

# Did early *Homo* migrate “out of” or “in to” Africa?

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The origin of our own genus remains frustratingly unclear. Although many of my colleagues are agreed regarding the “what” with respect to *Homo*, there is no consensus as to the “how” and “when” questions. Until relatively recently, most paleoanthropologists (including the writer) assumed Africa was the answer to the “where” question, but in a little more than a decade discoveries at two sites beyond Africa, one at Dmanisi in Georgia and the other at Liang Bua on the island of Flores, have called this assumption into question. The results of recent excavations at Dmanisi reported in PNAS (1), which suggest that hominins visited that site on several occasions between *ca.* 1.85 and *ca.* 1.77 Ma, together with recent reassessments of the affinities of *Homo habilis*, are further reasons for questioning the assumption that *Homo* originated in Africa.

The site of Dmanisi, which is 34 miles southwest of Tbilisi, is situated on a promontory at the confluence of two rivers, the Masavera and the Pinasaouri. Since the 1930s the main foci of excavations have been its Bronze Age and medieval archeology, but between 1983 and 1987 excavations in part of the medieval village resulted in the recovery of early Pleistocene fossils, and the first of many well-preserved hominin fossils, the D211 mandible, was recovered in 1991. The early Pleistocene sediments at Dmanisi, which are dominated by primary and locally reworked ashfalls, are divided into two major units: stratum A (with subunits A1–A4), which conformably overlies the Masavera Basalt, and stratum B (with subunits B1–B5), which overlies stratum A and is separated from it by a minor erosional disconformity (2).

## Digging Deeper at Dmanisi

Before the recent excavations all of the hominin fossils and archeological evidence from Dmanisi had come from stratum B. The 73 artifacts and 34 bone fragments recently recovered from stratum A (specifically from subunits A2a–A4a) at M5 have been interpreted as coming from a series of “living surfaces” on ash falls that were exposed long enough for soil formation to begin. Most of the artifacts were flakes, but there are a few cores and choppers; all are consistent with the simplest, mode 1, category of artifacts. The artifacts from stratum A are mostly made on a red tuff that was exploited more in-

tensively than the raw materials used to make the artifacts found in stratum B.

None of the sediments in any of the excavations at Dmanisi can be older than the underlying Masavera Basalt, which has been dated to *ca.* 1.85 Ma. The sediments that make up stratum B have been dated by magneto- and biochronology and by correlative argon–argon dating to *ca.* 1.77 Ma. In contrast, the sediments in stratum A all display a normal magnetic signal that is interpreted as the upper Olduvai subchron; this places them between 1.85 and 1.78 Ma (the latter being the age of the Olduvai–Matuyama boundary). The evidence from Dmanisi thus provides a minimum first appearance date (FAD) for hominins in the Caucasus, but it is very

## Evidence for *H. erectus* outside of Africa extends back to at least *ca.* 1.85 Ma.

likely that hominins were there long before *ca.* 1.85 Ma, for in the absence of long sections FADs are subject to substantial error (3).

Thus far, no hominin fossils have been recovered from the sediments of stratum A, but the archeological evidence is consistent with the hypothesis that the artifacts in stratum A were made by the hominin taxon that is sampled in stratum B. However, what type of hominin is that? Some have suggested that the hominin fossils recovered from Dmanisi may sample more than one taxon, but most observers see just one morph in the sample. At the time of their discovery the morphology of the first hominin fossils to be recovered did not fit neatly into what was then known about either *H. habilis* or *Homo erectus*, but subsequent *H. erectus* discoveries in East Africa (4, 5) have expanded our knowledge of that taxon. Most experienced observers agree that the Dmanisi hominins are appropriately assigned to *H. erectus*, but with the caveat that they lie at the primitive end of that taxon’s morphological spectrum; some observers have suggested they sample a taxon that is more primitive than *H. erectus* (6, 7).

## A More Primitive African Emigrant?

For a long time now, the conventional wisdom has been that the first hominins to leave Africa were morphologically and adaptively quite distinct from *Australopithecus* (e.g., they had body proportions much like tropical modern humans and were capable of imagining and manufacturing mode 2 artifacts), but this view has had to be modified because of the hominin fossils assigned to *Homo floresiensis* from Liang Bua (8). The hominin sample from Liang Bua now includes nearly 100 individually numbered specimens that are estimated to represent fewer than 10 individuals. The taxon *H. floresiensis* was immediately controversial for at least two reasons. First, the estimated geological age of the specimens of between *ca.* 17 and *ca.* 74 ka substantially overlaps the presence of modern humans in the region. Second, although its discoverers and describers acknowledged the small overall size of *H. floresiensis* (the stature of LB1 is estimated to be 106 cm and its body mass to be *ca.* 25–30 kg) it had an exceptionally small brain (*ca.* 417 cm<sup>3</sup>) for an adult hominin individual. A few researchers have suggested that the hominin fossils from Liang Bua sample a population of *Homo sapiens*—most likely antecedents of the small-statured Rampasasa people who live on Flores today—afflicted by either an endocrine disorder, or some other syndrome, that includes microcephaly. Both explanations, a unique endemically dwarfed hominin species or pathology, are exotic, but the researchers who espouse a pathological explanation for the individuals represented by LB1–15 need to explain what pathology results in an early *Homo*-like cranial vault, archaic hominin-like mandibular, dental, carpal, and pedal morphology, and a brain that although very small apparently has none of the morphological features associated with microcephaly. Initially it was suggested that *H. floresiensis* was an endemically dwarfed *H. erectus*, but the burden of subsequent analyses suggest that it may be an endemically dwarfed version of a more primitive *H. habilis*-grade hominin (9–12).

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## Homo Who?

Although I suggested that many of my colleagues are agreed regarding the “what” with respect to *Homo* (i.e., that the genus *Homo* includes the species *H. habilis*), in the past some of us have argued (13) that if a genus is both a clade and a grade, then there are grounds for excluding *H. habilis* from *Homo* because it is very likely not in the same grade as the type species of *Homo*, *H. sapiens*. The grade arguments involve a wide range of regional and functional morphology, including the relative size of the postcanine tooth crowns (13) and mandibular corpus (14), the proportions (15) and relative strength (16) of the limbs, carpal morphology (9), and diet as inferred from microwear evidence (17). All these lines of evidence suggest that the adaptive coherence of *Homo* would be compromised if *H. habilis* is included in *Homo*. Thus, if these arguments are accepted the origins of the genus *Homo* are coincident in time and place with the emergence of *H. erectus*, not *H. habilis*.

We have seen from the most recent evidence from Dmanisi (1) that evidence for *H. erectus* outside of Africa extends back to at least *ca.* 1.85 Ma, and some claim that fossils of *H. erectus* from Java may also be in that age range. However, what about the earliest evidence of *H. erectus* in Africa? There is uncontestable evidence of *H. erectus* in the form of the KNM-ER 3733 cranium from Koobi Fora, whose geological age is *ca.* 1.78 Ma, but

many point to an occipital fragment, KNM-ER 2598, whose geological age is *ca.* 1.87 Ma, as the earliest evidence of *H. erectus* in Africa. Thus, the new evidence from Dmanisi suggests that the FADs for *H. erectus* both inside and outside of Africa are much the same, but it must be remembered that both FADs are likely to be adjusted upward.

## Uncertain Origins

So what does all this mean for the origin of *Homo*? The following scenarios are compatible with the meager evidence we have; it would be misleading to claim that any of the scenarios are supported by that meager evidence. I am skeptical about the merits of including *H. habilis* in *Homo*, but if it is included then *Homo* most likely evolved in Africa, but “where” in Africa, “when,” and “from what” are all questions presently without reliable answers. If, on the other hand, *H. habilis* is excluded from *Homo*, then the meager evidence we have is consistent with *H. erectus*, and thus *Homo*, evolving from a *H. habilis*-grade taxon either within, or outside of, Africa. In the most parsimonious version of the “outside of Africa” scenario for the origin of *Homo*, *H. erectus* would have evolved from a *H. habilis*-grade hominin either in Asia or in Southeast Asia, and then *H. erectus* would have migrated to Africa some time before 1.87 Ma. This scenario is consistent with the aspects of the morphology of the Dmanisi and the Liang Bua hominins that are more primitive than the

condition seen in *H. erectus sensu stricto*. This primitive morphology is one of stumbling blocks for a “within Africa” scenario for the origin of *H. erectus* taxon, for it would mean the migration out of Africa of two hominins, first a *H. habilis*-grade taxon then *H. erectus sensu stricto*. Another stumbling block for an ancestor-descendant relationship between *H. habilis* and *H. erectus sensu stricto* within Africa is that both the ancestor and the descendant overlap in time in East Africa for several hundred thousand years (5).

## Even Dmanisi Is Not Enough

We must hope that researchers find more sites as productive as Dmanisi so that today’s meager evidence for the origin of *Homo* will soon be augmented. In the meantime we need to be realistic about what can, and what cannot, be deduced about hominin evolutionary history. It is sobering to realize that even in the case of a taxon such as *Homo neanderthalensis* that has an order of magnitude better fossil record than for early *Homo*, we still have much to learn about its origin and evolution.

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- Ferring R, et al. (2011) Earliest human occupations at Dmanisi (Georgian Caucasus) dated to 1.85–1.78 Ma. *Proc Natl Acad Sci USA* 108:10432–10436.
- Lordkipanidze D, et al. (2007) Postcranial evidence from early *Homo* from Dmanisi, Georgia. *Nature* 449:305–310.
- Bobe R, Leakey M (2009) Ecology of Plio-Pleistocene mammals in the Omo-Turkana Basin and the emergence of *Homo*. *The First Humans: Origin and Early Evolution of the Genus Homo*, eds Grine FE, Fleagle JG, Leakey RE (Springer, Dordrecht, The Netherlands), pp 173–184.
- Potts R, Behrensmeier AK, Deino A, Ditchfield P, Clark J (2004) Small mid-Pleistocene hominin associated with East African Acheulean technology. *Science* 305:75–78.
- Spoor F, et al. (2007) Implications of new early *Homo* fossils from Ileret, east of Lake Turkana, Kenya. *Nature* 448:688–691.
- Gómez-Robles A, et al. (2008) Geometric morphometric analysis of the crown morphology of the lower first premolar of hominins, with special attention to Pleistocene *Homo*. *J Hum Evol* 55:627–638.
- Martinón-Torres M, et al. (2008) Dental remains from Dmanisi (Republic of Georgia): Morphological analysis and comparative study. *J Hum Evol* 55:249–273.
- Brown P, et al. (2004) A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature* 431:1055–1061.
- Tocheri MW, et al. (2007) The primitive wrist of *Homo floresiensis* and its implications for hominin evolution. *Science* 317:1743–1745.
- Argue D, Morwood MJ, Sutikna T, Jatmiko, Saptomo EW (2009) *Homo floresiensis*: A cladistic analysis. *J Hum Evol* 57:623–639.
- Brown P, Maeda T (2009) Liang Bua *Homo floresiensis* mandibles and mandibular teeth: A contribution to the comparative morphology of a new hominin species. *J Hum Evol* 57:571–596.
- Morwood MJ, Jungers WL (2009) Conclusions: Implications of the Liang Bua excavations for hominin evolution and biogeography. *J Hum Evol* 57:640–648.
- Wood BA, Collard M (1999) The changing face of genus *Homo*. *Evol Anthropol* 8:195–207.
- Wood BA, Aiello LC (1998) Taxonomic and functional implications of mandibular scaling in early hominins. *Am J Phys Anthropol* 105:523–538.
- Green DJ, Gordon AD, Richmond BG (2007) Limb-size proportions in *Australopithecus afarensis* and *Australopithecus africanus*. *J Hum Evol* 52:187–200.
- Ruff C (2009) Relative limb strength and locomotion in *Homo habilis*. *Am J Phys Anthropol* 138:90–100.
- Ungar PS, Krueger KL, Blumenschine RJ, Njau J, Scott RS (2011) Dental microwear texture analysis of hominins recovered by the Olduvai landscape paleoanthropology project, 1995–2007. *J Hum Evol*, in press.