

Fast trains, slow boats, and the ancestry of the Polynesian islanders

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The question of the origins of the Polynesians has, for over 200 years, been the subject of adventure science. Since Captain Cook's first speculations on these isolated Pacific islanders, their language affiliations have been seen as an essential clue to the solution. The geographic and numeric centre of gravity of the Austronesian language family is in island Southeast Asia, which was therefore originally seen as their dispersal homeland. However, another view has held sway for 15 years, the 'out of Taiwan' model, popularly known as the 'express train to Polynesia'. This model, based on the combined evidence of archaeology and linguistics, proposes a common origin for all Austronesian-speaking populations, in an expansion of rice agriculturalists from south China/Taiwan beginning around 6,000 years ago. However, it is becoming clear that there is, in fact, little supporting evidence in favour of this view. Alternative models suggest that the ancestors of the Polynesians achieved their maritime skills and horticultural

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Neolithic somewhere between island Southeast Asia and Melanesia, at an earlier date. Recent advances in human genetics now allow for an independent test of these models, lending support to the latter view rather than the former. Although local gene flow occurring between the bio-geographic regions may have been the means for the dramatic cultural spread out to the Pacific, the immediate genetic substrate for the Polynesian expansion came not from Taiwan, but from east of the Wallace line, probably in Wallacea itself.

Introduction

The patterns of human diversity in the remote Pacific are unique. The vast expanse of the Polynesian triangle, from Tonga and Samoa to Hawaii, New Zealand and Easter Island, is peopled entirely by speakers of a single major group of languages, the Austronesian family, and the archaeological record shows that this peopling took place within the last 3,500 years. Migration models fell from favour amongst prehistorians during the 1960s and 1970s, but the remote Pacific clearly provides a case in which people must have settled the region from outside, bringing their languages and cultural practices with them.

Even though this much is clear, however, the ultimate ancestry of the Polynesians has remained a hotly disputed topic. Now, however, a new kind of evidence is coming into play. Although classical genetic markers (such as blood groups) have been studied for many years in the hope of elucidating the history of human populations, only in the last few years has the molecular revolution in genetics begun to impact on the study of the Pacific islands. There are obvious reasons why genetic data are crucial. Archaeologists attempt to reconstruct material culture and date it but, in the absence of written texts and skeletal remains, they have less success identifying the origins of the *manufacturers* of their assemblages. Similarly, linguists can reconstruct the branching history of their languages, but they have no direct evidence for the origins of the *speakers* of those languages. Furthermore, when archaeological and linguistic lines of evidence are combined, they may become mutually self-supporting to the extent of circularity – and this may have happened in the case of the modern consensus view of Pacific prehistory. Since genetics can now directly trace the ancestry of genetic lineages of modern individuals back through time on a genealogical tree, it provides the ideal test for hypotheses based on demographic assumptions. As the dust begins to clear, the genetic evidence looks set to revolutionise our understanding of the colonisation of the Remote Pacific¹.

Polynesian origins

Since Captain Cook's time, the question of Polynesian ancestry has usually been linked with the question of the origin of the Austronesian language family (Figure 1). These languages are spoken throughout Polynesia, through much of coastal Melanesia (the New Guinea coast, the Bismarcks, the Solomons, New Caledonia and Fiji), and throughout island Southeast Asia (Indonesia, East Malaysia and the Philippines) – but not inland in New Guinea (where Papuan languages are spoken), and not on the Southeast Asian mainland (with a few exceptions believed to be recent introductions).

There are three principal hypotheses concerning Polynesian ancestry (Figure 2). The first explicitly couples the Polynesian expansion with the spread of Austronesian languages through island Southeast Asia from mainland East Asia. This model, the predominant view at present, has been popularly called the 'express train to Polynesia'², but is better referred to as the 'out of Taiwan' model. It argues that the Austronesian language family as a whole evolved in Taiwan, 4,000–5,000 years ago, from a proto-language introduced

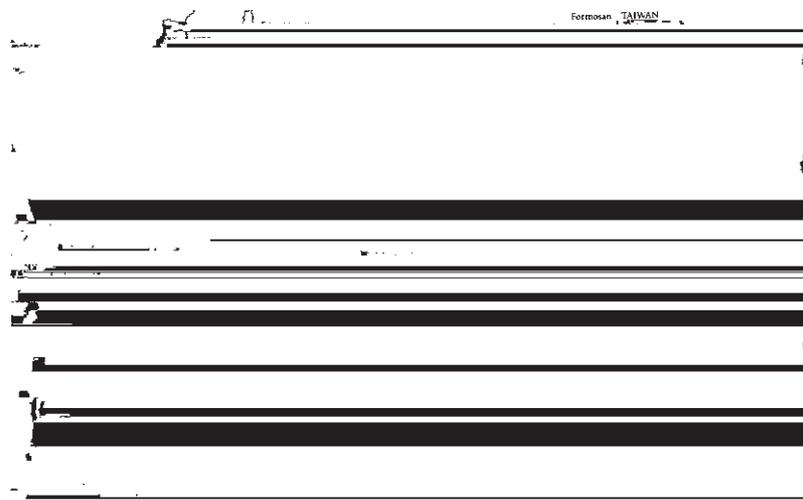


Fig. 1 Distribution of the Austronesian language family. This huge language family, as the name implies, is almost entirely located on islands of the southern Indo-Pacific region. Only the main high order groupings are shown here. For practical purposes, the most important division is between Oceanic and the Western Malayo-Polynesian group, with the languages of Wallacea sandwiched in between. Taiwanese languages form a divergent Formosan group.

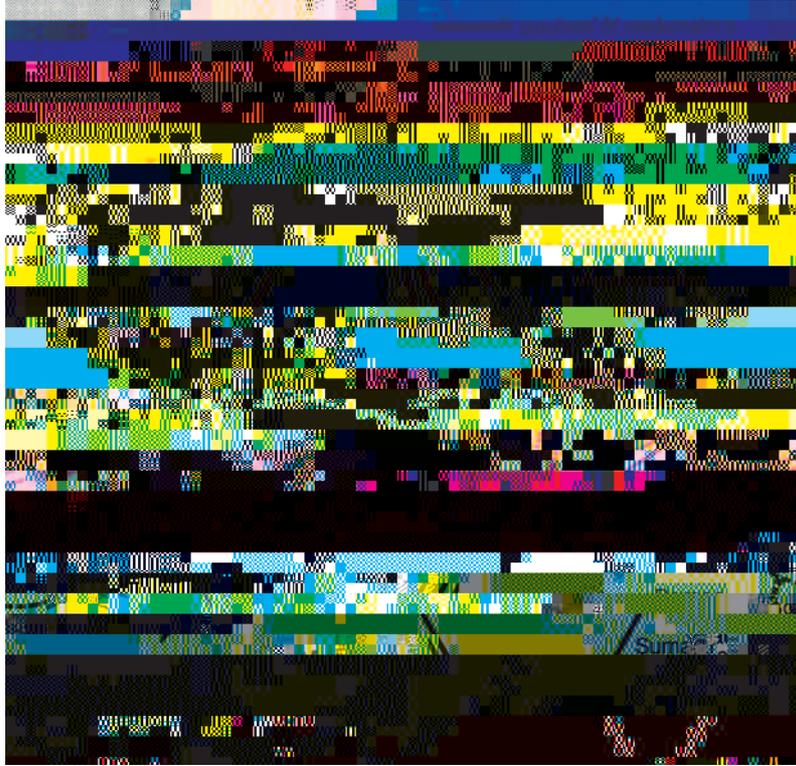


Fig. 2 *Origins of Polynesians. Map showing two main alternative views of Austronesian origins, on-shore and off-shore. The oldest view represented by Meacham (solid triangle), Terrell and Solheim (interrupted solid black line and circle) argues an Island Southeast Asian homeland (>5,000 BC). The 'out of Taiwan' view of a recent rapid migration from China via Taiwan (3,000–4,000 BC), spreading to replace the older populations of Indonesia after 2,000 BC, is shown as a red dotted line.*

from the south Chinese mainland by dispersing rice farmers 5,000–6,000 years ago^{3,4}. The Austronesian-speaking agriculturalists subsequently spread throughout the Philippines and into Indonesia, more or less replacing a putative indigenous hunter-gatherer population there. They moved on through the coastal parts of Melanesia (leaving the inland, horticulturalist populations of New Guinea intact), and finally spread out into the Pacific, into the previously unsettled territory of the Polynesian islands. On this view, the spread of genes, languages and culture (including the farming economy) were coeval.

However, several further hypotheses, all proposing offshore origins for the Polynesians, decouple the ultimate origins of the Polynesians from the spread of the Austronesian languages as a

whole. A second hypothesis argues, on the basis of lexical diversity within the Austronesian language family, that the Polynesians arose as a distinct people within Melanesia, and are therefore not closely related to Southeast Asians⁵. A third hypothesis argues that the Polynesians emerged from within island Southeast Asia, where the Austronesian languages themselves may previously have arisen⁶⁻⁸

The implications of this hypothesis for island Southeast Asia are quite staggering. According to the theory, until about 4,000 years ago island Southeast Asia was entirely inhabited by non-Austronesian-speaking 'Australoid' foragers. Today, apart from a few Papuan tongues (related to languages of west New Guinea) spoken in the eastern Nusa Tenggara, every single language in island Southeast Asia is now Austronesian. This implies that there was a near complete linguistic and ethnic replacement. It seems extraordinary that such an ethnic sweep – as this was supposed to be – should have left no relicts, linguistic or otherwise, of the former hunter-gatherer inhabitants of the huge island of Borneo, which ranks with New Guinea as one of the great tropical island wildernesses. If Austronesian languages had such difficulty replacing (let alone dominating) the pre-existing languages of Australia and New Guinea, how were they so extraordinarily successful in island Southeast Asia and in such a short time?

The answer given to this question has generally been that cultural and technological superiority of the incoming farmers, and their resulting higher demographic growth, led to the replacement of the foraging populations. This answer was modelled on a view of the spread of the European Neolithic, for which there is a much more substantial archaeological record. Archaeology, linguistics and the evidence of blood groups from genetics were all taken as supporting the view of a wave of advance of Indo-European speaking Near Eastern farmers overwhelming the indigenous foraging population. Recently, however, this view has been seriously undermined as a result of work in all three disciplines¹³.

There are reasons for thinking it may be no more appropriate in island Southeast Asia and the Pacific. In traditional societies of the region, the rigid conceptual dichotomy of one culture *versus* another breaks down – complementary and parallel development seem to be more the rule. While there are a few societies that are more or less exclusive nomadic hunter-gatherers, trading with more settled folk, many farming societies that live on the edge of, or within, the forest derive the bulk of their protein and vegetables from hunting and gathering. Polynesians show no evidence, present or past, of rice growing and cultivate the same root crops as Melanesians. Maritime foraging and boat skills, on the other hand, seem to have been important all the way from Southeast Asia to Polynesia. To describe modern Southeast Asian forest hunter-gatherers and Pacific marine foragers as 'devolved agriculturists' would seem to weaken the basis of the farming premise. In any case there are no attested cases of hunter-gatherer devolution in Borneo¹⁴.

The 'out of Taiwan' model has relied primarily on linguistics for the structure and geographic integrity of its migration route. This is a result of the branching structure of the Austronesian language tree.

ment in the 'out of Taiwan' tale. The south Chinese technology, proposed by Bellwood³ to motivate the expansion to Taiwan, was rice farming. Yet, the only islands in the Pacific that ever grew rice were the Marianas, and this practice could have resulted from a later, direct end-point colonisation from the nearby Philippines. The domesticated foodstuffs that the Pacific Austronesian speakers took with them were not rice, which spread only to Eastern Indonesia, but yams, bananas, breadfruit, sago, betel-nuts, coconuts and chickens. Such root and tree crops, and indeed the chicken, are indigenous to Southeast Asian and Melanesian cultures. Moreover, like terms for boat-building, the majority of the names for common Austronesian foodstuffs (with the notable exception of cereals) can only be reconstructed back to Proto-Malayo-Polynesian, and not Proto-Austronesian itself. This means that the 'out of Taiwan' argument entails that the entire subsistence basis of the advancing Austronesian speakers dramatically changed *en route* through island Southeast Asia^{3,15}; yet the subsistence base is intended to have driven the expansion in the first place.

One striking discontinuity is found in the distribution of domesticated pigs and dogs, regarded as specifically Austronesian gifts to New Guinea and the Pacific. The pig species that found its way first to New Guinea was not *Sus scrofa*, the common type in Eurasia and Southeast Asia, but *Sus papuensis*. This is regarded as a hybrid of *Sus scrofa* and *Sus celebensis*. The latter is indigenous to Sulawesi. It was domesticated there in the early Holocene, and was transported to Maluku and other parts of Wallacea where hybridization occurred¹⁶. This implies that pigs, although not initially part of the New Guinea horticultural revolution, may have been domesticated preceding the arrival of the hypothetical Taiwanese rice farmers in Wallacea some 4,000 years ago. New Guinea singing dogs, whose only near relation is the dingo, also appeared in New Guinea in association with humans between 5,000 and 6,000 years ago.

The case is weakened still further by the sheer paucity of evidence in island Southeast Asia for the spread of agriculture alongside the principal Neolithic archaeological markers, and the lack of clear origins for red-slipped pottery further back than the Philippines. Clearly, absence of evidence cannot be taken as evidence of absence. Even so, it is not always appreciated that, in comparison with the clear evidence for the spread agriculture into Europe, the evidence in island Southeast Asia is surprisingly weak³, relying to an alarming extent on the reconstructions of linguistic palaeontology.

An insular Polynesian homeland?

The principal alternative view is that Austronesian languages and the cultures of those that speak them evolved offshore from the Asian mainland, somewhere in the region they are spoken today

Terrell and Welsh¹⁰ have also argued that the ancestors of the Polynesians originated within the 'voyaging corridor' between Wallacea and the Solomon Islands, defined by Irwin⁹. Terrell has

Cranial morphology

This is the average outcome of polygenic factors and environment acting in concert; interpretation in genetic terms is highly problematic. Moreover, the skeletal record of the post-glacial but pre-Neolithic period in Southeast Asia is very poor, so that any attempt to date the onset of a 'Mongoloid' replacement is fraught. Where thorough studies have been carried out on modern Asian and Oceanic populations, however, the conclusion has been that Polynesians group somewhere between Southeast Asians and Melanesians, and not with Taiwanese or Chinese²⁰. Much of the early genetic study in Southeast Asia met with the same problems encountered elsewhere, and analogous to cranial morphology, namely that the classical autosomal markers being used were common to many populations, varying only slightly in frequency from one population to another. Work in the 1980s, on protein products of rare allelic variants and highly specific mapped globin gene abnormalities from Melanesia and Polynesia, started to change that.

Globin genes

The mapping of globin genes (Figure 3) in the 1980s suggested that there were two α -globin gene deletions, resulting in two forms of α -thalassaemia, found throughout coastal and lowland Melanesia, with potential as migration markers^{21,22}. One of these, the $\alpha^{3.7\text{III}}$ type, deletes one of the two genes that encode the α -globin part of the haemoglobin molecule. The $\alpha^{3.7\text{III}}$ type constitutes 60% of α -deletions found in the Austronesian speakers of the New Guinea north coast and the Bismarck Archipelago. It is also the dominant type found throughout the rest of island Melanesia, and is also found in Polynesia, although at lower rates than in Melanesia. It is, however, only found in Oceania and is rare in the highlands of New Guinea. The other type, $\alpha^{4.2}$, deletes the other of the two α -globin genes. In Melanesia, the latter is the dominant type in non-Austronesian speakers, especially of the north coast of New Guinea, where it is found either as a heterozygote or homozygote in 80% of the population. It also occurs throughout Austronesian speakers of island Melanesia, but at lower rates than the $\alpha^{3.7\text{III}}$ -deletion. Curiously, the $\alpha^{4.2}$ -deletion is notably *not* found in Polynesia^{23,24}.

In the case of both of these α -thalassaemia deletions, the flanking DNA sequences, known as α -haplotypes, indicate that they are local mutations (*i.e.*, not recently derived from Southeast Asia)²³. In other words, the $\alpha^{3.7\text{III}}$ -deletion may have travelled with Austronesian speakers right out to eastern Polynesia, but it arose locally, some-

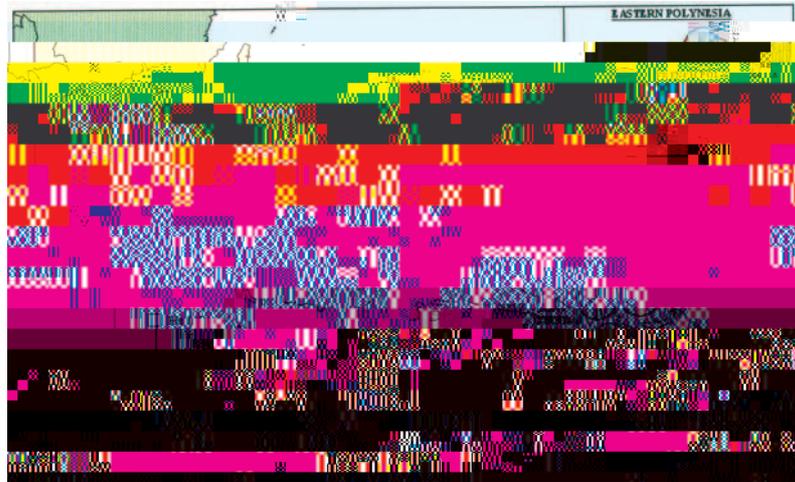


Fig. 3 Distribution of specific α -globin deletion haplotypes in Southeast Asia, Australasia and the Pacific. These ancient and unique deletions of α -globin genes, coding for part of haemoglobin molecule, have specific geographic distributions. Those in Oceania are not derived from anywhere west of the Wallace line, and certainly not from Taiwan. Ht1: Fil – (double alpha gene deletion); Ht 2: SEA – (Southeast Asian double alpha gene deletion); Ht 3: 4.2 kb single alpha deletion (Southeast Asian haplotype 1a); Ht 4: 3.7 kb deletion type I (Southeast Asian haplotypes 1a and 1a); Ht 5: 3.7 kb deletion type II; Ht 6: 4.2 kb single alpha deletion (Pacific haplotypes IIIa and IV); Ht 7: 3.7 kb deletion type I (Pacific haplotype IIIa); Ht 8: 3.7 kb deletion type III (Pacific haplotype IIIa). (Data from references 23, 24, 26, 45, 46.)

where along the voyaging corridor, around or off the north coast of New Guinea. Not only are they local, but these deletions may also be quite ancient. The unique $\alpha^{3.7\text{III}}$ -deletion has been around northern island Melanesia long enough to acquire a further mutation. This produces a variant haemoglobin molecule called Hb J Tongariki, which is found in some people on Karkar Island, off the north coast of New Guinea^{25,26}.

These observations suggest that the Polynesians' ancestors, if they were not local, must have stopped at least long enough to intermarry locally. There is, however, a problem with that supposed genetic interaction. If the Polynesians' ancestors stopped on the north coast of New Guinea long enough to pick up the $\alpha^{3.7\text{III}}$ -deletion, it seems strange that they failed to pick up the $\alpha^{4.2}$ -deletion as well, because it is present in over 80% of the non-Austronesian speaking people now living there. The $\alpha^{4.2}$ -deletion was carried only as far as the

Solomons and Vanuatu, and not further into Polynesia²⁴. The only possibility – apart from small canoes and extreme founder effects – that could explain this selective genetic divergence in northern Melanesia is that the contact area where the pre-Polynesians took on (or evolved) the $\alpha^{3.7\text{III}}$ -deletion was offshore from the New Guinea mainland. By offshore we might include the Bismarck Archipelago (Manus Island, New Ireland and New Britain) – all places where the $\alpha^{3.7\text{III}}$ -deletion is the dominant variant today. But this interpretation would suppose that these sailors bypassed the mainland north coast of New Guinea on their way out to the Pacific 3,500 years ago – quite within their powers, as they demonstrated later. In this case, they may have originated in Wallacea – the $\alpha^{3.7\text{III}}$ -deletion is not found in western Indonesia²⁶, but Wallacea has so far not been tested. Such a bypass interpretation certainly fits the aspect of the common archaeological model that identifies the proto-Polynesians with the Lapita material culture complex³, because, with one exception, there are no Lapita pottery sites anywhere on the New Guinea mainland.

An important monograph summarising contemporary knowledge on all aspects of the genetic trail into the Pacific (including the globin gene work) concluded in the summary chapter (p. 286), with the following little-remembered judgement²⁶: ‘The genetic data have not located a precise “homeland” for the pre-Polynesians, but evidence clearly indicates that they are mainly derived from a Southeast Asian population prior to ‘Mongoloid’ expansion.’

Mitochondrial DNA

For greater power to resolve prehistoric migrations by genetic means, however, we must turn to the non-recombining, uniparental loci: the mitochondrial DNA (mtDNA) and the Y chromosome. These are inherited only from the mother and the father respectively, and correspondingly clearly trace the female and male lines of descent without the shuffling that takes place at each generation with autosomal genes. Early work on mitochondrial DNA (mtDNA) in the control region highlighted what came to be known as the ‘Polynesian motif’²⁷ (Figure 4). This is a suite of four base substitutions, at nucleotide positions 16189, 16217, 16247 and 16261 with respect to the reference sequence, in the non-coding control region of mitochondrial DNA. These four substitutions identify a sub-group of haplogroup B – a widespread East Asian clade of mitochondrial lineages characterised by an intergenic 9-base-pair deletion²⁸. (A haplogroup, or clade, is a group of lineages which all descend from a particular mutation).

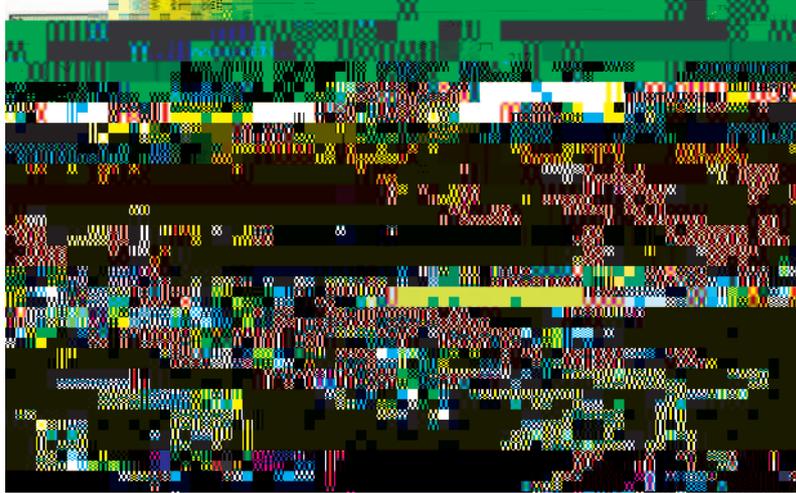


Fig. 4 Distribution of the defining mtDNA (maternal) 'Polynesian motif' and its ancestors in eastern Asia and the Pacific. The Polynesian motif is defined by three mtDNA mutations within haplogroup B, at positions 16217, 16247, and 16261, abbreviated to 217, 247, 261. It is derived from the ancestral sequence (which carries only the 217 mutation) by mutations firstly at 261 (to create the immediate ancestor) and then at 247 (to create the Polynesian motif). Age estimates of the motif itself are given for various regions. In Polynesia these correspond with archaeological dates

The Polynesian motif, so-called because it reaches very high frequencies in Polynesian populations, is actually distributed at varying frequencies throughout the coastal populations of Oceania, including Micronesia and coastal Melanesia^{27,29-32}. It is not found in highland New Guinea, and is virtually absent to the west of Wallace's line. (The main exception is Madagascar, where it does occur at high rates³³.) Its distribution thus also follows Austronesian linguistic boundaries. It excludes virtually all populations speaking Western Malayo-Polynesian languages; in other words, the whole of island Southeast Asia west of Wallace's line²².

Although the Polynesian motif is not found in the Philippines, Taiwan or China, we do find in these regions its immediate ancestor type, with only three of the four substitutions (at nucleotide positions 16189, 16217 and 16261). This does place the ancestors of the motif on the Asian mainland, and led to the initial interpretation that the mtDNA variation supported the 'out of Taiwan' model. But further

study led us to think that this view may have been mistaken. Since eastern Indonesia is the westernmost region in which the full motif type, defined by the substitution at position 16247, is now found (excluding Madagascar), then the 16247 mutation must have arisen in that region. This means that the age of the motif can be estimated using the molecular clock by dating the variation accumulated on the motif branch. The age of the most recent common ancestor of lineages with the motif is very approximately 17,000 years (95% credible region: 5,500–34,500 years)³⁴.

Genetic dating is approximate at best, but there is some internal validation for these dates in this case. The Pacific dispersals of the motif can be dated using the same mutation-rate calibration by assuming successive founder effects *en route*. These estimates place the arrival in Samoa at around 3,000 years ago, and in eastern Polynesia at around 1,000 years ago – consistent with the archaeological evidence³⁴. It therefore appears that the motif is at least 5,000 years old, and probably considerably older. However, the ‘out of Taiwan’ model is chronologically constrained by the appearance in eastern Indonesia of red-slipped pottery: Bellwood³

Austronesian origins, since it implies that one of the main insular mtDNA clusters, haplogroup B, has been present in the archipelago for more (probably considerably more) than 5,000 years. Whilst the 'out of Taiwan' model does allow for some pre-Neolithic gene flow from the mainland³, it becomes difficult to imagine language-shift on such a dramatic scale when indigenous continuity is so substantial³⁷. It may be more plausible to imagine that the Austronesian languages originated within the archipelago itself, as suggested by Meacham and Solheim^{7,8}. However, the effects of genetic drift acting between Wallacea and the Pacific have clearly been very severe. Further detailed work on insular Southeast Asian mtDNA variation will be necessary to establish the contribution, if any, of mainland agriculturists to the maternal genetic ancestry of the archipelago.

Y chromosome

Since the mtDNA-based arguments in favour of the 'slow boat' model were first proposed three years ago³⁴, revolutionary strides have been made in the study of the second non-recombining uniparental genetic system, the paternally inherited non-recombining part of the Y chromosome. Underhill and his colleagues³⁸ have identified more than 200 new stable markers, leading to the publication of a series of studies of the male line of descent in Southeast Asia and the Pacific^{35,39-42}. Some of these analyses have also included more rapidly evolving microsatellite markers, which involve mutational changes in the length of a repeating structure and can resolve much more closely related lineages. These have fuelled further doubts about the 'out of Taiwan' model for the origin of the Polynesians, and returned to an earlier twist in the story: namely, the size of the Melanesian contributions to the Polynesian gene pool. Working from largely similar data sets, but using markers of varying resolution and equivalence, a range of interpretations have been proposed, from predominantly Melanesian origins to predominantly insular Southeast Asian origins for Polynesians. It is worth trying to put these results together to see whether a coherent picture emerges.

As with mtDNA, Polynesian Y chromosomes show dramatic reductions in diversity, indicating strong founder effects. Just two Y-chromosome haplogroups dominate the Polynesian scene. One of these, defined by the Underhill marker M122, is clearly derived from East Asia or Southeast Asia, since it is common throughout those regions but absent from the New Guinea highlands^{35,40,41} (Figure 5). It occurs at highest frequencies, approximately 60%, on the south

Chinese mainland (and also in Han Taiwanese), and at around 50% in both Vietnam and the Philippines. It is almost absent from Taiwan aborigines, with the exception of the Ami where a few types have been elevated to almost 50%. It is present at around 30% in northern Borneo and Sulawesi, falls to around 15–20% in southern Sulawesi, southern Borneo, Java and Sumatra, and drops away to very low

mtDNA haplogroup B) from the mainland is also possible, and this might equally have been from south China, or Indo-China, or even both. The presence of shared microsatellite haplotypes within this haplogroup indicates a more recent dispersal than that of haplogroup 10 (see below), but does not preclude a pre-Neolithic, post-glacial entry. Unfortunately, genetic dating based on microsatellites is not yet sufficiently refined for a reliable age estimate for the dispersal; calibrations used in the past may soon require significant re-evaluation.

The distribution of the M38 sub-group of haplogroup 10 is striking (Figure 6). It is confined to eastern Indonesia, coastal Melanesia, and Polynesia, but is rare in the New Guinea highlands; indeed, it is the only form of the clade to be found in Melanesia and Polynesia, and the more common form found in eastern Indonesia. This distribution is reminiscent of the mtDNA ‘Polynesian motif’ described above, which is also restricted to eastern Indonesia, coastal Melanesia and Polynesia. As with the mtDNA haplogroup B, the distribution of variation within haplogroup 10 strongly suggests an ancient Asian ancestry, with the mutations to the derived types occurring in eastern Indonesia during the Pleistocene. Kayser and his colleagues³⁵ estimated that the derived type appeared very approximately 11,500 years ago, which is likely to be an under-estimate given the problems associated with microsatellite dating.

Kayser and his colleagues proposed that this result supports a primarily Melanesian origin for the Polynesians, arguing that the



*Fig. 6 Distribution of Oceanic-variant haplogroup 10 (DYS390.3del/RPS4Y711T) and haplogroup 24 (M4/M5) of the Y chromosome in eastern Asia and the Pacific. Whilst haplogroup 24 is characteristic of both the New Guinea lowlands and the less admixed highlands, it is nearly absent from Polynesia. By contrast the unique Oceanic variant of haplogroup 10 dominates Polynesia, yet is uncommon in the New Guinea highlands. Haplogroup 10 is, however, common in Wallacea and throughout lowland Melanesia. This suggests Melanesia as the immediate source and Wallacea as the ultimate source of the main Polynesian paternal lineages. (Data combined from references 35, 39, 40, 41. *DYS390* repeats of 21 or fewer are used where other markers are lacking.)*

Conclusion

It is possible that there was a Neolithic dispersal from the Asian mainland, via Taiwan, into the Indo-Malaysian archipelago: the Y-chromosome evidence is equivocal on this, and sufficient evidence from mitochondrial DNA is not yet in. However, the evidence of both genetic systems clearly indicates that any such dispersing populations were *not* the ancestors of the Polynesian islanders. Therefore, if the Polynesians were connected in some direct way with the earlier dispersals, it must have been via acculturation. However, there is a paradox here, when we consider the archaeological record: although there may be evidence for dispersals involving rice farming from South China into Taiwan, there was a shift within the archipelago such that the expansions of the Polynesians involved

and Cristian Capelli for permission to adapt his map of Y-chromosome haplogroup distributions.

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