Supporting Information

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Genetics

New Mitochondrial DNA Analyses. ***Background.*** Non-African mitochondrial DNAs (mtDNAs), except for those of sub-Saharan ancestry within the last few millennia, fall exclusively within two subclades, haplogroups M and N, which emerged within a clade of eastern African origin referred to as haplogroup L3 (1–4). Haplogroups M and N are found together throughout Asia and Australasia and among Native Americans, whereas (apart from rare "accidentals") only haplogroup N is found among West Eurasians and North Africans (5–7). The main exception, haplogroup M1, is distributed around the Mediterranean and in eastern Africa, provoking an early suggestion that it might trace a southern-route dispersal out of the Horn of Africa into Eurasia (8). Closer analysis of its distribution and the obvious center of gravity of M in general in southern Asia indicates rather that M1 spread west into the Mediterranean region ~40 ka and thence into eastern Africa (9). The distribution of M and N (and the major subclade of N, haplogroup R) indeed suggests a southern-route dispersal from eastern Africa, but with haplogroups N and R most likely originating ~60 ka in the Persian Gulf region, from which the (almost exclusively N and R) Near Eastern and European lineages would be derived, and M farther to the east in southern Asia (5, 6, 10–18).

The most recent estimate for the timing of the out-of-Africa dispersal from the male-specific part of the Y chromosome (MSY), and likely the most reliable to date (albeit with large confidence intervals) because it is based on almost 9 Mb of MSY genome sequence, is ~57–74 ka for haplogroup DR (perhaps better referred to as DF or CDEF, encompassing C, DE, and F, although C was not sampled), with 41–52 ka for GR (or haplogroup F) (19). The timing of the dispersal from Africa is, however, more likely to be between these two estimates than corresponding to the former, as the authors suggest. Haplogroup DF most likely arose within Africa, with C, D, and F each involved in the dispersal; haplogroup E is African, so that DE most likely arose within Africa, whereas C, D, and F are all non-African (20).

X chromosome (21) and autosomal, including complete-genome, analyses have suggested a similar pattern (22–28), in some cases arguing specifically for a single southern-route dispersal out of Africa followed by multiple waves of expansion in Asia (29, 30). The concordance of both the dating estimates and the very small founder population size with the mtDNA and MSY results strongly suggests that the autosomes are not concealing a significantly different picture for the initial modern human settlement of South Asia, which autosomal estimates again suggest most likely began ~55 ka (23).

Although there has been substantial work on the structure of autosomal variation in South Asia (31, 32), and many questions can be addressed only by using genome-wide variation, at present the precise details of the first settlement of South Asia can be most clearly elucidated by the genealogical and chronological reconstructions possible with the rapidly growing numbers of complete mtDNA genomes (currently approaching 15,000), supported by the much larger database of partial mtDNA sequences (33).

If haplogroup M originated in the Indian subcontinent, and N and R arrived from farther west, then the age of indigenous M lineages in India and founder ages of indigenous N and R should all estimate the minimum settlement time, with the age of L3 in sub-Saharan Africa providing an upper bound, because its root is the ancestor of both M and N (and R within N) and therefore necessarily predates them (2). [The age of L3 in Africa is itself further constrained by the age of L4 in Africa (1).] Advances in molecular-clock dating for mtDNA now allow for both greater accuracy (by correcting for purifying selection) and greater precision (by using the entire length of the molecule for the estimates) (34). The top of the 95% range on the estimate of the age of L3 in Africa using this clock with the most up-to-date African database is 79 ka using maximum likelihood (ML) and 67 ka using the ρ-statistic (Fig. 5) (2). Similarly the age of haplogroup N lineages in the Near East/Arabia, closest to their presumed point of origin, should provide a second upper bound for the settlement of South Asia, whether it was from the north or from the south. In this case the top of the 95% range is 72 ka for ML and 78 ka with the ρ-statistic (10). These estimates effectively rule out models that propose that mtDNA traces an earlier dispersal from Africa, ~80–100 ka (35).

Recent years have, however, also seen a rapid accumulation of complete-genome sequence data for mtDNAs from South Asia (15, 36–48). We have therefore updated the South Asian mtDNA database and reestimated founder ages for R and M in India (indigenous non-R haplogroup N lineages are virtually absent from the subcontinent), again using both ML and the ρ-estimator. Because haplogroup M apparently has an anomalously younger age in South Asia, we have also examined the regional patterns to find a possible explanation.

Materials and Methods. ***Dataset.*** We obtained 992 Indian complete mitochondrial DNA sequences from GenBank (15, 36–48). We also consulted the Web databank PhyloTree (49) to check for additional sequences not available in GenBank or for additional Indian sequences described in papers not explicitly related to Indian mitochondrial studies. This led us to add a further 6 sequences to the dataset (47).

We then excluded a number of sequences: those from the paper by Rajkumar et al. (42), which have been reported to contain errors (15), and 10 from the paper by Kumar et al. (40), which carry frame-shift indels in protein-coding regions, which are likely to be artifacts of the sequencing process (50–52). Finally, we further reduced the sequence set to include only haplogroups considered to have arisen within the subcontinent (48, 53): R5–8, R30–31, M2, M3, M4′67, M5, M6, M31–33, M34′57, M35, M36, M39, M40′62, M41–45, M48–50, M52′58, M53, M60, M61, M63, M64, and M66. We added a sequence from the L3a haplogroup (1, 54) as an outgroup, to root the phylogeny. The final dataset comprised 818 sequences: 129 from haplogroup R, 688 from haplogroup M, and the L3a (1) outgroup.

We scored variation in the mtDNA sequences as variants relative to the revised Cambridge Reference Sequence (rCRS) (55) and initially assigned each sequence to a haplogroup on the basis of its pattern of variants, using the program Haplogrep (56). Haplogroup nomenclature follows the system of Richards et al. (57) and is consistent with the most recent revision of PhyloTree (version 15) (49).

Phylogenetic reconstruction. We constructed a phylogenetic tree by departing from reduced-median networks generated by Network 4.6.0.0 software (58). Due to the large number of sequences in the dataset, we treated haplogroups M and R separately, and we also generated networks of the individual haplogroups separately. We further added idealized pseudosequences carrying only the defining basal mutations of M, R, and L3, and otherwise identical to the rCRS, to root the networks. We constructed the tree manually, with reference to the rooted and unrooted networks, resolving homoplasies by favoring faster-evolving mutations as the more likely to occur multiple times in the tree. We used the number of times a particular mutation was observed in a recent, comprehensive study of the worldwide mtDNA tree (34) as the basis for deciding whether one mutation was faster evolving compared with another.

Statistical analysis. We estimated coalescent ages of haplogroups R and M, and their subclades, on the basis of all of the substitution information in the molecule, using both the ρ-statistic (59, 60) and maximum likelihood. We used a mutation rate estimate for the whole molecule of one substitution event every 3624 y, correcting for purifying selection, using the method of Soares et al. (34). We excluded the highly variable and uncertain mutations around the polycytosine run, starting at position 16182, and the extreme hypervariable site 16519, from these age estimations.

We obtained the ML estimates using the program baseml from the package PAML 4 (61), using the HKY85 substitution model with gamma-distributed rates, approximated by 32 discrete categories, and a strict clock. The data we analyzed were sequence alignments of the whole mtDNA molecule, with the same highly variable mutations excluded as for the ρ-estimates. We analyzed the alignments using a partition model, dividing the data into two categories, coding region and control region: The first displays similar mutation densities across its extension and the second has a higher number of fast sites (34). We converted ML distances to age estimates, using the molecular-clock calculator of Soares et al. (34), as for ρ. We also repeated the analyses without enforcing a clock, to test the assumption that the data are clock-like, using the likelihood-ratio test. Each dataset analyzed passed this test.

There are two additional sources of uncertainty relating to the mutation rate. One is the branch length of the separation between human and chimpanzee as estimated by PAML (d) (34) and the other is the paleontologically estimated divergence time between humans and chimps (T). The age estimate for a clade (t) is calculated as $t=\frac{T}{d}\times\rho$, where T is the divergence time between the human and the chimpanzee, d is the average divergence in nucleotides between human and chimp mtDNAs and their common ancestor, and ρ is the average number of mutations in a given clade or the average branch length of a given clade (for ML estimates). d and ρ are both genetic measures with a given SE approximating a normal distribution. The divergence time between humans and chimps is itself uncertain, but the *Sahelanthropus tchadensis* cranium suggests an age of ~7 Ma—this fossil is likely within or very close to the base of the hominin lineage (62). It could be younger (the next candidates are *Orrorin tugenenis* and *Ardipithecus kadabba*, dating close to 6 Ma) but is very unlikely, on numerous independent grounds, to be much older (63). The beds enclosing *Sahelanthropus* are thought on faunal evidence to date to between 6.5 and 7.4 Ma (62); so we consider 7 Ma as the point estimate and a 95% confidence interval (CI) that covers the range 6.5–7.5 Ma, essentially the interval of the age of the beds enclosing the fossil [similar to the interval used by Endicott et al. (64)]. We take this to include any lineage sorting to the common mtDNA ancestor within *Sahelenthropus*, the time for which is likely (especially in what is assumed to be a very small population) to be small in comparison with the overall coalescence time (it is ~180 ka for extant humans and about three times as deep for modern chimpanzees) (65). This decision is justified as effectively tuning the result to the archaeological calibration points, discussed below, because the fossil split is inherently more uncertain; a deeper split would render several known archaeological time points too ancient. This yields a SE of 255,000 y. We now have three sources of uncertainty, which we combined as follows:

$$T = 7,000,000 \text{ (SE = 255,000)}$$

$$d = 1931.6 \text{ (SE = 133.78)}$$

ρ, which is dependent on each individual clade and estimate

$$\delta_t^2 = \left(\frac{\rho}{d}\right)^2 \times \delta_T^2 + \left(\frac{T\times\rho}{d^2}\right)^2 \times \delta_d^2 + \left(\frac{T}{d}\right)^2 \times \delta_\rho^2.$$

We then calculated the variance of the estimated time t, using the delta method, assuming minimal correlation between the three variables.

We next split the data into geographical groups to investigate the coalescent ages of M and R in different regions, using both ρ and ML. We recorded the state each sample was taken from and assigned these to one of six regions, corresponding to those described in Barik et al. (66) (Table S1). We also calculated ρ-estimates for M and N for data in each of the individual states. The capital of each state was used as the representative for geographical location of each dataset. We further included a data point representing East Asia, selecting a geographic point in the Yunnan province of China. The value of ρ for haplogroup R for this was directly taken from Soares et al. (34) because few new East Asian R lineages have been published since then. We calculated ρ of M in East Asia from the recent tree of Kong et al. (67). We displayed the results on a map, using the Kriging algorithm of the Surfer package.

We also generated Bayesian skyline plots (BSPs). We obtained BSPs from complete-sequence alignments (edited as before to exclude the highly variable mutations) with BEAST v1.6.2 (68, 69), using a relaxed clock (uncorrelated log-normal) and the HKY85 substitution model with two rate categories and each rate gamma distributed (approximated by 10 discrete categories). We set the mutation rate to 2.514×10^{-8}, the rate determined in a study of haplogroup U6 (70), based on a mean generation time assumption of 25 y. We ran the analyses for 10,000,000 generations, with a burn-in of 1,000,000. We determined each run to have converged to a stationary distribution by assessing the posterior trace, visualized in Tracer v1.5, which we also used to produce the skyline plots. We note that although skyline plots were developed for use on population data, it is likely that any demographic signal from individual haplogroups will reflect to some extent the demographic history of the regional population that carries this haplogroup as a whole, as suggested by previous studies (2, 70, 71).

To test whether the differences in diversity observed between different geographic regions were due to different times of expansion of haplogroup M in that region or simply due to different distribution and frequency of haplogroups with different overall mean lengths from the root of M, we took a phylogeographic approach and checked the tree for the most probable origin of each clade by taking into account branching structure, number of main subclades, and center of gravity. We made a broader classification of India into east, west, and south (insufficient data are available for northern India) and also northeast, because it yielded a very different profile from that of east India. With this approach, we aimed to date the age of M only on the basis of the basal lineages in each region, excluding later migrants that entered the region already carrying some diversity.

Results and Discussion. ***Phylogenetic reconstruction.*** The pattern of South Asian mtDNA variation is well established (12, 14, 15, 45, 46, 49, 53, 66, 72), with a number of basal and deep-branching indigenous haplogroups within haplogroups M and R recognized. Haplogroup N (aside from R) is almost absent, with the very rare N5 being the only potentially indigenous lineage seen in the population (73), so we focused on haplogroups M and R. All but two of the R sequences—Forn_Tor458 and Shar_Bi43—and four of the M sequences—Forn_Tor460, Forn_Tor456, Chan_PB88, and Sun_C4—fell into recognized subclades. For the remaining sequences, assignment to haplogroups was unproblematic, with the only concerns being the inclusion of sequences Forn_Tor472 and Sun_T135 in haplogroup M35, which may be due to long-branch attraction. This clade is defined by a single synonymous transition at position 12562. These sequences, which share the defining mutation, have no other polymorphisms in common with other members of M35, or with each other, and have 13 and 17 private mutations, respectively. If they share the transition at 12562 by chance, by virtue of having a large number of mutations among which 12562 happens to occur, then they are not related to the rest of M35 by descent. However, they do not carry an especially large number of mutations—the average for haplogroup M is 15—so they do not represent particularly long branches, and we therefore included them in M35.

Molecular dating. The ML estimates tended to be slightly higher than the estimates using the ρ-statistic, as often seen previously at greater time depths (33, 34). If ML is inferring hidden mutations, we may assume that the ML estimates should be the more accurate. The overall estimates for haplogroup M in India are 43.0 [38.2; 47.8] ka with ρ and 48.0 [39.6; 56.5] ka with ML, whereas for haplogroup R the values are 57.0 [46.2; 68.1] ka with ρ and 62.3 [54.7; 70.0] ka with ML (Fig. 5 and Table S2). The highest 95% upper bound for any of the estimates is therefore 70 ka, and thus none approach the age of the Toba eruption, at 74 ka. These estimates fit well with the upper bounds recently provided by estimates of N in Arabia (10) and L3 in Africa (2).

The only other possibilities for a pre-Toba entry of modern human maternal lineages into South Asia are (*a*) that there are non-L3 lineages that have not yet been identified in the extant modern human population or (*b*) that such lineages existed in the past but have gone extinct. Regarding *a*, the total number of non-African complete mtDNAs now available on GenBank is approaching 15,000 (compare PhyloTree, build 15), and the number of control-region sequences is >100,000, so there is little scope for the discovery of non-African non-L3 lineages, although of course one could never entirely rule it out.

Very low levels of admixture with any pre-Toba modern human population (as with Neanderthals) would, however, be unlikely to impact on the still relatively crude resolution of the autosomal analyses discussed in the main text. On the other hand, if the resident population were indeed Neanderthal, rather than anatomically modern, we have a possible answer to the conundrum of where the low levels of Neanderthal introgression thought to be present in non-African modern human genomes arose because, in the "southern-route" model, southern Asia, in the vicinity of the Persian Gulf, is likely to have been the main point of departure for all non-African populations (10). Neanderthals are known to have been present in northern Iraq at roughly 50–75 ka and may well have encountered advancing modern humans (74) close to the "Gulf Oasis" refuge area that may have harbored the earliest groups following their initial dispersal from eastern Africa (10, 75).

Impact of uncertainty in the molecular-clock calibration on age estimates. The above estimates are performed in the established way for mtDNA dating analyses (34, 51). However, given the critical importance of the age estimates for distinguishing the "pre-Toba" vs. "post-Toba" out-of-Africa models, it might reasonably be asked whether additional sources of uncertainty could affect the outcome. The obvious candidate is uncertainty in the calibration of the mtDNA mutation rate. There are two such additional sources of uncertainty: the human–chimp branch length as estimated by PAML (d) and the divergence time between humans and chimps (T). We investigated this possibility heuristically by combining estimates of these two sources of uncertainty with the uncertainty on the clade divergence estimated above. The effect of incorporating all three sources of error on the width of the 95% confidence intervals for our clade estimates can be seen in Table S3.

These results show that there is no case in which the upper bound exceeds even ~85 ka, and in only a few cases do they exceed the conventional 74-ka Toba cutoff. Given the error in the Toba age itself, which was estimated at 74 ± 2 ka as the weighted mean of several $^{40}Ar/^{39}Ar$ and K/Ar dates and thus has an approximate 95% range of 70–78 ka (76), the only cases are the ρ-estimate for haplogroup N in Arabia and the ML estimate for L3 in Africa (the ancestral lineage, necessarily predating the time of the settlement of Asia). In both cases, the alternative estimator gives a lower upper bound. All of the others (including all of the estimates for South Asia) have upper bounds below or at least only just reaching the age of the Toba eruption.

So, even when estimating (and undoubtedly exaggerating: see below) this level of uncertainty—albeit very imperfectly because it is impossible to model precisely—the upper bounds barely reach the (somewhat imprecise) age of the Toba eruption for the Asian founder lineages, and even for the African ancestor (the ultimate upper bound and necessarily older) only one of the two estimates has a reasonable chance of being older than Toba. The results continue to show that the settlement of South Asia is overwhelmingly likely to be post-Toba. A colonization at the earlier time suggested by the Petraglia et al. model, ~120 ka, is vanishingly improbable.

However, we stress that this approach very likely exaggerates the uncertainty inherent in the rate, because it ignores the fact that the clock has been calibrated in several ways and does not rely solely on the human–chimp divergence estimate. In the first place, for the paleontological calibration, Soares et al. (34) were also constrained by fossil estimates for a large range of primate species. For example, the rate they estimated suggests that gorillas diverged from humans almost 10 Ma, which is at the upper end of possible fossil estimates. Again (although there may well have been rate change for deeper points of the tree), the calibration point for humans and chimps pushes the deeper splits with orangutans, gibbons, and Old World monkeys to the fossil upper limits in each case. Indeed, we find that a BEAST analysis of mammalian whole-mtDNA genomes with several calibration priors that uses 8.25 Ma for the human–chimp split as a prior results in a posterior age estimate of 6.9 Ma (77). Thus, the mitochondrial evidence points securely to a divergence of ~7 Ma.

Obtaining maximum fossil estimates for divergence times is of course always problematic, but the Soares et al. rate has also been checked and confirmed using archaeological time points, such as the closely constrained (within a few hundred years at most) settlement of the Remote Pacific and the settlement of the Americas (34, 54). The latter, which is currently thought to be after ~16.5 ka (78), is constrained by the age of several subclades of haplogroup C1 (~14 ka) and their ancestor (~17 ka), supported by the age of the other major founder haplogroups, A2, B2, D1, and X2a, all dating from 13 ka to 15 ka (34, 79). Furthermore, using the corresponding rate for the first hypervariable segment of the control region, founder mtDNAs into southern Africa, dating to ~1.8 ka, closely match the arrival of the Chifumbaze complex, the archaeological signature for Bantu speakers (2, 80).

Moreover, Pereira et al. (70) and Soares et al. (2) have also adopted the Bayesian approach of Endicott and Ho (81) and Endicott et al. (82) (but with more realistic archaeological calibration points) to reestimate the rate and divergence times, with very similar results. Indeed, other researchers have independently provided similar estimates [e.g., Henn et al. (83) and Loogvali et al. (84); note that the faster synonymous rate of Kivisild et al. (85) is now superseded (84)]. An estimate for L3 that incorporates 10 almost complete prehistoric mtDNA genomes as calibration points comes to 78.3 (62.4–94.9) ka (86). The principal divergent estimates have been the Bayesian analyses of Endicott and Ho (81) and Endicott et al. (82), but these lead to anomalous conclusions and are very likely to be overestimated (51). However, in their case the estimate for L3 is ~16 ka (~23%) younger than that of Soares et al., which, if correct, would rule out a pre-Toba entry even more definitively.

We therefore stress that the upper bounds in Table S3 are very likely considerable overestimates. A simple measure of the uncertainty of the calibration based purely on the human–chimp split both is unrealistic (because it is not clear how to precisely estimate the uncertainty of the paleoanthropological calibration point) and yet at the same time exaggerates the uncertainty, because it does not take into account the fact that multiple paleontological and archaeological calibration points (as well as several distinct methodologies) have been used.

Finally, we note that the recent reevaluation of the human autosomal mutation rate via pedigree studies of complete human genomes has brought inferences from the mtDNA very closely into line with those from autosomal SNPs (87). The autosomal rate has been roughly halved by complete-genome data to ~0.5×10^{-9}/y (87–90), because earlier work based on a calibration against the divergence of humans from Old World monkeys did not allow for the well-documented rate slowdown on the great ape lineage resulting from their higher generation time (87). This reestimate now brings the timing of population divergence between Europeans and Asians from estimates of ~30 ka to 40–80 ka, in line with both the mtDNA evidence for the age of the Eurasian haplogroups M, N, and R and the archaeological record (87). Similarly, it increases the divergence time between modern humans and Neanderthals from ~350 ka to ~500 ka or more (87, 91), again in line with the mtDNA evidence (34, 64) and the widely accepted proposal that modern humans and Neanderthals share a common African ancestor, *Homo heidelbergensis*, ~500 ka (87). Several other estimates, such as the split between chimps and bonobos; humans and chimps; and humans, chimps, and gorillas also now show greater congruence between the autosomal and mtDNA estimates, as well as with the fossil record, although the slower autosomal rate would be problematic for the divergence of orangutans if extrapolated farther back in time (34, 91).

Scally and Durbin (87) do, however, question the timing of the Khoisan divergence from other Africans and the timing of the out-of-Africa dispersal, but in fact there is no real discrepancy in either case. The Khoisan split from other modern humans at the base of the human mtDNA and, especially given the enhanced drift in mtDNA lineages, it would not be unexpected for the mtDNA to underestimate the timing of the population divergence in this case.

In the more significant case of the timing of the dispersal from Africa, the authors date the autosomal split between Yorubans (from West Africa) and non-Africans, which is estimated at 90–130 ka, and compare this with the age of the mtDNA haplogroup L3, which, at ~70 ka, provides the mtDNA upper bound on the timing of the dispersal. However, West Africans diverged from eastern Africans well before the latter formed the source for the non-African gene pool and indeed well before the emergence of L3. A simple estimate for the split time from mtDNA data would be the divergence between L3′4′6 and L2, which is indeed ~110 ka (92).

In fact, though, these population divergence times are not appropriate for estimating the timing of the dispersal out of Africa. The mtDNA evidence clearly indicates that West Africa includes both subclades of L3 that arose since the dispersal out of Africa and more ancient lineages from L1 and L0 (2). Even present-day eastern Africa would not at all be representative of the source of non-African mtDNAs; again, L0 and L2 lineages have arrived from the south and west since the time of the exit, presumably accompanied by autosomal lineages that would inflate any estimate of the divergence from non-Africans. The suggestion of an earlier dispersal time is therefore an artifact of the misapplication of an oversimplistic and misleading population-genetics model—a possibility evidently recognized by its authors (ref. 87, p. 751). Unfortunately, their speculations have been reported without their due caution by the scientific press (93).

The authors stops short of arguing that the mtDNA rate has been overestimated—not surprisingly, given that several of their results are more in line with the mtDNA picture than with the faster autosomal rate used previously. A slower rate that implied an age for non-African mtDNAs of ~110 ka, we might add, would imply that the colonization of the Remote Pacific (well dated to ~3.1–3.3 ka) would have taken place ~6 ka and the settlement of the Americas (thought to be ~16.5 ka at most) at ~26 ka.

The best current autosomal estimate for the timing of the dispersal across Eurasia is the divergence of Europeans and Asians, which, at 40–80 ka, matches the estimates for the age of haplogroup N in Arabia and haplogroup R in South Asia (both ~60 ka) very closely and, although not completely ruling out a pre-Toba dispersal at ~74 ka, like the mtDNA evidence, does render it very unlikely.

Regional patterns: An eastern origin for haplogroup M. The point estimates for the ages of haplogroups M and R in South Asia are ~14 ka apart, which is somewhat unexpected if they both represent the same arrival along the southern route from Africa. Although the 95% age ranges do overlap slightly, data from China suggest that the point estimate for R in India is likely to be a fairly accurate proxy for the time of first settlement (ML age of R in China = 54.3 [41.2; 67.8] ka), but that the time depth of haplogroup M in India has been foreshortened (ML age of M in China = 57.3 [49.3; 65.5] ka, compared with 48.0 [39.6; 56.5] ka in India (Table S2)).

To investigate the geographical distribution of diversity within the subcontinent, we generated regional age estimates using ρ-values for both haplogroups M and R, and we also displayed estimates for each state on a map of the region, using the Surfer software (Table S4 and Fig. S1). The results suggest a correlation between the founder age and the sampling region for M, but not for R, with haplogroup R as a whole dating to ~57 ka (~62 ka with ML), and the regional estimates varying between 52–60 ka, but with considerable overlap in their confidence intervals. A Bayesian skyline plot of haplogroup R indicates a major expansion beginning at just over 50 ka, with a further expansion in the early Holocene (Fig. S2). For haplogroup M, however, the Pleistocene expansion signal in the skyline plot is stepped and begins at only ~40 ka, with further increments at ~30 ka and ~13 ka. [Interestingly, both plots show a dip from around 3,000 y ago, perhaps due to a reduction in the effective population size resulting from the establishment of the caste system and its marriage restrictions (94, 95).]

Moreover, for haplogroup M, the diversity values peak in the east, followed by the south and central regions, with the west, north, and northeast being the most recent. We repeated the regional analysis using both ML and BSP analyses for haplogroup M and obtained a similar pattern, although the order of the three youngest regions differed according to the method of analysis used. The BSPs suggest a steep rise in population in the east by ~40 ka, followed several thousand years later by similarly steep rises in the southern and then central regions (Fig. S3). Shallower increases follow in the west, north, and northeast at ~30 ka. These correspond to the establishment of a number of new basal haplogroups within M, with much shallower time depths than those established earlier in the east, as noted previously (96).

We wished to check whether the higher age estimates for M in east India and lower estimates in the remaining regions are the result of different frequencies of subclades in each region and the random length of each to the root of M (and therefore unrelated to the expansion time of M in each location). To do this, we adopted a phylogeographic approach to pinpoint a probable location of origin for each subclade of M, calculating regional diversities only from subclades that had evidently evolved in each region (Table S5). The age of M based on lineages that most probably arose in east India was even higher than before (~51.9 ka) and much closer to the age of M in China (~55.9 ka) with overlapping 95% confidence intervals. The age estimates for the west and northeast were much lower, at ~30 ka, indicating a probable expansion of the root type of M in those regions at around that time. South India shows an intermediate age estimate, but with very few basal lineages in the profile of the region.

These results suggest that whereas haplogroup R entered South Asia from the west ~60 ka, haplogroup M most likely expanded from east to west, via both the south and the central parts of the subcontinent. The simplest explanation for this pattern is that haplogroup M originated on the east coast of the subcontinent, during the southern-route dispersal from Africa to Southeast Asia, spreading early back around the coast to the south and into central India (97), with later expansions carrying it into the north and west, perhaps associated with the spread of microlithic technology, as suggested previously (96). Given the age estimates in East Asia (Table S2) (67), it is even possible that haplogroup M originated ~55–60 ka, in South China/Southeast Asia, and then spread west into eastern India ~50–55 ka, similarly expanding back around the eastern coastline and into the interior of the subcontinent from ~45 to 30 ka. Alternatively, and perhaps most parsimoniously in the context of the origins of both M and N from the root of L3, haplogroup M might have originated alongside haplogroup N, farther to the west in the Gulf region (10), as suggested in the simple version of the southern-route model (5), but became extinct in more western locations due to drift, as other L3 lineages must have done. The lack of appreciable frequencies of indigenous non-R haplogroup N lineages in the subcontinent, despite their presence in both West and East Eurasians and aboriginal Australasian populations (7, 67, 98), highlights the important confounding role of genetic drift during this time in human prehistory, so any conclusions remain necessarily rather tentative, but further data from Southeast Asia may help to resolve the issue.

Web resources. Tracer is available at http://tree.bio.ed.ac.uk/software/tracer/, Network 4 is at www.fluxus-engineering.com/sharenet.htm, PAML 3.14 is at http://abacus.gene.ucl.ac.uk/software/paml.html, PhyloTree is at www.phylotree.org/, Family Tree is at http://www.familytree.com/, and Calculator for converting ρ-values and ML estimates to age estimates is at www.hud.ac.uk/targ/furtherinformation/.

Archaeology

As outlined in the main text, there are two central components to the current models of Petraglia, Clarkson, Haslam, and others for the earliest anatomically and genetically modern human settlement of India and South Asia, which can be summarized as follows (96, 99–106):

i) Anatomically, genetically, and cognitively modern humans dispersed from Africa to South Asia sometime before the major eruption of the Mount Toba volcano (Sumatra) ~74 ka [and conceivably at a much earlier date closer to 100–130 ka (103)], equipped with a distinctively and diagnostically African form of Middle Stone Age (MSA) technology.

ii) At around 40–35 ka there was a radical, technologically complex, and rapid internal evolution from the preceding "Indian Middle Paleolithic" to the dramatically different bladelet and backed-microlith–dominated technologies of the so-called "Indian Microlithic tradition", which subsequently persisted with relatively little change within the subcontinent for a period of at least 35,000 y, until the middle stages of the Holocene (Neolithic) period (96, 101, 103). The rapid evolution from the "archaic" Middle Paleolithic to the fully "modern" microlithic technologies is attributed to a range of climatic and associated environmental changes during the later stages of Marine Interstadial Stage (MIS) 3 (96, 103).

These interpretations have been published in an impressive total of over a dozen coauthored papers by Petraglia and others over the past 5 y and can be illustrated by the following direct quotations from these papers.

Pre-Toba Modern Human Settlement of South Asia. "These pre- and post-Toba industries suggest closer affinities to African Middle Stone Age traditions .... than to contemporaneous Eurasian Middle Palaeolithic ones ... Technology more similar to the Middle Stone Age than the Middle Palaeolithic may suggest the presence of modern humans in India at the time of the YTT [Younger Toba Tuff] event" (Petraglia et al., ref. 99, pp. 115–116).

"We have suggested, based on a variety of data sets, that modern humans were present in the Indian subcontinent before the [Mt. Toba] super-eruption and that the populations survived this event" (Petraglia et al., ref. 96, p. 160).

"It has been hypothesized that *H. sapiens* occupied locality 3 both prior and subsequent to the YTT event ….. We propose that populations in South India at this time were *H. sapiens*, who continued to use Middle Palaeolithic techniques for the subsequent ~40,000 years in this region before indigenous demographic changes prompted and responded to a shift to microlithic technology" (Haslam et al., ref. 102, p. 13).

Middle Paleolithic to Microlithic Transition in South Asia. "To date, South Asia has played a minor role in most discussions of early microlithic innovation, other than as a passive recipient of technologies developed elsewhere [Mellars 2006]. Here we redress the balance by demonstrating that the origins and regional chronological variability of the Indian microlithic reflect dynamic human responses to local and regional environmental and demographic pressures in South Asia during the late Pleistocene and Holocene" (Clarkson et al., ref. 101, p. 327).

"We have argued elsewhere (Petraglia et al. 2009) based on archaeological, genetic and environmental data that the appearance of microlithic technology in South Asia around 30-35,000 years ago represents a local solution to increasing aridity and population pressure in the lead up to the LGM [Last Glacial Maximum] …. Lithic evidence from elsewhere in the Jurreru valley demonstrates the continuance of Middle Palaeolithic assemblages until 38kya, ruling out the possibility that the Indian Pleistocene microlithic was the result of the initial out of Africa spread of *Homo sapiens* (contra Mellars 2006). We therefore think it likely that modern humans brought lithic technologies characteristic of the Middle Palaeolithic/Middle Stone Age to India, rather than microlithic technology. This conclusively demonstrates that short-lived microlithic technologies such as the Howiesons Poort in South Africa are convergent and unrelated to the South Asian assemblages" (Clarkson et al., ref. 101, p. 343).

Pre-Toba Modern Human Settlement of India. As discussed in the main text, the entire argument for the presence of African-derived modern human populations in South Asia before and following the time of the mount Toba volcanic eruption rests at present entirely on archaeological evidence and specifically on the interpretation of the collections of stone artifacts recovered from below and immediately above thick deposits of Toba ash-fall deposits in recent excavations in the Jwalapuram district (Jurreru valley) of southeastern India (100). The age of the ash-fall deposits has been "bracketed" by optically stimulated luminescence (OSL) dating of the associated underlying and overlying sediments to between 77 ± 6 and 74 ± 7 ka (99, 101). A number of separate, adjacent localities have been excavated, with lithic artifacts from below the ash at sites 3 and 22 and above the ash at sites 3, 17, and 21 (100).

The claims that anatomically modern humans were present in India both before and immediately after the Mount Toba ash-fall deposits rest entirely on the interpretation of the technology of these pre- and post-Toba artifacts assemblages, which have been claimed repeatedly and in numerous recent publications to show close and explicit similarities to those from southern and eastern African MSA sites (99, 102, 103)—similarities that, it is claimed, can be plausibly explained only by an actual dispersal of human groups from Africa to India sometime before the time of the

Toba eruption at ~74 ka. Because the human populations inhabiting Africa from at least 150 ka onward are generally agreed to be of anatomically modern form [as at Herto and Omo in Ethiopia, dated, respectively, to ~165 and 190 ka (107, 108)], the inescapable implication must be that anatomically modern humans had dispersed from Africa to southern Asia before (at least) 74 ka.

In view of the critical importance of this interpretation of the archaeological material from the Jwalapuram sites to the whole model of a Pre-Toba dispersal of modern humans from Africa to southern and southeastern Asia, the credentials of the archaeological evidence invoked to support these conclusions demand close and rigorous scrutiny.

As discussed in the main text, the entire argument for the explicitly African origins of the Jwalapuram archaeological assemblages rests at present entirely on a metrically based, multivariate analysis of the available samples of residual "core" forms recovered from the recent excavations. When analyzed and presented in terms of a multivariate "discriminant function" analysis of a selected range of metrical and related attributes, these are claimed to show a much closer grouping with samples from African MSA sites than with core samples from a range of Middle Paleolithic or "Mousterian" sites in Europe and the Near Eastern region—as reflected in Fig. 3 of Petraglia et al. (99) and Fig. 9 of Haslam et al. (102). On close scrutiny, these analyses and the conclusions derived from them can be challenged and criticized on a range of different grounds:

i) First, the samples of core forms so far recovered and analyzed from the different Jwalapuram sites are based on a maximum of 20 cores from below the ash deposits (at sites 3a and 22) and only 10 cores from above the ash deposits (at sites 3 and 20) (Haslam et al., ref. 102, table 7). By any criteria these are extremely small samples to support any form of quantitative statistical analyses and comparisons of the core samples involved.

ii) Second, it should be emphasized that discarded core forms in any artifact assemblage are by their nature strictly "residual" products, whose size, shape, and residual flaking patterns were not dictated solely by strict "cultural" criteria, but very largely by "opportunistic" factors, based largely on such factors as the variable quality and flaking properties of the available raw material supplies, the size and shape of the stone nodules used, and the relative abundance or scarcity of these materials within the local environments of the sites. These factors will influence both the character of the flaking ("core-reduction") strategies that can be applied to different raw materials and the extent to which the cores are systematically "reduced" to progressively smaller (and usually simpler) forms, in response to the abundance or scarcity of the available raw material supplies (109–111).

It should be noted that that the majority of the cores analyzed from both below and above the Toba ash deposits were not of any very clearly defined or generally recognized specific core types (such as Levallois flake, Levallois point, discoidal, or typically blade forms) but overwhelmingly (in ~60–70% of the recorded specimens from both below and above the ash deposits) of distinctly atypical or amorphous forms of "multiple-platform" cores (Haslam et al., ref. 102, table 4; Haslam et al., ref. 104, table 7.1)—most probably a function of the relative scarcity of high-quality raw materials in the vicinity of the sites and the need to progressively reduce and remodel the core forms to obtain the maximum numbers of usable flakes from the available raw material supplies. Again, as a basis for specific cultural comparisons with European Middle Paleolithic and African MSA assemblages, these analyses are at best of highly dubious significance. It is equally notable that the majority of the lithic raw materials used on all of the Jwalapuram sites were not of fine-grained, high flaking quality (such as flint, fine-grained chert, chalcedony, or obsidian) but of much poorer quality rocks such as limestone (by far the dominant raw material used both below and above the ash deposits), together with relatively poor quality quartzite, crystal quartz, and dolerite—with much smaller components of more fine-grained chert and chalcedony (102, 104). Once again, this is a poor basis for far-reaching conclusions on the specific "cultural" affinities of the very small core samples available for the metrical analyses used.

iii) Third, there are some curious anomalies in the proposed "groupings" of the different geographical samples of core forms displayed in the two successive published versions of the "discriminant function analyses", applied to the full range of African and Eurasian samples used in the study (99). For example, it is claimed that the Jwalapuram post-Toba ash samples (based on a combined sample of only ~10 cores) group closely with the overall grouping of "South African" Middle Stone Age assemblages and not with the smaller grouping of "East African" assemblages (Petraglia et al., ref. 99, figure 3). However, because any dispersal of putatively modern human populations from Africa to Asia must inevitably have derived from East Africa rather than the far-removed areas of South Africa (several thousand kilometers to the south), this again presents some obvious problems for the interpretations proposed. In the same vein it should be noted that the overall grouping of South African assemblages includes a major component (over 30% of the total South African site samples) of the highly distinctive Howiesons Poort assemblages (Petraglia et al., ref. 99, figure 3), which, according to all of the recent dating evidence, cluster closely around 60–65 ka (112–114)—i.e., at least 10,000 y later than the proposed dispersal of populations from Africa to Asia before the time of the Toba eruption. How these assemblages can have any relevance to the proposed >74 ka African dispersal is difficult to visualize. Finally, it should be noted that most if not all of the South and East African assemblages included in the analyses are manufactured predominantly from very different, and for the most part more high quality and fine-grained, raw materials [such as silcrete, fine-grained quartzite, chalcedony, and obsidian (115–121)] than those used in the Jwalapuram sites—which are likely to have substantially distorted any metrical and morphological comparisons of the residual core forms between the African and the Indian sites, for the reasons outlined above. The same observation becomes even more pertinent to comparisons between the Indian Middle Paleolithic assemblages and the rich assemblages of Middle Paleolithic/Mousterian industries from both Europe and the Near East, where virtually all of the samples analyzed are manufactured from locally abundant and high quality flint supplies (109, 122, 123). How in this situation it can be claimed that "The Jwalapuram (Post-Toba-Tuff) core assemblage unambiguously clusters with contemporaneous sites from the South African MSA" (Petraglia et al., ref. 99, supporting information) is unclear to us.

Our conclusion, in short, is that the very small core samples analyzed from the Jwalapuram sites could just as easily be related to the contemporaneous Middle Paleolithic/Mousterian assemblages from Europe and the Near East, manufactured overwhelmingly by Eurasian Neanderthal populations [with the notable exception of the Israeli Skhul and Qafzeh assemblages (122, 124)], rather than to any hypothetically modern human populations from sub-Saharan Africa.

iv) Finally, leaving aside all these issues of the metrical analyses and interpretations of the small core samples from the Indian sites, it should be noted that, with a single highly dubious exception, the recent publications have failed to identify any specific retouched (i.e., shaped) tool forms in the Jwalapuram Middle Paleolithic assemblages, which could be held to provide any specific link with the range of African MSA technologies from which the Indian pre- and post-Toba assemblages are held to be derived. The sole exception is a claimed example of a possible "tanged" or "stemmed" point recovered from below the Toba ash deposits at Jwalapuram site 22 (102, 105), which could suggest a possible link with the Aterian industries of northern Africa, currently dated (very approximately) to ~60–100 ka (116, 125). From the small published illustration of this piece (Haslam et al., ref. 105, figure 9) it is difficult to see any convincing evidence of deliberate retouch or shaping of the critical stemmed extremity of the piece, as opposed to accidental damage of the piece, perhaps due to human trampling or to other human or geological site formation processes. In their presentation of the artifact assemblage from site 22, Haslam et al. report "high rates of artefact breakage and edge damage suggest destructive site formation processes at Jwalapuram localities 22 and 3 ….. Edge damage is difficult to separate from retouch on many flakes with modified lateral margins. The possibility cannot be ruled out …. that heavy trampling and rolling can account for much of the damage. Retouch often acts isolated, haphazard and alternating between dorsal and ventral surfaces without any appearance of creating a continuous edge" (Haslam et al., ref. 104, p. 81). However this isolated, supposedly tanged piece is interpreted, it could in no sense be described as a typically or convincingly Aterian form.

Equally if not more significant in this context is the apparently complete absence from the Indian Middle Paleolithic sites of the highly distinctive forms of extensively unifacially or bifacially flaked "leaf" or "pear-shaped" point forms, which form such a distinctive, widespread, and abundant element in both East and South African middle and later MSA sites [such as Aduma (126), Mumba (127), and other sites in East Africa and numerous sites in central and southern Africa (118, 119)] and clearly extend over the period of the putative dispersal of modern human groups from Africa to Asia around the time of the Toba eruption (largely defining what is sometimes termed in Africa the "Aduma" or "Bambatan" complex) (119, 126, 128) (Fig. S5). Why, one must ask, were these highly distinctive, numerically abundant, and geographically widespread forms in Africa not carried to India at the time of the hypothetical pre-Toba modern human dispersal to southern Asia? Two specimens of potentially retouched "point" forms were listed in the tool inventory from Jwalapuram locality 22 (Haslam et al., ref. 104, table 7.1 and figure 7.7), but in both cases the potential "retouch" on these pieces was confined to the immediate margins of the flakes and bears no resemblance whatever to the highly invasive forms of uni- or bifacial retouch that are effectively the defining hallmark of the African leaf or pear-shaped point forms from the eastern and southern African MSA sites referred to above. In view of the extent of accidental, peripheral edge damage or trampling present on a high proportion of the artifacts from Jwalapuram locality 22 (104, 105) referred to above, we see no basis for any comparison between these two pieces and the totally different, highly invasively retouched and shaped forms of uni- and bifacially shaped points that form such a ubiquitous and highly distinctive feature of the African MSA industries. Significantly, much closer analogies are apparent between these African, bifacially retouched points and the range of "Balangoda" point forms reported from Batadomba-lena and other early microlithic sites in Sri Lanka [Perera et al., ref. 129, figure 9; see below (129–131) and Fig. S5].

Finally, the same observation could be applied to one of the few truly distinctive forms of cores identified in African industries—i.e., the highly idiosyncratic "Nubian" types of Levallois point cores. Although these forms are abundant over a wide area of northeast Africa and the immediately adjacent areas of the Arabian peninsula during the period of MIS 5 between ~125 ka and 70 ka (132, 133), they are conspicuously absent from any Middle Paleolithic assemblages in the Indian subcontinent.

In short, as in the metrical analyses of the core assemblages discussed above, it seems impossible to identify a single distinctive technological element in the Indian Middle Paleolithic assemblages that could provide any convincing link—direct or indirect—with the known archaeological material from Africa. The absence of these distinctively African technological and typological features from the Indian sites must be seen as a further, major obstacle to the proposed dispersal of modern human groups from Africa to South Asia around—or before—the time of the Mount Toba eruption.

As noted in the main text, this conclusion now seems to have been accepted by the author responsible for the analysis and interpretation of the Jwalapuram industries. In a review of the whole of the pre-Toba dispersal debate recently published in *Nature*, Appenzeller (134) reports: "The archaeologist who analysed the oldest relics from the Jurreru Valley and provided key support for the claim that they are the handiwork of modern humans is no longer so sure. Chris Clarkson …. now thinks they might be the work of an unidentified population of archaic people. Clarkson and others say it is simply too soon to know for sure whether our ancestors were in India to watch the volcanic ash rain down 74,000 years ago …" (Appenzeller, ref. 134, p. 26). With this admission, the central pillar of the published case for a pre-Toba modern human colonization of India has now effectively collapsed.

African Howiesons Poort Industries. The so-called Howiesons Poort industries represent one of the most distinctive, abundant, and geographically widespread technologies in the archaeological records of the Middle Stone Age in Africa (114, 115, 135, 136). Their geographical distribution is most densely concentrated in the regions adjacent to the southern and southwestern coasts of South Africa (from Namibia in the northwest to the Mozambique border in the northeast) but the same or closely related technologies extend through central southern Africa [notably Zimbabwe and Zambia, where they are sometimes referred to as "Tshangulan" or "Magosian" industries (119)] and northward along a 2,000-km strip of central eastern Africa, as represented at the sites of Enkapune-ya-Muto in Kenya (137); Mumba (110, 127) and Naisiusiu (Olduvai Gorge) (138, 139) in Tanzania; and Mochena Borago, Norikiushin, and other sites in Ethiopia (140, 141) (main text Fig. 2). Recent OSL dating by Jacobs et al. (112) of 10 different South African sites has consistently yielded closely similar ages of between ~64.8 and 59.5 ka, suggesting an overall duration of these industries in South Africa of ~5,300 y (112)—although an apparently precocious occurrence of a similar industry has recently been dated at the site of Pinnacle Point 5–6 on the southern Cape coast to ~71,000 ka (142).

The chronology of the Howiesons Poort-like industries in eastern Africa is especially significant in the context of the present discussion and rests at present essentially on the dating of three sites—Mumba and Naisiusu (Olduvai Gorge) in Tanzania and Enkapune-ya-Muto in Kenya. In the long stratigraphic sequence at Mumba, recent OSL dating of newly excavated sections of the deposits has yielded dates for two separate levels containing characteristic microlithic/backed-segment industries, of respectively 56.9 ± 4.8 ka for the basal level and 49.1 ± 4.3 ka for the uppermost level (110, 113). These dates, performed using precisely the same techniques as those used at the South African sites, are broadly in agreement with earlier amino acid-racemization dates on ostrich eggshell for the same levels, on samples from the earlier excavations (115)—although the new excavations have effectively documented substantial stratigraphic mixing of materials from the immediately underlying and overlying levels, due the methods of excavation used in the earlier 1930s excavations on the site (110). In the Tanzanian site of "Naisiusiu" (i.e., located within the "Naisiusiu beds" at Olduvai Gorge) a level containing an effectively classic example of a Howiesons Poort industry (at least in terms of its microlithic component, dominated by small, geometric microliths made on typical bladelets) has recently been dated by ESR measurements on associated animal teeth to be between 59 ± 5 and 62 ±5 ka (138, 139) (Fig. 3).

Potentially the most significant East African site is that of Enkapune-ya-Muto (Kenya) where excavations by Ambrose (137) revealed a long stratigraphic sequence of industries containing typical microlithic and other backed-segment forms clearly spanning a substantial length of time and interpreted by Ambrose and others (115) as effectively documenting an evolutionary sequence from the earliest microlithic levels (described by Ambrose as the Endingi industry) into later industries of classic East African Later Stone Age (LSA) form. The basal (Endingi) microlithic level has not as yet been directly dated, but a level 1.3 m higher in the section (the "Sakutiek" level) produced a series of apparently reliable radiocarbon measurements on ostrich eggshell samples reaching back to at least ~45 ka, in calibrated radiocarbon terms (110, 137), and containing relatively abundant ($n = 13$) perforated, circular ostrich eggshell beads and associated "preform" specimens. Significantly, the uppermost microlithic level at the Mumba rock shelter also yielded three closely similar ostrich eggshell beads, claimed by the excavators to be securely stratified within this level and now (as noted above) dated by OSL to ~49 ± 4.3 ka (110, 113) (Fig. 3). The combined significance of these three sites is that they appear to demonstrate a clear continuity of microlithic and related backed-segment industries within eastern Africa spanning a total time range of at least 15,000 y—and including from at least 45–49 ka onward the manufacture of perforated ostrich eggshell beads, closely similar to those documented in the earlier stages of the of the microlithic industries of South Asia (see below and main text Fig. 4).

As noted above, the geographical range of the Howiesons Poort-type industries covers a vast area of sub-Saharan Africa, embracing a wide range of different environments, from the rich "Fynbos" habitats of the southern Cape coast region, extending into the arid environments of Namibia and Botswana, and through a range of varying habitats in central and east Africa and the Ethiopian highlands (114, 115, 117, 119, 135, 138) (main text Fig. 2). To expect to find technologically identical industries across this broad geographical and environmental range would clearly be unrealistic in both ecological and cultural terms, and such variations (for example, in the range of core-reduction strategies applied and some of the associated tool forms) have been documented in a number of recent studies (135, 143, 144). However, the one central element that defines all of these Howiesons Poort or "Howiesons Poort-like" industries is the occurrence (usually in high frequencies) of a range of highly distinctive microlithic or backed-segment forms, manufactured either from typical bladelet blanks [as at Klasies River and Naisiusiu (120, 121, 139)] or occasionally from more variable small flake blanks [as at Sibudu (144) and Mumba (110, 127)] (Fig. 3). Much if not all of this variation is probably related to the use of differing raw-material types in the different locations, with more fine-grained and high quality raw materials favoring the production of elongated bladelet forms [such as those from Klasies River in South Africa, manufactured predominantly from high quality, imported silcrete (117, 120, 121), and from Naisiusiu in Tanzania, produced largely from obsidian (139)] and more coarse-grained materials (quartz, quartzite, etc.) favoring the use of simpler flaking strategies—such as those at Sibudu in northeast South Africa (144) and Mumba in Tanzania (110, 127). The same raw material factors almost certainly influenced the sizes of the distinctive backed-segment forms, which range from relatively large forms up to ~5 cm in length at sites such as Klasies River and Mumba to very much smaller, classically microlithic forms (in some cases down to less than 1 cm in length) at the sites of Sibudu (South Africa), of Naisiusiu in Tanzania, and elsewhere (120, 121, 127, 139) (there is unfortunately at present no universally agreed metrical definition of microliths in the current literature).

However, the most striking feature of these backed-segment forms is their occurrence in a range of highly distinctive shapes, ranging from typically "crescentic" or "lunate" forms, through carefully shaped triangular and trapezoidal forms, to simple obliquely blunted types. This range of forms can be recognized equally clearly in both the South African sites (Klasies River, Diepkloof, Sibudu, etc.) and the East African sites such as Mumba and Naisiusiu (120, 121, 127, 139, 144, 145) (main text Fig. 3). It is this range of distinctively "geometric" backed-segment forms that provides both a strong element of unity to the African Howiesons Poort assemblages and such a striking resemblance to the effectively identical range of backed microlithic forms that characterize the earliest microlithic industries of South Asia—including those from the Jwalapuram 9 rock shelter in southeast India (101), Patne in northwest India (146), and the two sites of Batadomba-lena and Fahien-lena in Sri Lanka (100, 129, 131)—all securely dated by radiocarbon to between ~30 ka and at least 38–40 ka (see below and main text Fig. 3).

As stressed in the main text it is on present evidence impossible to identify any potential, alternative, sources for this highly idiosyncratic range of distinctively geometric microlithic forms from any other geographical regions of Eurasia, apart from the Howiesons Poort-like industries of sub-Saharan Africa, over the time range in question. The distinctive range of small, retouched bladelet forms that define the early Upper Paleolithic so-called "Proto-Aurignacian", "Ahmarian", "Baradostian", and related industries of Mediterranean Europe and the Near East over the period from ~40–45 ka [calibrated (cal.) before present (B.P.)] is of exclusively nongeometric forms, consisting of much simpler, straight-edged, "lamelles Dufour" forms (usually shaped by relatively light, inverse retouch on the ventral surfaces), together with pointed "Font-Yves/El Wad/Arjeneh" point forms, shaped by similar retouch on both edges of the tools (147). These forms are not recorded in any of the earlier microlithic industries of the Indian subcontinent and lack entirely any of the idiosyncratic triangular, crescentic, or trapezoidal steeply backed geometric forms that are the defining hallmarks of both the Indian microlithic and the African Howiesons Poort-like industries. The earliest occurrences of typically geometric microlithic forms in regions to the north and west (or east) of India appear first in some of the Gravettian industries of Central and Eastern Europe and in the analogous Kebaran industries of Israel, dated broadly to ~30 ka and ~20 ka (cal. B.P.), respectively, significantly later than the earliest dated microlithic industries in India (see below). In short, there is simply no other plausible origin for the Indian microlithic technologies, apart from the Howiesons Poort-like industries of the South and East African sites, which (for reasons discussed more fully in the main text) must inevitably have dispersed from East Africa in association with the initial Out-of-Africa dispersal of anatomically and genetically modern populations between ~50 and 60 ka.

In addition to this range of highly distinctive microlithic and backed-segment forms, other equally significant cultural features documented in the African Howiesons Poort sites include simple but highly shaped bone tools [principally carefully worked awls, as at Klasies River and Sibudu (120, 144)] and fragments of both ochre and ostrich eggshell engraved with distinctive "bounded criss-cross" and analogous "bounded cross-hatched" motifs from the Howiesons Poort levels at Diepkloof (148) and Klein Kliphuis (149) and the preceding Still Bay levels at Blombos Cave (150) (main text Fig. 4). In both cases these can be paralleled in the early South Asian microlithic assemblages by the small but highly shaped bone and antler tools recovered from Batadomba-lena and Fahien-lena (Sri Lanka) (129–131) and the Jwalapuram 9 rock shelter (101) and by the remarkable, double bounded criss-cross design incised on ostrich eggshell from the site of Patne in northwest India (146), radiocarbon dated to at least ∼30 ka (cal. B.P.). As argued in the main text, the combined similarities of all these cultural features in both the African Howiesons Poort and the early microlithic industries of South Asia would seem totally beyond the range of either pure coincidence or entirely independent and remarkably convergent cultural evolutionary processes in the two continents, over a time period that corresponds broadly with the genetically estimated age of the initial modern human dispersal from eastern Africa to southern Asia.

The technological and cultural origins of the Howiesons Poort industries remain one of the most hotly debated issues in African archaeology (112, 114, 117). The heavy concentration of these sites documented in the southwestern corner of South Africa (around the southern Cape coast and the closely adjacent areas of the south Atlantic coast: main text Fig. 2) clearly points to a center of gravity and probably a center of origin of these technologies within South Africa itself (recently reinforced by the dating of a closely similar industry at Pinnacle Point on the southern Cape coast to ∼71 ka (142)—although their precise relationships with the stratigraphically preceding "Still Bay" industries (as at Sibudu, Diepkloof, Apollo 11, and elsewhere) remain a matter of ongoing debate (114, 144, 145, 150, 151). If South Africa was the point of origin of the Howiesons Poort technologies, then their subsequent dispersal through central Africa and into many parts of East Africa could be attributed most parsimoniously to the transition from the great East African "megadrought" spanning the period from ∼100 to 60–70 ka to the onset of much wetter conditions, dated broadly to between ∼70 and 60 ka in the detailed sedimentary sequences recently recorded in the Lake Malawi deposits in eastern-central Africa (113, 152). A rapid and major demographic expansion northward from South Africa into eastern Africa at this time would seem largely predictable in ecological and demographic terms. The relationships between the Howiesons Poort technologies and specific genetic lineages in South and East Africa remain more debatable. A large-scale dispersal from South to East Africa does not appear to be reflected in the mtDNA evidence; L3 has deep antecedents in East Africa, and an origin in the South can be effectively excluded, and deep South African L0d and L0k lineages seem to be virtually absent from East Africa (2, 153). The dispersal of Howiesons Poort industries northward may have been mediated by sex-biased demographic dispersal, perhaps signaled by the sharing of subclades of deep-rooting Y chromosome haplogroups across South African Khoisan (A2 and A3b1) and Ethiopians (A3a and A3b2). The alternative is that the dispersal of Howiesons Poort-like technologies from South to eastern Africa was due not to a major dispersal of populations from south to north, but more to a dispersal (or cultural "diffusion") of the principal technological elements of the Howiesons Poort technologies [possibly reflecting the introduction of new bow-and-arrow technology (154)] into the preceding MSA populations already occupying East Africa (155–159). The claimed [but debatable (110)] co-occurrence of typical Howiesons Poort-like backed-segment forms with distinctively MSA uni- and bifacially flaked "points" in Bed V of the Mumba rockshelter (Tanzania) (110, 127) and (rather later and more reliably) in the recently reported sequence in the Mochena Borago rock shelter (Ethiopia) (140) could potentially provide evidence of this kind of technological diffusion and of assimilation processes in the East African sites.

Coastal Dispersal Models. For the past decade, the hypothesis of a primarily, if not exclusively, coastal pattern of dispersal of modern human populations from Africa eastward to South and Southeast Asia, and ultimately Australia, has been widely accepted as the most plausible and theoretically parsimonious model for the rapid dispersal of these populations across the so-called "southern" dispersal route (11, 17, 160–164). To a large extent this model has been driven by the apparent speed of this dispersal, implied by the documented presence of anatomically modern populations within Australia (a distance of ∼15,000 km along the inferred coastal route) by a date that, although still debated, can be estimated broadly at around 45–50 ka (165, 166) and conceivably (by some estimates) as early as 55–60 ka (167). Only by what has been termed this "coastal express" route (17), it is argued, could this dispersal from eastern Africa to Australia have been achieved within a period of at most ∼10,000 y.

As discussed briefly in the main text, this model can be supported by a range of ecological, economic, demographic, and related ethnographic observations, which can be summarized in more detail as follows:

i) The first and most obvious rationale underlying this rapid coastal dispersal model is that by expanding along a succession of coastal locations, the dispersing human groups would be able to retain a closely similar range of both coastal environments and their associated range of exceptionally rich, productive, diverse and long-term "dependable" food resources (see below) over most if not all of this coastal dispersal route. In this way the human groups would have been able to reduce to a minimum the degree of economic, technological, and no doubt social adaptations from one coastal location to another—a pattern that might well be described as a process of progressive "beach hopping" along the successive coastal habitats.

ii) Ever since the original pioneering paper by the geographer Carl Sauer in 1956, "Seashore: Primitive home of Man?" (164), it has been recognized that coastal environments provide a uniquely rich and ecologically diverse supply of food resources for human populations in most if not all regions of the world (161, 163, 168–170). Crucially, this is dependent on the immediate juxtaposition in these contexts of three separate and ecologically contrasting ecosystems, each with its own range of potential (and usually highly abundant and productive) food resources—i.e., the resources of the sea itself (fish, sea mammals, sea birds, etc.); the resources of the adjacent terrestrial habitats, providing a range of both animal and plant food resources; and the entirely separate range of potential food supplies provided by the intervening intertidal zone, typically including high concentrations of marine molluscs, various forms of crustaceae, and edible species of seaweed (161, 163, 164). The immediate juxtaposition of these three separate and contrasting ecosystems provides a potential wealth and diversity of human food resources, which can be paralleled in very few, if any, purely terrestrial environments (161, 168, 169).

iii) In human demographic terms, the critical importance is not merely the sheer wealth and abundance of these different coastal food resources (depending largely on the biotic and planktonic productivity of the inshore coastal sea waters) but also above all their exceptional diversity when viewed in human subsistence terms. Although the abundance of all these coastal food supplies can vary to some extent, both seasonally and over longer timescales, by a variety of ecological factors (161, 163) the prospect of all of these resources declining sharply and simultaneously at any point in time is much less than that in almost any purely terrestrial habitats, which are typically dependent on a much more limited range of potential food resources, many of which can be sharply and in some cases catastrophically reduced by factors such as exceptionally severe winters and associated snow cover, episodes of hyperaridity, shifts in the seasonal migration patterns of animal populations, and a range of other largely unpredictable environmental fluctuations (168, 169). In human demographic terms, the critical factor in this situation is the so-called "Liebig's law of the minimum", which dictates that the long-term densities of any biological populations that can be supported in any environment are ultimately controlled not by the overall, "average" abundance of essential food or other resources in the environment as a whole, but by the quantities of resources available during episodes of maximum scarcity, in both seasonal terms and over longer timescales of decades or even centuries (171). This factor in turn is normally critically determined by the overall diversity of essential food and other resources available in the respective environments and the low probability that all of these resources will decline, sharply and simultaneously, at any particular point in time. It is here, in short, that the high diversity of the combined marine, intertidal, and terrestrial food resources available to human groups occupying coastal situations can exert such a dramatic effect on the overall numbers and population densities that can be supported within these habitats on an effectively permanent basis—what is often defined as the long-term "carrying capacity" of the environments in question (172).

Ethnographic data on a wide range of recent hunter–gatherer populations occupying a range of different coastal environments clearly bear out the demographic implications of this model—as the exceptionally high densities of human populations recorded in areas such as the northwest coast of North America, the coastal Ainu populations of Hokkaido Island (Japan), and many populations along the exceptionally rich and productive Pacific coastlines of South America clearly reveal (168–170). There seems no reason to doubt that similar factors would have had a similar demographic effect on prehistoric hunter–gatherer populations—including the initial modern human founder populations dispersing progressively along the various coastlines of the southern dispersal route:

iv) The wealth, concentration, and above all economic diversity of coastal food supplies help to explain not only the attractions of coastal locations for the original, dispersing modern human founder populations in the different regions of southern and southeastern Asia, but also the economic and demographic mechanisms for their gradual, progressive expansion from west to east. Owing to the wealth, diversity, and long-term "reliability" of these coastal resources, it can be assumed (for the reasons outlined above) that once a new coastal location had been established by the initial human settlers, the human populations within that location would rapidly increase in numbers, until some form of either economic or social constraints led to significant population pressures on either the available economic resources themselves or the social integration mechanisms within the local groups, presumably leading to increased social and personal "competition" within the groups and potentially to associated social conflicts (172). These are precisely the kinds of economic and social pressures that would presumably lead to a "fissioning" of the original founder communities and a "budding off" of some segment of the original groups (perhaps groups of closely related families) into a new settlement location, located farther along the adjacent coastline. If the dispersal process was assisted by the use of boats or other watercraft [as most authors now assume, and which was presumably essential to make the at least 60-km sea crossing from southeast Asia to the late Pleistocene Australasian ("Sahul") landmass (161, 162, 165–167)], then the distances between the adjacent founder settlements could no doubt in some cases have been substantial. However, it should be kept in mind that to maintain the essential mating and other social contacts with the preceding "parent" groups, and to avoid the dangers of excessive genetic inbreeding within the newly established settlements, the distances between the new and parent communities must presumably have been kept within a viable traveling distance. Settlements separated by too great distances would presumably have been in danger of becoming socially and demographically isolated, with the consequent dangers of extinction of the "pioneering", progressively dispersing groups. This, in short, is the model we would envisage for effectively the entire process of geographic dispersal of the earliest modern human populations, across most, if not all, of the inferred southern coastal dispersal route.

v) Viewed from an archaeological perspective, one element that seems strongly predictable in this scenario is that the successive human settlements established along this coastal dispersal route are likely to have been tied very closely to immediately coastal locations and in most cases closely adjacent to the contemporaneous beaches (161, 163, 164). In theoretical terms this seems largely predictable from the obvious need to maintain a close monitoring of the state of the tide (and the consequent access to intertidal resources such as shellfish and crustaceans), the movements of sea mammals, and immediate access to boat travel. Equally if not more importantly this would also reduce to a minimum the distances over which relatively heavy economic resources, such as collections of shellfish and perhaps carcasses of sea mammals, together with coastal supplies of lithic raw materials for stone-tool manufacture or the maintenance of living structures and associated hearths and cooking facilities, derived from the adjacent beach deposits, needed to be carried.

The same prediction is supported by archaeological surveys of documented archaeological coastal sites in many areas of the world [frequently marked by substantial shell-midden accumulations (161, 163)], which are almost invariably located closely adjacent to the contemporaneous beaches, presumably for all of the reasons outlined above [as documented for example in many areas of South Africa (116, 173), Australia (165–167), northwestern America (168–170), and European Mesolithic contexts (174)]. The same could be said of the great majority of coastal settlements in recent ethnographic contexts, such as the American Northwest coast or the Japanese Ainu settlements (168–170), which are again almost invariably located adjacent to contemporary shorelines. It is salutary to recall that if the subsequent sea levels rose by only 10 m or so, the great majority of these coastal settlements would be either effectively destroyed by tidal action or submerged beneath several meters of the rising sea levels. The implications for coastal settlements of the initial modern human founder populations around the coastlines of southern and southeastern Asia, occupied at a time when worldwide sea levels were around 50 m or more below present sea levels, are even more self-evident:

vi) In addition to their obvious archaeological implications for the survival and visibility of coastal sites, one of the important environmental effects of the greatly reduced sea levels around the time of MIS 3 is that these heavily reduced sea levels would have exposed large areas of now submerged land around virtually all of the contemporaneous coastlines of southern and southeastern Asia (161, 163). The extent of these submerged "coastal plain" areas would of course have varied depending on the steepness and topography of the submarine contours in the different areas, but around most of the coastlines of southern Asia these exposed coastal-shelf habitats are likely to have ranged between at least ~20 and 50 km in width throughout the period of MIS 3, when the dispersal of the modern human populations is known (on genetic grounds) to have occurred. However, the key point to emphasize is that these "near coastal" terrestrial habitats would in most cases have provided rich supplies of plant and animal food resources to the coastally based human groups, in addition to the exceptionally rich resources provided by the strictly coastal (sea and intertidal) ecosystems themselves (161, 163, 164). The combination of these geographically extensive coastal lowland habitats and the resources of the coast itself could no doubt have allowed the initial, founder human groups to remain and flourish within the immediately coastal areas of South and East Asia for prolonged periods, without venturing beyond this broad "coastal strip" into the entirely different habitats within the more interior areas of the continent—quite possibly for periods of several millennia. As already emphasized, all traces of this initial, coastally based phase of occupation of southern Asia are now submerged below depths of up to 50–60 m of the subsequently rising sea levels (161).

vii) The factors that eventually induced an expansion of these initially coastally based populations into the very different and ecologically contrasting interior areas of India could have taken a variety of forms. We put the primary emphasis here on the sheer force of gradually increasing population numbers and densities within the initially colonized coastal regions—leading eventually to severe population pressures and overcrowding within these "primary" coastal occupation zones. In the earliest, founder stages of colonization these pressures (both economic and social) were presumably resolved by progressive dispersal and budding off of the original human groups farther along the adjacent coasts, as discussed above. However, with the continuing increase in population densities fostered by the sheer wealth and reliability of the coastal resources themselves, the point would eventually arise where these population pressures could be resolved only by demographic expansion into the interior areas of the continent (96). This would inevitably have required the development of a wide range of new economic and social adaptations to cope with the new and unfamiliar habitats and the consequent risks of various forms of resource failures and, no doubt, associated extinction of some of the initial, pioneering dispersals into the interior. Petraglia et al. (96) have argued that these pioneer dispersals into the Indian interior may also have been influenced from ~40 ka onward by a series of climatic changes that provided in certain contexts much richer and more productive food resources in some of the better-watered interior basins in the subcontinent. They have also argued, on the basis of paleobotanical evidence, that there was a marked decline in the extent and productivity of coastal mangrove communities at around the same time, which would have exerted further pressures on the coastal-living groups to move away from the coastlines into the adjacent interior habitats (96, 103). Our point, in short, is that all of these adaptive processes, both demographic and economic/environmental, would inevitably have taken substantial lengths of time, probably amounting to several millennia. It is for this reason that we see no conflict between our hypothesis of an initial colonization of the (now submerged) Indian coastlines from at least 50 ka onward and the subsequent, very clear evidence for a sharp increase in population densities within the interior areas of the continent from around 40–45 ka onward—a pattern that is reflected equally in both the current genetic evidence (notably a rapid proliferation of different subclades of the mtDNA M lineages from ~40 ka onward) and a broadly parallel increase in the numbers of dated microlithic industries within the interior areas of India, from approximately the same point in time (96); see also discussion *Genetics* and in main text). Exactly the same point has recently been emphasized by Hiscock in relation to the age of the initial colonization of Australia, where he comments that "The earliest sites found …. are not likely to date the arrival of humans but more likely reveal the time when population and landscape use had risen to the point of being archaeologically visible …. 44-46 ka BP must be considered a time when humans had established themselves across Australia, not necessarily the time at which colonisation occurred" (Hiscock, in O'Connell and Allen, ref. 175, p. 25). How exactly Petraglia et al. would account for these dramatic increases in population numbers within the Indian interior in terms of a general "environmental deterioration" (96) at around this time is, to us, more difficult to comprehend.

viii) How far we have to take account of any significant geographical barriers to this inferred pattern of coastal dispersal from Africa eastward to South and East Asia is potentially open to debate (162, 163). Field and Lahr (162) have discussed a number of such potential barriers to this coastal dispersal route, including the problems of crossing regions of "hyperarid" habitats such as the southern Arabian peninsula and regions adjacent to the Thar desert of Pakistan, combined with the potential problems of negotiating areas with exceptionally rugged or cliff-lined coastlines and the crossing of broad river estuaries, such as those of the Indus in northwestern India and the Ganges in northeastern India. In summary, however, they conclude that none of these potential coastal "barriers" are likely to have presented insurmountable obstacles to an overall pattern of dispersal across at least the greater part of the hypothetical southern dispersal route, even if these barriers may in certain contexts have slowed down the overall speed of dispersal. Although hyperarid habitats such as the Arabian peninsula (during the colder and drier episodes of MIS stages 4, 3, and 2) would have made the interior areas of the peninsula effectively impenetrable to human groups (due to the shortage of both freshwater supplies and exploitable food resources), they emphasize that this need not have impinged on the food resources available around the immediate coastlines of the peninsula, where the biotic productivity of the adjacent coastal waters is exceptionally high (main text Fig. 2). In terms of the availability of essential freshwater supplies along this coast, they note the occurrence of several springs and ephemeral streams along the present-day coastal zone. Potentially much more significant in this context is the evidence advanced by Faure et al. (176) that under conditions of substantially reduced sea levels, increased aquatic pressures in the coastal zones would have led to the emergence of now submerged freshwater coastal springs within the contemporaneous intertidal zones. Even if the distributions of freshwater supplies along this coast were relatively few and far between, they could well have been negotiated by the use of boats, from one freshwater source to another.

Overall therefore there seems no reason to regard the crossing of the South Arabian coast during the periods of MIS stages 4 and 3 as in any way an insurmountable, or even substantially difficult, barrier to the proposed coastal dispersal route from Africa eastward to southern and eastern Asia. With the use of boats or other watercraft, it is equally unlikely that the crossing of major river estuaries such as the Indus and the Ganges would have provided any major obstacle to the coastally dispersing groups. Whether any of these potential barriers would have substantially slowed down the speed of dispersal in certain areas is perhaps more debatable (162, 163). If the crossing of the, potentially arid, coastline of southern Arabia did have the effect of significantly reducing the rate of dispersal of the initial modern human groups across this geographical zone, this might conceivably explain the time needed for the divergence of the initial M and N mitochondrial lineages from the parent (East African) L3 lineage within the Arabian zone, as recently discussed by Richards et al. (16). However, to regard the crossing of the Arabian coast as an almost insurmountable obstacle to the current model of an explicitly coastal route of dispersal of the earliest modern human groups from Africa to southern Asia would seem difficult, if not impossible, to substantiate, on all of the grounds outlined above.

Earliest Microlithic Assemblages from South Asia. The most significant and best-documented sites for the earliest directly radiocarbon-dated phases of the microlithic technologies in the interior areas of South Asia are the rock-shelter site of Jwalapuram 9 (101) in the Kurnool district of southeast India and the two rock-shelter sites of Batadomba-lena and Fahien-lena (129–131) at the extreme southern tip of South Asia in present-day Sri Lanka—although joined at the time of the microlithic occupations to mainland India. The character and credentials of these important sequences are therefore worth examining in some detail. All of these locations must be regarded as strictly "interior" locations in environmental terms. The Jwalapuram complex of sites lies at around 250 km from the present-day eastern coastline of India, whereas the Sri Lankan sites are estimated to have been located at least 80 km from the contemporaneous coastline at the time of the microlithic occupations (129). The archaeological sequences at two of these critical sites (Jwalapuram 9 and Batadomba-lena) have recently been published in considerable detail (101, 129), although the final reports on both excavations are still to appear.

Jwalapuram 9. The excavated sequence in the Jwalapuram 9 rock shelter covers a depth of ~3.3 m, currently dated by a series of 12 radiocarbon measurements by the Oxford Radiocarbon Accellerator Laboratory on the aragonite fractions of samples of land-snail shells, ranging between ~34 ka (cal. B.P.) in the earlier levels to ~11.5 ka in the uppermost microlithic levels (101). One notable feature of the overall sequence of radiocarbon measurements (although curiously not referred to in the published report) is a major gap between the dates of 32–34 ka for the lower part of the sequence (stratum D) and the dates of 11.5–15 ka for the immediately overlying levels of stratum C—clearly indicating a substantial chronological and stratigraphic hiatus in the sequence spanning a period of ~15,000 y and coinciding broadly with the last glacial climatic maximum (Fig. S6). A potentially more serious question in this context lies in the reliance on dates produced entirely on land-snail shell samples for the dating of effectively the whole of the stratigraphic sequence. Because past experience has shown that ^{14}C dates based on shell samples have often produced dates that are several thousand years younger than dates on associated charcoal samples [even when based purely on the aragonite as opposed to calcite fractions of the shell samples (177–179)], it might be prudent to regard most if not all of these dates as essentially minimal ages for the levels in question. In the present context, for example, it is notable that the date secured on a shell sample from the uppermost level in the sequence (stratum C, at a depth of ~80 cm from the surface) yielded a date around 300 y younger than that of a charcoal sample from the same level in the deposits (Clarkson et al., ref. 101, table 1)—apparently reflecting some residual contamination of the shell sample by more recent carbon. If the same level of contamination were present in shell samples dated to ~34 ka toward the base of the microlithic sequence, this could translate into an underestimate in the true ages of these levels of up to 4,000 y [because the effect of any given level of contamination doubles with each increase in the half-life of the samples (177, 178)]. Whether this could be true of the measured ages of the dated shell samples throughout the Jwalapuram 9 sequence must presumably remain an open question, in the absence of further dates based on more methodologically reliable charcoal or bone samples. It should be noted that similar discrepancies have been encountered between the dating of shell and associated charcoal or bone samples in a number of European and Near Eastern sites, within broadly the same age range (179).

The archaeological material from the lowermost parts of this sequence was recovered from an excavated area of at most ~4 m^2. The archaeological material was summarized in some detail by Clarkson et al. in 2009 (101), including a series of graphs of the main features of the excavated lithic assemblages. Four main features of this sequence are especially relevant to the present discussions and are summarized briefly as follows:

i) Characteristic microlithic industries defined by a range of distinctive, clearly backed microlithic forms were recorded to an overall depth of between 2.30 and 2.80 m in the section as a whole, down to the lower part of stratum D, dated by two ^{14}C measurements on shell samples of ~34 ka (Fig. S6) and based for the most part on lithic assemblages of apparently reasonable size (although the precise numbers of retouched tools recovered from the different levels are not given in the published report). In the immediately underlying levels of the (currently undated) stratum E—recovered purely from the original, small deep sounding of at most 4 m^2 in area—it is stated that no retouched microliths were recovered, although the excavators stress that "their absence below 2.20 m may simply reflect small sample size" (Clarkson et al., ref. 101, p. 337). Within these basal levels, however, it is recorded that very high frequencies of typical microblade forms were recovered down to the base of layer E, where they represent the highest frequencies of these microblade forms recorded within the stratigraphic sequence as a whole. In this context one is forced to wonder exactly why these high frequencies of classic microblade forms were being produced in these basal levels, if not for the production of backed microliths. Our own reading of this situation is that, given larger assemblage sizes, the production of typical microlithic forms would be recorded to the base of the excavated Jwalapuram 9 sequence and to dates significantly older than the published radiocarbon measurements for the overlying levels, of ~34 ka. A reasonable inference from this situation in our view is that the overall sequence of microlithic assemblages in this site most probably extended back to around—and conceivably significantly before—40 ka, if the potentially problematic nature of ^{14}C dates based purely on snail-shell samples is taken into account. In any event, because it is stated that the excavated sequence encountered impenetrable, heavily concreted calcareous deposits at the base of the excavation, it is impossible to see the documented sequence in the Jwalapuram 9 rock shelter as reflecting more than a strictly minimum age for the production of microlithic technologies within the Jwalapuram region and, by implication, within this particular region of southeastern India as a whole.

ii) As to the actual shapes of the backed microlithic forms in the different levels we as yet have little information, beyond a single drawing of the tools recovered from the middle part of the sequence (spits 33 and 34). However, Clarkson et al. state that typically "symmetrical", "geometric" triangular and trapezoidal forms were the dominant types in the lower levels of the sequence, with increased frequencies of more elongated, "crescentic" or curved-backed forms in the overlying levels (101) (main text Fig. 3). As noted earlier, all of these forms are the classic hallmarks of the African Howiesons Poort industries, as encountered in sites in both southern and eastern Africa, at around the time of the genetically inferred age of the dispersal of modern human populations from East Africa to Asia. In Eurasian terms, the association of these forms with high frequencies of blade/bladelet production, typical forms of end scrapers and burins, and both highly shaped bone tools and perforated bead ornaments (see below) evokes an overall cultural repertoire of distinctively Upper Paleolithic form (124, 136), providing a stark contrast to the closely preceding industries of the Indian Middle Paleolithic tradition in the same region.

iii) The other important archaeological features documented in the Jwalapuram 9 excavations included a small (~2.5 cm) but clearly shaped fragment of deer antler, retaining an apparently clearly shaped barb, recovered from close to the base of the microlith-bearing levels at a depth of ~2.20 m, together with a further, shaped bone awl-like form from the adjacent levels (Clarkson et al., ref. 101, figure 5). From the overlying levels (dated to between 13 and 29 ka) there is a series of 25 rotary-perforated, circular-shaped bead forms, together with associated unfinished "preforms", manufactured predominantly from both local limestone and animal bone fragments (Clarkson et al., ref. 101, figure 6) (main text Fig. 4). These are effectively identical in shape and techniques of manufacture to those of the closely similar bead forms manufactured from ostrich eggshell fragments recovered from the earlier microlithic levels at the site of Patne in northwestern India and dated by radiocarbon measurements to ~30 ka (cal. B.P.) (146). As stressed in the main text, these bead forms are to all appearances identical in shape, size, techniques of manufacture, and associated, unfinished preform specimens to those of the range of ostrich-eggshell beads documented from the sites of Enkapune-ya-Muto in Kenya, Mumba in Tanzania, and numerous later sites in southern Africa (117) dated by radiocarbon in the Enkapune-ya-Muto sequence back to at least ~45 ka (cal. B.P.) (137) and by OSL measurements in the recently published Mumba sequence to ~49.1 ± 4.3 ka (110, 113) (main text Fig. 4). Whether the absence of similar bead forms in the lower levels of the Jwalapuram sequence has any significance, granted the small artifact sample sizes recorded from these lower levels, must clearly remain an open question. In addition, many fragments of red ochre were apparently recovered throughout most of the levels of the sequence (101), providing further potential (but more debatable) evidence for clearly "symbolic" behavior among the earliest recorded microlith-using groups in South Asia.

iv) Finally, it should be added that the rich faunal assemblages recovered from most of the levels of the Jwalapuram 9 sequence indicated the exploitation of a wide range of mammalian species, apparently reflecting a shifting mosaic of forested and more open habitats in response to climatic fluctuations in the vicinity of the site, throughout the greater part of the documented occupation sequence.

Sri Lankan Sites. The two rock-shelter sites of Batadomba-lena and Fahien-lena, located at distances of ~80 and 40 km, respectively, from the present-day coastline of southwest Sri Lanka (129–131) have yielded critical additional information on the earliest microlithic technologies within the interior areas of South Asia, which both complement and significantly expand on the finds from the Jwalapuram 9 site, some 1,000 km to the north, in the combined late Pleistocene land mass of present-day India and adjacent Sri Lanka. Major excavations at the Batadomba-lena site were initially undertaken by S. Deraniyagala between 1979 and 1986, excavating a total of 33 m^2 of the rock-shelter deposits, with a total depth of 2.8 m of archaeological deposits (131). On the basis of 10 radiocarbon measurements the deposits spanned a time range of ~20,000 y, from at least 32 ka (cal. B.P.) in the basal levels to ~12 ka in the uppermost levels, and yielded a total of over 44,000 artifacts (131). The entire archaeological sequence consisted of a closely similar range of characteristically geometric backed microlithic industries (main text Fig. 3), associated with a range of small but carefully shaped bone awls, perforated, circular sea-shell ornaments, and fragmentary human remains of at least 16 individuals, diagnosed by Kennedy and others as of distinctively anatomically modern human form (180, 181).

A much more limited but methodologically sophisticated excavation of deposits immediately adjacent to the large-scale excavations of Deraniyagala was undertaken by N. Perera and colleagues in 2005 and published in some detail in two recent publications (129, 130). Summarized briefly, the main discoveries of the combined Deraniyagala and Perera excavations in the basal levels of the sequence (levels 7b and 7c) were as follows:

i) These levels, despite reflecting relatively short and ephemeral visits to the site, contained the highest frequencies of backed microlithic forms recorded in the entire site sequence—with a progressive decrease in these microlith frequencies in the overlying levels. Although a total of only 23 complete microliths were recovered from the lowermost occupation level (layer 7c), the microlithic forms recovered from both this and the overlying levels comprised a range of distinctively geometric forms, including lunates and triangular and trapezoidal forms, apparently identical to those from the various levels of the Jwalapuram 9 rock shelter discussed above (101, 129) (main text Fig. 3). Virtually the whole (99.7%) of the lithic artifacts from these basal levels was manufactured from translucent, clear crystal quartz that, despite its difficult flaking qualities, included a significant component of typical bladelet forms and associated heavily reduced bladelet cores. Presumably due to the small size and limited flaking qualities of the available raw materials, the average size of the microliths was small, but included occasional specimens up to 2.8 cm in length. As at Jwalapuram 9, an additional distinctive feature of many of the microliths was the use of "bidirectional" or "bipolar" retouch to shape the backed edges of the tools (129), identical to that used in the production of similar backed-segment forms at Mumba, Enkapune-ya-Muto, Sibudu, and other African Howiesons Poort-like sites (110, 137, 139, 144).

ii) The same basal levels also yielded a series of carefully shaped bone and antler tools (principally small, sharply pointed awl-like forms, up to ~7 cm in length) together with a series of circular, rotary perforated bead forms manufactured from fragments of marine shells, evidently imported into the site from contemporaneous coastlines at least 80 km or more to the west (129) (main text Fig. 4). As Perera et al. (129) point out, these represent the earliest specimens of both bone tools and unequivocally symbolic ornamental items so far recorded in southern or southeastern Asia. Fragments of ochre were abundant in both the basal levels of the sequence, and the presence of ochre smearing on a human vertebra from the basal occupation level 7c (conceivably deriving from a disturbed burial) was taken to imply a specifically symbolic use for at least some of the ochre present in the site. As noted above, according to the studies by Kennedy (180) and others, all of the relatively abundant, although fragmentary, human remains recovered from all levels of the Batadomba-lena sequence—including the basal levels—are of distinctively anatomically modern form (180, 181).

iii) One further, especially notable technological element identified exclusively within the lowermost occupation level in the Batadomba-lena sequence (layer 7c) is the occurrence of one complete, and several unfinished specimens, of a highly distinctive, bifacially flaked, essentially leaf-shaped point form, ~3.6 cm in length, and again manufactured from clear crystal quartz—a form described by the excavators as a Balangoda point (Perera et al., ref. 129, figure 9) (Fig. S5). Although not apparently recorded from any of the other documented, early microlithic assemblages on the Indian mainland, this piece bears a striking resemblance to the similar forms of totally or partially bifacially flaked leaf or pear-shaped points that, as noted earlier, are such a distinctive and widespread feature of many of the middle and later Middle Stone Age industries of eastern and central Africa, such as Mumba, Aduma, Porc Epic, Mochena Borago, and other sites in East Africa and many other sites farther to the south, with ages apparently spanning the range from at least 50 ka back to ~80 ka (126–128). These forms could well be seen as a further distinctively African element within the (currently very small) range of the earliest South Asian microlithic industries. Its location closely adjacent to the proposed out-of-Africa coastal dispersal route is at least intriguing and potentially highly significant in the present context.

iv) Finally, the chronology of the basal occupation level in the Batadomba-lena sequence is dated by a single radiocarbon date on a charcoal sample (measured by the University of Waikato laboratory) of between 36.283 ka and 34.609 ka (cal. B.P.) at a 2 SD range (129).

Critical reinforcement of the age and character of this initial episode of microlithic occupation at Batadomba-lena is provided by the data recovered from a much shorter stratigraphic sequence recently excavated in the Fahien-lena rock shelter, located some 40 km to the southwest of the Batadomba-lena site (129). Despite the limited size of the excavated archaeological assemblage, this is again reported to have produced a number of extensively shaped bone and antler points, together with perforated sea-shell beads, and at least one geometric microlith. These were stratified some 60 cm below an overlying level radiocarbon dated by the Beta-Analytic laboratory to ~38 ka (cal. B.P.) (with a potential range of between 38.734 and 36.475 ka, at a 2 SD range). As Perera et al. comment, this provides an "indication that people who used microliths, bone and antler points and symbolism settled in the Sri Lankan rain forest between 40,000 and 38,000 cal. BP" (Perera et al., ref. 129, p. 263).

Two of the most significant observations made in the recent paper by Perera et al. are that the earliest currently dated microlithic industries in Sri Lanka (and, by analogy, the equivalent lower levels in the Jwalapuram 9 site discussed above) must be regarded as strictly minimal age estimates for the initial appearance of microlithic technologies in South Asia. In all three of the Indian and Sri Lankan sites, the basal microlithic industries lay either on bedrock or underlying sterile deposits, with no evidence at any of the sites for any preceding Middle Paleolithic occupation. Second, and equally importantly, they stress that all of these localities are located in strictly inland, interior habitats, substantially removed from the contemporaneous coasts (101, 129). This is especially true when due allowance is made for the large-scale reduction in global sea levels at the time of the human occupations (i.e., during MIS 3) and the consequent emergence of a broad expanse of now-submerged "coastal lowlands" around the entire coastlines of the Indian subcontinent, with environments and associated food resources very different from those of the adjacent inland, interior regions (96). They go on to stress that, with one or two highly questionable exceptions, no examples of clearly intermediate or "transitional" Middle Paleolithic-to-microlithic technologies have ever been documented in Sri Lanka (129)—a pattern that appears to be equally true of mainland India (with the highly dubious exception of the Patne site, where claims for a potentially transitional industry almost certainly reflect stratigraphic mixing between adjacent levels during excavation: C. Clarkson, personal communication). Finally, they draw attention (ref. 129, p. 265) to the (to our) patently obvious conclusion that in the face of all this evidence, the mechanisms and origins of the dramatically new, technologically idiosyncratic, and culturally modern replacement of archaic Middle Paleolithic technologies by the new microlithic technologies in the Indian subcontinent remain an issue totally open to debate (ref. 129, p. 265). Although they, along with Petraglia et al. (96), are tempted to stress the potential role of climatic and related environmental changes in this technological replacement of archaic Middle Paleolithic by entirely modern, symbolically structured microblade and microlithic technologies, they conclude that "it is possible that aspects of the later [i.e., post-Middle Palaeolithic, microlithic] record were deeply rooted in other, longer inhabited ecozones in Sri Lanka, from which they were introduced by foragers expanding into the interior at around 40,000 BP" (Perera et al., ref. 129, p. 265). This is precisely the interpretation that we have proposed throughout this paper, where we have argued for a substantial phase of occupation and a progressive process of population increase and ecological/economic adaptation, established initially around the immediate coastlines and closely adjacent (now submerged) coastal lowland habitats of south Asia, most probably from at least 50 ka onward. Significantly, in the Sri Lankan sites there is direct evidence for continuing contacts between the interior and coastal populations, in the form of the long-distance transport of imported marine shell ornaments, present in the earliest occupation levels of both the Batadomba-lena and Fahien-lena sites (129). This appears to provide further support to the hypothesis of an initial, coastal episode of occupation around the South Asian coastlines, by the earliest modern human founder populations in South Asia.

Finally, as discussed in the main text, a highly important discovery on the Indian mainland, from the site of Mehtakheri, in the Narmada valley of northwest India, has recently documented a typical microblade and backed-microlith industry dated by multiple OSL and associated radiocarbon meaurements to between ~45 and 55 ka. Although the paper is currently in press (182) and based on a comparatively small lithic assemblage, this site now appears to effectively demonstrate the presence of microblade-using and backed-microlithic–using groups in the interior areas of northern India from at least 45 ka, as predicted from the general model proposed in this paper.

Geographical Limits of Microlithic Technology. One point that now seems established beyond reasonable doubt is that the geographical limits of these highly distinctive microblade and geometric microlithic technologies are confined to the Indian subcontinent, with no currently documented traces of these technologies in regions farther to the east (11, 183, 184). The potential explanations of this pattern in terms of the current coastal dispersal model for the earliest modern populations from Africa eastward to eastern and southeastern Asia have been discussed elsewhere (183). Briefly, three separate, but interrelated factors are likely to have been significant in this context.

First, and most significant, we should recall that that any process of long-distance dispersal of (initially small) human populations across a distance of over 15,000 km from East Africa to southeast Asia and Australasia will inevitably be subject to a succession of repeated demographic, genetic, and cultural "founder effects", as they moved progressively eastward along the hypothetical coastal dispersal route. The impact of this factor has already been documented clearly in the both the genetic (25) and the craniometric (185) features of modern populations eastward from Africa to Australasia, and it is inconceivable that similar, founder-effect mechanisms would not operate to an analogous degree on the repertoire of cultural and technological features of the small, dispersing human groups involved—leading to a cumulative "loss" of specific technological and other cultural elements progressively from west to east and an associated apparent "simplification" in the cultural and technological repertoires of the dispersing human groups (186, 187). Further innovations could of course occur during this process, as reflected, for example, by the appearance of edge-ground and waisted axes in Australasia (166, 167) and a number of distinctive tanged and trapezoidal forms in the early "Upper Paleolithic" industries in Korea and Japan, respectively.

Second, we should recall that in the course of this eastward dispersal, the initial, founder human groups would have encountered a range of new, and in some cases sharply contrasting, environments, with a range of at least inland if not coastal economic resources that differed sharply from one region to another. This would impact most notably on the kinds of technologies required to effectively exploit the new ranges of both plant and animal resources within the inland habitats and at the same time have provided access to new raw materials for a range of technological equipment and the precise forms and techniques of manufacture of the artifacts produced (183).

Finally, and in the present context perhaps most significantly, the precise repertoire of the stone tool industries produced and used in the different locations, and the associated techniques of manufacture, would be heavily dependent on both the abundance and, above all, the variable flaking properties of the immediately available lithic raw material supplies in the different locations (109–111). It is now fairly generally recognized that the continued production of technologically "simple" or even archaic forms of pebble-tool and chopping-tool technologies (sometimes broadly referred to as "Hoabinhian") across large areas of southeastern Asia well into the late Pleistocene and even Holocene periods can be most plausibly explained in terms of the general scarcity of high quality, fine-grained rocks for tool manufacture and the enhanced reliance in many areas on much poorer (largely river or beach derived) coarse-grained rocks such as quartz and quartzite (11, 116, 184). What role the presence of bamboo as an entirely new raw material for the manufacture of a range of pointed or sharp-edged implements may have played in these contexts (now unfortunately effectively invisible in the surviving archaeological records of the southeast Asian sites) is still a matter of debate (111, 188). However, in any event, the general absence or scarcity of fine-grained, siliceous materials for stone tool manufacture throughout large areas of both inland and coastal southeast Asia would inevitably have imposed heavy constraints on the capacities of the human groups to produce highly controlled and standardized forms of flake and blade blanks—and especially the kinds of small, highly standardized "bladelet" blanks needed for the production of highly shaped microlithic forms (183).

It is potentially equally relevant in this context that if the use of microlithic technology was primarily if not entirely for the production of multicomponent hunting armatures [either in spears or quite probably as armatures for wooden arrows (115, 117, 121, 154)] for the hunting of relatively large game, then the functional need for this form of technology would decline as the eastward-dispersing groups moved into regions with abundant plant and small-game food resources in the increasingly tropical regions of eastern and southeastern Asia (189)—with the potential use of bamboo as an alternative material for the production of hunting equipment in these regions (111). It is for all these reasons that we find the absence of typically microlithic technologies during the initial stages of modern human dispersal in regions lying to the east and southeast of India not only unsurprising, but arguably largely predictable in both demographic and technological terms.

Early Modern Humans in the Arabian Peninsula? In view of its immediate proximity to northeastern Africa, the evidence from the Arabian peninsula for modern human dispersals has inevitably generated much interest and field research over the past few years (75, 132–134, 190–192). Climatically, most of this region, with the notable exception of the coastline (see above) must have been far too arid to support any substantial human occupation throughout the whole of MIS 4 and 2, and effectively all of the documented evidence for occupation derives from the period of MIS 5, between ∼125 and 70 ka, when climatic conditions were demonstrably much wetter and more economically productive than during the preceding MIS 6 and ensuing MIS 4 periods.

Recently, two major, but archaeologically very different, claims have been made for the possible expansion of modern human populations from northeast Africa into the Arabian peninsula during the wetter episodes of MIS 5. Potentially the most significant evidence derives from the extensive recent research of Rose et al. (132) in the western parts of the peninsula (most notably in the Dhofar region of Oman), which has documented large numbers of surface sites, characterized by the presence of distinctively Nubian forms of Levallois point cores (i.e., essentially cores with the pointed ends shaped by removals directed from the distal end of the core). Before the discovery and reporting of the Arabian sites, cores of this highly distinctive form had been restricted to a range of sites in the adjacent areas of northeast Africa, ranging from Ethiopia in the south to the Nile valley and the eastern margins of the Sahara desert in the north, with several of these sites dated by a range of dating methods to the period of MIS 5, between ∼114 and 100 ka (Rose et al., ref. 132, figure 1 and table 1). In our view, these sites provide strong and convincing evidence for the movement of human groups carrying the "Nubian core" technology across the intervening (relatively narrow, but chronologically fluctuating) Red Sea, at one or more points during the course of MIS 5.

In view of the well documented dispersal of anatomically modern human groups from northeast Africa into the closely adjacent area of Israel during the warmer and wetter conditions of the earlier part of MIS 5, ∼120–90 ka [as documented unequivocally by the skeletal remains from the sites of Skhul and Qafzeh in Israel (122)], it is possible and entirely plausible to suggest that the same conditions had facilitated and promoted an analogous dispersal of African-derived populations across the intervening Red Sea into the western parts of Arabia over broadly the same span of time. In this context, however, there are five main caveats to be kept in mind:

i) First, the highly distinctive Nubian technology bears no resemblance whatever to the very different, Middle Paleolithic/Levallois technologies found in association with the anatomically modern skeletal remains at the two Israeli sites (122, 132).

ii) Second, the recorded geographical distribution of the Nubian-type sites in Arabia is so far confined entirely to the western and south-central parts of the peninsula and is as yet unrecorded in any regions farther to the east (Rose et al., ref. 132, p. 18).

iii) Third, in the absence of any skeletal remains recorded in association with any of the Nubian sites, in either Arabia itself or in the adjacent regions of northeast Africa, the human forms responsible for these industries remain at present totally unknown.

iv) Fourth, even if we accept some movement of human groups between northeastern Africa and western Arabian during MIS 5, the actual direction of this dispersal remains for the present an essentially open question, as Rose et al. (ref. 132, p. 18) have recently stressed. As they point out, the only directly dated occurrence of Nubian artifacts in Arabia (at Aybut Al Auwal, dated to ∼106 ± 9 ka) is of broadly similar age to the earliest dated sites in northeast Africa, and the ages of the remaining Arabian sites remain unknown. In view of the apparently dense occupation of parts of the Arabian peninsula during much if not all of MIS 5, it must remain an open question whether this technology developed initially in northeast Africa or within the Arabian peninsula itself, perhaps due to an influx of populations from the north. Simply to apply the term Nubian to this technology (for purely historical research reasons) is clearly no proof that this is the region where the technology initially developed!

v) Finally (as emphasized in an earlier section) there is certainly no clear evidence documented so far for the occurrence of distinctively Nubian technology within the Indian subcontinent or anywhere to the east of the south-central region of the Arabian peninsula (Rose et al., ref. 106 and ref. 132, figure 1).

In short, as Rose et al. themselves have emphasized (ref. 132, p. 18), to regard the occurrence of Nubian technologies in Arabia as unambiguous proof of an early dispersal of anatomically modern humans from Africa into western Asia during the period of MIS 5 must remain at best hypothetical, in the current state of research—although it certainly cannot be ruled out on either demographic or archaeological grounds.

The second piece of evidence recently claimed to show—or strongly suggest—the presence of African-derived modern human populations in the Arabian peninsula during an early stage of MIS 5 (~125 ka) comes from recent excavations in the rock-shelter site of Jebel Faya in the United Arab Emirates, located in this case at the extreme eastern tip of the peninsula, close to the straits separating the Persian Gulf and the Gulf of Oman (Armitage et al., ref. 133). The critical evidence in this case derives from a small assemblage of artifacts (the exact number is not indicated) excavated from the basal level (layer C) in the rock-shelter sequence, with an associated single-grain OSL age estimate of ~125 ka (133). The lithic assemblage from this level is dramatically different from that of the Nubian sites in the western parts of the peninsula and is characterized by a number of small, bifacial "hand-axe" forms, the use of simple, centripetal Levallois flake and occasional blade-like technology, the absence of Nubian technology, and a single illustrated specimen of what is described as a "bifacial foliate" (Armitage et al., ref. 133, figure 2, no. 1), which is claimed to show affinities with the range of small, bifacial foliate forms recorded from a wide range of eastern and southern African MSA sites, spanning the range from ~50 to at least 80–100 ka, as discussed above (Fig. S4). In reality, this single foliate form bears little if any resemblance to the supposedly ancestral African forms, in terms of its size, its thickness, its overall shape (which is more appropriately described as essentially suboval, as opposed to leaf-shaped), and the fact that it is clearly manufactured from a nodule of raw material as opposed to a Levallois or some other form of flake—which is an almost invariable feature of the great majority of the East African MSA bifacial foliate forms (192). In the context of the Jebel Faya assemblage as a whole, this piece could just as easily be interpreted as a lateral (essentially "ovate") variant of the other typical bifacial hand-axe forms, which are the most distinctive feature of the (very small) Jebel Faya assemblage as a whole. In our view therefore the Jebel Faya layer C assemblage need represent nothing more than a local variant of a late "Acheulian" industry, of the kind that shows a wide distribution across Eurasia, extending from western France, as represented for example in the late MIS 6 levels of the Combe Grenal rock shelter in the Dordogne region (193), through parts of central and eastern Europe, and apparently into the Indian subcontinent (106)—as well as in many parts of southern and eastern Africa. As an argument for the presence of explicitly African-derived modern human populations in this region of eastern Arabia—and in the absence of any associated human skeletal remains—it is in our view difficult to attach any significance to this discovery, despite the evident interest of the site in more general archaeological terms.

Finally, one potential objection that has sometimes been raised against our model of a direct dispersal of microlithic/Howiesons Poort-like technologies from East Africa (via the mouth of the Red Sea) to India is the current lack of archaeological evidence for these industries in the intermediate zone along the southern coastlines of the Arabian peninsula. In reality, there are several reasons why we find this situation not merely unsurprising but largely predictable, in both archaeological and environmental terms. As noted above, current archaeological research and surveys for Paleolithic sites in most areas of Arabia is effectively still in its infancy (largely a product of research in the past decade) and the only Arabian sites we are aware of that dated to the critical time range of the out-of-Africa dispersal between ~50 and 60 ka derive from the Wadi Surdud in western Yemen (192), along the eastern margins of the Red Sea, which are marked by an almost total absence of retouched tool forms and bear no obvious resemblance to any documented African industries (192).

However, the most critical factors to be kept in mind in this context relate to the patterns of the now widely accepted, specifically coastal route of dispersal of the initial modern human populations from East Africa to Asia, along the southern dispersal route, discussed in detail in an earlier section. Here we argued that for a wide range of demographic, economic, and environmental reasons, the archaeological traces of these initial, founder human populations are likely to be tied very closely to the immediate coastlines of the different regions and for the most part closely adjacent to the contemporaneous beaches, where the dispersing groups could benefit from the complementary resources of three rich, immediately accessible, and entirely separate ecosystems and their associated food and other resources (those of the sea itself, the closely adjacent land areas, and the intermediate, and exceptionally productive, intertidal zone). This factor is especially pertinent along the southern coastline of the Arabian Peninsula, where the biotic productivity of the inshore coastal waters is exceptionally high (main text Fig. 2). As discussed earlier, all of these immediately coastal locations are now deeply submerged ~50–60 m below present sea levels, due to the massive rise in global sea levels during the past 20,000 y. As in the case of India, therefore, the discovery of archaeological sites reflecting this initial modern human dispersal along the coastlines of the Arabian peninsula is likely to be dependent on future underwater explorations, of the kind that are currently being developed and applied around the coasts of the Red Sea (161). It is true that as a result of the steeply shelving coastlines of southern Arabia, the widths of these now submerged contemporaneous coastal shelf or coastal plain areas are likely to have been relatively narrow. However, this of course is largely irrelevant to groups dependent very heavily if not exclusively on specifically coastal and intertidal food resources, and an adjacent coastal plain width of even a few kilometers would still have provided access to a substantial range of purely terrestrial (plant and animal) resources, in addition to the much richer, more diverse, and long-term reliable resources of the immediate coastlines themselves. As noted earlier, freshwater sources along the southern Arabian coast are likely to have been boosted by the emergence of freshwater springs within the contemporaneous (now submerged) intertidal zones (176). To venture farther into the relatively arid and economically unproductive areas of the peninsula would, in this situation, have been both unnecessary and ecologically improbable, except conceivably during one or two brief, wetter episodes during MIS 3. As noted earlier, it is for all these reasons—combined with the limited and localized extent of systematic surveys for Paleolithic sites across the Arabian peninsula—that we find the current lack of archaeological evidence for distinctively microlithic or Howiesons Poort-like industries around the present-day coastlines of the Arabian peninsula both unsurprising and effectively predictable, in the current stage of research.

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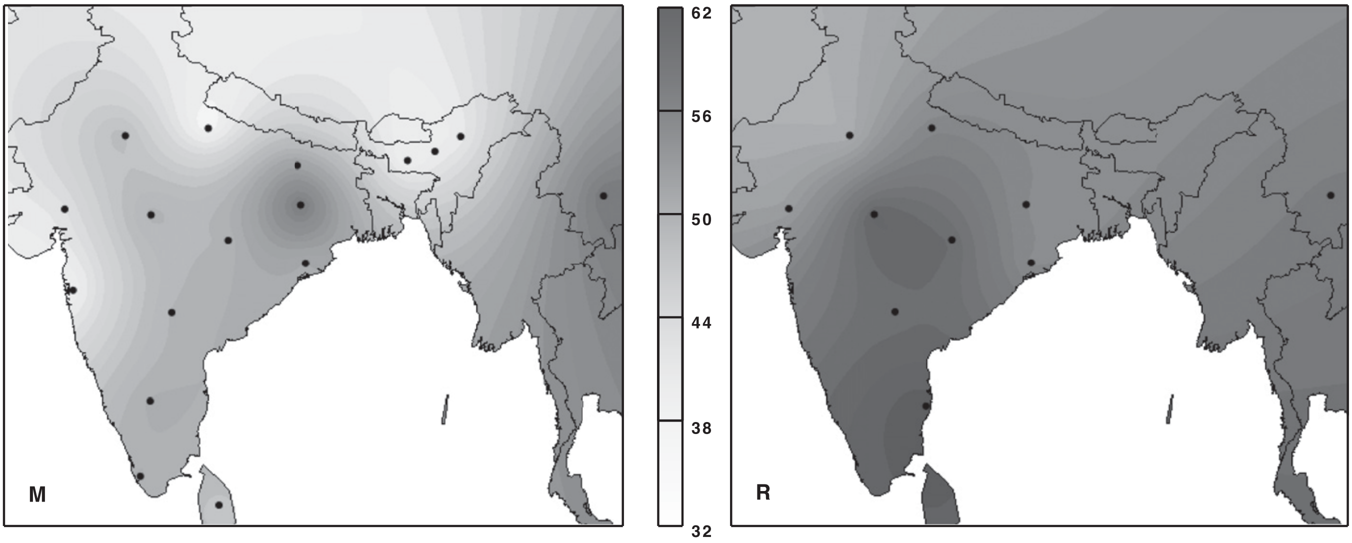

Fig. S1. Surfer maps of ρ-values (expressed as ka) for each state of India for which data were available (solid circles) for haplogroups M and R.

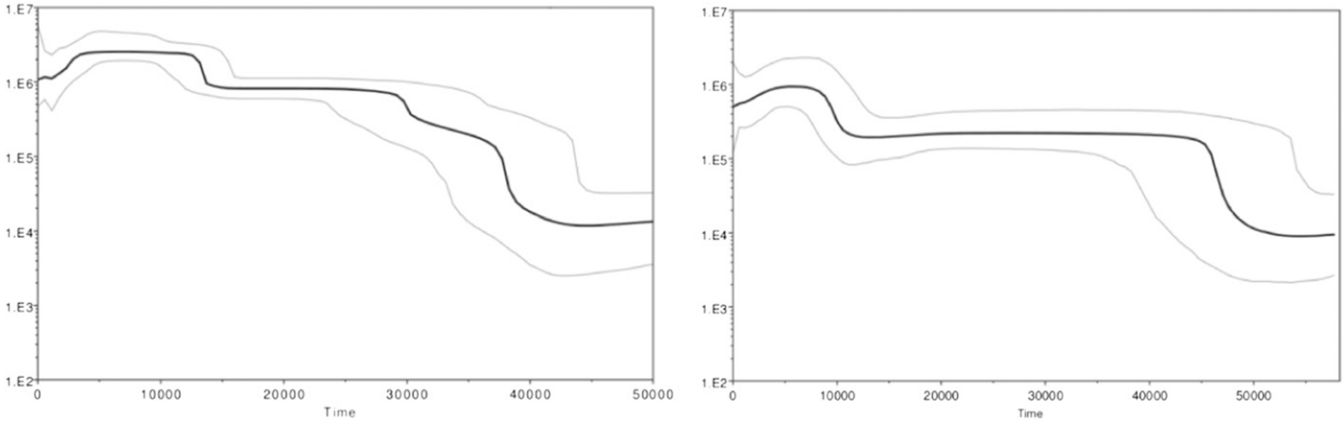

Fig. S2. Bayesian skyline plots of haplogroups M (*Left*) and R (*Right*) in India. The time axes run from 0 to 50 ka and from 0 to 60 ka, respectively, and the effective population size axis is logarithmic from 10^2 to 10^7 individuals.

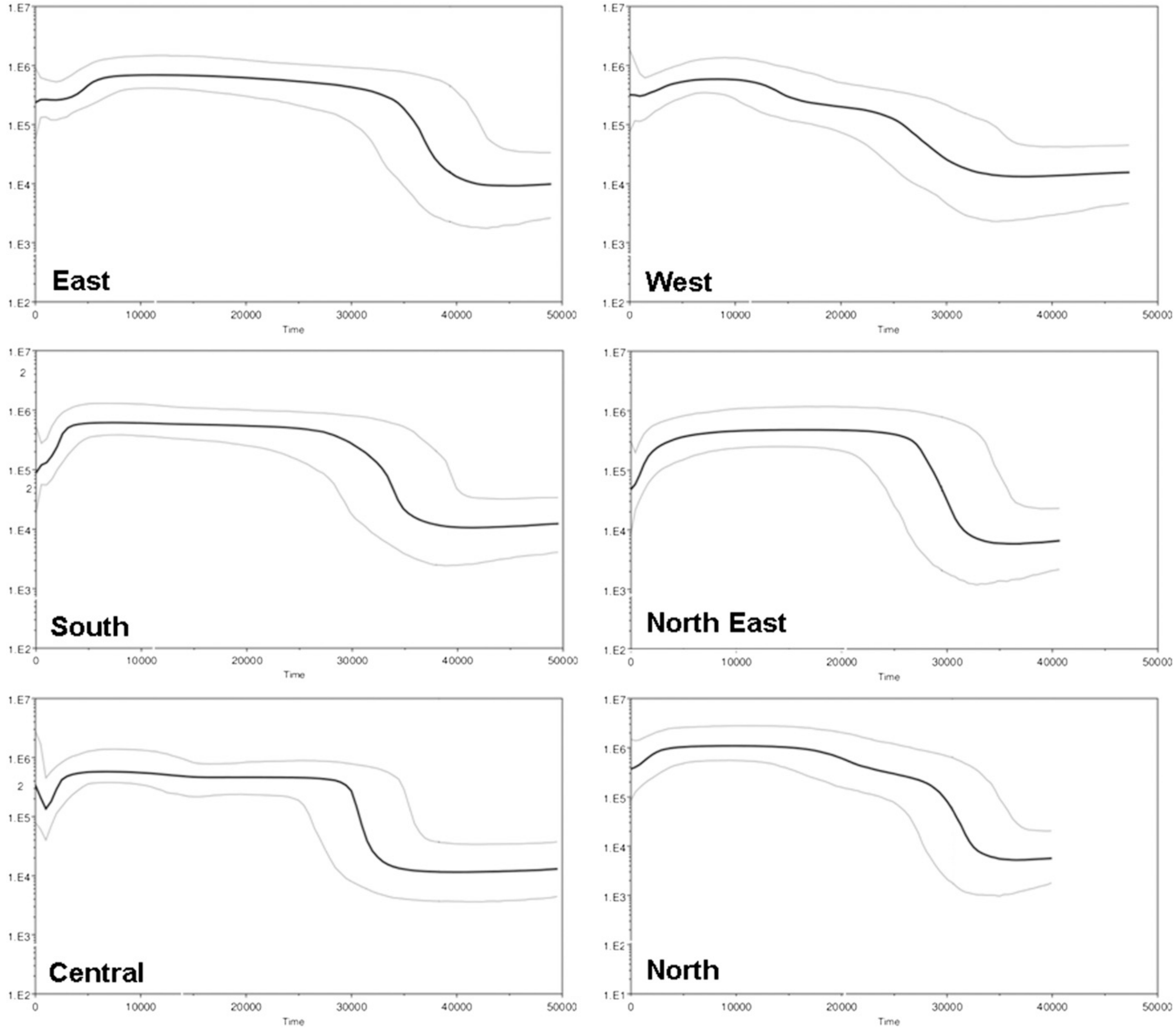

Fig. S3. Bayesian skyline plots of haplogroup M in regions of India. All diagrams are shown on the same scale: The time axis runs from 0 to 50 ka, and the effective population size axis is logarithmic from 10^2 to 10^7 individuals.

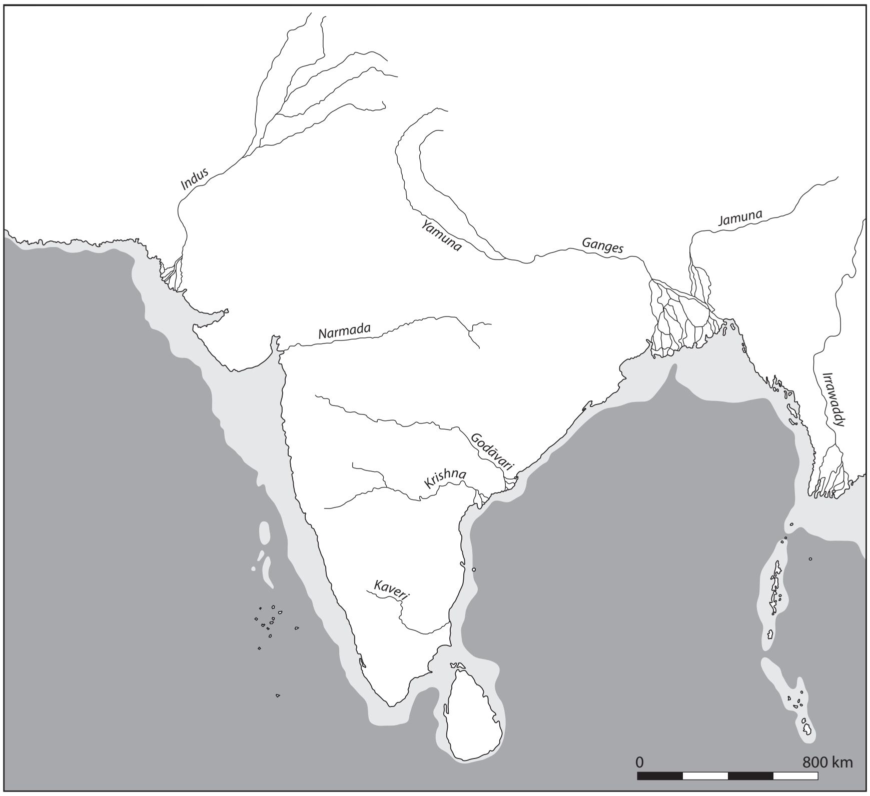

Fig. S4. Map to show the varying widths of the submerged continental-shelf areas around the coastlines of South Asia and the locations of the major river valleys in the Indian mainland. As discussed in the text, the greater number of rivers flowing into the eastern vs. the western Indian interior may explain the earlier expansion of the mtDNA M lineages into the eastern than into the western regions of the subcontinent (Figs. S1–S3). The greater width of the coastal-plain areas around the western than around the eastern coastlines would also have allowed for a longer period of population growth along the former coastline, before the initial founder populations were forced by population pressure, and rising sea levels, into the sharply contrasting environments of the western Indian interior.

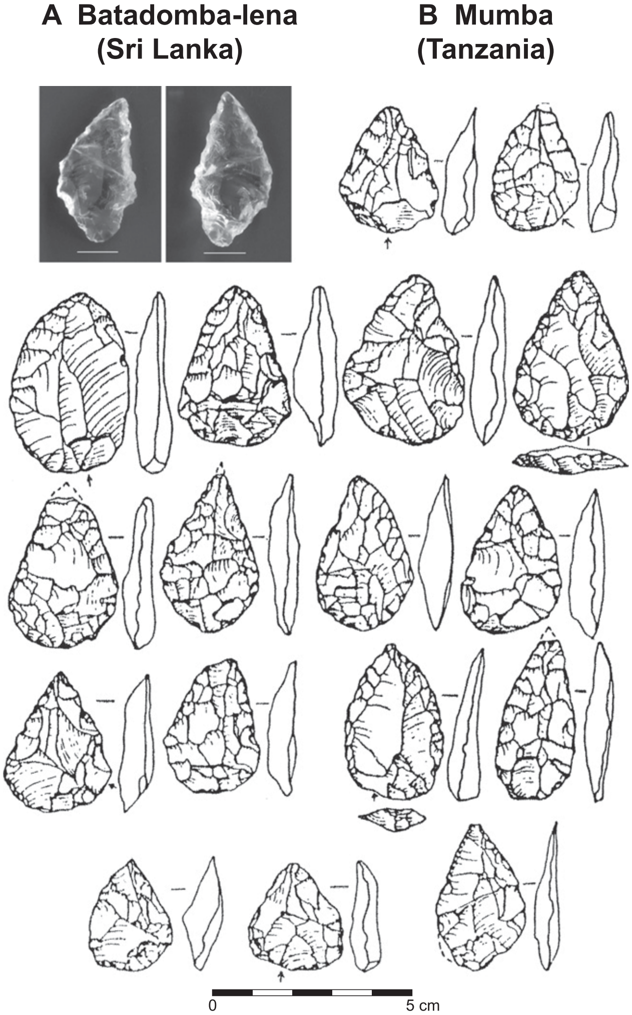

Fig. S5. (*A*) Bifacially flaked, leaf-shaped "Balangoda point" manufactured from clear crystal quartz from the basal microlithic level (layer 7c) at Batadomba-lena (Sri Lanka). (*B*) Similar forms of bifacial leaf points from the lower Howiesons Poort-like levels (layer V lower) in the Mumba rock shelter (Tanzania) (110, 129).

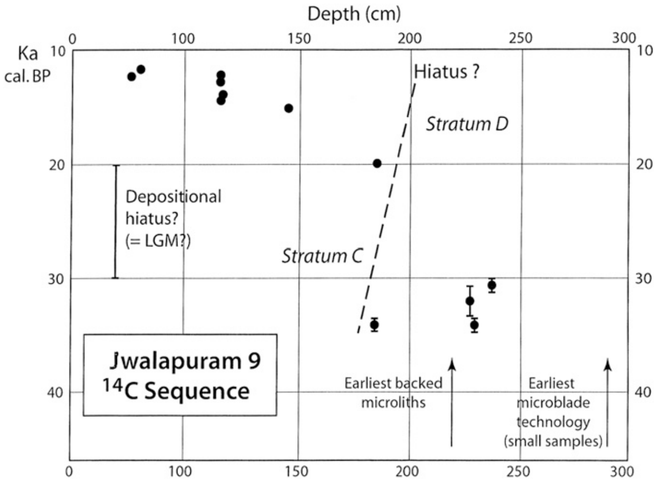

Fig. S6. Stratigraphic distribution of radiocarbon dates (based on land-snail shells) through the microlithic sequence in the Jwalapuram 9 rock shelter, indicating a major chronological hiatus between levels C and D and spanning the last glacial maximum from ~20–30 ka cal. B.P. Graph is reconstructed from data in Clarkson et al. (ref. 101, figure 4 and table 1). Note the absence of dates from the basal layer E, containing the highest frequency of microlithic bladelets in the entire sequence, with an absence of retouched microliths, probably due to the very small artifact sample size from this level (Clarkson et al., ref. 101, p. 337). For reasons discussed in the text, all of the dates shown should be regarded as essentially minimal estimates, owing to problems of potential contamination in the measured samples.

Table S1. Regional categories used in this study

Geographical divisions	States
Northeast	Assam, Arunachal Pradesh, Meghalaya, Sikkim
East	Bihar, Orissa, Jharkhand, West Bengal, Andaman Islands
Central	Madhya Pradesh, Chhattisgarh
North	Uttar Pradesh, Nepal
South	Andhra Pradesh, Karnataka, Kerala, Tamil Nadu, Sri Lanka
West	Rajasthan, Gujarat, Maharashtra, Pakistan, Punjab

Table S2. Summary of ages in years of haplogroups L3, N, R, and M

Haplogroup (region, method) (reference)	Age	95% lower bound	95% upper bound
R (South Asia, ML)	62,300	54,700	70,000
R (South Asia, ρ)	57,000	46,200	68,100
R (East Asia, ML) (34)	54,300	41,200	67,800
R (East Asia, ρ) (34)	55,700	46,300	65,300
N (Arabia/Southwest Asia, ML) (10)	61,100	50,400	72,100
N (Arabia/Southwest Asia, ρ) (10)	65,100	52,750	77,800
M (South Asia, ML)	47,970	39,610	56,530
M (South Asia, ρ)	42,960	38,210	47,770
M (East Asia, ML) (67)	57,300	49,260	65,530
M (East Asia, ρ)	55,900	48,800	63,100
L3 (Africa, ML) (2)	70,200	61,600	78,950
L3 (Africa, ρ) (2)	58,900	51,050	66,900

Table S3. Summary of ages in years of haplogroups L3, N, R, and M, including estimated clock calibration error

Haplogroup (region, method) (reference)	Age	95% lower bound	95% upper bound
R (South Asia, ML)	62,300	49,450	75,550
R (S South Asia, ρ)	57,000	42,650	71,850
R (East Asia, ML) (34)	54,300	38,500	70,800
R (East Asia, ρ) (34)	55,700	42,550	69,300
N (Arabia/Southwest Asia, ML) (10)	61,100	46,350	76,350
N (Arabia/Southwest Asia, ρ) (10)	65,100	48,650	82,150
M (South Asia, ML)	47,970	36,450	59,850
M (South Asia, ρ)	42,960	34,450	51,700
M (East Asia, ML) (67)	57,300	44,850	70,200
M (East Asia, ρ)	55,900	44,200	67,950
L3 (Africa, ML) (2)	70,200	55,600	85,200
L3 (Africa, ρ) (2)	58,900	46,350	71,850

Table S4. Summary of the regional coalescent ages in years of haplogroup M using ρ, ML, and BSP

	ρ			ML			BSP		
Region	Age	CI−	CI+	Age	CI−	CI+	Median age	HPD−	HPD+
East	47,420	41,590	53,350	50,440	29,330	72,830	43,930	38,000	51,390
South	45,700	37,190	54,430	47,340	24,770	71,470	42,780	35,610	51,750
Central	42,860	35,820	50,060	42,680	17,870	69,560	41,780	34,860	50,140
West	38,860	32,000	45,870	39,070	18,520	61,230	37,220	30,450	45,710
Northeast	36,260	29,620	43,050	37,450	12,690	64,480	33,530	28,270	39,450
North	36,110	30,990	41,330	41,270	22,600	61,120	34,390	29,370	39,390

Table S5. Summary of the regional coalescent ages in years of haplogroup M, using ρ, for lineages that evolved in situ in each region

Region	States	Clades	Age, ρ	CI−	CI+
West	Rajasthan, Gujarat, Maharashtra, Madhya Pradesh	M44, M35, M34′57, M56, M6, M4′67	28,150	22,750	33,650
East	Bihar, Orissa, Jharkhand, West Bengal, Uttar Pradesh, Chhattisgarh	M53, M52, M42, M40′62, M39, M33, M31, M61, M5, M2, and two basal samples	51,850	44,300	59,500
South	Andhra Pradesh, Karnataka, Kerala	M36, M3, and one basal sample	40,350	27,700	53,500
Northeast	Assam, Arunachal Pradesh, Meghalaya, Sikkim	M60, M50, M49, M48	31,600	18,950	44,850

These inferences were made using a phylogeographic approach. States included in each region for the purpose of this analysis are indicated, as well as the lineages that were inferred to originate in each region.