Supplementary Materials for

Ancient genomes document multiple waves of migration in Southeast Asian prehistory

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Other Supplementary Materials for this manuscript include the following:
(available at www.sciencemag.org/cgi/content/full/science.aat3188/DC1)

Tables S1 and S2 (Excel)
Materials and Methods

Description of archaeological sites

*Man Bac (Vietnam Neolithic)*

Man Bac is on the southern edge of the Red River Delta, 25 km from the current coast, in Yen Mo District, Ninh Binh Province, northern Vietnam. The site is well sheltered by surrounding steep karstic outcrops. Man Bac was comprehensively excavated in 1999, 2001, 2004–5 and 2007, revealing a wealth of material cultural and zooarchaeological remains in addition to 100 human burials [7]. While the pottery styles, including manufacture techniques and decoration, have a strong local influence, it is clearly associated with the broadly distributed Phung Nguyen culture in northern Vietnam. While the Phung Nguyen is often identified with the earliest introduction of bronze into northern Vietnam, there is no evidence for a knowledge of bronze at Man Bac, and indeed the dating of the introduction of Bronze into northern Vietnam is simply not known [27].

The site, while contextually complex, essentially consists of three major stratigraphic units, the upper two being associated with structures (as evidenced by extensive evidence for post holes) and everyday living (hearth, food remains, and general debitage). The lower layer, extending to approximately 2m in depth in parts, is for the most part free of general midden material and otherwise sterile except for the burials. In general, Man Bac displays evidence for elevated levels of fertility, cranio-dental morphological and mtDNA diversity, rice cultivation and domestic pig rearing as well as a broad and diverse continued reliance on hunting as part of the subsistence mix. Mortuary studies of Man Bac have indicated a loose age-based hierarchy and complex system of social identities, including a range of age-based transitions in childhood [28]. Further, Man Bac provided the backdrop to the development of the new sub-discipline “the bioarchaeology of care” with the adult quadriplegic case of Man Bac 09 [29, 30].

Samples used in this study:

- VN29 (05.MB.M16): Female, estimated 3900-3600 yBP
- VN31 (05.MB.M2): Male*, estimated 3900-3600 yBP
- VN34 (07.MB.H1.M6): Female*, 4080-3845 cal yBP (3630±35 BP, Poz-81116, date suspect due to C:N ratio of 3.68 – but reasonable based on archaeological context, and only slightly elevated C:N ratio)
- VN37 (07.MB.H1.M09): Male, 3825-3637 cal yBP (3445±20 BP, PSUAMS-2409)

*Sex assignment uncertain from skeletal material and reported based on genetic data
Nui Nap (Vietnam Bronze Age)

First surveyed in 1962 and subsequently excavated in 1976–77, Nui Nap is located at the base of a limestone mountain in Dong Hieu District, Thanh Hoa province, only 10km distant from the eponymous Dong Son site. Over 30 extended supine burials were recovered, including a broad range of mortuary offerings, including: bronze spear and arrow heads, daggers, axes, harpoons, vessels, earrings, drums, beads (including glass), pottery and even the occasional Han coin [24]. Nui Nap provides the first verified evidence of the use of betel nut (*Areca catechu*) in northern Vietnam [31] and along with other Bronze and Iron Age sites in the region, contributes to our understanding of the rise of infectious disease with the emergence of agricultural dependence [32].

Nui Nap is situated in a region conquered by the Han in the late first millennium BC, becoming the southern-most Han administrative region for much of the first millennium AD. Indeed, there are clear records for massive Han migration into northern Vietnam from the first century AD [24].

Samples used in this study:

- VN41 (78.NN.M4.KB): Female, estimated 2100-1900 yBP

Ban Chiang (Thailand Neolithic through Iron Age)

Ban Chiang, an UNESCO world heritage archaeological site that spans the pre-metal (Neolithic) to Bronze/Iron Ages, is located in the village of Ban Chiang, Nong Han District, Udon Thani Province, northeastern Thailand [16]. Radiocarbon dating, based primarily on artifacts from this site, suggests dates of ca. 2100 BCE to 200 CE [33]. Dating of the human and associated animal bones from the site suggests the initial settlement of Ban Chiang occurred ca. 1600–1450 BCE, with the transition to the Bronze Age occurring ca. 1100 BCE [34]. The archaeological sequence at Ban Chiang is known for its distinctive decorative pottery, ornaments, elaborate burial offerings, and early evidence of metallurgy and agriculture, including bronze artifacts and domesticated rice. A total of 142 burials from two separate sites in the village of Ban Chiang, about 100 meters apart, which were excavated under the direction of Chester Gorman (University of Pennsylvania) and Pisit Charoenwongsa (Thai Fine Arts Department-FAD) in 1974 and 1975, are described in ref. [16].

Samples used in this study:

- BCES B67: Female*, estimated 3500-3200 yBP (Early Period II-IV, Late Neolithic/Early Bronze Age)
- BCES B38: Female*, estimated 3200-3000 yBP (Early Period IV, Bronze Age)
• BCES B54: Male, estimated 3200-3000 yBP (Early Period IV, Bronze Age)
• BCES B27: Female, estimated 3000-2800 yBP (Early Period V, Bronze Age)
• BCES B16: Male*, estimated 2600-2400 yBP (Middle Period VII, Early Iron Age)
  *Sex assignment uncertain from skeletal material and reported based on genetic data

Oakaie (Myanmar Late Neolithic/Early Bronze Age)

Partial excavation of the Oakaie 1 (OAI1) cemetery in 2014–15 revealed forty single and six double burials of adults and juveniles, male and female, cut into a sterile volcanic tuff at varying depths and orientations. Funerary offerings included bivalve shells, pottery, stone beads and bracelets, bone bracelets, spindle whorls, a cowrie shell and a dog. Metal was found in only one grave, S15, in the form of a single bronze axe. A complex stratigraphy with significant ancient and recent disturbance currently precludes the definitive attribution of the burials without metal, including S28 and S29, to either the Neolithic or Bronze Age periods. In the absence of preserved collagen, radiocarbon dating was attempted using bone and tooth apatite and shells but most of the determinations are problematic, typically appearing too young. More reliable dating is provided by the extrapolation of charcoal dates and ceramic techno-typologies from closely neighbouring sites.

Indeed, OAI1 is but is one activity area of an extensive late Neolithic to early Bronze Age site located on the eastern bank of the Chindwin, approximately 100 km north of the confluence with the Irrawaddy. Nyaung’gan, the first late prehistoric site investigated by Myanmar archaeologists [35], lies 2.6 km to the NNE and a vast settlement and industrial zone extends over at least 1000 m to the south, west and north, with excavated locations OAI2–4. A series of 52 14C dates indicate occupation from the 12th to 8th centuries BC, with the Bronze Age transition probably falling in the 10th century. A major lithics industry is evident in the production of axe/adzes, beads, bracelets and other ornaments, partly derived from proximity to sources of volcanic rock but also using imported agate, carnelian, nephrite and other minerals. Archaeometallurgical analyses indicate on-site secondary production activity (founding) but that the copper used is consistent with imports from central Laos and central Thailand, and not with the nearby deposits at Monywa [36]. These combined data suggest that the population buried at OAI1 had some degree of interaction with groups over in excess of 1000 km of MSEA territory.

Samples used in this study:

• OAI1/S28: Female, estimated 3200-2700 yBP
• OAI1/S29: Female, estimated 3200-2700 yBP

Vat Komnou (Cambodia Iron Age)

The Vat Komnou cemetery, ca. 200 BCE – 200 CE, at the Angkor Borei site in southern Cambodia is located on the western edge of the Mekong Delta [17, 37]. The dates for this site fall within the Protohistoric Period or Iron Age (ca. 500 BCE – 500 CE). In addition to brick
architectural monuments, associated moats, and ponds, the Vat Komnou mortuary assemblage includes human burials, beads, ceramics, multiple pig skulls, and other faunal remains [37, 38]. A total of 111 individuals were sorted and analyzed from 57 burial features excavated at the Vat Komnou cemetery by the Lower Mekong Archaeological Project (LOMAP) in 1999 and 2000. Participating LOMAP Institutions are: University of Hawai‘i-Mānoa (USA), Ministry of Culture and Fine Arts (Kingdom of Cambodia), Royal University of Fine Arts (Kingdom of Cambodia), University of Glasgow (Scotland, UK), and Scottish Universities Environmental Research Centre (Scotland, UK). There was extensive commingling of the burials at the Vat Komnou cemetery due, in part, to its apparent re-use through time [38]. The Vat Komnou cemetery is one of the largest archaeological skeletal samples analyzed to date from Cambodia.

Sample used in this study:

- **AB40**: Male, 1890-1731 cal yBP (1885±30 BP, Poz-81120, date suspect due to C:N ratio of 3.75 – but reasonable based on archaeological context, and only slightly elevated C:N ratio)

Experimental design

DNA was extracted from archaeological samples as described below. Resulting genotype data were analyzed using population genetic tools to infer historical processes.

Ancient sample preparation and data processing

We screened a total of 146 ancient petrous bone samples for the presence of human DNA, following an established procedure [39–41]. We obtained bone powder in a dedicated clean room facility at University College Dublin and extracted DNA via published protocols [42, 43] in clean rooms at Harvard Medical School. A subset of the extracts were executed using silica magnetic beads instead of the standard silica spin columns (Table S1). From the extracts, we prepared double-stranded individually bar-coded libraries, some of which (including all libraries used for final analyses) we treated with uracil-DNA glycosylase (partial UDG treatment) to reduce the rate of characteristic cytosine-to-thymine errors in ancient DNA [44, 45]. For the majority of libraries, we used magnetic bead cleanup between enzymatic reactions and SPRI bead cleanup for the final PCR [46, 47] instead of MinElute column cleanups (Table S1). We initially used target capture hybridization to enrich the libraries for sequences overlapping the mitochondrial genome [48, 49] and in most cases a set of approximately 3000 nuclear SNP targets, and we then sequenced the enriched libraries on an Illumina NextSeq 500 instrument with 76-base-pair paired-end reads. From the output, we merged sequences that were within 1-base-pair edit distance of expected bar-codes and with at least 15 overlapping bases, trimmed bar-codes and adapters, and mapped the merged reads to the mitochondrial reference genome RSRS [50] or to the human reference genome (version hg19) as appropriate. Mapped
reads were then quality-filtered and de-duped, and two terminal bases were clipped to reduce damage (five for UDG-minus libraries), as described previously [39]. For libraries with evidence of nuclear DNA, we then enriched for sequences overlapping approximately 1.2 million genome-wide SNPs [40, 41, 51] (in some cases pooling libraries from the same individual prior to enrichment; Table S1) and sequenced to increased depth, processing the data in the same way. We called one allele at random per site to create pseudo-haploid genotypes and determined genetic sex by examining the factions of reads mapping to the X and Y chromosomes.

Because of the poor molecular preservation of the samples, we prepared multiple libraries for most individuals (102 libraries used in final analyses for 18 samples, out of 164 libraries screened for those samples; Table S1), which we then merged after data processing. All 102 libraries displayed ancient DNA damage (at least 14% C-to-T substitutions in the final base of mitochondrial screening sequencing reads), providing evidence of authenticity [45, 52], with noticeably high damage rates for these samples likely reflecting hot and humid local climates. During screening, we assessed possible contamination by measuring rates of apparent heterozygosity on the mitochondrial genome [51], and we performed follow-up heuristic analyses on the genome-wide data to test for the presence of potentially contaminating present-day human DNA (see below).

Mitochondrial DNA haplogroups were called with HaploGrep2 [53] using phylotree (mtDNA tree Build 17; 18 Feb 2016), with final calls based on comparisons between single-library results and reassembled multi-library merges for each individual (versions with all reads and with only reads showing evidence of damage). Y-chromosome haplogroups were determined from 15,100 targeted SNPs; mutations were compared with the tree provided by the International Society of Genetic Genealogy (http://www.isogg.org) via a modified version of the yHaplo software [54].

Present-day data

We generated new genome-wide SNP genotype data on the Affymetrix Human Origins array for 10 Htin and 10 Mlabri individuals [20, 55, 56]. All individuals gave informed consent for genome-wide analyses of population history and public sharing of anonymized data following publication. The sample collection was approved by an ethical review panel in Thailand, and genotyping of anonymized samples for studies of population history was approved by the Harvard Medical School Human Research Protection Program (Protocol 11661, approval date July 12, 2016). We merged these new data with published Human Origins samples [57-61] and with 1000 Genomes populations [62]. Han, Kinh, and Japanese data were taken from 1000 Genomes, whereas Dai were taken from Human Origins, except in the statistic $f_4$(Nui Nap, X; Y, Z), where we used all 1000 Genomes populations to increase power and retain symmetry of data sources. All analyses were performed using the set of 593,124 autosomal Human Origins SNPs, unless otherwise noted (“all 1240k SNPs” refers to the full set of about 1.15 million targeted autosomal SNPs).
Statistical analysis

Clustering and allele-sharing analyses

We performed PCA by computing principal components for present-day populations (except as noted) and then projecting ancient samples, using the “lsqproject” and “autoshrink” options in smartpca [63, 64]. We computed f-statistics and fit admixture graphs via ADMIXTOOLS [57], with standard errors estimated via block jackknife. For differences between f-statistics (in particular comparing VN29 and other Man Bac individuals), we used the qp4diff program in ADMIXTOOLS with “allsnps” mode, i.e., taking the union of all covered SNPs rather than the intersection. We note that no individuals in the study were identified as close relatives based on allele matching rates; for the coverage level of the Man Bac samples, we can confidently rule out any first-degree kinship but not more distant relationships. Our primary outgroup f3-statistics use Dinka as the outgroup, with a second set using Europeans (CEU) for replication (Table S2).

Analysis of possible contamination

Our initial methods to authenticate our data and estimate levels of possible contamination were based on established protocols implemented in our screening process. First, we observed characteristic ancient DNA damage patterns, with at least 14% C-to-T substitutions in terminal positions of molecules mapping to mtDNA (roughly twice the rate in non-UDG-treated libraries versus partial UDG libraries; min 37%, mean 62%, median 62%, max 74% for 26 non-UDG libraries; mean 31%, median 31%, max 46% for 101 of the 102 partial-UDG libraries used in analyses; Table S1). Such high damage rates (including ∼40% for VN29) make it less likely that the samples have substantial amounts of contamination but do not provide quantitative estimates. We also measured apparent heterozygosity at single-copy markers (mtDNA as well as the X chromosome in males), with mtDNA results shown in Table S1. Of the 102 libraries used in analyses, 42 yielded estimates of the mismatch rate, with a range of 0.1–20.5% (mean 7.0%, median 5.1%). However, we believe that the exact quantitative results are not always reliable for low-coverage libraries. Estimates based on the X chromosome are generally more stable, but we lacked sufficient coverage for the samples in this study to generate confident measurements with this method.

While the damage patterns and mtDNA matching results indicated reasonably good quality data, we wished to extend our quality control by examining potential effects of contaminating DNA on observed population genetic results. In the broad-scale PCA (Fig. S1), all samples are close to present-day East and Southeast Asians, with none displaying particular signs of greater affinity to Europeans (as might be expected if there were contamination). In the PCA focusing on East and Southeast Asia (Fig. 1B), none of the samples appear to be shifted unexpectedly in the direction of present-day populations such as Han or Kinh, and the ancient populations are all relatively homogeneous (especially considering the low coverage). We also
studied versions of the sample data restricted to sequencing reads showing ancient DNA damage patterns, but we found that the coverage was too low (generally at least 10 times thinner than the already low-coverage full data) to draw any informative conclusions. Finally, we computed \( f \)-statistics designed to detect excess affinity to potentially contaminating populations and did not find any such evidence at a level that would significantly affect our results (Table S3). We also note that if the VN29 sample from Man Bac were contaminated with present-day East Asian DNA, this would cause its apparent proportion of deeply splitting ancestry to be too low, preserving our observation of within-site heterogeneity.

Admixture graphs: core model

Native Americans such as Mixe are known to have a mixture of eastern and western Eurasian ancestry [65]. Since we are primarily interested here in results involving eastern Eurasian populations, we did not wish to make our models overly complicated by including western Eurasians. With the populations present in our core model, however, we needed to include an implicit western Eurasian component in Mixe; the proportion of this component was not constrained, so to simplify the fitting, we locked it at 30%. We also obtained similar results when replacing Mixe with Ulchi from the Amur River Basin (\( \sim \)5% western Eurasian ancestry).

Without additional unadmixed reference populations available in our admixture graphs, we did not have power to resolve the exact topology of the two source lineages for Austroasiatic-clade populations. The final model we present is the most parsimonious version, with an initial shared admixture event for Nicobarese, Mlabri, and Man Bac, but we can also fit all three populations with separate admixture events, which yields a very similar fit score but with two additional free parameters in the model. Formally, we cannot prove that the farmer lineages contributing to Nicobarese, Mlabri, and Man Bac represent a single migration out of China, as we did find one less parsimonious model (with statistically indistinguishable fit quality) in which the farmer component for Man Bac can be fit outside the Austroasiatic clade (or even the Austroasiatic-plus-Austronesian clade). However, we do not find evidence of substantial asymmetry between Man Bac and either Nicobarese or Mlabri with respect to other present-day Southeast Asians (Table S3), which supports our other lines of evidence for a shared ancestral admixture event.

Lastly, we fit a model for Man Bac with all 1240k SNPs, using full sequence data for other present-day populations, but with no other Austroasiatic speakers present, and the results (insofar as the models were overlapping) were very similar.

Admixture graphs: western Indonesians

Using our main graph topology, we obtained a significantly better fit for Barito (fit score—i.e., approximate log-likelihood—roughly 9 units better) as a mixture of Austroasiatic-clade and Austronesian (plus additional Papuan-related) ancestry as compared to only Austronesian and deeply-splitting ancestry. This is true even if the deeply-splitting ancestry is from the same source that contributes to Austroasiatic speakers, and also allowing for a
combination of two different deep ancestry components. In a less parsimonious topology for the Austroasiatic clade, with separate deep ancestry sources for Nicobarese, Mlabri, Man Bac, and western Indonesians, a simpler Austronesian-plus-indigenous model does fit successfully for Barito or Semende individually, but it is again worse when modeling Barito and Semende together (roughly 3.5 units worse with two additional free parameters). We also note that in the final version, we modeled the Austroasiatic-related (Nicobarese-related) component in western Indonesians as including the extra deep indigenous ancestry present in Nicobarese, but the alternative model (western Indonesians having ancestry splitting from the Nicobarese lineage prior to the second admixture event) also fits well, so we do not have the resolution to determine the order of those two events.

Admixture graphs: Dai and Lao

We model both Dai and Lao as three-way admixed (Fig. S4; evidence of admixture provided by negative $f_3$-statistics, e.g., $f_3$(Dai; Han, Nicobarese) = −0.0014, $Z = −3.3$; $f_3$(Lao; Dai, Nicobarese) = −0.0035, $Z = −7.8$). For Dai, the majority component is closely related to the farmer ancestry in Austroasiatic speakers, with additional northern East Asian (32%) and deep eastern Eurasian (5%, same Onge-related source as in Austroasiatic speakers) ancestry. For Lao, the first two components are the same (but in different proportions), while the third is from the Austroasiatic clade (close to the split of Mlabri and Nicobarese). Dai can also be modeled with the same three components as Lao, with a statistically indistinguishable fit. Lao, however, fits significantly better in the final model (fit score roughly 10 better) than in versions where they are modeled as either (1) a mixture of one component sister to Dai and one from the Austroasiatic clade, or (2) a three-way mixture using the same components as in Dai (i.e., with the same Onge-related ancestry as Austroasiatic speakers but not the same farmer ancestry). For both groups, the three sources do not indicate proximal mixing populations (given that the Mixe-related ancestry is likely derived ultimately from northern China), but they represent the key relevant components of ancestry relative to the reference populations in the model.

Admixture graphs: Juang

For Juang, the inferred western Eurasian component is itself admixed in reality, but for the purposes of our model, it fits best as closely related to the Ancient Northern Eurasian lineage forming part of the ancestry of Native Americans. The deep eastern Eurasian component splits close to the same point as Onge, East Asians, and the indigenous Austroasiatic component. A mixture of two components of this type is characteristic of Indian populations today [66]; Juang, however, is distinguished from most South Asians by its third, Austroasiatic-related source of ancestry.
Fig. S1.
PCA with diverse non-Africans.
Fig. S2.
Basic admixture graph for Man Bac with present-day Austroasiatic-speaking populations. All $f$-statistics relating the populations are predicted to within 1.3 standard errors of their observed values. Omitting VN29, the two fitted mixture proportions are 28% and 6%, and all $f$-statistics are predicted to within 1.5 standard errors; omitting VN29 and VN40, the figures are 27%, 6%, and 1.7. Dotted lines denote admixture events, with proportions as shown. Branch lengths are given in units of 1000 times $f^2$ drift distance (rounded to the nearest integer).
Fig. S3.
Extended admixture graph including Man Bac, present-day Austroasiatic-speaking populations, Dai, Semende, Barito, Lebbo, and Juang. All $f_2$-statistics relating the populations are predicted to within 1.8 standard errors of their observed values. Dotted lines denote admixture events, with proportions as shown. Branch lengths are given in units of 1000 times $f_2$ drift distance (rounded to the nearest integer).
Fig. S4.
Extended admixture graph including Man Bac, present-day Austroasiatic-speaking populations, Dai, Semende, Barito, and Lao. All $f$-statistics relating the populations are predicted to within 1.9 standard errors of their observed values. Dotted lines denote admixture events, with proportions as shown. Branch lengths are given in units of 1000 times $f_2$ drift distance (rounded to the nearest integer).
Table S1. (separate file)
Detailed library-level information for samples passing through screening process.

Table S2. (separate file)
Outgroup $f_3$-statistics.

Table S3. Additional $f$-statistics.

<table>
<thead>
<tr>
<th>Statistic</th>
<th>Populations X</th>
<th>$Z$-score(s)</th>
<th>Interpretation</th>
</tr>
</thead>
<tbody>
<tr>
<td>$f_4(X, \text{Han}; \text{Denisova}, \text{Chimp})$</td>
<td>Man Bac*, Nui Nap*, Barito, Lebbo</td>
<td>$-1.4, -0.6, 0.7, 4.4$</td>
<td>Significant Denisovan [67] ancestry in Lebbo but not Man Bac, Nui Nap, or Barito</td>
</tr>
<tr>
<td>$f_4(X, \text{Han}; \text{Altai}, \text{Chimp})$</td>
<td>All ancient*</td>
<td>$-2.3 &lt; Z &lt; 0.3$</td>
<td>No evidence of excess Neanderthal [68] ancestry in ancient samples</td>
</tr>
<tr>
<td>$f_4(X, \text{Nui Nap}; \text{Dinka}, \text{Man Bac})$</td>
<td>All present-day from Fig. 1B</td>
<td>All $&gt; 4.5$</td>
<td>Likely artificial apparent allele-sharing between ancient populations</td>
</tr>
<tr>
<td>$f_4(X, \text{Kin}h; \text{European, African})^\dagger$</td>
<td>All ancient ind.*</td>
<td>$-2.5 &lt; Z &lt; 1.3$</td>
<td>No evidence of significant European contamination</td>
</tr>
<tr>
<td>$f_4(X_1, X_2; \text{Japanese, Han})$; $f_4(X_1, X_2; \text{Japanese, Kin}h)$; $f_4(X_1, X_2; \text{Kinh, Han})^#$</td>
<td>All pairs of ancient individuals* from the same site (120 total statistics)</td>
<td>All but two $</td>
<td>Z</td>
</tr>
<tr>
<td>$f_4(\text{VN29}, \text{Man Bac}; \text{Australasian, Han})^*$</td>
<td></td>
<td>$3.0$</td>
<td>Replication of excess deep ancestry in VN29 (Bonferroni-corrected $p&lt;0.02$) using full sequence data for Papuan and Andamanese [69, 70]</td>
</tr>
<tr>
<td>$f_4(\text{X}1, \text{X}2; \text{X}3, \text{Nui Nap})$</td>
<td>Any combination of 1000 Genomes Dai, Kinh, Han, or Japanese</td>
<td>All $</td>
<td>Z</td>
</tr>
<tr>
<td>$f_4(\text{Lebbo, Kinh}; \text{Papuan, Onge})$</td>
<td></td>
<td>$27.0$</td>
<td>Extra deep ancestry in Lebbo is Papuan-related</td>
</tr>
</tbody>
</table>

*All 1240k SNPs. †1000 Genomes CEU and YRI. #$Computed indirectly as $f_4(X_1, Y; Z, W) - f_4(X_2, Y; Z, W)$ [19].
References and Notes


19. Materials and methods are available as supplementary materials.


