PALAEOANTHROPOLOGY

Small-brained and big-mouthed

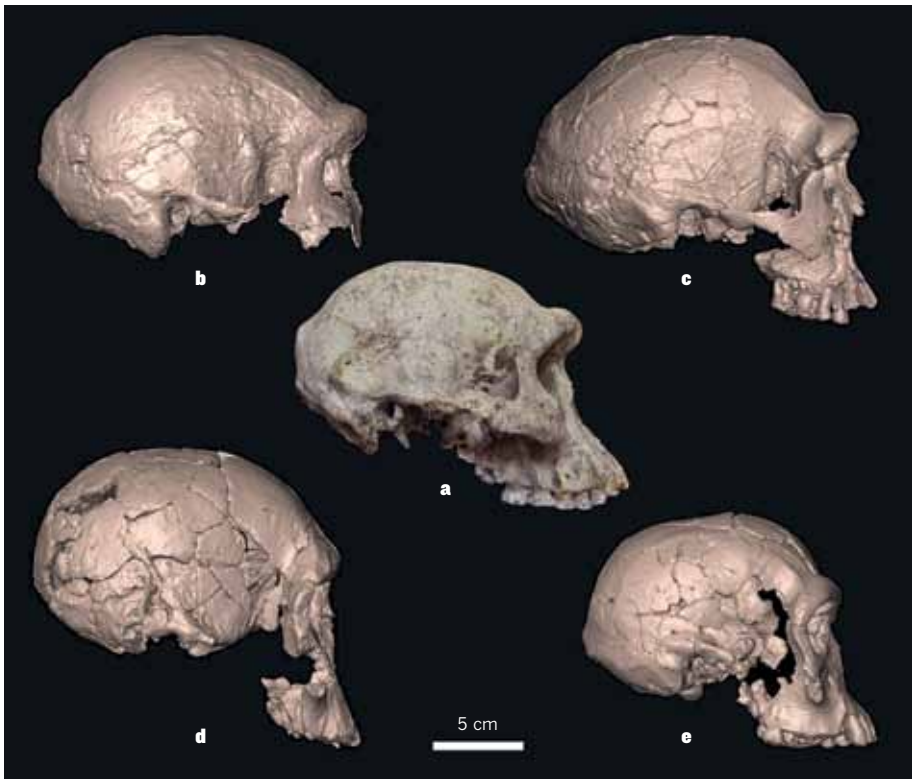
A complete hominin cranium found at the archaeological site of Dmanisi shows remarkably primitive morphology, prompting its discoverers to propose that early forms of the genus *Homo* evolved as a single, highly variable lineage.

FRED SPOOR

Hominins are species more closely related to humans than to chimpanzees. The oldest hominin fossils that have been found outside Africa are from 1.77-million-year-old strata at Dmanisi in the Georgian Caucasus[1]. These specimens show closest similarities to early *Homo erectus* fossils[2], but the discovery in 2000 of a large and robust mandible at the site led to the Dmanisi hominins being attributed to a new species, *Homo georgicus*[3], with this mandible as its holotype. But other researchers have considered whether the size and shape differences between Dmanisi mandibles indicate that these fossils represent more than one species[4,5]. Writing in *Science*, Lordkipanidze *et al.*[6] now provide the description and comparative analysis of the cranium associated with the large *H. georgicus* mandible — and use this to infer a taxonomy that breaks with a decades-long consensus on hominin evolution.

The new specimen is complete, and together with the mandible it forms the best-preserved adult skull of a hominin from the Early Pleistocene (the period from around 2.6 million to 0.8 million years ago). This exceptional find is made even more exciting by the fact that limb bones have been recovered that probably belonged to the same individual, and that it can be considered in the context of four other crania that were previously uncovered from the same location and that belong to broadly the same time period.

The latest cranium is characterized by a large and projecting face, combined with a brain size of 546 cubic centimetres, which is smaller than those of the other Dmanisi crania and any other specimen attributed to *H. erectus* (Fig. 1). In their analyses, Lordkipanidze *et al.* consider two broad issues: whether the variation shown by the five Dmanisi crania is greater than expected for a single species, and what the implications of this cranial variation are for the interpretation of the early fossil record of the genus *Homo*. With respect to the first question, the authors find the overall cranial shape variation of the Dmanisi sample to be consistent with that seen in chimpanzees or modern humans, such that it can be accommodated within a single species.



a, GURAM BUMBIASHVILI/GEORGIAN NATL MUS.

Figure 1 | A new cranium from Dmanisi. Lordkipanidze *et al.*[6] describe a fossil cranium from the Dmanisi site in Georgia, known by its accession number, D4500. Here, it is presented in comparison with early *Homo* specimens from Kenya, dated to between 1.6 million and 2 million years ago. The new cranium (**a**) has a projecting face and a braincase that is small but similar in shape to those of *Homo erectus* specimens KNM-ER 3833 (**b**) and KNM-ER 3733 (**c**). Specimens KNM-ER 1470 (**d**) and KNM-ER 1813 (**e**), which are attributed to the species *Homo rudolfensis* and *Homo habilis*, respectively, differ from these three crania in the shape of the braincase or face. Lordkipanidze and colleagues argue that the differences between all early *Homo* specimens, including the five shown here, can be accommodated within a single species, *H. erectus*. Surface reconstructions (**b**–**e**) derived from computed tomography images (**c**, left side, reversed).

The second issue focuses on whether the diversity of early *Homo* fossils reflects an evolutionary radiation of multiple species (*Homo habilis*, *Homo rudolfensis* and *Homo erectus*)[7–9], or a single, highly variable lineage[10]. On the basis of cranial shape analyses and a broad comparison of characteristics, the authors report that the morphological variation seen in the African fossil record of early *Homo* lies within the variation shown by chimpanzees, modern humans or the Dmanisi sample. This leads them to conclude that early *Homo* evolved as a single variable lineage, and to attribute the associated fossil record to a single species, *H. erectus* (this name has priority over others because it was the first one used for any of these fossils). Consequently, the authors retract *georgicus* as a species name, but re-use it in their designation of the Dmanisi sample as *Homo erectus ergaster georgicus*. This highly unusual infrasubspecific classification is probably the first use of a quadrinomial in primate taxonomy, and is not recognized by the International Code of Zoological Nomenclature.

The radical proposal to subsume the well-established taxa *H. habilis* and *H. rudolfensis* into *H. erectus* warrants careful scrutiny, and in my view the presented evidence is weak. It

is doubtful whether analyses of overall cranial shape have the diagnostic power to distinguish between closely related taxa, as is indeed demonstrated by some of the analyses presented in the report. Species are defined by specific morphological features, not by overall cranial shape. Lordkipanidze and colleagues' list of individual features could have been informative in this respect, but it is not analysed systematically, nor is a distinction made between traits that are derived (absent in the last common ancestor of a group) or primitive (already present in the last common ancestor) — a distinction that is essential to establishing phylogenetic relationships. Moreover, the features are categorized in a way that sometimes obscures, rather than highlights, important differences. For example, two crania attributed to *H. rudolfensis*[9] clearly differ from all other early *Homo* specimens in the degree of facial projection around the mouth. This distinction is not revealed in the authors' table of features because of the arbitrary way the associated angle is categorized. Finally, the authors make no reference to the available non-cranial fossil evidence, even though biomechanical analyses of specimens attributed to *H. habilis* and *H. erectus* indicate marked differences in locomotive behaviour[11].

The new cranium's small brain size, projecting face and large cheek teeth are primitive for *H. erectus* (in the conventional use of this species name), but the specimen also shows derived morphological features that are typically found in this species, but not in specimens attributed to *H. habilis* or *H. rudolfensis*. These include its thick and protruding brow ridges, the distinct shape of the occipital bone (Fig. 1) and the arrangement of the temporal bone in basal view. This pattern of combined primitive and derived morphology is seen in other Dmanisi specimens as well, but in the new cranium the primitive aspect is particularly prominent. As such, this morphology seems to correspond to what one would expect not too long after the *H. erectus* lineage diverged from a more generalized form of early *Homo*. It would also be compatible with the centrifugal model of speciation[12], in which central populations in Africa are more derived, and peripherally distributed ones in western Asia and southern Africa (such as *Homo* at the Swartkrans site) retain primitive features.

The discovery of the new Dmanisi cranium will greatly help with the evaluation of the fossil record of early *Homo* in eastern Africa, which is temporally and geographically more diverse, and generally less well-preserved. This should contribute to a better understanding of where and when the *H. erectus* lineage first emerged, and how it relates to other taxa of early *Homo*. ■

Fred Spoor *is in the Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig 04103, Germany, and University College London, UK.*
e-mail: f.spoor@eva.mpg.de

1. Lordkipanidze, D. *et al. Nature* **449,** 305–310 (2007).
2. Rightmire, G. P. & Lordkipanidze, D. in *The First Humans* (eds Grine, F. E., Fleagle, J. G. & Leakey, R. E.) 39–48 (Springer, 2009).
3. Gabunia, L., de Lumley, M. A., Vekua, A., Lordkipanidze, D. & de Lumley, H. *C.R. Palevol* **1,** 243–253 (2002).
4. Skinner, M. M., Gordon, A. D. & Collard, N. J. *J. Hum. Evol.* **51**, 36–49 (2006).
5. Rightmire, G. P., Van Arsdale, A. P. & Lordkipanidze, D. *J. Hum. Evol.* **54,** 904–908 (2008).
6. Lordkipanidze, D. *et al. Science* **342,** 326–331 (2013).
7. Wood, B. *Nature* **355,** 783–790 (1992).
8. Spoor, F. *et al. Nature* **448,** 688–691 (2007).
9. Leakey, M. G. *et al. Nature* **488,** 201–204 (2012).
10. Suwa, G. *et al. Anthropol. Sci.* **115,** 133 (2007).
11. Ruff, C. *Am. J. Phys. Anthropol.* **138,** 90–100 (2009).
12. Groves, C. P. *A Theory of Human and Primate Evolution* (Clarendon, 1989).