THE GENETIC HISTORY OF THE ORANG ASLI: UNITING PATCHWORK DATA

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ABSTRACT

The genetic history of the West Malaysian Orang Asli, or "first people," is only partially known. Few of the 19 or more ethnolinguistic groups have been studied. This work has found variation at the protein level and the DNA level. Genetical questions of broad interest include (1) the relationships among Orang Asli groups and (2) their relative affinities to other Asians. Both within and between Orang Asli groups, close neighbors can have large differences in allele frequencies, indicating ethnic microdifferentiation. Taking a larger perspective, a few groups have been compared genetically to other Southeast Asians, as well as to people elsewhere. Overall, these broad comparisons show Orang Asli to be distinctive from other Malaysians and other Southeast Asians. At the same time, Orang Asli fall into genetic alignment regionally between more northerly continental groups and insular groups to the south and east in important respects. Historically, Orang Asli distinctiveness can be ascribed in large part to small effective population size and continuous selection pressures. The cohesiveness of Orang Asli cultures and gene pools has long maintained an array of alleles at relatively high frequencies that provide resistance to endemic disease. Related cultural and genetic attributes suggest a long tenure by Orang Asli in the rainforest environment.

Key words: *Orang Asli history, genes, indigenes, Malaysia, ethnic relationships*

INTRODUCTION

The Orang Asli of West Malaysia number about 95,000. Their ethnolinguistic group sizes range from small (fewer than 200 people for the Mendriq) to medium (over 26,000 for the Semai). By tradition, most of the 19 groups were swiddeners or horticulturalists, but some emphasized fishing or rainforest foraging (Dentan *et al.* 1997). Today, some Orang Asli speak Aslian languages, a subdivision of the Austroasiatic stock, while others speak Austronesian languages (Benjamin 1986; 1998). But the Austronesian speakers may have spoken Aslian languages in the past, according to nineteenth century word lists (Gianno 1997). Austronesian languages reached the fringes of Malaya some 2000 years ago (Blust 1984-85), long after Austroasiatic languages were in place.

While genetics can help clarify ambiguities about Orang Asli prehistory, it has not yet had much success, partly due to the low number of pertinent genetic studies in existence. (The full names of the various genes I mention can be found in the endnote.)

The first genetic survey of Orang Asli groups was a product of the 1950's (Polunin and Sneath 1953), and no subsequent study has been as geographically comprehensive. Still, more recent studies provide data on a few groups. Here I examine this database to address two questions that have a historical dimension: (1) What are the genetic relationships among Orang Asli groups? and (2) How are Orang Asli related to other Asians?

GENETIC VARIATION OCCURS WITHIN ORANG ASLI GROUPS

Most of the data on genetic variation within Orang Asli groups pertain to the Semai and Temuan. Looking first at a fairly broad horizon, Semai from two states (Perak and Pahang) were shown to differ in allele frequencies for the G6PD and SAO genes, as well as in frequencies of allele 1 of the PGM1 gene (Lie-Injo 1976). More narrowly, Temuan villages within one state (Negri Sembilan) differ markedly in their genetic makeup (Baer *et al.* 1976). One village lacked the E allele for hemoglobin and the C allele for PGD, both of which occur in other Temuan areas. Another Temuan village lacked colorblind males, although colorblindness is fairly common elsewhere. A third village lacked G6PD-

deficient males, also a rather common Temuan trait. Micro-variation as a result of cultural and evolutionary forces, however, extends even to the level of adjacent hamlets (Fix and Lie-Injo 1975). For example, the frequency of the E allele for hemoglobin among seven related Semai settlements averaged 0.22 but ranged from 0.13 up to 0.51. The SAO allele frequency averaged 0.12 but ranged from 0.03 to 0.25.

Overall, variation within Orang Asli groups appears to be widespread. Nevertheless, generalizations based on small, localized surveys may be misleading in a wider context, unless the group itself is small and is broadly sampled.

GENETIC VARIATION OCCURS AMONG ORANG ASLI GROUPS

Lie-Injo (1976) analyzed three blood-group genes and over 10 others for several somewhat arbitrary subdivisions of Orang Asli, those popular in typological theories. These subdivisions were "Negritos," a misnomer for small forager groups of northern Orang Asli; "Senoi," largely Semai and Temiar in this instance; and the southerly "Aboriginal Malays," largely Temuan and Jakun. Considering all genes together, she found Negritos to be closest genetically to Malays and to be distant from Senoi and Aboriginal Malays, among the 10 groups surveyed. While Senoi were much closer to Aboriginal Malays in terms of blood groups, they were closest to Thais for other genes, resulting in them being equally related to Aboriginal Malays and to Thais overall. While Aboriginal Malays were closer to Senoi in terms of blood groups, their closeness to Malays in terms of other genes netted out to a position closer to Malays than Senoi. But, overall, Malays were much closer to Chinese and Thais than to any of the three Orang Asli subdivisions.

In a study of PepB variation in four Orang Asli groups, Welch (1973) found strong similarities between Temuan and Semelai and between Semai and Jakun, but not between other duos. The Semelai and Temuan also shared the rare B6 allele of the PepB gene, which was not found in the Semai or Jakun. In contrast, Semai alone had the rare B2 allele of this gene. And in a related study, Semelai and Temuan were most alike in their allele frequencies for the ADA gene, with Semai and Jakun also being alike in this regard (Welch et al. 1978).

More recently, Fix (1995) reviewed inter-group variation in detail for two traits (SAO and Hb E). Since these traits, among others, are central for understanding survival in malarious environments, I will discuss them in a later section.

As one might expect, not all genes display differences among groups. For example, the A allele of the SAP gene had frequencies statistically very similar in different Malaysian groups (range 0.42 to 0.53): two subdivisions of Orang Asli plus Malays, Chinese, and Indians (Tan and Teng 1978). And the same similarity prevails for the PGD gene (Lie-Injo and Welch 1972).

Overall, these data reveal some differences among Orang Asli groups. In comparative terms, genetic variation within the Orang Asli domain was found to be at the same level as, for example, within the Taiwan Chinese or within the Amerindian Pima, according to one analysis (Chen et al. 1995). But it is also true that Orang Asli groups have many commonalities (Fix 1995; Baer 1995).

OUTSIDE CONNECTIONS: "CLASSICAL" GENE STUDIES

First of all, I should mention that the widely read book by Cavalli-Sforza et al. (1994) listed many, but not all, the 100 Temuan are listed separately in their tables, other groups are melded into headings such as "Malays and Aboriginal Malays" or "Mon-Khmer unspecified," leading to some confusion.

Lie-Injo (1976) was the first to analyze the relationship of Orang Asli with non-Asli groups. Although she found relationships between Orang Asli subdivisions and Malays, Thais, and Chinese, her results were not based on Orang Asli ethnic-group designations and thus were somewhat coarse-grained. Moreover, the fact that Malays were found to be much more closely related to Chinese and Thais than to any Orang Asli category emphasizes Malay distinctiveness from Orang Asli. Indeed, as Sumatra was the homeland of Malay speakers (Maxwell 1997), their separateness from Orang Asli is not surprising.

A paper by Chen et al. (1995) that compared Orang Asli to other ethnic groups was reportedly on Kensiu, traditionally a hunting-gathering population, but may have been on the broader and vaguer category called Negrito. I am unsure which group was studied because these authors considered only blood-group variation as cited in the compilation of Roychoudhury and Nei (1988), undoubtedly derived from the only report on blood groups in northern Orang Asli (Polunin and Sneath 1953). In terms of the 130 human groups studied by Chen and coworkers, the so-called Kensiu were closest to Kam, Zhuang, and Thai (three groups of S. China or S. E. Asia speaking Daic languages). They were much less closely related to a Taiwan indigenous group (Atayal), or to Polynesians, Micronesians, Filipinos, Balinese, Sumatran Batak, or Malays. This conclusion is counter to the findings of Lie-Injo (1976), who placed Negritos somewhat closer to Malays than to Thais. Moreover, Nei and Roychoudhury (1982) compared the Malaysian Negrito category with seven other Asian-Pacific populations, including Aboriginal Malays. The Negritos were loosely related to Aeta of the Philippines and to Aboriginal Malays, but Negritos and Aboriginal Malays were farther from a tripartite cluster of Filipinos, Chinese, and Malays. Aboriginal Malays were somewhat closer to Filipinos.

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Using similar data, Kirk (1979) compared Senoi to 20 other Asian-Pacific populations, surveying 13 genes. His analysis put Senoi outside a cluster consisting of Ainu, Japanese, Ryukyuan, Atayal, Chinese, Malays and Sumatran Batak.

Gajra et al. (1994, 1997) studied several forms of lipoproteins in Semai from Betau, Pahang, first by standard biochemical tests and later by DNA tests. Among the 8 groups compared biochemically, Semai were genetically more like Finns and Sudanese than like Malays, in terms of apolipoprotein E allele frequencies. The DNA work compared Semai only with Swedes, Finns, and Italians. Since Orang Asli had been rumored to have little coronary heart disease, the researchers looked to see if a particular genotype distinguished their Semai sample from Europeans. While they detected inter-group differences, they presented no correlative data on heart disease. Other variables possibly relevant to heart disease, including life expectancy (lower in Orang Asli) and malnutrition (commoner in Orang Asli), were not studied.

A more comprehensive study (Saha et al. 1995) compared Semai to 14 other Asian populations, notably including Khmers, in terms of either 7 or 13 variable genes, using composite data. Ignoring a few statistical problems in this analysis, Semai were most closely related to Khmers, while at some distance Malays were most closely related to southern Chinese. Various Indian populations, as well as Koreans and Japanese, were also distant from the Semai. Such findings were based on a study of 7 genes; but when 13 genes were analyzed, the Semai were closest to Javanese, followed by Khmers, with other populations again being quite different. Still, the results with respect to Khmers are of interest because the Semai language is related to Khmer in the Mon-Khmer section of the Austroasiatic stock.

OUTSIDE CONNECTIONS: MITOCHONDRIAL DNA (MTDNA) AND NUCLEAR DNA STUDIES

Closure has not yet been reached on the question of the external relationships of the Orang Asli, from the perspective of mtDNA studies. No study has looked at more than a handful of Southeast Asian groups, out of the hundreds in existence. The report by Ballinger et al. (1992) did include several groups of Orang Asli. They studied various facets of mtDNA, which is maternally inherited, including the well-known 9-base pair mtDNA intergenic deletion that is widespread in Asia. Out of 32 Orang Asli mtDNA samples (unrelated?), they found one person, a Semai, with this deletion, for a frequency of 3%. A caveat here is that 5 of the 32 Orang Asli were reportedly Semai, 6 were "extrapolated" Semai, and another 6 were "extrapolated" to be either "Temiang" or Semai (Ballinger, pers. comm. 1992);

on this basis a single Semai with the deletion represents at least 6% of the Semai sampled (1/17) but possibly as high as 9% (1/11).

In contrast, Melton et al. (1995) reported that 37% of 30 unrelated Semai exhibited this 9-base pair deletion, a higher frequency than reported previously. By the analysis of Melton's group, Semai were closer to Filipinos, East Indonesians, and Javanese than to Malays, Singaporean Chinese, or Barito-area Borneans. In a later paper that excluded Orang Asli, Melton and Stoneking (1996) used sequence-specific oligonucleotide probes; by this finer analysis they found that Malays were most closely related to Singaporean Chinese and more distantly to Javanese and East Indonesians, but they bore little relationship to the Borneans or Filipinos. Putting these two reports together, Semai were close to Filipinos while Malays were close to Chinese; but Semai and Malays were not close to each other.

Ballinger et al. (1992) also studied their Orang Asli samples for affinities to other Asians: Vietnamese, Malays, Chinese, Koreans, and five groups of indigenous East Malaysians. In this analysis they took into account the 9 base-pair deletion and also other variable aspects of mtDNA. The 32 Orang Asli studied, representing four ethnic groups, did not cluster together. They were interspersed among other Asians in terms of their mtDNA phenotype. For example, two "Jeni" (later assigned to the Jehai group) had closest mtDNA affinities with a Vietnamese in one direction and a Korean in another and were fairly distant from Orang Asli of other ethnic groups. Small sample sizes, however, preclude drawing strong conclusions from such a result. Temiar, Semai and other Orang Asli studied were interspersed among indigenous people from Sabah, East Malaysia, and to a lesser extent among Koreans, Malays, Chinese, and Vietnamese. Overall, various Orang Asli individuals, or ethnic clusters, showed broad Asian affinities. These results stand in some contrast to the known linguistic affiliations of Orang Asli (Benjamin 1998). Neither their Austroasiatic nor their Austronesian languages are closely related to Korean, Chinese, or even the indigenous languages of Sabah. Upon averaging the Orang Asli data, however, they were found to be closer to Vietnamese than to other groups studied; and Malays were closer, on average, to Sabahans.

In papers by another research group, six Orang Asli (unidentified) were compared to members of four other Asian groups. In terms of trinucleotide repeat polymorphisms in nuclear DNA, these six were closest to Cambodians, presumably Khmers (Watkins et al. 1995), a finding that seems to reinforce that of Saha et al. (1995). But by other measures at the DNA level (Jorde et al. 1995), the six were closer either to Cambodians or to Japanese than they were to Vietnamese or Chinese.

I interpret these scattered reports to mean that while Orang Asli show general affinities to other Asians, Semai at least show closer affinity to Khmers, to whom they are related linguistically (Table 1).

TRIANGULATION: DNA, PROTEINS, AND EVOLUTIONARY FORCES

As I reported elsewhere, the Aslian-speaking Orang Asli slot into a west-to-east distribution for particular alleles. Table 2 shows the intermediate position of Aslian speakers between northerly continental groups and insular Southeast Asian groups. Most of these alleles appear to be "neutral," neither relatively positive nor negative for survival. But a few are considered to be selectively advantageous, or positive

The two evolutionary forces that have received the most attention on Orang Asli are natural selection and gene flow (gene migration), but genetic drift is also of interest. These three forces are intertwined with demographic-social factors such as

population size and structure, kin-structured population moves, and the fission or fusion of population units (Fix 1982). Beyond population size *per se*, genetic drift may have caused wide fluctuations in allele frequencies over the past millennium, as outside groups recurrently introduced ravaging diseases such as cholera, smallpox, typhoid and others. So-called "demographic momentum" toward larger populations would have been severely curtailed by such epidemics.

In terms of natural selection, several genetic traits have been tested for associated anti-malarial effects. To variable extents, SAO, G6PD deficiency and Hb E have demonstrated such effects (Baer 1988, 1995; Fix 1995; Foo *et al.* 1992). In addition, Hirayama *et al.* (1996) have suggested that a HLAB variant common in Temuan and in a Semai-Temiar mixed sample also provides resistance to malaria, since HLA proteins are part of the immune response to the parasite in the liver; this variant appears to be uncommon in nearby populations. As is well known, various kinds of parasites

Table 1. Summary of groups genetically closest to various West Malaysian ethnic categories (nd=no data).

Northern Orang Asli	Senoi or Semai	Semelai	Temuan, Jakun, or "Aboriginal Malay"	Malay	Reference
Malay	(Senoi) Abor. Malay + Thai	nd	(Ab. Malay) Malay	Chinese + Thai	Lie-Injo 1976
nd	(Senoi) Jakun	Temuan	(Temuan) Semelai; (Jakun) Semai	nd	Welch 1973; Welch *et al.* 1978
Kam, Zhuang, + Thai	nd	nd	nd	Sumatran Batak	Chen *et al.* 1995
Abor. Malay + Aeta	nd	nd	(Abor. Malay) Filipino	Chinese	Nei and Roychoudhury 1982
nd	(Senoi) 7 groups from Japan to Sumatra	nd	nd	Atayal	Kirk 1979
nd	Finn + Sudanese	nd	nd	Javanese	Gajra *et al.* 1994
nd	Khmer; Javanese + Khmer	nd	nd	So. Chinese	Saha *et al.* 1995
nd	Filipino	nd	nd	So. Chinese	Melton *et al.* 1995; Melton and Stoneking 1996
Vietnamese + Korean	Sabah people + various others	nd	nd	Sabah people	Ballinger *et al.* 1992
nd	(Senoi?) Cambodian	nd	nd	nd	Watkins *et al.* 1995

Table 2. Presence/absence of variant alleles in Southeast Asian subregions, in west-to-east format (nd=no data). TK, AA, and ASL are Mainland subregions, where TK stands for the Tai-Kadai language group, AA stands for non-Aslian Astroasiatic, and ASL stands for Aslian. WMP and CMP are Island subregions, where WMP stands for the Western Malayo-Polynesian language group and CMP stands for the Central Malayo-Polynesian group. Pap stands for Papuan groups in New Guinea, and Aus stands for Australian aborigines. Positive (+) and negative (-) refer to the reported presence or absence of an allele. (Modified from Baer 1995)

	T K	A A	A S L	W M P	C M P	P A P	A U S
Hb*CoSp	+	-	+	+	-	-	-
PGM1*7	+	nd	+	+	-	-	-
PGM1*6	+	nd	+	+	-	-	-
AK1*2	+	+	+	+	+	-	-
Tf*DChi	+	+	+	+	+	-	-
Hb*E	+	+	+	+	+	-	-
SAO	nd	nd	+	+	+	+	-
PepB*2	nd	nd	+	-	+	+	-
PGM2*9	nd	nd	-	+	+	+	-
GPT*6	-	nd	nd	+	-	+	-
PepB*6	nd	nd	+	+	-	+	+

share the Orang Asli's ecological niche. Since in parasitism two or more species are forced, in a way, to evolve together, it seems likely that yet undiscovered human genes have entered into the history of Orang Asli survival through the millennia.

SAO is a dominant trait, lethal in utero when in double dose (homozygous). Among Orang Asli its reported allele frequency is highest in the state of Negri Sembilan (0.19, in Temuan), but the allele is known from the Malay Peninsula eastward into New Guinea. In malarious environments it may be a balanced polymorphism, maintained by the ability of SAO carriers to inhibit or impede the growth of malarial parasites in their ovate red blood cells.

Among Orang Asli groups, G6PD deficiency reaches its highest allele frequency in the Jah Hut of Pahang. Because of the gene's X-chromosome location, the deficiency trait is more common in males than females. Many kinds of G6PD deficiency alleles exist throughout the world. The trait is widespread in Southeast Asia and into the Pacific as far as Palau. The G6PD enzyme is involved in energy metabolism, and its deficiency indirectly forestalls the growth and development of malarial parasites. (The deficiency is also a counter indication for administering primaquine as an antimalarial drug in Malaysia, because of ensuing metabolic problems.)

Hb E extends roughly from India eastward into western Indonesia, reaching its highest frequencies in Khmers and in Aslian speakers such as Semai and Temiar. Its geographical extent and centralized high frequencies suggest that it is an ancient variant with a selective advantage in western Southeast Asia associated with the Austroasiatic language stock. (Known slight differences in the allele at the DNA level favor this argument [Orkin et al. 1982].) Various evidence points to an advantage for Hb E in combating malaria (Baer 1998). If the Hb E allele arose in the Thai-Cambodian-Laos border area and diffused 1500 km or more to the south (to Pahang state on the Malay Peninsula, for example), how long would this diffusion take in human generations? An average advance of 2 km per generation would produce an answer to this question of 750 generations. Assuming an average generation time of 20 years, one might estimate Hb E arising about 15,000 years before it reached Pahang. But if the generation time averaged 25 years, Hb E may have arisen 19,000 years before reaching Pahang. Since Semai are not thought to have arrived in Pahang very recently, Hb E might have arisen much earlier than 15,000 to 19,000 years ago. In contrast to my simplistic view, however, Fix (1981) presented a detailed scenario suggesting that Hb E has existed only for the past 5000 years, approximately.

While high frequencies of Hb E are associated with the central Aslian branch of Austroasiatic languages, particularly Semai and Temiar speakers, high frequencies of SAO are associated with more southerly groups, particularly the Austronesian-speaking Temuan, who have little Hb E. That is, these two genetic ways of counteracting malaria are linguistically differentiated. If gene flow were high between these two Orang Asli areas, the genetic-cum-linguistic differentiation would not be expected. Although the distance between the two areas is small, the topography presented traveling difficulties in the past. Thus, isolation by topography, rather than strictly by distance, was likely one factor in this genetic differentiation. A buffer zone created by cultural factors may have been another factor. At the same time, since malaria was a continuous threat in both Semai-Temiar and Temuan areas, the frequency of Hb E was kept opportunistically high in Semai-Temiar and the frequency of SAO was likewise kept high in Temuan by natural selection.

Gene flow and genetic drift. The micro level

The question of gene flow (gene migration) is of particular note here for Semelai vs. Temuan. These adjacent groups speak languages belonging to different language stocks. Yet in terms of genetics, especially the PepB findings, they appear to be closely related. This result may be entirely due to intermarriage, whereby genes migrate from one group to another. While marriage between Semelai and Temuan does occur, at least on a small scale, Benjamin (1998) also suggested that Temuan living near Semelai might once have been Semelai speakers. I would guess that Semelai are even closer genetically to the neighboring Temoq, their closest linguistic relatives (Benjamin 1998), but no genetic reports on Temoq exist.

Gene flow also exists between Semai and Temuan (Fix 1995) and between other groups, a process that may be more a recent than a prehistoric phenomenon. And genetic drift has, in various guises, been shown to be a factor in differences among related Semai hamlets (Fix 1982), although comparable work is lacking on other groups.

Gene flow and genetic drift. The regional level

A number of uncommon alleles studied throughout Southeast Asia show a west-to-east trend (Baer 1995). Such alleles found in Mainland Southeast Asia link it to Island Southeast Asia, but they tend to peter out before reaching New Guinea or Australia. Contrary to what one might think, this continental-insular linkage does not necessarily require a prehistoric movement of people. It may, for example, reflect very recent movements or ecosystem-selection differences. Some authors, however, attribute this loss of certain alleles toward the east to genetic drift, ie, chance loss associated with small-population characteristics. Nevertheless, since Aslian speakers share at least 67% (6/9) of these uncommon alleles with the northwesterly Tai-Kadai language group, as well as 89% (8/9) with the much larger Western Malayo-Polynesian population that speaks Austronesian languages, these Orang Asli are firmly ensconced in prehistory in a Southeast Asian continuum.

It is interesting and relevant that, besides genetic traits, some cultural traits also position Orang Asli between Mainland and Island Southeast Asia (Baer 1995). Such traits include the use of a blowpipe; the thunder-god complex of ideas, including the injunction against mockery of animals; and possibly certain beliefs about twin births. And Pleistocene flake tools — as found on the Malay Peninsula — also are found in continental East Asia and in Indonesia (Anderson 1987).

Overall, then, it is likely, if unprovable, that Orang Asli have been generally *in situ* for a long time, perhaps long before the last ice age. The Malayan high ground could have served as a refugium in relation to the emergence and drowning of the Sunda shelf during the late Pleistocene; such "pumping action" could have led to groups oscillating between shelf areas and uplands (Baer 1995).

ON RECONSTRUCTING GENETIC HISTORY: A SUMMARY

Historical genetics is an ongoing endeavor, as new research techniques and new theories about evolutionary change arise. Yet it is already clear from genetic findings that Malayan prehistory cannot be encapsulated in terms of separate waves of migrating peoples, so-called megatrends, but rather was richly textured by many biocultural and evolutionary processes. Certainly gene flow or diffusion was one of these. Genetic drift was another. Not the least, natural selection relative to endemic disease was a third.

Finally, both genetic and eco-cultural components of Orang Asli life have been entwined in the past and will continue to be so in the future.

NOTE

Full names of genes or alleles mentioned in the text or tables:

ADA: the gene for adenosine deaminase.

AK1: gene 1 for adenylate kinase.

Duffy: the gene for Duffy blood group

G6PD: the gene on the X chromosome for glucose-6-phophate dehydrogenase; a marked deficiency of this enzyme is often designated as G6PD–(G6PD negative).

GPT: the gene for glutamic pyruvate transaminase.

Hb CoSp: the Constant Spring allele of the alpha-hemoglobin gene.

Hb E: the E allele of the beta-hemoglobin gene.

HLAB: the B gene for human leucocyte antigen.

PepB: the B gene for peptidase.

PGD: the gene for 6-phosphogluconate dehydrogenase.

PGM1: gene 1 for phosphoglucomutase.

PGM2: gene 2 for phosphoglucomutase.

SAO (or OV): the gene for Southeast Asian ovalocytosis, also known as the erythrocyte band 3 gene and as the transmembrane anion-exchange, or AE1, gene.

SAP: the gene for saliva acid phosphatase.

Tf: the gene for transferrin.

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