Population increase and environmental deterioration correspond with microlithic innovations in South Asia ca. 35,000 years ago

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Genetic studies of South Asia's population history have led to postulations of a significant and early population expansion in the subcontinent, dating to sometime in the Late Pleistocene. We evaluate this argument, based on new mtDNA analyses, and find evidence for significant demographic transition in the subcontinent, dating to 35–28 ka. We then examine the paleoenvironmental and, particularly, archaeological records for this time period and note that this putative demographic event coincides with a period of ecological and technological change in South Asia. We document the development of a new diminutive stone blade (microlithic) technology beginning at 35–30 ka, the first time that the precocity of this transition has been recognized across the subcontinent. We argue that the transition to microlithic technology may relate to changes in subsistence practices, as increasingly large and probably fragmented populations exploited resources in contracting favorable ecological zones just before the onset of full glacial conditions.

archaeology | environment | genetics | lithic technology

Global population data reveal South Asia to be one of the most densely populated regions in the world, with some 1.5 billion people occupying an area of ≈4.4 million square kilometers. Recent genetic findings suggest that this high-density pattern has very ancient roots; it has been estimated that between ≈45 and 20 ka, most of humanity lived in South Asia (1). This evidence is thought to reflect a Late Pleistocene population expansion in the subcontinent that is unparalleled elsewhere. In addition, both archaeological and genetic models postulate South Asia as a key region on the proposed southern route for Out-of-Africa dispersals (2–5). Despite the importance of the region, however, archaeological data from South Asia rarely feature in discussions of human evolution, and little attempt has been made to bring South Asia's archaeological record to bear on discussions of its unique population dynamics. This paper brings together genetic, paleoenvironmental and archaeological data pertaining to Late Pleistocene population dynamics in the Indian subcontinent. We begin by reexamining genetic findings pertaining to Pleistocene population trajectories, drawing upon new analyses of available mtDNA data from South Asia to argue for possible population increase at ca. 35–28 ka in South Asia, due to expansion of indigenous lineages. We then synthesize available paleoenvironmental evidence relating to Late Pleistocene climate and landscape change in the Indian subcontinent to better understand environmental transformations at this time period, creating the first reconstructed vegetation zone map for South Asia at ca. 30 ka. Finally, to test how these genetic and paleoenvironmental patterns fit with on-the-ground evidence for human occupation and activities, we examine in detail new archaeological data pertaining to demography and technological change in the subcontinent beginning at 35–30 ka. In particular, we argue for the development of microlithic technology in the subcontinent at this early time period. The findings suggest a concordance of diverse datasets, which collectively provide support for the notion of a significant Late Pleistocene population expansion in South Asia and its correlation with both overall environmental deterioration and microlithic technological innovation.

Discussion

Population Growth Recorded in mtDNA Haplogroups. Population geneticists broadly agree that modern humans occupied South Asia from at least 50 ka, based on genetic coalescence data and fossil evidence for the colonization of Australia (2, 6, 7). Demographic analysis of relative regional population sizes across the world using mtDNA complete sequence data suggests that after the out-of-Africa dispersal event, the first and most dramatic global population expansion occurred in South and Southeast Asia, where most of the human population was purportedly living between 45 and 20 ka (1). Further indications of the effects of population growth are recorded in the history of the South Asian major founder haplogroup M, which includes two-thirds of extant Indian mtDNA lineages.

Studies of human mtDNA have shown that South Asian populations harbor the highest genetic diversity outside Africa (suggesting long-term high effective population size). The puzzling fact remains, however, that the coalescent time of haplogroup M in India using both functional and nonfunctional coding region sites appears to be ≈30% younger (ca. 45 ka) than the respective age estimate from the global sample (65 ka), which does not make sense given South Asia's central position on Out-of-Africa dispersal routes. One suggested explanation for this unexpected observation is that after initial settlement, the demographic history of the Indian subcontinent was staggered

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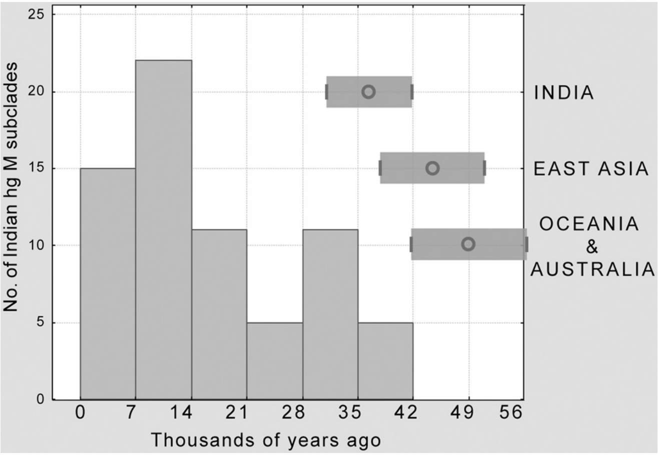

Fig. 1. Distribution of Indian haplogroup (hg) M subclades age estimates (bar graph), with a peak 35–28 ka ago indicating a locally derived demographic event at this time. A second, larger population expansion is seen following the Last Glacial Maximum and continuing into the Holocene. Also shown are the regional hg M coalescence times for India, East Asia, and Oceania, with means (circles) and standard error range. The Indian coalescence date is anomalously young, as a result of the later significant deviations from a random demographic expansion history.

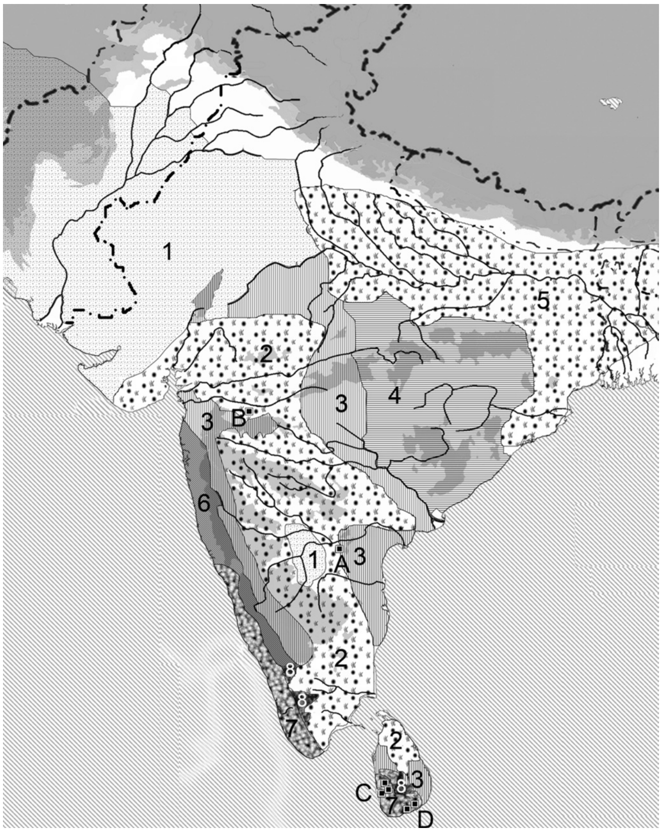

Fig. 2. South Asia, showing reconstructed vegetation zones for ca. 30 ka ago and location of microlithic sites. Sites indicated by letters are as follows: **A,** Jurreru Valley; **B,** Patne; **C,** Sri Lanka caves, from north to south Beli-lena Kitulgala, Batadomba-lena and Fa Hien; and **D,** Sri Lanka coastal sites 49 and 50. Vegetation zones indicated by numbers are as follows: **1,** desert and semidesert (*Caligonum-Salvadora-Prosopis-Acacia* and scattered grasses); **2,** savannah and tropical dry deciduous woodland mosaic (*Acacia-Anogeissus-Terminalia*, *Hardwickia* in some localities, abundant gatherable grasses and legumes); **3,** dry deciduous woodlands, including teak; **4,** dry deciduous woodlands, including *Shorea-Hopea*; **5,** deciduous *Shorea-Hopea* woodland and grassland/marsh mosaic; **6,** moist deciduous and scattered evergreen taxa; **7,** Tropical evergreen and semievergreen forest refugia; **8,** tropical/subtropical mountain forests.

by several indigenous Late Pleistocene expansion events ≈30 ka (8), a scenario earlier proposed on the basis of mtDNA hypervariable region analyses (9). Alternatively, differences in genetic diversity between world populations in mtDNA coding regions could be due to natural selection, a possibility that we decided to test.

In light of the hypothesis for a staggered population increase in South Asia, we conducted an analysis comparing haplogroup M coalescence estimates derived from India and neighboring regions by using synonymous substitutions (to minimize potential problems caused by different efficiencies of purifying selection under different population sizes) (Fig. 1) (see *Methods*). Relative to the rest of the world, the Indian M lineages show a 20% younger age estimate, undermining the role of purifying selection as the sole cause of the discrepancy. We note, however, that background selection, which removes synonymous variation linked to deleterious mutations, would possibly also contribute to and make coalescence estimates based on synonymous variation younger in populations with higher population size. The Indian-specific haplogroup M subclades (Fig. 1) include a significant proportion with coalescent ages ≈35–28 ka ago, well above the level seen in the periods immediately before and after this time frame. This anomaly may be explained as resulting from abnormal population increase at this time, or relative isolation of different groups [which would increase long-term effective population size (10)], or both. The genetic information is therefore consistent with a demographic event involving founders of local origin, possibly with some separation of populations, occurring in India ≈35–28 ka.

Environmental Conditions in South Asia 35–30 KA. What environmental conditions did populations in South Asia face 35–30 thousand years ago? Whereas paleoenvironmental data for South Asia unfortunately remain limited, synthesis of existing regional and global datasets nonetheless provides some insights into this question. Populations at this time lived during the later part of Oxygen Isotope Stage 3 (OIS 3), a period when the global climate had moved toward full glacial conditions. This climatic shift was tied to the downturn from peak Northern Hemisphere summer insolation (Fig. S1), resulting in a strong reduction in summer (southwest) monsoon rainfall across South Asia (11, 12). Drying associated with monsoon decrease is reflected in several regional datasets within and just beyond the northern area of the subcontinent, including high dust-particle spikes and lower δ^{18}O values in the Dunde Ice Cap (Qinghai, China) and Guliya Ice Cap (Tibet) (13). Pollen and plant macrofossils from Lake Zeribar in Iran, which lies at the western margin of the South Asian region, indicate a mosaic of desert and shrubland 35 ka, with limited tree growth restricted to sheltered valleys and stream and lake edges (14). Conditions became worse after 34 ka, when lake margin vegetation disappeared, and indications are that Zeribar water levels dropped and turned brackish. Regional pollen from the Arabian Sea near South India (15) and from southern Arabia (16) indicates desert–steppe shrubs and virtually no woodland. The overall implication is that the region from Iran eastward to the Thar Desert in Pakistan and India would have been dry and relatively inhospitable (Fig. 2).

Superimposed on such a general cooling trend, the latter part of OIS 3 in South Asia is characterized by abrupt oscillations in temperature on a ca. 200-year cycle (13); vegetation zones would have been highly variable during this period. High values of salt-tolerant desertic pollen indicators suggest drier conditions during glacial maxima, and these begin to increase in Arabian

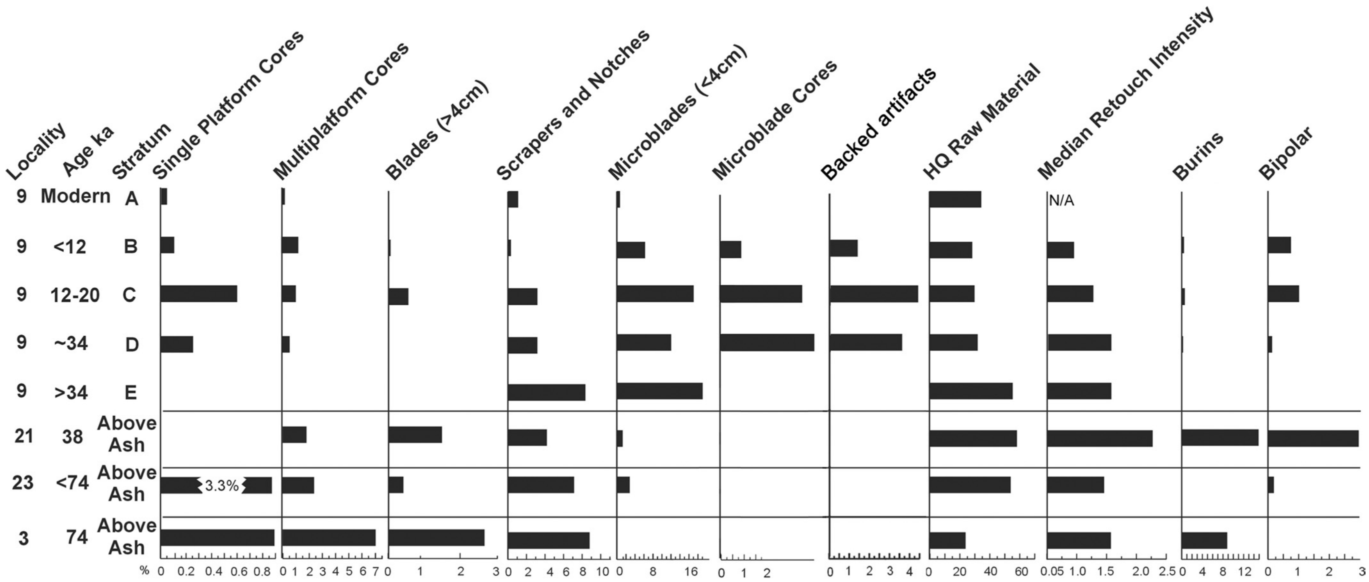

Fig. 3. Lithic technology in the Jurreru Valley. Note the major technological change between 38 and 34 ka from single and multiplatform cores with scrapers, blades, and burins to an assemblage dominated by microblades, microblade cores, and backed artifacts (indicating systematic microlith production). Percentages are proportions in relation to the total artifact assemblage in strata (Locality 9) or in above-ash contexts (Localities 3, 21, and 23).

sea-pollen counts from 35 ka. It is clear, however, that in certain cases wet evergreen tropical forests persisted, probably in refugia in Sri Lanka and the southwestern parts of the Indian peninsula, as indicated by the presence of endemic tropical evergreen taxa disjunct from sister taxa in Assam and mainland Southeast Asia (17), and the continuous presence of the tropical evergreen *Artocarpus* seeds throughout the sequence at Beli-lena Kitulgala cave in Sri Lanka (18). Between 35 and 25 ka, grass pollen levels in India show a marked decline, which probably mainly reflects loss of grassland to desert in much of northwest India.

Overall, for peninsular India, ca. 35 to 25 ka, we have reconstructed a semiglacial-period mosaic environment, consisting of deserts, savannahs, tropical deciduous woodlands, and limited tropical forests (Fig. 2, Fig. S2). Most taxa show levels similar to those found in glacial periods, with notably reduced evergreen forests, and total arboreal pollen much lower than the preceding period at ≈40 ka. Nevertheless, total tree pollen counts indicate the continued, if more limited, presence of trees, presumably from tropical dry (deciduous) taxa, some semidesert shrubs, and a slight rise in evidence for freshwater wetland. There is an absence of mangrove pollen, indicating less attractive coastal environments than those that existed earlier or under Holocene conditions. However, as areas of previous evergreen forest cover contracted and were replaced by a mosaic of dry deciduous woodlands and savannah, it is likely that parts of southern India became more favorable to foragers than they had been previously. Against this ecologically variable backdrop, human populations would have responded in diverse ways, with population decreases in some areas offset by demographic increases, dispersals, and population packing in others. Higher numbers of individuals in what will likely have become gradually smaller favorable ecological zones would have placed increased pressure on local food resources.

The Microlithic Transition in South Asia. Given this genetic and paleoenvironmental context, the question that arises is whether the archaeological record provides any support for population increase and whether occupations were spatially differentiated according to vegetation zones. As a proxy for relative population size, we collected published data on systematically studied Middle Paleolithic and Late Paleolithic (consisting of blade and bladelet technologies) sites across South Asia (19). Our tabulation demonstrates that Late Paleolithic sites ($n = 402$) are more than 2.5 times as numerous as Middle Paleolithic ($n = 153$) sites, even though the Middle Paleolithic ranged over a considerably longer time frame. Examining site counts by Late Pleistocene vegetation zones demonstrated that the Thar Desert and savannah zones show a 2-fold increase in site counts from the Middle Paleolithic to the Late Paleolithic, whereas sites in the deciduous zones show a 5-fold increase in site counts. Although site preservation and visibility conditions may partly account for archaeological site counts, population history also probably contribute to this pattern; thus, we suggest that population increases disproportionately affected deciduous zones, as would be expected under drier climatic conditions. This hypothesis broadly supports the notion of demographic increase and denser occupation in more favorable habitats.

Unfortunately, this analysis provides only an approximate and not unproblematic assessment of change in population size, particularly because information is derived from surface survey, with ages dated through lithic typologies. To more firmly establish the timing and nature of the Middle Paleolithic to Microlithic transition in South Asia, it is necessary to examine well-excavated localities with stratified deposits and chronometric ages. We analyzed data from 3 of the most reliable archaeological locations in South Asia, revealing new findings concerning the origin and development of the microlithic industry in the region. Given the importance of these analyses, we present them here in some detail.

Recent multidisciplinary investigations by our team at Jwalapuram, in the Jurreru River valley in southern India (Fig. 2), have revealed preserved stratified deposits spanning the past 78 ka (20, 21), allowing a rare insight into technological change in southern India over this period. Here we provide a major synthesis of data from all the main localities in the Jurreru Valley, covering multiple field seasons from 2003–2009; included are significant data from several localities. The Jurreru Valley lithic sequence described here is derived from 3 excavated open-air sites (Jwalapuram Localities 3, 21, and 23) and 1 rock-shelter site (Jwalapuram Locality 9) (Fig. 3). The lower levels of the open-air localities contain a distinct chronostratigraphic marker in the form of a volcanic ash (tephra) layer

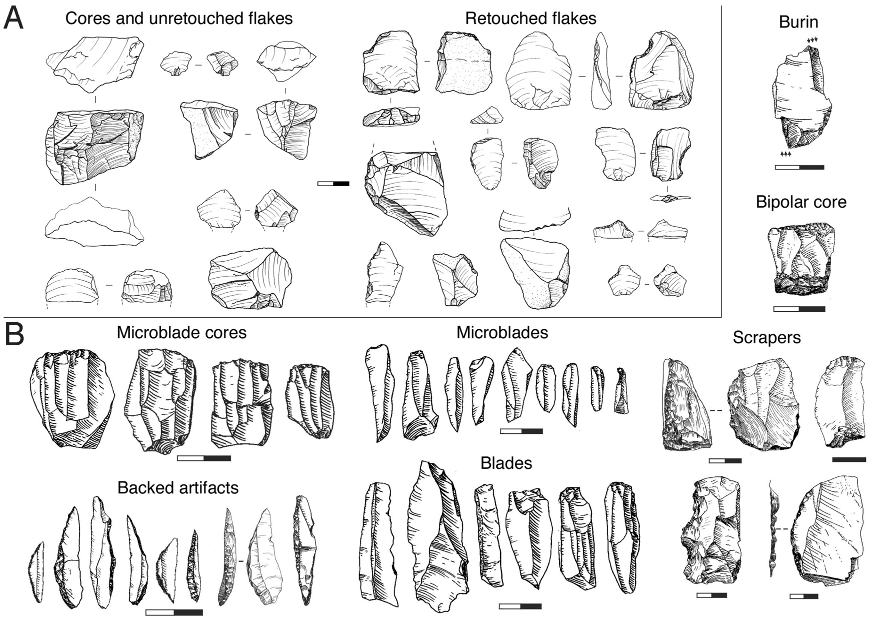

Fig. 4. Stone artifacts from the Jurreru Valley. (*A*) Middle Paleolithic artifacts from Locality 23. (*B*) Microlithic cores and artifacts from Locality 9, with other artifact forms from the site. All scales are in cm.

deposited from the Sumatran Toba supereruption at ca. 74 ka (5). The sequence following the ash-fall returned a series of optically stimulated luminescence (OSL) and radiocarbon ages ranging from immediately post-Toba to the terminal Pleistocene.

Comprehensive technological attribute analysis of the open-air assemblages (OSL dated to ca. 74 ka and 38 ka) demonstrates that intersite variability is minor over the period represented. Multiplatform and radial cores dominated, with roughly equal exploitation of local limestone, chert, and chalcedony. In all sites, flakes are small and squat with some increase through time in the proportion of retouched pieces (Fig. 4*A*). Rare production of both blades (>4 cm length) and microblades (<4 cm) is noted, although microblade cores are absent and production of these forms is considered fortuitous. Maximum peaks in retouch intensity, burination, bipolar reduction and use of high-quality stone are seen ≈38 ka in Locality 21. These assemblages fall chronologically and typologically within the Indian Middle Paleolithic (22).

The first clear qualitative and quantitative shift in Jurreru Valley lithic technology occurs with the introduction of systematic microblade and backed artifact production in the lower levels of the Jwalapuram Locality 9 rock-shelter. This site has the best-dated and analyzed Late Pleistocene sequence in India, and constitutes a significant addition to the South Asian archaeological record. Excavations have revealed stratified deposits to a depth of >3 m (Fig. S3), with 3 1-m^2 units yielding more than 53,000 artifacts from 7 distinct stratigraphic layers.

Flake production throughout the Locality 9 sequence is focused on the creation of small, elongated flakes from uni- and bidirectional blade cores (Fig. 4*B*). Scrapers are most prevalent in the earliest period of occupation, represented in sediments >250 cm in depth and >34 ka in age. Blades >4 cm in length are present at the site but never prominent. Backing of microblades to create asymmetric (i.e., lunate) and symmetric forms (i.e., trapezes and triangles) makes its first appearance at a depth of ≈210 cm (bracketed by ages of ca. 34 and 20 ka; Table S1), and remains at high frequency until just before the time total artifact discard rates peak ≈20 ka. The use of high-quality chalcedony becomes important after this time. The first evidence for systematic microblade production is found some 40 cm below the first backed microblades, demonstrating that the former slightly predates 34 ka, and indicating a staged introduction of microlithic technology at the site.

Some 750 km to the northwest of the Jurreru River Valley, the Patne site in Maharashtra is amongst India's most important Late Pleistocene localities, with dense stone tool assemblages in stratified deposits extending over a 10-m composite profile (23). A calibrated radiocarbon age of 30.4–29.8 ka on an ostrich eggshell was obtained from deposits 4 m deep (Table S1). Our technological analysis conducted on 1,630 lithic artifacts has revealed distinct changes in reduction techniques through time at Patne (Fig. S4). Lithic technology in the earliest phase is characterized by the production of large parallel flakes and flake blades, with scrapers dominating the industry and an absence of backed artifacts. The technology of this early phase is Middle Paleolithic. The overlying levels continue the production of blades alongside short, squat flakes, but also include limited evidence of backing as well as the first appearance of microlithic backed blades. It is, however, in the layers dated to ca. 30 ka that backed microliths become the principal artifact type. Innovations include a wide range of backed artifact shapes (e.g., lunates, trapezes, triangles), indicating increased specialization in microlithic tool forms over time. This industry is accompanied by the production of small blades and flake blades, with the former more likely to be retouched. Backing is predominant among the retouched forms.

A third archaeological area with both well-stratified deposits and chronometric information is found in Sri Lanka. The lowland wet zone of Sri Lanka's Sabaragamuva province has produced some of the region's most significant early microlithic industries, from 3 major Pleistocene cave excavations at Fa Hien, Batadomba-lena, and Beli-lena Kitulgala (Table S1) (18). Fa Hien is the earliest dated Sri Lankan cave site, with radiocarbon ages on charcoal documenting occupation from ca. 38–36 to 28.5 ka, and again in the early to mid-Holocene. The Pleistocene levels are characterized by microblades as well as larger flakes and contain the earliest skeletal evidence for anatomically modern *Homo sapiens* in South Asia (24). Technology at Batadomba-lena consists of geometric backed microliths and rare small blades in all levels, with their initial appearance occurring somewhere between 39 and 30 ka and continuing through to the terminal Pleistocene. *H. sapiens* remains are associated with the early age range. Beli-lena Kitulgala records a sequence dating from 32–27 ka to the Holocene through dozens of radiocarbon and thermoluminescence (TL) ages (25), with geometric backed microliths from the lowest levels.

Although the cave sites do not preserve extensive premicrolithic deposits, these sequences are complemented by 2 open-air sites on Sri Lanka's southern coast. Both Sites 49 (Bundala) and 50 (Patirajavela) display distinct lower and upper artifact horizons separated by a discard hiatus (18). Equivalent sedimentary context and cultural content of the 2 layers at each site permits joint discussion of these localities. The lower horizon of both sites contains a Middle Paleolithic industry with discoidal cores, medium-sized and large spheroidal prepared cores, a relatively high proportion of tools >4.5 cm, and an absence of nonlithic artifacts. By contrast, the upper horizon at both sites is associated with the introduction of numerous geometric microliths, backed bladelets, bladelet cores, and Balongoda points in a dense deposit, and a dramatic reduction in the proportion of larger artifacts. At both sites, the upper horizon is TL-dated to ca. 28.5–28.3 ka, whereas at Site 50 the lower horizon is capped by TL ages of ca. 70–64.4 ka (Table S1). There is therefore a clear convergence of available Sri Lankan ages for the proliferation of microlithic technology between ca. 35 and 28 ka.

New radiocarbon ages from Jwalapuram, in combination with those from other well-stratified and dated localities demonstrate for the first time that the origin of the microlithic industry across South Asia begins in the Late Pleistocene, with an onset at ca. 35 ka. Across geographically separated sites, a long-standing Middle Paleolithic tradition gave way at this time to a significantly altered approach reliant on standardized small blade tools. These findings are backed up by those from other sites across the subcontinent, where early microliths have also been reported but less systematically documented. In all, 122 calibrated radiocarbon ages have been obtained for microlithic industries across South Asia (Fig. S5), and they indicate continuity of microlithic industries from ca. 35 ka into the Holocene. Although the initial appearance of the microlithic industry in South Asia has traditionally been viewed as a Holocene phenomenon (26), these findings as a whole clearly demonstrate a much earlier onset. The radiocarbon counts steadily increase from the Late Pleistocene to the Holocene, potentially reflecting, at least in part, increasing population size.

Conclusion

This paper presents a unique synthesis of both published and unpublished datasets from an evolutionarily critical region of the world. Our analysis of the mtDNA data from the region indicates the emergence of a number of new haplogroup M subclades at 35–28 ka, although whether this is indicative of significant population size increase or the relative isolation of groups is unclear. Our sense, based on the paleoenvironmental and archaeological data, is that both processes would have been relevant. Our paleoenvironmental synthesis suggests an increasingly fragmented environment that may well have separated populations, and the overall archaeological site counts are broadly (although not without caveats) indicative of a general increase in population size.

What is most clear from our analysis is that the time period in question coincides with the appearance of a new subsistence technology based on the use of diminutive stone blades. Recognition of this pattern represents an important contribution to our understanding of regional variation in the appearance of microlithic industries and has important evolutionary implications. It indicates that South Asia has an old and long-enduring microlithic tradition, complementary to other regional records, such as that found in Africa. Furthermore, it suggests that processes of Late Pleistocene resource diversification and intensification seen elsewhere, including Africa, the Levant and Europe (27, 28) may also have taken place in South Asia. Mass-produced, interchangeable microliths represent a technologically advantageous strategy, being light, portable and straightforward to replace, thus ensuring ease of tool-edge maintenance and enhancing the reliability of the tool over time (29, 30). Microliths, as components of barbed projectiles, may have been economically advantageous in that associated weaponry could have increased success in capturing mobile prey through improved hunting technologies. Microlithic tools served a number of functions (31), but it is often argued that they were components of serial armatures which increased the maintainability and reliability of tools during time-stressed hunting trips (29) and increased penetration and blood loss through multiple cutting edges and internal fragmentation of the adhering barbs (32–34). It seems likely that the use of microliths in South Asia is associated with changes in subsistence practices, and the various archaeological, genetic, and paleoenvironmental findings presented here, although not conclusive, suggest that this use may have been necessitated in this region by a combination of landscape fragmentation, overall environmental deterioration, and increased population packing.

Population expansion and population pressure remain, as always, difficult processes to demonstrate for prehistoric time periods (35–38). Whereas genetics offers a new tool through which to approach the topic, neither the genetic nor archaeological records for South Asia are currently sufficient to rule on the question of Late Pleistocene population dynamics with absolute certainty. Nonetheless, the findings presented here and their concordance around a date of 35–30 ka for the emergence of a number of new processes and technologies, do suggest a critical avenue for future research. In particular, they highlight the need to further explore the issue of Pleistocene demographic history. Such early demographic shifts may help explain not only Late Pleistocene archaeological findings in a number of regions, but also more specifically help to understand the factors that led to remarkably dense human inhabitation of the South Asian landscape.

Methods

Attribute analysis of flakes, retouched flakes and cores from the Jurreru Valley open-air sites and rock-shelter followed methods outlined in detail in ref. 39. More than 40 attributes were recorded for all complete artifacts from Locality 9 and on all recovered artifacts from Localities 3, 21, and 23. The same methods were applied to the Patne sample. A note on terminology: Both ''microblade'' and ''microlith'' are relative terms relating to the size of artifacts, and definitions vary widely in the literature according to region and individual researcher. We developed a definition relevant to the Indian microlithic record based on quantitative analysis of our data rather than applying an arbitrary definition from outside South Asia. Microblades are defined in this study as thin elongate flakes (length:width >2:1; width > thickness) with less than 20% dorsal cortex, exhibiting 1 or more dorsal ridges running roughly parallel to the percussion axis and a percussion axis length of <40 mm. For elongate flake lengths at the microlithic Locality 9 site, this size cutoff represents a natural falloff in the frequency distribution and coincides with the upper bound at 2 standard deviations above the mean (Fig. S6). See *SI Methods* for further technological details and definitions.

The analyses of mtDNA haplogroup age distributions were based on the published complete mtDNA coding region sequences from South Asia, East Asia, and Oceania (8, 40, 41). Coalescent time estimates with standard errors for clades defined by at least 2 sequences were obtained by rho statistic (42) by using a molecular clock calibrated for synonymous substitutions (43).

Radiocarbon ages were calibrated by using the OxCal calibration program, version 4.0.5 (44). Ages <20,500 radiocarbon years have been calibrated with the IntCal 04 dataset. For measured ages >20,500 radiocarbon years, we have compared the data with the dataset in ref. 45 by using OxCal software; however, this comparison is currently an estimate, as there is no agreed calibration curve for this period, and comparison to different records would give different results. TL and OSL ages are determined directly in calendar years and do not require calibration. See Table S1 for further details.

ANTHROPOLOGY

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