

Supplementary Note 1: The Teouma site

The Teouma Lapita site is located on the south coast of Efate Island, Vanuatu, and is currently 800 meters from Teouma Bay. Tectonic uplift, volcanic ashfalls prior to and during the period of human utilisation of the site, and alluvial deposition from an adjacent stream have altered its immediately coastal location during Lapita times. Excavations by a joint ANU-Vanuatu National Museum team took place between 2004 and 2010¹⁻³, during which 68 burial features, including remains of just over 100 individuals were found, concentrated in a band running northeast to southwest, parallel to the former beach and some 10-15m wide. Teouma has numerous indicators of being an initial colonisation site for Efate, including extinct faunal remains, early ceramic forms and decoration, and New Britain obsidian. This combined with the extensive and previously very rare Lapita skeletal remains underline its significance to those investigating colonization in this region.

There are two key zones of the site; the Cemetery Zone (CZ) and the Midden Zone (MZ) located to the east of the Lapita cemetery, that both comprise three layers. The Lapita midden contained a number of domesticated species (i.e., *Sus scrofa*, *Gallus gallus* and the commensal *Rattus exulans*), as well as a large number of bones from indigenous birds and animals, many now extinct, including land tortoise (*Meiolania damelipi*), crocodile (*Mekosuchus kalpokasi*) and a range of bird species^{2,4,5}. Layer 3 of the Midden Zone (MZ3) deposit is considered to be contemporary with Layer 3 of the cemetery (CZ3) and both are emplaced onto a pre-human tephra deposit⁶. A later midden deposit (Layer 2 Cemetery Zone [CZ2]), up to 50 cm thick, covered the cemetery and extended downslope over the former beach and within alluvial deposits from the adjacent stream, representing a shift to purely habitation use at the main site. This is associated with Post-Lapita Arapus and Early Erueti ceramics currently dated to c. 2800-2500 BP². Continued tectonic uplift and alluvial deposition led to abandonment of the settlement as immediate access to the sea became problematic because of shoreline progradation. Layer 1 from both zones has not been dated but represents natural post-occupation accumulation, rich in tephra from the 2300 BP eruption of Nguna Island to the north. In Area 7C some 70m south of the main Teouma site further burials were located, dating to within the Erueti phase at about 2400 BP⁷.

An extensive dating program has been undertaken at the site on a range of materials including charcoal and marine shell, as well as human, terrestrial native fauna and domesticate bones^{8,9}. That analysis places the start date of the Lapita deposits at 2920-2870 cal BP with a possible use as early as 3000 cal BP, and an end date of 2870-2750 cal BP. The results are in keeping with evaluation of the burials (36 direct dating on human cranial and infracranial elements⁸), which places earliest use of the cemetery at c. 2970 cal BP with regular use underway by c. 2940-2880 cal BP and the last internment occurring c. 2770-2710 cal BP. Continued use of the area is evident by the later burials nearby dating to the end of the Erueti phase and by components of the

CZ2 midden deposits of post-Lapita age.

The exceptionally well-preserved and extensive Lapita skeletal remains have provided an opportunity to start to establish a population profile, gaining insights into the health, morphology and diet of a group of Lapita settlers who were among the first to have ventured into Remote Oceania. The 68 burials at Teouma display a wide range of mortuary practices and indicate that ritual was a multi-faceted and on-going process, rather than a one-off event. The burials were generally placed in shallow graves dug into the underlying tephra deposits amongst gaps in the uplifted reef and coral boulders on the upper part of the beach. Evidence indicates manipulation of the corpse prior to burial or at least during the early stages of decomposition and of the skeletal remains after body decomposition. All the adult burials had their skulls, and often many other bones, removed during this process and only a few of these bones were secondarily re-deposited at the site^{1,3,10,11}. Nine skulls were found out of a total of 52 infracranial skeletons in articulation. Although disconnected from infracranial skeletons, the cranial elements appears to have belonged to the same group as shown by similarities in isotopic values measured in bone collagen and dental enamel. Seven of them, belonging to female and male adults, were preserved well enough for morphological examination. Five of them were useable for metrical analysis that demonstrated that each displays a lack of Australian or Papuan affinities and an alignment with ancient and more recent Asiatic populations¹². Ancient DNA was successfully obtained from three skulls from striking mortuary contexts: a jar burial containing a single skull (B17), an alignment of three skulls lying on the chest of a skeleton without a skull (B10B), and a triangular bone arrangement, with skulls at each vertex, lying on the legs of a skeleton without a skull (B30A).

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Supplementary Note 2: The Talasiu site

The Talasiu site (TO-Mu-2) is located on the palaeoreef-limestone shoreline of the Fanga 'Uta Lagoon around 10 kilometers from Nuku'alofa and immediately north of Lapaha Village. The site consists of a dense shell midden deposit ~90 cm thick covering some 450 square meters and includes fire features and burials. The palaeoshoreline at Talasiu is fronted by reclaimed land that was deposited in the lagoon during the expansion of the Tu'i Tonga chiefdom 800-200 cal. BP. During the Lapita period in Tonga (2900-2650 cal. BP) (95.4% prob.)¹, the Talasiu site would have been an attractive location for human settlement as it overlooked an embayment holding large numbers of sessile and gregarious shellfish close to a fresh water solution channel, with gardening soils immediately inland. The site was first investigated in 1957 by Jack Golson (ANU) and in the 1980s by Dirk Spennemann (ANU) who surface collected pottery (including sherds decorated with dentate-stamping) lithics and human bone^{2,3}. Site monitoring after road grading in 2008 identified a concentration of burned and partially burned human bone which was excavated and found to be a cremation mortuary context containing the incomplete remains of four individuals⁴. In 2011, new burials were found eroding from the road cut and as the area was about to be intensively gardened a rescue archaeology project to recover human remains was directed by Frederique Valentin (CNRS) and Geoffrey Clark (ANU) in 2013-2014 with the support of the Ministry of Internal Affairs (Kingdom of Tonga) and funded by the French Government (MAEDI, Commission des fouilles à l'étranger).

The site stratigraphy consists of a series of six layers distinguished by varying quantities of shellfish, ceramics, charcoal and bone resting on sterile basal clay (Layer 6). The 95% probability range of radiocarbon determinations obtained on coconut endocarp (n=5), unidentified charcoal (n=2), worked shell grave goods (n=3) and human bone sample on articulated burials (n=6) fall between 2870 and 2340 cal. BP. Calibrated charcoal and bone ¹⁴C ages between 2600 and 2300 BP are influenced by curve flattening resulting in multiple curve intercepts and a substantial widening in the calibrated age range of determinations. However, a high-resolution chronology based on U-Th dating of coral files and AMS determinations on short-lived material demonstrates the Lapita period on Tongatapu spanned 2900-2650 cal. BP¹ and it is highly likely that the midden and burials at Talasiu date to ~2700-2600 cal. BP² and are of late Lapita/immediately post-Lapita age.

Analysis of the midden using archaeozoological and microbotanical techniques provided evidence for a broad spectrum mixed economy in Tonga². Pottery was predominantly plain with dentate-stamped vessels bearing simple open designs typical of late Lapita ceramics throughout the deposit. Shell artefacts included short and long shell units, broad *Conus* spp. rings, and narrow rings made in *Conus* spp. and *Tridacna* spp. that are characteristic Lapita ornaments. Lithics included adzes, flakes, grind stones and oven stones. Thin-section and compositional study of the lithics with pXRF and LA-ICP-MS identified obsidian flakes from Tafahi in

northern Tonga⁵, adzes made in volcanic material chemically sourced to Central Tonga, eastern Fiji and Samoa, and manuports and grindstones/oven stones from nearby 'Eua Island and Central Tonga^{2,5,6}.

The 19 late-Lapita/immediately post-Lapita burial contexts at Talasiu were placed at the base of the midden or interstratified within the midden. Intact lenses of ash and marine shell overlying several burials conclusively demonstrate that interments were made during midden formation. The burials were single or multiple interments containing the skeletal remains of one to six individuals (male and female adults and children of various ages). Field evidence indicates a wide range of mortuary practices involving primary burial in various positions, secondary deposits of burnt⁴ or unburnt bone, including placement of isolated skulls, and post-decomposition removal of skulls and long bones. This diversified mortuary pattern recalls that of late Lapita and immediately post-Lapita burials from sites in Vanuatu⁷, while the body treatment of some individuals is the same as at the Lapita site of Teouma⁸⁻⁹. These 19 burial contexts have yielded the skeletal remains of 62 individuals, providing an opportunity to obtain information on health, diet and morphology of a group of late Lapita/immediately post-Lapita people from Tongatapu, using macroscopic and microscopic observations and biogeochemical and palaeomolecular data.

Preliminary metrical analysis performed on one skull (BG3) shows that the individual lacks Australian or Papuan affinities and instead has affinities to mainland Asian populations, as do the Teouma Lapita skulls¹⁰. Ancient DNA was successfully obtained from the right petrous bone of burial SK10, a single primary interment of an adult female with a marine-adjusted calibrated age of 2680-2340 cal. BP (95.4% confidence interval; see **Extended Data Table 1**). The SK10 ¹⁴C calibration is influenced by the radiocarbon plateau around 2600-2300 BP, which results in a wide spread in the calibrated age range. It is important to note that this burial was sealed by a layer of intact midden which is inferred from essentially identical radiocarbon results on carbonized coconut shell from the upper/middle and basal layers to have been deposited around 2700-2600 cal. BP².

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Supplementary Note 3: Population history graph models

We used admixture graph models to model the population history of Oceania and Polynesia. For our main analyses, we used *qpGraph*^{1,2} to test systematically a variety of historical models, and to assess their fit to the data, but see also our complementary analysis with *TreeMix* documented in the **Methods** section and **Extended Data Figure 4**. For *qpGraph*, we focused on assessing whether graphs fulfill the criterion that all or nearly all f_4 -statistics predicted by the model are consistent with the empirical statistics. We refer to individual f_4 -statistics with $|Z| > 3$ between empirical and predicted statistics as 'outliers', providing evidence for unmodeled shared genetic drift between populations. We also assess the relative fit of models by considering a sum of squared differences-statistic (RMSE) summarizing the overall fit between predicted and empirical f -statistics, but note that the distribution of this statistic under arbitrary admixture graph models is not known.

We focused on a set of populations representing broad genetic and geographic diversity:

1. Outgroup: African Yoruba
2. Unadmixed Papuans: New Guinean Highlanders
3. Mainland East Asia: Dai Chinese
4. Indigenous Taiwanese: Atayal
5. Philippines population without Papuan ancestry: Kankanaey
6. Philippines population with Papuan ancestry: Mamanwa
7. Northern Solomons Papuan-speakers who are a mixture of Papuan and First Remote Oceanian ancestry: Nasioi (HGDP Bougainville)
8. Solomon Islander Austronesian-speakers who are a mixture of Papuan and First Remote Oceanian ancestry: Kolombangara
9. Polynesians: Tongan
10. Australians

A 'skeleton graph' of a tree-like population history that fits the ancient DNA data

We first added Lapita_Vanuatu to all 8 possible edges of a skeleton phylogeny of (Yoruba, (New_Guinea, (Dai, (Atayal, Kankanaey))))), which we found fitted the data without outliers either using all SNPs or only transversions. Two principal graph topologies fitted with no outliers, one of which modeled the Lapita_Vanuatu as being most closely related to the Kankanaey of the Philippines, and the other which modeled the Lapita_Vanuatu, Atayal, and Kankanaey as a trifurcation. Since the trifurcation model also had a slightly greater chi-squared statistic (RMSE=1.71) than the model in which the Lapita_Vanuatu share on the order of $F_{ST} = 0.001$ drift with the Kankanaey lineage (RMSE=1.58), we continued to use the latter graph, but note that the shared drift between the Kankanaey and Lapita_Vanuatu is small.

Adding populations to the skeleton graph

We proceeded by adding four genetically differentiated populations as mixtures of all 45 possible pairs of edges of the graph: the Polynesian Tongans, the Solomon Islander Kolombangara, the Northern Solomons Nasioi (HGDP Bougainville), and the Philippine Mamanwa³.

Tongans, Kolombangara, and Nasioi

We found that Tongans, Kolombangara and Nasioi can only be fit as having derived their ancestry from the First Remote Oceanian lineage on the one hand, and the New Guinean Highlander lineage on the other hand, with no outlier statistics and $\chi^2 < 1.9$ for all three populations. All other graphs for Tongans and Kolombangara have 32 or more outlier statistics, and $\chi^2 > 15$. The second best fitting graph for Tongans posits that Tongans received their Austronesian ancestry from the Atayal lineage, but this graph has 50 outlier f_4 -statistics; for example f_4 (Yoruba, Tongan; Atayal, ancient Oceanians) which is predicted to be ~ 0 in this graph is empirically 0.021 ($Z=9.6$). In addition, this graph has a chi-squared statistic of $\chi^2 = 41$ compared to 1.6 for the best fitting graph. For Nasioi the second best fitting graph has 10 outlier statistics, but a slightly smaller χ^2 -statistic (5.3). We conclude that there is overwhelming evidence that all three populations received their non-Papuan ancestry from a source most closely related to the Lapita_Vanuatu, which in this paper we call the First Remote Oceanian lineage.

Mamanwa

We found that there were three phylogenies that fit the Mamanwa without outliers. One portion of Mamanwa ancestry was in all cases derived from the lineage leading to New Guinean Highlanders, but the second source was either the First Remote Oceanian lineage, the Kankanaey lineage, or the lineage ancestral to Kankanaey and the Lapita_Vanuatu. In all three cases the inferred drift length separating this second source of the Mamanwa ancestry to the (Lapita_Vanuatu, Kankanaey) ancestral node was $F_{ST} = 0.0001$. We are thus not able to uniquely place the Mamanwa with respect to the First Remote Oceanians and Kankanaey, but use the placement along the Kankanaey lineage due to a smaller chi-squared statistic.

Modeling Tongans, Solomon Islanders and Bougainville populations simultaneously

We next proceeded to testing all possible models that included two populations out of the set (Tongan, Kolombangara, Nasioi). To do this we used the unique fitting graph for each population from our initial additions to the skeleton graph, and added the two others as mixture between all possible edges of that graph. We find that for all these combinations of populations there are at least 23 graph topologies without outliers, and we thus do not have enough resolution in the data to distinguish between different graphs that include these populations simultaneously. We therefore focus on graphs where only one of these populations is included at the same time.

Adding populations to a skeleton graph with Australians

We also consider a graph that models Australians as a clade with New Guineans (Yoruba, ((New_Guinea, Australian), (Dai, (Atayal, (Kankanaey, Lapita_Vanuatu))))). The Lapita_Vanuatu fit in this graph as a clade with Kankanaey without outliers, but when we add Tongan, Kolombangara, Nasioi and Mamanwa as admixed between all possible 66 pairs of graph edges, there are no solutions without outlier statistics. For the Tongan, Kolombangara, and Nasioi, the best fitting graph posits that they are mixed between the Lapita_Vanuatu and New Guinea Highlander lineages, although both the Nasioi and Tongan graph show outliers (2 and 7, respectively) suggestive of unmodeled affinity to Australians. For Tongans:

$f_4(\text{New_Guinea, Australia; Dai, Tongan})$: model = -0.011118, empirical = -0.006075, ($Z = 4.9$)

$f_4(\text{New_Guinea, Australia; Atayal, Tongan})$: model = -0.011118, empirical = -0.005472, ($Z = 4.9$)

The Mamanwa are optimally fitted as a lineage basal to Australians and New_Guineans, but a single $Z = 3$ outlier ($f_4[\text{Yoruba, Mamanwa; New_Guinean, Australian}]$) suggests that the portion of Mamanwa ancestry related to Papuans and Australians is slightly closer to Australians. The difference between this statistic and the statistic in **Table S1** (see below) is that the graph statistic is based on transversion SNPs where we have at least one Lapita_Vanuatu genotype.

Graphs that can account for the excess affinity between Oceanians and Australians

We have shown that when we model the non-First Remote Oceanian ancestry of Tongans as entirely Papuan—with the lineage leading to Australians basal to both lineages—we observe more allele sharing between Tongans and Australians than is predicted by this model. In contrast, differences between Australians and Papuans affinity are not detectable in non-Oceanians, who are approximately symmetrically related to Australians and Papuans (**Table S1**).

Table S1. Australians and New Guinean Highlanders are approximately symmetrically related to non-Oceanians based on the statistic $f_4(\text{Yoruba, X; Australian, New_Guinea})$.

<i>X</i>	f_4	<i>Z</i>
Primate_Chimp	0.000044	0.1
Dinka	0.000078	0.5
Sardinian	-0.000558	-1.6
Onge	0.000287	0.7
Dai	0.000214	0.6
Atayal	0.000261	0.6
Karitiana	0.000289	0.6
Mixe	0.000076	0.2
Mamanwa	0.000819	2.3
Tongan	0.002998	7.7
Kolombangara	0.002590	6.6

We tested different permutations of a graph where either Papuans, Australians, or Tongans are admixed (and excluded the Kankanaey for simplicity), and found that the only permutation tested that resulted in no outliers posited that the Papuan population that contributed ~25% of the ancestry of Tongans also contributed ~45% of the ancestry of Australians (**Extended Data Figure 3**). An alternative graph that only has a single $Z=3.17$ outlier posits that the non-First Remote Oceanian portion of Tongan ancestry is itself admixed between Papuan- and Australian-related sources. We cannot statistically distinguish between these two models, but conclude that there is evidence for complexity in the history of Papuans, Australians and Polynesians.

Graph model with Tongans and Mamanwa

Combining the observations from the systematic tests of all possible placements of different populations on skeleton graphs above, we find that:

1. Tongans, Nasioi and Kolombangara are generally fitted as mixed between the same two lineages: First Remote Oceanian represented by the ancient samples, and Papuan.
2. The Philippine Mamanwa can be fitted as being mixed from a lineage related to the Philippine Kankanaey, and a lineage that split off prior to the separation of the ancestors of Papuans and Australians.
3. Australians cannot be successfully fit as an outgroup to the non-First Remote Oceanian ancestry in Tongans, and will be treated separately.

We found that a graph with Mamanwa and Tongans results in an excellent fit with no outliers. We also confirmed that Tongans could be successfully replaced with Nasioi or Kolombangara without resulting in a poor fit.

Extended graph model with archaic human genomes and Onge Andaman Islanders

In the above, we do not model the Neanderthal ancestry that separates non-Africans from Africans, or the Denisovan ancestry that separates Australians and Papuans from other populations. While this ancestry is important when considering the histories of these populations, the reason that we can successfully fit Australians and Papuans without modeling their Denisovan ancestry in our graphs is that the difference in archaic ancestry between the Australians and Papuans and mainland non-Africans can be accounted for by shifting the bifurcation point with Yoruba Africans. If multiple African populations with different divergences from non-Africans had been included the Denisovan component of Australian and Papuan ancestry would be expected to share different amounts of drift with the African populations as they have different degrees of relatedness to non-Africans. This would make it impossible for a model that does not model the archaic admixtures to accommodate the real data.

To fit an extended model incorporating archaic admixture inferred by previous studies, we used chimpanzee as an outgroup, and both the archaic Denisova and Altai Neanderthal genomes^{4,5}. Following previous findings, we modeled the Denisovans as being admixed between the Neanderthal lineage and a more basal ('unknown archaic') lineage⁴. We also modeled

Neanderthal admixture in the ancestral non-African population⁶, and Denisovan admixture in the ancestral population of Australians and Papuans⁷. As a final expansion of our population history model, we added the Andamanese Onge on the lineage ancestral to Australians and Papuans but diverging prior to the Denisovan admixture event³. We found that the resulting graph (**Figure 3A**) fits well given the large number of populations included. There are only two outliers that deviate by slightly more than 3 standard errors from empirical statistics:

$f_4(\text{Yoruba, Tongan; Denisova, Altai}): \text{model} = 0.001284, \text{empirical} = 0.006947, (Z = 3.1)$

$f_4(\text{Atayal, Mamanwa; Onge, Tongan}): \text{model} = -0.010912, \text{empirical} = -0.007444, (Z = 3.2)$

The first outlier could be interpreted as suggesting unmodeled affinity between Tongans and Neanderthals, but the second one is more difficult to interpret, as it is consistent for example with unmodeled affinity between Mamanwa and Tongan or Onge and Atayal.

Adding the ancient Tonga sample

For the graph we display in **Figure 3**, we do not include the Mamanwa but added the Lapita_Tonga sample which despite being represented by only a single individual can be adequately fitted as being a clade with the Lapita_Vanuatu sample. The three minor outliers with Z-scores between 3 and 3.5 were all for population configurations that have little to do with the history of admixture and population splits in Oceania that we are most interested in:

$f_4(\text{Yoruba, New_Guinea; Yoruba, Dai}): \text{model} = 0.143671, \text{empirical} = 0.133643, (Z = 3.3)$

$f_4(\text{Yoruba, Dai; Yoruba, Dai}): \text{model} = 0.193597, \text{empirical} = 0.183619, (Z = 3.0)$

$f_4(\text{Yoruba, Dai; Dai, Atayal}): \text{model} = 0.004789, \text{empirical} = -0.000185, (Z = 3.4)$

We note that we can also fit modified models with the Lapita_Tonga as being a clade with the First Remote Oceanian lineage contributing to present-day Tongans with approximately the same support, but we chose to conservatively display the graph in **Figure 3**.

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