

A Fourth Hominin Skull From Dmanisi, Georgia

DAVID LORDKIPANIDZE,^{1,*} ABESALOM VEKUA,^{1,2} REID FERRING,³
G. PHILIP RIGHTMIRE,^{4,5} CHRISTOPH P.E. ZOLLIKOFE,⁶
MARCIA S. PONCE DE LEÓN,⁶ JORDI AGUSTI,⁷
GOCHA KILADZE,¹ ALEXANDER MOUSKHELISHVILI,¹
MEDEA NIORADZE,⁸ AND MARTHA TAPPEN⁹

¹Georgian National Museum, Tbilisi, Georgia

²Institute of Paleobiology, Tbilisi, Georgia

³Department of Geography, University of North Texas, Denton, Texas

⁴Department of Anthropology, Binghamton University, Binghamton, New York

⁵Department of Anthropology, Peabody Museum, Harvard University,
Cambridge, Massachusetts

⁶Anthropologisches Institut, Universität Zürich, Zürich, Switzerland

⁷ICREA-Institute of Human Paleoecology (URV-DURSI), Tarragona, Spain

⁸Georgian Archeological Center, Tbilisi, Georgia

⁹Department of Anthropology, University of Minnesota, Minneapolis, Minnesota

ABSTRACT

Newly discovered *Homo* remains, stone artifacts, and animal fossils from Dmanisi, Republic of Georgia, provide a basis for better understanding patterns of hominin evolution and behavior in Eurasia ca. 1.77 million years ago. Here we describe a fourth skull that is nearly complete, lacking all but one of its teeth at the time of death. Both the maxillae and the mandible exhibit extensive bone loss due to resorption. This individual is similar to others from the site but supplies information about variation in brain size and craniofacial anatomy within the Dmanisi paleodeme. Although this assemblage presents numerous primitive characters, the Dmanisi skulls are best accommodated within the species *H. erectus*. On anatomical grounds, it is argued that the relatively small-brained and lightly built Dmanisi hominins may be ancestral to African and Far Eastern branches of *H. erectus* showing more derived morphology. Anat Rec Part A, 288A:1146–1157, 2006. © 2006 Wiley-Liss, Inc.

Key words: early Pleistocene; craniofacial morphology; systematics; species; paleodeme; *Homo erectus*; human evolution

Dmanisi is situated in the Georgian Caucasus. For more than 20 years, the site has been known to contain fauna of Plio-Pleistocene antiquity, and in 1991 a hominin mandible (Gabunia and Vekua, 1995) was recovered during excavations in Block 1, one of three excavation areas that have yielded hominin remains. The jaw is well preserved, with a complete dentition. It has been compared to *Homo erectus* (Bräuer and Schultz, 1996; Rosas and Bermúdez de Castro, 1998). Later, two crania were found in Block 1 (Gabunia et al., 2000), a second mandible was discovered in Block 2 (Gabunia et al., 2002), and a complete subadult skull was collected in Block 2 (Vekua et al., 2002). Remarkable for its small

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*Correspondence to: David Lordkipanidze, Georgian National Museum, 3, Rustaveli Avenue, 0105 Tbilisi, Georgia. Fax: 995-32-982129. E-mail: dlordkipanidze@museum.ge

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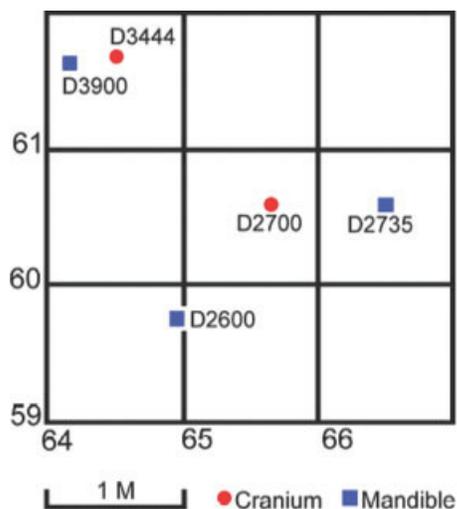


Fig. 1. Block 2 excavation site map.

size, the latter specimen exhibits primitive characters, but like the 1991 mandible and the first two crania, it shows anatomical resemblances to *H. erectus* (Rightmire et al., 2006). To date, our field and laboratory investigations have been directed toward clarifying the sedimentary context within which the fossils occur, gathering taphonomic evidence bearing on site formation, reconstructing the paleoecology of the region in which the hominins lived, establishing the phylogenetic position of the Dmanisi paleodeme, and addressing questions concerning paleobiogeography. Dmanisi seems to document a very early dispersal of hominins from Africa, and it is clear that western Asian populations were important in the origin, evolution, and range expansion of *H. erectus*.

During the 2002–2003 excavations at Dmanisi, a new hominin cranium (D3444) and associated mandible (D3900) were recovered along with lithic artifacts and mammal bones in Unit 64/61 of Block 2 (Fig. 1) (Lordkipanidze et al., 2005). Here we provide information concerning the stratigraphic context of these discoveries and describe the new skull in greater detail.

Stratigraphic Context and Taphonomy of Block 2 Hominins

Radiometric and paleomagnetic data show that all of the Dmanisi fossils were buried shortly after the Olduvai-Matuyama reversal at ca. 1.77 million years (Ma) (Gabunia et al., 2000). Critical geochronological control is provided by an extensive, 30–40 cm thick zone of groundwater calcretes, which envelop the stratigraphic contacts of all the hominin-bearing sediments, and also the higher portions of the uneroded and unweathered Mašavera Basalt. Even conservative estimates of the basalt weathering rate indicate that the sediments containing the Dmanisi hominins were deposited and sealed by the calcretes in less than 10,000 years (Fig. 2). Rapid burial of the Dmanisi fossils is further supported by their physical and microstratigraphic proximity as well as their remarkably intact taphonomic condition. Cranium D3444 and mandible D3900, and immediately

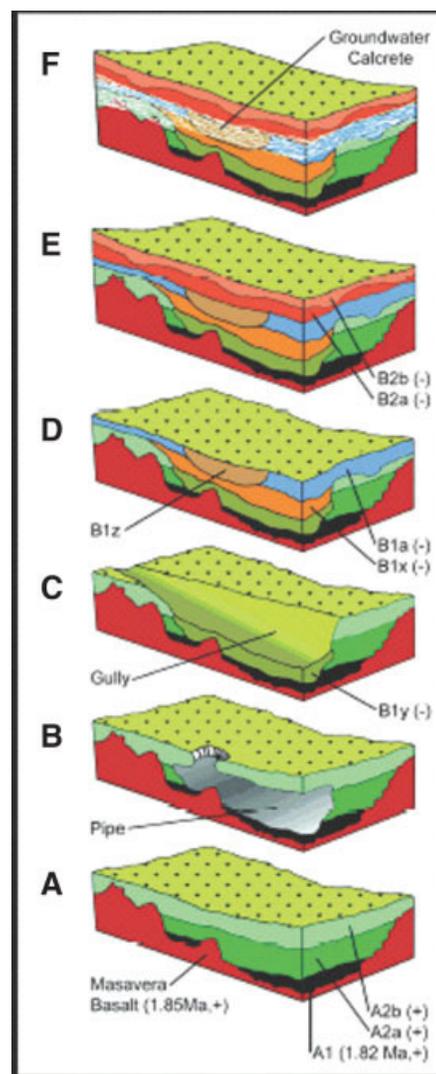


Fig. 2. Geologic history of Block 2 at Dmanisi. Rapid burial and excellent preservation of hominin fossils and associated artifacts and fauna at Dmanisi were enhanced by serial episodes of ashfall deposition and also by piping, a pseudokarstic process that resulted in very short cycles of gully construction and filling. **A:** Deposition of Strata A1–A2 ashes (1.82 Ma, normal polarity) on the uneroded Mašavera Basalt (1.85 Ma, normal polarity). **B:** Piping of A deposits with breaching to surface. **C:** Formation of gullies along the axis of collapsed pipe, and accumulation of Stratum B1y (reverse polarity, as for all the subsequent sediments at site) with bones, artifacts, and hominin fossils D3444, D3900, D2600. **D:** Deposition of B1x sediment, with artifacts, fauna, and hominin fossils D2700, D2735; B1a ashfall deposits veneer site, followed by erosion and filling of B1z gully. **E:** Episodic ashfalls accumulate as Stratum B2, with stratified occupation surfaces. **F:** Calcareous soil formation in B2b deposits, with penecontemporaneous precipitation of subsurface groundwater calcretes enveloping buried geologic contacts and higher parts of Mašavera Basalt. These diagenetic cements seal the underlying deposits and constrain potential age range of all hominin remains to period less than required for weathering of basalt, conservatively estimated to be less than 10,000 years.

associated vertebrate and archaeological remains, were situated 35 cm apart in Stratum B1y, in a heterogeneous granular to sandy silt that is the basal fill of a broad gully formed along the axis of a collapsed pipe. These

sediments, which also contain the D2600 mandible (Gabunia et al., 2002), are just above an erosional contact with Stratum A1, and ca. 50 cm below the Stratum B1x deposits containing the D2700/D2735 skull (Vekua et al., 2002). There are no soils or erosional unconformities in this thin sedimentary succession, demonstrating that the fossils and the associated evidence of human activities accumulated in an extremely brief interval of time.

The new cranium and lower jaw were found within a dense concentration of bones, including hundreds of mammal specimens in very good condition, most in weathering stage 0 and 1 (after Behrensmeyer, 1978) and sometimes in articulated sections, suggesting burial while the ligaments were still attached (Tappen et al., 2006). Many bones from Stratum B1 are whole or represented by more than half the element. Fracture morphology indicates that the material was broken while still fresh, with virtually no evidence for geological transport or postburial breakage. Carnivore tooth marks are the most frequent type of perimortem bone modification and occur on nearly 7% of the 2,000 specimens examined to date. This figure is greater than reported for many fossil accumulations interpreted as dens (Pickering, 2002) but less than found in modern dens (Cruz-Uribe, 1991). The presence of juveniles, coprolites, and long bone shafts with chewed ends implies that carnivores were among the primary agents of bone accumulation, but artifacts together with some stone tool-marked bones indicate that hominins also helped to shape the faunal assemblage (Tappen et al., 2006).

Archaeology

Dmanisi preserves a complex archaeological record of numerous reoccupations, which are registered in both stratigraphic and spatial concentrations of artifacts and faunal remains across all areas of the site. Excavations in Block 2 have revealed a series of horizons throughout Stratum B that contain artifacts, manuports, and culturally modified bones directly associated with hominin remains in Stratum B1. The manuports are ca. 5–10 cm diameter cobbles most commonly of basalt or andesite, carried to the site from terrace deposits and/or channel gravel sources, which at the time of occupations were located at least several hundred meters away. Several large manuports, measuring up to 35 cm in length, were derived from both gravels and Cretaceous bedrock and were presumably used for heavier pounding or breaking activities.

At the time of its discovery in August 2002, the D3444 cranium was embedded in hard matrix, and the endocranial cavity was partially filled with stratified sediment. The sediments enveloping the fossil were discontinuously indurated with groundwater and vadose zone carbonates, necessitating removal of the specimen in a block (Fig. 3). The block was transported to the Georgian National Museum in Tbilisi, where the cranium was prepared by G. Kiladze. Photographs, CT scans, and casts of the block were made during the exposure of the specimen, providing a uniquely detailed chronicle of its context. The D3900 mandible was found in 2003, lying immediately adjacent to the spot from which the cranium had been excavated earlier.

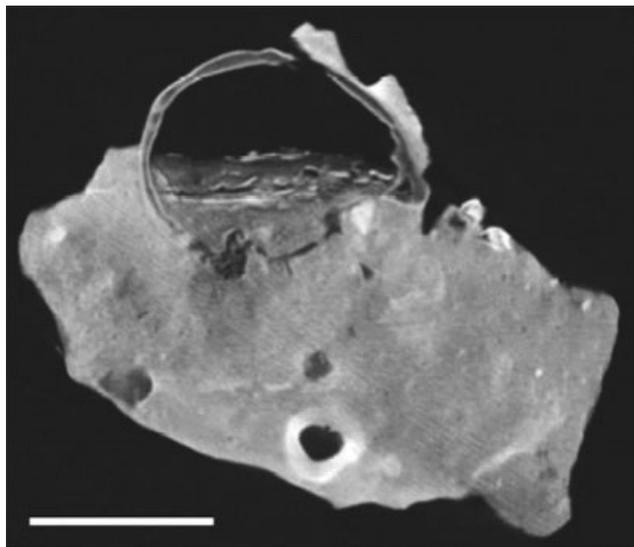


Fig. 3. CT cross-section through the matrix block containing the D3444 cranium. The endocranial cavity is partially filled with stratified sediment. Note the dense concentration of faunal elements around the cranium. Scale bar = 10 cm.

MATERIALS AND METHODS

We present descriptions of the D3444 cranium and D3900 mandible and report a series of standard measurements based on landmarks that are readily identifiable (Tables 1 and 2). Supplementary measurements are given in the text. Endocranial volume can be estimated using the method of seed-filling and also from CT reconstructions. CT imaging was performed at the Oncology Center and the Medical-Diagnostic Center of Tbilisi University using Toshiba Xpeed and Philips medical CT scanners. Following sequential data acquisition, cross-sectional images were reconstructed with standard and bone filters.

Anatomical descriptions encompass the vault, cranial base, and facial skeleton. A number of nonmetric characters are considered. Form of the supraorbital tori, glabellar protrusion, supratoral flattening, creasing associated with the temporal lines, elevation of the temporal squama, midline eminences and keeling, the extent of torus formation and muscle scarring on the occiput, prominence of the mastoid process and its associated crests, expression of a juxtamastoid (or occipitomastoid) eminence, morphology of the mandibular fossa, construction of the tympanic plate and its orientation in relation to the petrous bone are described according to conventions established by Weidenreich (1943) and continued by Rightmire (1990), Tobias (1991), Wood (1991), Antón (2003), and Kimbel et al. (2004).

Facial characters include the course followed by the nasofrontal and frontomaxillary sutures, shape of the individual nasal bones, keeling of the saddle, the relationship of the lateral margin of the aperture (Weidenreich's "crista nasalis") to the floor of the nose, presence of lateral and/or spinal crests (terminology of McCollum et al., 1993), and topography of the nasal floor (Robinson, 1954; McCollum, 2000). As viewed from the front, the lateral boundary of the piriform aperture is scored

TABLE 1. Cranial Measurements (mm) for the Dmanisi hominins and selected representatives of earlier *Homo*

	Dmanisi			Early <i>Homo</i>		<i>H. erectus</i> (Africa)			<i>H. erectus</i> (Asia)			
	D2700	D2280	D2282	D3444	ER1813	ER1470	ER3733	ER3883	WT15000	Sangiran 2	Sangiran 4	Sangiran 17
Whole vault	155	177	—	163	145	168	182	182	—	—	—	207
Cranial length	92	—	—	—	82?	—	107	102	—	—	—	115
Basion-nasion length	100?	—	—	—	94?	—	118	—	—	—	—	129?
Basion-prosthion length	101	—	—	—	98?	—	111?	102	106?	—	—	114?
Basion-bregma height	126	136 ^a	—	132	113	>138	142	140	131	141	147	161
Max. cranial breadth	119	132 ^a	—	120	112	135?	132	129	—	126	132	140
Biauricular breadth												
Frontal bone												
Supraorbital torus thickness												
Central	8	11	10.5	10	9	8	8	11	—	12	—	17
Lateral	6	9	5.5	9	6.5	6.5	9	7	—	8	—	13
Min. frontal breadth	67	75	66	67.5	65	71	83	80	73	82	—	95
Max. frontal breadth	85?	105	87?	91?	—	92	110	105	—	102	—	119
Biorbital chord	90	105?	96?	98	91	109	109	110	96	—	—	115
Postorbital constriction index ^b	74.4	71.4	68.7	68.8	71.4	65.1	76.1	72.7	76.0	—	—	82.6
Frontal sag. chord	89	101	—	93	80	93	104	101	—	—	—	118?
Frontal sag. arc	95	108	>95	101	90	104	119	118	—	—	—	—
Frontal angle	150	149	—	148	139	140	139	140	—	—	—	—
Parietotemporal region												
Max. biparietal breadth	117	119	116?	122	100?	120	131	134	128?	137	140	142
Parietal sag. chord	87	91	82	98	74?	84	82	90	93	98?	—	108?
Parietal sag. arc	91	96	85	105	77?	89	85	95	107	103?	—	—
Lambda-asterion chord	65	70	68	71	64	80	81	74	63	82?	80?	74
Lambda-asterion arc	70	75	72	74	69	88	88	79	76	92?	87?	—
Occipital bone												
Biasterionic breadth	105	104	103?	104	93?	108?	119	115	106	122	126?	124
Occipital sag. chord	70?	76?	—	79	78?	86?	88	75?	69	>71	82	81?
Occipital sag. arc	87?	97?	—	95	96?	105?	118	101?	93	—	108	—
Occipital angle	115.6	108?	—	117	114?	—	103	101	—	—	105	100
Lambda-ionion chord	45?	46?	46?	50	55?	60?	57	48	38	45?	47	52
Inion-opisthion chord	39?	47?	—	42.5	40?	45?	53	51	50	45?	56	57
Occipital scale index ^c	86.6	102.1	—	85.0	72.7?	75.0?	92.9	106.2	131.5	100.0?	119.1	109.6
Foramen magnum length	30	—	—	—	—	—	37	33	36	—	40?	39
Foramen magnum breadth	28?	—	—	28	—	—	32?	26?	27	—	31	29?
Foramen magnum area ^d	660?	—	—	—	—	—	930?	674?	763	—	974?	888?

^aObtained by doubling the measurement to the midline.

^bCalculated as the ratio of min. frontal breadth to the biorbital chord.

^cCalculated as the ratio of the inion-opisthion chord to the lambda-ionion chord.

^dCalculated as π (1/2 length) (1/2 breadth).

TABLE 2. Facial Measurements (mm) for the Dmanisi hominins and selected representatives of earlier *Homo*

	Dmanisi			Early <i>Homo</i>		<i>Homo erectus</i>			
	D2700	D2282	D3444	ER1813	ER1470	ER3733	ER3883	WT15000	Sangiran 17
Nasion-prosthion length	69 ?	—	—	64	90 ?	81	—	77 ?	>75
Biorbital chord	90	96 ?	98	91 ?	109	109	110	103	114 ?
Nasion angle	136	—	142	153	151	155	151	138	141 ?
Nasal bridge width	18 ?	—	21	—	—	22	22	32	24 ?
Nasal bridge height	9.0	—	9.0	—	—	8.0	9.0 ?	9.5	9.0 ?
Nasal bridge index ^a	50.0	—	42.8	—	—	36.3	40.9	29.6	37.5
Nasal bridge angle	90	—	98	—	—	108	101	119	106
Orbit breadth	35	—	38	34	41 ?	44 ?	45	39 ?	44
Orbit height	31	—	32	30	36 ?	35	36	42 ?	40
Midorbital chord	55	—	51	60	64 ?	73	—	70	66 ?
Naso-orbital angle	129	—	130	—	136 ?	135	—	123	123
Nasal breadth	28	27	28	24	27	36 ?	—	36	29
Nasal height	50	—	50	44	58 ?	53	—	57	52 ?
Clivus length	>20	28	—	24 ?	36 ?	30 ?	—	22	25 ?
Bimaxillary chord	97 ?	91 ^b	93	86 ?	98 ?	101	—	100	116 ?
Subspinale angle	143 ?	154 ?	140	144 ?	161 ?	143	—	133	125 ?
Prosthion angle	107 ?	107 ?	—	108 ?	112 ?	102	—	103	—
Cheek height	28	30 ?	25 ?	27	40 ?	34	—	30	37
Max. malar height	39	43.5 ?	40	—	—	53 ?	>58	53 ?	57 ?
Palate breadth	37 ?	39	—	35 ?	—	—	—	40	—
Palate length	55 ?	54	—	54 ?	—	—	—	—	—

^aCalculated as the ratio of nasal bridge height to nasal bridge width.

^bObtained by doubling the measurement to the midline.

as rounded or relatively sharp. The development of a canine jugum and the extent to which this swelling reaches superiorly are noted. Lateral to the jugum, there may be a furrow-like sulcus rather than a broader “canine fossa” situated above the premolar roots. The form of the malar incisure and the cheek itself, morphology of the hard palate, and positioning of the entrance to the incisive canal are all recorded following Rightmire (1998).

Craniofacial anatomy and measurements provide a basis on which to compare D3444 to specimens recovered earlier at Dmanisi. The latter include an adult calvaria (D2280) and the partial cranium of a young adult (D2282) found in 1999, as well as a smaller subadult cranium (D2700) recovered in 2001. Because the form of the D3900 mandibular corpus has been affected by resorption, it cannot be compared metrically with the other Dmanisi jaws (D211, D2600, and D2735). Similarities and differences of the new skull to hominins from other sites are also noted. Here only the more complete *H. erectus* individuals from Koobi Fora (Kenya), Sangiran, Sambungmacan and Ngandong (Java), and Zhoukoudian (China) are considered, along with two additional crania from Koobi Fora that are usually referred to as *H. habilis* and *H. rudolfensis*. Such comparative treatment is purposefully limited, and a more comprehensive analytical study of the Dmanisi paleodeme is given by Rightmire et al. (2006).

State of Preservation

The new cranium is almost complete (Fig. 4). There is a gap in the parietal on the left side, and the anterior portion of the foramen magnum and the basioccipital are missing. On the left, the petrous temporal is broken out. The body of the sphenoid seems to have been crushed, and this region is blocked with matrix contain-

ing bone fragments. The interior of the vault has been cleaned, and parts of the posterior, middle, and, to a lesser extent, the anterior cranial fossae are intact. Much of the facial skeleton is in good condition. On the right, there is some damage to the lower margin of the cheek. No teeth are present, and the maxillary alveolar processes are heavily resorbed. There is little doubt that the edentulous lower jaw (D3900) recovered near the cranium must belong to the same individual. It is well preserved; only the left ascending ramus is missing (Fig. 5).

Endocranial Volume

Cranial capacity as measured with seed is close to 650 cm³. However, this result is dependent on restoring parts of the cranial base that are missing, just anterior to the foramen magnum. CT reconstruction of the complete endocast yields an estimate of 625 ± 5 cm³.

Frontal and Midvault

The glabellar prominence is broad and projecting above the nasal root. Glabella itself is situated in a slight indentation between the medial-most elements of the supraorbital torus. Where it is best preserved on the right side, the brow attains maximum thickening (ca. 12 mm) at a tubercle produced from the outer lip of a well-defined supraorbital notch. At the center of the orbit, thickness is reduced to 10 mm, while the lateral portion of the torus is thinner and bar-like. As in the other Dmanisi crania, there is little definition of a supratatorial sulcus. The least frontal width measured at the temporal lines is 67.5 mm, and breadth taken lower in the temporal fossae is 78 mm. With an index of postorbital constriction of 68.8, D3444 is comparable to D2282, and it is apparent that marked frontal narrowing is a char-

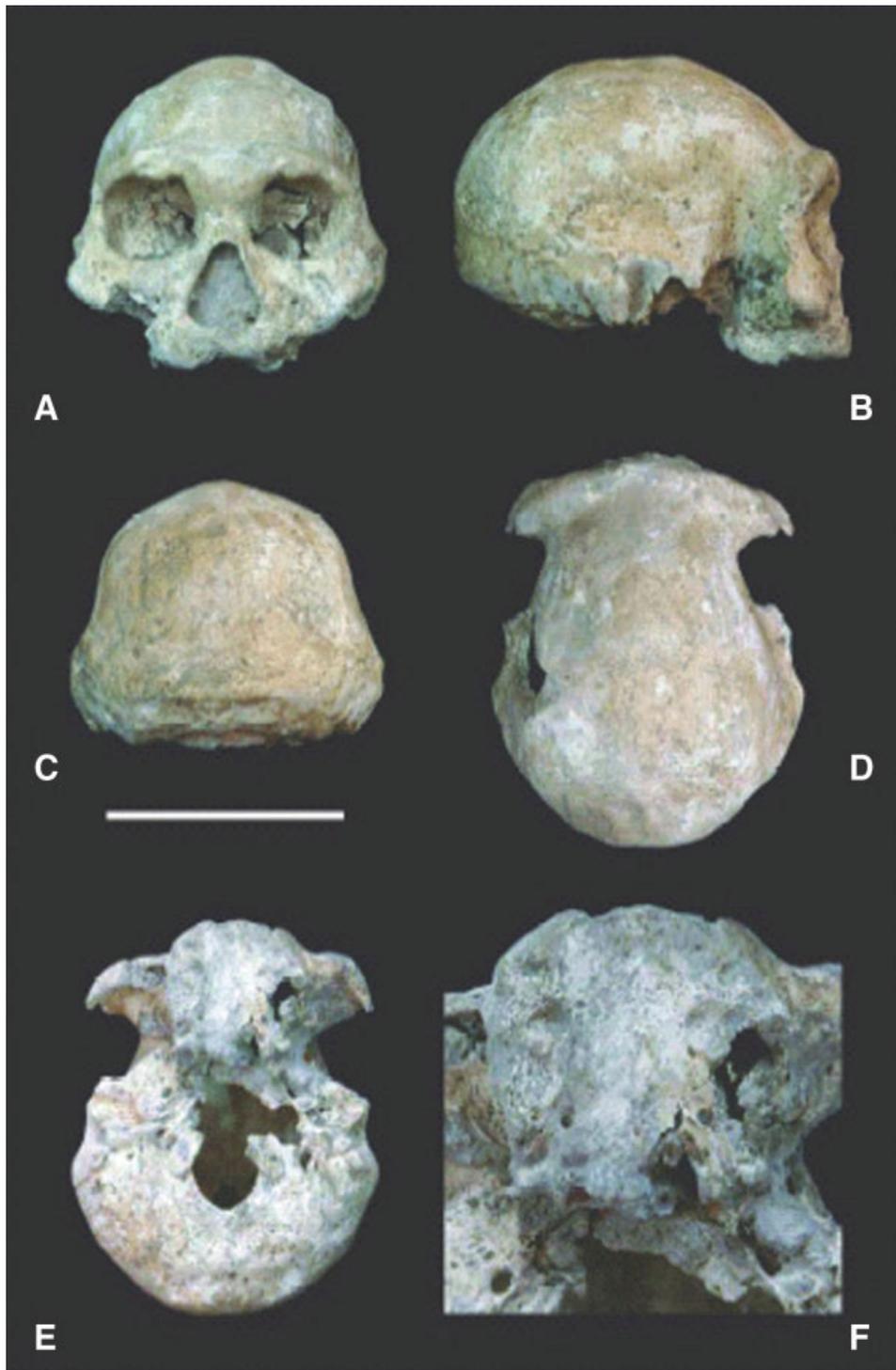


Fig. 4. The D3444 cranium. **A:** Frontal view. **B:** Right lateral view. **C:** Posterior view. **D:** Superior view. **E:** Inferior view. **F:** Occlusal view. Scale bars = 10 cm (A–E); 5 cm (F).

acteristic that all of the Dmanisi individuals share with australopiths and early *Homo*. Behind the brows, the frontal profile is quite flat, and there is no midline keeling.

At bregma, there is a low eminence, and this swelling follows the coronal suture for a short distance on either

side of the midline (Fig. 4D). A blunt sagittal keel is also present. This becomes more prominent posteriorly, where the bone is raised on both sides of the suture but seems to subside centrally. Here the pattern of (double) keeling resembles that in D2280.



Fig. 5. The D3900 mandible. **A:** Right lateral view. **B:** Frontal view. **C:** Occlusal view. Scale bar = 5 cm.

The chord from bregma to lambda is 98 mm, while the arc is 105 mm. The parietals of D3444 are thus lengthened in comparison to those of the other Dmanisi individuals, including D2280. This part of the vault is narrow in relation to its length, as the lambda-asterion dimensions are close to those of D2280 and only slightly greater than the measurements for D2700. The *H. erectus* crania from Koobi Fora also exhibit substantial variation in this feature. KNM-ER 3883 is similar in its proportions to D2280, while the parietals of KNM-ER 3733 are relatively broad.

At their closest approach to the midline, the temporal lines are ca. 70 mm apart. These lines are raised throughout their courses. On each side, the inferior line produces a strong ridge as it curves toward the supramastoid crest. The crest itself is much more prominent in D3444 than in D2700. This structure is damaged in the other Dmanisi crania, but there are no indications that it could have been so well developed. Below the supramastoid crest, there is a shallow sulcus, which extends posteriorly onto the angle of the parietal bone.

Here it separates the angular torus from the faint (superior) temporal line and the nuchal lines below. In the floor of the sulcus, there is a clear incisure, where a tongue of the parietal is inserted between the squamous and mastoid portions of the temporal bone.

The squamous temporal is intact on the right side, and above it a number of fine striations radiate onto the parietal surface. Maximum height of the squama above the outer lip of the zygomatic root is 29 mm. As noted by Weidenreich (1943) for the Zhoukoudian skulls and later confirmed by other workers for African *H. erectus*, the temporal is highest anteriorly. Its upper border is straight relative to the (arched) condition in recent humans and slopes posteroinferiorly to meet the parietal incisure. The tympanic bone outlining the auditory porus is slightly damaged, but this opening (still filled with matrix) must be oval in shape and oriented approximately vertically. As in the other Dmanisi crania, the porus is recessed relative to the shelf-like root of the zygomatic process.

Occipital Bone

The biasterionic width for D3444 (104 mm) is essentially the same as that for the three other Dmanisi specimens. Occipital length (79 mm) is slightly greater than in D2700 or D2280. In side view, the occiput is flexed, and the upper scale is oriented vertically. Its surface is less convex than that of D2700. Height of this plane is 50 mm, while the chord from inion to opisthion is 42.5 mm. The index of scale lengths is thus 85.0. This result is very close to the figure obtained for D2700, and both individuals have relatively short nuchal planes, as is usual for African *H. erectus*. A transverse torus is developed on the D3444 occiput. This ridge is low and mound-like, and more similar to that in KNM-ER 3733 than to the sharply sculpted torus of D2280. Its upper margin is diffuse, but there is slight supratoral hollowing. The lower border is delimited more clearly by the superior nuchal lines. Centrally, the junction of these lines may be abraded, but it is evident that there was no prominent linear tubercle like that in D2280. On each side, the superior line can be followed laterally toward the occipitomastoid suture, but D3444 resembles the other Dmanisi fossils in lacking any retromastoid tuberosities.

The nuchal plane shows only moderate relief (Fig. 4C). No external occipital crest is preserved in the interval between the transverse torus and the inferior nuchal lines. At the confluence of the inferior lines, there is a low bulge, and a thin crest passes from here to the rim of the foramen magnum. Superiorly, to either side of the midline, the attachments for the semispinalis capitis muscles are slightly hollowed. Laterally, below the (faint) inferior lines, the areas occupied by rectus capitis posterior major are restricted in extent but appear flattened. Closer to the midline, the impressions left by rectus capitis posterior minor are depressed. However, some of this excavation must reflect erosional damage to the cortex. Overall, the nuchal surface that is bounded by the transverse torus and the occipitomastoid sutures is flattened, as in the D2280 adult, rather than rounded as in the D2700 subadult. The differences are likely a consequence of growth.

Breadth of the foramen magnum is 28 mm. Length of this opening cannot be measured, but in its size and

shape, the foramen must resemble that of D2700. On the right side, the occipital condyle is complete. Its length is 20.5 mm, and the maximum breadth is 12.0 mm. Behind the condyle, a shallow fossa is present, and its floor is pierced by a small canal. Anteriorly, the hypoglossal canal is damaged on the right side but patent on the left.

Mastoid Region

D3444 is the only Dmanisi cranium to retain a complete mastoid process, and this structure is preserved on each side. The mastoid is short and cylindrical in form. Superiorly (at its base), each process is thickened by the mastoid crest, which traverses the surface in a posterior-to-anterior direction rather than curving downward toward the apex. Above this transverse ridge are the supramastoid sulcus and the strong supramastoid crest. This parallel orientation of the sulcus and crests is not apparent in the D2280 cranium, where the larger, probably more pyramid-like, process and its associated ridges are less complete. In D2282, the process is small, but its shape is indeterminate because of crushing. In the otherwise very well preserved D2700 cranium, both mastoids have been broken away entirely.

The D3444 processes are very inturned, so that the distance between their tips is only 102 mm. By contrast, the breadth measured higher at the supramastoid crests is 132 mm. This inward canting of the long axis coupled with short length allows the mastoid apex to protrude downward only slightly, relative to either the rim of the auditory porus or the more medial aspect of the cranial base. As a result, the digastric incisure is very shallow. It is broad at its posterior terminus and also where it passes forward toward the wall of the petrosal crest. The stylomastoid foramen is situated within this channel, where it lies lateral to the petrosal spine. Because the digastric fossa itself is widened behind the mastoid process and extends onto the lateral margin of the nuchal plane, its orientation in relation to the foramen and the styloid root differs somewhat from that in D2280. In D2280, as in the Zhoukoudian skulls and some other *H. erectus* specimens, the digastric incisure deviates laterally toward the stylomastoid foramen and does not intersect with the styloid pit. In D3444, however, the long axis of the incisure passes through both structures.

The broad digastric impression is bounded medially by a low ridge, just perceptible on the left but more distinct on the right side. This ridge ends posteriorly in a small flange-like tubercle, set 1 cm or so behind the mastoid tip. The tubercle seems to give (added) attachment for the belly of the digastric muscle. Medial to it, there is a channel, situated fully on the temporal but bounded by bone that is heaped up along the occipitomastoid suture. This channel trends anteriorly toward the stylomastoid foramen, and in its floor, there is a narrow groove, possibly for the occipital artery. The adjacent occipitomastoid junction is raised to form an eminence, separated by ca. 15 mm from the mastoid process. Just where it is highest, along the suture line, this eminence follows the scar left by the superior oblique muscle. Therefore, it may be termed an occipitomastoid crest.

In these anatomical details, D3444 resembles the condition noted for several of the crania from Sambungma-

TABLE 3. States for characters identified in the Dmanisi crania and mandibles

Plesiomorphies for *Homo*

- cranial capacity low (600 to 775 cm³)
- frontal narrowing pronounced (postorbital constriction index 68.7 to 74.4)
- mastoid region inflated and laterally projecting
- occipital transverse torus poorly expressed or absent
- occipital scale index low (85.0 to 102.1)
- midfacial contour projecting
- canine jugum prominent and bounded laterally by maxillary sulcus
- zygomaticoalveolar incisure present
- hard palate shallow
- palatal opening to incisive canal situated posteriorly
- mental eminence slight or absent
- symphysis buttressed internally (superior transverse torus)

Synapomorphies with *H. erectus* (*sensu lato*)

- supraorbital torus bar-like and projecting
- bregmatic eminence with parietal sagittal keel
- angular torus present
- temporal squama low with straight upper border
- mastoid tip inturned and flattened posteriorly
- low petrotympanic angle (140° to 150°)
- petrous pyramid smooth (“dense”) in appearance
- foramen lacerum restricted
- nasal saddle prominent

Possible synapomorphies with Asian *H. erectus*

- parasagittal flattening (depression) of parietal surfaces
- paramastoid and occipitomastoid crests present

Possible autapomorphies in the Dmanisi paleodeme

- sagittal keel double
- tympanic plate relatively delicate
- supratubarius process absent
- M3 reduced in size

can and Ngandong in Java. Although the mastoid process and its associated structures are quite small in the Dmanisi specimen compared for example to the much more rugose Ngandong 12 individual, the low ridge medial to the digastric fossa and the stronger occipitomastoid crest correspond to the components of the juxtamastoid eminence described originally by Weidenreich (1951). In the Ngandong crania, there is a “paramastoid” crest, separated by the groove for the occipital artery from the more medial occipitomastoid crest. Both structures contribute to what may more generally be termed a juxtamastoid complex (e.g., Rightmire, 1990). Expression of this complex in D3444 constitutes a synapomorphy with Asian *H. erectus* (Table 3). This character is unlikely to link the Dmanisi population directly with the later Pleistocene Ngandong group, but along with other observations, it suggests that an evolutionary relationship between Dmanisi and the earlier Java hominins is certainly plausible. The evidence from the mastoid region emphasizes the scope of variation to be expected within both Western and Far Eastern *H. erectus*. Also, it once again underscores the fact that the cranial base of earlier *Homo* differs in many respects from that of recent humans.

Mandibular Fossa and Tympanic Plate

The glenoid fossa is virtually intact on the right side (where the tubercle of the zygomatic root is preserved

on a separate fragment; Fig. 4E). Width measured from the entoglenoid process to the ectoglenoid margin is 32 mm. The cavity is thus larger than that of D2700 and probably close in width to that of D2280. Its overall proportions are quite similar to those of D2280. As in the latter specimen, the anterior wall has a convex contour but is curved forward centrally, so as to give the fossa an open (but moderately deep) appearance. There is no clearly defined articular tubercle separating the fossa from the flattened preglenoid planum. Where it crosses this planum, the sphenotemporal suture has begun to close. One of its segments can be followed posteriorly toward the entoglenoid pyramid, where it passes several mm lateral to both the foramen ovale and the foramen spinosum. Detail on the entoglenoid pyramid itself is lost, but this structure must be partly of temporal origin. The sphenoid bone does not contribute to the medial border of the mandibular cavity, and there is no downward projecting sphenoid spine.

As the (posterior) tubercle of the zygomatic bone is present, the full extent of lateral projection of the glenoid articulation can be ascertained. About two-thirds of the cavity is tucked directly under the braincase, but the remainder lies beneath the zygomatic root, lateral to the exterior wall of the vault. This morphology is generally characteristic of *H. erectus*, whereas in recent humans, nearly the entire glenoid surface can be accommodated medially, underneath the substantially expanded braincase. The postglenoid process is lip-like, with a flattened anterior face. It is decidedly less massive than that in D2700. The rear of the D3444 mandibular fossa is composed of the tympanic plate, oriented almost vertically. The plate curves slightly as it reaches inward, where it makes contact with the entoglenoid pyramid. This configuration is similar to that observed in D2700, while in D2280 there is a little more separation of the tympanic from the entoglenoid process. Neither in D2700 nor in D2280 is there much development of a recess marking the medial boundary of the fossa. In D3444, however, the rounded entoglenoid region is oriented so as to create a more crevice-like constriction, where it meets the tympanic plate posteriorly. In this feature, the D3444 individual more clearly approaches the condition described for (some of) the Zhoukoudian hominins (Weidenreich, 1943) and most African *H. erectus* (Rightmire, 1990).

The tympanic bone is slightly damaged laterally, where it forms the rim of the external auditory porus. This part of the plate is not greatly expanded. Indeed, the entire tympanic is relatively delicate in its construction (as in the other Dmanisi crania), rather than thickened, as is usual for Asian and African *H. erectus*. Its inferior border is free from (not fused with) the mastoid process. The blunt petrosal crest slopes downward to produce a prominent spine, adjacent to the jugular opening. This petrosal spine is less projecting but somewhat more massive than that developed in the D2700 subadult. On its posterior aspect, there is a vertical groove, ending on the right side in an empty pit. On the left, the spine itself is damaged, but the groove can be followed superiorly, where it contains the broken root of a (small?) styloid process. Similar traces of styloid development have been noted in some of the East African *H. erectus* crania (Rightmire, 1990), but this process is said to be missing altogether in the Zhoukoudian specimens.

It is absent also in several of the Sangiran fossils. More medially, the D3444 tympanic bone is incomplete, but there is no indication that a supraturbarius process was present.

On the right, much of the petrous temporal is preserved, but its (inferior) surface shows signs of erosion. The jugular fossa is intact, as is the relatively small carotid canal. The apex presents several longitudinal gouges along which cancellous tissue is exposed. There is a general resemblance to the morphology of the D2700 petrous bone, but fewer details can be made out. In D3444, the petrosphenoid contact is present, but all of the basioccipital is missing. It is not possible to see whether a foramen lacerum remained open or whether this structure was constricted, as is usual for *H. erectus*. Orientation of the petrous pyramid within the cranial base can be assessed, and it is clear that the long axis of the pyramid is set in a more nearly sagittal position, relative to the inferior crest of the tympanic bone, than is true for *H. sapiens*. This angulation of the tympanic and petrous axes was noted for *Sinanthropus* by Weidenreich (1943), and it is well documented for other populations of *H. erectus* (Table 3).

Facial Skeleton

The D3444 face is comparatively massive (Fig. 4A) and shows none of the distortion that has affected D2282. There is hard matrix still partially filling the nasal cavity and the paranasal sinuses, but the bone surrounding the orbits is intact, as is some of the orbital interior on each side. Although the ethmoid has been crushed, it is possible to measure the interorbital pillar. Width taken between the anterior lacrimal crests is 21 mm. Height taken from this chord to nasion is 9 mm, and the nasal bridge index is 42.8. The bridge is thus less strongly convex than that of D2700 and more comparable in shape to that of the Koobi Fora specimens. At the frontonasal suture, the nasal bones together are 13 mm wide. These elements narrow slightly in their middle parts and broaden again below. They are broken inferiorly. It is apparent that the nasal bones are set at an angle to one another, so that the saddle is tented but lacks any sharp midline keel. From the side, the nasal profile is gently concave, rather than flattened as in D2700.

The piriform aperture closely resembles that of D2700 in both size and shape. Superiorly, its walls are sharp and everted. If the nasal bones were complete, the saddle would be elevated, relative to the orbital rims. In this degree of nasal prominence, D3444 differs from D2700 and also individuals such as KNM-ER 3733. On the floor of the aperture, the remnants of an incisive crest are preserved. This midline ridge extends forward to produce a blunt tubercle, which projects slightly beyond the nasal sill. Spinal crests that are now faint, but may well have been stronger in their unweathered condition, pass laterally and set the nasal sill off from the clivus immediately below. Just where they turn upward, the borders of the aperture may be described as rounded by the criteria of McCollum et al. (1993). Any lateral crests that were developed have been lost. The sill itself is flattened, and it slopes inward away from the nasal rim more steeply than in D2700. At its posterior pole, there seems to be a distinct step downward

onto the surface of the hard palate (as in the other Dmanisi specimens). The rear of the nasal cavity is filled with matrix. To prevent potential damage during physical preparation, additional anatomical details will be resolved with the aid of CT scanning.

Most of the subnasal part of the facial skeleton has been altered and/or lost through bone remodeling. Enough of the clivus has survived to show that there is little swelling laterally, below the nasal margin, that can be associated with a canine jugum. Such juga are expressed in D2700 and are more prominent in D2282. Their absence in D3444 is unexpected, as this individual is adult and probably a male. It appears that the entire maxillary dentition was lost before death, and the alveolar processes and the clivus were remodeled as the sockets were resorbed.

As a consequence of bone loss due to remodeling, the D3444 midface appears somewhat orthognathic in comparison to that of D2700. Cheek height measured from the orbital rim to the most lateral aspect of the inferior maxillary margin is 25 mm, but height measured more medially, to the lowest point of the masseter attachment on the zygomatic arch, is 30 mm. On the left side, there are two infraorbital foramina. The principal opening is about midway between the orbital margin and the lower border of the cheek. Exiting from the foramen there is a faint vertical groove. This feature is less well marked than in D2700, and it does not reach more than a few mm inferiorly. In neither D3444 nor D2700 is this maxillary sulcus expressed as clearly as it is in D2282 and some African and Far Eastern *H. erectus*. Indeed, the infraorbital region of D3444 is flattened. There is minor hollowing both at the base of the cheek, where the maxillary zygomatic process merges with the wall of the nasal aperture, and also laterally along the zygomaxillary suture. However, no true canine fossa is developed.

Where it arises from the body of the maxilla, the zygomaticoalveolar pillar is quite massive, with an antero-posteriorly thickened root. This morphology is also characteristic of D2700 and D2282. The pillar turns laterally to become almost horizontal, and the incisure is relatively open. At the masseter origin, the inferior border of the cheek curves upward, carrying the muscle scar for 12 or 13 mm toward the zygomaxillary suture. All along its course, the masseter attachment is rugose, but there is no malar tubercle. The contour of the cheek is rounded but becomes flatter posteriorly. Maximum vertical height of the zygomatic bone is 40 mm on the left side and 38 mm on the right.

Shape of the dental arcade cannot be determined with any confidence, but the palatal roof is preserved. In its proportions, the D3444 hard palate must be similar to those of the other Dmanisi individuals. Length from staphylion to orale cannot be measured, but the distance from staphylion to the incisive fossa is 36 mm. The equivalent chords for D2700 and D2282 are ca. 39 mm. In both of the latter faces, the entrance to the incisive canal is set well back from the anterior tooth roots, as in other *H. erectus*. If it is assumed that this posterior displacement of the canal is about the same in all three crania, then the restored internal length of the D3444 palate must exceed 51 mm. Width can be assessed from the spacing between the greater palatine foramina, which are in place on each side. Taken as a minimum, this distance is 23 mm for D3444, 22 mm for D2700, and

25 mm for D2282. These measurements suggest that the palate of D3444 may be broad relative to that of D2700 and more comparable in shape to that of D2282. The D3444 palate also appears to be shallow, most probably as a consequence of resorption of the alveolar processes following tooth loss. Posteriorly, there is weak development of a midline torus. Surface relief is otherwise very slight, as in the other Dmanisi palates.

Mandible

In the D3900 mandible, all sockets but those for the canine teeth have been resorbed (Fig. 5). It is clear that the left canine persisted in its socket at the time of death. The alveolus for the right canine is partially resorbed, indicating antemortum tooth loss. Overall, D3900 has been reduced in size as a consequence of remodeling, and in its principal linear dimensions the specimen is now slightly smaller than D2735.

What remains of the symphysis is low, and there is a distinct midline eminence. However, this blunt projection must be viewed as an effect of the remodeling process, and in its original state the symphysis would have been both higher and more uniformly flattened in profile. On the right side, a single large mental foramen is located about 13 mm above the base. This passage slopes downward into the mandibular canal. Just posterior to the foramen, the lateral wall of the body presents an eroded appearance, and this may be a further indication of pathology.

Internally, an alveolar planum recedes from the region where the incisors were implanted. Below this shelf, there are traces of a pit containing small genial tubercles. The morphology of the subalveolar fossa has been mostly obliterated. On the right, some roughening/scalloping of the internal aspect of the angle reflects attachment of the lateral pterygoid muscle. The angle itself is slightly everted. Here the ramus is very thin, and there is a small perforation situated about 5 mm from the base.

DISCUSSION

Age and Sex

The D3444/D3900 skull is clearly adult. Assessing individual age from human skeletal remains is problematic, particularly when only a cranium and mandible can be examined. Sinus development, vault thickness, suture closure patterns, and overall morphology can be recruited in an attempt to refine this estimate, but it is not possible to provide a precise age at death. Even for recent populations, cranial synostosis is known to be of low utility as an age indicator (Meindl and Lovejoy, 1985). For archaic species such as *H. erectus*, where growth and maturation likely differed from the norms established within *H. sapiens*, the method must be used with caution (e.g., Antón, 1999).

Sex can be determined with more confidence when craniofacial features are well preserved. For recent humans, size and general rugosity provide a first impression, and this can be confirmed by reference to glabella and the supraorbital region, the mastoid and supramastoid crests, muscle attachment areas on the occiput, orbital proportions, construction of the zygomatic arches, definition of tubercles associated with the bony chin, and shape of the angles of the mandible. For D3444 and D3900, sex must be evaluated within the context provided by the Dmanisi assemblage. Four other individuals provide information

about variation in cranial and mandibular morphology in this ancient population.

The D3444 cranium displays many of the features anticipated in males of the genus *Homo*. The glabellar region is broad and prominent above the nasal root, and the supraorbital tori are projecting. Mastoid crests are strongly developed, and the mastoid portion of the temporal bone is laterally inflated. On the occipital, a blunt transverse torus is bounded inferiorly by hollowing associated with the nuchal muscles. The upper face is relatively broad, and the cheek is massive. To a greater extent than the D2700 subadult or even the larger D2280 braincase, D3444 shows "male" morphology. If this is a correct interpretation, then it is evident that within the archaic Dmanisi population, at least one older male was relatively small in size. That some other males were larger is almost certainly documented by the D2600 mandible, which has been attributed to the (new) species *H. georgicus* by Gabunia et al. (2002).

Tooth Loss and Bone Remodeling

The edentulous face of D3444/D3900 presents a striking contrast to other Dmanisi individuals. The appearance of the specimen may reflect aging or pathology. Applying clinical comparative standards (Atwood, 1971), such advanced alveolar bone atrophy indicates substantial tooth loss (96.8% as calculated following Cuzzo and Sauter, 2004) several years before death. Further studies are necessary to identify the ultimate causes of the observed pattern. Nonetheless, we are aware of no other fossil hominins that display such extensive tooth loss and remodeling. Also, recorded instances of wild nonhuman primates showing comparable masticatory impairment are extremely rare. We know of only one example: the skull of a fully adult but completely edentulous wild-shot male chimpanzee from Cameroun [illustrated by Miles and Grigson (1990) and held in the collections of the Powell-Cotton Museum, Kent, U.K.]. The extent of alveolar bone atrophy and remodeling suggests that this animal had lost all of its teeth some years before death.

Because no apes live today in a temperate environment similar to that at Dmanisi, the behavioral and even social implications of the edentulous hominin specimen must be considered within the biocultural context preserved at the site. It is evident that D3444/D3900 survived for a significant period without consuming foods that required heavy chewing. Inferences regarding subsistence must be drawn with caution (Lebel et al., 2001; DeGusta, 2002). However, it may be hypothesized either that this individual was able to survive without help by utilizing softer plant foods and extracting animal brain and marrow with stone tools and manuports, or that the Dmanisi hominins could offer assistance to individuals beyond the level observed in nonhuman primates (Lordkipanidze et al., 2005). Currently, neither hypothesis can be falsified, but they raise provocative questions regarding the social attributes of early *Homo*. We argue that the Dmanisi hominins were capable of exploiting a wide spectrum of food sources on an individual basis and/or as a group. While there are at present no data on plant consumption at Dmanisi, animal carcass processing is well documented at the site. Animal foods including both meat and softer tissues may have been an important portion of the diet, and it is reason-

able to assume that the population survived the winter by greatly increasing acquisition and consumption of faunal resources.

Taxonomic and Phyletic Implications

Apart from facial remodeling, D3444 and D3900 are similar to the crania and jaws discovered earlier. With the possible exception of the D2600 mandible (Gabunia et al., 2002), all of this material can be assigned to a single paleodeme (Rightmire et al., 2006). D3444 is likely an older adult and may be a male. Treated together, the Dmanisi skulls show several traits that appear to be primitive, in the sense that they are present in species of *Australopithecus* and other Plio-Pleistocene African hominins (Table 3). These characters include low cranial capacity, midfacial projection, flexion of the malar pillar, frontal constriction, inflation of the mastoid region, weak expression of an occipital transverse torus, a shallow palate, a thickened vertical mandibular symphysis with little/no mental eminence, a sloping alveolar planum, and internal transverse tori.

In many other aspects of their morphological bauplan, the Dmanisi hominins resemble *H. erectus*. Traits clearly diagnostic for this species are an elevated nasal saddle and a bar-like supraorbital torus, sagittal keeling on the parietals, a low temporal squama with a straight upper border passing downward toward asterion, flexion of the occiput, and a constricted foramen lacerum. As noted by Gabunia et al. (2000), the Dmanisi skulls are broadly similar to those referred to as African *H. erectus* (= *ergaster*). However, the Caucasus fossils share some characters only with the Far Eastern populations. Such synapomorphies include parasagittal flattening of the posterior vault, and the occurrence of both paramastoid and occipitomastoid crests, as in the Ngandong assemblage from Java. Other traits, such as a double sagittal keel (D3444 and D2280), a relatively delicate tympanic plate, and the architecture of the medial glenoid fossa, may be regarded as autapomorphic (uniquely derived) for the Dmanisi hominins.

Regional variation is to be expected within any polytypic species. Patterns of morphology in diverse local populations may reflect periodic isolation and opportunities for drift, or adaptation to novel environmental circumstances. Characters that appear to be stable within fossil assemblages, and differ consistently on a regional basis, may provide clues concerning the evolutionary history of populations making up *H. erectus*. In overall size and proportions, the Dmanisi crania appear primitive. Some workers will prefer to emphasize resemblances to early *Homo* or *Australopithecus* in their considerations of taxonomy and phylogenetic relationships. However, the Dmanisi vault, cranial base, and facial skeleton display a suite of traits that are best interpreted as synapomorphies with *H. erectus* (Table 3). On anatomical grounds, it can be argued that the Dmanisi hominins are close to a stem, relative to which other allopatric groups of *H. erectus* are somewhat more derived. The evidence is consistent with viewing the Dmanisi paleodeme as ancestral to African and Far Eastern branches of the species (Rightmire et al., 2006).

Just where *H. erectus* evolved is presently uncertain. An African origin has been widely advocated, but this scenario is no longer the only one tenable (Dennell and

Roebroeks, 2005). The evidence available (mainly from the eastern Rift in Africa and the southeast Asian tropics) is still too sparse to permit a realistic biogeographic reconstruction of this event. But an Asian origin for *H. erectus* must now be considered (cf. Asfaw et al., 2002). Dmanisi, dated at ca. 1.77 Ma, is ancient enough to meet the requirements of such an hypothesis, and the site is in an area of western Asia from which populations could relatively easily have dispersed to eastern Africa. Our findings also suggest movement of populations from the Caucasus across southern Asia to the Far East. At present, there are few archaeological traces marking the passage of hominins through this region at the beginning of the Pleistocene, but it is likely that the first occupations involved small groups, having little impact on the landscape. As the Dmanisi paleodeme is expanded by additional discoveries, it will be possible to explore these questions of systematics and dispersal with greater confidence.

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