DOI: 10.1002/evan.21863

ISSUES

Evolutionary Anthropology WILEY

What kind of hominin first left Africa?

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Funding information

Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: 302127/2015-1; Fundação de Amparo à Pesquisa do Estado de São Paulo, Grant/Award Numbers: 2013/22631-2. 2016/04809-7: Wenner-Gren Foundation. Grant/Award Number: 8991

Abstract

Recent discoveries of stone tools from Jordan (2.5 Ma) and China (2.1 Ma) document hominin presence in Asia at the beginning of the Pleistocene, well before the conventional Dmanisi datum at 1.8 Ma. Although no fossil hominins documenting this earliest Out of Africa phase have been found, on chronological grounds a pre-Homo erectus hominin must be considered the most likely maker of those artifacts. If so, this sheds new light on at least two disputed subjects in paleoanthropology, namely the remarkable variation among the five Dmanisi skulls, and the ancestry of Homo floresiensis.

KEYWORDS

early Pleistocene, Homo floresiensis, Homo georgicus, Out of Africa

INTRODUCTION 1

In the conventional paleoanthropological narrative Homo erectus, first documented in Java, was the first hominin to exit Africa and enter Eurasia. As currently articulated, this scenario depends heavily on evidence from the Georgian site of Dmanisi, where five skulls and some associated postcrania, dated to ca. 1.8 million years (Ma),¹ have been allocated to H. erectus.² Under this reasoning, the first appearance of H. erectus in Asia soon followed its first appearance in Africa, currently dated at ca. 2 Ma in South Africa.³

Recent discoveries of stone tools in Jordan⁴ and in China⁵ date back to 2.5 and 2.1 Ma, respectively, and suggest a new and starkly different picture. On a purely chronological basis, these dates push the first Out of Africa event back by 700 thousand years, strongly suggesting that a pre-erectus hominin must have been involved in this expansion. In this note we present a short summary of recent discoveries in Jordan and China and discuss how this new evidence sheds light on at least two widely disputed subjects in paleoanthropology, namely the remarkable variation among the five Dmanisi skulls, and the ancestry of Homo floresiensis.

Since the early 1980s, the Dawgara Formation in the Zarga Valley, Jordan, has been known for the occurrence of cores and flakes artifacts within its fluvial sediments.⁶ Early findings were confirmed by surveys in the late 1990s, when Mammuthus meridionalis, Equus cf. tabeti, and Bos primigenius were also reported in the upper part of the Dawgara Fm.⁷ The Zarga Valley was then revisited between 2013 and 2016 by a Brazilian-Italian team, with the aim of providing a robust chronostratigraphic framework for the several artifact-bearing sites.

Three major fluvial terraces are observed at the confluence between the Zarga River and its tributary the Dulayl. The highest (oldest) of these lies 40-50 m above the modern river, and it consists of fluvial sediments belonging to the Dulayl (at the bottom) and Dawqara (at the top) formations, respectively, the two separated by a basaltic lava flow. The top of the Dawgara Fm is capped by a thick caliche produced by pedogenic processes. Megafaunal remains are encountered throughout the succession,^{4,7} but stone tools have been found only above the basalt layer, within the Dawqara Fm. Artifacts occur at several stratigraphic levels, suggesting an almost continuous hominin occupation of the Zarqa Valley during the deposition of the Dawqara Fm.⁴ Techno-typologically, the lithic assemblage of Dawqara is composed of pebble-cores and flakes.

Age estimates of the Dawqara Fm have been obtained by integrating 40 Ar/ 39 Ar on basalt (2.52 ± 0.01 Ma), U–Pb laser ablation on caliche (1.98 ± 0.2 Ma), and magnetostratigraphy. The results from these independent dating methods are in mutual agreement, and pin down the deposition of the Dawgara Fm to the period between 2.52 Ma and the Matuyama-Olduvai geomagnetic reversal at 1.95 Ma.⁸ By linear interpolation, the artifact-bearing stratigraphic levels have been dated to 2.48, 2.24, 2.16, 2.06, and 1.95 Ma, respectively.4

Far to the east, in China, the Loess Plateau is a large layered deposit of wind-blown dust deposited during the last 2.6 Ma by winter monsoon winds. As loess is mostly composed of fine-grained sediments (silt, 2-62 µm), pebble- to cobble-sized stone tools are easily identified; and, in 2018, artifacts dating by magnetostratigraphy from 2.1 to 1.3 Ma were reported.⁵ These results provide independent support for the claim of artifacts as old as 2.2 Ma from the Longgupo Cave.⁹ the chronology of which is provided by combined electron spin resonance (ESR) and uranium series dating methods. Like the Dawgara assemblage, the Chinese Plateau lithic assemblage also consists of pebble-cores and flakes.

The evidence collected in these two Asian regions during the last few years is composed of a large sample size, especially in the Jordan case, including features (e.g., dominant noncortical cores and flakes, bulbar scars) that allow it to be classified as "anthropological origin probable, natural origin improbable," according to Shea's^{10,11} criteria for recognizing anthropic agency in stone artifact assemblages. This lithic evidence thus documents an initial exit of hominins from Africa at around 2.5 Ma, and to their presence in China by 2.1 Ma. No fossil hominins documenting this earliest Out of Africa phase have been found either in Jordan or in China, leaving Dmanisi as still the oldest hominin fossil site outside Africa.

DMANISI FOSSILS 2

Dmanisi has been systematically explored by a Georgian-led team since 1993. The age of the site is well bracketed between 1.85 and 1.78 Ma,¹ and five hominin crania (Figure 1) have been found at the site, along with a pebble-cores and flakes lithic industry interpreted as Oldowan.² These skulls vary considerably in morphology, and the species names attributed to them have varied wildly. The situation became even more complicated following the discovery of the extremely distinctive Skull 5 in 2005.12,13 For some, including the Georgian team, the latest conclusion is that all five skulls can be ascribed to one single population, to which an unprecedented quadrinomen was given: Homo erectus ergaster georgicus.¹² In contrast, for others a more primitive hominin, or more likely two hominin speciesif not two genera-are represented at Dmanisi.^{14,15,16} For those who espouse a single variable lineage at this locality, the extreme morphological diversity in the sample is explained by what would be a highly unusual combination of biological age differences, sexual dimorphism, and facial remodeling due to tooth loss and other dental pathologies.^{2,17}

The Dmanisi team described the five hominin skulls from the site as having a combination of primitive (habilis-like) and derived (erectuslike) traits. As Rightmire et al.¹ put it, "it is becoming clear that the Caucasus hominins share features with African Homo habilis but had not yet evolved a full suite of the characters diagnostic of later H. erectus" (p. 12). For instance, cranial capacity ranges between 546 and 730 cm³, well below the average of 904 cm³ found in specimens often attributed to H. erectus.¹⁸ Some other characteristics that allegedly revealed a mosaic of primitive and derived traits included brow ridges that are only moderately thickened, and a supra-orbital sulcus that is minimal but associated with a very marked post-orbital constriction. The occipital is flexed, but a transverse torus is not uniformly present, while the face is prognathic with a relatively massive midface. Lordkipanidze et al.¹⁹ similarly reported that the postcranial anatomy of the Dmanisi hominins showed a surprising mosaic of primitive and derived features. Primitive features included small body size and an absence of humeral torsion, while derived ones included body proportions similar to modern humans and lower limb structure suggesting this form was already an obligate biped. All in all, Lordkipanidze et al.¹⁹ concluded that "the first hominin species currently known from outside Africa did not possess the full suite of derived locomotor traits apparent in African H. erectus and later hominins" (p. 309). Still, a major problem in all of this is that (just as at



FIGURE 1 The five hominin crania from Dmanisi, from left to right: Skull 1 (D2280), Skull 2 (D2282), Skull 3 (D2700), Skull 4 (D3444), and Skull 5 (D4500). Courtesy of the Georgian National Museum [Color figure can be viewed at wileyonlinelibrary.com]

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Dmanisi) nothing known from Africa bears the cranial apomorphies that define the H. erectus holotype from Java. What is more, something rather similar appears to apply to H. habilis, which has never been adequately defined in morphological terms. Indeed, this African "species" is essentially a taxonomic wastebasket into which a motley assortment of hominin fossils dating between ca. 2.5 and 1.8 Ma has been rather heedlessly tossed, so that the more informal "early Homo" might be a preferable term for this grouping.²⁰ Despite this needless complication, and in agreement with evidence from Jordan and China, the heterogeneity we see at Dmanisi can be much more easily interpreted if we invoke a member of the "early Homo" group as the first hominin to leave Africa and as the ancestor of the Dmanisi hominins. Accepting that Skull 5 (the mandible of which would more properly be the holotype of Homo georgicus) is entirely distinctive from everything else at Dmanisi, we prefer to ascribe the remaining four skulls to another species, which is not *H. erectus*, since none of them has any of the apomorphies of the Trinil holotype. Neither it is clear, for similar reasons, that the remaining Dmanisi individuals are appropriately referred to Homo ergaster (a.k.a. "African H. erectus"). Indeed, it is still an open question whether those four skulls might actually belong to more than one species.

3 | FLORES FOSSILS

On the other side of Asia, the discoveries at Liang Bua cave, Flores (Indonesia), remain controversial to this day. Brown et al.²¹ described the remains of a short-statured hominin (LB1), including a cranium, a mandible and some postcranial elements. Additional bones of LB1

were discovered later, together with another mandible (LB6) and skeletal remains from 5 to 7 different individuals.²² The distinctive features of these fossils, including short stature (106 cm), a small cranial capacity (417 cm³ as measured by Falk et al.²³) and a mix of features seen in both australopiths and Homo,²⁴ were thought by the discoverers to be distinctive enough to describe a new species, H. floresiensis. The Liang Bua remains were recently dated to between 98 and 67 ka,²⁵ apparently antedating the presence of Homo sapiens on the island. The picture was, and still is, very complex, with a lot of open questions. The lack of a connection between Flores and the neighboring continent, for example, suggests that these small-brained hominins had developed some form of ocean navigation capability.²⁶ The complexity of the artifacts found at Liang Bua also raised questions about the identity of their makers.²⁷ Interestingly, observations on the LB1 endocast suggested that the species may have had relatively high cognitive capabilities.²³ But the most intriguing question of all concerns the origin of this unusual form. From the very beginning three different interpretations were heatedly debated: that the bones represent anatomically modern humans with genetic or metabolic disorders^{28,29}; that the new species is derived by dwarfing from the Asian H. erectus^{30,31,32}; or that H. floresiensis is descended from an earlier lineage of Homo.33,34

The various pathologies suggested in defense of the first hypothesis have all been convincingly dismissed.^{31,35} Microcephaly, for example, has been rejected in multiple analyses,^{36,37,38} as has Down Syndrome.^{33,39} What is more, the description of new and similar skeletal remains from Mata Menge, Flores, has finally confirmed the validity of *H. floresiensis* as a distinctive anatomical entity.⁴⁰ These findings suggest a complex hominin evolutionary history for Flores, since the

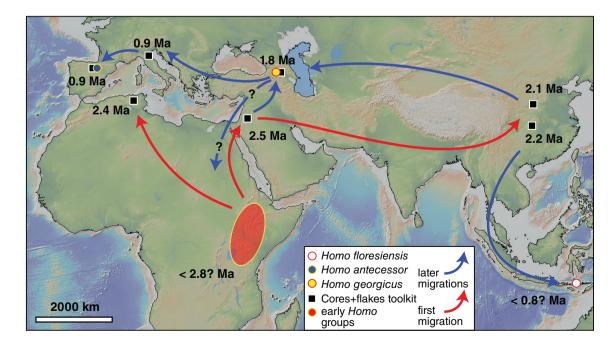


FIGURE 2 Tentative scenario for the first Out of Africa expansion at ca. 2.5 Ma according to the recent findings from Jordan and China, and later migrations stemming from the early *Homo* lineage. See text for discussion and references [Color figure can be viewed at wileyonlinelibrary.com]

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island has been inhabited at least since ca. 700 ka, leading up to the extinction of the "hobbit-like" hominin around ca. 50 ka.⁴¹

The biggest question, however, remains open: did H. floresiensis derive from H. erectus through dwarfing (via an unusually intense "island effect"), or did it descend from a more primitive, smaller-bodied, hominin? Some studies of the cranium and dentition of LB1,^{30,42} of its endocast,⁴³ of its calvaria,⁴⁴ and of the mandibular fragment and teeth,⁴⁰ have favored the hypothesis that *H. floresiensis* is descended from H. erectus. However, as noted by Gómez-Robles,⁴⁵ the traits that point away from H. erectus and to a more primitive ancestor come mostly from the postcranial remains, which were not included in the abovementioned analyses. The study of the external cranial morphology of LB1 by Gordon et al.46 agrees with the hypothesis that H. erectus and H. floresiensis shared a common ancestor, but the authors hint that LB1 may be more similar in morphology to H. habilis than to H. erectus. A much more comprehensive phylogenetic analysis was carried out by Argue et al.³⁴ who supported previous findings^{24,36} that H. floresiensis is more likely a sister either to H. habilis alone, or to the clade that includes H. habilis, H. erectus, H. ergaster, and H. sapiens.

The main objection to the Argue group's hypotheses has been the lack of archeological evidence for a pre-*erectus* hominin dispersal from Africa.⁴⁵ But at 2.5 and 2.1 Ma, respectively, the stone tools from Jordan and China may resolve this issue. If what we may–for lack of a better term, and in the absence of a morphologically coherent definition for our own genus–describe as "early *Homo*" was actually the first hominin to leave Africa, we would have a ready explanation for the more primitive, more australopith-like features of its descendant *H. floresiensis*—including the latter's short stature and archaic body proportions (relatively long arms vs. legs). As, indeed, we would also have for the Oldowan characteristics of its associated lithic industry.^{47,48,49}

4 | CONCLUSIONS

In the light of recent findings, then, we propose the following tentative scenario to account for the diversity of extinct hominins found outside Africa (Figure 2). Namely, that something which on account of our inadequate current taxonomic framework we have to call "early Homo" differentiated in Africa, possibly as early as 2.8 Ma.⁵⁰ Subsequently, one or more members of this group reached the Mediterranean fringe⁵¹ and spread Out of Africa at 2.5 Ma. After successfully expanding over Asia, at least one of those hominins (but likely more, as argued by those advocating diversity at Dmanisi) gave rise to new species that reached the Caucasus by around 1.8 Ma, and thence Europe by ca. 0.9 Ma^{52,53,54} and maybe back to Africa.⁵⁵ The eastward expansion (or occupation) in Asia of small-bodied and archaically-proportioned hominins continued, possibly in multiple waves; and, by ca. 0.8 Ma, representatives of this group had penetrated as far as insular southeast Asia, where H. floresiensis ultimately emerged as the result of a mild "island effect." H. erectus probably also differentiated in eastern Asia,⁵⁶ but that is another story.

ACKNOWLEDGMENTS

Research funded by FAPESP (2013/22631-2; 2016/04809-7), the Wenner-Gren Foundation (8991), and CNPq (302127/2015-1). We thank A. Margvelashvili for the photo of the five hominin crania from Dmanisi and C.J. Lepre for helpful comments. Constructive comments on the manuscript by J.J. Shea and an anonymous reviewer are also appreciated.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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How to cite this article: Scardia G, Neves WA, Tattersall I, Blumrich L. What kind of hominin first left Africa? *Evolutionary Anthropology*. 2020;1–6. https://doi.org/10.1002/evan.21863