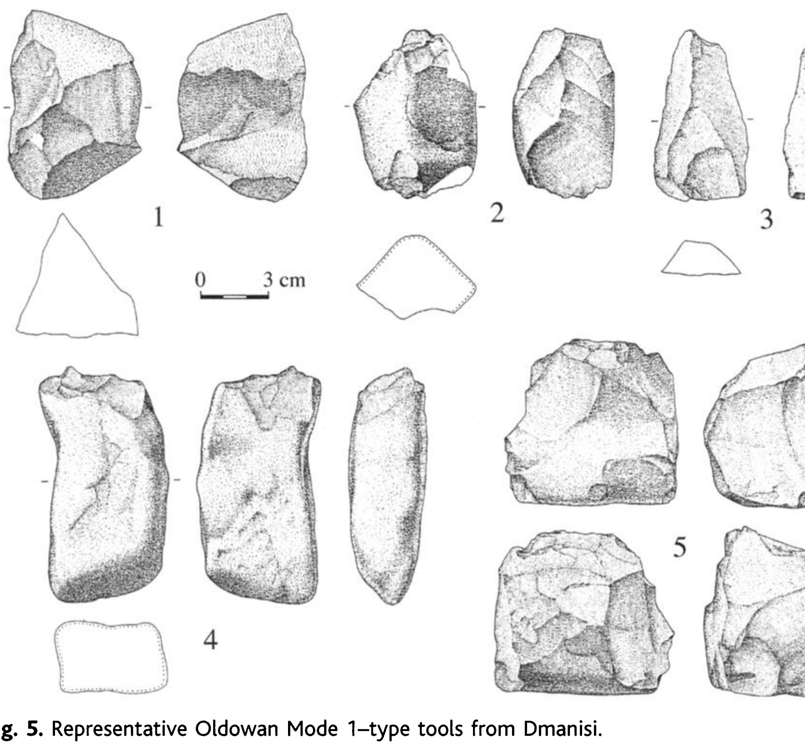

Fig. 5. Representative Oldowan Mode 1–type tools from Dmanisi.

In contrast, 23 samples of the fossil-bearing infills within unit A all gave reverse polarity directions (fig. 2 in Web appendix 2). The reverse polarity of the infills clearly establishes their noncontemporaneity with the surrounding normal polarity unit A strata and supports our lithologic and stratigraphic correlation of the infills with the basal reverse polarity sediments of unit B. Although a few fossil mammals, notably a partial rhinoceros (*Dicerorhinus etruscus etruscus*) mandible (*20*), have been recovered from undisturbed Olduvai normal unit A1 sediments, the bulk of the vertebrate fossils, the hominids, and stone artifacts come from the Matuyama reverse infills within unit A or from overlying unit B.

The vertebrate fauna from Dmanisi points to a latest Pliocene–earliest Pleistocene age. *Struthio dmanisensis*, *Ochotona cf. largerli*, *Hypolagus brahygnathus*, *Apodemus dominans*, *Kowalskia sp.*, *Cricetus sp.*, *Mimomys tornensis*, *Mimomys ostramosensis*, *Parameriones cf. obeidiensis*, *Gerbillus sp.*, *Marmota sp.*, *Canis etruscus*, *Ursus etruscus*, *Martes sp.*, *Megantereon cultridens*, *Homotherium crenatidens*, *Panthera gombaszoegensis*, *Pachycrocuta perrieri*, *Mammuthus (Archidiskodon) meridionalis*, *Equus stenonis*, *Dicerorhinus etruscus etruscus*, *Gazella borbonica*, *Soergelia sp.*, *Dmanisibos georgicus*, *Cervus perieri*, *Eucladocerus aff. senezensis*, Cervidae *cf. Arvernoceros*, *Dama nestii*, and Paleotraginae are indicative of the Late Villanyian (Mammalian Neogene Zone 17) and Early Biharian Mammal (Mammalian Quaternary Zone 1) ages of Europe that span the Plio-Pleistocene boundary (*27*). In particular, the rodents *Mimomys ostramosensis* and *Mimomys tornensis*, which occur intermixed with the other fossils, indicate a latest Pliocene, Olduvai Subchron age (1.95 to 1.77 Ma). The fauna predate the occurrence of *Allophaiomys pliocaenicus*, which dates in Europe to the earliest Pleistocene [the basal part of the post-Olduvai Matuyama dated slightly younger than 1.77 Ma (*23*, *27*)].

Lithic artifacts from Dmanisi are consistent with a late Pliocene–early Pleistocene age.

Over 1000 artifacts consisting of rare choppers, chopping tools, a few scrapers, and numerous flakes have been recovered from unit A and B strata (Fig. 5). The artifacts are made entirely from local basalt sources using an Oldowan (Mode 1) technology (*3*, *21*). No bifaces or developed Oldowan artifacts have been found. Most of the artifacts retain sharp edges,which suggests little transport, although no refits of flakes on tools were observed. The Dmanisi artifacts are compatible with pre-Acheulean assemblages of East Africa that appear as early as 2.4 Ma (*28*), predating Acheulean assemblages that first appear about 1.6 Ma (*29*).

Thus, the paleomagnetic and geochronologic data indicate that the fossil-bearing sedimentary rocks at Dmanisi are constrained within the Matuyama chron [calibrated between 1.77 and 1.07 Ma (*23*)]; the sedimentological relations, archaeological assemblage, and particularly the associated MN17-MQ1 vertebrate fauna indicate an age near the base of this chron or in the uppermost part of the Olduvai Subchron (*27*). Combined, the data restrict the age of the Dmanisi site to just above the Pliocene-Pleistocene boundary, slightly younger than the Olduvai-Matuyama boundary or about 1.7 Ma (*23*, *27*). This finding is consistent with the morphology of the Dmanisi hominid fossils and their proposed affinity with latest Pliocene—earliest Pleistocene *H. ergaster* from Koobi Fora, Kenya.

Implications of the new discoveries. Unlike all other hominids found outside of Africa so far, the new Dmanisi specimens show clear affinities to African *H. ergaster* rather than to more typical Asian *H. erectus* or to any European hominid. The morphological affinities of the Dmanisi fossils expand the known geographic range of *H. ergaster* (i.e., the African morphotype of *H. erectus*) outside of Africa and into more northerly latitudes, suggesting that the *H. ergaster* morphology may be more than simply a minor geographic variant encompassed within the greater *H. erectus* range of variation. Given the early age and the presence of some Asian *H. erectus* features of the Dmanisi hominid crania, mandible, and dentition, we suggest that these hominids may represent the species that initially dispersed from Africa and from which the Asian branch of *H. erectus* was derived (2).

Situated at the apparent crossroads of hominid dispersal into Europe, it is unexpected that the Dmanisi hominids do not exhibit closer affinities with the later European lineages. However, the early age of the Dmanisi hominids, which predates the earliest occurrence of *Homo* in Western Europe by more than half a million years, supports the view that Western Europe was occupied relatively late in hominid evolution and perhaps explains the lack of morphological continuity between the regions. The Dmanisi site suggests a rapid dispersal from Africa into the Caucasus via the Levantine corridor, apparently followed by a much later colonization of adjacent European areas (*30*).

However, in combination with evidence from Indonesia (*31*), the early age of the Dmanisi hominids and their associated Mode 1 (Oldowan) technology argue for early pre-Acheulean migrations out of Africa and into Asia (*7*). Despite the abundance of suitable raw materials in the Dmanisi area, the presence of Mode I tools probably reflects the early pre-Acheulean age of the site and suggests that similar associations recorded with early East and Southeast Asian *H. erectus* (*32*) may also reflect early dispersal into Asia rather than habitat differences. Later post–1.0 Ma differences in assemblages may result from subsequent migrations or other phenomena (*5*). The early age and Oldowan technology of the Dmanisi site also suggest that the initial hominid dispersal from Africa was driven not by technological innovation (*6*) but more likely by biological and ecological parameters, including the increasing energy requirements of larger hominid body size, perhaps met by greater exploitation of animal protein (*7, 33*). Based on known relationships between home range size and diet quality in primates (*8*), such a foraging shift would allow larger home range sizes and greater dispersal capabilities than were typical of earlier hominids.

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