

Cite as: M. Lipson *et al.*, *Science*
10.1126/science.aat3188 (2018).

Ancient genomes document multiple waves of migration in Southeast Asian prehistory

Mark Lipson,^{1*} Olivia Cheronet,^{2,3,4} Swapan Mallick,^{1,5} Nadin Rohland,¹ Marc Oxenham,⁶ Michael Pietrusewsky,⁷ Thomas Oliver Pryce,^{8,9,10} Anna Willis,¹¹ Hirofumi Matsumura,¹² Hallie Buckley,¹³ Kate Domett,¹⁴ Nguyen Giang Hai,¹⁵ Trinh Hoang Hiep,¹⁵ Aung Aung Kyaw,¹⁶ Tin Tin Win,¹⁶ Baptiste Pradier,⁹ Nasreen Broomandkhoshbacht,^{1,17} Francesca Candilio,^{18,19} Piya Changmai,²⁰ Daniel Fernandes,^{2,3,21} Matthew Ferry,^{1,17} Beatriz Gamarra,^{3,4} Eadaoin Harney,^{1,17} Jatupol Kampaunsai,^{22,23} Wibhu Kutanan,²⁴ Megan Michel,^{1,17} Mario Novak,^{3,25} Jonas Oppenheimer,^{1,17} Kendra Sirak,^{3,26} Kristin Stewardson,^{1,17} Zhao Zhang,¹ Pavel Flegontov,^{20,27†} Ron Pinhasi,^{2,3*‡} David Reich^{1,4,17*‡}

¹Department of Genetics, Harvard Medical School, Boston, MA 02115, USA. ²Department of Anthropology, University of Vienna, 1090 Vienna, Austria. ³Earth Institute, University College Dublin, Dublin 4, Ireland. ⁴School of Archaeology, University College Dublin, Dublin 4, Ireland. ⁵Medical and Population Genetics Program, Broad Institute of MIT and Harvard, Cambridge, MA 02142, USA. ⁶School of Archaeology and Anthropology, Australian National University, Canberra, ACT 0200, Australia. ⁷Department of Anthropology, University of Hawai'i at Mānoa, Honolulu, Hawai'i 96822, USA. ⁸Centre National de la Recherche Scientifique, 75016 Paris, France. ⁹UMR 7055 Préhistoire et Technologie, Université Paris Nanterre, 92023 Nanterre, France. ¹⁰CEA/CNRS UMR 3685 NIMBE, 91191 Gif-sur-Yvette, France. ¹¹College of Arts, Society and Education, James Cook University, Townsville, Queensland 4811, Australia. ¹²School of Health Science, Sapporo Medical University, Sapporo 060-8556, Japan. ¹³Department of Anatomy, University of Otago, Dunedin 9054, New Zealand. ¹⁴Division of Tropical Health and Medicine, College of Medicine and Dentistry, James Cook University, Townsville, Queensland 4811, Australia. ¹⁵Department of Prehistoric Archaeology, Vietnam Institute of Archaeology, Hanoi, Vietnam. ¹⁶Department of Archaeology, Ministry of Religious Affairs and Culture, Mandalay, Myanmar. ¹⁷Howard Hughes Medical Institute, Harvard Medical School, Boston, MA 02115, USA. ¹⁸Soprintendenza Archeologia Belle Arti e Paesaggio per la Città Metropolitana di Cagliari e per le Province di Oristano e Sud Sardegna, 09124 Cagliari, Italy. ¹⁹Physical Anthropology Section, University of Pennsylvania Museum of Archaeology and Anthropology, Philadelphia, PA 19104, USA. ²⁰Department of Biology and Ecology, Faculty of Science, University of Ostrava, 70103 Ostrava, Czech Republic. ²¹CIAS, Department of Life Sciences, University of Coimbra, Coimbra 3000-456, Portugal. ²²Department of Biology, Faculty of Science, Chiang Mai University, Chiang Mai 50200, Thailand. ²³Center of Excellence in Bioresources for Agriculture, Industry and Medicine, Chiang Mai University, Chiang Mai 50200, Thailand. ²⁴Department of Biology, Faculty of Science, Khon Kaen University, Khon Kaen, 40002, Thailand. ²⁵Institute for Anthropological Research, 10000 Zagreb, Croatia. ²⁶Department of Anthropology, Emory University, Atlanta, GA 30322, USA. ²⁷Institute of Parasitology, Biology Centre, Czech Academy of Sciences, 37005 České Budějovice, Czech Republic.

*Corresponding author. Email: mlipson@genetics.med.harvard.edu (M.L.); ron.pinhasi@univie.ac.at (R.P.); reich@genetics.med.harvard.edu (D.R.)

†P.F. holds part-time positions as a research assistant at the Faculty of Science, University of South Bohemia, Ceske Budejovice, Czech Republic and at the Institute for Information Transmission Problems, Russian Academy of Sciences, Moscow, Russia.

‡These authors contributed equally to this work.

Southeast Asia is home to rich human genetic and linguistic diversity, but the details of past population movements in the region are not well known. Here, we report genome-wide ancient DNA data from eighteen Southeast Asian individuals spanning from the Neolithic period through the Iron Age (4100–1700 years ago). Early farmers from Man Bac in Vietnam exhibit a mixture of East Asian (southern Chinese agriculturalist) and deeply diverged eastern Eurasian (hunter-gatherer) ancestry characteristic of Austroasiatic speakers, with similar ancestry as far south as Indonesia providing evidence for an expansive initial spread of Austroasiatic languages. By the Bronze Age, in a parallel pattern to Europe, sites in Vietnam and Myanmar show close connections to present-day majority groups, reflecting substantial additional influxes of migrants.

The archaeological record of Southeast Asia documents a complex history of human occupation, with the first archaic hominins arriving at least 1.6 million years ago (yBP) and anatomically modern humans becoming widely established by 50,000 yBP (1–3). Particularly profound changes in human culture were propelled by the spread of agriculture. Rice farming began in the region approximately 4500–4000 yBP and was accompanied by a relatively uniform and widespread suite of tools and pottery styles showing connections to southern China (4–7). It has been hypothesized that this cultural transition was effected by a

migration of people who were not closely related to the indigenous hunter-gatherers of Southeast Asia (5, 7–10) and who may have spoken Austroasiatic languages, which today have a wide, but fragmented, distribution in the region (4, 5, 11–14). In this scenario, the languages spoken by the majority of present-day people in Southeast Asia (e.g., Thai, Lao, Myanmar, Malay) reflect later population movements. However, no genetic study has resolved the extent to which the spread of agriculture into the region and subsequent cultural and technological shifts were achieved by movement of people or ideas.

Here we analyze samples from five ancient sites (Table 1; Fig. 1A): Man Bac (Vietnam, Neolithic; 4100–3600 yBP), Nui Nap (Vietnam, Bronze Age; 2100–1900 yBP), Oakaie 1 (Myanmar, Late Neolithic/Bronze Age; 3200–2700 yBP (15)), Ban Chiang (Thailand, Late Neolithic through Iron Age; 3500–2400 yBP (16)), and Vat Komnou (Cambodia, Iron Age; 1900–1700 yBP (17)). We initially screened a total of 350 next-generation sequencing libraries generated from petrous bone samples (specifically the high-yield cochlear region (18)) from 146 distinct individuals. For libraries with evidence of authentic ancient DNA, we generated genome-wide data using in-solution enrichment, yielding sequences from eighteen individuals (Table 1, table S1) (19). Because of poor preservation conditions in tropical environments, we observed both a low rate of conversion of screened samples to working data and also limited depth of coverage per sample, and thus we created multiple libraries per individual (102 in total in our final data set).

We initially analyzed the data by performing principal component analysis (PCA) using two different sets of present-day populations (19). First, compared to a set of diverse non-Africans (East and Southeast Asian, Australasian, Central American, and European), the ancient individuals fall close to present-day Chinese and Vietnamese when projected onto the first two axes, with Man Bac, Ban Chiang, and Vat Komnou shifted slightly in the direction of Onge (Andaman Islanders) and Papuan (fig. S1). To focus on East and Southeast Asian diversity, we then used a panel of 16 present-day populations from the region, with three primary directions in the first two dimensions represented by Han Chinese, Austroasiatic-speaking groups (Mlabri and Htin from Thailand, Nicobarese, and Cambodian, but not Kinh), and aboriginal (Austroasiatic-speaking) Taiwanese (right, left, and top, respectively; Fig. 1B; compare (20)). Man Bac, Ban Chiang (all periods), and Vat Komnou cluster with Austroasiatic speakers, while Nui Nap projects close to present-day Vietnamese and Dai near the center, and Oakaie projects close to present-day Myanmar and other Sino-Tibetan speakers. Present-day Lao are intermediate between Austroasiatic speakers and Dai, and western Indonesians (Semende from southern Sumatra and Barito from southeastern Borneo) fall intermediate between Austroasiatic speakers and aboriginal Taiwanese.

We measured levels of allele sharing between populations via outgroup f_3 -statistics and obtained results consistent with those from PCA (table S2). Nominally, the top sharing for each ancient population is provided by another ancient population, but this pattern may be an artifact due to correlated genotype biases between different ancient samples (table S3). Restricting to present-day comparisons, Man Bac, Ban Chiang, and Vat Komnou share the most alleles with Austroasiatic-speaking groups (as Austroasiatic-

speaking groups do with each other); Nui Nap with Austroasiatic speakers, Dai, and Kinh; and Oakaie with Sino-Tibetan-speaking groups. We also computed statistics $f_4(X, \text{Kinh}; \text{Australasian}, \text{Han})$, where “Australasian” is a union of Papuan and Onge, to search for signals of admixture from outside the East Asian clade in test populations X (increasingly positive values for increasing proportions of deeply-splitting ancestry). Present-day Myanmar, Lao, western Indonesians, and Austroasiatic speakers all yield significantly positive values, as do the majority of the ancient samples, with approximately equal results for Mlabri, Nicobarese, and Man Bac (Fig. 2). The Man Bac individuals are additionally mostly similar to each other, except for one, VN29, which is significantly higher than the population mean (Bonferroni-corrected Z -test, $p < 0.02$ (19)). Vat Komnou and Ban Chiang also yield high positive values, while Oakaie is modestly positive, and Nui Nap is close to zero ($Z = 1.1$).

Next, we built admixture graph models to test the relationships between the Vietnam Neolithic samples and present-day Southeast Asians in a phylogenetic framework. We began with a scaffold model containing the Upper Paleolithic Siberian Ust’-Ishim individual (21) as an outgroup and present-day Mixe, Onge, and Atayal, to which we added Man Bac, Nicobarese, and Mlabri. The latter three were inferred to have ancestry from a Southeast Asian farmer-related source (~70%, forming a clade with Atayal) and a deeply diverging eastern Eurasian source (~30%, sharing a small amount of drift with Onge; f -statistics indicate that this source is also not closely related to Papuans, South Asians, or the 40,000 yBP Tianyuan individual (22); table S3). The allele sharing demonstrated by outgroup f_3 -statistics can be accommodated along the farmer lineage, the deeply-splitting lineage, or a combination of the two, but given the closeness of the mixture proportions among the three groups, we found that the most parsimonious model (Fig. 3, fig. S2) involved a shared ancestral admixture event (29% deep ancestry; 28% omitting VN29), followed by divergence of Man Bac from the present-day Austroasiatic speakers, and lastly a second pulse of deep ancestry (5%) into Nicobarese (19).

Finally, to assess the relationships among additional present-day populations, we fit two extended admixture graphs (figs. S3, S4), with the first including Dai, Semende, Barito, Lebbo (from east-central Borneo), and Juang (an Austroasiatic-speaking group from India), and the second including Dai, Semende, Barito, and Lao. The western Indonesians could be fit well with three (but not two) sources of ancestry: Austroasiatic-related, Austroasiatic-related, and Papuan-related (table S3), in respective proportions of ~67%, 29%, and 4% (Semende); ~37%, 60%, and 2% (Barito); and ~55%, 23%, and 22% (Lebbo) (19). The Austroasiatic-associated component was inferred to be closer to

Nicobarese than to Mlabri or Man Bac, forming a “southern” Austroasiatic sub-clade (Fig. 3B). For Juang, we also obtained a good fit with three ancestry components: one western Eurasian, one deep eastern Eurasian (interpreted as an indigenous South Asian lineage), and one from the Austroasiatic clade (fig. S3). The Austroasiatic source for Juang (proportion 35%) was inferred to be closest to Mlabri, as supported by statistics $f_4(\text{Juang, Palliyar; Mlabri, X}) > 0$ for $X = \text{Atayal, Man Bac, or Nicobarese}$ ($Z = 5.1, 2.8, 2.3$), creating a “northern” Austroasiatic sub-clade. Separately, we found that Lao also possesses ancestry from the Austroasiatic clade (47%; fig. S4) but cannot be fit as a simple mixture of the same two components found in Nicobarese and Mlabri (residual statistic $Z = 3.4$ without a source to explain distantly shared ancestry between Lao and Mixe) (19).

Our results provide genetic support for the hypothesis that agriculture was first practiced in Mainland Southeast Asia by (proto-) Austroasiatic-speaking migrants from southern China (4–6, 11–13). We find that all eight of our sampled individuals from Man Bac (as well as individuals from Ban Chiang and Vat Komnou) are closely related to present-day Austroasiatic speakers, including a shared pattern of admixture, with one, VN29, exhibiting significantly elevated indigenous ancestry. By comparison, studies of cranial and dental morphology have placed Man Bac either close to present-day East and Southeast Asians (“Neolithic”), intermediate between East Asians and a cluster containing more ancient hunter-gatherers from the region plus present-day Onge and Papuan (“indigenous”), or split between the two clusters (7, 8, 23). The simplest explanation for our results is that the majority of our Man Bac samples represent a homogeneous Neolithic cluster, with recent local contact between farmers and hunter-gatherers leading to additional hunter-gatherer ancestry in VN29 and perhaps VN40 (7, 8). This model would imply that the incoming farmers had already acquired 25–30% hunter-gatherer ancestry, either in China or Southeast Asia, establishing the characteristic Austroasiatic-affiliated genetic profile seen in multiple populations today. The wide distribution of this profile across Southeast Asia (in some cases in admixed form) also supports a coherent migration with early shared admixture. The symmetric position of aboriginal Taiwanese and the majority East Asian ancestral lineage in Man Bac (and Austroasiatic speakers) with respect to Native Americans points to an origin for the farming migration specifically in southern China (contrasting with $f_4(X, \text{Atayal; Mixe, Dinka}) > 0$ for northern East Asians $X = \text{Han, Japanese, or Korean}$, $Z > 4.5$). Conversely, the signal of allele-sharing between Lao and Native Americans points to admixture in Lao from a population affected by Han Chinese migrations, with a plausible explanation for our results being mixture between resident Austroasiatic speakers and incoming Tai speakers

within historical times (5).

Our findings also have implications for genetic transformations linked to later cultural and linguistic shifts in Southeast Asia and beyond. We observe substantial genetic turnover between the Neolithic period and Bronze Age in Vietnam, likely reflecting a new influx of migrants from China (24). Late Neolithic/Bronze Age Myanmar individuals from Oakaie also do not possess an Austroasiatic genetic signature, in their case being closer to populations speaking Sino-Tibetan languages (including present-day Myanmar), pointing to an independent East Asian origin. Outside of Mainland Southeast Asia, we document admixture events involving Austroasiatic-related lineages in India (where Austroasiatic languages continue to be spoken) and in Borneo and Sumatra (where all languages today are Austronesian). In the latter case, the shared ancestry with Nicobarese (in addition to separate Papuan-related and Austronesian-associated components) supports previous genetic results and archaeological hints of an early Austroasiatic-associated Neolithic expansion to western Indonesia (25, 26). Overall, Southeast Asia shares common themes with Europe, Oceania, and sub-Saharan Africa, where ancient DNA studies of farming expansions and language shifts have revealed similar instances of genetic turnover associated with archaeologically attested transitions in culture.

REFERENCES AND NOTES

1. C. Higham, Hunter-gatherers in southeast Asia: From prehistory to the present. *Hum. Biol.* **85**, 21–43 (2013). doi:10.3378/027.085.0302 Medline
2. M. Oxenham, H. R. Buckley, The population history of mainland and island Southeast Asia, in *The Routledge Handbook of Bioarchaeology in Southeast Asia and the Pacific Islands*, M. Oxenham, H. R. Buckley, Eds. (Routledge, 2016), pp. 9–23.
3. C. J. Bae, K. Douka, M. D. Petraglia, Human colonization of Asia in the Late Pleistocene: An introduction to supplement 17. *Curr. Anthropol.* **58** (S17), S373–S382 (2017). doi:10.1086/694420
4. C. Higham, Languages and farming dispersals: Austroasiatic languages and rice cultivation, in *Examining the Farming/Language Dispersal Hypothesis*, P. Bellwood, C. Renfrew, Eds. (McDonald Institute for Archaeological Research, 2002), pp. 223–232.
5. P. Bellwood, *First Farmers: The Origins of Agricultural Societies* (Blackwell, Oxford, 2005).
6. Z. Chi, H.-C. Hung, The emergence of agriculture in southern China. *Antiquity* **84**, 11–25 (2010). doi:10.1017/S0003598X00099737
7. M. F. Oxenham, H. Matsumura, K. D. Nguyen, *Man Bac: The Excavation of a Neolithic Site in Northern Vietnam* (ANU Press, 2011).
8. H. Matsumura, M. F. Oxenham, Y. Dodo, K. Domett, N. K. Thuy, N. L. Cuong, N. K. Dung, D. Huffer, M. Yamagata, Morphometric affinity of the late Neolithic human remains from Man Bac, Ninh Binh Province, Vietnam: Key skeletons with which to debate the ‘two layer’ hypothesis. *Anthropol. Sci.* **116**, 135–148 (2008). doi:10.1537/ase.070405
9. Z. Chi, H.-C. Hung, Later hunter-gatherers in southern China, 18,000–3000 BC. *Antiquity* **86**, 11–29 (2012). doi:10.1017/S0003598X00062438
10. H. Matsumura, M. F. Oxenham, Demographic transitions and migration in prehistoric East/Southeast Asia through the lens of nonmetric dental traits. *Am. J. Phys. Anthropol.* **155**, 45–65 (2014). doi:10.1002/ajpa.22537 Medline
11. C. F. Higham, Archaeology, linguistics and the expansion of the East and Southeast Asian Neolithic, in *Archaeology and Language II: Correlating Archaeological and Linguistic Hypotheses*, R. Blench, M. Spriggs, Eds.

- (Routledge, 1998), pp. 103–114.
12. I. Pejros, V. Shnirelman, Rice in Southeast Asia: A regional interdisciplinary approach, in *Archaeology and Language II: Correlating Archaeological and Linguistic Hypotheses*, R. Blench, M. Spriggs, Eds. (Routledge, 1998), pp. 379–389.
 13. P. Bellwood, M. Oxenham, B. C. Hoang, N. K. Dzung, A. Willis, C. Sarjeant, P. Piper, H. Matsumura, K. Tanaka, N. Beavan-Athfield, T. Higham, N. Q. Manh, D. N. Kinh, N. K. T. Kien, V. T. Huong, V. N. Bich, T. T. K. Quy, N. P. Thao, F. Campos, Y.-I. Sato, N. L. Cuong, N. Amano, An Son and the Neolithic of southern Vietnam. *Asian Perspect.* **50**, 144–175 (2011). [doi:10.1353/asi.2011.0007](https://doi.org/10.1353/asi.2011.0007)
 14. P. Sidwell, R. Blench, The Austroasiatic Urheimat: The southeastern riverine hypothesis, in *Dynamics of Human Diversity: The Case of Mainland Southeast Asia*, N. J. Enfield, Ed. (Pacific Linguistics, 2011), pp. 317–345.
 15. T. O. Pryce, A. A. Kyaw, L. Andia, L. Champion, C. Colonna, A. Favereau, K. Myat Myat Htwe, X. Peixoto, B. Pradier, A. Willis, F. Valentin, A. Zazzo, Dating the Myanmar Bronze Age: Preliminary 14C dates from the Oakaie 1 cemetery near Nyaung'gan. *J. Indo-Pacific Arch.* **39**, 38–49 (2015). [doi:10.7152/jipa.v39i0.14902](https://doi.org/10.7152/jipa.v39i0.14902)
 16. M. Pietrusewsky, M. T. Douglas, *Ban Chiang, a Prehistoric Village Site in Northeast Thailand, Volume 1, The Human Skeletal Remains* (Univ. of Pennsylvania Museum of Archaeology and Anthropology, 2002).
 17. R. M. Ikehara-Quebral, M. T. Stark, W. Belcher, V. Vuthy, J. Krigbaum, R. A. Bentley, M. T. Douglas, M. Pietrusewsky, Biocultural practices during the transition to history at the Vat Komnou Cemetery, Angkor Borei, Cambodia. *Asian Perspect.* **56**, 191–236 (2017). [doi:10.1353/asi.2017.0008](https://doi.org/10.1353/asi.2017.0008)
 18. R. Pinhasi, D. Fernandes, K. Sirak, M. Novak, S. Connell, S. Alpaslan-Roodenberg, F. Gerritsen, V. Moiseyev, A. Gromov, P. Raczky, A. Anders, M. Pietrusewsky, G. Rollefson, M. Jovanovic, H. Trinhhoang, G. Bar-Oz, M. Oxenham, H. Matsumura, M. Hofreiter, Optimal ancient DNA yields from the inner ear part of the human petrous bone. *PLOS ONE* **10**, e0129102 (2015). [doi:10.1371/journal.pone.0129102](https://doi.org/10.1371/journal.pone.0129102) [Medline](#)
 19. Materials and methods are available as supplementary materials.
 20. M. A. Abdulla, I. Ahmed, A. Assawamakin, J. Bhak, S. K. Brahmachari, G. C. Calacal, A. Chaurasia, C.-H. Chen, J. Chen, Y.-T. Chen, J. Chu, E. M. C. Cutiongco-de la Paz, M. C. A. De Ungria, F. C. Delfin, J. Edo, S. Fuchareon, H. Ghang, T. Gojabori, J. Han, S.-F. Ho, B. P. Hoh, W. Huang, H. Inoko, P. Jha, T. A. Jinam, L. Jin, J. Jung, D. Kangwanpong, J. Kampuansai, G. C. Kennedy, P. Khurana, H.-L. Kim, K. Kim, S. Kim, W.-Y. Kim, K. Kimm, R. Kimura, T. Koike, S. Kulawonganunchai, V. Kumar, P. S. Lai, J.-Y. Lee, S. Lee, E. T. Liu, P. P. Majumder, K. K. Mandapati, S. Marzuki, W. Mitchell, M. Mukerji, K. Naritomi, C. Ngamphiw, N. Niikawa, N. Nishida, B. Oh, S. Oh, J. Ohashi, A. Oka, R. Ong, C. D. Padilla, P. Palittapongarnpim, H. B. Perdigon, M. E. Phipps, E. Png, Y. Sakaki, J. M. Salvador, Y. Sandraling, V. Scaria, M. Seielstad, M. R. Sidek, A. Sinha, M. Srikummool, H. Sudoyo, S. Sugano, H. Suryadi, Y. Suzuki, K. A. Tabbada, A. Tan, K. Tokunaga, S. Tongshima, L. P. Villamor, E. Wang, Y. Wang, H. Wang, J.-Y. Wu, H. Xiao, S. Xu, J. O. Yang, Y. Y. Shugart, H.-S. Yoo, W. Yuan, G. Zhao, B. A. Zilfail; HUGO Pan-Asian SNP Consortium; Indian Genome Variation Consortium, Mapping human genetic diversity in Asia. *Science* **326**, 1541–1545 (2009). [doi:10.1126/science.1177074](https://doi.org/10.1126/science.1177074) [Medline](#)
 21. Q. Fu, H. Li, P. Moorjani, F. Jay, S. M. Slepchenko, A. A. Bondarev, P. L. F. Johnson, A. Aximu-Petri, K. Prüfer, C. de Filippo, M. Meyer, N. Zwyns, D. C. Salazar-García, Y. V. Kuzmin, S. G. Keates, P. A. Kosintsev, D. I. Razhev, M. P. Richards, N. V. Peristov, M. Lachmann, K. Douka, T. F. G. Higham, M. Slatkin, J.-J. Hublin, D. Reich, J. Kelso, T. B. Viola, S. Pääbo, Genome sequence of a 45,000-year-old modern human from western Siberia. *Nature* **514**, 445–449 (2014). [doi:10.1038/nature13810](https://doi.org/10.1038/nature13810) [Medline](#)
 22. M. A. Yang, X. Gao, C. Theunert, H. Tong, A. Aximu-Petri, B. Nickel, M. Slatkin, M. Meyer, S. Pääbo, J. Kelso, Q. Fu, 40,000-year-old individual from Asia provides insight into early population structure in Eurasia. *Curr. Biol.* **27**, 3202–3208.e9 (2017). [doi:10.1016/j.cub.2017.09.030](https://doi.org/10.1016/j.cub.2017.09.030) [Medline](#)
 23. J. Corny, M. Galland, M. Arzarello, A.-M. Bacon, F. Demeter, D. Grimaud-Hervé, C. Higham, H. Matsumura, L. C. Nguyen, T. K. T. Nguyen, V. Nguyen, M. Oxenham, T. Sayavongkhamdy, F. Sémah, L. L. Shackelford, F. Détroit, Dental phenotypic shape variation supports a multiple dispersal model for anatomically modern humans in Southeast Asia. *J. Hum. Evol.* **112**, 41–56 (2017). [doi:10.1016/j.jhevol.2017.08.017](https://doi.org/10.1016/j.jhevol.2017.08.017) [Medline](#)
 24. M. F. Oxenham, *Bioarchaeology of Ancient Vietnam* (BAR International Series 2781, Hadrian, 2016).
 25. M. Lipson, P.-R. Loh, N. Patterson, P. Moorjani, Y.-C. Ko, M. Stoneking, B. Berger, D. Reich, Reconstructing Austronesian population history in Island Southeast Asia. *Nat. Commun.* **5**, 4689 (2014). [doi:10.1038/ncomms5689](https://doi.org/10.1038/ncomms5689) [Medline](#)
 26. T. Simanjuntak, The western route migration: A second probable Neolithic diffusion to Indonesia, in *New Perspectives in Southeast Asian and Pacific Prehistory*, P. J. Piper, H. Matsumura, D. Bulbeck, Eds. (ANU Press, 2017), pp. 201–212.
 27. M. Oxenham, Mainland Southeast Asia: Towards a new theoretical approach. *Antiquity* **89**, 1221–1223 (2015). [doi:10.15184/ajqy.2015.106](https://doi.org/10.15184/ajqy.2015.106)
 28. M. Oxenham, H. Matsumura, K. Domett, N. K. Thuy, N. K. Dung, N. L. Cuong, D. Huffer, S. Muller, Health and the experience of childhood in Late Neolithic Viet Nam. *Asian Perspect.* **47**, 190–209 (2008). [doi:10.1353/asi.0.0001](https://doi.org/10.1353/asi.0.0001)
 29. M. F. Oxenham, L. Tilley, H. Matsumura, L. C. Nguyen, K. T. Nguyen, K. D. Nguyen, K. Domett, D. Huffer, Paralysis and severe disability requiring intensive care in Neolithic Asia. *Anthropol. Sci.* **117**, 107–112 (2009). [doi:10.1537/ase.081114](https://doi.org/10.1537/ase.081114)
 30. L. Tilley, M. F. Oxenham, Survival against the odds: Modeling the social implications of care provision to seriously disabled individuals. *Int. J. Paleopathol.* **1**, 35–42 (2011). [doi:10.1016/j.ijpp.2011.02.003](https://doi.org/10.1016/j.ijpp.2011.02.003) [Medline](#)
 31. M. F. Oxenham, C. Locher, N. L. Cuong, N. K. Thuy, Identification of *Areca catechu* (betel nut) residues on the dentitions of Bronze Age inhabitants of Nui Nap, northern Vietnam. *J. Archaeol. Sci.* **29**, 909–915 (2002). [doi:10.1006/jasc.2001.0767](https://doi.org/10.1006/jasc.2001.0767)
 32. M. F. Oxenham, N. K. Thuy, N. L. Cuong, Skeletal evidence for the emergence of infectious disease in bronze and iron age northern Vietnam. *Am. J. Phys. Anthropol.* **126**, 359–376 (2005). [doi:10.1002/ajpa.20048](https://doi.org/10.1002/ajpa.20048) [Medline](#)
 33. J. C. White, E. G. Hamilton, The transmission of early bronze technology to Thailand: New perspectives. *J. World Prehist.* **22**, 357–397 (2009). [doi:10.1007/s10963-009-9029-z](https://doi.org/10.1007/s10963-009-9029-z)
 34. C. F. Higham, K. Douka, T. F. Higham, A new chronology for the Bronze Age of northeastern Thailand and its implications for Southeast Asian prehistory. *PLOS ONE* **10**, e0137542 (2015). [doi:10.1371/journal.pone.0137542](https://doi.org/10.1371/journal.pone.0137542) [Medline](#)
 35. E. Moore, P. Pauk, Nyaung-gan: A preliminary note on a Bronze Age cemetery near Mandalay, Myanmar (Burma). *Asian Perspect.* **40**, 35–47 (2001). [doi:10.1353/asi.2001.0012](https://doi.org/10.1353/asi.2001.0012)
 36. T. O. Pryce, K. M. M. Htwe, M. Georgakopoulou, T. Martin, E. Vega, T. Rehren, T. T. Win, T. T. Win, P. Petchey, J. Innanchai, B. Pradier, Metallurgical traditions and metal exchange networks in late prehistoric central Myanmar, c. 1000 BC to c. AD 500. *Archaeol. Anthropol. Sci.* (2016). [doi:10.1007/s12520-016-0436-7](https://doi.org/10.1007/s12520-016-0436-7)
 37. M. T. Stark, Pre-Angkorian settlement trends in Cambodia's Mekong delta and the lower Mekong archaeological project. *Bull. Indo-Pac. Prehist. Assoc.* **26**, 98–109 (2006).
 38. R. Ikehara-Quebral, "An assessment of health in Early Historic (200 BC to AD 200) inhabitants of Vat Komnou, Angkor Borei, southern Cambodia: A bioarchaeological perspective," thesis, University of Hawai'i at Mānoa (2010).
 39. W. Haak, I. Lazaridis, N. Patterson, N. Rohland, S. Mallick, B. Llamas, G. Brandt, S. Nordenfelt, E. Harney, K. Stewardson, Q. Fu, A. Mittnik, E. Bánffy, C. Economou, M. Francken, S. Friederich, R. G. Pena, F. Hallgren, V. Khartanovich, A. Khokhlov, M. Kunst, P. Kuznetsov, H. Meller, O. Mochalov, V. Moiseyev, N. Nicklisch, S. L. Pichler, R. Risch, M. A. Rojo Guerra, C. Roth, A. Szécsényi-Nagy, J. Wahl, M. Meyer, J. Krause, D. Brown, D. Anthony, A. Cooper, K. W. Alt, D. Reich, Massive migration from the steppe was a source for Indo-European languages in Europe. *Nature* **522**, 207–211 (2015). [doi:10.1038/nature14317](https://doi.org/10.1038/nature14317) [Medline](#)
 40. I. Mathieson, I. Lazaridis, N. Rohland, S. Mallick, N. Patterson, S. A. Roodenberg, E. Harney, K. Stewardson, D. Fernandes, M. Novak, K. Sirak, C. Gamba, E. R. Jones, B. Llamas, S. Dryomov, J. Pickrell, J. L. Arsuaga, J. M. B. de Castro, E. Carbonell, F. Gerritsen, A. Khokhlov, P. Kuznetsov, M. Lozano, H. Meller, O. Mochalov, V. Moiseyev, M. A. R. Guerra, J. Roodenberg, J. M. Vergès, J. Krause, A. Cooper, K. W. Alt, D. Brown, D. Anthony, C. Lalueza-Fox, W. Haak, R. Pinhasi, D. Reich, Genome-wide patterns of selection in 230 ancient Eurasians. *Nature* **528**, 499–503 (2015). [doi:10.1038/nature16152](https://doi.org/10.1038/nature16152) [Medline](#)
 41. I. Lazaridis, D. Nadel, G. Rollefson, D. C. Merrett, N. Rohland, S. Mallick, D.

- Fernandes, M. Novak, B. Gamarra, K. Sirak, S. Connell, K. Stewardson, E. Harney, Q. Fu, G. Gonzalez-Fortes, E. R. Jones, S. A. Roodenberg, G. Lengyel, F. Bocquentin, B. Gasparian, J. M. Monge, M. Gregg, V. Eshed, A.-S. Mizrahi, C. Meiklejohn, F. Gerritsen, L. Bejenaru, M. Blüher, A. Campbell, G. Cavalleri, D. Comas, P. Froguel, E. Gilbert, S. M. Kerr, P. Kovacs, J. Krause, D. McGettigan, M. Merrigan, D. A. Merriwether, S. O'Reilly, M. B. Richards, O. Semino, M. Shamooun-Pour, G. Stefanescu, M. Stumvoll, A. Tönjes, A. Torroni, J. F. Wilson, L. Yengo, N. A. Hovhannisyann, N. Patterson, R. Pinhasi, D. Reich, Genomic insights into the origin of farming in the ancient Near East. *Nature* **536**, 419–424 (2016). [doi:10.1038/nature19310](https://doi.org/10.1038/nature19310) [Medline](#)
42. J. Dabney, M. Knapp, I. Glocke, M.-T. Gansauge, A. Weihmann, B. Nickel, C. Valdiosera, N. García, S. Pääbo, J.-L. Arsuaga, M. Meyer, Complete mitochondrial genome sequence of a Middle Pleistocene cave bear reconstructed from ultrashort DNA fragments. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 15758–15763 (2013). [doi:10.1073/pnas.1314445110](https://doi.org/10.1073/pnas.1314445110) [Medline](#)
43. P. Korlević, T. Gerber, M.-T. Gansauge, M. Hajdinjak, S. Nagel, A. Aximu-Petri, M. Meyer, Reducing microbial and human contamination in DNA extractions from ancient bones and teeth. *Biotechniques* **59**, 87–93 (2015). [doi:10.2144/000114320](https://doi.org/10.2144/000114320) [Medline](#)
44. A. W. Briggs, U. Stenzel, M. Meyer, J. Krause, M. Kircher, S. Pääbo, Removal of deaminated cytosines and detection of in vivo methylation in ancient DNA. *Nucleic Acids Res.* **38**, e87 (2010). [doi:10.1093/nar/gkp1163](https://doi.org/10.1093/nar/gkp1163) [Medline](#)
45. N. Rohland, E. Harney, S. Mallick, S. Nordenfelt, D. Reich, Partial uracil-DNA-glycosylase treatment for screening of ancient DNA. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **370**, 20130624 (2015). [doi:10.1098/rstb.2013.0624](https://doi.org/10.1098/rstb.2013.0624) [Medline](#)
46. M. M. DeAngelis, D. G. Wang, T. L. Hawkins, Solid-phase reversible immobilization for the isolation of PCR products. *Nucleic Acids Res.* **23**, 4742–4743 (1995). [doi:10.1093/nar/23.22.4742](https://doi.org/10.1093/nar/23.22.4742) [Medline](#)
47. N. Rohland, D. Reich, Cost-effective, high-throughput DNA sequencing libraries for multiplexed target capture. *Genome Res.* **22**, 939–946 (2012). [doi:10.1101/gr.128124.111](https://doi.org/10.1101/gr.128124.111) [Medline](#)
48. T. Maricic, M. Whitten, S. Pääbo, Multiplexed DNA sequence capture of mitochondrial genomes using PCR products. *PLOS ONE* **5**, e14004 (2010). [doi:10.1371/journal.pone.0014004](https://doi.org/10.1371/journal.pone.0014004) [Medline](#)
49. M. Meyer, Q. Fu, A. Aximu-Petri, I. Glocke, B. Nickel, J.-L. Arsuaga, I. Martínez, A. Gracia, J. M. B. de Castro, E. Carbonell, S. Pääbo, A mitochondrial genome sequence of a hominin from Sima de los Huesos. *Nature* **505**, 403–406 (2014). [doi:10.1038/nature12788](https://doi.org/10.1038/nature12788) [Medline](#)
50. D. M. Behar, M. van Oven, S. Rosset, M. Metspalu, E.-L. Loogväli, N. M. Silva, T. Kivisild, A. Torroni, R. Villems, A “Copernican” reassessment of the human mitochondrial DNA tree from its root. *Am. J. Hum. Genet.* **90**, 675–684 (2012). [doi:10.1016/j.ajhg.2012.03.002](https://doi.org/10.1016/j.ajhg.2012.03.002) [Medline](#)
51. Q. Fu, M. Meyer, X. Gao, U. Stenzel, H. A. Burbano, J. Kelso, S. Pääbo, DNA analysis of an early modern human from Tianyuan Cave, China. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 2223–2227 (2013). [doi:10.1073/pnas.1221359110](https://doi.org/10.1073/pnas.1221359110) [Medline](#)
52. S. Sawyer, J. Krause, K. Guschanski, V. Savolainen, S. Pääbo, Temporal patterns of nucleotide misincorporations and DNA fragmentation in ancient DNA. *PLOS ONE* **7**, e34131 (2012). [doi:10.1371/journal.pone.0034131](https://doi.org/10.1371/journal.pone.0034131) [Medline](#)
53. H. Weissensteiner, D. Pacher, A. Kloss-Brandstätter, L. Forer, G. Specht, H.-J. Bandelt, F. Kronenberg, A. Salas, S. Schönherr, HaploGrep 2: Mitochondrial haplogroup classification in the era of high-throughput sequencing. *Nucleic Acids Res.* **44**, W58–W63 (2016). [doi:10.1093/nar/gkw233](https://doi.org/10.1093/nar/gkw233) [Medline](#)
54. G. D. Poznik, Identifying Y-chromosome haplogroups in arbitrarily large samples of sequenced or genotyped men. *bioRxiv* 088716 [Preprint]. 19 November 2016. <https://doi.org/10.1101/088716>.
55. S. Xu, D. Kangwanpong, M. Seielstad, M. Srikumool, J. Kampuansai, L. Jin, The HUGO Pan-Asian SNP Consortium, Genetic evidence supports linguistic affinity of Mlabri—A hunter-gatherer group in Thailand. *BMC Genet.* **11**, 18 (2010). [doi:10.1186/1471-2156-11-18](https://doi.org/10.1186/1471-2156-11-18) [Medline](#)
56. W. Kutanan, J. Kampuansai, S. Fuselli, S. Nakbunlung, M. Seielstad, G. Bertorelle, D. Kangwanpong, Genetic structure of the Mon-Khmer speaking groups and their affinity to the neighbouring Tai populations in Northern Thailand. *BMC Genet.* **12**, 56 (2011). [doi:10.1186/1471-2156-12-56](https://doi.org/10.1186/1471-2156-12-56) [Medline](#)
57. N. Patterson, P. Moorjani, Y. Luo, S. Mallick, N. Rohland, Y. Zhan, T. Genschoreck, T. Webster, D. Reich, Ancient admixture in human history. *Genetics* **192**, 1065–1093 (2012). [doi:10.1534/genetics.112.145037](https://doi.org/10.1534/genetics.112.145037) [Medline](#)
58. I. Lazaridis, N. Patterson, A. Mittnik, G. Renaud, S. Mallick, K. Kirsanow, P. H. Sudmant, J. G. Schraiber, S. Castellano, M. Lipson, B. Berger, C. Economou, R. Bollongino, Q. Fu, K. I. Bos, S. Nordenfelt, H. Li, C. de Filippo, K. Prüfer, S. Sawyer, C. Posth, W. Haak, F. Hallgren, E. Fornander, N. Rohland, D. Delsate, M. Francken, J.-M. Guinet, J. Wahl, G. Ayodo, H. A. Babiker, G. Bailliet, E. Balanovska, O. Balanovsky, R. Barrantes, G. Bedoya, H. Ben-Ami, J. Bene, F. Berrada, C. M. Bravi, F. Brisighelli, G. B. J. Busby, F. Cali, M. Churnosov, D. E. C. Cole, D. Corach, L. Damba, G. van Driem, S. Dryomov, J.-M. Dugoujon, S. A. Fedorova, I. Gallego Romero, M. Gubina, M. Hammer, B. M. Henn, T. Hervig, U. Hodoglugil, A. R. Jha, S. Karachanak-Yankova, R. Khusainova, E. Khusnutdinova, R. Kittles, T. Kivisild, W. Klitz, V. Kučinskas, A. Kushniarevich, L. Laredj, S. Litvinov, T. Loukidis, R. W. Mahley, B. Melegh, E. Metspalu, J. Molina, J. Mountain, K. Näkkäläjärvi, D. Nesheva, T. Nyambo, L. Osipova, J. Parik, F. Platonov, O. Posukh, V. Romano, F. Rothhammer, I. Rudan, R. Ruizbakiev, H. Sahakyan, A. Sajantila, A. Salas, E. B. Starikovskaya, A. Tarekgn, D. Toncheva, S. Turdikulova, I. Uktveryte, O. Utevska, R. Vasquez, M. Villena, M. Voevoda, C. A. Winkler, L. Yepiskoposyan, P. Zalloua, T. Zemunik, A. Cooper, C. Capelli, M. G. Thomas, A. Ruiz-Linares, S. A. Tishkoff, L. Singh, K. Thangaraj, R. Villems, D. Comas, R. Sukernik, M. Metspalu, M. Meyer, E. E. Eichler, J. Burger, M. Slatkin, S. Pääbo, J. Kelso, D. Reich, J. Krause, Ancient human genomes suggest three ancestral populations for present-day Europeans. *Nature* **513**, 409–413 (2014). [doi:10.1038/nature13673](https://doi.org/10.1038/nature13673) [Medline](#)
59. P. Qin, M. Stoneking, Denisovan ancestry in East Eurasian and Native American populations. *Mol. Biol. Evol.* **32**, 2665–2674 (2015). [doi:10.1093/molbev/msv141](https://doi.org/10.1093/molbev/msv141) [Medline](#)
60. P. Skoglund, C. Posth, K. Sirak, M. Spriggs, F. Valentin, S. Bedford, G. R. Clark, C. Reepmeyer, F. Petchey, D. Fernandes, Q. Fu, E. Harney, M. Lipson, S. Mallick, M. Novak, N. Rohland, K. Stewardson, S. Abdullah, M. P. Cox, F. R. Friedlaender, J. S. Friedlaender, T. Kivisild, G. Koki, P. Kusuma, D. A. Merriwether, F.-X. Ricaut, J. T. S. Wee, N. Patterson, J. Krause, R. Pinhasi, D. Reich, Genomic insights into the peopling of the Southwest Pacific. *Nature* **538**, 510–513 (2016). [doi:10.1038/nature19844](https://doi.org/10.1038/nature19844) [Medline](#)
61. N. Nakatsuka, P. Moorjani, N. Rai, B. Sarkar, A. Tandon, N. Patterson, G. S. L. Bhavani, K. M. Girisha, M. S. Mustak, S. Srinivasan, A. Kaushik, S. A. Vahab, S. M. Jagadeesh, K. Satyamoorthy, L. Singh, D. Reich, K. Thangaraj, The promise of discovering population-specific disease-associated genes in South Asia. *Nat. Genet.* **49**, 1403–1407 (2017). [doi:10.1038/ng.3917](https://doi.org/10.1038/ng.3917) [Medline](#)
62. 1000 Genomes Project Consortium, A. Auton, L. D. Brooks, R. M. Durbin, E. P. Garrison, H. M. Kang, J. O. Korbel, J. L. Marchini, S. McCarthy, G. A. McVean, G. R. Abecasis, A global reference for human genetic variation. *Nature* **526**, 68–74 (2015). [doi:10.1038/nature15393](https://doi.org/10.1038/nature15393) [Medline](#)
63. N. Patterson, A. L. Price, D. Reich, Population structure and eigenanalysis. *PLOS Genet.* **2**, e190 (2006). [doi:10.1371/journal.pgen.0020190](https://doi.org/10.1371/journal.pgen.0020190) [Medline](#)
64. L. T. Liu, E. Dobriban, A. Singer, ePCA: High dimensional exponential family PCA; <https://arxiv.org/abs/1611.05550> (2016).
65. M. Raghavan, P. Skoglund, K. E. Graf, M. Metspalu, A. Albrechtsen, I. Moltke, S. Rasmussen, T. W. Stafford Jr., L. Orlando, E. Metspalu, M. Karmin, K. Tambets, S. Rootsi, R. Mägi, P. F. Campos, E. Balanovska, O. Balanovsky, E. Khusnutdinova, S. Litvinov, L. P. Osipova, S. A. Fedorova, M. I. Voevoda, M. DeGiorgio, T. Sicheritz-Ponten, S. Brunak, S. Demeshchenko, T. Kivisild, R. Villems, R. Nielsen, M. Jakobsson, E. Willerslev, Upper Palaeolithic Siberian genome reveals dual ancestry of Native Americans. *Nature* **505**, 87–91 (2014). [doi:10.1038/nature12736](https://doi.org/10.1038/nature12736) [Medline](#)
66. D. Reich, K. Thangaraj, N. Patterson, A. L. Price, L. Singh, Reconstructing Indian population history. *Nature* **461**, 489–494 (2009). [doi:10.1038/nature08365](https://doi.org/10.1038/nature08365) [Medline](#)
67. M. Meyer, M. Kircher, M.-T. Gansauge, H. Li, F. Racimo, S. Mallick, J. G. Schraiber, F. Jay, K. Prüfer, C. de Filippo, P. H. Sudmant, C. Alkan, Q. Fu, R. Do, N. Rohland, A. Tandon, M. Siebauer, R. E. Green, K. Bryc, A. W. Briggs, U. Stenzel, J. Dabney, J. Shendure, J. Kitzman, M. F. Hammer, M. V. Shunkov, A. P. Derevianko, N. Patterson, A. M. Andrés, E. E. Eichler, M. Slatkin, D. Reich, J. Kelso, S. Pääbo, A high-coverage genome sequence from an archaic Denisovan individual. *Science* **338**, 222–226 (2012). [doi:10.1126/science.1224344](https://doi.org/10.1126/science.1224344) [Medline](#)
68. K. Prüfer, F. Racimo, N. Patterson, F. Jay, S. Sankararaman, S. Sawyer, A. Heinze,

- G. Renaud, P. H. Sudmant, C. de Filippo, H. Li, S. Mallick, M. Dannemann, Q. Fu, M. Kircher, M. Kuhlwilm, M. Lachmann, M. Meyer, M. Ongyerth, M. Siebauer, C. Theunert, A. Tandon, P. Moorjani, J. Pickrell, J. C. Mullikin, S. H. Vohr, R. E. Green, I. Hellmann, P. L. F. Johnson, H. Blanche, H. Cann, J. O. Kitzman, J. Shendure, E. E. Eichler, E. S. Lein, T. E. Bakken, L. V. Golovanova, V. B. Doronichev, M. V. Shunkov, A. P. Derevianko, B. Viola, M. Slatkin, D. Reich, J. Kelso, S. Pääbo, The complete genome sequence of a Neanderthal from the Altai Mountains. *Nature* **505**, 43–49 (2014). [doi:10.1038/nature12886](https://doi.org/10.1038/nature12886) [Medline](#)
69. S. Mallick, H. Li, M. Lipson, I. Mathieson, M. Gymrek, F. Racimo, M. Zhao, N. Chennagiri, S. Nordenfelt, A. Tandon, P. Skoglund, I. Lazaridis, S. Sankararaman, Q. Fu, N. Rohland, G. Renaud, Y. Erlich, T. Willems, C. Gallo, J. P. Spence, Y. S. Song, G. Poletti, F. Balloux, G. van Driem, P. de Knijff, I. G. Romero, A. R. Jha, D. M. Behar, C. M. Bravi, C. Capelli, T. Hervig, A. Moreno-Estrada, O. L. Posukh, E. Balanovska, O. Balanovsky, S. Karachanak-Yankova, H. Sahakyan, D. Toncheva, L. Yepiskoposyan, C. Tyler-Smith, Y. Xue, M. S. Abdullah, A. Ruiz-Linares, C. M. Beall, A. Di Rienzo, C. Jeong, E. B. Starikovskaya, E. Metspalu, J. Parik, R. Villems, B. M. Henn, U. Hodoglugil, R. Mahley, A. Sajantila, G. Stamatoyannopoulos, J. T. S. Wee, R. Khusainova, E. Khusnutdinova, S. Litvinov, G. Ayodo, D. Comas, M. F. Hammer, T. Kivisild, W. Klitz, C. A. Winkler, D. Labuda, M. Bamshad, L. B. Jorde, S. A. Tishkoff, W. S. Watkins, M. Metspalu, S. Dryomov, R. Sukernik, L. Singh, K. Thangaraj, S. Pääbo, J. Kelso, N. Patterson, D. Reich, The Simons Genome Diversity Project: 300 genomes from 142 diverse populations. *Nature* **538**, 201–206 (2016). [doi:10.1038/nature18964](https://doi.org/10.1038/nature18964) [Medline](#)
70. M. Mondal, F. Casals, T. Xu, G. M. Dall'Olio, M. Pybus, M. G. Netea, D. Comas, H. Laayouni, Q. Li, P. P. Majumder, J. Bertranpetit, Genomic analysis of Andamanese provides insights into ancient human migration into Asia and adaptation. *Nat. Genet.* **48**, 1066–1070 (2016). [doi:10.1038/ng.3621](https://doi.org/10.1038/ng.3621) [Medline](#)

ACKNOWLEDGMENTS

We thank Iosif Lazaridis, Vagheesh Narasimhan, Iñigo Olalde, and Nick Patterson for technical assistance; Nicole Adamski and Ann-Marie Lawson for aiding with lab work; and Minh Tran Thi, Rona Ikehara-Quebral, Miriam Stark, Michele Toomay Douglas, and Joyce White for help with archaeological samples. **Funding:** This work was supported by the French Ministry for Europe and Foreign Affairs (T.O.P.), Japan Society for the Promotion of Science (grant 16H02527; H.M.), Statutory City of Ostrava (grant 0924/2016/ŠaS; P.C.), Moravian-Silesian Region (grant 01211/2016/RRC; P.C.), Irish Research Council (grant GOIPG/2013/36; D.F.), Thailand Research Fund (grant MRG5980146; W.K.), University of Ostrava (IRP projects; P.F. and P.C.), Czech Ministry of Education, Youth and Sports (project OPVVV 16_019/0000759; P.F. and P.C.), National Science Foundation (HOMINID grant BCS-1032255; D.R.), National Institutes of Health (NIGMS grant GM100233; D.R.), an Allen Discovery Center of the Paul Allen Foundation (D.R.), and the Howard Hughes Medical Institute (D.R.). **Author contributions:** N.R., P.F., R.P., and D.R. supervised the study. M.O., M.P., T.O.P., A.W., H.M., H.B., K.D., N.G.H., T.H.H., A.A.K., T.T.W., B.P., and R.P. provided samples and assembled archaeological and anthropological information. M.L., O.C., S.M., N.R., N.B., F.C., D.F., M.F., B.G., E.H., M.M., M.N., J.O., K.Si., K.St., Z.Z., R.P., and D.R. performed ancient DNA laboratory and data processing work. P.C., J.K., W.K., and P.F. provided present-day data. M.L., S.M., and D.R. analyzed genetic data. M.L., R.P., and D.R. wrote the manuscript with input from all coauthors. **Competing interests:** The authors declare no competing interests. **Data and materials availability:** The aligned sequences are available through the European Nucleotide Archive under accession number PRJEB24939. Genotype datasets used in analysis are available at <https://reich.hms.harvard.edu/datasets>. All the skeletons for which we newly report ancient DNA data are curated by coauthors of this paper, who affirm that the sampling of the skeleton was performed with appropriate permissions.

SUPPLEMENTARY MATERIALS

www.sciencemag.org/cgi/content/full/science.aat3188/DC1

Materials and Methods

Figs. S1 to S4

Tables S1 to S3

References (27–70)

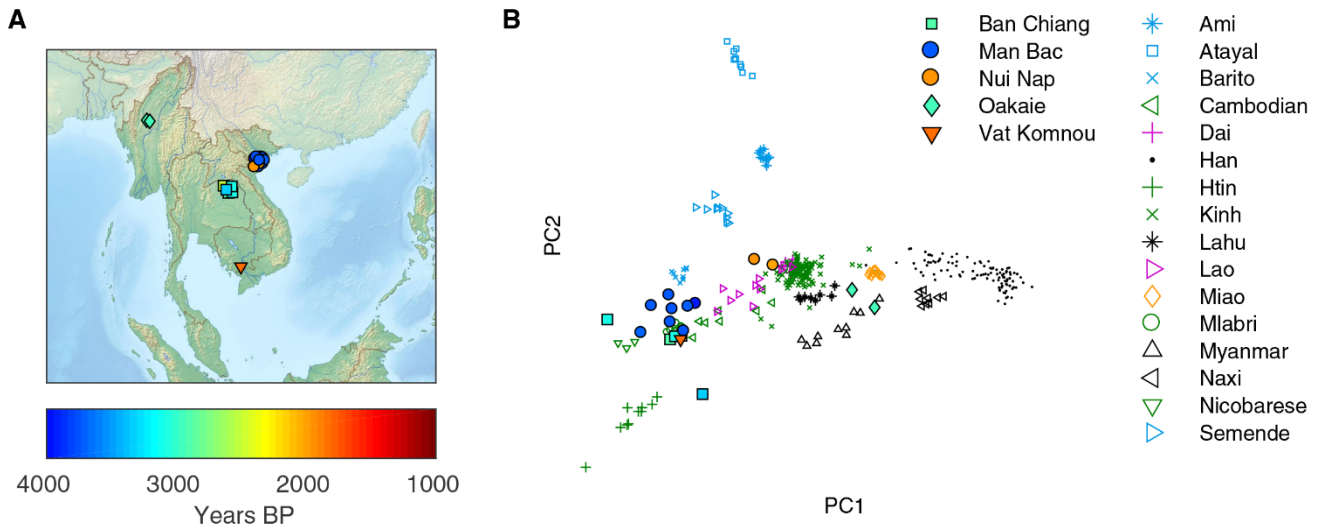


Fig. 1. Overview of samples. (A) Locations and dates of ancient individuals. Overlapping positions are shifted slightly for visibility. (B) PCA with East and Southeast Asians. We projected the ancient samples onto axes computed using the present-day populations (with the exception of Mlabri, who were projected instead due to their large population-specific drift). Present-day colors indicate language family affiliation: green, Austroasiatic; blue, Austronesian; orange, Hmong-Mien; black, Sino-Tibetan; magenta, Tai-Kadai. Map data from <http://www.freeworldmaps.net/asia/southeastasia/physical.html>.

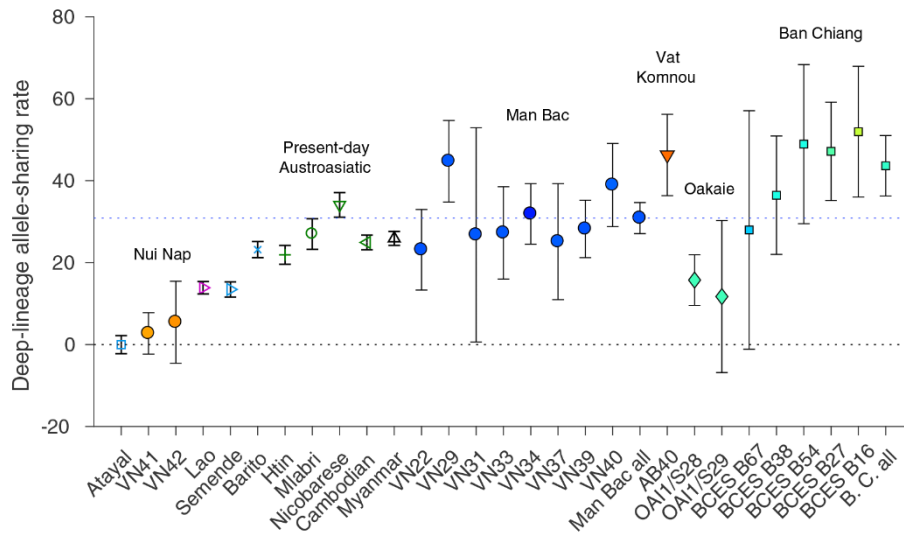


Fig. 2. Relative amounts of deeply diverged ancestry. The Y-axis shows $f_4(X, \text{Kinh}; \text{Australasian}, \text{Han})$ (multiplied by 10^4) for populations X listed on the x-axis (present-day as aggregate; ancient samples individually, except for points labeled “all”). Symbols are as in Fig. 1. Bars give two standard errors in each direction; dotted lines indicate the levels in Man Bac (top, blue) and Kinh (zero, black). B. C., Ban Chiang.

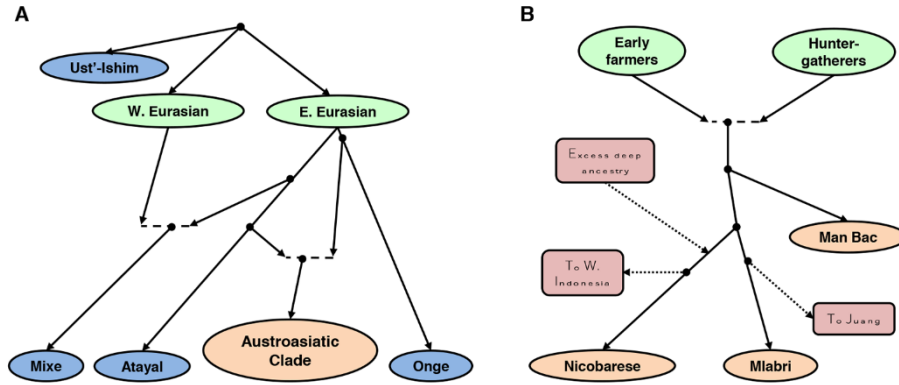


Fig. 3. Schematics of admixture graph results. (A) Wider phylogenetic context. **(B)** Details of the Austroasiatic clade. Branch lengths are not to scale, and the order of the two events on the Nicobarese lineage in (B) is not well determined (19).

Table 1. Sample information.

ID	Lib.	Date (yBP)	Site	Country/period	Lat.	Long.	Sex	Mt Hap	Y Hap	Cov.
VN22	6	3835–3695	Man Bac	Vietnam N	20.1	106.0	F	M13b	..	0.048
VN29	9	3900–3600	Man Bac	Vietnam N	20.1	106.0	F	M7b1a1	..	0.049
VN31	1	3900–3600	Man Bac	Vietnam N	20.1	106.0	M	No call	No call	0.005
VN33	2	3900–3600	Man Bac	Vietnam N	20.1	106.0	M	B5a1a	O2a	0.028
VN34	10	4080–3845	Man Bac	Vietnam N	20.1	106.0	F	M7b1a1	..	0.106
VN37	4	3825–3635	Man Bac	Vietnam N	20.1	106.0	M	M7b1a1	CT	0.019
VN39	11	3830–3695	Man Bac	Vietnam N	20.1	106.0	M	M7b1a1	O2a1c1b1a	0.102
VN40	6	3820–3615	Man Bac	Vietnam N	20.1	106.0	M	M74b	O1b1a	0.041
VN41	5	2100–1900	Nui Nap	Vietnam BA	19.8	105.8	F	C7a	..	0.373
VN42	6	1995–1900	Nui Nap	Vietnam BA	19.8	105.8	M	M8a2a	F	0.042
OAI1/S28	20	3200–2700	Oakaie 1	Myanmar LN/BA	22.4	95.0	F	D4q	..	0.178
OAI1/S29	4	3200–2700	Oakaie 1	Myanmar LN/BA	22.4	95.0	F	D4h1c	..	0.011
BCES B67	1	3500–3200	Ban Chiang	Thailand LN/BA	17.4	103.2	F	F1f	..	0.005
BCES B38	1	3200–3000	Ban Chiang	Thailand BA	17.4	103.2	F	B5a1a	..	0.017
BCES B54	1	3200–3000	Ban Chiang	Thailand BA	17.4	103.2	M	B5a1c	CT	0.010
BCES B27	7	3000–2800	Ban Chiang	Thailand BA	17.4	103.2	F	M74b2	..	0.030
BCES B16	1	2600–2400	Ban Chiang	Thailand IA	17.4	103.2	M	M72a	F	0.017
AB40	7	1890–1730	Vat Komnou	Cambodia IA	11.0	105.0	M	B5a1a	O	0.047

Calibrated radiocarbon dates are shown in bold (95.4% confidence interval, rounded to nearest 5 years); dates in plain text are estimated from archaeological context. Lib., number of sequencing libraries; Cov., average coverage level for 1.2 million genome-wide SNP targets; N, Neolithic; LN, Late Neolithic; BA, Bronze Age; IA, Iron Age.

Ancient genomes document multiple waves of migration in Southeast Asian prehistory

Mark Lipson, Olivia Cheronet, Swapan Mallick, Nadin Rohland, Marc Oxenham, Michael Pietrusewsky, Thomas Oliver Pryce, Anna Willis, Hirofumi Matsumura, Hallie Buckley, Kate Domett, Nguyen Giang Hai, Trinh Hoang Hiep, Aung Aung Kyaw, Tin Tin Win, Baptiste Pradier, Nasreen Broomandkhoshbacht, Francesca Candilio, Piya Changmai, Daniel Fernandes, Matthew Ferry, Beatriz Gamarra, Eadaoin Harney, Jatupol Kampaunsai, Wibhu Kutanan, Megan Michel, Mario Novak, Jonas Oppenheimer, Kendra Sirak, Kristin Stewardson, Zhao Zhang, Pavel Flegontov, Ron Pinhasi and David Reich

published online May 17, 2018

ARTICLE TOOLS

<http://science.sciencemag.org/content/early/2018/05/16/science.aat3188>

SUPPLEMENTARY MATERIALS

<http://science.sciencemag.org/content/suppl/2018/05/16/science.aat3188.DC1>

REFERENCES

This article cites 57 articles, 8 of which you can access for free
<http://science.sciencemag.org/content/early/2018/05/16/science.aat3188#BIBL>

PERMISSIONS

<http://www.sciencemag.org/help/reprints-and-permissions>

Use of this article is subject to the [Terms of Service](#)