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*, *H. 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 *H. 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.

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1. 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 (Messager 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 (e.g., 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. Martinón-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 Homo 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