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### Title

Genetic Dendrograms and Malaysian Population History

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From Darwin's time in biology and even before Darwin in linguistics, the tree diagram has been the primary formal depiction of descent (Fig. 1).

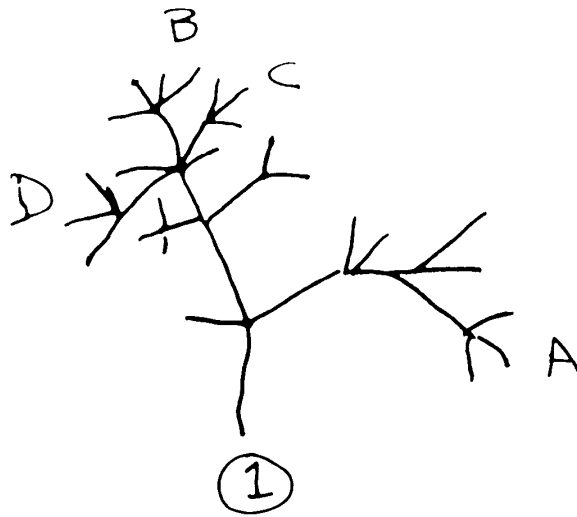


Fig. 1. Darwin's tree diagram from the 1836 Notebook B.

More recently, interest in phylogenetic methods in studying cultural diversity has extended the use of dendrograms to cultural anthropology (Mace, et al. 2005). Within genetics, and by extension, anthropological genetics, the proliferation of research on the non-recombining portion of the genome (mtDNA and NRY chromosome) has been presented predominately in the form of gene trees showing divergence of the genome from an ancestral state (Fig. 2).

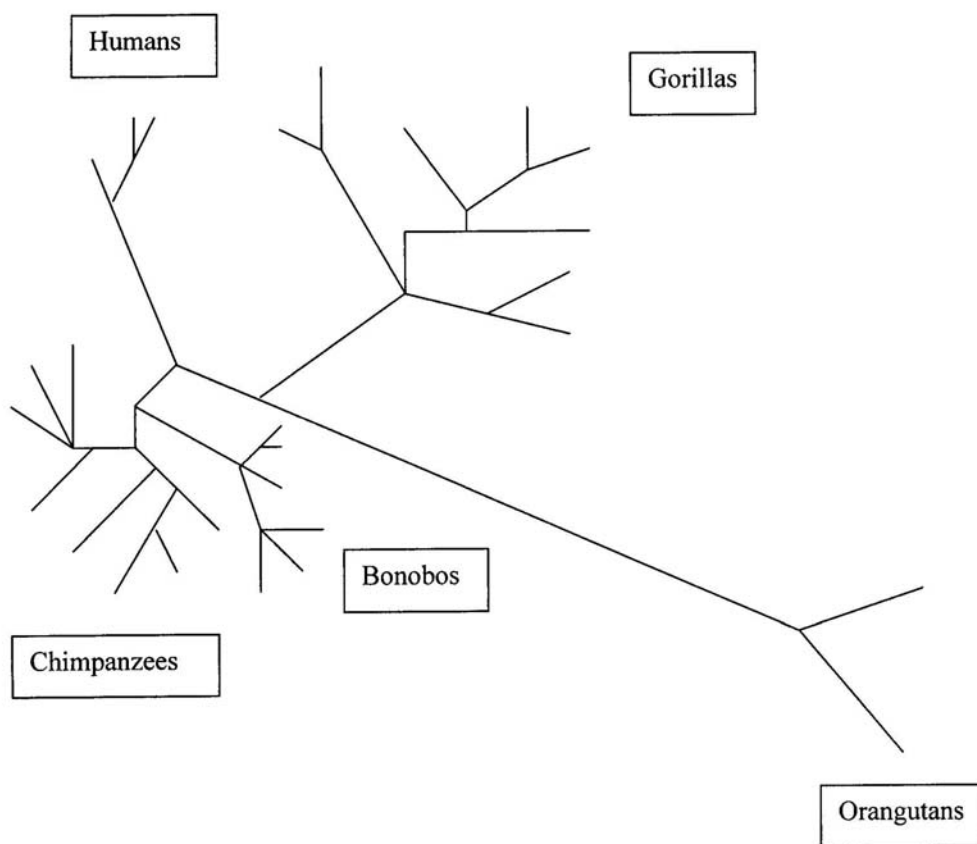


Fig. 2. Unrooted tree – mitochondrial DNA – HVS 1. Note the similarity to Darwin’s sketch. (Redrawn and simplified from (Jobling, et al. 2004). The chimpanzee and to a lesser extent, the human, limbs are much “twiggy” in the original).

The underlying logic of the dendrogram depends on a branching process: units fission, then diversify through time. Differences (or conversely, similarities) among present units (haplotypes, populations, etc.) then are a function of time since separation. This model of differentiation is generally correct for the evolution of species, genes, and languages (although see David Kronenfeld’s paper in this issue for some problems with trees in historical linguistics). However, when the units are capable of exchanging material (genes, traits, etc.), the indefinitely diverging branches of a tree no longer fit reality. In genetics, below the level of the biological species (which are by definition incapable of

exchanging genes with other species), gene flow and natural selection can reconnect the separate gene pools thereby reversing divergence. For human population history, the pattern of divergence and convergence might better be modeled as a reticulating network (Moore 1994) (Fig. 3) or the classic lattice diagram (Fig. 4) of Franz Weidenreich (1946).

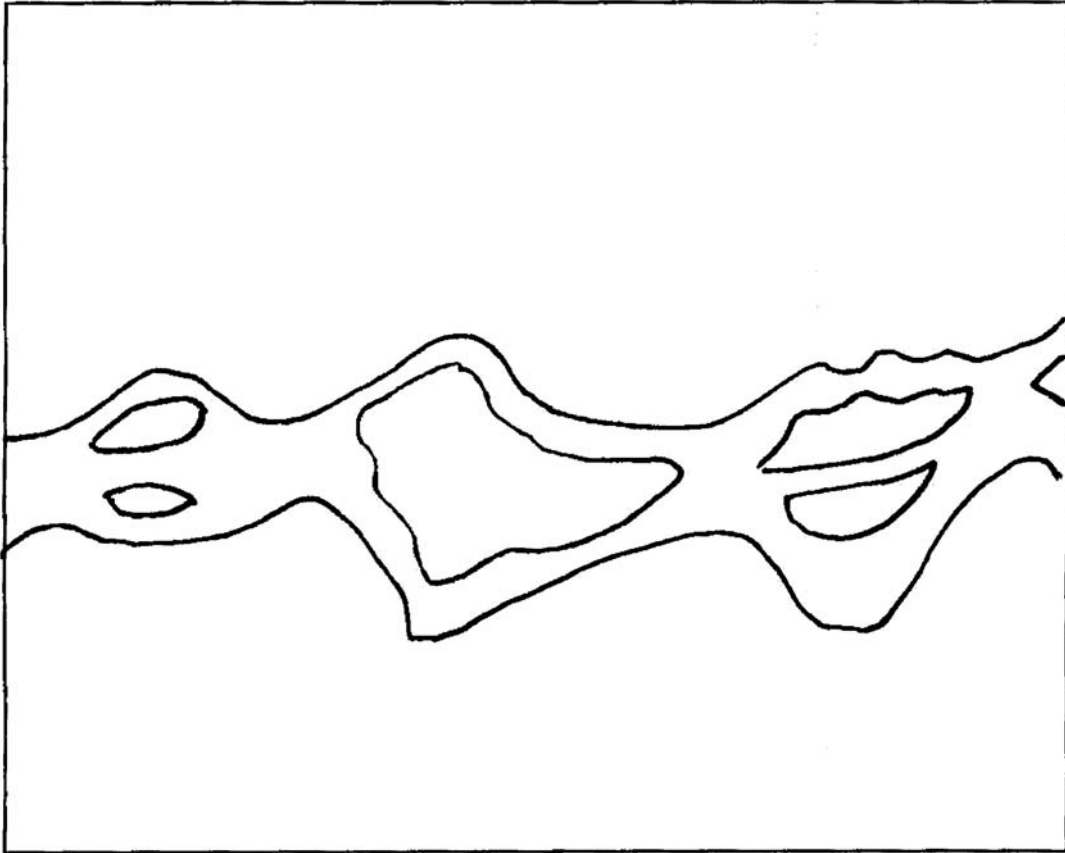


Fig. 3. River channel with reticulate branching (Redrawn from Chorley, et al. 1984).

Horizontal [Spatial] Differentiation

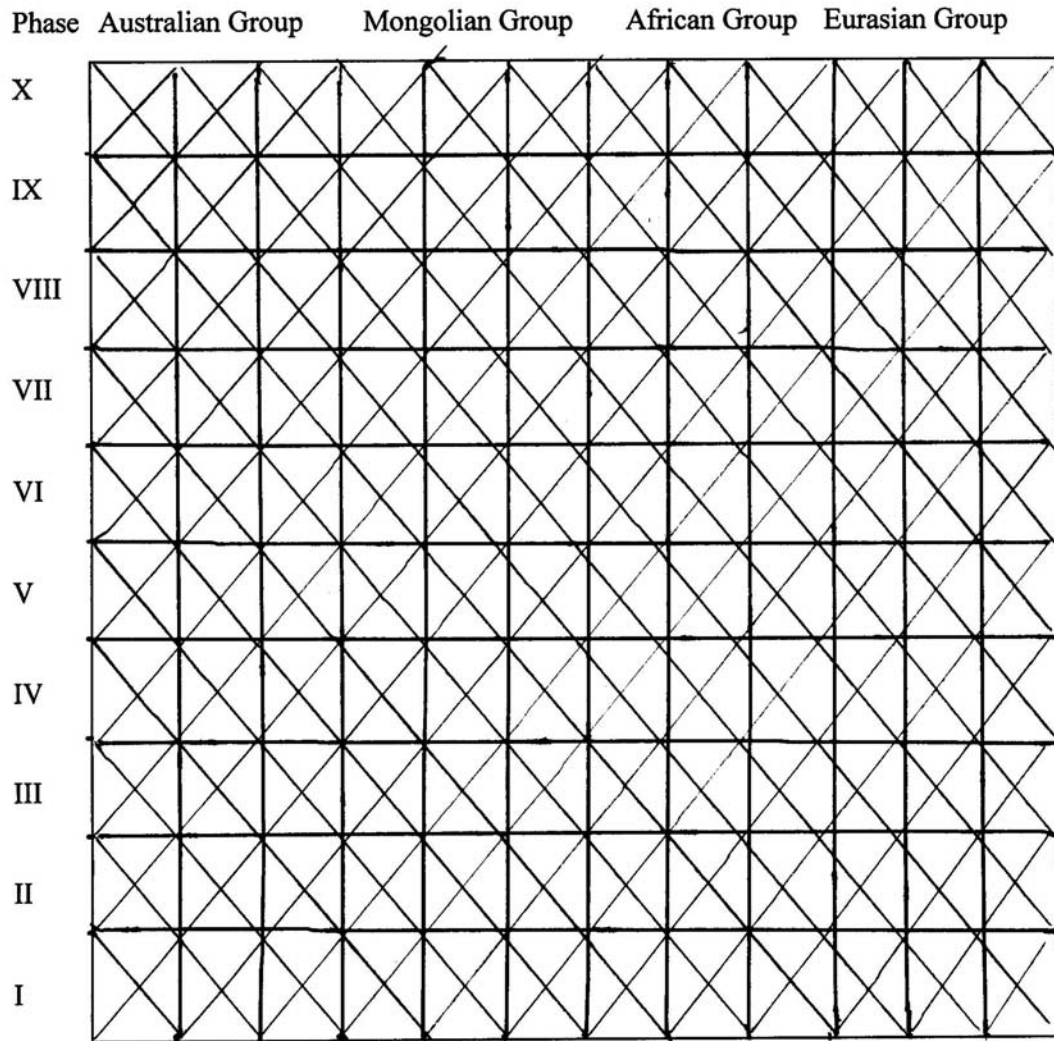


Fig. 4. Franz Weidenreich's (1946) representation of human evolution with vertical lines of descent linked together by horizontal connections through gene flow.

To illustrate this point, this paper will critically examine genetic dendrograms based on "classical" loci as well as mitochondrial DNA in the context of the history of Malaysian Orang Asli populations.

## The *Orang Asli* of Malaysia and SE Asian Population History

The *Orang Asli* (“original people” in the Malay language now used instead of “aborigines”) are the indigenous people of the Malayan Peninsula comprising three groups: Semang foragers, Senoi farmers, and “Melayu Asli” farmer-traders (Benjamin 1985), as shown in Table 1 and Fig. 5.

Table 1. The three ‘traditions’ of Malayan Orang Asli

<u>Tradition</u>	<u>Language</u>	<u>Technology/economy</u>
Semang (“Negritos”)	Northern Aslian	nomadic foragers
Senoi (includes Semai & Temiar)	Central Aslian	sedentary swiddeners
Melayu Asli (“Aboriginal Malays”)	Southern Aslian	sedentary farmers, traders

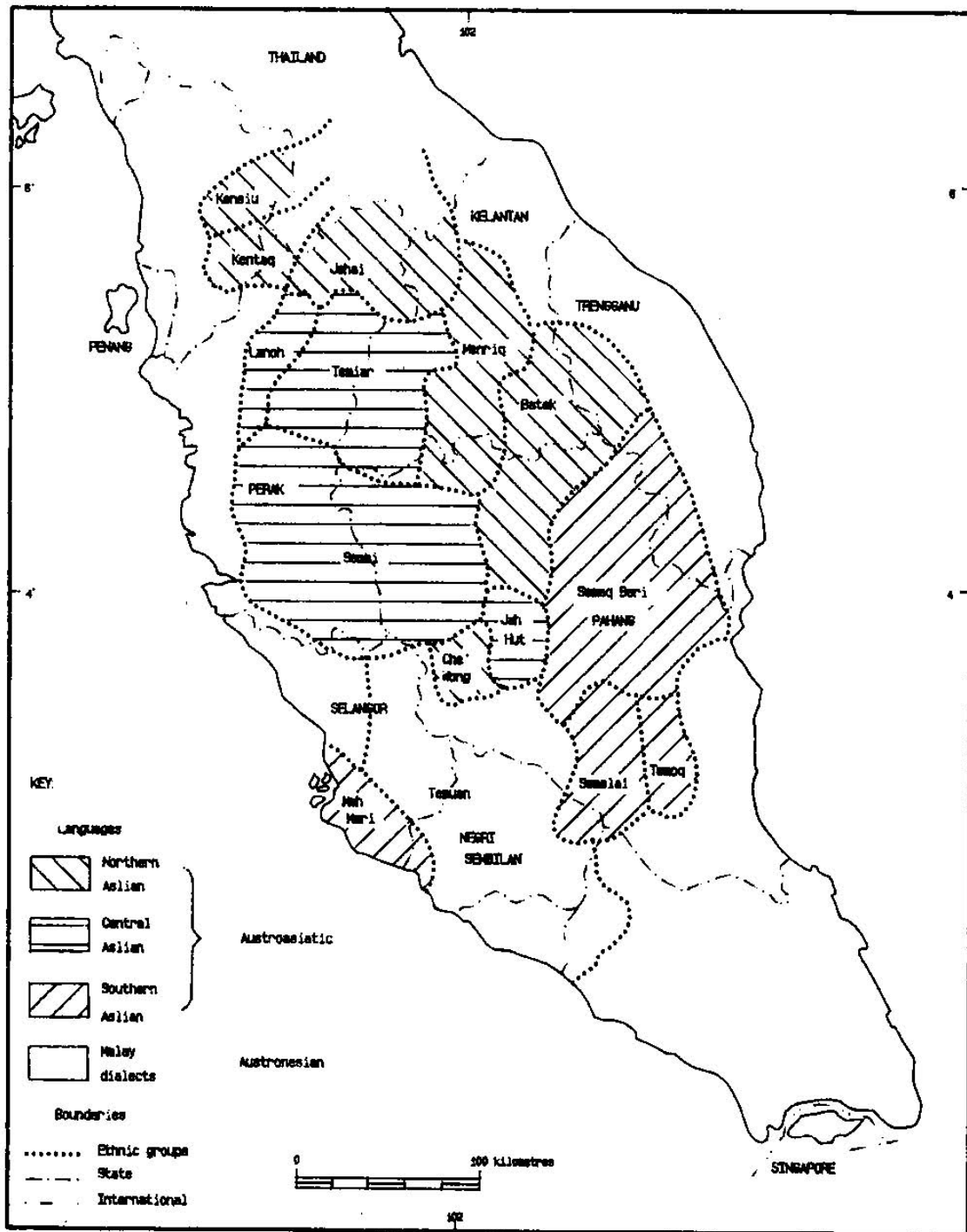


Fig. 5. Map of Orang Asli groups.

The origins of the three *Orang Asli* groups have been interpreted as a successive series of migrations (Carey 1976). The most ancient brought the ancestors of the present-day Semang foragers to the peninsula. Later waves introduced farming Senoi ancestors (including those of the Semai) followed by the farming-trading *Melayu Asli* or “aboriginal Malays”. Although this explanation for present day cultural (and biological) diversity harkens back to the *Kulturkreislehre* school of cultural diffusion, in some measure it continues to have support among current scholars (Bellwood 1993).

An alternative model was put forward by Geoffrey Benjamin (1976; 1985) who argued that cultural differentiation arose in situ on the peninsula through a process of competitive displacement between the economies. Benjamin’s (1976) model was based partly on the pattern of shared languages among the Orang Asli (all are speakers of Mon-Khmer languages of the Austroasiatic family) and a socio-cultural argument for a kind of competitive displacement among the economies and cultures of the three groups. The migration idea as championed by Peter Bellwood (1993) ascribes the expansion of Austroasiatic-speaking rice farmers via demic diffusion from a homeland in China through Southeast Asia down to the Peninsula. Thus range-expanding Senoi agriculturalists would have displaced the original hunter-gatherer Semang inhabitants from some of their lands. The linguistic similarity between Senoi and Semang would have come about through adoption of farmer languages by the foragers on the model of the Agta of the Philippines and the Pygmies of central Africa (Headland and Reid 1989).

Clearly trees of genetic descent based on these two different population histories should be quite different. If dendrograms reflect population histories of fission and divergence, Orang Asli genetic relationships should provide a tool for deciding between



these alternative models. To alleviate suspense, they don't. To be fair, this failure is partially due to too few data. Very little genetic information is available for the Orang Asli and almost none for the Semang. However, as we shall see, what data there are argue against any simple tree model of population history in the Malayan Peninsula.

### **“Classical Markers”**

“Classical” genetic loci, including blood groups, enzymes and structural proteins such as hemoglobin, have been used to construct dendrograms representing genetic affinities among a series of sampled populations. Genetic similarity thus implies a common evolutionary history of populations (Cavalli-Sforza, et al. 1994), as shown in Fig. 6.

However, such trees offer little evidence bearing on Orang Asli origins and migrations. The Semai were included among a number of other Southeast Asian populations in a tree based on 31 “classic markers” (Cavalli-Sforza et al. 1994). They are shown as clustering closest to the Zhuang, a Tai-speaking ethnic group of South China whereas they are quite distant from the Khmer, the contiguous population of Cambodia with whom they share a close linguistic tie. Interestingly, another tree constructed from a different set of “markers” and a somewhat different set of Southeast Asian populations, is quite different from the Cavalli-Sforza et al. dendrogram, linking Orang Asli (specifically, Semai) and Khmer closely and separating this cluster from other populations (Saha, et al. 1995). It is shown in Fig. 7. In neither study are there data on the other Orang Asli groups.

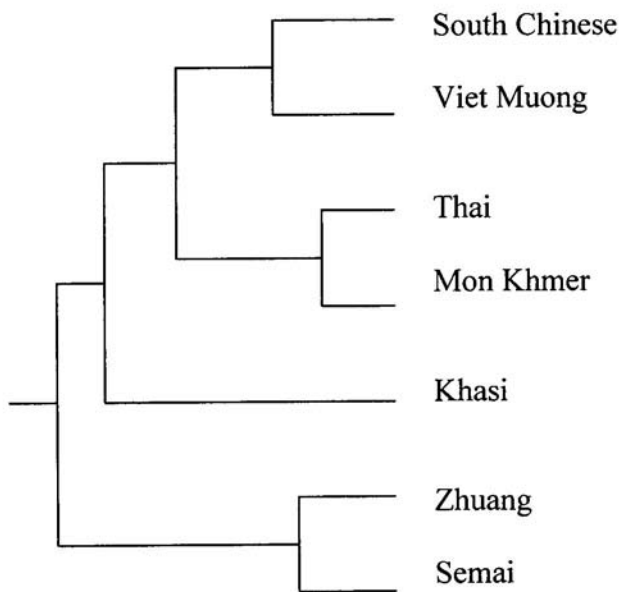


Fig. 6. Dendrogram of selected Southeast Asian populations (redrawn and simplified from (Cavalli-Sforza, et al. 1994).

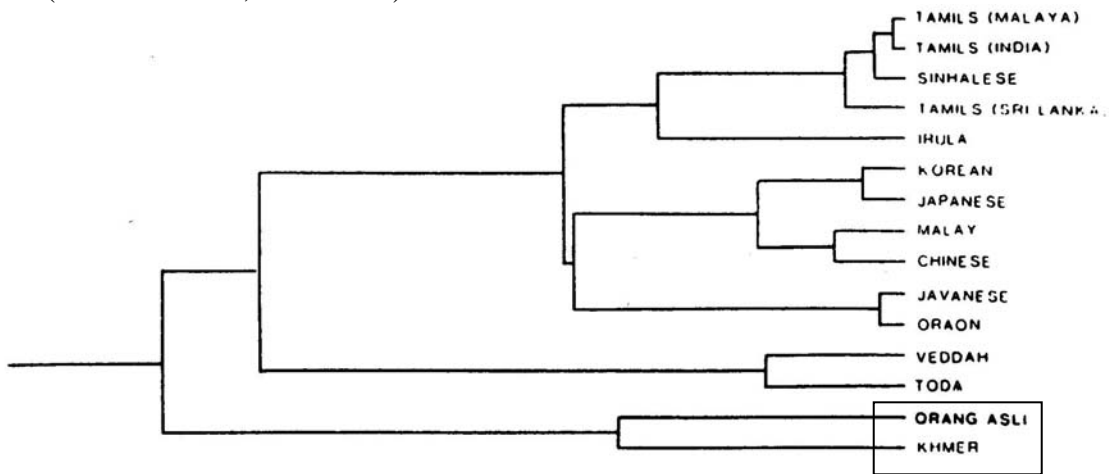


Fig. 7. Dendrogram linking Orang Asli (specifically, Semai) and Khmer (Saha 1995)

This comparison illustrates some pitfalls with genetic inference on the history of populations. Trees are constructed from matrices of genetic similarity/difference. If all loci are “marking” the same history of population fission, migration, isolation, and random differentiation, then all dendrograms should be identical. However, this may not

always be the case. Consider the fact that one of these trees includes hemoglobin E (Hb\*E), an allele conferring some resistance to malaria. This non-neutral allele attains high frequency in several mainland Southeast Asian populations (including the Khmer) and, for the same reason, malarial selection, in the Semai. Not surprisingly, then, Khmer and Semai show genetic “affinity”.

In the case of Hb\*E, shared ancestry as part of the wide-spread Austroasiatic (Mon-Khmer) speaking mainland Southeast Asian population may explain the presence of this allele among the Semai, but its *high frequency* surely depends on natural selection.

Similarly the historical evidence records the introduction of another adaptive allele, ovalocytosis (Southeast Asian Ovalocytosis or SAO), via migration from a *Melayu Asli* group. In this case, however, a common *population* history between Semai and other populations with high frequencies of SAO is less likely than for Hb\*E. While Hb\*E is found in mainland Southeast Asia, SAO occurs in a wide swath from coastal Papua-New Guinea through island Southeast Asia (Fix 1995), as shown in Table 2. Among the southern Semai, we perhaps find an adaptive allele protecting against malaria in the process of being introduced from a neighboring population (Melayu Asli) who likely received the gene through intermarriage with trading partners, Austronesian-speaking Malays, seafarers ranging over the entire extent of the islands. SAO demonstrates a *link* (gene flow) with island Southeast Asia but does not necessarily show the *origins* of Orang Asli from this region. The cause of high frequencies of SAO in coastal New Guinea and Melayu Asli (as well as some local Semai populations) is malarial selection. A few migrants would be sufficient to spread the allele, and where advantageous, it increased in frequency.

Table 2. *Hemoglobin E and ovalocytosis frequencies*

<u>Population</u>	<u>Ovalocytosis (SAO)</u>		<u>Hb*E</u>	
	<u>N</u>	<u>% Positive</u>	<u>N</u>	<u>q<sub>E</sub></u>
Negritos	?	<2.0	?	0.024
Senoi				
Temiar	?	6.7	80	0.319
Semai				
Perak	242	6.6	332	0.255
Pahang	545	21.3	520	0.215
Melayu Asli				
Temuan	315	35.2	406	0.015
Semelai			41	0.171
Malays				
Selangor	?	<0.3	536	0.015
Negri Sembilan	629	13.2	629	0.026
Trengganu			249	0.111
Indonesians				
Sulawesi	?	40.0-50.0		
Bali			219	0.018
Minangkabau	83	7.2	235	0.011
New Guinea				
Kar Kar Island	334	13.8		
Thailand				
Khmer			133	0.327

Indeed, it may be difficult to demonstrate that gene flow is the cause for the presence of an allele in a population. Recent work (Ramos-Kuri, et al. 2005) has identified exactly the same 27 base pair deletion that characterizes SAO in Mexico. A colleague suggested the Manila Galleon as a migrant source but it is not impossible to rule out an alternative explanation for this sporadic occurrence; i.e., a new mutation. Thus, there are multiple causal factors that must be considered to understand any genetic distribution. As a consequence, “(h)istory may not be read simply from gene trees” (Fix 2000:16).

## **Molecular markers**

A problem with classical loci is their lack of specificity. As Majumder (2005:293) notes, “Since genes move as people move, the commonly used method to trace trails of human migration is to identify *specific genetic signatures* in the source population and look for these signatures in extant populations along the suspected migration route” (emphasis added). It would appear that the molecular signature of SAO (deletion of a particular sequence of DNA) would satisfy this requirement. But a similar deletion phenotype, the famous 9 bp deletion in the mitochondrial (mt) DNA genome that is the basis of the “Polynesian motif” (as well as haplogroup B, a common Native American type), is quite widespread and several origins for the basic deletion have been posited (Schurr and Wallace 2002).

Even where we may presume a common mutational origin, molecular genetic markers may only record *ancient* history over a wide geographic region. Neither Hb\*E nor SAO mark Senoi or Orang Asli ethnic populations but rather demonstrate shared histories and gene flow on a spatial scale from eastern India to Papua-New Guinea.

Similarly, the mtDNA 9bp deletion has a wide distribution including the Semai Senoi, where 11 of 30 individuals carry the trait (Melton, et al. 1995), as shown in Fig. 8. Because the genome is inherited maternally, there is no recombination among loci so that successive mutations accumulate on the chromosome. Melton and colleagues (1995) propose that the original deletion occurred perhaps 60kya and was widely spread through Southeast Asia.

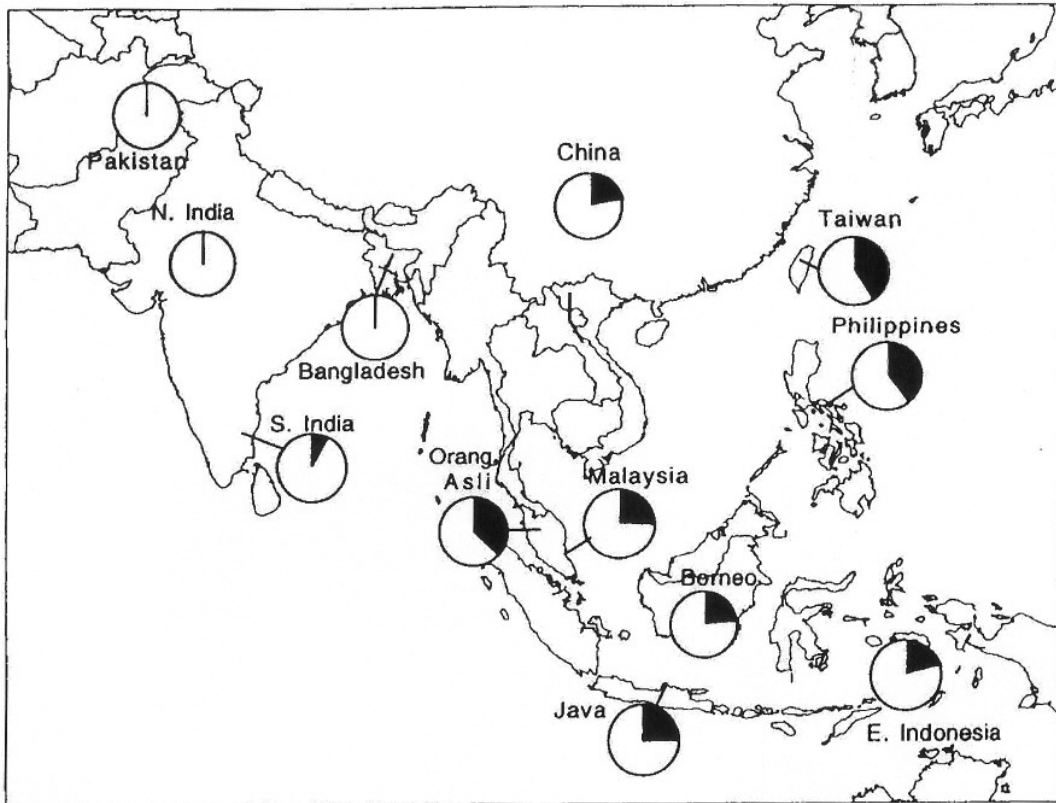


Fig. 8. Distribution of the 9bp deletion in mitochondrial DNA (from Melton, et al. 1995).

A dendrogram formed by adding three additional substitutions in the control region of mtDNA shows a “star cluster” pattern, deep branches extending far back to the ancestral form, indicating that these divisions are *all* ancient (Fig. 9). This pattern has been widely observed in mtDNA data world-wide and has been explained as a population bottleneck followed by population increase, a demographic event that Rogers and Jorde (1995) believe would have obscured more recent population history.

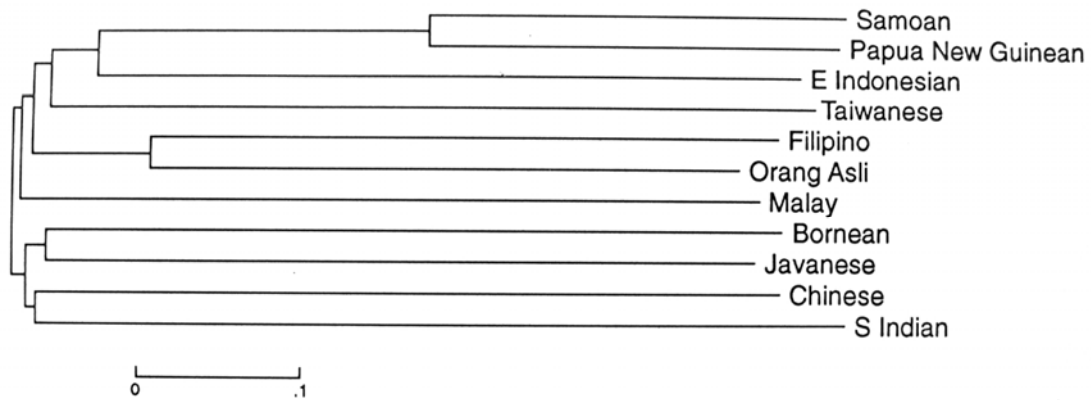


Fig. 9. mtDNA dendrogram (from Melton et. al. 1995).

This conclusion is reinforced by the haplotype tree of Ballinger et al. (1992), as shown in Fig. 10. Some 33 Orang Asli of various ethnicities (but probably mostly Semai Senoi) are located in almost every branch of this tree. Some Orang Asli haplotypes are close to those found in present-day Sabah indigines, Koreans, Vietnamese, and Malays. Again, the mtDNA data do not uniquely mark origin(s), subgroups (Semang, Senoi, or Melayu Asli), or population movements of the Orang Asli.

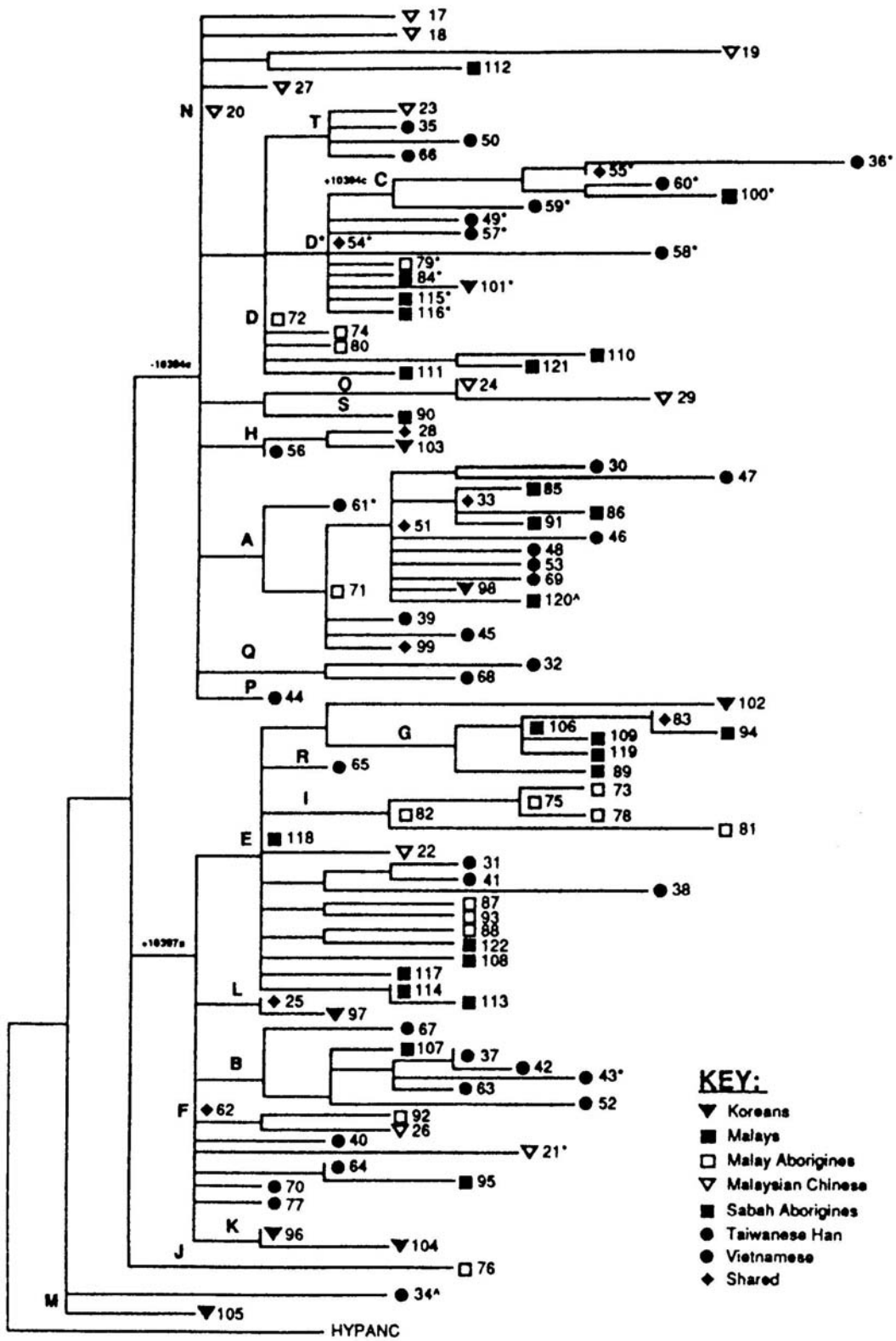


Fig. 10. mtDNA dendrogram (from Ballinger, et al. 1992).



More recently, analysis of mtDNA from 260 Orang Asli from all three subgroups has been claimed to support a “single, rapid coastal settlement of Asia” (Macaulay, et al. 2005). Figure 11 shows their reconstructed dendrogram of Asian mtDNA haplogroups. Based on molecular clock estimates, the basal haplogroup, L3, the African clade ancestral to M and N is approximately 84ky old, with M and N arising circa 63ky ago. These dates (if correct) would suggest that M and N (and the nearly contemporary R) were carried by the original anatomically modern *Homo sapiens* migrants dispersing from Africa. Note that the filled terminal haplotypes in Fig. 11 indicate Orang Asli. Maccaulay and colleagues (2005:1035) interpret this to mean that the “Orang Asli harbor “relict” mtDNA lineages with time depths of ~44,000 to 63,000 years. Their restricted distribution makes it very likely that these lineages diverged around that time within mainland southeast Asia. The Orang Asli would thus be “relict populations” (Forster and Matsumura 2005) preserving ancient mtDNA signatures of the first colonization of southern Eurasia by modern humans. In this scenario, the Orang Asli survived in a “glacial refuge”, avoiding later “waves of replacement...during the late Holocene” (Maccaulay et al. 2005:1035).

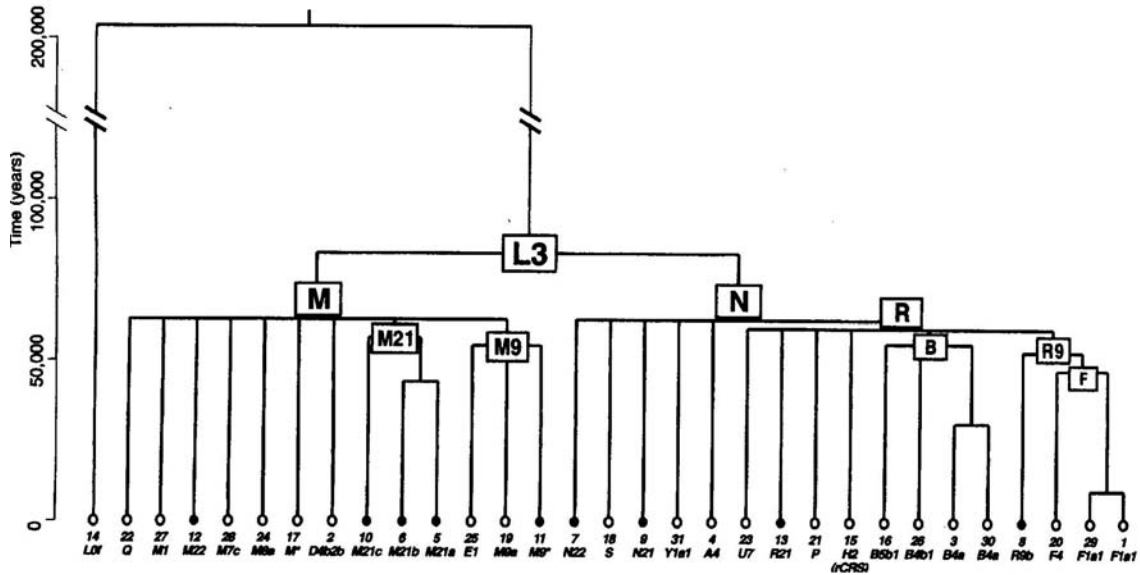


Fig. 11. Orang Asli mtDNA dendrogram (from Macaulay, et al. 2005).

Interestingly, all three subgroups of Orang Asli show “relict” haplotypes (although only one Semai was typed – the rest of the Senoi sample being Temiar – N=51). This may constitute evidence for the *in situ* differentiation hypothesis of Orang Asli origins discussed above, or may only be an indication of gene flow amongst these populations after their successive arrival in the Peninsula.

## Conclusions

If dendrograms are explicitly presented as simply visual representations of genetic similarity among populations (as Cavalli-Sforza sometimes seems to argue), then there is no problem. However, the very notion of a tree of descent implies a model of divergence in isolation. The naïve interpretation when viewing a tree is always the branches follow separate evolutionary trajectories. This is not the case for the Orang Asli and, I would argue, for most human populations. The genetic dendrogram, then, is a ubiquitous but often misleading formalism and should be recognized as such.

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