Hominin population bottleneck coincided with migration from Africa during the Early Pleistocene ice age transition

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Two recently published analyses make cases for severe bottlenecking of human populations occurring in the late Early Pleistocene, one case at about 0.9 Mya based on a genomic analysis of modern human populations and the low number of hominin sites of this age in Africa and the other at about 1.1 Mya based on an age inventory of sites of hominin presence in Eurasia. Both models point to climate change as the bottleneck trigger, albeit manifested at very different times, and have implications for human migrations as a mechanism to elude extinction at bottlenecking. Here, we assess the climatic and chronologic components of these models and suggest that the several hundred-thousand-year difference is largely an artifact of biases in the chronostratigraphic record of Eurasian hominin sites. We suggest that the best available data are consistent with the Galerian hypothesis expanded from Europe to Eurasia as a major migration pulse of fauna including hominins in the late Early Pleistocene as a consequence of the opening of land routes from Africa facilitated by a large sea level drop associated with the first major ice age of the Pleistocene and concurrent with widespread aridity across Africa that occurred during marine isotope stage 22 at ~0.9 Mya. This timing agrees with the independently dated bottleneck from genomic analysis of modern human populations and allows speculations about the relative roles of climate forcing on the survival of hominins.

hominin bottleneck | Early Pleistocene | migrations | glacioeustatic drop | climate change

Genomic data from modern human populations were used to construct a model showing that "human ancestors went through a severe population bottleneck … between around 930,000 and 813,000 y ago" (1). The bottleneck was attributed to a "0.9 Mya event" associated with a decrease in marine surface temperature, an inferred long period of drought, and extensive mammal turnover in Africa and Eurasia; this timing is the nominal age of marine isotope stage (MIS) 22. Published a few weeks later in the same journal (2), paleoenvironmental analyses on a deep-sea core from the Bay of Biscay were used to show that an interval of climate variability between ~1.154 Mya and ~1.123 Mya and culminating with MIS 34 may have caused a drastic decrease in early hominin habitat and a depopulation of Europe (which was obviously presumed to have been already populated). So which event caused bottlenecking, MIS 22 or MIS 34?

During cruise VM28 in the western equatorial Pacific of the once (and now restored as the Mandalay) three-masted schooner Vema, operated as a research vessel by the Lamont-Doherty Geological (now Earth) Observatory of Columbia University, two long piston cores of pelagic carbonates were recovered on successive days (May 8 and 9, 1971) on the Ontong-Java Plateau—V28-238 and V28-239—and became the subject of pioneering oxygen isotope and magnetostratigraphic analyses (3, 4). MIS 22 was identified to occur before the Matuyama/Brunhes (M/B) boundary [now at 0.78 Mya (5)] but after the Jaramillo subchron (whose termination is now placed at 0.99 Mya) and explicitly regarded as a full glacial stage, possibly "a 'first glaciation' marking the end of the 'pre-glacial Pleistocene'" (3) and "the first glaciation of duration and intensity similar to the glacial stages of the Brunhes epoch" (4). Following affirmation of variations in Earth's orbit as the pacemaker of Pleistocene ice ages (6), spectral analysis conducted on the records from the same (V28-238 and -239) cores (7) showed an increase in amplitude of the 100 ky component of cyclicity at about 0.9 Mya that is "practically identical to the change in record character picked by Shackleton and Opdyke (…) at the stage 22/23 boundary." Oxygen isotope data from ODP 677A from the Panama Basin confirmed that "Oxygen isotope stage 22 […] was of similar magnitude to the most extensive glacials of the Brunhes and constitutes a logical base for the middle Pleistocene" (8) whereas data from ODP 806B from the Ontong-Java Plateau allowed the identification of a clear switch in climatic cyclicity from earlier obliquity-dominated to mixed (eccentricity and obliquity) cycles at

Significance

The timing and causes of hominin (pre-*Homo sapiens*) migrations out of Africa have been of recent interest. Two scenarios, one based on modern genomic data and the other on the chronology of hominin sites, indicate population bottlenecking in the Early Pleistocene. An ice age is invoked as bottleneck trigger in both cases even though they differ in timing, and therefore in the actual event that triggered depopulation. Our assessment of the chronology of key hominin sites in Eurasia leads us to conclude that bottlenecking occurred at the first major ice age of the Pleistocene, ~900,000 y ago, in agreement with the genomic model, and coincided with a major diaspora from Africa into Eurasia when hominins came close to extinction.

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the beginning of MIS 22, which was referred to as the mid-Pleistocene climate revolution (9).

In stacked records (10), the change from cyclicity with the highest spectral power in the obliquity range (~40 ky) to cyclicity with the highest power in the short eccentricity range (~100 ky) looks more gradual, with the ~100 ky frequency component first emerging at ~1.25 Mya to then experience a lull and subsequently reemerged with renewed and persistent power at (and since) ~0.9 Mya (11). This spectral character suggested the use of the term mid-Pleistocene climate transition (MPT) (12) instead of revolution even though MIS 22 still stands out as the first major (~80 kyr-long) ice age and glacioeustatic low-stand of the Pleistocene (11). In fact, an attempt (13) to separate the effects of temperature and global ice volume on the δ^{18}O data used in the stacked record (10) concluded that the MPT was not gradual but rather an abrupt event centered on MIS 24 to 22 (their "900-ka event") related to an abrupt increase in Antarctic ice volume. Manifestations of a distinct late Early Pleistocene transition centered on MIS 22 (hereafter EPT-MIS22) include the full continentalization of the Po and Danube flood plains in Europe (14). The Galerian migration hypothesis (15) for the first peopling of Europe was built on this critical event of climate change at 0.9 Mya. In contrast, MIS 34 has a maximum benthic δ^{18}O value of about 4.6‰ (8) that is similar to pre-MIS 22 δ^{18} O maxima that are typically in the range 4.4 to 4.6‰ and considerably less than the 5.0‰ of MIS 22. When these benthic δ^{18}O values are translated into glacioeustatic change by applying a simple extrapolation from data for the last glacial maximum (LGM) (16), pre-MIS 22 low-stands including MIS 34 correspond to 70 to 85 m below present-day sea-level compared to MIS 22 at about 110 m below. Hence, while acknowledging the insightful paleoenvironmental data and modeling provided for MIS 34 (2), we maintain that the first most relevant event of Early Pleistocene climate change with the greatest potential to affect hominin populations is EPT-MIS22 at ~0.9 Mya.

The Early Hominin Record of Europe and Western Asia

The inventory of early hominin sites from Europe plus the Middle East and western Asia used to link MIS 34 to apparent depopulation (2) shows two main clusters of ages: one cluster with eight sites (5 from Europe and 3 from the Middle East) at 0.8 to 0.9 Mya and a second cluster with seven sites (4 from Europe, 2 from the Middle East and 1 from Russia) at about 1.2 to 1.4 Mya; there are also two additional sites from Russia and Georgia at around 1.9 Mya. MIS 34 at 1.15 Mya falls toward the beginning of the apparent age gap between the two main site clusters and was thus regarded as a potential trigger for hominin depopulation of Europe. But the actual ages of sites reputedly older than ~0.9 Mya from Europe, and for that matter, from the Middle East and western Asia, that were used to suggest depopulation at MIS 34 (2) are highly disputable (15).

This prompted our critical re-evaluation of the chronostratigraphies of these and other early out-of-Africa hominin sites. The inventory of suitable sites was assembled using strict chronostratigraphic criteria: i) sites should be reported in accessible publications in a clear stratigraphic context, possibly accompanied by metered logs and correlative lithological descriptions; ii) sites should be provided with documented chronostratigraphies based on experimental methods; and iii) experimental data should be presented and illustrated (e.g., demagnetization data and principal component analysis for magnetostratigraphy, mineralogy and protocols for radiometric dating, etc.). Trapped charge dating methods (e.g., electron-spin resonance) and burial ages based on cosmogenic nuclides (e.g., ^{26}Al/^{10}Be) are of growing value but require careful knowledge of, respectively, environmental dose rates and cosmic ray fluxes to reduce experimental uncertainties and may not be yet suitable as discriminatory dating methods. We thus give strong preference to sites with hominin remains and/or lithic tools that are placed in well-documented and continuous magnetostratigraphies composed of at least one magnetic polarity reversal as providing the most robust age constraints. These sites are shown in Fig. 1.

European sites with demonstrable magnetostratigraphies and included in our inventory (Fig. 1) are Sima del Elefante (20) and Gran Dolina (21) (see *SI Appendix* for details), Cùllar (22), Solana del Zamborino (23), and Barranc de la Boella (24), all from Spain, Monte Poggiolo in Italy (25), and Kozarnika in Bulgaria (26). Hominin sites in the Middle East at the gates of Europe with demonstrable magnetostratigraphies are Evron (27) and Gesher Benot Ya'aqov (28) in Israel. Together, these earliest hominin sites in Europe (7 sites) and the Middle East (2 sites) have well-substantiated ages that cluster at around 0.9 Mya (Fig. 1). Additional sites provisionally not included in our current inventory, but which do not disagree with such a young age, are Happisburgh, United Kingdom, with tools in reverse-polarity-only strata considered to shortly pre-date the M/B boundary (29), and Vallparadis, Spain, with disputed tools (30, 31) in post-Jaramillo and pre-Brunhes strata (32). In contrast, sites that at the present state of knowledge do not seem to meet the criteria outlined above and yet are reputed as among the oldest in Europe, the Middle East and western Asia (2) are Fuente Nueva-3 and Barranco León (Spain), Pirro Nord (Italy), 'Ubeidiya (Israel), Sinyaya Balka and Rodniki, and Kermet (Russia), Kocabas (Turkey), and Dmanisi (Georgia). These sites are discussed in *SI Appendix* with some additional comments below on Dmanisi in the Caucasus.

Dmanisi. At Dmanisi (Georgia), virtually all of the hominin remains come from reverse magnetic polarity Unit B or related sediment that is erosively piped into older strata of normal magnetic polarity (Unit A) down to basal tuffs overlying the Masavera basalt that is also of normal polarity and specifically attributed to the Olduvai subchron based on ^{39}Ar/^{40}Ar dating of the basalt (33–36). By these accounts, Unit B with fossils is considered of Matuyama age immediately post-dating the end of the Olduvai subchron (1.77 Mya) assuming no significant temporal gaps between Units A-B and the Masavera basalt (*SI Appendix*, Fig. S1A; see also Fig. 1, Dmanisi age option#1). However, Unit B with the fossils has erosive contacts and in the absence of additional constraints, it is not possible to estimate with any accuracy when the erosion and piping took place during the Matuyama Chron. The absence of weathering surfaces between units, taken as evidence for continuous deposition, is hardly significant due to the erosive context of fossiliferous Unit B.

The critical attribution of Unit B to immediate post-Olduvai time (rather than post-Jaramillo time, for example) heavily depends on mammal biostratigraphy (33). A recent reassessment of the Dmanisi fauna (37) finds, however, that "Dmanisi compares most closely with a subgroup of Greek, Italian, and Spanish localities that are slightly younger than Dmanisi itself" and that are generically attributed to the Late Villafranchian or even the Epivillafranchian, this latter straddling, in standard mammal time scales, the Jaramillo subchron up to shortly before the M/B boundary (0.78 Mya), where it is replaced by the Galerian mammal age. In any case, even those Epivillafranchian sites with fossil mammals similar to Dmanisi are not securely placed to either before or after the Jaramillo, that is, older or younger than ~1 Mya (see discussion in *SI Appendix*). An alternative hypothesis that cannot be discarded by the available chronostratigraphic constraints is that erosion and infill of Unit B

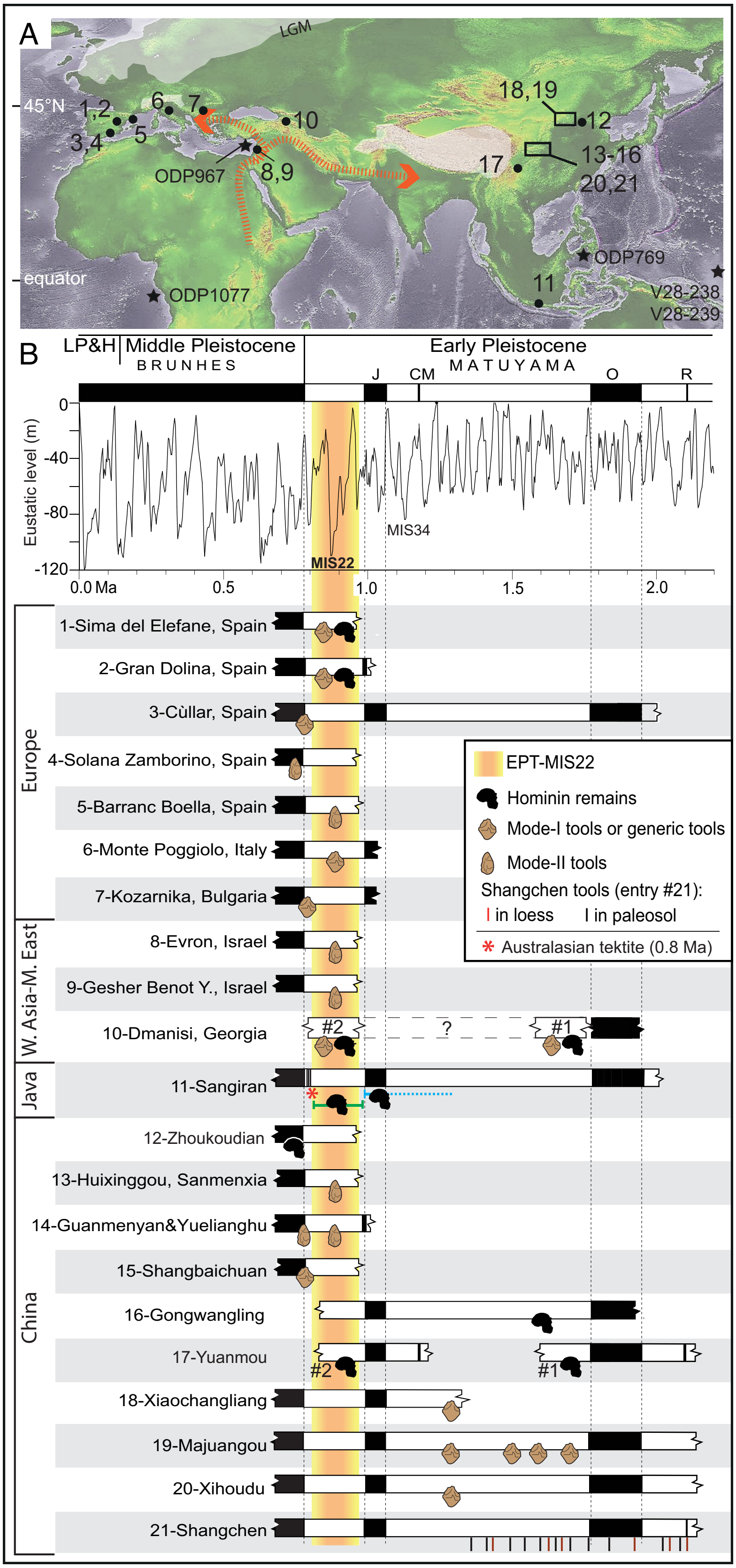

Fig. 1. Early hominin sites with reported artifacts or osteological remains from Europe, the Middle East, and Asia that meet chronostratigraphic criteria described in the text. (*A*) Locations of the hominin sites as well as of key ODP and Vema coring sites discussed in the text on a world reconstruction of sea level during the LGM as an analog to the first major ice age of the Pleistocene at MIS 22 (source: US NOAA; public domain image). Also indicated is the extent of ice caps at LGM. Generic migration pathways out of Africa and into Eurasia at MIS 22 are indicated by dashed lines. (*B*) Glacioeustatic curve derived from $\delta^{18}O$ benthic data from ODP 677 (8) and the Pleistocene geomagnetic polarity time scale (black bar is normal polarity, white bar is reverse polarity) (5). Glacioeustatic drops associated with MISs for this discussion (MIS 22 and MIS 34) are labeled. The magnetochronologies of key hominin sites discussed in the text are reported with the same numbering as in *A*. Gesher Benot Y. (entry #9) is Gesher Benot Ya'aquov. For Dmanisi (entry #10) and Yuanmou (entry #17), two chronology options are shown (option #1 and option #2) and discussed in the text. For Sangiran (entry #11), the chronostratigraphic distribution of the older (syn- to pre-Jaramillo) and younger (post-Jaramillo to Australasian tektite level at 0.8 Mya) hominin groups are indicated by the blue and green bar, respectively. The vertical orange band centered on MIS 22 indicates the independently determined timing of the population bottleneck (1) that also corresponds to a peak in C4 plants (17) and Saharan dust (18, 19). J is Jaramillo, CM is Cobb Mountain, O is Olduvai, and R is Reunion subchrons.

took place much later than commonly assumed as immediately after the Olduvai (36), but instead during EPT-MIS22. More positively, this eventually testable scenario (*SI Appendix*, Fig. S1*B*; see also Fig. 1, Dmanisi age option#2) could explain the extensive carving and piping as due to base-level reduction during an enhanced eustatic low-stand (MIS 22) and the subsequent Unit B infilling with subsequent aggradation during an eustatic high-stand (MIS 21). In any case, these two profoundly different age models, both of which are theoretically conceivable in the context of the complex stratigraphy at Dmanisi, serve to indicate that the Dmanisi fossils can neither confirm nor refute an initial post-Jaramillo versus pre-Jaramillo peopling of western Asia.

The Eastern Asia Hominin Record

Having critiqued the 1.2 to 1.4 Mya hominin sites in Europe and at the Gates of Europe as having poorly substantiated ages and illustrated the complexity of the widely cited Dmanisi site with a claimed occupation age of ~1.8 Mya, we shift focus to sites in eastern Asia starting with the iconic *Homo erectus* locality of Sangiran in Java and then review records from parts of China that would have hominin presence extend back to 2.1 Mya, older than *H. erectus* in Africa. These sites are shown in Fig. 1.

Sangiran. The Sangiran area in central Java is a key hominin locality on which an old out-of-Africa scenario has been built that has reverberated extensively in the literature. A widely quoted ^{39}Ar/^{40}Ar weighted mean age of 1.66 Mya reported for two specimens from a pumice-rich layer mapped within the Pucangan (Sangiran) Formation was used to date the oldest hominin fossils in the Sangiran region [(38); see also ref. 39]. However, some of the Sangiran fossils were reported coming from a magnetostratigraphic interval between the Jaramillo subchron to just below the M/B boundary (40), close to the well-known Australasian tektite horizon that is found in Sulu Sea ODP Site 769A just below the M/B boundary in MIS 20 (~0.8 Mya) (41), prompting the suggestion (42) that the inconsistency in dated volcanic materials with the tektite evidence was due to reworking of the volcanic materials. It nevertheless appears that two distinct hominin fossil groups may exist at Sangiran (43) (Fig. 1): a younger group, straddling levels of the Bapang Formation from just below the M/B boundary as recently defined (44), down to the boundary with the underlying Grenzbank unit with a U-Pb age of 0.97 Mya; and an older group from just below the Grenzbank unit down to the base of the Jaramillo (40) in the underlying Sangiran Formation and possibly extending further down to estimated ages of ~1.3 Mya when the area became fully continental. This robust radiometric and magnetostratigraphic age model would have the dweller-occupants at syn- to-pre-Jaramillo time appear to have been substituted by newer arrivals to Java at the EPT-MIS22 (post-Jaramillo time) facilitated by the large drop in sea-level that exposed the Sunda shelf (43) and which we contend was part of the same out-of-Africa hominin expansion that reached Europe at about this time (Fig. 1). A recently published ^{26}Al/^{10}Be cosmogenic nuclide burial age of 1.78 Mya (45) for the same level with a more secure U-Pb date of 0.97 Mya (43) suggests there are poorly constrained assumptions with the burial age technique, as indicated for some other sites such as Sima del Elefante (Atapuerca, Spain) (*SI Appendix*).

China. The Zhoukoudian *H. erectus* ("Peking Man") cave site near Beijing, one of the richest and most important Paleolithic sites in the world, dates sometime after the M/B boundary (0.78 Mya) located by magnetostratigraphy (46) between layers 14 and 13 at 33 m depth in the 41 m-thick sediment fill of the karstic fissure (44) (Fig. 1). Cosmogenic ^{26}Al/^{10}Be burial dating on sediment samples from hominin fossil-bearing layers 10 to 7 at 5 to 19 m above the placement of the M/B boundary yield what were regarded as consistent results with a weighted mean age (uncertainty at $\pm 1\sigma$) of 0.81 ± 0.11 My (47) that excluded an aberrant result from a sediment sample a few meters above in layer 6.

There is nonetheless mounting evidence of earlier hominin presence elsewhere in China, especially in the time interval between the end of the Jaramillo and the beginning of the Brunhes (0.99 to 0.78 Mya) (48). This includes a tektite level (from same event as recorded in Sangiran, Sulu Sea, and elsewhere in the general region) in the Bose Basin of southern China where it was dated with ^{39}Ar/^{40}Ar to 803 ± 3 ka (~0.8 Mya) and is associated with Acheulean (Mode 2) tools (49, 50) (not shown in Fig. 1 in absence of magnetostratigraphy), as well as sites with tools reported as Acheulean at Huixinggou (51), Guanmenyan and Yuelianghu (52), and with lithic artifacts at Shangbaichuan (53), all from the Loess Plateau of central China and correlated to just below the M/B boundary (Fig. 1). There are also pre-Jaramillo sites with hominin remains, provided that the provenance of the fossils are correctly reconstructed from finds made decades earlier. The "Lantian" *H. erectus* was traced to post-Olduvai strata in the Gongwangling magnetostratigraphic profile correlated to around 1.6 Mya (54) (Fig. 1), whereas in the Yuanmou Basin of southwest China, a reverse polarity magnetostratigraphic sequence with two normal polarity intervals correlated to the Olduvai and Reunion subchrons yielded hominin incisors with affinities to *H. erectus* in reverse polarity strata interpreted as post-Olduvai at a nominal age of 1.7 Mya (55) (Fig. 1, Yuanmou age option #1). An alternative option that does not seem to violate the available magnetostratigraphic age constraints would be to correlate the two normal polarity intervals, respectively, to the Jaramillo and Cobb Mountain subchrons, which would imply a post-Jaramillo age for the hominin remains (Fig. 1, Yuanmou age option #2).

Lithic artifacts also have been reported in pre-Jaramillo strata usually ranging in age from ~1.3 to ~1.7 Mya and as early as 2.1 Mya from the Loess Plateau of central and north China, including (but not limited to) Xiaochangliang (56), Majuangou (57), Xihoudu (58), and Shangchen (59) (Fig. 1). Age constraints for these sites from the Chinese Loess Plateau are typically provided by densely sampled, high resolution magnetostratigraphies. Notably, the Shangchen loess-paleosol sequence displays in a 75-m-thick section an impressively detailed and unambiguous polarity sequence for much of the Matuyama and into the Brunhes chron (Fig. 1). A total of 17 layers with abundant lithics interpreted as rudimentary tools have been reported in the section across an interval from about 2.1 Mya near the Reunion subchron and across the Olduvai subchron to ~1.3 Mya within the Matuyama. Curiously, no putative tool levels have been reported from the lithologically similar overlying strata, which continue across the Cobb Mountain and Jaramillo subchrons and into the Brunhes Chron (59).

Pan-Eurasia Hominin Dispersal at ~0.9 Mya during the EPT-MIS22

The large ambiguity in age control of Eurasian hominin sites assigned ages greater than about 1.1 Mya is a significant issue with the MIS 34 depopulation model (2). At the very least, we suspect that the number of hominin sites in Eurasia which may turn out to have substantiated ages greater than ~1.1 Mya is likely to be small, and thus, attribution of population fluctuations to specific triggers, such as MIS 34, will be difficult to distinguish from vagaries of discovery of sparse occurrences.

On the other hand, there is a robust concentration of Eurasian hominin sites at around 0.9 Mya (Fig. 1), which coincides with a reported age gap of hominin sites in Africa and an independently dated genomic inference of a severe human bottleneck (1). The timing corresponds to MIS 22, a powerful climate trigger perhaps 1/3 larger in terms of ice volume and the modeled climate effects of MIS 34 (2). The genomic bottleneck model is intriguingly connected to the Galerian migration hypothesis (15), which stated that "Europe was first inhabited in the late Early Pleistocene … possibly during the waning stages of MIS 22 and the ensuing MIS

22/21 transition at ~0.9 to ~0.85 Mya" when "(m)igrations occurred in the form of expansions of the Galerian food web, to which hominins presumably belonged, through a Po-Danube conduit that connected the Gates of Europe (e.g., Turkey, the Levant, Caucasus) with Europe. This conduit opened, meaning that it became terrestrial and ecologically sustainable for Galerian food web expansions, for the first time during the EPT".

We suggest that the genomic bottleneck model can be linked to an expanded, pan-Eurasian version of the Galerian migration hypothesis. Complementing the validated European sites (entries #1 to 7 in Fig. 1), this would include hominin sites from the Middle East (#8 and 9), the younger hominin group with *H. erectus* in Java associated with the Australasian tektite horizon (#11), and sites in China (#12 to 15) altogether comprised between the end of the Jaramillo and the beginning of the Brunhes (0.99 to 0.78 Mya). This cluster of reasonably validated early hominin sites can be explained as part of a major exodus from Africa that coincided with the hominin population bottleneck at the time of MIS 22. Hominins apparently spread rapidly northward out of Africa (where the genetic bottleneck was found in modern central African populations) and across the breadth of Eurasia: eastward to Java (Sangiran), south China as well as north China, possibly displacing or substituting earlier populations. In virtually the same time frame, hominins expanded for the first time westward into Europe along the Danube-Po terrestrial migration conduit, reaching as far west as Spain and as far north as the UK (15) (Fig. 1*A*; see also Fig. 13 in ref. 15). The migrations were not confined to hominins but involved entire African food chains including large mammals like elephants (15) and thus they should have occurred preferentially along open terrestrial conduits (e.g., Po-Danube) rather than across seaways such as the oft-cited Gibraltar Strait (e.g., ref. 60), which is ~300 m deep at the main sill and was submerged even during MIS 22 and all subsequent glacioeustatic low-stands.

The close correspondence in the timing of the pan-Eurasian migration to MIS 22, the first major glaciation of the Pleistocene, points to associated climate changes that may have triggered and literally paved the way for the EPT-MIS22 migration out of Africa. The large (~110 m) glacioeustatic drop opened land routes across shallow waters that were heretofore submerged in the Levant, Black Sea area, the Danube-Po conduit, and the northern Adriatic and allowed more ready egress of hominins and closely associated Galerian fauna. At the same time, MIS 22 is associated with a marked increase in Saharan dust production as revealed by data from ODP Site 967 in the eastern Mediterranean (18, 19) as well as a marked increase in C4 plants as revealed by data from ODP Site 1077 in the Angola Basin (17). Lower sea surface temperatures in the equatorial Atlantic during MIS 22 resulted in diminished monsoonal circulation, the main source of moisture more inland over the African landmass (17). Hence, we suggest that the enhanced aridity during MIS 22 that caused the spread of savanna and arid zones across much of continental Africa pushed early *Homo* populations in Africa to adapt or migrate to avoid extinction. Ironically, the same threatening climate event at MIS 22 produced a major glacioeustatic low-stand that opened escape routes via land bridges from Africa. Rapid migration in response to a severe climate trigger and concomitant means to escape is what can account for the pan-Eurasia EPT-MIS22 migration out-of-Africa at 0.9 Mya and contribute to the modern genomic evidence in modern African populations of the bottleneck (1).

The 0.9 Mya migration pulse per se does not rule out the existence of earlier hominin populations in Eurasia. The old versus young chronology for Dmanisi hominin fossils (*SI Appendix*, Fig. S1; entry #10 in Fig. 1) is testable, for example, through improved regional faunal biostratigraphy and its age calibration. The older, syn- to pre-Jaramillo hominin group at Sangiran (#11), the Lantian (Gongwangling) hominin fossils (#16), the Yuanmou hominin fossils (#17 in Fig. 1, assuming age option #1), as well as the artifacts from the loess plateau of China credibly extending from ~1.3 to 2.1 Mya (#18 to 21), may signal a much earlier migration that somehow left little evidence from ~1.3 Mya to 0.9 Mya but may have been influenced by early stages of the MPT. Alternatively, these rudimentary lithic artifacts (59) may have been produced by other than *Homo*, perhaps similar to the Lomekwi toolmakers that at 3.3 Mya predate the oldest fossil specimens attributed to *Homo* in West Turkana, Africa (61). But even if confirmed, these allegedly much earlier migrations may not have seriously influenced the genomic memory of modern African populations for the bottleneck at 0.9 Mya.

Data, Materials, and Software Availability. All study data are published as cited or included in the article and/or *SI Appendix*.

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