Skull 5 from Dmanisi: descriptive anatomy, comparative studies, and evolutionary significance

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Abstract

A fifth hominin skull (cranium D4500 and mandible D2600) from Dmanisi is massively constructed, with a large face and a very small brain. Traits documented for the first time in a basal member of the *Homo* clade include the uniquely low ratio of endocranial volume to basicranial width, reduced vertex height, angular vault profile, smooth nasal sill coupled with a long and sloping maxillary clivus, elongated palate, and tall mandibular corpus. The convex clivus and receding symphysis of skull 5 produce a muzzle-like form similar to that of *Australopithecus afarensis*. While the Dmanisi cranium is very robust, differing from OH 13, OH 24, and KNM-ER 1813, it resembles *Homo habilis* specimens in the “squared off” outline of its maxilla in facial view, maxillary sulcus, rounded and receding zygomatic arch, and flexed zygomaticoalveolar pillar. These characters distinguish early *Homo* from species of *Australopithecus* and *Paranthropus*. Skull 5 is unlike *Homo rudolfensis* cranium KNM-ER 1470. Although it appears generally primitive, skull 5 possesses a bar-like supraorbital torus, elongated temporal squama, occipital transverse torus, and petrotympanic traits considered to be derived for *Homo erectus*. As a group, the Dmanisi crania and mandibles display substantial anatomical and metric variation. A key question is whether the fossils document age-related growth and sex dimorphism within a single population, or whether two (or more) distinct taxa may be present at the site. We use the coefficient of variation to compare Dmanisi with *Paranthropus boisei*, *Homo erectus*, and recent *Homo sapiens*, finding few signals that the Dmanisi sample is excessively variable in comparison to these reference taxa. Using cranial measurements and principal components analysis, we explore the proposal that the Dmanisi skulls can be grouped within a regionally diverse hypodigm for *Homo erectus*. Our results provide only weak support for this hypothesis. Finally, we consider all available morphological and paleobiological evidence in an attempt to clarify the phyletic relationship of Dmanisi to *Homo* species evolving >2.0 to 1.0 Ma.

Introduction

The Early Pleistocene site at Dmanisi in the Georgian Caucasus is well known for its diverse fauna, exceptionally well preserved hominin remains, and quantities of stone artifacts. The first human mandible (D211) was recovered from Block 1 in 1991 (Gabunia and Vekua, 1995), and two crania followed in 1999 (Gabunia et al., 2000). A second mandible (D2600) was found later in Block 2 (Gabunia et al., 2002). To date, excavations in Blocks 1 and 2 have produced an adult braincase (skull 1), a young adult (skull 2), a juvenile (skull 3), an aged edentulous individual (skull 4), and a mature adult (skull 5, comprising cranium D4500 and mandible D2600) (Vekua et al., 2002; Lordkipanidze et al., 2006, 2013; Rightmire et al., 2006), the subject of this study. Postcranial bones from Block 2 include vertebrae, ribs, clavicles, humeri, a lower limb, and partial foot. Much of this material is quite complete and yields valuable information concerning the body mass and proportions, stature, and locomotor capabilities of the Dmanisi hominins (Lordkipanidze et al., 2007; Pontzer et al., 2010). Field and laboratory investigations continuing for more than 30 years have been directed toward clarifying the sedimentary context within which the fossils and artifacts occur (Gabunia et al., 2000; Lordkipanidze et al., 2006; Ferring et al., 2011), gathering taphonomic evidence bearing on site formation (Tappen et al., 2007), reconstructing the paleoecology of the Dmanisi region (Messenger et al., 2010), addressing questions concerning the archaeological record (Baena et al., 2010; Mgeladze et al., 2011), and understanding the paleobiology and evolutionary significance of the hominin assemblage (Rightmire and Lordkipanidze, 2009; Pontzer et al., 2010; Lordkipanidze et al., 2013).

Radiometric and paleomagnetic data show that the Dmanisi fossils were buried shortly after the Olduvai-Matuyama reversal, ~1.77 million years ago (Ma) (Gabunia et al., 2000). Rapid burial leading to near-perfect preservation of remains was effected by serial episodes of ash fall deposition and also by subterranean piping, an erosional process that resulted in very short cycles of gully construction and filling. Deposition of strata A1–A2 ashes on the Mašavera Basalt (1.85 Ma, normal polarity) was followed by piping of A deposits with breaching to the surface, pipe collapse and formation of gullies, and accumulation of reverse polarity stratum B sediments with bones and artifacts (Lordkipanidze et al., 2006). Skull 4, skull 5, and associated vertebrate and archaeological remains were situated in stratum B1y, in a heterogeneous granular to sandy silt filling the base of a broad gully formed along the axis of a collapsed pipe. These sediments are just above an erosional contact with stratum A1, and ~ 50 cm below the stratum B1x deposits containing juvenile skull 3 and associated postcranial elements. There are no soils or erosional disconformities in this thin sedimentary succession, demonstrating that the fossils and traces of human activities accumulated in an extremely brief interval of time (Lordkipanidze et al., 2006).

Ongoing research has revealed 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. Recently completed excavations in the M5 sector, to the west of the main excavation blocks, have yielded in situ stone flakes, cores, and heavily weathered

animal bones from the older stratum A deposits, dating to ~1.85 Ma. Coupled with the findings from Blocks 1 and 2, this evidence demonstrates that there were repeated occupations at Dmanisi over several thousands of years (Ferring et al., 2011). It is likely that the local hominin population was relatively large and well established, rather than sparse and ephemeral (Lordkipanidze et al., 2013).

The Dmanisi crania and mandibles display a substantial range of anatomical and metric variation. This observation raises the question of whether the fossils document age-related growth and sex dimorphism within a single population (Lordkipanidze et al., 2006; Rightmire et al., 2006; Van Arsdale, 2006), or whether two (or more) distinct taxa may be present at the site (Schwartz, 2000; Schwartz and Tattersall, 2003; Skinner et al., 2006). Our previous resampling analyses have showed that for individual measurements, the level of size variation within Dmanisi mandibular pairs (eg. D2600/D211) may be greater than in *Homo sapiens* and, for some dimensions of the corpus and dental arcade, excessive relative to that of *Pan troglodytes* or even *Gorilla gorilla* (Rightmire et al., 2008). However, when a multivariate nested resampling analysis (see Van Arsdale, 2006) is applied, the Dmanisi hominins differ no more than would be expected for individuals within a relatively dimorphic ape population (Van Arsdale and Lordkipanidze, 2012). Resampling statistics can also be used with geometric morphometric data. Shape variation among either the five Dmanisi calvaria, or the three more complete crania, has been compared with variation in samples of *P. troglodytes*, *Pan paniscus*, and modern *H. sapiens* (Lordkipanidze et al., 2013). For the calvarial analysis, the Dmanisi maximum inter-individual distance is greater than the resampled maximum distance in 347/1000 cases for *P. troglodytes troglodytes*, 779/1000 cases for *P. t. verus*, 1000/1000 cases for *P. t. schweinfurthii*, 747/1000 cases for *P. paniscus*, and 804/1000 cases for *H. sapiens*. When the entire cranium is considered, the maximum phenetic distance between Dmanisi individuals is below the 95th percentile values in all *P. troglodytes* demes, and close to the 95th percentile value for *P. paniscus* and modern humans. These results indicate that the magnitude of calvarial and cranial shape variation within the Dmanisi sample is similar to that within most (but not all) *Pan* demes and recent humans.

Other workers find evidence for multiple taxa. On the basis of mandibular measurements, Skinner et al. (2006) have suggested that either the Dmanisi population was so sexually dimorphic as to raise doubts about its status within *Homo*, or D2600 should be grouped separately from the other specimens. Martínón-Torres et al. (2008: 270) also comment on the “unusual” morphology of D2600 as pointing to “the likely existence of two distinct paleodemes” at the site. Bermúdez de Castro et al. (2014) affirm that the small Dmanisi mandibles resemble *Homo habilis* and/or *Homo ergaster*, whereas D2600 documents a different growth pattern. Both Bermúdez de Castro et al. (2014) and Schwartz et al. (2014) refer skull 5 to *Homo georgicus* (Gabunia et al., 2002). Schwartz et al. (2014: 360) comment that denying skull 5 a distinct identity “is effectively to deny the utility of morphology in systematics, a radical proposition to which few would subscribe.”

Dmanisi marks the earliest documented occurrence of human fossils outside of Africa. The fossils have previously been described as *H. erectus* with similarities to the Turkana Basin hominins (Gabunia and Vekua, 1995; Vekua et al., 2002; Antón, 2003), regarded as early *H. erectus* retaining primitive features (Rightmire et al., 2006), likened to *H. ergaster* (Gabunia et al., 2000), and attributed to the (new) species *H. georgicus* (Gabunia et al., 2002; de Lumley et al., 2006). Also, it has been suggested that the small-brained Dmanisi specimens fall beyond the limits of “any morphological or behavioral characterization” of genus *Homo*, implying that all of the material should be placed in a separate taxon (Tattersall, 2016: 3).

We have noted that several of the Dmanisi skulls resemble KNM-ER 3733 and other *H. erectus* individuals from the Turkana Basin (Rightmire et al., 2006). Similarities to *H. erectus* fossils from Sangiran (Java) are present but less numerous. In addition, the midface of skull 5 exhibits morphological similarities to the AL 666-1 maxilla from Hadar, the SK 847 partial cranium from Swartkrans, and the OH 65 palate (Lordkipanidze et al., 2013). All of these specimens share a suite of features that is near-universally accepted as diagnostic for the genus *Homo*. These observations reinforce the strong African affinities of the Dmanisi population and appear to place it within *H. erectus*, considered to be a geographically widespread and polytypic species.

In this article, we describe the anatomy of skull 5 in detail, address the question of age at death, and confirm that this individual is a very robust male. The relationship of skull 5 to other Dmanisi individuals is clearly a key issue, not yet resolved. Our account of similarities and differences among the crania, mandibles, and teeth provides a comprehensive basis for evaluating the null hypothesis that only one taxon is represented at the site. We use the coefficient of variation (CV) to compare Dmanisi with appropriate reference groups including recent humans and fossil hominins. Our second goal is to clarify the evolutionary role played by the Dmanisi population. We begin with the hypothesis that the Dmanisi skulls are best grouped within a regionally diverse hypodigm for *H. erectus*. Using assessments of discrete characters along with measurements, we compare the Dmanisi hominins to representatives of *H. erectus* from Africa and Asia, early *Homo*, *Australopithecus*, and *Paranthropus*. Principal components analysis (PCA) based on size-adjusted cranial measurements offers a method for simplifying such comparisons and serves as a test of our working hypothesis. We then consider all available morphological and paleobiological evidence in an attempt to clarify the affinities of Dmanisi to currently recognized species of *Homo*.

Materials and methods

We provide anatomical descriptions for skull 5 as a whole, the frontal bone and midvault, the occipital bone, the mastoid region, the tympanic plate and petrous temporal, the mandibular fossa, the temporal fossa and pterygoid process, the facial skeleton, the palate, the mandible, and the dentition. Numerous non-metric characters are considered. Fifty-seven linear dimensions and

angles measured on the braincase, cranial base, face, mandible, and teeth are listed with their definitions in the Supplementary Online Material (SOM) Table S1.

Skull 5 and other individuals from Dmanisi (Table 1) were compared to fossils representing *Paranthropus*, *Australopithecus*, and earlier *Homo* (Table 2). Reference populations selected for our study of relative variation include *P. boisei*, acknowledged to be one of the most securely documented of earlier hominin taxa. *Paranthropus boisei* was probably quite sexually dimorphic in skull size (Wood and Constantino, 2007). Our sample of *H. erectus* includes fossils from Africa and eastern Asia. Within this polytypic species, there is variation related to time, geographic region, and dimorphism in local populations (Antón, 2003; Villmoare, 2005; Terhune et al., 2007; Baab, 2008a, 2016). Our third comparator is modern *H. sapiens*. We utilized samples of sub-Saharan African crania measured by de Villiers (1968) and Howells (1973, 1989), thus capturing the variation present in one continental region rather than differences expressed world-wide.

To evaluate the variation within the Dmanisi assemblage and other samples, we applied the coefficient of variation (CV). When the number of individuals is small, the CV may be modified as $(1 + 1/4N) \times (100s/\bar{X})$, where N = sample size, s = standard deviation, and $\bar{X}$ = arithmetic mean (Sokal and Braumann, 1980). The resulting unbiased statistic is V^* .

To explore relationships of the Dmanisi assemblage to early *Homo* and *H. erectus* (Table 2), we used PCA, conducted with JMP release 8.0.2 (distributed by SAS Institute Inc.). Principal components analysis finds linear combinations of the original measurements, computed so as to account for maximum variance among the specimens (Cooley and Lohnes, 1962; Reyment and Jöreskog, 1993). The first component explains the largest percentage of total variance. Subsequent axes are computed to maximize the variance not described previously, subject to the constraint of orthogonality. Often just the first few PCs are retained, as two- or three-dimensional maps showing patterns in the data (Cavalli-Sforza et al., 1994; Zelditch et al., 2004).

Results and preliminary discussion

Preservation of skull 5

The basicranium, vault, and face of D4500 are virtually complete (Fig. 1). There is minor damage to the frontal on the left side, where a wedge of cortex has been broken out behind the brow ridge. A few mm more medially, there is a puncture made by an excavator's nail as the specimen was being uncovered in the site. Higher on the vault, there is an oval depression just to the right of the midline, approximately one third of the way between the brow and the coronal suture. The floor of this depression is eroded and pierced by a small foramen. This canal passes inward through both tables of the bone. D4500 has suffered (premortum) trauma to the right zygomatic region, where the arch is broken and displaced medially. Computed tomography (CT) imaging suggests the presence of an old (healed) fracture and also a more recent break. On the left side, the mandibular fossa is flattened, and definition of the ectoglenoid process and articular

tubercle has been lost. These alterations, along with lipping along the lateral and anterior margins of the deformed temporomandibular joint (TMJ), constitute evidence of osteoarthritis (Rando and Waldron, 2012). The nasal aperture is partially plugged with stony sediment, and additional matrix adheres to the floor of the left orbital cavity. Other aspects of facial morphology are unobscured. All of the maxillary teeth are present, but the incisors and canines show extreme attrition. There are indications of abscessing (or cyst formation) associated with the apex of the right lateral incisor root and perhaps also the left central incisor. The premolar crowns are heavily worn, especially on the left side. Only the right P⁴ retains enamel on the buccal cusp and at the lingual margin. The M¹ surfaces display deeply excavated dentine surrounded by thin borders of enamel. On the M² crowns, the buccal cusps are partially preserved, and on the M³s, much of the enamel cap has survived (small islands of dentine are exposed).

The D2600 mandible is less complete (Fig. 1). The symphyseal region is intact, but on the left side the corpus is damaged below P₃, and the posterior part of the alveolar process has been heavily eroded. There are obvious pathologies (radicular lesions, remodeling associated with premortum or antemortum tooth loss) related to dental attrition (Gabunia et al., 2002; Rightmire et al., 2008; Margvelashvili et al., 2016). Cancellous tissue is exposed in a deep pit at the apex of the right lateral incisor root, about midway between the alveolar margin and the base. The anterior teeth are reduced to stumps from which nearly all of the enamel has been lost. On the left, P₄ and M₁ are missing, and their alveoli have been partially resorbed. The M₂ crown has been reduced to dentine, and its roots are fully exposed buccally. On the right, P₄ has been lost. A small portion of the M₁ crown base remains in place, along with its root system. As in the maxilla, the molars exhibit a steep wear gradient. Only the M₃ crowns retain appreciable amounts of enamel. Both rami are heavily damaged. The mandibular condyles and coronoid processes are preserved, but the left condyle exhibits flattening of its articular surface. This area is marked by many small pits/irregularities, and there is minor osteoarthritic lipping at the articular margins.

Biological age

Assessing individual age from human skeletal remains is problematical, particularly when only a cranium and mandible can be examined. Dental development, wear on the occlusal surfaces, cortical bone remodeling, suture closure patterns, and overall morphology can be recruited in an attempt to refine an estimate, but it is often not possible to provide a precise age at death (Lovejoy, 1985; Işcan, 1989; Buikstra and Ubelaker, 1994; Jackes, 2000). For non-modern populations, or for archaic species where patterns of growth and maturation almost certainly differed from the norms established within *H. sapiens*, the utility of standards based on living humans is uncertain.

In skull 5, dental eruption has been completed, and all of the teeth show heavy wear. Prominent cranial superstructures, including an angular torus and cresting in the mastoid region along with full differentiation of tabular bone and diploë, indicate that this individual is a mature

adult. Sagittal vault contours reflecting extreme frontal flattening and occipital flexion (Antón, 1999) support this diagnosis. Further information relevant to the age of skull 5 comes from the pattern of ectocranial suture closure. As assessed directly from the specimen or from CT imaging, the spheno-occipital synchondrosis is fused. The coronal and sagittal sutures are fully fused. However, large portions of the lambdoid suture remain open on both sides. In the face, the nasofrontal sutures are unfused, and the nasal bones are clearly outlined. Contacts between the frontal and the zygomatic bone are open.

Trends in cranial synostosis characteristic of earlier *Homo* remain largely unknown. Weidenreich (1941, 1943, 1951) concluded that suture closure must have progressed rapidly in *H. erectus* at Sangiran and Ngandong, and application of his reasoning would identify skull 5 as an “adolescent” or young adult. Evidence provided by cranial superstructures, vault contours, the mandible, and the teeth does not fit with such an assessment. It is far more likely that skull 5 is an older adult, still showing incomplete sutural fusion in some portions of the vault and face. Rates of synostosis in the Dmanisi hominins might have been delayed relative to those in African apes and approximated the condition usual for later *Homo*. If this were the case, then the method of Meindl and Lovejoy (1985) would be applicable. A composite score (9) based on the lateral anterior system places skull 5 in an interval of 33–76 years, with an estimated age at death of 51.9 years. Scoring for the vault sutures provides an estimate of 48.8 years. Skull 5 appears to be advanced in age, relative to most other members of the Dmanisi population.

Sex

Cranial and mandibular form are known to be useful in sex determination. For recent humans, size and general rugosity provide a first impression, to be confirmed by reference to glabella and the supraorbital region, the mastoid and supramastoid crests, muscle attachment areas on the occipital, orbital proportions, construction of the zygomatic arches, definition of tubercles associated with the bony chin, and shape of the angles of the mandible (Krogman and Işcan, 1986; Buikstra and Ubelaker, 1994; Ubelaker, 1999). For archaic hominins, it is presumed that size differences (usually among adults) will be a useful guide to intersexual variation as well as other variation between individuals within populations. However, patterns of dimorphism for the cranium, mandible and teeth differ between species, implying that one cannot simply compare variation across traits and assume that each will yield a similar signal of dimorphism for any particular group (Plavcan, 2001, 2002, 2012). Patterns established for modern humans, or other reference populations, should not be assumed uncritically to be appropriate templates applicable to ancient *Homo*. A conservative position is that the sex of a given specimen can be determined with relative confidence only in the context provided by other penecontemporary individuals thought to represent the same species.

At Dmanisi, five crania now provide information about variation in morphology. D2280 has the largest vault with a capacity of 730 cm³. The thickened brow ridge, angular torus, and sculpted nuchal lines are in keeping with identification as an (adult) male (Rightmire et al.,

2006). D2282 is severely damaged, but its relatively thin supraorbital torus, small mastoid process, and smooth occipital are suggestive of female status. The gracile morphology of the D211 mandible supports this diagnosis. The D3444 cranium carries a number of features anticipated in males of the genus *Homo* (Lordkipanidze et al., 2006). The glabellar region is broad and prominent, supraorbital tori are projecting, mastoid crests are strongly developed, and there is a blunt transverse torus on the occipital. Skull 5 is more massively constructed still. If D4500/D2600 is indeed conspecific with other Dmanisi individuals (our null hypothesis), the very robust face, prominent juga associated with large canine roots, and high mandibular corpus with marked lateral and marginal relief leave little doubt that this hominin is male.

Anatomical descriptions of the cranium (D4500), mandible (D2600), and dentition

Skull 5 as a whole Endocranial capacity of D4500 as determined from CT scans is 546 cm³. In superior view (SOM Fig. S1), the braincase is ovoid in contour and somewhat elongated anteriorly, where there is marked postorbital constriction. A faint double midline keel is present posteriorly on the parietals. In its midsagittal profile (Fig. 2), the vault appears angular rather than globe-like. The glabellar region is inflated and overhangs the nasal root. A slightly hollowed supratral shelf extends posteriorly to the base of the extremely inclined frontal squama. The height at vertex is reduced relative to that of other Dmanisi individuals (Table 3). Maximum cranial breadth is comparable to that of D2280, but width across the parietals is less than in other Dmanisi specimens. These proportions, along with the very large supramastoid crests and laterally extensive zygomatic roots, give the cranium a squat bell shape when viewed from the rear (SOM Fig. S2).

The face is large in relation to the braincase. The midface is broad, and the bizygomatic diameter exceeds that of D3444 (SOM Fig. S3). Upper facial height must also be greater than in D3444, although the latter exhibits bone loss that precludes locating prosthion other than approximately. The infraorbital plates appear flattened, lying mostly in the coronal plane, while the zygomatic arches are rounded and curve gently posteriorly. This is the condition expected for *Homo*. In *A. africanus* and *Paranthropus robustus*, the midfacial contour (in horizontal cross section) appears more segmented, with a bulge localized at each “corner” of the zygomatic arch (Kimbel et al., 2004). From slightly above the level of the nasal sill, the pillar-like and laterally swollen C/P³ juga jut forward, carrying between them the premaxillary portion of the face. The inclination of the sellion-prosthion line with the symphyseal profile produces an angle of 130° in skull 5 (versus 175° in *H. sapiens*). This forward displacement of the inferior nasoalveolar clivus and the mandibular symphysis differentiates the archaic face from that of recent *Homo*. The sloping clivus, prominent C/P³ juga, and receding symphysis produce a muzzle-like form. This morphology is primitive and shared with *A. afarensis*.

The frontal bone and midvault The glabellar region is very prominent relative to the supraorbital tori. Glabella itself is more inflated than in D2280, and there is no intertoral groove. Nasion is positioned far inferiorly and is more deeply recessed than in D2280 or D3444. This downward

displacement of the nasal root is apparently the reason why D4500 has a frontal angle of only 141°, while other Dmanisi crania have larger angles reflecting less elevation of the squama above the frontal chord. The tori themselves pass outward from the central eminence with no upward curvature, to form continuous horizontal bars across the orbits. On these surfaces, a vermiculate bone pattern is clearly evident. To either side of the glabellar prominence, faint channels pass obliquely upward. Shallow supraorbital notches are situated inferiorly. Measured at the center of the orbit, vertical height of the torus is ~12 mm. The brow ridge remains robust laterally, and there is no attenuation of its thickness near the zygomaticofrontal suture.

Viewed from above, the anterior margin of the frontal is convex. The supraorbital tori curve posteriorly, and on each side, the trigon is carried well to the rear of the glabellar point. The supraorbital trigon itself is relatively broad anteroposteriorly, as in most early *Homo* specimens, rather than elongated and bar-like as in *Australopithecus*. D3444 is similar in form to D4500, whereas in D2280, the supraorbital outline is straighter, with extremities that are less receding. The supratral shelf is broad and slightly hollowed. This hollowing extends laterally, following the arc described by the brows. Behind the shelf, the frontal rises very gradually. There is neither frontal keeling nor a bregmatic eminence. A double sagittal keel (6-8 mm separation of the two limbs) is just palpable on the posterior parts of the parietals. Otherwise, the midvault is smooth, without obvious pits. D4500 differs from several of the other Dmanisi crania in that the parasagittal surfaces are neither flattened nor depressed. The biparietal arch is low but rounded in the coronal plane.

The frontal is strongly narrowed behind the orbits. Least frontal breadth measured at the temporal lines (frontotemporale-frontotemporale) is only 65 mm, and it is apparent that D4500 shows greater constriction than do other Dmanisi crania. The (inferior) temporal lines are slightly crested anteriorly and converge as they approach the coronal suture. There is no clear demarcation of separate superior lines, either on the frontal or on the parietal surfaces. At the point of maximum proximity (near bregma), the temporal lines are separated by 43-44 mm. This distance is 7 mm to 26 mm less than in the other Dmanisi individuals, implying relative hypertrophy of the temporalis muscles and/or reduction in vault surface area associated with the small brain.

The temporal line can be followed posteriorly as it arcs across the parietal. Midway along this course, the line becomes more strongly crested, but it subsides before turning downward toward the mastoid angle. Here, a blunt angular torus is present, just at the junction with the temporal bone. The torus is continuous with a horizontally oriented supramastoid crest that is mound-like and undercut by a deep (supramastoid) sulcus. The root of the zygoma is similarly expanded, to produce a ~15 mm wide, shallow gutter. The entire zygomatic arch is substantially more robust than that of D3444. Below the posterior portion of the root, the auditory porus is oval in outline, with its long axis tipped slightly posteriorly from vertical. The porus is deeply recessed (6.7 mm on the left, 6.9 mm on the right). Its rim is thickened (4 to 5 mm), especially inferiorly where a number of small bony nodules are developed.

On the left side, behind the sphenoid greater wing, the squamous temporal rises steeply to a height of 31 mm above the zygomatic shelf. On its most anterior aspect, the squama presents a short but distinct groove (6 to 7 mm wide), passing downward into the infratemporal fossa. This channel must have carried a small bundle from the tendon for the temporalis muscle. Where it abuts the sphenoid wing, the groove is bounded by a crest continuous with the sphenotemporal suture. The superior portion of the squama is somewhat inflated in relation to the parietal surface, and there are no (parietal) striations radiating upward from this border. Here, the squamosal suture is near-horizontal and remains so for about two-thirds of its length, giving the temporal bone an elongated appearance. Posteriorly, the suture slopes downward, as described by Weidenreich (1943) for the Zhoukoudian crania. Such a flattened (rather than arched) contour is observed frequently in Asian and African *H. erectus*, but there is variation (Terhune and Deane, 2008). Posteriorly, a small tongue of the parietal (the “angle incisural du parietal” of Delattre and Fenart, 1960) protrudes into a notch (incisure) in the temporal bone, either above (left side) or just below (right side) the supramastoid crest. The sutural pattern in the asterionic region is like that of most (not all) representatives of *Homo* (Kimbel and Rak, 1985).

The occipital bone Although there is minor damage to surface features near the occipitomastoid contact on the right side, the entire occipital bone is well preserved. In rear view, the upper portion of the squama is rounded in outline, and the angle formed by the lambda-asterion chords is obtuse, as in other Dmanisi crania. The biasterionic breadth is 93 mm. This value is appreciably (>10 mm) less than that for other Dmanisi crania. The chord from lambda to inion (47 mm) exceeds the value (46 mm) obtained for D2280 and D2282. Thus, the D4500 occipital is relatively high and narrow. These proportions accentuate lateral projection of the mastoid processes and supramastoid crests, when the cranium is viewed posteriorly. Much the same bell-like outline characterizes D3444, although this individual is less heavily constructed (SOM Fig. S2).

The occipital plane is close to vertical but highly distinctive in appearance. The upper part of this surface presents obvious swelling, extending across the midline and filling the region just below the lambdoid margin. On the right side, this feature is plateau-like, and it reaches downward for at least 25 mm. On the left, the mound is irregular in form. CT scans show that the tabular bone is not greatly thickened, while the diploë is locally expanded. We term this feature the “lambdoid hump”. Inferiorly, there is a shallow sulcus, passing for 50 to 55 mm horizontally, across the midline. This sulcus is slightly deeper on the left side, where there are several localized depressions. Below it, an occipital torus is well defined. This transverse ridge is more rugged than that expressed in any of the other Dmanisi hominins. From the midline, the torus curves upward in a low arc and passes toward the mastoid. On the left side, a small retromastoid tuberosity is present, about two-thirds of the way between the center of the squama and the occipitomastoid boundary. The lower border of the torus is sculpted by the superior nuchal lines. These lines are crested medially, where they spring from the linear tubercle. They can be traced laterally but subside below the asteria, before reaching the mastoid region. The linear tubercle

itself is massive, triangular in form, and strongly beaked with its apex directed downward. In its very high relief relative to the nuchal surface, this tubercle differs from that in D2280. Other Dmanisi individuals show less development of markings associated with the neck musculature.

On the nuchal plane of the occipital, an elevated external crest links the linear tubercle with opisthion, suggesting a substantial nuchal ligament (SOM Fig. S4). The crest is bilaminar, and CT images show that this midline defect extends superiorly, into the occipital plane. A well-developed (but more delicate) external occipital crest is present also in KNM-ER 3733 from Koobi Fora, Sangiran 4 from Java, and several of the Ngandong individuals, all referred to *H. erectus* (Rightmire, 1990). As noted by Weidenreich (1943), the crest is poorly expressed in the Zhoukoudian crania. To either side of the midline, moderately deep pits are present between the superior and inferior nuchal lines. The bone lining these pits is quite thin, and small sections have been damaged. These features may coincide with the attachments for the semispinalis capitis muscles. Other regions of the nuchal plane are rounded, but flattened scars left by the obliquus superior muscles are apparent.

The basilar part of the occipital is broad posteriorly but narrows as it passes forward to join the body of the sphenoid. The chord from basion to hornion (at the contact of the vomer with the sphenoid rostrum) is 34 mm. On its external surface, the basioccipital preserves a trace of the weakly developed, midline pharyngeal tubercle. The foramen magnum is oval in contour (28.6 mm wide, 33.5 mm in length) and level (inclination 0°) with respect to the Frankfort Horizontal (FH). There is no tendency for the foramen to be inclined either positively as in chimpanzees (+19°), *Australopithecus* (+20° in Sts 5) and *Paranthropus* (+7° in OH 5), or negatively as in modern humans (-8°) (Tobias, 1991; Kimbel et al., 2004). The occipital condyles are large (left side, 20 mm long by 11 mm wide) and present strongly convex articular surfaces. Both hypoglossal canals are partially blocked with matrix. Lateral to each condyle, the jugular process is irregular and mound-like. In D4500, this process is substantially larger than is usual for modern humans, and it extends laterally as well as anteriorly toward the tympanic bone. Immediately behind the condyles, there are fossae to receive the superior facets of the atlas when the head is tilted backward. On the left side, this condylar fossa is deeply excavated. Posteriorly, the margin of the foramen magnum is turned downward, relative to the adjacent nuchal surface. This portion of its rim is thickened.

The mastoid region The mastoid process is mostly complete on the left side. In D3444, the only other Dmanisi individual for which the mastoid region is intact, the process is short and cylindrical in form, with little cresting. In contrast, the D4500 mastoid projects downward to a level well below that of the adjacent occiput. Length estimated by the method of Howells (1973) is 32 mm. Anteriorly, the mastoid wall is fused to the tympanic plate, and there is no intervening fissure. D4500 resembles D2280 in this respect, but expression of a tympanomastoid fissure is variable, even within the Dmanisi assemblage. In lateral view, the process is quadrilateral in outline, rather than cylindrical or pyramid-shaped. Anteriorly, a mastoid crest is heavily developed. The upper part of this crest bulges outward as a knob-like tubercle, while its lower

aspect slopes medially. Compared with the maximum cranial breadth (135.5 mm), the distance between the mastoid tips is only 103 mm. Laterally, the surface of the mastoid is markedly hollowed. Its inferior portion is compressed from side-to-side, to form an elongated, flange-like structure. Where it is well preserved (on the left), this flange is continuous with a bony ridge, applied to the outer margin of the obliquus superior impression. The raised oblique line passes for 18-20 mm posteriorly, to approach the superior nuchal line. Such strong relief along with the very marked supramastoid crest, massive zygomatic root, and broad temporal gutter constitutes a distinctive suite of morphologies emphasizing the extreme robusticity of the new skull in relation to other Dmanisi individuals.

Medial to the mastoid process, there is a deep channel. This digastric incisure can be traced for a distance of ~19 mm, as it passes anteriorly and somewhat laterally toward the stylomastoid foramen (located between the anterior wall of the mastoid process and the tympanic plate). In its relationship to the foramen and the more medially situated petrosal spine, the digastric notch is similar to that of D2280. Both crania match the condition described for *Sinanthropus* by Weidenreich (1943). Medially, the incisure is bounded by a ridge-like juxtamastoid eminence. On the right, where the occipitomastoid suture remains open, it is clear that the eminence lies on the temporal bone. This ridge extends posteriorly, nearly joining the complex made up of the superior oblique line and the flange-like mastoid. In possessing a strongly developed juxtamastoid process, D4500 differs from D2280. In lacking any second (paramastoid) crest, D4500 differs also from the condition described for D3444 (Lordkipanidze et al., 2006). Evidently, there is substantial variation in occipitomastoid morphology within the Dmanisi assemblage.

The tympanic plate and petrous temporal The tympanic plates are well preserved, if slightly damaged at their lateral margins (Fig. 3). These structures are thickened and oriented vertically. The “crista petrosa” (Weidenreich, 1943) is blunt, rather than delicate and sharp as in modern humans. On both sides, the “spine of the crista petrosa” is remarkably strong, extending downward for a length of 8-9 mm, almost as far as the mastoid tip. This petrosal spine is thickened at its base, anteroposteriorly flattened, and resembles a compressed pyramid. Its anterior face is slightly hollowed and conforms to the contour of the tympanic plate, thus forming a continuation of the (non-articular) rear wall of the TMJ. On its posterior aspect, the spine presents a distinct channel. This groove narrows as it passes obliquely upward, toward the more laterally placed stylomastoid foramen. No styloid process is present.

Medial to the projecting petrosal spine, the tympanic is massive but still slightly crested inferiorly. Directly behind, the carotid canal opens upward, into the petrous bone. Still more medially, the tympanic terminus is expanded, to form a eustachian process (the “supratubarius process” of Weidenreich, 1943, or the “infratubarius process” of Delson et al., 2001). This structure is large and conical, and it tapers inward to a point, directed somewhat inferiorly. D4500 generally resembles the hominin pattern, where there is medial extension of the tympanic axis past the carotid foramen. In apes, the eustachian process tends to be truncated medially,

leaving the basal surface of the petrous bone uncovered (Kimbel et al., 2014). Nevertheless, the supratubarius process is distinctive, being far more robust than that expressed in any of the other Dmanisi specimens. It approaches (or surpasses) the development seen in some *H. erectus* from Zhoukoudian, Sangiran (particularly Sangiran 4), and Ngandong (Weidenreich, 1943, 1951; Aiello and Dean, 1990; Rightmire, 1990).

Both petrous pyramids are complete and undeformed. Unlike most other hominin fossils, D4500 has sustained very little damage to this most fragile but informative region of the cranial base. The angle subtended by the petrous apex with the long axis of the tympanic bone is 143 - 144° as measured from CT scans. In comparison to *H. sapiens*, the pyramid assumes a more sagittal orientation, in relation to the coronally aligned tympanic plate. Such reduction of the petrotympanic angle is not documented in *H. habilis* (in which cranial bases are poorly preserved) but is characteristic of the Zhoukoudian fossils (Weidenreich, 1943), southeast Asian, and African representatives of *H. erectus* (Rightmire, 1990; Spoor et al., 2007).

The basal surface of the petrous bone has an irregular appearance, and some tiny pores are present. However, the bone is smoother and less eroded in appearance than expected for a recent human. On the left, the inner margin of the pyramid closely approaches the wall of the basioccipital. The foramen lacerum is thus crevice-like and much reduced in area. On the right side, there is slightly more space between the petrous apex and the occipital, but there may be minor damage to the bony contacts.

The mandibular fossa The mandibular fossa is complete on both sides. On the right, the distance from the entoglenoid apex to the ectoglenoid process is 28.5 mm, while fossa breadth measured following Wood (1991) is 28 mm (right) or 30 mm (left). The fossa of D4500 is quite shallow, relative to that of D2280 or D3444. Similar morphology is present in some *H. habilis* (OH 13, KNM-ER 1805, KNM-ER 1813) and African *H. erectus* (KNM-ER 3733) (Tobias, 1991; Wood, 1991). In typical crania of *H. erectus* from China and Java, the joint cavity tends to be narrower from side to side and deeper (Weidenreich, 1943; Rightmire, 1990; Kaifu et al., 2008). The entoglenoid pyramid of D4500 is of squamous temporal origin. The sphenotemporal suture passes a mm or two more medially, and in this zone of near contact there is no downward-trending sphenoid spine. The squamotympanic fissure is oriented mediolaterally. Where it passes behind the entoglenoid process, the fissure is associated with a distinct crevice, delineating the medial-most extent of the glenoid surface. The anterior wall of the fossa curves forward centrally and is quite low. In D2280, this wall is somewhat steeper. No bar-like tubercle is developed, and the articular surface merges smoothly with the flattened preglenoid planum. On the right side, a postglenoid process is expressed only as a very low, lip-like mound, applied to the tympanic plate. Here, D4500 differs from the other Dmanisi crania, where a postglenoid tubercle tends to be more prominent. In keeping with the very strong development of the zygomatic root in this individual, there is marked lateral extension of the TMJ. Nearly two-thirds of the mandibular articular surface is carried beyond the external wall of the vault, to lie below the protruding

zygomatic shelf. Similar morphology occurs in other *H. erectus* specimens, but in D4500 it is expressed to an extreme degree.

The temporal fossa and the pterygoid process The temporal fossa as circumscribed by the zygomatic arch, sphenoid greater wing, and anterior temporal squama is quite spacious. The area enclosed within this opening, at about the level of the arch, can be measured from CT scans. On the left, this area is 139.9 mm², and on the (damaged and compressed) right side it is 124.8 mm². In part, the large size of the fossa results from anteroposterior elongation of the greater wing of the sphenoid. The surface of this wing is gently concave superiorly, where it meets the frontal bone. Inferiorly, within the fossa, a rounded channel is cut deeply into the sphenoid wall. This broad, almost half-circular gutter for a portion of the temporalis tendon is continued downward, and at its outlet, a strong spine is present anteriorly.

Despite being almost paper-thin, the bone of both pterygoid processes is largely intact. The pterygoid fossa is relatively open (shallow), but its roof presents relief suggestive of strong muscle attachments. Anterior and posterior pits are present, separated by a blunt, obliquely oriented ridge. The lateral plate is strongly projecting and flares outward, so that its distance from the smaller medial plate increases below. This lateral lamina is distinctive not only in its large size but also in its shape. The plate extends rearward, and its root reaches to a location just medial to the foramen spinosum. Here, it contributes to the cranial wall. Such architecture has the effect of incorporating both the foramen spinosum and foramen ovale into the pterygoid process of the sphenoid. Rather than lying in the roof of the infratemporal fossa, as is the norm for modern populations, foramen ovale opens into the lateral plate, by way of a funnel-like channel.

The face The face is especially broad centrally, with massive, outwardly flaring cheek bones, a large bimaxillary chord, and a wide nasal aperture (SOM Fig. S3, Table 4). Angles measured in the midline indicate that the nasal saddle is less elevated and the subnasal region (at subspinale) less projecting than is the case for other Dmanisi specimens. The midsagittal profile of the face presents three well defined contours with transitions between them. The nasal saddle is concave, as is the middle contour formed by the lateral margin of the nasal aperture. The lowermost facial (or nasoalveolar) contour (Kimbel et al., 1984) is convex, flowing smoothly into the procumbent central incisors. The jugum for the canine is conjoined with bone enclosing the mesio-buccal part of the P³ root, and this compound pillar squares off the corner of the upper jaw. Such morphology distinguishes *Homo* from *A. afarensis*, *A. africanus*, and *A. sediba*, where there is superomedial tapering of the midfacial outline (Rak, 1983; Kimbel et al., 1997; Berger et al., 2010).

The D4500 interorbital pillar (approximately 23 mm in width) is slightly less robust than that of D2280. The frontal processes of the maxillae are oriented mainly in the coronal plane, giving the entire nasal root a flattened appearance. This region is deeply recessed, relative to the inflated

glabellar region. The anterior lacrimal crests are preserved, and the lacrimal bones themselves present thickened anterior margins. The width of the nasal bridge at the anterior crests is 21 mm. The subtense to nasion is 11.0 mm. Both nasal bones are intact, and their combined width at the frontonasal suture is 10.5 mm. The bones narrow slightly in their middle parts but broaden out below. The resulting hourglass-like shape is less pronounced than in D2700. In side view, the nasal profile is strongly concave (more so than is the case for D3444). Superiorly, there is a definite midline keel, but inferiorly the bridge is flattened, and there is no elevation of the nasal surfaces relative to the frontal processes of the maxillae. This condition differs from that inferred for D3444, where the saddle must have been (somewhat) higher in relation to the orbital rims.

The piriform aperture is broad relative to that of other Dmanisi hominins (D2700 and D3444). Superiorly, its wall is thin, and the sharp leading edges are slightly everted. It is apparent that the lateral margins of the aperture slope forward, and the entrance to the nasal floor lies anterior to rhinion. This is the pattern documented for other Dmanisi individuals and more generally for early *Homo*, whereas for recent humans, the wall of the nose is likely to be vertical or even set back below the overhanging nasal saddle. The D4500 nasal sill is smooth, and there is no central tubercle marking attachment of the nasal septum. Neither spinal crests nor lateral crests are present. Inside the piriform aperture, a low intermaxillary (incisive) crest is developed, but there is no discrete step separating the sill from the nasal floor behind. This configuration of subnasal elements is “continuous-smooth” in the terminology of McCollum (2000).

Because there is no anterior nasal spine, the position of subspinale cannot be determined in the usual way. As with the nearly coincident landmark nasospinale, the inferior aspect of the nasal sill can be used as a guide. Length of the maxillary clivus measured from subspinale/nasospinale to prosthion is ~33 mm. This dimension is greater than in D2282 or D2700. The surface of the clivus immediately below the nasal sill is depressed relative to the rounded jugal pillars. Inferiorly, the subnasal profile becomes strongly convex in the sagittal plane and moderately so in the horizontal plane. Alveolar prognathism is pronounced, and the clivus joins FH at an angle of 39° (versus 90° in *H. sapiens*). There are deep vertical corrugations associated with the incisor roots. In numerous locations, thin plates of surface bone are missing from the outer alveolar margin. The I¹ roots are bowed and partially exposed within their sockets. A number of the molar and premolar roots are also exposed, in some instances all the way from the cervix to the root apex. This loss of cortical bone can be attributed to excessive tooth wear and more generally to aging.

Large infraorbital foramina are situated approximately 12 mm below the orbital rims. From each foramen, a furrow passes directly downward. As in *H. habilis*, *H. erectus*, and the other Dmanisi crania, this maxillary sulcus delimits the lateral extent of jugal swelling. In D4500, the furrow terminates inferiorly in a palpable depression, centered where the maxillary wall recedes behind the P³ root(s). A similar pit occurs bilaterally in the face of D2700, where it is still more pronounced (Rightmire et al., 2006). Neither the maxillary sulcus nor the localized, inferiorly placed depression associated with it corresponds to a canine fossa. Such a generalized excavation

of the maxillary wall, situated below and medial to the infraorbital foramen, is typically developed in the smaller cheek of modern *H. sapiens* (Maddux and Franciscus, 2009).

Cheek height measured on the maxilla is 30 mm, while vertical height of the zygomatic bone taken from its inferior margin to the uppermost part of its frontal process is 44.5 mm. The infraorbital surface of the maxilla appears rugose but is generally flattened. This plane is oriented vertically. On the left side (and less evidently on the right), a diffuse hollow is centered on the maxillary surface a few mm laterally from the infraorbital foramen. This feature again differs from the human canine fossa, as it is not associated with any flexion of the infraorbital region in relation to the nasal wall. Along the zygomaticomaxillary boundary, the cheek is slightly flexed. The body and frontal process of the zygomatic bone are oriented anterolaterally, resembling the human condition. As it ascends, the frontal process curves posteriorly. Its upper terminus thus appears recessed, where it joins the overhanging and bulbous lateral extremity of the supraorbital torus.

The zygomaticoalveolar pillar has its origin directly above the M₁/M₂ interalveolar septum. Where it arises from the body of the maxilla, this structure is anteroposteriorly thickened, as in the other Dmanisi specimens. The strut curves outward and continues to rise slightly as it approaches the zygomaticomaxillary suture. There is no noticeable development of a malar tubercle. While flexion is not acute enough to produce a true incisure, the contour in skull 5 is *Homo*-like. This configuration of the zygomaticoalveolar pillar differs from that in *A. africanus*, *P. robustus*, and *P. boisei*, where the lower margin of the crest “never curves to face inferiorly but instead follows a straight, diagonal path from its origin on the maxilla to its termination at the lateral end of the zygomatic bone” (Kimbel et al., 2004: 69). In *A. sediba*, “the zygomaticoalveolar crests are long, straight, and steeply inclined, resulting in a high masseter origin” (Berger et al., 2010: 196).

From a point several mm in advance of the zygomaticomaxillary suture, the lower margin of the zygomatic arch presents a laterally inclined bevel, associated with the masseter origin. Anteriorly, this muscle scar carries a series of distinct pits and appears eroded. Above it, there is a shallow sulcus, extending horizontally along the outer aspect of the arch. On the left (undamaged) side of the face, this sulcus can be traced for a short distance after it has crossed onto the zygomatic process of the temporal bone.

The palate The D4500 palate is long and relatively narrow (Fig. 4). External length (prosthion to the posterior aspect of the maxillary tuberosity) is 74.5 mm. External (maxilloalveolar) width is 69 mm measured at M¹ and 72 mm at M². The cheek tooth rows diverge only slightly in relation to the midline. This divergence is progressive, and there is no tendency for the palate to narrow at the level of the M³s. The surface appears shallow at the front but slopes (gently) upward posteriorly. This arch is high and vaulted at the level of the molar teeth. In this respect, D4500 resembles AL 666-1 from Hadar (Kimbel et al., 1997) but differs from other Dmanisi specimens

and also from the shallower *H. habilis* palates from Olduvai (OH 13, OH 24) (Tobias, 1991) and Koobi Fora (KNM-ER 1813) (Wood, 1991).

The palatal surface displays many small irregularities and some pitting, as is true for recent humans. However, in the location of its incisive fossa, D4500 differs markedly from the modern condition. The entrance to the incisive canal is situated at the level of the P⁴ roots, approximately 28 mm from orale. Such posterior displacement of the fossa, accompanied by inclination of the canal itself, has been documented for *H. erectus* from both the Far East and Africa (Rightmire, 1998). Posteriorly, a low ridge is present in the midline, where it is restricted to the palatine surfaces. Laterally, a greater palatine groove can be traced for a few mm on the right side, and the associated foramen is well preserved. The lesser palatine foramina are no longer intact. On the left side, the maxillary tuberosity is eroded. Enough bone has survived to show that this structure reaches posteriorly for about 12 mm, to make contact with the palatine pyramidal process. Externally, the maxillary tuberosity appears to be fused directly to the pterygoid process of the sphenoid.

The mandible The mandible is long with cheek tooth rows that are nearly parallel, mirroring the form of the D4500 palate. Height of the symphysis greatly exceeds that of D211 or D2735, as do heights of the corpus taken at P₃ and M₁ (Fig. 5, SOM Fig. S5, Table 5). Breadths at the symphysis and of the corpus are more comparable to those of the other Dmanisi jaws. Consequently, the corpus breadth/height ratio measured at M₁ is only 51.2 for D2600, whereas this robusticity index is substantially greater for D211 and D2735. Height of the ascending ramus cannot be measured directly without the missing gonial angle, but D2600 is clearly much larger in this dimension than other Dmanisi individuals. Overall, D2600 is massively built, as is the D4500 face.

Morphology of the symphyseal region has likely been altered (contra Schwartz et al., 2014) in response to extreme dental attrition, pathology associated with this condition, and the aging process (Van Arsdale, 2006; Rightmire et al., 2008; Margvelashvili et al., 2011, 2013, 2016). The upper part of the symphyseal profile is dominated by the outwardly bowed and partially exposed incisor roots, while the inferior aspect is flattened and receding. A very weak central eminence is flanked by prominent and elongated anterior marginal tubercles. To either side of the midline, pillars extend upward, accommodating the very deep canine roots. These canine pillars (partially conjoined with the P₃ juga as in the D4500 maxilla), are separated from the base by a horizontal sulcus. This intertoral sulcus can be followed posteriorly to about the position of the first molar teeth. A superior lateral torus is moderately prominent. On the right, a single mental foramen is located below midcorpus at P₃/P₄. On the left, two foramina are present. Width of the extramolar sulcus at the center of the M₃ crown is 8 mm on the right side and 8.5 mm on the left.

On the internal aspect of the symphysis, the post-incisive plane is hollowed to form a deep basin, set below the incisors and reaching posteriorly to the level of the first premolars. The

superior transverse torus is rounded and of low relief. Below it, there is a localized depression, containing several small irregular projections. An inferior transverse torus is very restricted in its lateral extent. Associated with it there is a plate-like mental spine projecting posteriorly. Digastric impressions are shallow but indistinct, and at the symphyseal midline there is a pair of small spines, oriented inferiorly.

As in D2735 and to a lesser extent D211, the lingual aspect of the alveolar process of D2600 is swollen to form a mandibular torus adjacent to the P₄ sockets and the M₁s (SOM Fig. S5). Below the torus, the sublingual fossa is deepest at the level of the M₁ roots. A mylohyoid line is strongly defined below the second and third molar teeth. This line passes posteriorly and obliquely upward, where it becomes roughened by many small bony nodules. The resulting ridge constitutes the inner margin of an elongated retromolar space, extending for about 10 mm beyond the distal aspect of the M₃ crown. Posteriorly, the alveolar prominence courses upward onto the ramus, where it is continuous with a massive triangular torus (Weidenreich, 1936). The bifurcation of this triangular mound into endocoronoid and endocondyloid crests is preserved, but the entrance to the mandibular canal is damaged. The mandibular foramen is situated well above the occlusal plane.

The dentition Both upper and lower dentitions are heavily worn and generally in poor condition (Fig. 4, SOM Fig. S5). Judging from root orientation, the maxillary incisors were strikingly procumbent. Structural non-occlusion of the incisors, the rounded labial and lingual wear surfaces of these teeth, and labiolingually oriented striations suggest that the anterior dentition was used in paramasticatory activities such as gripping (Lordkipanidze et al., 2013; Martín-Francés et al., 2013).

The D4500 P³s have three roots, while the P⁴s are double-rooted with the buccal root exhibiting two canals. The P³ associated with skull 3 has a single root, apparently representing fused buccal and lingual components. The P⁴ of skull 2 has a single mesiodistally compressed root (Macaluso, 2006). Such variation is common in other early *Homo* populations. The P³ of OH 16 has a single flat root with a bifid tip; OH 13 exhibits a double root, and OH 24 presents three roots (two buccal, one lingual). Tobias (1991) notes that root number in the P³ is polymorphic. Two early *H. erectus* P³s from Java have three roots, but *H. erectus* P³s at Zhoukoudian tend to be double-rooted with varying degrees of coalescence. This polymorphism has persisted for a long period, and P³s with one, two, and three roots continue to occur at widely different frequencies among populations of modern *H. sapiens*. The P₃s of D2600 have two divergent roots (the distal root with two canals) (Gabunia et al., 2002). The P₃s of skull 2 are single-rooted, while the P₃ of skull 3 has two roots following the Tomes' pattern (Macaluso, 2006).

For the most part, cusp morphologies have been obliterated by wear. Only in the case of the maxillary second and third molars, and the mandibular third molars, are portions of the crown surface preserved. For the D4500 M²s, enamel is present on the buccal cusps and at the margins

of the crowns. Quite clearly, crown outlines are rhomboidal and dominated by the mesial cusps, as in most *H. habilis* (Tobias, 1991) and early African *H. erectus* (Brown and Walker, 1993). This pattern is present in other (less worn) Dmanisi specimens. In D2282, the well preserved crown of (left) M^2 has a rhomboidal outline and displays a relatively large protocone and an extensive mesial marginal ridge (Macaluso, 2006). The D2700 M^2 s have paracones that appear enlarged and mesiobuccally prominent.

Dimensions of the dentition have been affected by attrition. Only labiolingual diameters can be estimated for the (upper) incisors. Interproximal wear has reduced the MD lengths of the canines and (to a degree) the premolars. Buccolingual (BL) breadths can be measured more reliably (Table 6, Table 7). It is apparent that the upper canines and premolars are quite large in comparison to those of other Dmanisi individuals. For the P^4 , estimated crown area is 137 mm^2 for skull 5, whereas crown areas are 93 mm^2 for D2280 and 78 mm^2 for D2700. Upper molar dimensions for D4500 are also relatively large, and this distinction is particularly clear for M^2 and M^3 . Fewer mandibular teeth are preserved. There is some indication that the D2600 C_1 and P_3 are larger than other Dmanisi homologues. The P_4 s are missing, and the remaining M_1 is so damaged that it cannot be measured. M_2 and M_3 are substantially larger in D2600 than in D211 or D2735. In addition to such differences, it is important to point out that neither D4500 nor D2600 exhibits any size reduction of the M_3 s relative to the M_2 s. In this respect, skull 5 is unique within the Dmanisi assemblage.

Is skull 5 conspecific with other Dmanisi individuals?

It is probable that skull 5 and the other fossils are sampled from a single paleopopulation (Lordkipanidze et al., 2013; Zollikofer et al., 2014), and this constitutes our null hypothesis, supported by the observation that the Dmanisi crania, mandibles and teeth display a commonality of form. This “total morphological pattern” (Le Gros Clark, 1964; Tobias, 1985) includes (small) brain size ranging from 546 cm^3 to 730 cm^3 . The ratio of endocranial volume (cube root) to external basicranial (biauricular) width is reduced relative to that of other early *Homo*. Brow ridges are prominent in the adults (less thickened in D2700). Supratoral hollowing is minimal, the frontal profile is flattened, and postorbital constriction is very marked. There is midline keeling on the vault. The parietal surfaces tend to be depressed, giving the cranium a poorly filled appearance. Breadth at the supramastoid crests far exceeds the biparietal width. The occipital is flexed (especially D2280, D4500), and the upper scale is greater than or equal to the lower (nuchal) plane in length. The glenoid fossa extends well out onto the underside of the zygomatic root. The facial skeleton is prognathic, and the midface is relatively massive. There is little relief on the surface of the nasal sill. The zygomaticoalveolar pillar curves outward to produce an incisure. The three mandibles for which the dentition is preserved share similar arcade proportions. D211 and D2735 are relatively robust but absolutely smaller than D2600. The corpus presents a thickened vertical symphysis, a sloping post-incisive plane, and internal transverse tori. All of the Dmanisi specimens possess anteriorly projecting marginal tubercles,

mandibular tori adjacent to P₄, and a distinctive pattern and location of the mental foramina (Lordkipanidze et al., 2006; Rightmire et al., 2006; Van Arsdale and Lordkipanidze, 2012).

Relative variation Variation is apparent at Dmanisi, as should be anticipated for any adequate sample drawn from a biological population. Table 8 provides comparisons of both CV and V* for cranial capacity and dimensions of the vault, basicranium, face, and palate. Comparison of CV or V* for endocranial volume among *H. sapiens*, *P. boisei*, *H. erectus* and Dmanisi alongside a CV value of 13.0 for six early *Homo* crania including KNM-ER 1470 (Tobias, 1991) gives no indication that variation within the Dmanisi paleodeme is excessive, relative to that in most other hominins. Cranial height appears to be especially variable at Dmanisi. Indeed, the sample encompasses specimens ranging in vertex height from 91 mm (D2280) to only 73 mm (D4500). The resulting V* exceeds values calculated for *P. boisei* and a large sample of *H. erectus*. Variation in parietal arc length is also somewhat greater at Dmanisi than for *H. erectus*, but V*s for other linear dimensions of the vault are lower for Dmanisi than for *P. boisei* and similar to or lower than for *H. erectus*. For cranial base width, V*s for Dmanisi and *H. erectus* are comparable, but variation at Dmanisi is only 50% as great as that within *P. boisei*. Mandibular fossa breadth is far less variable at Dmanisi than in the other taxa. The most variable group is *H. erectus*, as the TMJ is relatively wide in early African specimens but narrow and deep in later Asian crania. Because of small sample size, comparisons of facial dimensions must be limited, particularly for *H. erectus*. Fortunately, the supraorbital region is often intact. Supraorbital torus thickness displays a high level of variation at Dmanisi, as in other groups. This is expected, given previous assessments of brow form in hominoid primates, hominins, and recent humans (Picq and Hylander, 1989; Ravosa, 1991; Lieberman, 2000; Rightmire, 2008). Biorbital (upper facial) breadth tends to be less variable at Dmanisi than in *H. erectus*. Other dimensions (of the cheek and nasal aperture) are less variable at Dmanisi than for *P. boisei*. The Dmanisi sample is clearly more variable than recent Africans in cranial height and parietal arc length. For certain other vault dimensions and for basicranial width, V*s at Dmanisi are close to CVs for modern humans, and for the frontal and occipital arcs, and maximum cranial breadth, Dmanisi V*s fall below the *H. sapiens* values. The bimaxillary chord shows high relative variation at Dmanisi, principally because the D4500 midface is so massively constructed in comparison to that of D2280, D2700 and D3444. Other midfacial measurements are more variable in the modern human sample. Overall, the V* values reported in Table 8 convey few clear signals that the Dmanisi crania are excessively variable in comparison to recent *H. sapiens*.

The Dmanisi assemblage compared with other hominins

Form of the braincase Endocranial capacity of D4500 is lower than that of other Dmanisi specimens. The brain is comparable in size to that of the smallest mature individuals (e.g., KNM-ER 1805, KNM-ER 1813, DH1, DH3) hitherto referred to genus *Homo*. D4500 is only marginally larger than Stw 505 (*A. africanus*) from Sterkfontein (Conroy et al., 1998) and has essentially the same capacity as AL 444-2 (*A. afarensis*) from Hadar (Kimbel et al., 2004). Considered as a group, the Dmanisi hominins fall at the lower end of, or outside, the range of

endocranial capacity observed for *H. erectus* (Fig. 6). Indeed, D4500 along with D2700 and D3444 lie more than three standard deviations below the mean calculated for 27 African and Asian representatives of this species. Small brain size is reflected in the reduced ratio of endocranial volume (cube root) to base (biauricular) width. Comparisons provided in Table 9 show that D4500 has the lowest volume-to-base breadth index observed for any *Homo*, while other Dmanisi hominins are comparable to the (very few) *H. habilis* and *H. rudolfensis* crania that can be measured. Most *H. erectus* have proportionately larger brains, but several of the Asian fossils (Sangiran 17, Sambungmacan 4, Zhoukoudian XII) have especially massive bases.

The D4500 vault is lower at vertex than other Dmanisi individuals but not extraordinary in its length or breadth dimensions (Table 3). The height/length index is reduced, and the breadth/height ratio is increased, in relation to KNM-ER 1813, KNM-ER 1470, and all of the more complete *H. erectus* braincases (Table 9). This contrast is still more pronounced in the case of *H. naledi*, where the breadth/height index (~ 1.32) suggests a relatively high and narrow braincase (Berger et al., 2015). Overall cranial globularity can be expressed as a function of length, maximum breadth, and height (Lieberman et al., 2002). Not surprisingly, D4500 has a globularity index (0.35) lower than that of nearly all early *Homo* and *H. erectus*. Only the much larger and relatively elongated cranium of Ngandong 6 is comparable.

All of the Dmanisi crania exhibit anterior frontal narrowing. This morphology can be assessed using different landmarks. One method compares minimum frontal breadth to the biorbital chord, to quantify postorbital constriction in relation to the brow ridges. Table 9 indicates that the D4500 frontal is the most constricted, while D2280, D2282, and D3444 have indices falling near the lower limits established for species of ancient *Homo*. Only D2700 has a somewhat higher index, probably as a consequence of its subadult status. Had this individual lived a little longer, it would have developed a face that was wider superiorly, implying brows that were more laterally extensive in relation to the braincase (Richtsmeier and Walker, 1993). Alternatively, postorbital breadth measured lower in the temporal fossae can be paired with maximum frontal breadth, or with maximum cranial width (the frontoparietal index). The index of frontal narrowing listed in Table 9 compares postorbital breadth with maximum biparietal width, in an effort to capture form of the anterior braincase without including the supramastoid cresting that is common in archaic hominins. In this ratio, D4500 is similar to other Dmanisi individuals. All of the values recorded at Dmanisi fall well within the range for African and Asian *H. erectus*.

Flexion of the rear portion of the vault is expressed by the occipital angle. This angle is lower (indicating more pronounced flexion) in *H. erectus* than in diminutive representatives of *H. habilis* (OH 13, OH 24, KNM-ER 1813) or the more voluminous crania of recent humans. At the same time, there is variation in the degree of angulation recorded in regionally distinct groups of *H. erectus*. Angles tend to be lower at Ngandong and at Zhoukoudian, while some African crania (Daka, KNM-ER 42700) give higher readings (Asfaw et al., 2002; Antón, 2003; Spoor et al., 2007; Gilbert and Asfaw, 2008; Kaifu et al., 2008). At 107° , the D4500 occipital angle is comparable to that of D2280 and toward the high end of the range for all *H. erectus*. D2700 and

D3444 have still more rounded posterior vaults and thus approach the condition seen in *H. habilis* or *H. sapiens*.

Occipital scale proportions also vary in earlier *Homo*. Chord lengths of the lower (nuchal) and upper (occipital) segments of the squama can be compared as the occipital scale index (Table 9). This index is higher (>1.0) in Sangiran and Zhoukoudian representatives of *H. erectus*, reflecting proportional dominance of the nuchal plane. The occipital scale is relatively longer in some African populations and also at Ngandong (Rightmire, 1990; Kaifu et al., 2008, 2013). At Dmanisi, the ratio tends to be reduced. D4500 follows this pattern and presents an unusual “humped” upper scale that is expanded relative to the nuchal region. The D4500 index is similar to that of KNM-ER 3733 or Daka but not quite so low as in *H. habilis* or *H. rudolfensis*.

The cranial base External (biauricular) width of the D4500 cranial base is 129 mm. This measurement is slightly less than that for D2280 but exceeds the values obtained for D2700 and D3444 (Table 3). Basicranial (basion-nasion) length is 97 mm. Base area (calculated as width $\times$ length) for skull 5 is thus 12513 mm², while the area for D2700 is only 10948 mm². This finding bears on the observation (above) that D4500 has an exceptionally low ratio of brain volume to base breadth. While the brain is reduced in comparison to that of nearly all early *Homo*, the basicranium is not. In its base area, skull 5 is larger than D2700, KNM-ER 1813, and OH 24 and probably close to D2280 (for which basion-nasion length can only be estimated). Indeed, skull 5 is similar to the Daka cranium and only slightly smaller than KNM-ER 3883 or Ngawi (*H. erectus* specimens with substantially larger braincases).

Proportions within the cranial base are also informative. A chord connecting the centers of the carotid canals can be taken to approximate the width of the central basicranium (Kimbel et al., 2014). For D4500, this chord is 52.4 mm. The bicarotid measurement can be standardized by comparing it to total external (biauricular) breadth. Such a ratio serves to distinguish the relatively wide base characteristic of modern humans from the narrower basicranium of *P. troglodytes*, *P. paniscus*, and *G. gorilla* (Kimbel et al., 2014). For D4500, the bicarotid breadth is 40.6% of the biauricular breadth. This result lies below the range calculated for modern humans and toward the high ends of the distributions for the great apes. The ratio for skull 5 is close to that for the AL-333-45 (*A. afarensis*) partial cranium from Hadar but marginally below the range observed for *A. africanus* (Kimbel et al., 2014). For D2700, the standardized bicarotid breadth is ~46%, comparable to the ratios obtained for early African *Homo* (44.4-49.1, $n=3$) and *H. erectus* (43.9-49.6, $n=3$) and just within the lower part of the distribution for *H. sapiens* males. Clearly there is variation within the Dmanisi assemblage, and in this context the proportions of the skull 5 base appear relatively primitive.

Length of the (posterior) portion of the cranial base can be measured as the basion-hormion chord. For D4500, this chord is 34 mm. If this value is again treated as a percentage of the biauricular breadth, the result is 26.3%. For the subadult D2700 cranium, with an unfused sphenoccipital synchondrosis, the relative basicranial length is about 23.5%. The Dmanisi

values fall within the ranges estimated for *H. sapiens* males and females, close to the result (25%) for Sts 19, but below the ratio of 29% recorded for Sts 5. In contrast, all of the great apes, including the bonobos, have external cranial bases that are absolutely and relatively lengthened (Kimbel et al., 2014). It is apparent that the Dmanisi population exhibits the relatively short basicranium that is diagnostic for *Australopithecus*, *Paranthropus*, and *Homo* (Aiello and Dean, 1990).

As revealed by CT imaging, the interior of the D4500 vault is partly filled with hard matrix, and portions of the sphenoid body are obscured or damaged. Nevertheless, the cranial base angle (CBA) can be reconstructed with reasonable accuracy. Cranial base angle 1 (described by the basion-sella line and the sella-foramen caecum line) is 146°-148°. For modern human adults, this angle averages ~ 135°, and in chimpanzees it is ~ 157°. Cranial base angle 4 (formed by the sphenoid clivus in relation to the planum sphenoidale) is 122°-124°. For adult *H. sapiens*, this angle is only 111° (McCarthy, 2001). Angulation of the base cannot be measured reliably for *H. habilis* or *H. rudolfensis* specimens. In *H. erectus*, CBA1 ranges from 138° in KNM-ER 42700 (Spoor et al., 2007) to 145° in KNM-ER 3733 (Lieberman, 2011). Thus, the cranial base of D4500 is less flexed than that of recent humans but resembles the condition documented in at least one of the *H. erectus* specimens for which good data are available.

Facial proportions The facial skeleton of D4500 is larger than that of other Dmanisi individuals (Table 4). Differences are most marked for the midorbital chord, bimaxillary width, and length of the nasoalveolar clivus. The low facial breadth index (Table 9) confirms that D4500 is relatively broader in the midface than across the orbits, as is D2700. D2282 and D3444 have higher indices, showing the upper face to be wider in comparison to the cheeks and nasal aperture. KNM-ER 1470 and KNM-ER 1813 also have relatively broad upper faces, while the small sample available for *H. erectus* suggests that there is variation within this species. Facial height for D4500 (74 mm) exceeds that for KNM-ER 1813 (64 mm) but is a little lower than the norm for *H. erectus* (~ 80 mm, $n = 3$) and substantially less than the height (90 mm) measured for KNM-ER 1470.

Facial topography can be assessed from angles registering midline projection in the transverse plane. The nasion angle measures prominence of the nasal root relative to the biorbital chord. In D4500, this angle is 147°, showing nasion to be slightly less prominent than in D3444 or D2700. Crania referred to *H. habilis*, *H. rudolfensis*, and *H. erectus* generally have higher angles (>150°), suggesting even greater depression of the nasal root (Rightmire et al., 2006). The nasal bridge itself seems to be more tented in the Dmanisi sample than in African or Far Eastern *H. erectus*. A third (naso-orbital) angle reflects elevation of the nasal saddle above the lower orbital margins. In this respect, the D4500 face is flattened, not only in comparison to other Dmanisi specimens but also all ($n = 3$) *H. erectus* for which the midface is preserved. In angles measuring forwardness of subspinale or prosthion in relation to the bimaxillary chord, the Dmanisi crania are comparable to KNM-ER 1813 and KNM-ER 3733. In neither D4500 (154°) nor D2282

(154°) does the subspinale angle approach the high value (161°) recorded for KNM-ER 1470. This latter individual is particularly flat-faced (Wood, 1991; Rightmire et al., 2006).

The maxillary clivus is longer in D4500 than in other Dmanisi faces. Clivus length also exceeds that of KNM-ER 1813 and representatives of *H. erectus* (Rightmire et al., 2006). Among earlier *Homo* specimens that can be measured, only AL 666-1 and KNM-ER 1470 are comparable in this dimension (Kimbel et al., 1997). Prognathism can be quantified as an angle measured in the midsagittal plane. The nasospinale-prosthion angle is taken relative to the FH (Kimbel et al., 2004), while the clivus and subnasal angles are calculated relative to the alveolar plane or postcanine alveolar margin (Leakey et al., 2012; Lordkipanidze et al., 2013). Prognathism data for the Dmanisi hominins, early *Homo*, and *Australopithecus* are given in Table 10. As assessed from the clivus angle, D4500 is slightly more prognathic than D2282 but comparable to D2700, OH 65, and KNM-ER 1813. Inclination of the clivus relative to the FH distinguishes D4500 from AL 666-1 (less prognathic) but aligns the Dmanisi face with the (sloping) profiles characteristic of *A. afarensis* and (some) *A. africanus*. Skull 5 differs most clearly from *H. rudolfensis*, where the subnasal region is more orthognathic.

Internal length of the D4500 palate (68 mm) is greater than in *H. habilis* (Tobias, 1991; Wood, 1991) but close to an estimate of 67 mm for Sangiran 4 (G.P. Rightmire, unpublished data). Internal breadth measured at M² is 37.8 mm. The resulting palatal index (0.56) is low compared to that of D2282 or D2700. Palate shape in D4500 also differs from that in KNM-ER 1813 and *H. erectus* (Table 9). Additional comparisons suggest contrasts with AL 666-1 (index = 0.63) (Kimbel et al., 2004) and KNM-ER 62000 (index = 0.64, allowing for additional growth in the adult) (Leakey et al., 2012). Rather than resembling early *Homo*, the elongated and relatively narrow palate of D4500 is similar to that of *A. afarensis* (mean index = 0.54, $n = 4$) and *A. africanus* (mean index = 0.55, $n = 3$) (Kimbel et al., 2004). The same (primitive) proportions are present in the great apes.

The face in relation to the braincase In *Homo*, the facial skeleton and particularly its masticatory components (the maxillary and zygomatic regions and the mandible) tend to be smaller in relation to the braincase than is true for *Australopithecus* and *Paranthropus*. Indeed, reduced size of the face has been cited as one of the defining characters of *H. habilis* as well as later humans (Leakey et al., 1964; Howell, 1978; Chamberlain and Wood, 1987; Wood, 1992; Rightmire, 2010; Lieberman, 2011). Whether, or to what extent, this expectation is met by skull 5 and the other Dmanisi hominins is thus a matter of some interest. Evidence already presented shows that the face of skull 5 is quite massively constructed, whereas the Dmanisi endocranial volumes are small in comparison to those of other *Homo*. The sizes of morphological components among the Dmanisi and comparator samples were assessed from geometric means based on appropriate linear measurements (Coleman, 2008). Seven dimensions of the facial mask and palate were used to construct one measure of overall size (GM_{face}). A second geometric mean (GM_{vault}), based on height, length, breadths, and midsagittal arcs measured for the braincase, was also calculated.

Face and braincase dimensions along with the geometric means (GM_{face} and GM_{vault}) for Dmanisi individuals, selected early *Homo*, *H. erectus*, Sts 5, and OH 5 are given in Table 11. For D2700, $GM_{\text{face}} = 60.9$, while $GM_{\text{vault}} = 98.1$. Quantified in this way, facial size is 62.1% of braincase size. Comparable figures are 64.9% for KNM-ER 1813, 67.4% for KNM-ER 1470, 61.2% for KNM-ER 3733, and 57.2 % for Sangiran 17. In the case of Sts 5, the face-to-braincase proportion increases to 75.6%. For the hyper-robust OH 5 cranium, the ratio is 87.3%. It is apparent that, for representatives of *Homo*, the face is reduced in relation to the vault. This is not the simple consequence of an evolutionary decrease in facial massiveness. Indeed, the face of Sangiran 17 (late *H. erectus*) is only marginally smaller than that of KNM-ER 1470 (*H. rudolfensis*), and its GM_{face} value is otherwise exceeded only by OH 5 (*P. boisei*). Expansion of the braincase is also an important trend in *Homo*, especially for later *H. erectus*. For D4500, GM_{face} is comparable to that for KNM-ER 3733. However, GM_{vault} is lower than in D2700. The D4500 braincase is also substantially smaller than those of either D2280 or D3444 and clearly falls toward the low end of the *Homo* size distribution. As a consequence, the face is almost 72% as large as the vault. Such a ratio exceeds that obtained for KNM-ER 1470, and the face-to-braincase relationship for Dmanisi skull 5 approaches that seen in *Australopithecus*.

The mandible In its great symphyseal and corpus heights, and tall ascending ramus, D2600 complements the massive D4500 face. D2600 stands apart from the other Dmanisi mandibles, being higher at the symphysis and less robust at midcorpus than D211 (Fig. 5). Similar differences are apparent between skull 5 and the subadult individual D2700/D2735 (SOM Fig. S5). In corpus breadth, and particularly corpus height, D2600 is larger than LD 350-1, a hemi-mandible identified as the oldest known representative of *Homo* by Villmoare et al. (2015). D2600 also exceeds the dimensions of most penecontemporary (~2.0 – 1.5 Ma) *Homo* specimens from Africa. Of these, OH 13 is among the most diminutive, although the corpus is still very robust. KNM-ER 730 and KNM-ER 992 (attributed to *H. erectus*) are somewhat larger but not a match to D2600 in symphyseal, body, or ascending ramus heights. KNM-ER 1802 consists of the partial body of an adult mandible, placed with *H. rudolfensis* by Wood (1991, 1992) but set apart from this taxon by Leakey et al. (2012) and likened to *H. habilis* by Spoor et al. (2015). As measured by corpus cross-sectional area at M_1 , KNM-ER 1802 approaches (Spoor et al., 2015) or slightly exceeds (Wood, 1991) the size of the Dmanisi jaw.

Only KNM-ER 60000, a complete mandible grouped tentatively with KNM-ER 1470 and the KNM-ER 62000 partial face (Leakey et al., 2012), presents overall proportions approximating those of D2600. KNM-ER 60000 has a high symphysis (43 mm), a robusticity index of 52.6 at M_1 , and a corpus cross-sectional area of 597 mm². In other features, resemblances are less apparent. KNM-ER 60000 has a markedly inclined (receding) symphyseal face and a thickened, more everted base. Viewed from the side, the basal profile is upwardly concave, so that the mandible rests on its symphysis and very deep gonial angles. Corpus heights measured sequentially along the tooth row are not uniform. Here, direct comparison with D2600 is complicated by the fact that the base is broken below M_3 , and the angle of the mandible is

missing. Inspection of the remaining basal contour suggests only that the gonial portion of D2600 may have curved less strongly downward (as in D2735). The Koobi Fora KNM-ER 60000 ramus seems to be taller, particularly at the coronoid process. Also, the anterior border of the ramus curves forward as it ascends from the alveolar process. Only about half of the M₃ crown is visible from the side. In D2600, anterior curvature of the ramus is somewhat less pronounced. The entire M₃ outline is exposed, and the retromolar space is elongated. In both specimens, the extramolar sulcus is wide and deep. Also, the lingula is elevated above the occlusal plane.

Form of the dental arcade provides a further basis for comparisons. Arcade shape can be expressed as an index comparing breadth (measured between the lingual margins of the M₃ crowns) to length (taken from a line joining the lingual borders of the central incisors to a line tangent to the distal borders of the M₃s). D2600 has a shape index (0.69) slightly lower than that of D211 (~0.71), and both Dmanisi specimens have relatively broad arcades. This is the condition documented for LD 350-1 (index ~0.77 as measured from the mirror image reconstruction prepared by Villmoare et al., 2015). Sangiran 22 (index = 0.81) also has a broad, parabolic dental arch, while KNM-ER 60000 has a somewhat more elongated shape (0.63). U.W. 101-1277 (attributed to *H. naledi*) has an index of 0.75. The Dmanisi contours differ from those of OH 7 (index = 0.51), OH 13 (0.58), and probably KNM-ER 1802 as reconstructed by Leakey et al. (2012) and Spoor et al. (2015), where the arcade is narrower and U-shaped.

Dental dimensions Dental comparisons are provided in Tables 12 and 13. In their BL dimensions, the D4500 canines and cheek teeth are (slightly) larger than those of AL 666-I. The Dmanisi upper premolars and first molars are comparable in overall crown size to Olduvai *H. habilis* (and OH 65) but fall outside the range observed for early African *H. erectus*. The D4500 M² is slightly larger than all Olduvai homologues but does not quite match the size of KNM-ER 1590 (*Homo* sp. indet). The Dmanisi M³ crown stands out as the largest in the early *Homo* inventory, falling just within the range for *P. boisei* as depicted by Leakey et al. (2012).

For D2600, measurements cannot be taken accurately for the anterior teeth, the premolars, or the M₁s. The Dmanisi M₂ is slightly smaller than that of KNM-ER 806 (a set of isolated teeth compared to *H. erectus* by Wood, 1991) but exceeds the dimensions recorded for (other) African *H. erectus*. M₂ falls within, but toward the low end of, the range observed for early *Homo* (Leakey et al., 2012). As with the upper third molar, the M₃ of D2600 is a relatively massive tooth, larger than all African *H. erectus* homologues. In M₃ crown size, D2600 is close to KNM-ER 60000 and comparable to hominins from Olduvai (particularly OH 4, OH 16, and OH 27).

Principal components analysis of cranial form

An important question concerns measurement selection. Because many of the archaic *Homo* crania considered here lack at least portions of the facial skeleton, it is appropriate to emphasize dimensions of the braincase and the base. Previous studies of the interactions of brain size, the

cranial base, and the neurocranium suggest that in *H. erectus*, as in later humans, the brain and the basicranium should independently influence the shape of the cranial vault (Lieberman et al., 2000; Rightmire, 2013). Thus, endocranial volume (VOL) and base breadth (AUB) can be considered to be key variables. Glabella-occipital length (GOL), maximum breadth (XCB), and vertex height (PVH) provide information about overall cranial proportions. Postorbital breadth (LFB) is an indicator of anterior frontal narrowing. The biasterionic chord (ASB) and occipital angle (OCA) vary with the width and curvature of the posterior vault. Mandibular fossa breadth (FOS) appears to differ between *H. habilis* and regional populations of *H. erectus* (Spoor et al., 2007). The supraorbital torus is often well preserved. This structure is variably developed within groups, but torus thickness (TOR) emerges as an important contributor to one of five factors (rotated components) identified in a previous PCA of skull form in *H. erectus* (Rightmire, 2013).

Four of the Dmanisi crania (D2280, D2700, D3444, D4500) are quite complete and can be measured without difficulty. One individual (KNM-ER 1813) referred to *H. habilis* is reasonably intact. Another (OH 24) has been heavily restored but provides useful information. KNM-ER 1470 is largely complete but has sustained some plastic deformation (Walker, 1981). Linear measurements for *H. habilis* and *H. rudolfensis* are from Tobias (1991), Wood (1991), and Rightmire (1993), but occipital curvature for KNM-ER 1470 is approximated from comparisons with other specimens. *Homo erectus* crania are listed in Table 2. Sources for data are given by Rightmire (2013). OH 9, Ngandong 1, Sambungmacan 1, and Sambungmacan 4 are slightly damaged, and means have been substituted for missing observations. Averages for vertex height, occipital angle, and mandibular fossa breadth are calculated for the appropriate local group (Africa, or Sambungmacan with Ngandong). For the 21 *H. erectus* individuals included in the analysis, only four of 210 observations are affected, amounting to just 1.9% of total information.

For PCA, endocranial volume is converted to its cube root. Occipital sagittal curvature is measured as an angle in degrees. Linear dimensions of the vault are adjusted for size using the geometric mean calculated from GOL, PVH, XCB, LFB, ASB, AUB, FOS, and TOR. This procedure yields a shape variable that has been shown to perform well in comparisons of humans and diverse anthropoid primates (Jungers et al., 1995). Subscripts applied to the variable name (eg., AUB_{adj} or TOR_{adj}) are used to flag this size adjustment. Data for all specimens included in the PCA are listed in Table 14. The first principal component (PC) accounted for 42.9% of total variance, while the second, third, and fourth components explained lower amounts (31.2%, 9.9%, and 5.6% respectively) of this variation. Subsequent components (PCs 5 – 10) accounting for < 5% of the variance can be set aside. Inspection of the coefficients (Table 15) shows that PC1 is weighted strongly (and negatively) for mandibular fossa breadth. Frontal narrowing is also important, and there are further contributions from vertex height and brain volume. Principal component 2 is influenced principally by variation in supraorbital torus thickness. Maximum cranial breadth and basicranial width also receive significant loadings. Principal component 3 is loaded for cranial length. Biauricular breadth is again important, and biasterionic width is weighted negatively. Principal component 4 is driven mainly by occipital sagittal curvature.

Scores on the first two axes are plotted in Fig. 7 (lower frame). The Dmanisi individuals have large values for FOS_{adj} and are driven toward the negative pole of PC1. KNM-ER 1813, OH 24, OH 9, and Ngawi also have relatively broad TMJs, while the Ngandong and Zhoukoudian hominins have narrow mandibular fossae and fall in positive territory. KNM-ER 1470, KNM-ER 3733, and Sangiran IX are intermediate. Relatively broad frontals contribute to the positive placement of the Ngandong population, while frontal narrowing is emphasized for Dmanisi and for OH 9. Small brain sizes also carry the Dmanisi specimens toward the tail of the distribution on PC1. On PC2, massive supraorbital tori (loaded negatively) and relatively narrow vaults cause OH 9, Daka, Sangiran 17, and Ngawi to receive low scores. D2700, OH 24, KNM-ER 1813, and *H. erectus* specimens from Koobi Fora have gracile brows and load positively on this axis. KNM-ER 1470 with low TOR_{adj} but very high XCB_{adj} lies at the positive pole of PC2.

On PC3 (Fig. 7, upper frame) there is a tendency for relatively long crania with broad bases (Ngandong 6, Zhoukoudian III, XI, and XII) to score positively, while individuals with relatively wide occipitals (D2700, KNM-ER 42700, Ngandong 11) fall in negative territory. D4500 with high AUB_{adj} but very low ASB_{adj} is driven positively in relation to other Dmanisi specimens. Principal component 4 is not plotted in the figure. Individuals with rounded occipitals have positive scores, while crania with flexed sagittal profiles lie toward the negative end of the distribution. D2280 and D3444 cluster closely with *H. habilis* crania KNM-ER 1813 and OH 24, but all of these specimens fall within the range of *H. erectus*.

Figure 7 shows principal patterns of shape variation in our sample of early *Homo* and *H. erectus*. However, summarizing multivariate variation along the first few PCs implies that some of the information contained in the original measurements is not represented in these graphs. It is apparent, for example, that the *H. erectus* skulls do not cluster closely by geographic region. Individuals from Ngandong, Sambungmacan, and Zhoukoudian constitute a sort of East Asian group (positive scores on axis 1), but several of the crania from Sangiran and Ngawi are relatively distant. African *H. erectus* crania are also dispersed, particularly on PC2. Interpretation is not straightforward. While trends in FOS_{adj} , TOR_{adj} , cranial length, and brain size are reflected in the shapespace of the first three PCs, variation in other characters loaded on the components with lower eigenvalues is not adequately accounted for. When only the first two PCs are considered, it is evident that the Dmanisi crania cluster together. D2280 is included within the 95% density ellipse constructed for the *H. erectus* sample, but other Dmanisi individuals are not. D4500 occupies an extreme (negative) position on PC1, while D2700 is also removed from the *H. erectus* distribution, on axis 1 as well as axis 2. It should be noted that the 95% ellipse centered on Dmanisi includes KNM-ER 1813 and OH 24, both referred to *H. habilis*. Principal component 3 does not further distinguish D2280, D2700, D3444, or the *H. habilis* crania from *H. erectus*. However, it has the effect of distancing D4500 from *H. habilis* as well as African and Asian *H. erectus* specimens.

Characters shared by the Dmanisi specimens with Australopithecus and /or ancient Homo

Skull 5 from Dmanisi possesses attributes not hitherto observed in a basal member of the *Homo* clade. The facial skeleton is exceptionally large in relation to the braincase. Other notable characters include the low cranial vertex, angular vault profile, lambdoid hump, marked lateral extension of the mandibular cavity, flange-like mastoid process, horizontally oriented foramen magnum, channel-like opening of foramen ovale into the lateral pterygoid plate, gradual transition from the nasal floor onto the long, sloping nasopalveolar clivus, muzzle-like lower face, relatively narrow palate, very deep mandibular symphysis, and enlarged (posterior) dentition. The robust architecture of D4500 differs from that of D2282 or D2700 and also the gracile, rounded braincases and diminutive faces of OH 13, OH 24, and KNM-ER 1813. Instead, there are similarities to specimens such as KNM-ER 1805 (Lordkipanidze et al., 2013), and to *Australopithecus*.

D4500 also shares features with the 2.33 Ma AL 666-1 maxilla and partial dentition from Hadar, attributed to *Homo* by Kimbel et al. (1997). Both the D4500 palate and the Hadar specimen are strongly vaulted at the level of the molar teeth. In occlusal aspect, the incisor row is weakly arched and projects only a short distance anterior to the bicanine line. The P³ crown is compressed mesiodistally, and the resulting oval outline is longer at its buccal margin. The P³s of D4500 have three roots, as does the (right) P³ of AL 666-1. The P⁴ crown is oval in outline with a longer lingual half. The (right) P⁴ of D4500 is well enough preserved to permit measurement of crown shape. The length/breadth index for this tooth is 0.73. The P⁴ is thus relatively broad and comparable in its proportions to *A. afarensis*, *A. africanus*, and AL 666-1 (Kimbel et al., 1997). The crown index falls substantially below the means of 0.80 given for ($n = 7$) *H. habilis* at Olduvai Gorge (Tobias, 1991) and 0.78 (range 0.75 to 0.79) calculated for ($n = 8$) *H. habilis* from eastern and southern Africa (Kimbel et al., 1997). However, the P⁴ of D2282 (shape index = 0.79) is elongated and narrow, as in *H. habilis*. Clearly, premolar crown shape varies significantly within the Dmanisi sample.

For D4500 and AL 666-1, M² is larger than M¹. D4500 does not exhibit any size reduction of the M³s relative to the M²s. The AL 666-1 third molar is represented only by its roots. Nevertheless, this hominin may also lack the M³ reduction that characterizes African *H. erectus* (Kimbel et al., 1997). If M¹ < M² < M³ is the correct size sequence for AL 666-1, then both the Hadar specimen and D4500 are similar to *Australopithecus* and (most) *H. habilis*.

The D4500 upper molar cusp proportions are obscured by attrition. Loss of structural detail is most pronounced in the case of the first molars, and for this tooth, it is not possible to assess the relative sizes of the paracone and metacone. In the D2282 M¹s, the paracone and metacone are equal in area, while for D2700, the metacone area is greater than that of the paracone. This is the condition shared by *Australopithecus* with early *Homo* (Quam et al., 2009). Given the limited evidence available, it can be hypothesized that both the Dmanisi individuals and AL 666-1 lack the derived M¹ cusp size ratio (paracone > metacone) seen in *H. erectus* and later humans.

In other characters, D4500 seems to be more primitive than AL 666-1. The Dmanisi palate is elongated and narrow, whereas the Hadar dental arcade is evenly parabolic in shape. D4500 presents no clear division of the floor of the nasal aperture from the subnasal portion of the maxilla, and there is no anterior nasal spine. In AL 666-1, the nasal floor is strongly angled in relation to the nasoalveolar clivus, and the anterior spine is strong and tubercle-like (Kimbel et al., 1997). Subnasal prognathism also appears to differ in the two hominins. Although there is incomplete agreement in results obtained from angles defined using slightly different horizontal planes, the nasospinale-prosthion angle measuring inclination of the clivus relative to FH distinguishes D4500 (39°) from AL 666-1 (47°). The Dmanisi face is aligned with the (more sloping) profiles characteristic of *A. afarensis* and (some) *A. africanus*, while the Hadar maxilla resembles that of KNM-ER 1813 (Table 10).

Interestingly, skull 5 from Dmanisi presents elements of the same primitive morphology that is apparent in the ~2.8 Ma LD 350-1 mandible from the Afar. The anterior corpus profile of D2600 is receding (although flattened rather than bulbous), and there is little indication of a bony chin. Only a very weak symphyseal eminence is present, accompanied by prominent anterior marginal tubercles. LD 350-1 has an inclined symphysis bearing a distinct keel but lacking any mentum osseum. Both mandibles share a suite of attributes differentiating them from *Australopithecus* or *Paranthropus* and aligning them with early *Homo*, including alveolar and basal corpus margins that are approximately parallel and an ascending ramus that is rooted posteriorly, so as to expose in side view a substantial portion of the M_3 crown.

Resemblances to H. habilis

The average endocranial capacity at Dmanisi (631cm^3 , $n = 5$) falls close to the mean of 610cm^3 reported for *H. habilis* by Wood (1992) but far below the norm for African and Far Eastern *H. erectus* (Fig. 6). Body mass estimates (Lordkipanidze et al., 2007; Grabowski et al., 2015) obtained from postcranial elements likely associated with skull 5 place this individual within the range of variation for early *Homo*, and at the lower end of variation of African *H. erectus* and modern humans (Holliday, 2012; see also Pontzer, 2012). The encephalization quotient (EQ) calculated for skull 5 (body mass estimate from Lordkipanidze et al., 2007) is ~2.3, similar to values reported for species of *Australopithecus*. Encephalization quotient obtained with the lower mass estimate of Grabowski et al. (2015) is ~2.9. For one possible hypodigm of *H. habilis*, a relatively high EQ of 3.6 has been proposed (McHenry and Coffing, 2000). However, very few postcranial bones can be associated unambiguously with this species. Only two *H. habilis* individuals (OH 62 and KNM-ER 3735) are represented by postcrania as well as skull parts, and in both cases the limbs are extremely fragmentary (Haeusler and McHenry, 2007; Wood, 2009). Estimates for body mass should be questioned (Holliday, 2012). Also, both OH 62 and KNM-ER 3735 appear to be quite small-bodied in comparison to nearly all other early *Homo* specimens from Koobi Fora (Grabowski et al., 2015), and if they are atypical for *H. habilis*, this sampling bias will result in EQs that are inflated. Until there is firm evidence to the contrary, it may be

hypothesized that in relative as well as absolute brain size, the Dmanisi population is comparable to early *Homo* from Africa.

While D4500 differs from OH 13, OH 24, and KNM-ER 1813 in face-to-braincase proportions, postorbital constriction, and cranial globularity, even this most robust of the Dmanisi individuals resembles *H. habilis* in its inflated and laterally projecting mastoid region and relatively wide and flattened mandibular cavity lacking any true articular tubercle. Like *H. habilis*, skull 5 displays a squared-off outline of the maxilla in facial view, a maxillary sulcus, and outward curvature of the zygomaticoalveolar pillar. If the maxillary sulcus (a narrow channel, not associated with any buttressing of the wall of the nasal aperture) is considered to differ from the “maxillary furrow” (a longer, continuous groove setting the entire anterior pillar/canine jugum apart from the more peripheral part of the face) of *A. africanus*, or the vestigial “fossula” of *P. robustus* as described by Rak (1983) and Kimbel et al. (2004), then this facial morphology can be described as synapomorphic for early *Homo*.

D2282, D2700, and D3444 present supraorbital tori that are well defined but not greatly thickened. Several of the Dmanisi crania follow *H. habilis* in having a rounded rather than strongly flexed occipital, with little or no expression of a transverse torus. D2700 is similar to KNM-ER 1813 in orbital proportions, nasal bone shape, midfacial profile (the “nasocanine contour” of Kimbel et al., 1984), and slope of the maxillary clivus in relation to the alveolar plane (Table 10). D2700 also has a very shallow palate.

Other traits shared by Dmanisi with *H. habilis* but not *Australopithecus* are expressed in the dentition. Although the D4500 M²s are heavily worn, enamel is preserved on the buccal cusps and at the periphery of both crowns. Quite clearly, the D4500 crown outlines are rhomboidal and dominated by the mesial cusps, as in most *H. habilis* (Tobias, 1991) and early African *H. erectus* (Brown and Walker, 1993). Such an asymmetric, rhomboidal occlusal outline differs from the squarer, more symmetric shape seen in *Australopithecus* (Kimbel et al., 1997).

The D2600 P₃ crown is ovoid in form with “weak projection of the distolingual margin and an obliquely oriented sagittal axis” (Macaluso, 2006: 74). The P₃ crowns that are preserved for D211 and D2735 are also asymmetrical, and these teeth share with *H. habilis* a smaller breadth, a more centered polygon and a less frequently opened anterior fovea than in *Australopithecus* (Martín-Torres et al., 2008). The remaining (right) M₁ crown of D2600 is in very poor condition. Other Dmanisi M₁s are long but narrow when compared to those of *Australopithecus* (Martín-Torres et al., 2008). This is the derived condition expected for early *Homo*.

Contrasts/similarities with specimens referred to H. rudolfensis

D4500 differs in many respects from KNM-ER 1470. Particularly striking are the contrasts in size and globularity of the braincase. In addition, D4500 has a bar-like supraorbital torus, parietal keeling, and a massive occipital transverse torus. D2280 also has a prominent supraorbital torus, midline keeling on the vault, and a deep mandibular fossa. KNM-ER 1470 displays almost no

supratoral hollowing, neither a bregmatic eminence nor any sign of a sagittal keel, and a shallow glenoid fossa. Although the occipital is damaged, there is apparently little development of any transverse torus.

Facial topography distinguishes the Dmanisi hominins from specimens referred to *H. rudolfensis*. Angles reflecting forwardness of subspinale or prosthion in relation to the bimaxillary chord show that midline projection in the transverse plane is greater in D2282, D2700, and D4500 than in KNM-ER 1470. Alveolar prognathism measured in the sagittal plane is also more pronounced. Clivus angles at Dmanisi are more acute than those for KNM-ER 1470 and KNM-ER 62000, and the latter individuals are quite flat-faced. D4500 has an elongated palate, whereas “the overall shape of the palate of KNM-ER 1470 is broad and short” (Wood, 1991: 73). Both maxilloalveolar and internal palatal widths for the Dmanisi crania are far less than any reasonable estimates for the Koobi Fora adult.

Although the skull 5 subnasal profile is (strongly) prognathic, there is some resemblance to KNM-ER 1470 in the shape of the anterior dental arcade. In occlusal view, the D4500 incisor row is weakly arched, projecting only a short distance anterior to the bicanine chord. The outer alveolar contour curves posterolaterally around the C¹ and buccal roots of the P³ (both contributing to the formation of the prominent jugum). Behind the P³, the wall of the maxilla angles more sharply backward. KNM-ER 1470 is described as possessing “a well-defined P³ jugum mark[ing] the ‘corner’ between the lateral and anterior surfaces of the maxillary alveolar process, so that the canine alveoli are fully part of the anterior row” (Leakey et al., 2012: 201). Unfortunately, this parallel between Dmanisi and *H. rudolfensis* cannot be drawn with confidence, as the KNM-ER 1470 palate is damaged, leaving only the incomplete alveoli for the anterior teeth in place.

Pairing D2700 with KNM-ER 62000 provides a more secure basis for comparisons. These specimens are of about the same developmental age. D2700 has incompletely erupted M³s, while KNM-ER 62000 presents unerupted M³s still in the crypts above the M²s (Leakey et al., 2012). Although D2700 has sustained some damage to the anterior palate and incisor alveoli, it is clear that the pillar-like maxillary juga are associated principally with the large canine roots. In occlusal outline, these jugal swellings bulge forward, so that the canine sockets are positioned laterally in relation to the incisor row. Here, there is a resemblance to KNM-ER 62000. The latter specimen is said to be quite similar to KNM-ER 1470, and in both cases the canine alveoli are incorporated into a straight anterior tooth row (Leakey et al., 2012).

As noted (above), the D2600 mandible is similar in symphysis height, corpus robusticity, and ramus size to KNM-ER 60000. The two jaws are alike in their extremely wide and deeply excavated extramolar sulci, and they share discrete features such as elevation of the lingula above the occlusal plane. How to interpret these similarities is presently unclear, pending final taxonomic attribution of the Koobi Fora specimen.

Characters shared with H. erectus

The low, relatively angular shape of the D4500 vault is not matched in African or Asian assemblages of *H. erectus*. D4500 does share aspects of form with other Dmanisi crania, and among the latter, D2280 is perhaps the most similar to African *H. erectus*. D2280 is slightly smaller than KNM-ER 3733 in most dimensions, and proportional differences are apparent in the relatively long parietal arc, low biparietal breadth, and high occipital scale index of the Dmanisi individual. However, these differences are not much more marked than those between the Turkana Basin specimens themselves. As a group, the Dmanisi fossils have frequently been likened to *H. erectus* (Gabunia and Vekua, 1995; Gabunia et al., 2000; Vekua et al., 2002; Antón, 2003; Rightmire et al., 2006; Lordkipanidze et al., 2006, 2013; Spoor, 2013; Baab, 2016).

The total morphological pattern expressed in the Dmanisi paleopopulation includes a number of traits that serve to describe *H. erectus* as a species. Supraorbital tori are prominent and vertically thickened. A sagittal keel, low temporal squama, angular torus, relatively great breadth across the supramastoid crests, flexed occipital with transverse torus, laterally extended glenoid articular surface, and reduced petrotympanic angle are typical for *H. erectus*. The nasal saddle is elevated relative to the orbital rims, faint spinal/lateral crests may define the nasal sill, and the zygomaticoalveolar pillar is commonly flexed to produce an incisure. The three Dmanisi mandibles for which the dentition is preserved share a relatively short and broad dental arcade with *H. erectus*, and teeth associated with skulls 2 and 3 resemble those of *H. erectus* in numerous details.

Elements of this pattern must constitute a key part of any diagnosis for *H. erectus*. However, not all characters likely to have diagnostic value (high taxonomic valence) are manifest to the same degree in each member of the Dmanisi assemblage (Table 16). The occipital is flexed with a strong transverse torus in D2280 but lacks relief in D2282. The tympanic plate is particularly robust and carries a thick petrosal spine in D4500, but the same structures are considerably more delicate in D2700. These differences underscore the presence of variation. The data in Table 16 provide only limited evidence supporting the inclusion of the Dmanisi fossils within the *H. erectus* hypodigm. Nevertheless, to a greater extent than D3444 or other Dmanisi individuals, D4500 shares characters of the vault, cranial base, and face with the oldest *H. erectus* specimens from Java including Sangiran 4 (Rightmire, 1990), Sangiran 27 (Indriati and Antón, 2008), and Sangiran 31 (Kaifu et al., 2010). Similarities include the low, bell-like shape of the braincase in posterior view, the extreme robusticity of cranial superstructures, a long, medially directed mastoid process, a massive tympanic plate, and a deep, elongated palate.

Characters shared with H. naledi

In its endocranial capacity, D4500 is only marginally below the figure of 560 cm³ reported for a (composite) male representative of *H. naledi* (Berger et al., 2015). The Dmanisi crania may also resemble *H. naledi* in possessing a well developed though weakly arched supraorbital torus,

slight parasagittal keeling between bregma and lambda, and prelambdoid flattening. There is a strong angular torus. D4500 appears to differ from the Dinaledi specimens which have a relatively high vertex, only slight postorbital constriction, widely spaced temporal lines, and parietal bossing. The *H. naledi* specimens display sexually dimorphic development of nuchal muscle markings, but DH1 and DH4 lack the massive transverse occipital torus of D4500, rather resembling the more gracile Dmanisi individuals. *Homo naledi* differs from all of the Dmanisi crania (and *H. erectus*) in its clearly defined external occipital protuberance, overlying the linear tubercle. Also, “almost the entire mandibular fossa is positioned medial to the temporal squama” (Berger et al., 2015: 19). In D4500, nearly two-thirds of the TMJ is carried beyond the external wall of the vault, to lie below the protruding zygomatic shelf. In D2280, and in many *H. erectus* crania, the fossa is again positioned more laterally, in comparison to the derived condition described for *H. naledi*. The Dinaledi petrotympanic is said to be distinctly coronally oriented, rather than angled as in the Dmanisi assemblage (and *H. erectus*). The crista petrosa is weakly developed, but “there is a strong Eustachian process” (Berger et al., 2015: 19).

The face of *H. naledi* is poorly preserved. There is part of a maxilla (U.W. 101-1277), and a little of the left orbit has survived. The nasoalveolar clivus is described as “flat and square-shaped,” while the (reconstructed) palatal arch is parabolic rather than elongated (Berger et al., 2015: 19). This morphology is clearly *Homo*-like, although the subnasal portion of the maxilla slopes forward, as in in D2700 and D4500. The one nearly complete mandible (U.W. 101-1261) from the Dinaledi Chamber is less robust (corpus breadth/height) than D211 or D2735. The teeth of *H. naledi* are described as quite small in comparison to samples of *H. habilis* and *H. erectus* and similar in their dimensions to much later *Homo* (Berger et al., 2015).

Discussion

Among Early Pleistocene *Homo* specimens, skull 5 is unprecedented in its preservation of anatomical detail. Frontal flattening, occipital proportions, mandibular form, and extreme dental attrition all point to an advanced age for the Dmanisi individual. This assessment is supported by the pattern of ectocranial cranial suture closure, and the scoring technique of Meindl and Lovejoy (1985) provides an estimate for age at death of close to 50 years. For a representative of non-*sapiens Homo*, the utility of this approach must, of course, be questioned. Skull 5 is clearly an adult, older than D2700/D2735 or D2282/D211. But how skull 5 should be seriated (sorted on the basis of one or more age factors) in relation to skull 4 remains uncertain. The edentulous condition and facial remodeling evident in D3444/D3900 may reflect pathology in addition to senescence (Lordkipanidze et al., 2006; Margvelashvili et al., 2013). Unfortunately, aging methods presently available, including novel approaches such as transitional analysis (Milner and Boldsen, 2012), offer little additional guidance.

The well-developed cranial superstructures, massive midface, high mandibular corpus, and tall ramus almost certainly identify D4500/D2600 as a male individual. This very robust morphology is coupled with a brain smaller than that of other Dmanisi specimens. Given the

tendency in extant large-bodied apes and humans for males to exceed females in brain size by 8% to 15% (Tobias, 1971; Wood et al., 1991), this observation is surprising. It may be hypothesized that the patterning of sex differences at Dmanisi differs from that in recent humans. Confirmation of such a finding will raise obvious doubts as to whether the (largely) size-based attributions of sex to *H. habilis* specimens from Olduvai Gorge or *H. erectus* crania from Koobi Fora and Sangiran can have much validity. Antón (2012) and Antón and Snodgrass (2012) follow other authors in assigning sex to D2280, D2282, D3444 and other *Homo* specimens, but analyses of sex dimorphism based on presumed male-female differences in brain size may be flawed. Indeed, the pattern and extent of variation within ancient hominin populations is only beginning to become clear.

Proportions of skull 5

D4500 displays distinctive proportions that are likely to be structural correlates of a small brain developing on a wide cranial base. At 546 cm³, the endocranial capacity of D4500 is lower than that of nearly all early *Homo* fossils. At 129 mm, the external base breadth is almost as large as that for D2280, KNM-ER 3733, KNM-ER 3883, Daka, Sangiran 4, and Ngandong 1. The size-adjusted variable AUB_{adj} for D4500 exceeds values for other Dmanisi specimens and falls in the uppermost part of the range observed for *H. erectus*. Despite its reduced relative bicarotid width (possibly a primitive retention), skull 5 presents an enlarged basicranial platform.

The interactions of brain size and the base with vault shape have been studied in living primates (Dutterloo and Enlow, 1970; Sirianni and Swindler, 1985) and in recent humans (Sperber, 1989; Lieberman et al., 2000; Bastir et al., 2010). In the case of extinct hominins, where fossilized remains of immature individuals are scarce or damaged, it becomes important to draw inferences concerning cranial development from the variation present among adults. This has been done for a large sample of *H. erectus* from localities in Africa and Asia (Rightmire, 2013). Correlations and partial correlations for endocranial capacity, the cranial base, and the vault for *H. erectus* have been compared with those of *H. sapiens*, and it is possible to identify patterns of covariation that parallel, or differ from, those described for recent humans. Within the archaic species, it is the form of the base, rather than the brain, that primarily determines the breadth of the neurocranium. Cranial base size also covaries with the length of the braincase (Rightmire, 2013). In this pattern of interactions, *H. erectus* is clearly distinct from *H. sapiens*, where variations in brain size significantly influence both width and length of the vault (Lieberman et al., 2000). In addition, the smaller brain of *H. erectus* constrains neurocranial expansion more than in later humans, particularly affecting vault height.

As anticipated for archaic *Homo*, the large basicranium of skull 5 appears to have a strong influence on vault proportions. Breadth of the D4500 vault is comparable to that of D2280 and only slightly less than breadths for much more voluminous specimens from Koobi Fora and Sangiran. Poor encephalization results in a uniquely low cranial vertex, and this reduction in height drives overall vault size downward. As measured by the geometric mean (Table 11), the

D4500 vault is smaller than that of D2700 and near the end of the *Homo* range. At the same time, GM_{face} is nearly as large as that for KNM-ER 3733. Also, the face of skull 5 is set (far) forward from the anterior cranial fossa. Size and orientation of the facial skeleton are important determinants of brow ridge size (Lieberman, 2000, 2011), and the D4500 supraorbital tori are prominent and thickened. An expected consequence of this upper facial robusticity is postorbital constriction, and frontal narrowing is indeed more marked in D4500 than in other Dmanisi specimens.

In comparison to D2282 and D2700, skull 5 has a long and forward sloping nasoalveolar clivus. The palatal arch is deep and vaulted in coronal cross section at the level of the molar teeth. In this respect, D4500 resembles AL 666-1 from Hadar but not the shallower *H. habilis* palates from Olduvai (OH 13, OH 24) and Koobi Fora (KNM-ER 1813). Also, the D4500 palate is relatively long and narrow as in *Australopithecus*, rather than parabolic in shape as in D2282 and *H. erectus* (Table 9). How to interpret these features of skull 5 is not entirely clear. One question involves statistical significance. There is near overlap in arch depth and palatal width/length proportions between the very small samples that are available for ancient *Homo*. In its palatal index, D4500 differs only slightly from KNM-ER 1813, while the latter is close to AL 666-1. Also, it is likely that (some of) the variation observed is associated with masticatory function, known to generate mechanical loading in the face. Especially in archaic hominins capable of producing strong bite forces, the palate and the mandible will be subject to high twisting and shearing stresses concentrated near the occlusal plane (Lieberman, 2011). The unusual dental wear patterns in skull 5 (Van Arsdale, 2006) attest to the presence of such differences within the Dmanisi population. Most probably, traits that are integrated within the masticatory complex should not be accorded high taxonomic value.

The D2600 mandibular arcade has about the same shape index (0.69) as does D211 (~0.71), and both Dmanisi arcades are relatively broad. This is the condition documented for LD 350-1 and the (few) *H. erectus* specimens that can be measured. Here, there is a paradox. For skull 5, there seems to be a mismatch between the relatively short mandibular dental arch and the narrow, elongated palate belonging to the same individual. An explanation lies in the palatal morphology of the specimen. The maxillary tuberosities, horizontal plates of the palatine bones, and staphylion are positioned well posterior to the third molar teeth. The palate itself is thus *Australopithecus*-like in its (low) width/length index. However, the maxillary dental arcade has proportions that are more *Homo*-like, providing a good occlusal fit to the mandibular dentition.

The Dmanisi hominins document one taxon

Previous resampling analyses demonstrate that patterns of mandibular corpus and dental arcade size variation at Dmanisi are not unexpected in human and African ape comparators (Rightmire et al., 2008; Van Arsdale and Lordkipanidze, 2012). Geometric morphometric comparisons of cranial form also fail to reject the (null) hypothesis that the Dmanisi hominins represent a single taxon (Lordkipanidze et al., 2013). Using the size-independent coefficient of

variation (CV or V^*), we have evaluated cranial characters at Dmanisi in relation to the variation observed in recent humans from Africa and in extinct hominins. For endocranial volume, variation within the Dmanisi assemblage is comparable to that in both *H. sapiens* and *H. erectus* (Table 8). Vertex height and parietal sagittal arc length at Dmanisi are more variable than is the case for *H. erectus*, but for most measurements of the braincase and the basicranium, values of CV or V^* at Dmanisi are similar to or lower than for *H. erectus* and consistently lower than for *P. boisei*. Mandibular fossa breadth is far less variable at Dmanisi than in the comparator groups.

Craniofacial traits exhibiting substantial variation include supraorbital torus thickness, the bimaxillary chord, and cheek height. High variation in torus thickness appears to be the norm. For the other characters, data for *H. erectus* are limited, but dimensions of the cheek and nasal aperture are less variable at Dmanisi than for *P. boisei*. Both Dmanisi and modern humans tend to show greater variation in the facial skeleton than in the neurocranium or the skull base. This result is consistent with the findings of Wood and Lieberman (2001). Both upper and lower jaws may be expected to exhibit high levels of within-species variation, associated with growth and phenotypic plasticity (Enlow, 1990; Enlow and Hans, 1996; Wood and Lieberman, 2001).

Principal components analysis provides useful information concerning proximity of the Dmanisi specimens to one another in a morphospace of multiple dimensions. On the first two PCs explaining 74.2% of total variation, the Dmanisi crania cluster together on the basis of their relatively wide mandibular fossae, narrow frontals, small brains, and gracile brows. As estimated from the individual scores (the PC map) or the density ellipses, this cluster takes up only a small portion of the space occupied by all *H. erectus*. For Dmanisi, scores on PC1 and PC2 cluster to about the same extent as is true for the Zhoukoudian individuals (all from one Middle Pleistocene locality). Both the Dmanisi and Zhoukoudian score-ranges are reduced in comparison to those for the assemblage from Ngandong in Java. On PC3, D2280, D2700, and D3444 group closely together, but D4500 with high AUB_{adj} and very low ASB_{adj} plots positively. Here the Dmanisi cluster is expanded, relative to either Zhoukoudian or Ngandong. On PC4, accounting for 5.6% of variation, the range for Dmanisi is comparable to that for the (six) Ngandong individuals.

These analyses support the taxonomic integrity of the Dmanisi assemblage, with the caveat that the relatively broad basicranium and narrow occipital of D4500 set it toward the periphery of the Dmanisi shape distribution. In our view, neither these differences, nor the proportions of the D2600 mandible, offer sufficient grounds for labeling skull 5 as the “holotype of the morphologically very distinctive species *H. georgicus*” (Schwartz et al., 2014: 360). Variation due to growth and dimorphism is to be expected among individuals sampled from any hominoid population. Early hominins probably displayed patterns of variation that are not present in any living taxon, and the nature of such differences is being revealed by new discoveries.

Affinities of the Caucasus population

The Dmanisi hominins share an array of characters with *H. habilis*. Average brain volume is similar to that calculated for a sample of early *Homo* from Olduvai Gorge and Koobi Fora (not including KNM-ER 1470). This conclusion is not altered by the estimate of 778 cm³ as the endocranial volume for OH 7 (Spoor et al., 2015). Several of the Dmanisi crania are relatively gracile, with rounded occipitals lacking well developed transverse tori. D2700 resembles KNM-ER 1813 in orbital proportions, midsagittal profile, and palate shape. Other similarities can be found in the dentition. The D2282, D2700, and D4500 M²s have crown outlines that are rhomboidal in shape and dominated by the mesial cusps, as in most *H. habilis*. The Dmanisi P₃ crowns are asymmetrical, sharing width/length proportions and discrete features with *H. habilis* (Macaluso, 2006). The Dmanisi M₁s are long but narrow when compared to those of *Australopithecus* (Martín-Torres et al., 2008).

This comparative evidence must be weighed carefully. Many of the similarities of D2700 to KNM-ER 1813 are likely to be size and/or age dependant. If D2700/D2735 had grown to full maturity, changes affecting the brow ridges, cranial superstructures, and the face might have set this individual apart from gracile *H. habilis*. Some other characters that appear to link the Dmanisi assemblage with *H. habilis* are primitive, in the sense that they are common not only to earlier *Homo* but also *A. afarensis* and (in some cases) extant apes. Such traits may serve to situate the Dmanisi population near the stem of the *Homo* clade, and they are a useful part of any species description. But symplesiomorphies do not link Dmanisi more closely to *H. habilis* than to other groups of hominins.

The Dmanisi fossils differ in many respects from *H. rudolfensis*. Contrasts in vault form and facial topography are especially marked. Nevertheless, there may be overlap in the shape of the anterior palate between the most orthognathic Dmanisi individuals (particularly D2700) and *H. rudolfensis* (the KNM-ER 62000 subadult). There are similarities in symphyseal and corpus heights, and corpus robusticity, between D2600 and KNM-ER 60000 (grouped with *H. rudolfensis* by Leakey et al., 2012). However, the taxonomic status of the Koobi Fora mandible remains unsettled. An analysis based on shape variables obtained from the dental arcade places KNM-ER 60000 closer to D2600 and other specimens from Dmanisi than to KNM-ER 1482, thus raising a question as to whether KNM-ER 60000 might actually represent *H. erectus* (Spoor et al., 2015). If this is the case, comparisons of D2600 with KNM-ER 60000 reflect variation among conspecifics rather than resemblances/differences between species.

Given the overall morphology of the cranial vault, basicranium, and lower jaw, the Dmanisi hominins might reasonably be aligned with *H. erectus* (Gabunia and Vekua, 1995; Rightmire et al., 2006; Spoor, 2013; Baab, 2016). A number of traits considered to be diagnostic for *H. erectus* are expressed in the Dmanisi population. A bar-like browridge, sagittal keel, flexed occipital, medially inclined mastoid process, low petrotympanic angle, smooth petrous pyramid, and reduced (crevice-like) foramen lacerum can be documented, but there is much individual variation. Insofar as facial form can be assessed, Dmanisi is again generally concordant with *H. erectus*. Many of these facial resemblances are primitive (shared with earlier *Homo*). The few

derived states (e.g., an elevated nasal saddle) linking Dmanisi to *H. erectus* vary within groups and may not be very useful for purposes of taxonomy (Rightmire (1998).

Multivariate analysis offers an additional perspective on affinities. Principal component 1 (42.9% of variance) is influenced strongly by mandibular fossa breadth, frontal narrowing, and brain size. The Dmanisi crania with relatively broad TMJs, constricted frontals, and reduced brain volumes are driven toward the negative pole. There is some overlap in scores with African *H. erectus*, but Far Eastern *H. erectus* assemblages lie toward the opposite end of the distribution on PC1. Principal component 2 (31.2% of total variance) is heavily weighted for supraorbital development and cranial breadth(s). Gracile supraorbital tori coupled with relatively broad vaults tend to shift the Dmanisi hominins positively, in reference to some (not all) of the 21 *H. erectus* specimens included in the analysis. Scores on PC1 and PC2 place three of the Dmanisi crania outside the 0.95 density ellipse constructed for *H. erectus*. D3444 lies very close to KNM-ER 1813. Indeed, these two individuals are remarkably alike in (size adjusted) mandibular fossa breadth, frontal narrowing, vertex height, and supraorbital torus thickness. D2700 approaches OH 24, again demonstrating broad resemblances between the Dmanisi population and *H. habilis*. When the three most important axes are considered (Fig. 7), it is evident that density ellipses for Dmanisi overlap only partially with those for *H. erectus*. Overall, the PC results seem to provide little support for the hypothesis grouping Dmanisi within the *H. erectus* hypodigm.

The Dmanisi hominins cannot unequivocally be referred either to *H. habilis* or to *H. erectus*. There is a continuum of forms, within which skull 5 may be counted as the most primitive in terms of brain size, cranial globularity, and basicranial proportions. D4500 displays a broad and flattened mandibular fossa similar to that of OH 13, KNM-ER 1805, and KNM-ER 1813. In its muzzle-like lower face, elongated palate, and molar size sequence, skull 5 resembles *Australopithecus*. Skull 2 is much more gracile, with a larger brain, reduced supraorbital development, a rounded occipital, and a *H. erectus*-like mandible. Skull 4 carries robust cranial superstructures but has a higher volume-to-base ratio and a more globular vault. Skull 1 has the largest brain and can be described as the specimen most like (African) *H. erectus*. These observations raise critical questions concerning the recognition of species-level diversity in Plio-Pleistocene *Homo*.

Diversification in early Homo

Homo habilis as described by Leakey et al. (1964) was represented by specimens from Olduvai Gorge that appeared different from *H. erectus*. Almost immediately, however, there were voices questioning whether enough morphological space could be found between *H. erectus* and *Australopithecus* to accommodate a new taxon (Campbell, 1964; Robinson, 1965). During subsequent decades, controversy over the nature and relationships of *H. habilis* never fully quieted (Spencer, 1997). Tobias himself held firmly to the belief that a single dimorphic species could encompass specimens from Olduvai Gorge, Koobi Fora, Sterkfontein, and Swartkrans (Tobias, 1991). On the basis of comprehensive studies of the fossils from Koobi

Fora, Wood (1985, 1991) proposed instead that the *H. habilis* hypodigm should be restricted to smaller brained, relatively prognathous individuals, while a second taxon (*Homo* sp. nov.) might be required for the more encephalized but flat-faced cranium of KNM-ER 1470. Wood (1992) then recognized both *H. habilis* and *H. rudolfensis* as distinct from early *H. erectus* (or *H. ergaster*). This model offers a “bushy” version of phylogeny, with a radiation of *Homo* species beginning well before 2.0 Ma ago. At least three (perhaps four) *Homo* lineages then existed in eastern Africa, over a long period (Lieberman et al., 1988; Rightmire, 1993; Strait and Grine, 2004; Spoor et al., 2007; Kimbel, 2009; Lieberman, 2011; Wood and Leakey, 2011; Antón, 2012; Leakey et al., 2012; Joordens et al., 2013).

Relatively speciose versions of hominin taxonomy have become quite widely accepted (Wood and Boyle, 2016). Nevertheless, there is continuing disagreement about the allocation of fossils to each species. Much of this confusion stems from the difficulty in identifying characters that are diagnostic, or “peculiar to a given taxon and by which it can be differentiated from other similar or closely related ones” (Mayr, 1969: 266). In the absence of such criteria, the boundaries between early *Homo* and *H. erectus* remain indistinct. This problem has become acute, as existing specimens are reassessed (Baab, 2008b, 2016; Spoor et al., 2015) and new fossils are described (Leakey et al., 2012; Lordkipanidze et al., 2013). A further challenge, not often acknowledged, is the need to explain the potential sympatry and synchrony of multiple *Homo* lineages (at Koobi Fora, for example), under the assumption that they inhabited similar ecological niches based on the acquisition of protein from animal carcasses (Kimbel, 2009; White, 2013; see also Ackermann and Smith, 2007). If multiple species are to be recognized, then questions concerning their ecology and adaptations must be explored more fully, in order to identify behaviors that might result in niche differentiation within a single lake basin.

Our morphometric findings lead us to hypothesize that *H. erectus* and *H. habilis* constitute a single evolutionary lineage, rooted in Africa and dispersing later into Eurasia, as documented by the Dmanisi population. Such arguments are not new (Tobias, 1991; White, 2009, 2013; Lordkipanidze et al., 2013; Van Arsdale and Wolpoff, 2013). We advance our case on grounds that: 1) variation in face-to-braincase size, facial prognathism, mandibular form, and tooth size within the Dmanisi paleodeme encompasses morphologies seen in *Australopithecus*, early *Homo*, and *H. erectus*; 2) PCA demonstrates that the Dmanisi crania are intermediate in form between *H. erectus* and *H. habilis*; 3) traits considered to be derived for *H. erectus* can be identified at Dmanisi but are not expressed in all individuals; and 4) derived states tend to be fixed in chronologically later populations of *H. erectus* from Africa and the Far East.

Support for our hypothesis comes from the observation that *H. erectus* and *H. habilis* appear to be largely time-successive and perhaps sympatric in East Africa. KNM-ER 3733 is dated at 1.63 Ma (Lepre and Kent, 2015), and most other *H. erectus* cranial, mandibular, and postcranial remains from the Turkana Basin have age estimates of 1.60 Ma to 1.43 Ma (McDougall et al., 2012). Craniodental fossils from Konso in southern Ethiopia are ca. 1.4 Ma in age (Suwa et al., 2007). OH 13 from middle Bed II Olduvai has an age estimated as 1.65 Ma, while OH 24 and

OH 7 from lower Bed I are dated at 1.90 Ma to 1.85 Ma (Suwa et al., 2007; Spoor et al., 2015). OH 24 and OH 7 are assigned dates of 1.90 Ma to 1.85 Ma (Suwa et al., 2007; Spoor et al., 2015). *Homo habilis* specimens at Koobi Fora range in age from 1.75 Ma to 1.65 Ma (Suwa et al., 2007; McDougall et al., 2012; Spoor et al., 2015). If KNM-ER 1802 is allocated to *H. habilis*, then the first appearance for this species is at ~2.0 Ma (McDougall et al., 2012). Thus, there is the option of defining the two morphs as successional species (Simpson, 1961) or chronospecies. The boundaries between such taxa can be defined only arbitrarily, and chronospecies do not add to lineage diversity.

Given the uncertainties surrounding determination of first and last appearances and dating inferred from placement of marker horizons, it is possible that early *H. erectus* at Koobi Fora may be as old as some *H. habilis* specimens, indicating overlap on geological if not ecological time scales. KNM-ER 2598 is part of an occipital bone bearing a prominent and rounded transverse torus similar to that of *H. erectus*. This specimen was found in the uppermost upper Burgi Member and assigned an age of 1.9 Ma to 1.88 Ma (Feibel et al., 1989). However, KNM-ER 2598 was collected from a lag surface and may have weathered from a stratigraphically younger deposit (White, 1996). The fossil would then have had to survive on the surface for a long period, without breaking up completely. KNM-ER 1813 has been dated at either 1.9 Ma to 1.88 Ma (Feibel et al., 1989), or within the limits of the Olduvai Subchron (1.95 Ma to 1.78 Ma) (Feibel et al., 2009). Alternatively, KNM-ER 1813 and other Area 123 hominins may be considerably younger (~1.65 Ma), as argued by Gathogo and Brown (2006). This controversy awaits resolution. If *H. erectus* and *H. habilis* do in fact occur together in the Turkana Basin, an anagenetic relationship between the two taxa may be “implausible” (Spoor et al., 2007: 690).

At Dmanisi there can be no doubt that populations sharing characters with both *H. erectus* and *H. habilis* predate specimens such as OH 13, OH 16, and KNM-ER 1805, but Dmanisi is geographically distant from East Africa. The Caucasus discoveries suggest an initial dispersal of *Homo*, prior to the time more than 1.9 Ma ago when hominins had evolved a full suite of characters anticipated in *H. erectus*. Dmanisi can be regarded as a very early outpost in Asia, relevant to the subsequent peopling of Java and China (Rightmire and Lordkipanidze, 2010). Not only the robust morphology of skull 5 but also features of skull 4 are echoed in the most ancient specimens from the Far East. Nothing in the paleontological record dictates that such dispersals must always have progressed from west to east, and the possibility of back migration(s) from western Asia into eastern Africa must also be considered (Rightmire et al., 2006; Spoor et al., 2007; Suwa et al., 2007).

A key question concerns the phyletic placement of the Dmanisi hominins. We view this population as part of an anagenetic sequence, within which *H. habilis* and *H. erectus* are ancestor and descendant. The competing hypothesis situates Dmanisi near the base of a *H. erectus* lineage already differentiated (split) from *H. habilis*. The claim that *H. habilis* is directly ancestral to *H. erectus* would be strengthened by a comprehensive phylogenetic analysis showing the earlier species to be more plesiomorphic anatomically than its putative descendant and confirming that

character state changes between temporally ordered assemblages of fossils are “congruent with hypothesized polarity transformations based on outgroup conditions” (Kimbel et al., 2006: 135). A different outcome, such as the identification of autapomorphic (uniquely derived) characters in older, supposedly ancestral site assemblages, would favor alternative hypotheses, invoking a more complex (speciose) evolutionary history for genus *Homo*.

Undertaking a full cladistic analysis will be difficult, given the obvious limitations of the existing record. No matter which of the various hypodigms proposed for *H. habilis* is selected, site-samples from Olduvai and the Turkana Basin remain very small. Crania are mostly incomplete and, apart from the Olduvai hand (OH 7), foot (OH 8) and lower limb (OH 35), postcranial elements are too fragmentary to provide useful information. Characters must be drawn mainly from the mandible and the dentition. Dmanisi provides a chronologically intermediate sample of well-preserved remains, including skulls and teeth. After ~1.65 Ma, *H. erectus* is represented throughout the Turkana Basin, but only two adult crania are relatively intact. The KNM-ER 992 mandible is complete with dentition, but other jaws are damaged. Most of them are isolated finds, without associated cranial material. From Konso, a partial *H. erectus* mandible with teeth is available, but the Konso cranial bones are badly broken. Until additional fossils are recovered and securely dated, constructing a strong test of hypotheses concerning the phylogeny of early *Homo* will present a significant challenge.

Homo rudolfensis remains enigmatic. The hypodigm for this species is still very small, including one nearly complete adult cranium (KNM-ER 1470) along with a juvenile face (KNM-ER 62000) showing similar morphology. Several damaged mandibles have been attributed to *H. rudolfensis* (Wood, 1992), but the identification of one of these specimens (KNM-ER 1802) has been questioned (Leakey et al., 2012). Our results demonstrate that D4500 is quite different from KNM-ER 1470 in aspects of vault form, facial topography, clivus angle, and palatal proportions. Many of the same distinctions are apparent when other Dmanisi specimens are compared with the Koobi Fora cranium. In a PCA based on vault measurements, the Dmanisi crania cluster with *H. habilis* and *H. erectus*, but KNM-ER 1470 falls at the extreme positive pole of axis 2, suggesting unique morphology. A similarity between Dmanisi and *H. rudolfensis* may lie in the form of the anterior dental arcade, as can be demonstrated most clearly when D2700 is compared with the KNM-ER 62000 subadult. In both palates, the canine jugal swellings bulge forward, so that the canine alveoli and the incisor row form a flat arc. Given the preponderance of evidence, we are inclined to favor the hypothesis of Wood and others, holding *H. rudolfensis* to be a distinct evolutionary lineage.

Conclusions

Dmanisi opens a rare window on the Plio-Pleistocene, allowing systematic assessment of variation within a geographically and temporally restricted population of early hominins. The Dmanisi assemblage is almost certainly composed of males as well as females, and mature adults occur alongside subadult specimens. There is much variation in craniomandibular morphology

and tooth size. Skull 5 in particular displays a number of unique features, most probably related to its small brain, large cranial base, and extreme dental attrition. At the same time, the Dmanisi individuals share a basic anatomical bauplan, suggesting that they represent a single taxon. This conclusion is supported by analyses of relative variation. Values of CV or V* for cranial height and parietal arc length are high at Dmanisi, but for most dimensions of the vault, basicranium, and face, variation at Dmanisi is about the same or less than that seen in comparators including *P. boisei*, *H. erectus* and *H. sapiens*.

The Dmanisi skulls and teeth have frequently been grouped with *H. erectus*. Nevertheless, brain size is dramatically reduced in comparison to the norm for this species, and D4500 has one of the lowest endocranial capacities on record for early *Homo*. Skull 5 resembles *Australopithecus* in its muzzle-like lower face and displays a suite of traits not seen before in early *Homo*. Skull 2 and skull 3 have larger brains but follow *H. habilis* in having gracile supraorbital tori, rounded rather than strongly flexed occipitals with little or no expression of a transverse torus, and primitive facial profiles. Other traits shared with *H. habilis* are expressed in the dentition. The many instances of overlapping morphology make it difficult to identify diagnostic traits by which the Dmanisi fossils can be sorted. The assemblage seems clearly to be *Homo* but cannot unequivocally be grouped with either *H. habilis* or *H. erectus*.

We propose that *H. habilis*, the Dmanisi population, and *H. erectus* constitute segments of a single evolutionary lineage. “Bushy” versions of phylogeny, postulating an early radiation within *Homo* and subsequent coexistence of three or more species in eastern Africa, may be unnecessarily complex and are difficult to justify on morphological grounds. Rather than extraordinary diversification with phenotypic divergence, it is the apparent congruence of some aspects of craniofacial form, accompanied by variation in others, that characterizes hominin populations evolving 2.5 to 1.0 Ma.

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Figure legends

Figure 1 Skull 5 from Dmanisi (scale bar = 5 cm). The D4500 cranium and dentition are complete and remarkably well preserved. The face is large and projecting in relation to the braincase. The D2600 mandibular corpus is damaged and exhibits significant pathologies (radicular lesions resulting in resorption of periapical bone, remodeling associated with premortum/antemortum tooth loss). Both ascending rami are broken.

Figure 2 Skull 5 lateral views (scale bar = 5 cm). The glabellar region is inflated and overhangs the nasal root. The nasal saddle is less elevated and the subnasal region is less projecting than in other Dmanisi specimens. The midsagittal profile of the face presents three well defined contours. The nasal saddle is concave, as is the middle contour formed by the lateral margin of the nasal aperture. The lowermost facial (or nasoalveolar) contour is convex, flowing smoothly into the procumbent central incisors.

The vault appears angular in profile, rather than globular. A slightly hollowed supratotal shelf extends posteriorly to the base of the extremely inclined frontal squama, and height at vertex is reduced relative to other Dmanisi individuals. The temporal line arcs posteriorly across the parietal. Midway along this course, the line becomes crested, but it subsides before turning downward toward the parietal angle. A blunt angular torus is continuous with a horizontally oriented and mound-like supramastoid crest. The auditory porus is oval in outline, with its long axis tipped slightly posteriorly from vertical.

Figure 3 The D4500 mastoid, tympanic, and petrous regions (scale bar = 2 cm). The tympanic plate is massively constructed, and the conical eustachian process is larger than in other Dmanisi crania. The foramen lacerum is crevice-like, as in *H. erectus*.

Figure 4 The D4500 palate and dentition (scale bar = 2 cm). The anterior teeth exhibit extreme wear and have been reduced to stubs. The (right) P⁴ is relatively broad and comparable in its proportions to *A. afarensis*, *A. africanus*, and AL 666-1. The crown index falls substantially below the mean for *H. habilis*. The upper molar (especially the M³) crowns are large relative to those of early *Homo*. The palatal (breadth/length) index for D4500 is low compared to D2282 or D2700, or *H. habilis*. The elongated and relatively narrow Dmanisi palate is similar in form to that of *A. afarensis*.

Figure 5 Lateral views of two Dmanisi mandibles (scale in cm). a) D2600 is massively constructed, with a high symphysis. The upper part of the symphyseal profile is dominated by the outwardly bowed and partially exposed incisor roots, while the inferior aspect is flattened and receding. A very weak central eminence is flanked by prominent and elongated anterior marginal tubercles. Height of the ascending ramus cannot be measured directly, but D2600 is clearly much larger in this dimension than other Dmanisi hominins. b) D211 has a substantially lower corpus, exhibiting damage inferiorly. At the symphysis, both a central eminence and strong marginal tubercles are present. D211 is clearly a younger individual, in comparison to

D2600. The gap in ages may be substantial, and it is quite likely that growth-related changes would have decreased the differences in corpus size and proportions between the two specimens.

Figure 6 Plot of cranial capacities for 27 adult *H. erectus* specimens ($\bar{X} = 1008.5 \text{ cm}^3$, $s = 128.5 \text{ cm}^3$). Distributions based on normal density and empirical density are depicted. Subadult specimens KNM-ER 42700 and KNM-WT 15000 are plotted separately. The Dmanisi hominins fall at the lower end of, or outside, the range observed for *H. erectus*. Indeed, D4500 along with D2700 and D3444 lie more than three standard deviations below the distribution mean.

Figure 7 Principal components analysis based on 10 cranial measurements. Scores on the first two components for four Dmanisi individuals, 21 *H. erectus* specimens, OH 24, KNM-ER 1813, and KNM-ER 1470 are plotted in the lower frame. Principal component 1 is influenced strongly by mandibular fossa breadth, frontal narrowing, and brain size. The Dmanisi crania with relatively broad TMJs, constricted frontals, and reduced brain volumes are driven toward the negative pole. There is some overlap in scores with African *H. erectus*, but southeast Asian *H. erectus* assemblages lie toward the opposite end of the distribution on PC1. Principal component 2 is weighted for supraorbital development and cranial breadths. Gracile supraorbital tori coupled with relatively broad vaults tend to shift the Dmanisi hominins positively, in reference to some (not all) *H. erectus*. Principal component 1 and PC3 are plotted in the upper frame; PC3 is loaded for cranial length, base breadth, and occipital width. D4500 with high AUB_{adj} but very low ASB_{adj} is driven positively in relation to other Dmanisi specimens. When all three axes are considered, it is evident that 0.95 density ellipses for Dmanisi overlap only partially with those for *H. erectus*.

Table 1 Five skulls from Dmanisi

	Specimen number	State of preservation
Skull 1 (adult)		
Calvaria	D2280	complete, minor damage
--	--	mandible missing
Skull 2 (young adult)		
Cranium	D2282	crushing, significant damage to face, occipital region
Mandible	D211	damage to base, rami missing
Skull 3 (subadult)		
Cranium	D2700	complete, minor damage
Mandible	D2735	complete, condyles missing
Skull 4 (old adult)		
Cranium	D3444	complete but edentulous, midfacial/alveolar parts resorbed
Mandible	D3900	complete but edentulous, alveolar bone heavily resorbed
Skull 5 (mature/old adult)		
Cranium	D4500	complete
Mandible	D2600	body complete, angles missing, rami damaged, severe pathology

Table 2 Early hominin crania used in comparative analyses

Taxon	Geographic region	Locality/Specimen number	Parts preserved
Earliest <i>Homo</i>	East Africa	LD 350-1	partial mandible
		AL 666-1	maxilla
<i>H. habilis</i>	East Africa	OH 7 ^a	parietal bones, partial mandible
		OH 13 ^a	partial cranium, mandible
		OH 16	teeth
		OH 24	cranium
		OH 62	cranial fragments
		KNM-ER 1805	partial cranium, mandible
		KNM-ER 1813	cranium
<i>H. rudolfensis</i>	East Africa	KNM-ER 1470	cranium
		KNM-ER 62000 ^a	partial face
<i>H. erectus</i>	East Africa	KNM-ER 3733 ^b	cranium
		KNM-ER 3883 ^b	calvaria, partial face
		KNM-ER 42700 ^b	calvaria
		KNM-WT 15000 ^{a, b}	cranium
		OH 9 ^b	calvaria
		Daka ^b	calvaria
	Java	Trinil	calotte
		Sangiran 2	calotte, partial base
		Sangiran 4	calvaria, palate
		Sangiran 10	partial calotte
		Sangiran 12	partial calotte
		Sangiran 17 ^b	cranium
		Sangiran IX ^b	calotte, maxilla

		Bukuran	calotte, partial base
		Ngawi ^b	calvaria
		Sambungmacan 1 ^b	calvaria
		Sambungmacan 3 ^b	calotte, partial base
		Sambungmacan 4 ^b	calvaria
		Ngandong 1 ^b	calotte
		Ngandong 6 ^b	calotte, partial base
		Ngandong 7 ^b	calvaria
		Ngandong 10 ^b	calotte, partial base
		Ngandong 11 ^b	calotte, partial base
		Ngandong 12 ^b	calvaria
	China	Zhoukoudian II	calotte
		Zhoukoudian III ^{a, b}	calotte, partial base
		Zhoukoudian V	partial calotte
		Zhoukoudian X	calotte
		Zhoukoudian XI ^b	calotte, partial base
		Zhoukoudian XII ^b	calotte
<i>H. naledi</i>	South Africa	DH1	partial cranium, mandible
		DH3	partial cranium
<i>Homo</i> sp. indet.	East Africa	OH 65	palate
		KNM-ER 1482	partial mandible
		KNM-ER 1802	partial mandible
		KNM-ER 42703	partial maxilla
		KNM-ER 60000	mandible
	South Africa	SK 847	partial cranium
<i>Paranthropus boisei</i>	East Africa	OH 5 ^a	cranium

<i>Australopithecus afarensis</i>	East Africa	AL 333-45	partial cranium
		AL 444-2	cranium, partial mandible
<i>A. africanus</i>	South Africa	Sts 5	cranium
		Sts 19	calvaria
		Sts 71	partial cranium
		Stw 505	cranium
<i>A. sediba</i>	South Africa	MH1 ^a	partial cranium, partial mandible
		MH 2	partial mandible

^a subadult or young adult specimens.

^b included in PCA.

Table 4 Facial measurements (linear dimensions in mm, angles in degrees) in the Dmanisi specimens

	D2282	D2700	D3444	D4500
Basion-prosthion length	--	100	--	126.7
Nasion-prosthion height	--	69	--	74
Biorbital chord	96	90	98	102
Nasion angle	--	136	142	147
Nasal bridge width	--	18	21	21
Nasal bridge height	--	9	9	11
Nasal bridge angle	--	90	98	--
Orbit breadth	--	35	38	38.5
Orbit height	--	31	32	32.6
Midorbital chord	--	55	51	60
Naso-orbital angle	--	129	130	146
Nasal breadth	27	28	28	31
Nasal height	--	50	50	46
Clivus length	28	>20	--	33
Bimaxillary chord	91 ^a	97	93	110
Subspinale angle	154	143	140	154
Prosthion angle	107	107	--	102
Cheek height	30	28	25	30
Max. malar height	43.5	39	40	44.5
Palate breadth	39	37	--	37.8
Palate length	54	55	--	68
Palate depth at M ²	15	12.5	--	18

^a Obtained by doubling the measurement to the midline.

Table 5 Mandibular measurements (in mm) in the Dmanisi specimens^a

	D211	D2600	D2735
Symphysis height	30.8	49	34
Symphysis thickness	16.8	21	16
Corpus height (min.) at P ₃	27.5	44.1	26.5
Corpus breadth at P ₃	18.5	21	18.5
Corpus height (min.) at M ₁	--	(41)	22.5
Corpus breadth at M ₁	18.4	(21)	19
Robusticity index at M ₁	--	(51.2)	84.4
Cross-sectional area ^b at M ₁	--	(676.2)	335.7

^a Where damage is appreciable, () indicates that only an estimate is possible.

^b Calculated as π (1/2 height) (1/2 breadth).

Table 9 Brain size, cranial base, vault proportion, and facial shape indices in the Dmanisi specimens and comparators

	D2280	D2282	D2700	D3444	D4500	ER 1470	ER 1813	<i>H. erectus</i>
Volume/base breadth ^a	0.068	-	0.071	0.071	0.063	0.067	0.071 ⁱ	(N = 24) 0.067 - 0.081
Cranial height/length ^b	0.51	-	0.49	0.50	0.43	0.55	0.51	(N = 23) 0.48 - 0.56
Cranial breadth/height ^b	1.49	-	1.64	1.60	1.86	1.50	1.52	(N = 25) 1.37 - 1.63
Globularity ^b	0.39	-	0.40	0.41	0.35	0.45	0.40	(N = 22) 0.35 - 0.46
Postorbital constriction ^c	0.71	0.69	0.74	0.69	0.64	0.65	0.71	(N = 14) 0.72 - 0.93
Frontal narrowing ^d	0.72	0.67	0.66	0.64	0.68	-	-	(N = 24) 0.61 - 0.79
Occipital scale ^e	1.02	-	0.87	0.85	0.77	0.75	0.73	(N = 20) 0.72 - 1.19
Facial breadth ^f	-	1.05	0.93	1.05	0.93	1.11	1.06	(N = 2) 0.98 - 1.08
Orbital ^g	-	-	0.88	0.84	0.85	0.88	0.88	(N = 3) 0.79 - 0.91
Palatal ^h	-	0.72	0.67	-	0.56	-	0.61	(N = 2) 0.72 - 0.74

^a Cube root of brain volume/biauricular breadth.

^b Indices describing vault proportions are calculated from glabella-occipital length, maximum cranial breadth, and porion-vertex height. Globularity = (breadth×height/length²).

^c Postorbital constriction index = minimum frontal breadth/biorbital chord

^d Frontal narrowing index = postorbital breadth/maximum biparietal breadth.

^e Occipital scale index = inion-opisthion chord/lambda-inion chord.

^f Facial breadth index = biorbital chord/bimaxillary chord.

^g Orbital index = orbit height/orbit breadth.

^h Palatal index = internal palate breadth/internal palate length.

ⁱ If volume and base breadth for the KNM-ER 1813 reconstruction (Benazzi et al., 2014) are used instead, the index is increased (0.082).

Table 10 Measurements of alveolar prognathism (in degrees) for Dmanisi, other early *Homo*, and *Australopithecus*^a

	Clivus angle (Lordkipanidze et al., 2013)	Subspinale/nasospinale- prosthion angle (Kimbel et al., 2004)	Subnasal angle (Leakey et al., 2012)
D2282	45	-	-
D2700	43	-	-
D4500	42	39 ^b	-
SK 847	46	-	-
OH 65	41	-	39
KNM-ER 1813	42	47	44
KNM-ER 1470	(55)	-	52
KNM-ER 62000	56	-	55
AL 666-1	47	49	42
Sts 5	36	37	-
Sts 71	35	47	-
AL 444-2	-	39	-

^a Where damage is appreciable, () indicates that only an estimate is possible.

^b Estimated by Y. Rak (pers. comm).

Table 12 Dental dimensions (in mm) for D4500 compared to those of early *Homo*^a

	C		P ³		P ⁴		M ¹		M ²		M ³	
	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL
D4500	(8.4)	10.9	(8.6)	13.6	(10)	13.7	12.2	14	14.5	15.8	14.4	16.4
OH 13	-	-	9.3	11.2	8.9	11.4	12.5	12.8	13	13.8	12.4	13.7
OH 16	10	9.8	10.2	12.2	9.9	12.1	14.7	13.7	13.9	16.4	13.1	16.7
OH 24	-	-	9.5	12.2	10.2	12.5	13.7	13.2	-	-	12.4	14.2
OH 62	-	-	-	-	-	-	-	-	-	16	-	15.5
OH 65	9.7	9.4	9.2	12.8	9	13.1	13	13.6	12.8	14.4	11	14
ER 1805	-	-	8	11.5	-	-	13.2	13.4	12.8	13.5	13.6	14.6
ER 1813	8.5	8.4	8.1	11.3	8.5	11.5	12	13	11.8	13.9	11.2	13.2
ER 42703	-	-	9	-	8.8	12.4	12.6	13.3	13	14.1	12.5	14.1
ER 62000	-	-	-	-	9.7	11.1	13.9	13.3	14.4	14	13.3	13.5
AL 666-1	-	10.2	9.2	12.5	9	12.6	12.9	12.4	13.5	14.4	-	-

^a Measurements generally taken on the left side (MD = mesiodistal; BL = buccolingual). If unavailable, the right side was used instead. Where interproximal wear is appreciable, or there is additional damage, () indicates that only an estimate is possible. Data for D4500 are uncorrected for attrition (Margvelashvili, Rightmire). Values for OH 13, OH 16, and OH 24 are corrected for attrition by Tobias (1991). Data for OH 62 are from Johanson et al. (1987). Data for OH 65 are uncorrected (Blumenschine et al., 2003). Values for ER 1805 and ER 1813 are corrected for attrition by Wood (1991). Data for ER 42703 are from Spoor et al. (2007). Data for ER 62000 are from Leakey et al. (2012). Values for AL 666-1 are corrected for attrition by Kimbel et al. (1997).

Table 13 Dental dimensions (mm) for D2600 compared to those of early *Homo*^a

	C		P ₃		P ₄		M ₁		M ₂		M ₃	
	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL
D2600	(10.5)	(8.2)	(9.5)	11.9	-	-	-	-	13.7	13.6	15.3	13.1
OH 7	8.8	10.1	9.7	10.3	10.3	10.7	14.8	12.2	15.6	13.5	-	-
OH 13	8.1	7.6	9.5	8.3	9.6	9.7	12.9	11.6	13.9	12.1	14.8	12.2
OH 16	-	-	10.8	11.4	10.8	10.9	14.8	12.7	16.3	15.1	16.0	14.4
ER 1482	-	-	-	-	9.7	(12.2)	(13.2)	(13.3)	15.0	14.0	-	14.6
ER 1802	-	-	10.7	11.5	12.1	11.8	14.9	13.2	17.0	14.2	-	-
ER 1805	-	-	-	-	-	-	-	-	14.3	12.9	15.0	12.2
ER 60000	-	8.3	8.9	9.5	8.8	9.8	12.8	11.4	14.0	12.8	15.7	12.9
LD 350-1	-	-	-	-	8.7	10.3	(12.2)	-	13.2	12.5	13.0	12.2

^a Measurements generally taken on the left side (MD = mesiodistal; BL = buccolingual). If unavailable, the right side was used instead. Where interproximal wear is appreciable, or there is additional damage, () indicates that only an estimate is possible. Data for D2600 are uncorrected for attrition (Margvelashvili, Rightmire). Values for OH 7, OH 13, and OH 16 are corrected for attrition by Tobias (1991). Values for ER 1482, ER 1802, and ER 1805 are corrected for attrition by Wood (1991). Data for ER 60000 are from Leakey et al. (2012). Values for LD 350-1 are corrected for attrition by Villmoare et al. (2015).

Table 15 Eigenvalues and coefficients for the first four principal components based on analysis of ten variables^a

Component	PC1	PC2	PC3	PC4
Eigenvalue	4.29	3.12	0.99	0.56
VOL	0.375	-0.316	0.060	0.066
OCA	-0.295	0.294	-0.207	0.657
GOL _{adj}	0.338	0.199	0.481	-0.170
PVH _{adj}	0.385	0.150	-0.261	0.478
XCB _{adj}	0.205	0.452	0.179	-0.074
AUB _{adj}	-0.021	0.445	0.465	0.191
ASB _{adj}	0.314	0.264	-0.445	-0.284
LFB _{adj}	0.422	-0.025	-0.314	0.005
FOS _{adj}	-0.432	0.124	-0.206	-0.315
TOR _{adj}	0.043	-0.511	0.254	0.289

^a Higher loadings on each component are indicated in bold. Variable abbreviations defined in the text.

Table 16 Expression in the Dmanisi crania of characters considered diagnostic for *H. erectus*^a

	D2280	D2282	D2700	D3444	D4500
Cranial vault					
Supraorbital torus bar-like, thickened	+++	++	+	+++	+++
Midline keeling on parietals	++	++	+++	++	+
Parasagittal flattening or depression	+	+++	+++	+	+
Temporal squama low, elongated posteriorly	++	-	++	++	+++
Angular torus prominent	+++	+	+	+	+++
Flexion of occipital	++	-	+	+	++
Occipital transverse torus	++	+	+	++	+++
Cranial base					
Glenoid fossa extends (far) laterally	+	-	+	++	+++
Mastoid process inclined medially	+	-	-	+++	+++
Tympanic plate thickened	+	++	+	+	+++
Petrosal spine robust	+	++	+	++	+++
Petrotympenic angle reduced	++	-	+	++	++
Eustachian (supratubarius) process tuber-like	+	-	+	-	+++
Petrous pyramid smooth (dense)	-	++	++	-	++
Foramen lacerum narrow	+++	-	+	-	+++
Face					
Nasal saddle elevated relative to orbital rims	-	-	+	++	+
Spinal/lateral cresting of nasal sill	-	+	+	++	+

^a Character expression is indicated as + (slight), ++ (moderate), +++ (strong), or – (indeterminate).

Table 3 Vault and cranial base measurements (mm for linear dimensions, angles in degrees, or as stated) for the Dmanisi specimens

	D2280	D2282	D2700	D3444	D4500
Whole vault					
Endocranial volume (cm ³)	730	650-660	600	625	546
Glabella-occipital length	177	--	155	163	169
Basion-bregma height	--	--	101	--	92.5
Porion-vertex height	91	--	77	82.5	73
Max. cranial breadth	136 ^a	--	126	132	135.5
Frontal bone					
Supraorbital torus thickness					
Central	11	10.5	8	10	12
Lateral	9	5.5	6	9	--
Min. frontal breadth	75	66	67	67.5	65
Postorbital breadth	86	78	77	78	75
Max. frontal breadth	105	87	85	91	92
Biorbital chord	105	96	90	98	102
Nasion-bregma chord	101	--	89	93	94
Nasion-bregma arc	108	>95	95	101	107
Glabella-bregma arc	98	95	88	90	91
Frontal angle	149	--	150	148	141
Parietotemporal region					
Max. biparietal breadth	119	116	117	122	110
Bregma-lambda chord	91	82	87	98	82
Bregma-lambda arc	96	85	91	105	84

Lambda-asterion chord	70	68	65	71	58
Lambda-asterion arc	75	72	70	74	68
Occipital bone					
Biasterionic breadth	104	103	105	104	93
Lambda-opisthion chord	76	--	70	79	64.5
Lambda-opisthion arc	97	--	87	95	86.5
Occipital angle	108	--	115.6	117	107
Lambda-inion chord	46	46	45	50	47
Inion-opisthion chord	47	--	39	42.5	36
Base					
Basion-nasion length	--	--	92	--	97
Biauricular breadth	132 ^a	--	119	120	129
Bi-foramen ovale diameter	55	--	--	--	53.5
Foramen magnum length	--	--	30	--	33.5
Foramen magnum breadth	--	--	28	28	28.6
Foramen magnum area ^b	--	--	660	--	752.5
Mandibular fossa breadth	28	--	28	30	29

^a Obtained by doubling the measurement to the midline.

^b Calculated as π (1/2 length) (1/2 breadth).

Table 6 Mesiodistal (MD) lengths and buccolingual (BL) breadths (in mm) for the maxillary dentition in the Dmanisi specimens^a

	I ¹		I ²		C		P ³		P ⁴		M ¹		M ²		M ³	
	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL
D2282 ^b	-	-	-	-	-	-	-	-	8.6	10.8	12.7	12.9	13.0	12.4	-	-
D2700	12.6	7.6	8.2	6.9	9.7	9.5	8.9	11.5	6.8	11.5	13.0	13.0	12.7	12.8	10.0	11.9
D4500	-	(10.4)	-	(8.9)	-	(10.9)	(8.6)	13.6	(10.0)	13.7	12.2	14.0	14.5	15.8	14.4	16.4

^a Measurements generally taken from the left side. If this tooth is missing or damaged, the right side was used instead. Where interproximal wear is appreciable, or there is additional damage, () indicates that only an estimate is possible.

^b Values corrected for attrition by Macaluso (2006).

Table 7 Mesiodistal lengths and buccolingual breadths (mm) for the mandibular dentition in the Dmanisi specimens^a

	I ₁		I ₂		C		P ₃		P ₄		M ₁		M ₂		M ₃	
	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL
D211 ^b	6.2	5.9	6.4	6.3	8.6	7.9	8.9	9.6	8.0	9.6	13.0	12.5	11.5	11.6	10.7	10.6
D2735	-	-	8.1	7.5	9.7	9.4	9.6	10.5	7.6	9.5	13.2	11.3	13.1	10.3	-	-
D2600	-	-	-	-	(10.5)	(8.2)	(9.5)	11.9	-	-	-	-	13.7	13.6	15.3	13.1

^a Measurements generally taken from the left side. If this tooth is missing or damaged, the right side was used instead. Where interproximal wear is appreciable, or there is additional damage, () indicates that only an estimate is possible.

^b data from Gabunia and Vekua (1995)

Table 8 Relative variation in dimensions of the cranial vault, base, and facial skeleton

	Dmanisi			<i>P. boisei</i> ^a			<i>H. erectus</i> ^b			<i>H. sapiens</i> ^c	
	N	CV	V*	N	CV	V*	N	CV	V*	N	CV
Endocranial capacity	5	10.8	11.3	5	4.2	4.4	27	12.7	12.8		~13.7
Glabella-opisthocranion	4	5.6	5.9	4	12.0	12.7	25	5.4	5.4	283	4.3
Porion-vertex height	4	9.6	10.2	6	6.2	6.4	26	6.0	6.1	283	4.4
Glabella-bregma arc	5	4.4	4.6	4	12.1	12.9	22	5.8	5.9	156	5.1
Bregma-lambda arc	5	9.4	9.8	-	-	-	25	7.0	7.1	156	6.2
Lambda-opisthion arc	4	5.9	6.3	-	-	-	22	5.3	5.4	156	7.3
Max. cranial breadth	4	3.5	3.7	4	10.9	11.5	26	4.2	4.2	283	4.4
Max. biparietal breadth	5	3.8	4.0	4	9.0	9.5	27	5.2	5.2	-	-
Biauricular breadth	4	5.2	5.5	5	10.5	11.0	25	5.3	5.3	283	3.8
Biasterionic breadth	5	4.9	5.1	5	7.4	7.7	27	5.7	5.7	283	4.4
Mandibular fossa breadth	4	3.3	3.5	5	7.3	7.7	18	23.3	23.6	-	-
Supraorbital torus thickness	5	14.4	15.1	4	20.7	22.0	25	18.1	18.2	-	-
Biorbital chord	5	5.2	5.5	-	-	-	16	5.8	5.9	283	4.3
Bimaxillary chord	4	8.7	9.3	-	-	-	-	-	-	283	5.5
Cheek height	4	8.3	8.9	4	13.8	14.6	-	-	-	283	11.0
Max. malar height	4	6.4	6.7	-	-	-	-	-	-	283	7.2
Nasal breadth	4	6.1	6.4	4	9.8	10.4	-	-	-	283	6.6
Palate breadth	-	-	-	4	3.9	4.1	6	13.3	13.8	283	6.0

^a Cranial data from Tobias (1991), Wood (1991), Suwa et al. (1997), Holloway et al. (2004), and Kimbel et al. (2004).

^b Endocranial capacities from Weidenreich (1943), Begun and Walker (1993), Baba et al. (2003), Widiyanto and Zeitoun (2003), Holloway et al. (2004), Spoor et al. (2007), Gilbert and Asfaw (2008), Kaifu et al. (2011), and Lordkipanidze et al. (2013). Measurements of porion-vertex height, glabella-bregma arc, and mandibular fossa breadth provided by F. Spoor (pers. comm.). Dimensions for the Bukuran cranium from Kaifu et al. (2008). Data for Ngawi from Widiyanto and Zeitoun (2003), but sagittal arcs taken from a cast. Sangiran IX documented by Arif et al. (2001) and Kaifu et al. (2011). Measurements of the Zhoukoudian crania from Weidenreich (1943) and casts held by the Peabody Museum at Harvard University. Dimensions for KNM-ER 42700 from Spoor et al. (2007). Data for Daka from Gilbert and Asfaw (2008). Other measurements taken by G.P.R. on the original fossils.

^c CV is based on pooled samples for 283 Dogon, Teita, and Zulu crania (Howells, 1973, 1989) or 156 Natal Nguni crania (de Villiers, 1968).

Table 11 Face and braincase dimensions (in mm) compared for Dmanisi, other *Homo*, *Australopithecus*, and *Paranthropus*

	D2700	D4500	OH 5	Sts 5	ER 1470	ER 1813	ER 3733	S 17
Facial dimensions								
Nasion-prosthion height	69	74	104 ^a	77 ^b	90	64	81	>75
Biorbital chord	90	102	103 ^a	94 ^b	109	91	109	114
Midorbital chord	55	60	66 ^a	61 ^a	64	60	73	66
Bimaxillary chord	97	110	115 ^a	98 ^a	98	86	101	116
Cheek height	28	30	47 ^a	25 ^b	40	27	34	37
Maxillo-alveolar breadth (M ²)	61 ³	72	82 ^c	66 ^b	>80 ^b	65 ^b	66 ^b	74 ^a
Palate length (internal)	55	68	79 ^c	69 ^b	58 ^d	54	55 ^a	57 ^a
GM (face)	60.9	68.8	81.9	65.0	73.3	60.1	69.7	72.2
Cranial vault								
Glabella-occipital length	155	169	173 ^c	147 ^c	168	145	182	207
Porion-vertex height	77	73	75 ^c	70 ^b	91.5 ^b	75	92	101
Max. cranial breadth	126	135.5	142 ^c	111.5 ^c	>138	113	142	161
Biasterionic breadth	105	93	89 ^c	74 ^c	108	93	119	124
Bregma-lambda arc	91	84	80.5 ^c	91.5 ^c	89	77	85	109
Lambda-opisthion arc	87	86.5	82 ^c	72 ^c	105	96	118	121
Lambda-asterion arc	70	68	59 ^c	62 ^c	88	69	88	92 ^a
GM (vault)	98.1	96.3	93.8	86.0	109.5	92.6	114.0	126.1

^a Estimated from a cast.

^b Data from Wood (1991).

^c Data from Tobias (1967).

^d Estimate only, based on other *Homo* ($n = 5$).

Table 14 Variables and *Homo* crania ($n = 28$) included in principal components analysis^a

	VOL	OCA	GOL _{adj}	PVH _{adj}	XCB _{adj}	AUB _{adj}	ASB _{adj}	LFB _{adj}	FOS _{adj}	TOR _{adj}
ER-3733	9.46	103	2.48	1.25	1.93	1.8	1.62	1.24	0.42	0.11
ER-3883	9.29	101	2.43	1.21	1.87	1.72	1.53	1.17	0.4	0.14
ER-42700	8.99	114	2.5	1.42	1.96	1.8	1.62	1.29	0.33	0.11
WT-15000	9.58	118	2.36	1.22	1.9	1.7	1.43	1.22	0.35	0.17
OH 9	10.21	108	2.37	1.18	1.73	1.56	1.42	1.15	0.37	0.22
Daka	9.95	107	2.22	1.25	1.72	1.6	1.43	1.17	0.34	0.23
San 17	10.01	100	2.45	1.19	1.9	1.65	1.58	1.19	0.28	0.2
San IX	9.54	104	2.42	1.21	1.85	1.64	1.52	1.13	0.36	0.18
Ngawi	9.54	99	2.24	1.19	1.75	1.62	1.47	1.22	0.38	0.19
Sam 1	10.11	106	2.4	1.28	1.81	1.64	1.52	1.28	0.31	0.18
Sam 3	9.71	107	2.34	1.32	1.91	1.8	1.57	1.32	0.25	0.18
Sam 4	10.02	95	2.34	1.18	1.83	1.71	1.56	1.36	0.3	0.17
Ng 1	10.54	98	2.52	1.38	1.97	1.67	1.65	1.36	0.23	0.17
Ng 6	10.77	99	2.56	1.27	1.8	1.72	1.46	1.25	0.29	0.18
Ng 7	10.04	103	2.44	1.28	1.86	1.67	1.57	1.34	0.25	0.19
Ng 10	10.43	105	2.58	1.36	2.03	1.76	1.62	1.4	0.22	0.16
Ng 11	10.71	95	2.55	1.4	2	1.69	1.64	1.44	0.23	0.15
Ng 12	10.29	100	2.53	1.34	1.9	1.7	1.59	1.35	0.24	0.17
Zhou III	9.71	102	2.59	1.31	1.99	1.92	1.61	1.21	0.23	0.17
Zhou XI	10.05	103	2.53	1.24	1.91	1.87	1.49	1.22	0.27	0.18
Zhou XII	10.1	102	2.52	1.29	1.9	1.95	1.48	1.23	0.23	0.19
D2280	9	108	2.43	1.25	1.86	1.81	1.42	1.18	0.38	0.15
D2700	8.43	115.6	2.38	1.18	1.93	1.82	1.61	1.18	0.43	0.12
D3444	8.55	117	2.36	1.19	1.91	1.74	1.5	1.13	0.43	0.14
D4500	8.24	107	2.44	1.05	1.96	1.86	1.34	1.08	0.42	0.17
ER-1813	7.99	114	2.35	1.21	1.83	1.82	1.51	1.13	0.42	0.14
OH 24	8.39	120	2.36	1.23	1.94	1.9	1.58	1.19	0.43	0.11

ER 1470	9.08	115	2.45	1.34	2.01	1.97	1.58	1.18	0.35	0.11
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^a San = Sangiran; Sam = Sambungmacan; Ng = Ngandong; Zhou = Zhoukoudian. Variable abbreviations defined in the text.

Figure

Figure

Figure

petrous apex

eustachian (supra-tubarius) process

petrosal spine

tympanic plate

mastoid (inferior aspect)

foramen lacerum

Figure

Figure

Figure