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mtDNA Suggests Polynesian Origins in Eastern Indonesia

To the Editor:

mtDNA evidence has previously been interpreted as providing strong support for a model of rapid expansion of the Polynesian peoples from a homeland in Taiwan or southern China ~6,000 years ago into the remote Pacific. Here, we argue that the evidence is consistent with an alternative view, namely, that the Polynesian expansion originated within the Indonesian archipelago.

Several studies have been published concerning the settlement of the remote Pacific that use the phylogeographic analysis of mtDNA, either large-scale sampling and control-region sequence analysis (Lum et al. 1994; Redd et al. 1995; Sykes et al. 1995) or sequence-specific oligonucleotide analysis (Melton et al. 1995). These have distinguished two main hypotheses concerning Polynesian origins. The first hypothesis, often referred to somewhat incongruously as the "express train to Polynesia" (Diamond 1988), was proposed by Bellwood (1991, 1997). This suggests that the Polynesians originated in a demic expansion of Austronesian-speaking agriculturalists from the southern China mainland, ~6,000 years ago, and spread successively to Taiwan, the Philippines, eastern Indonesia, and then Melanesia, reaching Fiji by ~3,500 years ago and radiating across the Pacific to fill the Polynesian triangle by ~1,000 years ago. They would have absorbed and replaced the local hunter-gatherer populations in Southeast Asia, who would have been of Australo-Melanesian ancestry. The principal alternative view, argued by Terrell (1986), is that the Polynesians evolved locally in Melanesia or, at least, within the voyaging corridor between the mainland and the Solomon Islands, defined by Irwin (1992).

Melton et al. (1995) and Redd et al. (1995) analyzed the history of a COII/tRNA^{Lys} intergenic 9-bp deletion by means of a suite of characteristic control-region transitions at positions 16189, 16217, 16247, and 16261 of the first hypervariable segment (according to the Cambridge Reference Sequence; Anderson et al. 1981). They referred to this as the "Polynesian motif," because of its high frequencies in Polynesia, despite its occurrence farther west (Hagelberg and Clegg 1993; Redd et al. 1995). They traced the origin of this motif to Taiwan and proposed that this represented the Polynesian homeland, in line with the Bellwood (1997) hypothesis, while acknowledging that the motif itself probably arose in eastern Indonesia. Sykes et al. (1995) agreed in tracing the origin of the motif to Taiwan but also pointed out that the lack of the motif in Taiwan, Borneo, and the Philippines might complicate the issue. In addition, they pointed out, along with Lum et al. (1994), that somewhat <5% of Polynesians had control-region sequences derived from Melanesia. Furthermore, Sykes et al. (1995) distinguished a third hypothesis, proposed by Heyerdahl (1950), suggesting that Polynesian ancestry may have been from South America, a view that received little or no support from the mitochondrial evidence (Sykes et al. 1995; Bonatto et al. 1996).

Although the evidence is therefore strong that Polynesians derive most of their maternal lineages from Southeast Asia, a fourth hypothesis has received little attention. This view, in contrast to the "express train" model of an agricultural expansion from Taiwan, suggests that the Austronesian speakers originated neither in southern China nor in Taiwan but toward the center of island Southeast Asia, in the vicinity of the Sulawesi-Mindanao region of the Philippines and Indonesia (Solheim 1994) or perhaps over the entire region of island Southeast Asia in which Austronesian languages are now spoken (Meacham 1984–85). This would suggest that the extant inhabitants of island Southeast Asia were the descendants of earlier Pleistocene settlers rather than of Neolithic people from the mainland. Meacham (1984–85) cites the paucity of extant Austronesian speakers on the southern Chinese mainland—or, indeed, any historical evidence for their existence there—in support of this view. There is also anthropometric evidence that Polynesians closely resemble island Southeast Asian populations but not aboriginal Taiwanese or southern Chinese populations (Pietrusewsky 1997).

Combining the published mitochondrial evidence al-

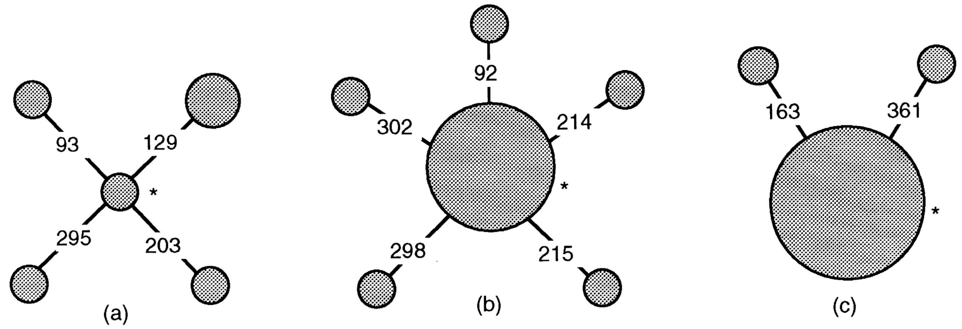

Figure 1 Phylogenetic tree of mitochondrial sequence haplotypes containing the "Polynesian motif" in (*a*) eastern Indonesia, (*b*) Papua New Guinea, and (*c*) American Samoa (data of Redd et al. 1995), in the part of the first hypervariable segment of the control region encompassing bp 16090–16365. The circles represent sequence haplotypes, with area proportional to frequency. The links represent transitional mutations (less 16,000) from the central motif sequence, which deviates from the Cambridge Reference Sequence by transitions at 16189, 16217, 16247, and 16261 (labeled with an asterisk [*]).

lows us to assess this model and to refine our model of predominantly Southeast Asian origins of the Polynesians. Although elevated to very high frequencies throughout Polynesia, probably as a result of severe population bottlenecks and expansions, the Polynesian motif is not exclusively Polynesian but also occurs at moderate frequencies in island Melanesia, coastal New Guinea, eastern Indonesia, and even Madagascar (Melton et al. 1995; Redd et al. 1995; Soodyall et al. 1995; Sykes et al. 1995). The motif evolved, via a transition at position 16247, from a sequence haplotype characterized by transitions at positions 16189, 16217, and 16261. Whereas the full motif itself is rather restricted geographically, the ancestral haplotype and others derived from it are found throughout island Southeast Asia, China, and even, at low frequencies, as far afield as Mongolia and India (Melton et al. 1995; Kolman et al. 1996). Its diversity in Taiwan, calculated by use of the statistic ρ (Forster et al. 1996), suggests a divergence time of ~30,000 years, although with a wide 95% credible region.

On the other hand, the Polynesian motif itself is much more restricted geographically, with the highest diversity in eastern Indonesia, a considerable decrease on the New Guinea coast, and the lowest diversity in Polynesia. This suggests that it arose in eastern Indonesia (Melton et al. 1995; Redd et al. 1995). Phylogenetic trees of the sequences characterized by the motif in the data of Redd et al. (1995), from eastern Indonesia, Papua New Guinea, and Samoa, are shown in figure 1. With these data and those of Sykes et al. (1995), we can use the

Table 1

Divergence Time Estimates for the "Polynesian Motif" in Eastern Indonesia, Coastal Papua New Guinea, Samoa, and the Cook Islands, and Its Ancestor Haplotype in Taiwan

Ancestral Sequence Haplotype	Sampling Location	N	ρ	Mean Divergence Time t (years)[a]	Central 95% Credible Region (years)[a]
16189–16217–16261	Taiwan[b]	14	1.14	30,500	17,500–47,000
16189–16217–16261–16247	Eastern Indonesia[c]	6	.83	17,000	5,500–34,500
16189–16217–16261–16247	Coastal Papua New Guinea[b,c]	22	.23	5,000	1,500–10,000
16189–16217–16261–16247	Samoa[b,c]	38	.13	3,000	1,000–6,000
16189–16217–16261–16247	Cook Islands[b]	48	.04	1,000	0–3,000

[a] To the nearest 500 years. For divergence times based on samples sequenced over different extents of hypervariable segment I (HVS I), a weighted mutation rate was used: $\mu = (N_1\mu_1 + N_2\mu_2)/(N_1 + N_2)$, where N_1 and N_2 are the numbers of samples sequenced over the two ranges and μ_1 and μ_2 are the rates appropriate to those ranges. The credible regions (Berger 1985) encompass the central 95% of the posterior density of t, under the assumption of a Jeffreys' prior for t and a likelihood appropriate for a perfectly starlike coalescent tree. It should be noted that the credible regions quoted on t do not take into account uncertainties in the mutation rate.

[b] Data are from Sykes et al. (1995), using a transition rate of 1 in 26,600 years for the truncated HVS I sequences from positions 16189–16375.

[c] Data are from Redd et al. (1995), using a transition rate of 1 in 20,180 years (Forster et al. 1996) for HVS I sequences from positions 16090–16365.

statistic ρ to calculate divergence times for the motif in various regions (table 1). Whereas the ages estimated for the populations of New Guinea, Samoa, and central Polynesia are ~5,000, ~3,000, and ~1,000 years, respectively, indicating successive recent bottlenecks predicted by the hypothesis of expansion from the west, the age for the population of eastern Indonesia (the Moluccas and Nusa Tenggara) is much greater, ~17,000 years.

Given the wide 95% credible regions associated with these age estimates, one cannot, on the basis of these data, confidently rule out either a Taiwanese or even a Melanesian origin for the Polynesians, especially given that much of island Melanesia has yet to be sampled. Nevertheless, they lend little support to the "express train" model. The most likely explanation for these data is that, although the ancestry of the motif goes back to the Southeast Asian Pleistocene era, the Polynesian expansion itself did not originate in either Taiwan or southern China but within tropical island Southeast Asia—most probably in eastern Indonesia, somewhere between southeastern Borneo and the Moluccas, given the almost complete absence of the full motif in western Indonesia and the Philippines (Melton et al. 1995; Sykes et al. 1995). This might also explain the appearance of the motif in Madagascar, in a population speaking an Austronesian language more closely related to Indonesian than to Polynesian languages (Soodyall et al. 1995). It is consistent with the hypothesis that the Austronesian languages originated within island Southeast Asia during the Pleistocene era and spread through Melanesia and into the remote Pacific within the past 6,000 years.

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