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REPORTS

Matrilineality and the Melanesian Origin of Polynesian Y Chromosomes[1]

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Linguists and archaeologists are in general agreement that the Austronesian languages originated in Southeast Asia on or near Taiwan around 3000 B.C. and that Austronesian-speakers dispersed through Island Southeast Asia, reaching Melanesia by 1450 B.C. and Western Polynesia by 950 B.C. (Shutler and Marck 1975, Bellwood 1978, Blust 1984–85, Pawley and Ross 1993, Kirch 2000; see fig. 1). This dispersal, because of its rapidity, has been characterized as the Express Train to Polynesia (Diamond 1988). This model is supported by genetic data showing a predominantly Asian origin of Polynesian mitochondrial DNA (mtDNA) (Melton et al. 1995, Redd et al. 1995, Sykes et al. 1995). Recently, however, Kayser et al. (2000) have shown a Melanesian origin of Polynesian Y chromosomes favoring a Slow Boat to Polynesia model with substantial population interaction components in relation to indigenous non-Austronesian (Papuan) populations in Melanesia. Our hypothesis is that the predominance of maternally transmitted mtDNA of Asian origin and the significant presence of paternally transmitted Y chromosomes of Melanesian origin in Polynesian ancestry can be accounted for as an effect of matrilocal residence and matrilineal descent in Proto-Oceanic society.

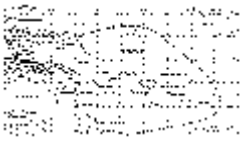

Fig. 1. The distribution of the Austronesian and non-Austronesian languages in Oceania. The heavy lines delineate major subgroups of the Austronesian languages. SHWNG, South Halmahera-West New Guinea; CMP, Central Malayo-Polynesian (courtesy of P. V. Kirch).

For present purposes matrilineal descent groups are lineages or clans in which membership is traced exclusively through female links to a founding ancestor. In matrilocal residence a married couple lives "with or near the female matrilineal kinsmen of the wife" (Murdock 1967). In a matrilineal chiefdom, as hypothesized for Proto-Oceanic society (Hage 1999*a*, Hage and Harary 1996), a man is succeeded by his sister's son. In a patrilineal descent group membership is traced exclusively through male links to a founding ancestor and a man is succeeded by his son. In patrilocal residence a

married couple lives "with or near the male patrilineal kinsmen of the husband." In a cognatic descent group membership is traced through either male or female links. Double descent (not to be confused with cognatic descent) refers to the presence of both matrilineal and patrilineal descent groups in the same society.

GENETIC DATA

There are three lineages of Polynesian mtDNA (Melton et al. 1995, Redd et al. 1995, Sykes et al. 1995). The predominant lineage, accounting for 90–95% of Polynesian mtDNA, is a haplotype possessing a 9-base-pair intergenic deletion shared with Asian populations. The greater diversity of this haplotype in Indonesia, the Philippines, and Taiwan implies an Asian origin and an eastward expansion of Austronesian-speakers into Polynesia. A second haplotype, accounting for 3.5% of Polynesian mtDNA, is also found in Melanesia, in Vanuatu and in coastal New Guinea (Sykes et al. 1995).

Kayser et al. (2000) have discovered three haplotypes (lineages) of Polynesian Y chromosomes. The dominant haplotype, DYS 390.3del/RPS4Y711T, accounts for 82% of Cook Island, 70% of Western Samoan (Forster et al. 1998, Hagelberg et al. 1999), 26% of Coastal Papua New Guinean, and 9–12% of Indonesian Y chromosomes. This haplotype is not found in any other Southeast Asian or Asian population. It originated in Melanesia an estimated 11,500 years ago, long before the intrusion of Austronesian-speakers into Melanesia about 3,500 years ago. A second haplotype, M122C/M9G, is infrequent in Polynesia, accounting for 7.1–10.7% of Polynesian Y chromosomes, but frequent in East and Southeast Asia. It probably originated in Asia on the order of 11,000 years ago (Kayser et al. 2000:1242).

Kayser et al. conclude from the Y-chromosome data that the express-train model should be replaced by a slow-boat model in which the Austronesian-speaking (Oceanic) ancestors of the Polynesians moved slowly across Melanesia, "mixing extensively" with indigenous non-Austronesian-speaking (Papuan) populations, leaving behind their genes and "incorporating" many Melanesian non-Austronesian genes.

This model is consistent with cultural and archaeological evidence of Austronesian–non-Austronesian interaction and with the linguistic "pause" in the spread of the Austronesian languages between the arrival of the Lapita archaeological culture in 1450 B.C. and about 1100 B.C. On general comparative grounds, some century or centuries of change would seem to be required to account for the common linguistic innovations that mark all Austronesian Oceanic languages (and no other [living] Austronesian languages). Several related studies of Polynesian DNA confirm Kayser et al.'s genetic data.

Underhill et al. (2001) found that 43% (25/54) of Maori and 41% (7/17) of Polynesians in their sample had the DYS 390.3 deletion. Following Kayser et al., they interpret this as unequivocal evidence for an important Melanesian lineage in Polynesian ancestry. By contrast, the mtDNA 9-base-pair deletion was present in 85% of their Maori sample; the remaining 15% belonged to European haplogroups.

Hagelberg et al. (1999) found the DYS 390.3 deletion in Melanesia—in the Trobriand Islands (9%), in the Tolai of New Britain (19%), in the Roro of the south coast of New Guinea (17%)—and in western Samoa (70%) but not in Southeast Asia or the New Guinea Highlands. Forster et al. (1998) found the DYS 390.3 deletion in 6% of Papuan New Guinea Highlanders and in 25% of north-coast New Guineans.

Lum et al. (1998) cite genetic data showing that Polynesians and Micronesians have predominantly (95%) Asian mtDNA but share 30% of their nuclear DNA with Near Oceanic, Papuan-speaking Melanesians.

MATRILOCAL RESIDENCE AND MATRILINEAL DESCENT IN PROTO-OCEANIC SOCIETY

Kayser et al.'s model does not specify the type of "intermixing" between Austronesian- and non-Austronesian-speaking populations in Melanesia, but we suggest that it took place in the framework of matrilocal residence and matrilineal descent in Proto-Oceanic society. By "Proto-Oceanic" we mean the language at the end point of its common development in the Bismarcks before the various incremental and abrupt dispersals that led to more localized varieties of speech. By "Proto-Oceanic society" we mean, formally, what can be reconstructed, linguistically, about the social vocabulary of Proto-Oceanic-speakers and what we infer from that about their society. By "Lapita society" the archaeologists mean what was surely the same community and what can be inferred about it through archaeology, comparative ethnography, and comparative linguistics (Kirch 1997, Green 2002). Proto-Oceanic (Lapita) society was a sophisticated maritime and horticultural society of Austronesian origin which developed in the region of the Bismarck Archipelago in western Melanesia around 1500 B.C. The society was based on an extensive voyaging and exchange network (Kirch 2000). By 1100 to 1200 B.C. daughter societies were expanding eastward, arriving in the Fiji-Tonga-Samoa area by 950 B.C. (Kirch 2000). After a "long pause" in Western Polynesia of as much as 1,000 years, as evidenced by numerous innovations in Proto-Polynesian (Pawley and Ross 1993), colonization resumed, reaching all islands in Eastern Polynesia by A.D. 1000.

There are two complementary, interconnected perspectives on the relation between matrilineal institutions and long-distance voyaging (Hage and Marck 2002). The first perspective is due to Harris (1980, 1985), who argues, generally, that the development of matrilocal residence and matrilineal descent is favored under conditions of prolonged male absence for purposes of trade, warfare, or resource exploitation. In contrast to patrilocal residence, in which absent husbands must rely on wives "whose alien descent group loyalties override any obligation to [their] husband[s]" (Harris 1980:97), matrilocal residence allows absent brothers to rely on their lineage sisters to manage their common corporate interests. Ethnographic examples of this model include the Iroquois, the Huron, the Mundurucu (Harris 1985:282), and the Haida (Hayden 1993). Historical and archaeological evidence includes the development of matrilocality in eastern North America following upon changes in subsistence practices that required extended male absence in hunting, trading, and raiding expeditions (Harris 1980:97, citing Trigger 1978). A significant Caribbean parallel is Keegan and Maclachlan's (1989) reconstruction of the initial colonization of the West Indies as the expansion of a matrilineal-matrilocal society of long-distance seafarers and traders.

The second perspective is due to Lévi-Strauss (1984), who observed with reference to Micronesia that males are easily assimilated to matrilineal descent groups. He also pointed out that matrilineal institutions, because of their inherent instability (resulting from conflicts between men over the control of their own and their sisters' children), are apt to disappear when societies become isolated (p. 183):

Some Micronesian societies have lived in relative isolation; elsewhere migrations, wars and intermarriages have mixed up the populations. Further, we find in the first group of societies a retreat from matrilineal institutions; left to themselves, these institutions, by reason of their well known instability, have a tendency to evolve spontaneously towards other forms. Contrariwise, they provide the second group of societies with a sort of common denominator and a convenient means ... of incorporating [male] immigrants.

In Micronesia the continuation of matrilineal descent was clearly associated with the continuation of regular long-distance voyaging (Hage and Marck 2002). In the isolated atolls of the eastern Carolines (Pingelap, Mokil, and Ngatik), in the outlier atolls of the Marshalls (Enewetok and Ujelang), and in the atoll groups (Kiribati), where regular long-distance voyaging declined or never developed, matrilineal descent gave way to patrilineal, double, or cognatic descent. The same thing happened in western Polynesia during the long pause, when interisland voyaging came under the control of chiefly elites involved in a prestige-goods system (Kirch 2000).

In matrilineal societies paternity is not an overriding issue. It matters little who the father is, since only women continue the lineage. In the Micronesian and larger Oceanic context, if husbands and fathers were lost (always a possibility in seafaring) they could be readily replaced by other men, Papuan as well as Oceanic.

In the "classic" theory of kinship (Murdock 1949, Lowie 1950, Fox 1983), the development of social organization proceeds from changes in residence rules to changes in descent rules to changes in kinship terminology. By Proto-Oceanic times residence (matrilocality), descent (matrilineality), and kinship terminology (bifurcate merging) were perfectly aligned. Many of the daughter societies of Proto-Oceanic retained this pattern while others underwent changes in residence—from matrilocal to avunculocal (a male-centered residence in a matrilineal society in which a married couple lives with or near the maternal uncle of the husband), changes in descent from matrilineal to double, patrilineal, and cognatic, and changes in kinship terminology from bifurcate merging to generational.

The evidence for matrilineal descent in Proto-Oceanic society as presented in Hage (1998) can be summarized briefly. Linguistically, Proto-Oceanic kinship terminology was bifurcate merging in type, with one term for father and father's brother (**tama*) and a separate term for mother's brother (**matuqa*) (Milke 1958). Cross-culturally, bifurcate-merging terminologies are associated with unilineal—matrilineal or patrilineal—descent 85% of the time and (using a slightly different sample) with unilocal residence 91% of the time (Hage 1999*a*). The rare bifurcate-merging terminologies found in nonunilineal (cognatic) societies are best interpreted as survivals of earlier unilineal regimes, bearing in mind the lag between changes in descent rules and kin terms.

Ethnographically, matrilineal descent is widespread in Oceanic-speaking societies in Micronesia, in the Caroline and Marshall Islands, and in Island Melanesia in the Huon Gulf and parts of New Britain and New Ireland (in the Bismarcks), Bougainville, the Solomon Islands, and Vanuatu (Allen 1984). Double descent (usually interpreted as a sign of the transition from matrilineal to patrilineal descent [Murdock 1940, Fox 1983]) is also found in Oceanic-speaking societies in Melanesia. It results when an integrated matrilineal society is undermined by patrilineal institutions, beginning typically with a shift from matrilocal to patrilocal residence. Patrilineal descent groups then become important in economic and political contexts, eventually leaving matrilineal descent groups with few functions other than exogamy, hospitality, and ritual. Classic examples of double descent in Oceania are Yap in Western Micronesia and Pukapuka in Central Polynesia. In Island Melanesia double descent is found in a number of societies in the Admiralty Islands, the Huon Gulf, Vanuatu, and Fiji (Murdock 1967). In Murdock's *World Ethnographic Atlas* (1967) 74% (26/35) of all unilineal Oceanic-speaking societies have either matrilineal or double descent. Historical linguistic evidence from Island Melanesia (Malaita) reveals shifts from matrilineal to patrilineal descent but not the converse (Blust 1986–87).

Not all Oceanic-speaking societies are matrilineal, but the majority of them display a matricentric orientation that we interpret as the historical residue of a matrilineal Proto-Oceanic society. If Proto-Oceanic society was patrilineal, one would expect a continuing patricentric orientation in daughter societies. In Burton et al.'s (1996) analysis of social structure in world ethnographic regions, matricentric traits include "localized or dispersed matrilineal groups, matrilocal or uxorilocal residence, monogamy, and the absence of marriage exchange ... generational aunt terms, bifurcate merging aunt terms and Crow cousin terms" (p. 93). Oceanic-speaking societies in Melanesia, Polynesia, and Micronesia are generally matricentric (fig. 2).

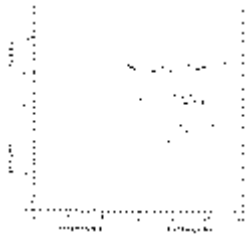

Fig. 2. Social structural traits of Oceanic-speaking societies based on Burton et al. (1996). M, Melanesia; P, Polynesia; I, Micronesia (from Hage 1998, courtesy of the Polynesian Society).

The relative unimportance of paternity in matrilineal societies in Oceania is clearly illustrated in the matrilineal chiefdoms of the Marshall Islands in eastern Micronesia (Hage and Harary 1996). Male ancestors were often omitted from chiefly genealogies. In the words of an early ethnographer, "When Kabua [a paramount chief of the Ralik chain of the Marshalls] dictated the genealogical tree of his ancestors to me and mentioned only women, I asked him to name the men too as is generally customary in Polynesia. He laughed and said that they were completely irrelevant, and therefore he did not know them" (Krämer 1906:431). Children in the Marshalls were considered chiefly (*iroij*) if their mothers were chiefly.

DISCUSSION

It is sometimes assumed in population genetics that patrilocal residence and patrilineal descent are the norm (Cavalli-Sforza 2000), but there are significant numbers of matrilineal societies in the world (Murdock 1967). If the Austronesian ancestors of the Polynesians were patrilineal, one would expect to find Polynesian Y chromosomes of predominantly Asian origin and mtDNA of mixed Asian and Melanesian non-Austronesian origin, the frequency of the latter depending on the frequency with which Austronesian-speaking men married indigenous non-Austronesian-speaking women. The predominance of Asian mtDNA and the high frequency of Melanesian Y chromosomes in Polynesian DNA imply the presence of matrilocal residence and matrilineal descent in Proto-Oceanic society. While founder effects in Polynesia and at various points along the way from the northwestern Melanesian Proto-Oceanic homeland could skew the actual level of Melanesian contributions to the Y-chromosome situation amongst Proto-Oceanic-speakers, it would be unlikely for the mitochondrial DNA to be so profoundly skewed in the *opposite* direction by early Polynesian settlement times. The founding population of Polynesia was dominated by Southeast Asian mitochondrial DNA and Melanesian non-Austronesian Y-chromosome DNA, and such a skewed sex-based difference is more likely the result of the long-term systematic effects of ancestral marital patterns than the chance result of compounded founder effects from the Proto-Oceanic homeland along the route to Western Polynesia. The genetic data are consistent with the linguistic and comparative ethnographic data supporting a hypothesis of matrilineal descent in the early Oceanic ancestors of the Polynesians. It would not have taken many generations to reach a high level of Melanesian Y-chromosome admixture in Polynesian DNA. If 10% of the Y-chromosome DNA in each generation came from outsiders, in 300 years (12 generations) the proportion of original DNA would have been (.9) ^12~ 28%.

Two studies of matrilineality and genetic diversity lend further support to our model. Oota et al. (2001) have shown that genetic diversity varies with residence rules. In a comparison of six closely related groups—three patrilocal and three matrilocal—from northern Thailand, mtDNA diversity was higher in all the patrilocal than in any of the matrilocal groups. Conversely, Y-STR haplotype diversity was higher in all the matrilocal than in any of the patrilocal groups. According to these researchers, the linguistic, cultural, regional, and economic similarities among the six groups make it unlikely that some factor other than residence could account for these differences.

An analogue to our model of the Oceanic settlement of Polynesia is provided by the Herero (Henry Harpending, personal communication). The Herero, pastoralists who represent the southwestern arm of the Bantu expansion (Pennington and Harpending 1993), are self-consciously ethnic, and group membership is determined exclusively by the mother. There are many liaisons with non-Herero, and offspring of these liaisons are Herero only if their mothers are Herero. One manifestation of this mating pattern is reduced genetic diversity compared with that of other Bantu-speaking people in southern Africa (Harpending and Chasko 1976). Another is lack of mitochondrial diversity, indicating bottlenecking and a restricted maternal ancestry. Vigilant et al. (1991) describe mitochondrial DNA sequences of a world sample of 189 people including 27 Herero. Whereas the sample of 162 non-Herero had 125 distinct sequences the sample of 27 Herero had only 10. An expanding group with strong matrilineal ideology like that of the Herero would show, centuries later, a restricted and geographically specific origin of

mitochondrial DNA but a diverse and widespread origin of Y-chromosome and nuclear DNA. This is the pattern that we propose to account for the discrepant origins of Polynesian mitochondrial and Y-chromosome DNA.

It has been put to us that the significant presence of Melanesian non-Austronesian Y chromosomes in Polynesian DNA could be more simply explained by a skewed sex ratio —more males in the boats than females. We would argue that sex ratios in colonizing expeditions were not markedly skewed. As Kirch (1997) observes, the Lapita expansion favored a high rate of population growth. The vulnerability to extinction of small colonizing "propagules" would have favored more nearly balanced sex ratios. If the social motivation for the Lapita expansion was primogeniture (Kirch 1997; Hage 1999*a*, *b*), the colonizing expeditions were probably led by junior, polygynous collaterals of chiefs. It is hard to imagine that men would have set off without women. Further, there is no need to assume that women would have been in the way on colonizing expeditions; they could well have been part of the crew. Lum et al. (1998) have suggested the possibility of male-biased gene flow after initial colonization in the context of predominantly male interisland voyaging and matrilineal descent. The details of this scenario are not given. In our view matrilineal descent and voyaging networks were part of the colonization process itself.

Not all population geneticists are in agreement with the analysis of genetic data in Kayser et al. (2000), Underhill et al. (2001), and Hagelberg et al. (1999). Su et al. (2000) found that one Y-chromosome haplotype, M4G/MST/M9G, is present in Melanesia but not in Polynesia and concluded that "the contribution of Melanesian Y-chromosomal haplotypes to the Polynesian expansion is very low or negligible" (p. 8227), but they did not include in their analysis the DYS 390.3 del/RPS4Y711T haplotype. Hurles et al. (2002) found that two lineages account for 81% of nonadmixed Polynesian Y chromosomes. Lineage 26.4 is found in Polynesia and Southeast Asia; lineage 10.2 is found only in Polynesia and Melanesia, but "it appears that 10.2 owes its ancestry, much like that of its phylogenetic predecessor, the DYS390.3 chromosomes (Kayser et al. 2000), to a source population in Melanesia and/or eastern Indonesia" (p. 300). Oppenheimer and Richards (2001*a*, *b*) believe that a subgroup of the mitochondrial haplotype with the intergenic 9-base-pair deletion called "the Polynesian motif" originated in Wallacea in eastern Indonesia 17,000 years B.P. (95% credible region: 5,500–34,500 years). They also suggest a possible eastern Indonesian origin of the Y-chromosome haplotype DYS 390.3. They argue that Austronesian origins lie within tropical Southeast Asia, but with the exception of Dyen (1965) and Terrell, Kelly, and Rainbird (2001), no linguists and few archaeologists credit this idea. As Diamond (2001) has written, they overlook the linguistic, archaeological, and genetic evidence that locates Austronesian origins in Taiwan and ultimately China.

Oppenheimer and Richards (2001*a*, *b*) and other geneticists are now making regular but unreferenced claims that the "linguists," "linguistics," or "the standard archaeo-linguistic model" do not allow much "mixing" of Austronesian-speakers with populations they encountered in their journey through time and space to Remote Oceania. While Oppenheimer and Richards contrast this with Terrell's (1998, Terrell et al. 2001) "entangled bank" model, neither Oceanic linguists nor theoretical linguists have actually made anything resembling a "no-mixing" claim. In this and his Wallacea

homeland "model" of Austronesian origins, Terrell has simply created "linguistic" models with no foundation in linguistics.

The "express-train" and "slow-boat" terminologies refer, in current parlance amongst biological scientists, not to the speed with which Austronesian dispersal/encroachment into the Pacific occurred but to the character of the social interactions along the way. The amount of time it took was already known to be about 500 years in Oceania. This figure will change if the archaeology changes, not if the biological science changes. Neither the linguists nor the archaeologists have said or implied that the apparent speed of dispersal meant that Austronesian-speakers were not interacting with non-Austronesian-speakers along the way. The contrast between express trains and slow boats, although convenient for geneticists' (Lum et al. 1998; Kayser et al. 2000; Oppenheimer and Richards 2001*a*, *b*; Underhill et al. 2001) purposes, is misleading. Most archaeologists, if forced to use catch phrases, would prefer some form of Green's (1990) Triple I—intrusion, innovation, and integration—model of Austronesian (Oceanic) and non-Austronesian interaction. The question is, how did these populations interact? Here we have suggested an answer: they interacted as most matrilineal societies do.

CONCLUSION

We propose that the predominance of maternally transmitted mtDNA of Asian origin and the significant presence of paternally transmitted Y chromosomes of Melanesian non-Austronesian origin in Polynesian ancestry can be accounted for as an effect of matrilineal institutions of residence and descent in Austronesian Proto-Oceanic society. The matrilineal hypothesis is supported by abundant linguistic, ethnographic, and cross-cultural evidence, and the genetic data are consistent with this evidence.

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