HUMAN GENOMICS

Ancient DNA reveals five streams of migration into Micronesia and matrilocality in early Pacific seafarers

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Micronesia began to be peopled earlier than other parts of Remote Oceania, but the origins of its inhabitants remain unclear. We generated genome-wide data from 164 ancient and 112 modern individuals. Analysis reveals five migratory streams into Micronesia. Three are East Asian related, one is Polynesian, and a fifth is a Papuan source related to mainland New Guineans that is different from the New Britain–related Papuan source for southwest Pacific populations but is similarly derived from male migrants ~2500 to 2000 years ago. People of the Mariana Archipelago may derive all of their precolonial ancestry from East Asian sources, making them the only Remote Oceanians without Papuan ancestry. Female-inherited mitochondrial DNA was highly differentiated across early Remote Oceanian communities but homogeneous within, implying matrilocal practices whereby women almost never raised their children in communities different from the ones in which they grew up.

Modern humans arrived in Near Oceania at least 47,000 years before present (BP) and spread through Australia, New Guinea, the Bismarck Archipelago, and the Solomon Islands (*1*, *2*). After 3500 to 3300 BP, humans expanded into previously unoccupied Remote Oceania (Fig. 1A).

In the southwest Pacific, the earliest archaeological sites are associated with artifacts of the Lapita complex, appearing in the Bismarck Archipelago as early as ~3350 BP and reaching the unoccupied islands of Remote Oceania by 3000 to 2850 BP (*3*, *4*). Ancient DNA from 11 individuals from Vanuatu and Tonga 3000 to 2500 BP indicates that these pioneers were related distantly to Neolithic southeastern Chinese (*5*), more closely related to Neolithic and Iron Age people of Taiwan (*6*), and most closely related to the ancestors of present-day north-central Philippine groups such as Kankanaey Igorot (*7*–*10*). However, the primary ancestry of many southwest Pacific Islanders today is "Papuan" (our term to describe the primary ancestry of peoples of New Guinea, the Bismarck Archipelago, and the Solomon Islands), which genetic data has shown is due to a secondary expansion that began ~2500 BP (*7*–*10*).

The first people to reach the Mariana Archipelago arrived around 3500 to 3200 BP (*11*–*14*). Their material culture (*15*) differed markedly from the Lapita assemblages in the southwest Pacific, with Marianas Redware ceramics being more similar to those found at sites in the Philippines and at the northern tip of Sulawesi (*16*). This study uses a revised chronology for the archaeology of the Mariana Islands that terms the earliest three periods of occupation from 3500 to 1600 BP "Unai" (table S1). The burials that we analyze date to 2800 to 2200 BP (Middle to Late Unai) and thus may not reflect the ancestry profile of Early Unai inhabitants. After 1100 BP, distinctive megaliths (latte) began to appear in the Mariana Islands, along with other material cultural changes marking the "Latte" period. The oldest evidence of human occupation in Palau in Western Micronesia dates to ~3000 BP (*17*). The oldest evidence in Central Micronesia is ~2000 BP; ceramics at these sites are similar to late Lapita pottery and shell artifacts and thus could reflect roots in earlier Lapita cultures in either northern New Guinea or in the southwest Pacific (*18*, *19*).

Linguistic relationships among Malayo-Polynesian (MP) languages that comprise all Austronesian languages outside of Taiwan provide an independent source of information about the cultural and geographic origins of Micronesian peoples (fig. S1). The CHamoru (*20*) language spoken by the indigenous people of the Mariana Islands is a first-order branch within MP; Palauan is another. All other Micronesian languages and languages of the southwest Pacific and Polynesia comprise a third major branch, Central-Eastern Malayo-Polynesian (CEMP) (*21*–*23*). Most Micronesian CEMP languages form a Nuclear Micronesian subgroup, which has been hypothesized to have developed somewhere between the Admiralty Islands and Vanuatu and to have spread near the end of the Lapita period ~2500 BP (*24*). By contrast, Yap's language is believed to be an early offshoot of Proto-Oceanic derived directly from protolanguages that branched during the Lapita expansion, although Yapese was also subsequently affected by borrowings from other languages (*25*). The people of Kapingamarangi and Nukuoro atolls in the Caroline Islands speak Polynesian languages, suggesting replacement of the original languages by Polynesian immigration (*26*, *27*).

To test alternative models of population history, we generated genome-wide ancient DNA data for 164 individuals from five archaeological sites and coanalyzed them with published data from two ~2200 BP individuals from

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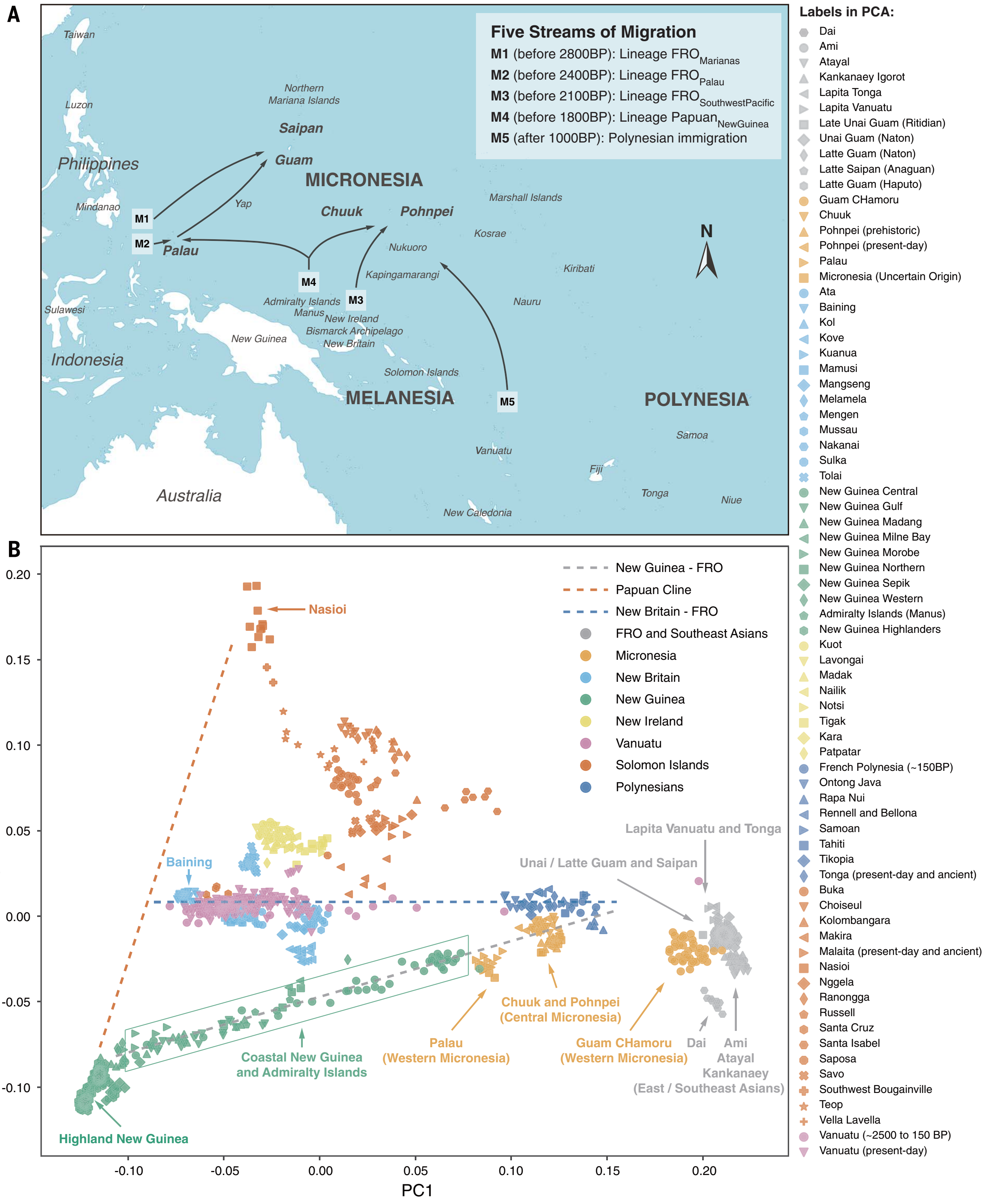

Fig. 1. Map and PCA. (**A**) Map showing five inferred streams of migration into Micronesia. (**B**) PCA results. Axes are computed with Dai, Nasioi, and Papuans; others are projected.

Guam (*28*). A total of 109 individuals (2800 to 300 BP) were from the Unai and Latte periods in Guam, 46 (600 to 200 BP) from the Latte period in Saipan, and 11 (500 to 300 BP) from Na Island and the nearby Nan Madol site in Pohnpei's protected lagoon in Central Micronesia (*20*).

We prepared samples in clean rooms, extracted DNA, built sequencing libraries, enriched for a common panel of ~1.2 million single-nucleotide polymorphisms (SNPs), and sequenced them (*20*). For individuals with evidence of high contamination, we restricted analysis to sequences with evidence of characteristic ancient DNA damage (*20*). The analyzed individuals had a median of 558,971 SNPs with data (table S2). We also genotyped 112 present-day Micronesians mainly from Guam, Palau, Chuuk, and Pohnpei (tables S3 and S4). We obtained 31 direct radiocarbon dates, 30 of which were on the same samples we analyzed

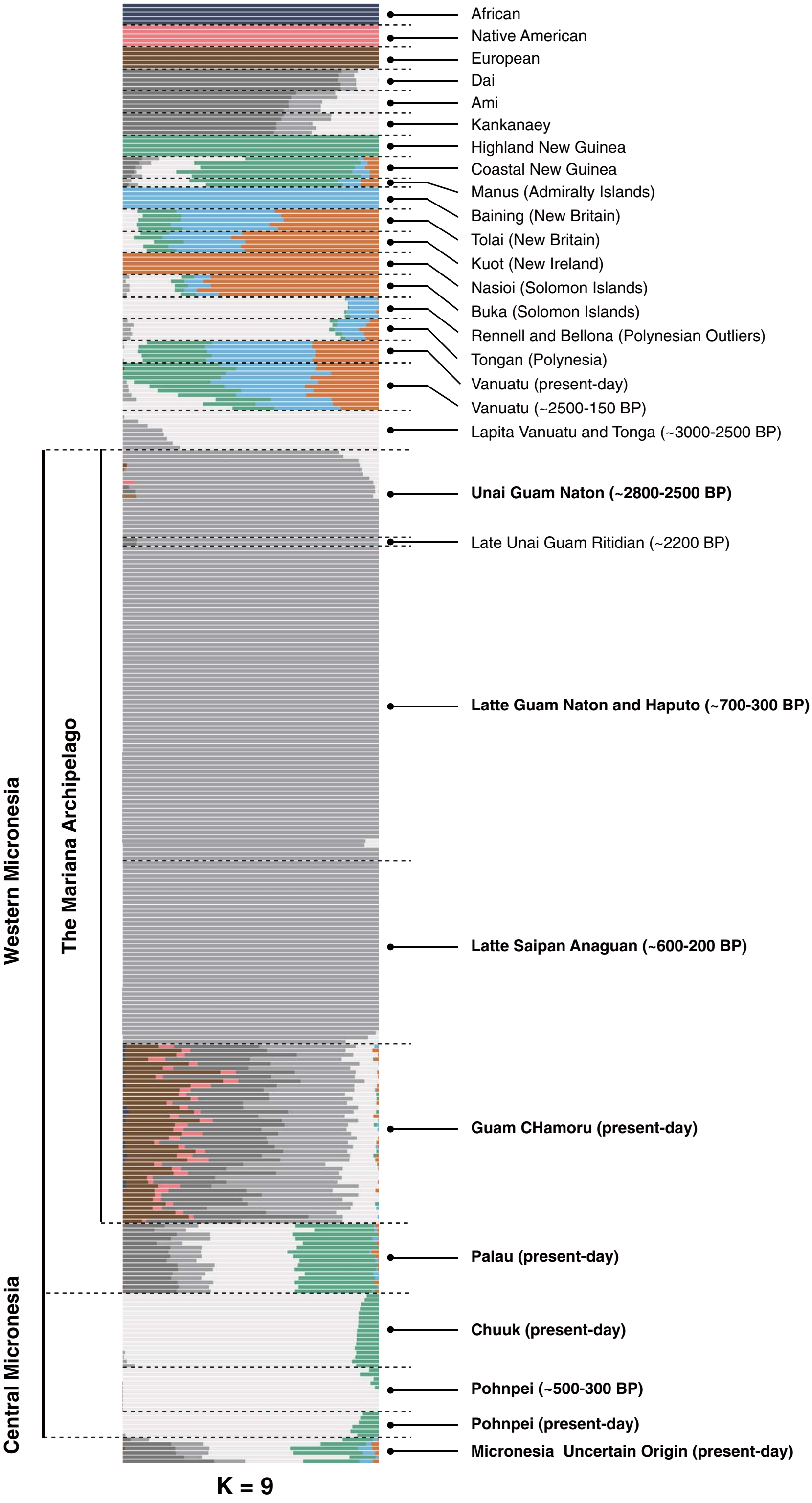

Fig. 2. Clustering analysis. Unsupervised ADMIXTURE (K = 9 clusters). New data are in boldface.

for DNA (tables S5 and S6). We coanalyzed our newly produced data with published data from 95 prehistoric individuals and 1642 present-day individuals from globally diverse populations (table S7).

Overview of population structure

We carried out principal components analysis (PCA) (Fig. 1B and figs. S2 and S3) by computing axes using shotgun data of present-day Dai (southern China), Nasioi (Solomon Islands), and New Guineans (from the Eastern Highlands and Middle Sepik areas) and then projecting other individuals. The first principal component (PC) corresponds to the proportion of East Asian–associated ancestry, henceforth "First Remote Oceanian (FRO)" (PC1; lower on left, higher on right); the second PC differentiates Papuan ancestry from the Solomon Islands to New Guinea (PC2; up to down). The Unai, Latte, and Lapita individuals cluster with present-day people from the Philippines (Kankanaey) and Taiwan (Ami and Atayal) on the right, corresponding to high East Asian–associated ancestry. Two clines are visible. The first (dashed blue) links groups with high proportions of FRO ancestry to New Britain, Vanuatu, and Polynesia; the second (dashed gray) links to groups from New Guinea, the Admiralty Islands, Palau, and a genetically homogeneous group of Central Micronesians (Chuuk, Pohnpei, and prehistoric Pohnpei). This suggests admixture in variable proportions between FRO and Papuan ancestry from at least two different sources—more related to New Britain in the first case and New Guinea in the second. f_3-statistics reveal patterns qualitatively similar to those shown in the PCA (fig. S4 and table S8).

We also computed the symmetry statistic f_4 (X, Kankanaey Igorot; New Guinea Highlanders, Dai) to test which individuals had significant Papuan admixture (using Kankanaey as a baseline with no evidence of Papuan ancestry) (table S9). Unai and Latte individuals had little or no Papuan ancestry; except for four Latte individuals, we observed non-significant Z-tests based on the normally distributed score being $|Z| < 3$ standard errors from zero. Lapita individuals from Vanuatu and Tonga had a small, but nonzero, proportion of Papuan ancestry (0.4 to 4.4% and 3.3 to 7.7%, respectively) (*7–10*). Papuan admixture was present in all prehistoric and present-day individuals from Pohnpei (~27%) and all present-day people from Chuuk (~27%) and Palau (~38%). In modern CHamoru, the inferred Papuan ancestry is consistent with zero, making CHamoru the only genetically analyzed indigenous Remote Oceanian group without evidence of such ancestry.

Unsupervised clustering using ADMIXTURE recapitulates the patterns in the PCA and differentiates the FRO components of First Remote Oceanians (we show K = 9 clusters in Fig. 2; see also figs. S5 to S8). Two clusters correspond to East Asian–associated ancestry, with a light gray component maximized in Lapita individuals and a dark gray component maximized in Mariana individuals. Pohnpei and Chuuk in Central Micronesia primarily have a light gray Lapita-associated component. Modern CHamoru of Guam is the population with the highest proportion of dark gray, suggesting local continuity. Palau and Central Micronesia only have the green Papuan-associated

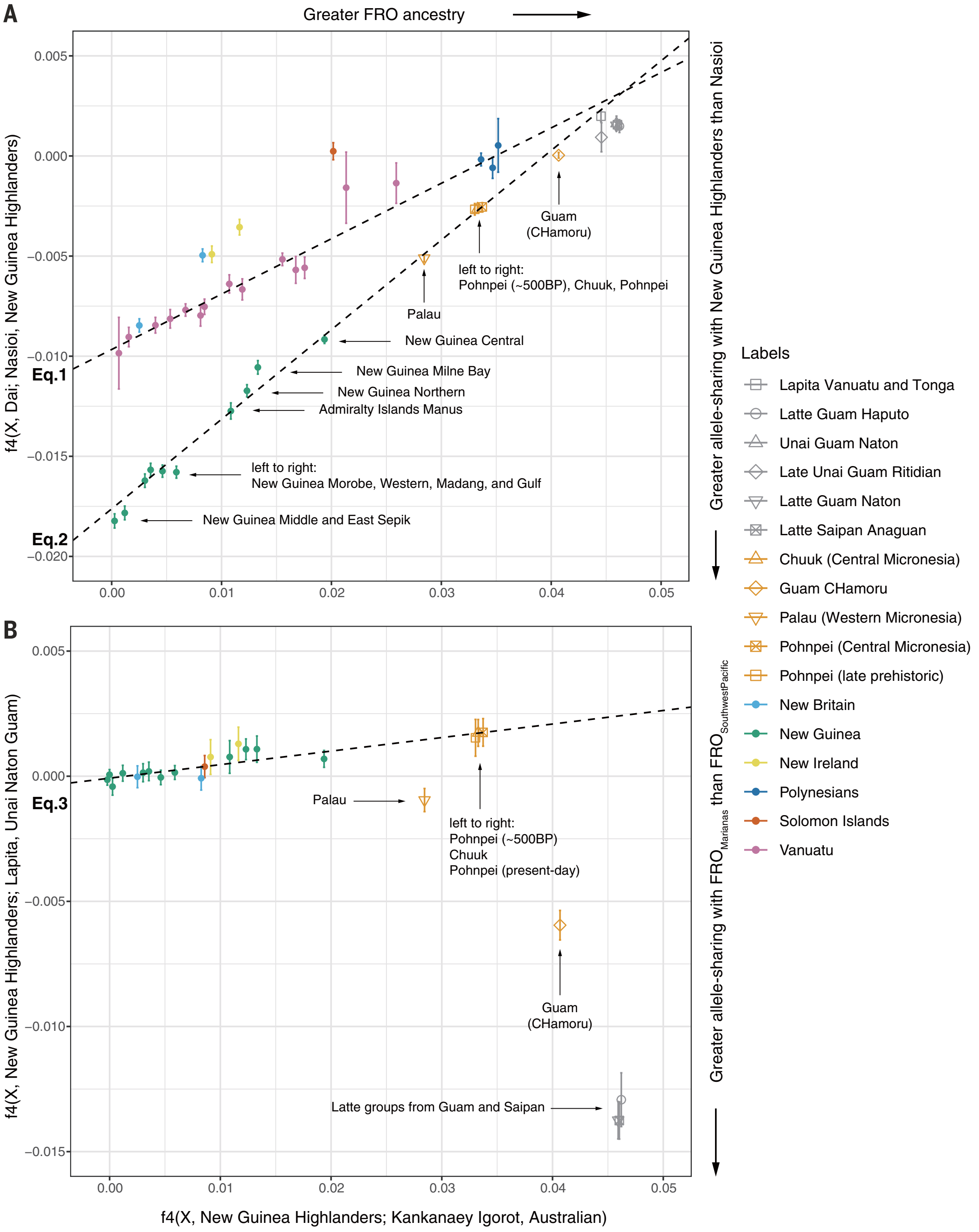

Fig. 3. Different Papuan and East Asian affinities. (**A** and **B**) Test for differential (A) Papuan and (B) FRO affinities using a merge of the 1240K and MEGA data (~169,000 SNPs). Equation 1 (Eq. 1) is computed with all groups from Vanuatu and Polynesians, Eq. 2 with all Micronesian and New Guinea–related groups except those from Guam and Saipan, and Eq. 3 with all present-day groups except Micronesians. We show one standard error in each direction on the *y* axis. We merged Lapita individuals from Vanuatu and Tonga. See fig. S9 for the same analysis performed on individuals for whom we have ~397,000 SNPs genotyped on a merge of 1240K and Human Origins data.

component maximized in New Guinea, without the orange-blue-green mixture characteristic of New Britain, the southwest Pacific, and Polynesia, suggesting previously undocumented Papuan spreads into Micronesia.

Evidence for at least five streams of migration into Micronesia

To determine the minimum number of migration streams into Micronesia needed to explain the data, we computed a statistic f_4(X, New Guinea Highlanders; Kankanaey Igorot, Australian) proportional to FRO ancestry and correlated it to statistics sensitive to different types of East Asian and Papuan-associated ancestry (*9*). We identified at least five distinct migratory streams, as follows.

(M1 to M3) Three streams of FRO migration into Micronesia including a previously unknown lineage. We plotted a statistic measuring affinity to the two previously identified (*7*, *28*) lineages $\mathrm{FRO}_{\mathrm{SouthwestPacific}}$ and $\mathrm{FRO}_{\mathrm{Marianas}}$, specifically, f_4(X, New Guinea Highlanders; Lapita, Unai) against our statistic measuring overall FRO ancestry proportion. All populations from the southwest Pacific and Polynesia fall on a line with a positive slope, implying closer affinity to Lapita than to Unai consistent with the Lapita-associated lineage being the source of their East Asian–associated ancestry (all residuals $|Z| < 2$ after regression; Fig. 3B and fig. S9B). Individuals from Central Micronesia (Pohnpei and Chuuk, and some other present-day Micronesians) also closely track the line (all residuals $|Z| < 2$), suggesting FRO ancestry from the Lapita expansion. By contrast, present-day individuals from Palau and the Mariana Islands yield negative f_4-statistics (all residuals $|Z| > 4$), implying FRO

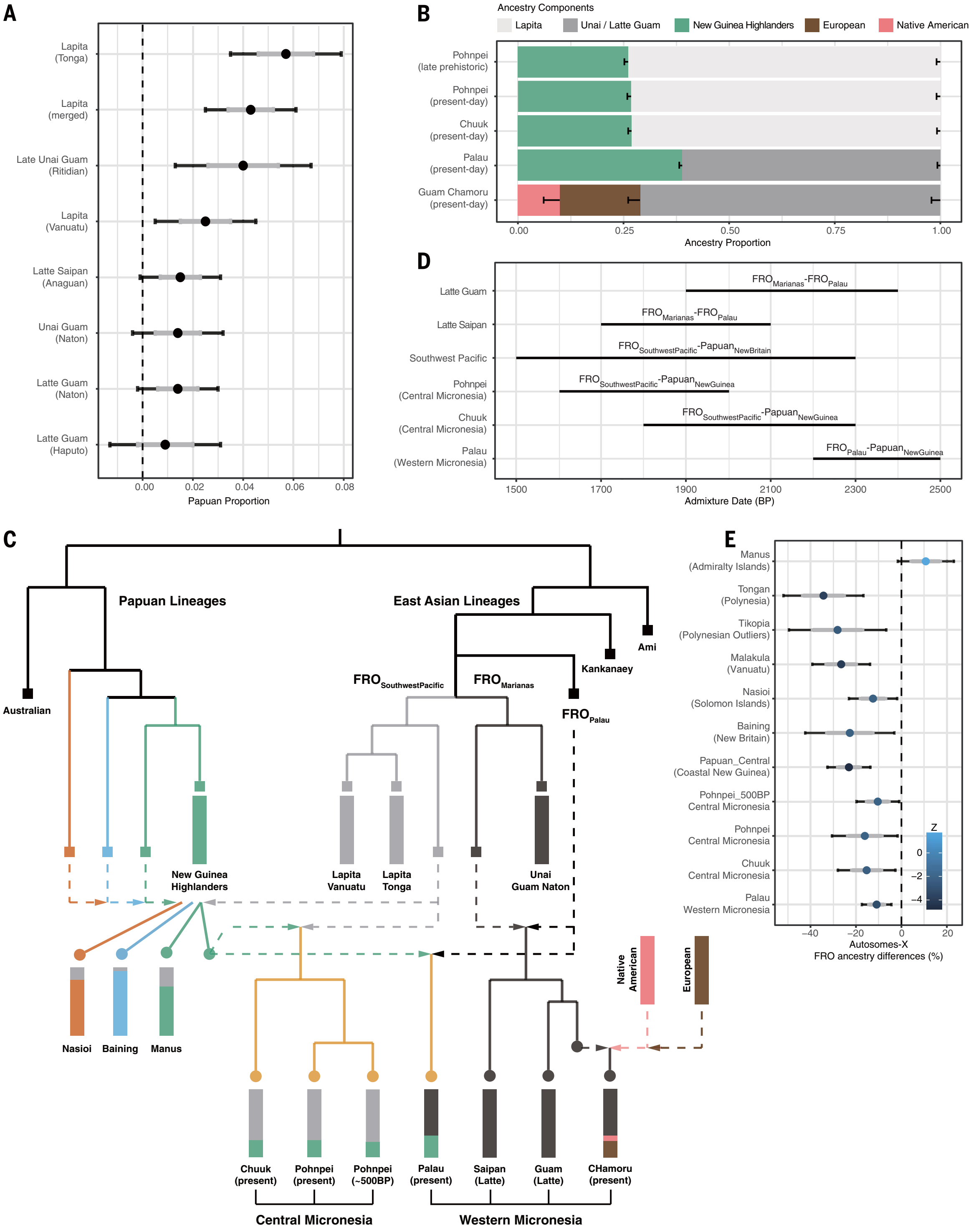

Fig. 4. Quantification of admixture events. (**A**) Proportions of Papuan ancestry in FRO and Latte groups. Thick and thin error bars show one standard error and 95% confidence interval, respectively. (**B**) Ancestry proportions from *qpAdm*. Each group is represented by a horizontal bar and partitioned into colored segments, representing different sources of their ancestry. Error bars show one standard error. (**C**) Admixture graphs. Arrow pairs (head to head) denote admixture events. The heights of the colored bars give mixture proportions. (**D**) Date of admixture. Ranges show one standard error in each direction. (**E**) Difference between FRO ancestry estimates on the autosomes and the X chromosome.

sources less closely related to the Lapita individuals (tables S12 and S13). We confirmed with f_4-symmetry statistics that all the prehistoric Remote Oceanian groups with nearly entirely East Asian–associated ancestry (Lapita, Unai, and Latte) descended from a common ancestral FRO population (table S22), which split earlier from the ancestors of indigenous and Iron Age Taiwanese and even earlier from those of Kankanaey Igorot. A surprise is that despite the fact that the Latte and Unai individuals share more alleles with each other than either group does with Lapita, there is not a simple tree relating these three groups, with the statistic f_4(Latte, Unai; Lapita, diverse East Asians) yielding many significant negative Z values (maximum $|Z| > 4$; table S26). This suggests that the Latte individuals harbor admixture from a basal FRO lineage, which split from the lineages ancestral to Unai and Lapita before they separated from each other, a scenario that fits the data in explicit admixture graph modeling (Fig. 4C and figs. S12 to S15). We call this third lineage FRO$_{\text{Palau}}$

because the proportion of this lineage is maximized in modern Palauans (where we estimate that it contributes 62% ancestry versus 15% in Latte individuals) (fig. S13A).

(M4) A previously unknown stream of Papuan migration into Micronesia. We computed f_4(X, Dai; Nasioi, New Guinea Highlanders), where the latter two populations are differentiated Papuan groups, and plotted it against our statistic measuring FRO proportion. Modern and prehistoric groups from the southwest Pacific and Polynesia fall on a line that also includes New Britain (all residuals $|Z| < 2$; Fig. 3A and fig. S9A), consistent with ancestry from a New Britain–associated source we call Papuan$_{\text{NewBritain}}$ (*8*–*10*). By contrast, all prehistoric and present-day individuals from Micronesia with evidence of Papuan ancestry fall below the line (all residuals $|Z| > 4$), mirroring the two-cline pattern in the PCA (tables S10 and S11). When we fit a separate line for Micronesians, New Guinea, and the Admiralty Islands, we observe no outliers with $|Z| < 2$, consistent with a previously unknown spread of Papuan ancestry from a lineage Papuan$_{\text{NewGuinea}}$ more closely related to New Guinea and the Admiralty Islands on its northern fringe.

(M5) Polynesian gene flow into Micronesia. We computed f_4(X, Tolai; Kankanaey Igorot, diverse Polynesians) (tables S14 to S20), and plotted it against our f_4-statistic proportional to FRO ancestry (figs. S10 and S11), a procedure that provides a sensitive test of Polynesian-specific admixture. Late prehistoric individuals from Pohnpei closely track the baseline, providing no evidence of Polynesian admixture. One present-day Micronesian (Jk2812) deviates from the line (maximum $|Z| = 3.3$) (table S21). We do not have a record of the island from which this individual came, so characterization of the Polynesian impact on Micronesia will require further sampling.

A working model for Micronesian population history

We started with a model previously used to study southwest Pacific lineages (*8*, *9*) and then added lineages and admixture events, testing alternative models for fit (Fig. 4C and figs. S12 to S15). With so many populations, the space of possible admixture graph topologies is vast, and the topology we show is unlikely to be a the only fit to the *f*-statistics. Nevertheless, identifying an admixture graph model is useful to demonstrate that all the features described in our analysis of individual *f*-statistics can jointly fit the data. We confirmed key inferences about admixture proportions and closest phylogenetic relatives of analyzed groups using *qpWave* and *qpAdm* (tables S22 to S25), which does not require making specific assumptions about deep phylogenetic relationships and allows us to test whether there are any groups that harbor genetic drift that is not present in the populations used as proxies for their ancestry (*20*). Finally, we used admixture linkage disequilibrium to estimate the ages of some detected admixture events with the software DATES (Fig. 4D and table S27).

(i) The Mariana Islands: Distinctive FRO ancestry without Papuan admixture. The Unai individuals from Guam whose radiocarbon dates range from 2800 to 2200 BP derive from the FRO$_{\text{Marianas}}$ lineage (M1) and have homogeneous ancestry. Later Latte individuals from Guam and Saipan after 700 BP derive ~85% of their ancestry from the same source (fig. S13A), with substantial continuity also confirmed by their harboring the same mitochondrial haplogroups E1 and E2 that are seen in the Unai period. The Latte individuals also derived ~15% ancestry from a previously unidentified FRO$_{\text{Palau}}$ lineage (M2), which we estimate mixed with FRO$_{\text{Marianas}}$ 45 to 50 generations before the Latte individuals lived (2400 to 1700 BP, assuming 28 years per generation). The admixture date shows that this migration and mixture process cannot be invoked to explain the origin of the Latte archaeological phenomenon in the Mariana Islands, which began much later at ~1100 BP.

The modern CHamoru from Guam are admixed with European (~19%) and Native American (~9%) ancestry (Fig. 4B), plausibly associated with Spanish colonial activities from the mid-16th century onward (*29*). Their remaining ancestry is entirely FRO. Although our analyses of modern CHamoru did not allow us to unambiguously determine their FRO source, they show a greater genetic affinity to FRO$_{\text{Marianas}}$ than to FRO$_{\text{SouthwestPacific}}$ (Fig. 3B), and their mitochondrial haplogroups E1 and E2 are also found in the Unai and Latte individuals, suggesting that they derived much of their East Asian–associated ancestry from earlier groups in Guam.

(ii) Palau: Mixture of FRO$_{\text{Palau}}$ and Papuan$_{\text{NewGuinea}}$ ancestry. Present-day Palauans are inferred to have ~62% FRO$_{\text{Palau}}$ ancestry (M2) from the same lineage that admixed in a smaller proportion into the Latte individuals (fig. S13A) and ~38% Papuan$_{\text{NewGuinea}}$ ancestry (M4). We estimate the date of FRO$_{\text{Palau}}$-Papuan$_{\text{NewGuinea}}$ admixture to be ~2500 to 2200 BP, suggesting the possibility of Papuan migration into this region by this time.

(iii) Central Micronesia: Mixture of FRO$_{\text{SouthwestPacific}}$ and Papuan$_{\text{NewGuinea}}$. We infer genetic homogeneity in central Micronesia over space and time, with Pohnpei and Chuuk having similar proportions of ~73% FRO$_{\text{SouthwestPacific}}$ (M3) and ~27% Papuan$_{\text{NewGuinea}}$ ancestry (M4) and forming a clade with the 11 individuals from prehistoric Pohnpei (Fig. 4B). FRO$_{\text{SouthwestPacific}}$ is a better single-source proxy for the primary First Remote Oceanian ancestry in Central Micronesia than FRO$_{\text{Marianas}}$, but an entirely FRO$_{\text{SouthwestPacific}}$ source fails in *qpAdm* when Unai and Latte are included as outgroups, suggesting that both FRO$_{\text{SouthwestPacific}}$ and FRO$_{\text{Marianas}}$ contributed. These findings also illuminate the origins of Nuclear Micronesian languages. Central Micronesians lack the Papuan ancestry that is predominant in the Solomon Islands, providing evidence against one of the three main candidate geographic regions (*24*). They also lack the Papuan$_{\text{NewBritain}}$ signature that was ubiquitous in Vanuatu by the time of the peopling of Central Micronesia, providing evidence against another candidate region. Instead, *qpAdm* shows that the people of Manus are a better proximate source for the Papuan$_{\text{NewGuinea}}$ ancestry than those of mainland New Guinea (table S24), increasing the likelihood of the third candidate—the Admiralty Islands—as the source for these languages and for the stream of migration that brought them. This should not be interpreted as implying that people specifically from Manus Island were the true source, but rather that the source was probably a genetically similar population from the Admiralty Islands or a coastal region along the northern fringe of mainland New Guinea.

We infer dates of FRO$_{\text{SouthwestPacific}}$-Papuan$_{\text{NewGuinea}}$ mixture in Chuuk and Pohnpei of 2100 to 1800 BP, showing that these lineages came into contact at least by the time of the peopling of Central Micronesia around 2000 BP and raising the possibility that the M3 and M4 lineage expansions into Central Micronesia came as part of an already mixed stream of people speaking early Nuclear Micronesian. An alternative, however, would accommodate a different perspective on the origins of Nuclear Micronesian languages, allowing M3 to have come from a FRO$_{\text{SouthwestPacific}}$ group that spoke a Southeast Solomonic language (*30*), to be joined later by an M4 Papuan-Admiralties group that did not displace already established Nuclear Micronesian languages. Such a scenario of language continuity despite population replacement would parallel the situation posited for Vanuatu (*8*, *9*). We do not yet have data from Yap but, given that Yapese is an earlier branching Proto-Oceanic language, we hypothesize that the indigenous Yap islanders might derive from a different mixture of source populations than other Central Micronesians.

Matrilocality in early Pacific islanders

We observed a notable degree of mitochondrial DNA differentiation between the FRO$_{\text{Marianas}}$ and the FRO$_{\text{SouthwestPacific}}$ lineages. All of the Unai individuals with mitochondrial haplogroup determinations and without evidence of high contamination carried haplogroups E1 and E2 (table S2), whereas all of the Lapita individuals had haplogroup B4 (*7*–*10*). All three haplogroups were found in Iron Age Taiwanese (*5*, *6*), consistent with the finding that the Iron Age Taiwanese were relatively undrifted descendants of a population that was also ancestral to the Unai and Lapita individuals. Such a high level of mitochondrial differentiation is surprising given the intermediate degree of autosomal differentiation as measured by F_{ST}, a standard statistic measuring population genetic differentiation, which is 0.083 between the Unai and Lapita groups. This raises the possibility of greater genetic drift on the maternal than paternal line during the early divergence and radiation of FRO lineages.

We carried out simulations to determine the probability that completely different mitochondrial macrohaplogroups spread over the two populations since they diverged, under the null assumption that males and females had the same demographic behavior and given the observed genetic drift on the autosomes (fig. S16). This null hypothesis is rejected (P = 0.0014, Fisher's exact test) (*31*). The P values are not sensitive to assumptions about the split time of the $\mathrm{FRO_{Marianas}}$ and the $\mathrm{FRO_{SouthwestPacific}}$ lineages (table S28). These patterns are qualitatively opposite to those in Neolithic and Bronze Age Europe, where patrilocal patterns of greater female than male mobility among households have been inferred by analyzing ancient DNA data (*32*, *33*). Matrilocality in early Remote Oceanians has been hypothesized based on genetic and ethnographic studies of present-day communities, many of which have matrilocal practices in which women tend to raise their children in the same households in which they grew up (*34*, *35*). Our results provide direct evidence for the practice of matrilocality among FRO populations.

These findings concerning matrilocality among the ancestors of Lapita and Unai individuals with little if any Papuan ancestry are not related to previous evidence of sex-biased admixture between Papuan and FRO ancestry in some Pacific populations (*7*). However, a new finding of this study does concern sex-biased mixture. Specifically, we find that the Papuan ancestry in Palau and Central Micronesia was primarily derived from male ancestors, based on significantly more Papuan ancestry on the autosomes than on the X chromosome ($|Z|$> 2.2 to 3.3) (Fig. 4E and table S29) (*7*). This is notable because each of the three cases of FRO-Papuan admixture that are now documented (Palau, Central Micronesia, and southwest Pacific and Polynesia) involved a different pair of Papuan and FRO groups. These events must have been independent, and yet all share the feature of Papuan ancestry being transmitted primarily by male ancestors.

Family structure and population size during the Latte period

We measured runs of homozygosity (ROH) that were longer than 4 centimorgans (cM) for 113 Latte individuals with high-enough-quality data to allow such analyses (table S30). Only two had single stretches of ROH longer than 50 cM, indicating that close-kin unions were avoided in Latte people. Nine individuals from Guam and nine from Saipan had at least one ROH longer than 20 cM, suggesting that mating pairs of close relatives such as second or third cousins on both islands were relatively common. Shorter ROH signals (>4 cM) were also abundant, implying a limited pool of reproductive partners in every generation. We estimated the size of the population from which the Latte individuals in Guam and Saipan were drawing their reproductive partners to be 315 to 356 individuals in Guam and 361 to 424 individuals in Saipan (table S32).

We further analyzed long shared DNA segments [identical by descent (IBD) blocks] between the X chromosomes of male individuals (one from Guam and the other from Saipan). We identified 149 pairs of individuals who shared IBD segments longer than 8 cM (table S31). This puts an upper bound on N_e, the size of the mating population in the combined Mariana Islands, of 1203 to 1712 (95% confidence interval) (table S32). If there were restricted migration between islands, or if there were temporal variation in the dates of the individuals we compared, these numbers would be overestimates. This implies a long-term small population size or strong founder event in Latte history.

We identified 122 pairs of closely related Latte individuals (up to third-degree relatives) (fig. S17 and table S33). Eighty of 125 Latte individuals that were studied had one or several close relatives.

Discussion

A notable finding of this study is that the phenomenon of primarily male Papuan migrants mixing with previously resident FRO populations ~2500 to 2000 BP occurred at least three times, because the pairs of mixing sources were different in three regions (Fig. 4D). One of these migration and mixture processes occurred at an average date of ~2500 to 2200 BP, with $\mathrm{Papuan_{NewGuinea}}$-$\mathrm{FRO_{Palau}}$ mixture forming modern Palauans. A second occurred ~2300 to 1600 BP, with $\mathrm{Papuan_{NewGuinea}}$-$\mathrm{FRO_{SouthwestPacific}}$ mixture forming ancient and modern Central Micronesians. A third occurred ~2300 to 1500 BP, with $\mathrm{Papuan_{NewBritain}}$-$\mathrm{FRO_{SouthwestPacific}}$ mixture forming the ancestry of ancient and modern people of the southwest Pacific and Polynesia (*7*). All three mixtures were sex asymmetric, with most of the Papuan ancestry deriving from males (Fig. 4C). Even in the Mariana Islands, where there is no evidence of Papuan mixture, the inferred $\mathrm{FRO_{Palau}}$-$\mathrm{FRO_{Marianas}}$ mixture date in Latte individuals is ~2400 to 1700 BP, providing a fourth example of migration and mixture in Remote Oceania occurring on average ~2500 to 2000 BP, well after the initial peopling events that involved entirely FRO groups.

A high-resolution ancient DNA time transect in Vanuatu has revealed the dynamics of this process in the southwest Pacific, where an initial $\mathrm{FRO_{SouthwestPacific}}$ migration stream likely from New Britain changed into a primarily male $\mathrm{Papuan_{NewBritain}}$ stream in the late Lapita period, likely deriving from the same source region and following previously established communication routes (*36*). Our results raise the possibility of similar processes in at least two other regions. The oldest pottery discovered in Pohnpei at ~2000 BP, which resembles that of late Lapita (*19*), provides an archaeological correlate for a spread of mixed $\mathrm{FRO_{SouthwestPacific}}$-$\mathrm{Papuan_{NewGuinea}}$ ancestry into this region. Parallel processes could have drawn $\mathrm{Papuan_{NewGuinea}}$ ancestry into Palau and $\mathrm{FRO_{Palau}}$ ancestry into the Mariana Islands.

Our identification of the $\mathrm{FRO_{Palau}}$ lineage raises the possibility that the three FRO lineages correspond to the first-order three language splits in Malayo-Polynesia: $\mathrm{FRO_{Marianas}}$ leading to the CHamoru language and associated with the Unai burials dated to ~2800 BP; $\mathrm{FRO_{SouthwestPacific}}$ leading to CEMP languages and associated with the Lapita archaeological complex and burials dating to ~3000 BP in Vanuatu; and $\mathrm{FRO_{Palau}}$ bringing ancestral Palauan and plausibly the first ancestry type in Palau because mitochondrial DNA of 3000 to 1800 BP remains from Chelechol ra Orrak suggests East Asian ancestry (*37*).

The ordering of the FRO lineage splits is also important. The fact that the $\mathrm{FRO_{Palau}}$ lineage split first cannot be explained by the theory that there was a single First Remote Oceanian spread into the Mariana Islands (*28*, *38*), which then gave rise to the other lineages, because in this case, $\mathrm{FRO_{Marianas}}$ would have branched first. The theory of a Mariana population being ancestral to all FRO lineages is further challenged by the mitochondrial DNA evidence. If this theory were correct, the most parsimonious expectation is for the haplotypes observed in the Unai individuals from Guam at 2800 to 2200 BP (E1 and E2) also to be observed in the Lapita individuals at 3000 to 2500 BP. However, only mitochondrial haplotype B4a1a1 (the "Polynesian motif") is observed. Therefore, our results point to a scenario in which three First Remote Oceanian lineages branched from a trunk of MP speakers in Island Southeast Asia, with at least three independent streams of migrations into Remote Oceania.

Since colonial times, Pacific peoples have been divided into "Melanesians," "Polynesians," and "Micronesians," driven by theories of shared origins (*39*). However, our results show that people in Micronesia have a diversity of ancestral origins even within the same geographic region, implying that the term "Micronesian" should be used as a geographic label without implying a specific biological profile.

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SUPPLEMENTARY MATERIALS

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Science

Ancient DNA reveals five streams of migration into Micronesia and matrilocality in early Pacific seafarers

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Human migrations into Micronesia
The movements of ancient humans can be difficult to ascertain from their current population genetic structure. Studying the peopling of the Micronesian islands, Liu *et al*. examined 164 ancient human remains from five different archaeological sites in remote Oceania from different prehistoric time frames, along with 112 present-day individuals from the same area. They combined these new data with the results of previous studies and also compared their results with linguistic studies. Their analysis revealed successive movements from island Southeast Asia that differ from those in the southwest Pacific. Furthermore, co-analysis of Micronesian and southwest Pacific ancient DNA indicates that the first people who colonized the Pacific islands had a population structure in which men moved to find their mates, whereas women rarely moved to join men. —LMZ

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