

A Complete Skull from Dmanisi, Georgia, and the Evolutionary Biology of Early Homo

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As already noted by Darwin, recognizing species diversity comes “at the expense of admitting much variation” within species [(33), p. 51]. Together with data from *Au. afarensis* paleodemes such as A.L. 333 (34–36), Dmanisi adds to the growing evidence that intrademic and intraspecific variation in Plio–Pleistocene fossil hominids tends to be misinterpreted as species diversity, especially when single fossil specimens from different localities are compared with each other (37). Evidence from skull 5 and the other four Dmanisi specimens indicates that cranial shape variation within early *Homo* paleodemes was similar in mode and range to that seen within modern *Pan* demes. Furthermore, Dmanisi indicates that an important proportion of character state variation in nonmetric features reflects intrademic variation rather than real species diversity. These findings have several implications for the interpretation of morphological diversity in the fossil record of early *Homo*.

When seen from the Dmanisi perspective, morphological diversity in the African fossil *Homo* record around 1.8 Ma probably reflects variation between demes of a single evolving lineage, which is appropriately named *H. erectus*. The hypothesis of multiple independent lineages (paleospecies) (15, 31) appears less parsimonious, especially in the absence of empirical evidence for adaptation to separate ecological niches. The hypothesis of phyletic evolution within a single but polymorphic lineage raises a classificatory but not evolutionary dilemma, and it is premature to describe the rate(s) of evolution in this lineage, given the small available samples. Specimens previously attributed to *H. ergaster* are thus sensibly classified as a chronosubspecies, *H. erectus ergaster*. The Dmanisi population probably originated from an Early Pleistocene expansion of the *H. erectus* lineage from Africa, so it is sensibly placed within *H. e. ergaster* and formally designated as *H. e. e. georgicus* to denote the geographic location of this deme [thus retracting the species status given earlier to mandible D2600 (12)].

Given the scattered and fragmentary fossil record in Africa that predates Dmanisi, questions of earliest African *Homo* phylogenetics and classification remain unresolved. It remains to be tested whether all of the fossils currently allocated to the taxa *H. habilis* and *H. rudolfensis* belong to a single evolving *Homo* lineage. Although we regard this null hypothesis as parsimonious and fully compatible with new evidence from Dmanisi, alternative scenarios exist. Given the range of variation seen in the Dmanisi paleodeme, there is no convincing signature, at present, of early *Homo* cladogenesis. The African fossils that postdate the Dmanisi ensemble show brain size increase and correlated change in craniofacial morphology within the evolving lineage of *H. erectus*. Moreover, it is likely that both the underpinning of the East Asian dispersal of *H. erectus*, as well as the roots of subsequent *H. erectus* evolution in Africa (for example, OH 9, Daka), shared greater craniofacial robusticity.

The new evidence from the ancient Dmanisi deme of early *Homo* reinforces the strong African affinities previously recognized for this early Eurasian outpost of our genus (7). Variation between continents may thus provide insight into the evolutionary population dynamics of early *Homo*. It is well known from the upper Pleistocene dispersal of modern humans from Africa that genetic and phenetic variation within demes decreases with geographic distance from Africa, due to serial founder effects and population bottlenecks. For example, modern human phenetic variation in western and eastern Asia is 95 and 85% of African variation, respectively (38). The expansion of early *Homo* from



Africa, Australia, and America); *P. troglodytes*: *P. t.*

troglodytes (solid squares and pictures), *P. t. verus* (vertical rectangles), *P. t. schweinfurthii* (horizontal rectangles); *P. paniscus* (open squares). Black

symbols indicate adult individuals; gray symbols indicate subadult individuals. Large symbols indicate male and female averages. Shape component SC1 captures within-group cranial variation from large-faced/prognathic to small-faced/orthognathic individuals; SC2 captures shape change associated with grade shifts in neurocranial size between taxa.

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Africa might have occurred at longer time scales, so direct comparisons must remain tentative. Nevertheless, the observation that Dmanisi conserves a substantial proportion of cranial shape and its variation among early African Homo speaks for genetic continuity between Africa and Eurasia. Because intrademic variation at Dmanisi is similar to that found in extant and extinct near relatives, the effective population size of early Homo in western Asia might have been similar [$N_e > 10,000$ (39)]. Furthermore, the remarkably large and robust dentognathic remains of early *H. erectus* from Java (Trinil/Sangiran) (40, 41) exhibit close affinities with skull 5 (tables S2 to S4). This provides evidence for morphological (and presumably underpinning genetic) continuity across large geographic distances, and for the preservation in East Asia of an appreciable proportion of the variation originally present within paleodemes of early Homo in Africa (20, 42–44) (fig. S8).

Contrasting with early Homo population continuity across continents, current paleontological data indicate a low degree of similarity between contemporaneous mammalian genera in Africa and at Dmanisi (5), implying a generally low rate of faunal exchange between Africa and Asia before and around 1.8 Ma (45). As suggested earlier (46), the populational, ecological, and evolutionary dynamics of early Homo probably differed significantly from those of coeval large mammals, including other hominid lineages. Theoretical considerations indicate that the long-range dispersal rate of a population mainly depends on rates of reproduction and local habitat expansion (47) and that intragroup cooperation can play an important role in population persistence (48). Various features such as derived lower limb and foot morphologies (5, 49), tool-mediated widening of the dietary niche toward meat eating (4, 6), and increased levels of intragroup cooperation (3) might have led to increased rates of reproduction, survival, and mobility in early Homo and the consequent establishment of stable populations outside Africa. Skull 5 and the other members of the Dmanisi paleodeme now indicate that early Homo expanded from Africa to ultimately establish substantial populations in western Asia. This earliest hominid dispersal pre-dated any significant increase in brain size. Further analyses are required to test and modify the attendant hypotheses. Ultimately, identifying hominid paleodemes and assessing within-deme variation (32) will be key to understanding mechanisms of evolution and geographic dispersal of early Homo.