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## Human Diversity and its History

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### ABSTRACT

In the last decade a large amount of new genetic data from human populations has appeared. The most informative of the new loci are STR (short tandem repeat) polymorphisms, because they are not subject to the ascertainment biases that affect classical markers and SNPs (single nucleotide polymorphisms). These loci show a marked diversity cline away from Africa, as they should if a version of the SOM (single origin model) is correct for our species. But the new data have not given us many insights into ancient population history and movements: they generally show that neighboring populations are similar to each other and that similarity declines with geographic distance. Much interesting human history has been blurred and erased by recurrent local gene flow. Other genetic and non-genetic markers, like language and physical appearance, may have better “memories” and tell us more about ancient populations movements and relationships.

### Introduction

New technology for ascertaining and typing genetic markers has given anthropologists a flood of data in the last decade. Today single publication can present more and better data than the sum of everything available in the literature before 1985 or so. The new data have essentially confirmed the SOM model of human history, in which we are descended from a small founding population that was probably in Africa.

Many of us did not foresee that we would infer demographic history from genetic data. On the other hand we did foresee that more and better genetic data would let us read this history of population relationships, migrations, and the genesis of human genetic diversity. In this paper we suggest that the new data from neutral markers paint a rather dull picture of high levels of local gene flow everywhere and unremarkable correlations between genetic distances and geographic distances between populations. In a sense the new wealth in data has been a disappointment.

When populations exchange neutral genes there is essentially blending of gene frequencies, so red and white each become pink over time. Markers that do not blend in this way may give us

better information about population history. Languages, for example, do not blend like gene frequencies. Instead there is “majority advantage” in which immigrants just learn the indigenous language (Renfrew 1987). Prominent visible “racial” traits may also have enjoyed such majority advantage, so that appearance can tell us more about ancient relationships than can gene frequencies.

## **Human Demographic History**

### ***Small Effective Size of Humans***

Findings from many genetic systems suggest that the effective size of humanity is on the order of 10,000 breeding individuals. Since this estimate is wrong by a factor of a million or so today, the implication is that our ancestry is some specific small isolated population of archaic humans (SOM) rather than the whole array of *Homo erectus* relatives that occupied the temperate Old World for one to two million years (MRM, multiregional model).

Haigh and Maynard Smith (1972) suggested that there was a bottleneck in our ancestry on the basis of the spectrum of substitutions in hemoglobin. Subsequently the number 10,000 has become widely established as the summary effective breeding size of humans (Li and Sadler 1991). This could reflect either a population that was this small for a very long time else a severe transient bottleneck during which the number of our ancestors was much less than this. Estimates from nuclear genes (Harding et al. 1997; Hey 1997; Zietkiewicz et al. 1998), mtDNA (mitochondrial DNA) (Rogers and Jorde 1995), the HLA system (Takahata and Satta 1998, in press) and from human-specific alu insertions (Sherry et al. 1997) all converge on a similar figure.

### ***Expansion from Small Size***

The tree of human mitochondrial DNA is star-like as if it is recording a major population expansion in our history (Di Rienzo and Wilson 1991; Slatkin and Hudson 1991; Rogers and Harpending 1992; Harpending et al. 1993). The pattern in mtDNA is clear, but it could be the result of selection as well as population expansion. The expansion hypothesis has been in limbo for several years, since no such pattern is apparent in several nuclear genes (Harding et al. 1997; Hey 1997; Zietkiewicz et al. 1998). Recently, however, there have appeared several papers analyzing STR polymorphisms (Shriver et al. 1997; Di Rienzo et al. 1998; Kimmel et al. 1998; Reich and Goldstein 1998). These all find strong evidence of a major population expansion in our history. Given the new findings, it seems safe to go back to the mitochondrial estimates of the timing of this expansion: these vary from 120,000 to 30,000 years ago, with heterogeneity among populations. Uncertainty about mtDNA mutation rates is great, so these numbers should be treated with caution.

Can we relate the expansion visible in our DNA to anything in the fossil and archaeological records? There are at least four candidates for the correspondence. First, Mode 3 stone tool

technologies appear about 250,000 years ago in Africa and Europe<sup>1</sup>. Second, human fossils that are equivocally modern appear in Africa and the Levant 100,000 or more years ago associated with Mode 3 technologies. Third, the Toba super-eruption at 71,000 years ago may have caused widespread ecological devastation and extinction on earth, and the expansion may be recovery from that event (Rampino and Ambrose 1998). Fourth there is a dramatic invasion of Europe by bearers of Upper Paleolithic (Mode 4) technologies 40,000 years ago. We do not believe that there is compelling evidence favoring any of these alternatives.

### ***Dispersal of Modern Humans***

In Europe and western Asia north of the Himalayas there is a clear record of the spread of modern humans from Africa. Most of Europe was occupied rapidly although pockets of Neanderthals apparently persisted for millennia, even adopting some of the new tool technologies.

South of the Himalayas the record is not so clear. If there was a separate southern exodus there is little record of it until Australia, which was occupied between 35,000 and 40,000 years ago (O'Connell and Allen 1998) by bearers of Mode 3 technology. Mode 4, thought by many to be diagnostic of modern humans, never appeared in Australia. There are at least two scenarios about the history of Australia that are plausible.

The first scenario is that there was a southern branch of the human expansion that did not bear Mode 4 technologies, implying that Mode 4 is not a marker of modern humanity but only a marker of a society where males were not continuously engaged in parental investment.

In a famous paper the Whittings (Whiting and Whiting 1975) point out that there are consistent differences between societies where males are familial and those where males are “aloof” from women and the family. In the latter males are more likely to be belligerent and gaudy: it is in these among technologically primitive societies where fancy artistic expression occurs as either a manifestation or a side-effect of male competition. In the former kind of society males are likely to be occupied working to provision their offspring. Certainly there are many foraging societies where there is no production of fancy technology like that of Mode 4 cultures. We can compare the drab limited technology of Kalahari Bushmen, for example, with the rich diversity of weapons and art from central African societies.

The second scenario is that there was a single expansion of moderns out of Africa. Modern humans reached Australia from southeast Asia much later, and the old technologies and fossils from Australia, like Mungo and Kow Swamp, are those of another species of archaics, not of modern humans. This is not a popular scenario today, but it deserves consideration. Under this model the arrival of modern humans in Australia occurred not 40,000 years ago but perhaps

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<sup>1</sup> Modes refer to a regular sequence of complexity of stone tools made by humans and human ancestors during the Pliocene and Pleistocene (Clark 1977). Mode 1 is pebble tools, Mode 2 adds the Acheulian hand axe technology, Mode 3 contains flakes made from prepared cores, Mode 4 is the technology of the Upper Paleolithic with blades and worked bone, and Mode 5 is the microlithic technology associated with the Mesolithic.

5,000 with the appearance of a small tool technology, the dingo, and an apparent tenfold increase in population (Bellwood 1997).

### **Diversity Patterns:**

{FIGURES ONE AND TWO ABOUT HERE}

Figures 1 and 2 summarize world patterns in microsatellite diversity from two separate sources: Figure 1 is based on results from Lynn Jorde's laboratory at the University of Utah (Jorde et al. 1995), while Figure 2 is based on results from Kenneth Kidd's laboratory at Yale (Calafell et al. 1997).

The left panels in each figure show how genetic diversity declines away from Africa. The horizontal axes are genetic distances from the African mean. The vertical axes are average heterozygosity. The pattern is clear in each case: the more genetically different a population is from African populations the lower its genetic diversity. This pattern is in good agreement with a model of human expansion that includes series of bottlenecks during colonization episodes in which diversity was lost. By the time we reached interior South America, according to the evidence of the Surui of Amazonia, we had lost about one quarter of our neutral genetic diversity.

The right panels in each figure are plots of the leading two principal components of the normalized allele size covariance matrix among populations. This is the (least squares) best two dimensional picture of genetic distances among populations. In each case we see that there is a general concordance between geography and genetic distance: neighbors are genetically similar. In figure 1 there is apparent "clumping" into three traditional races: African, European, and Asian, with the Biaka and Mbuti as slight outliers. This could reflect real differences from other African populations or it could reflect the small number of individuals from each population in the Jorde data. In figure 2 the picture is dominated by the genetic distinctiveness of small and probably isolated populations that have undergone a lot of gene frequency change due to drift. Compare, for example, the isolated Surui with the large cosmopolitan Maya.

### **Problems**

The rich new data that have become available support two general conclusions. First,  $F_{st}$ , a standard measure of heterogeneity among populations, is about ten percent among major continental groups. Essentially the same number has been known since 1972 or so. Second, there is a cline in neutral genetic diversity outward from Africa. This is a new finding that relies on microsatellite loci. With their large number of alleles they are not subject to the ascertainment bias that affects classical polymorphisms and SNPs. Older studies, summarized in (Cavalli-Sforza et al. 1994), did not show any clear diversity gradient because most of them had been found in Europeans, thus selecting for markers most diverse in Europeans.

Any account of the expansion of modern humans must account for the ten percent difference among continental areas as well as the diversity cline away from Africa. A popular idea in anthropology is that these race differences developed *in situ* as a consequence of geographically restricted gene flow, but this does not seem possible. In a collection of completely isolated

populations, each of size  $N$ , drawn from a common founding population,  $F_{st}$  should increase approximately as

$$F_{st}(t) \sim 1 - e^{-\frac{t}{2N}}$$

so that if  $N \sim 10,000$ , for example after the expansion and dispersal of humans, it would require approximately 50,000 years for differences that we observe today to accumulate. We know that 50,000 years ago humans were about to begin their colonization of Europe and west Asia and may have already reached Australia, and there must have been many more than 10,000 in these populations spread over several continents. Since there is such clear geographic patterning in genetic distances between populations, there must also have been substantial gene flow among populations. Such gene flow would retard the accumulation of  $F_{st}$ . In populations with hundreds of thousands of members  $F_{st}$  is essentially frozen over time scales of interest to us.

How can we account simultaneously for an expansion from a small population of only several thousands of adults, a global  $F_{st}$  of ten percent, and the diversity cline away from Africa? Since  $F_{st}$  is essentially frozen in populations greater than several tens of thousands, these neutral differences must have accumulated in small populations. Two models that have been proposed are the “divided Eden” model in which the small ancestral population was itself subdivided into races, and the “Cain model” in which colonizing populations are small for a long time so that a series of founder effects occurs during colonization of new areas. We can generate neutral gene distributions in a computer simulation of human history that match our origin from a small population, contemporary  $F_{st}$ , and contemporary diversity clines by either mechanism, and so far we have not found a way to distinguish their effects.

## A New Direction

The emerging picture from new and plentiful data about neutral markers is one of a smooth relationship between geographic and genetic distances with some perturbations due to recent history and to language. These findings suggest that there has been a lot of gene flow between neighbors and that isolation by distance, rather than history, dominates the distribution of neutral genes in human populations. We believe it is time to extend our domain of inquiry to marker systems where history is better preserved. In their pioneering study of human race differences, Nei and Roychoudhury (Nei and Roychoudhury 1974) hint at a new direction. They say that their finding of rather small race differences “does not apply to those genes which control morphological characters such as pigmentation and facial structure.” Darwin (1871) thought that our race differences were driven by sexual selection, a view defended by Diamond (1992) who shows that environmental selection accounts of race differences in skin color and other traits do not bear close scrutiny. If skin color were a response to climate, Tasmanians should have turned white. If this view of differences in appearance is correct, even in part, then physical appearance, like language, could carry a signature of history much deeper than the signature in neutral genes.

When gene flow occurs between populations gene frequencies blend in a linear way, so that over time differences between the populations are erased as history yields to local migration-drift equilibrium. But both language and sexually selected appearance may respond very differently to contact and admixture. We think it is time for biological anthropology to turn its attention again to language and to external appearance, but we realize that both these topics are, putting it mildly, unfashionable. We will discuss a simple model showing how traits like this should preserve deep history and discuss several examples.

### ***Language and Rh among Basques***

The Basques of the Pyrenees speak a language that is perhaps distantly related to languages of the Caucasus mountains but is otherwise unique in the world. A common theory is that they are a relic of an earlier occupation of Europe that was overrun by later invaders, perhaps the Indo-Europeans. Their genes are mostly similar to those of their neighbors except that they have a frequency of Rhesus negative that is greater than one-half. Following Ruhlen (1994) imagine that there has been some small level of gene flow, one percent per generation, into the Basque population from their new neighbors for five thousand years, say 250 generations. Then of the neutral genes in the Basque population today only  $.99^{250} \sim$  eight percent are descended from ancient Basque genes. The neutral parts of the genome have essentially been replaced.

But consider the language spoken by these immigrants. Since they arrive in small numbers they and their children learn Basque and, save for occasional loan words, have little effect on the language. The Basque language has persisted over millennia while the neutral genome has been replaced. Meanwhile, natural selection at the Rh locus is such that the common type is favored. If the original state was all or mostly Rh negative, then there would be ongoing selection against any Rh positive genes introduced by immigrants. In this way, both language and the Rh system preserve deeper history than neutral genes. Rh and language share the property that there is selection for the common type. Sexual selection for external appearance may follow similar dynamics.

### ***A Model of Majority Advantage***

Simple models of single diallelic loci can give us insights that are robust. Here we discuss the simplest model we can write of the process we envision, but the dynamics of a quantitative trait should be much the same.

Consider an allele  $A$  whose frequency in a population is  $p$ . The genic fitness of  $A$  is proportional to its frequency with selection intensity  $s$ , so that

$$W(A) = sp$$

$$W(a) = s(1 - p).$$

Gene frequency change follows

$$\frac{dp}{dt} = sp(1-p)(2p-1)$$

If  $p$  is greater than one half selection will drive  $A$  to fixation while if  $p$  is less than one half the allele  $a$  will go to fixation.

Now put this population in an island model, so that it is one of many demes that receive  $M$  immigrants per generation from the whole array of islands. Assume that half the islands have  $p > 0.5$ , half  $p < 0.5$ , and that the overall mean is just  $P = 0.5$ . The effective size of each island is  $G$  genes. Local frequency change is described by

$$\frac{dp}{dt} = sp(1-p)(2p-1) + \frac{M}{G}\left(\frac{1}{2} - p\right)$$

for which there are two interior stable points, one on either side of the grand mean  $P = 1/2$ .

Polymorphism persists if  $\frac{2M}{sG} < 1$ , that is if twice the migration rate is less than the selection intensity. If the migration rate is high enough it overwhelms local selection and the whole system quickly goes to fixation, that is to monomorphism of either  $a$  or  $A$ .

At the equilibrium between migration and local selection for the common type diversity among islands due to selection is

$$F_{st} = 1 - \frac{2M}{sG} \quad (1)$$

while neutral traits would follow migration-drift equilibrium for which

$$F_{st} = \frac{1}{2M+1} \quad (2)$$

These are abstract but we can obtain a feel for magnitudes involved by using some human data and plausible population parameters.  $F_{st}$  among continental groups is about ten percent, implying from equation (2) that  $M \sim 4.5$  corresponding to 2 diploid migrants per generation. Relethford (Relethford 1994) estimates  $F_{st}$  for human skin color to be about 0.6, that is six times as great as that of neutral genes. If the effective size of our human islands is  $G = 10,000$ , equation (1) implies  $s \sim .001$ . This is a very low intensity of selection, a level that is probably undetectable by epidemiological methods.

### **World Languages**

{FIGURE 3 ABOUT HERE}

Language ought in some cases to follow something like our model of common type advantage, as we proposed for Basque. Figure 3 is a map (redrawn from Ruhlen 1994) of world languages lumped into the largest possible groups by Ruhlen. This degree of lumping is very controversial,

but it may suggest interesting patterns. There does seem to be support for a North–South, rather than East–West, division of Eurasia. In the North there are two language families: Dene-Caucasian in scattered patches including several in the New World, and Eurasiatic. The pattern is one in which the Eurasiatic languages underwent a later expansion at the expense of Dene-Caucasian leaving behind relics (including Chinese!). South of the Himalayas there are more groups each more restricted reflecting perhaps lower mobility or the absence of subsistence innovations that allowed the wide expansions seen in the North.

This pattern in world languages supports the southern-branch theory of the expansion of modern humans. There are two families north of the Himalayas, with Dene-Caucasian perhaps the more ancient and associated with a pre-agricultural expansion and Euro-Asiatic superimposed on it. In the tropical regions there are four families in Asia and Oceania. The Indo-European intrusion into India and the Sino-Tibetan intrusion into southeast Asia may be relative recent events.

### ***Kalahari Bushmen***

An interesting case for the retention of old appearance in the face of gene flow is provided by Kalahari Bushmen. (They are called *San* in some recent literature, but this is a nasty word to use to someone in the central Kalahari, and we avoid it.) These are people who historically made their living by either foraging or keeping small stock in southern Africa. They resemble, to European eyes at least, east Asians. They have yellowish rather than black skin, epicanthic folds, shovel-shaped incisors, and many newborns have “Mongoloid spots” at the base of the spine. The Asian appearance is not just a perception of Europeans. In the !Kung language there are three kinds of mammals: !a is an edible animal like a warthog or a giraffe, !oma is an inedible animal like a jackal, hyena, black African, or European, and zhu is a person. Vietnamese in Botswana were immediately identified as zhu by Bushmen. In other words, their perception of their similarity to Asians is the same as ours (i.e. Europeans’).

Immediately to the north of the !Kung there are groups of so-called “Black Bushmen” across Africa. The most familiar of these are the Berg Dama of Namibia. These people speak Khoisan languages related to Nama Hottentot but in appearance they are completely like their Bantu-speaking neighbors. Our model suggests that intermediate appearance should be unstable and that selection should drive appearance rapidly toward one “type” or the other. The “Black Bushmen” may have received just enough gene flow from Bantu invaders to cause a switch to the other adaptive peak with rapid (in evolutionary time) loss of the earlier Bushman appearance.

Are there critical tests of this model? The model predicts retention of shared genes affecting external appearance between Bushmen and east Asians, but retention of nothing else. Hence, in agreement with the model, neutral Bushman genes seem completely African as shown in figure 2. The other more interesting prediction must wait for identification of the genetic basis of skin color and other aspects of physical appearance for a critical test.

If there is any validity to our hypothesis, other similarities in appearance that anthropologists in the early part of this century described might in fact be real signatures of ancient population expansions and movements that should be the basis for archaeological work. The idea of a Vedda-Australian-Ainu connection and the similarities of Negrito peoples around the Pacific rim and African Pygmies are examples of such hypotheses.



## Conclusion

We have outlined some of the more interesting problems in the history of our species and considered how various categories of data may help resolve them.

It is widely accepted (but not necessarily correct!) that modern humans appeared in Africa and expanded from this homeland within the last 100,000 or so years. While the northern branch is readily apparent in the archaeological record of Europe and west Asia, the early appearance of humans in Australia at 40,000 to 50,000 years ago suggests that there was a southern branch of the human exodus that roughly followed the Indian ocean coast. The hypothesis of a southern branch receives support from the distribution of language macro-families in the Old World and from the presence of modern humans in Tasmania. This island had been separated from Australia for thousands of years before the other candidate for the peopling of Australia, the event 5,000 years ago when dogs and microliths appeared and population increased by roughly a factor of ten. The surprising implication of the model of a separate southern branch is that Mode 4 technologies — fancy blade tools and worked bone — are not a distinctive signature of new human cognitive capacities but mere signs of male leisure in a new rather empty ecosystem.

Spectacular advances in typing neutral markers have provided large numbers of markers from various human populations. These markers should be free of the ascertainment bias that made comparisons of genetic diversity across populations unreliable. These markers show a diversity cline away from Africa and a pattern of population difference that looks like rather smooth isolation by distance but with marked clumping into groups that are rather like traditional “major races.” More populations need to be sampled before this clumping can be carefully evaluated.

Populations that have seemed on other grounds to be distinct from their neighbors turn out not to be distinct when we look at neutral markers. Bushmen of southern Africa, for example, appear as simply another African population. We suggest that other marker categories like language and external appearance might provide a deeper look at human history. These share with the Rh system the property that selection should favor the common type or, in the case of sexually selected appearance, some exaggeration of the common type. Under such dynamics they would “resist” the effects of gene immigration while neutral markers should “blend”. We do not have a critical test now of this hypothesis but there are clear predictions about genes controlling external appearance that have not yet been identified.

The ultimate test of these hypotheses about human origins will be identifying traces of past movements in the archaeological record. We need to develop closer ties among linguistics, archaeology, and genetics in the study of human history.

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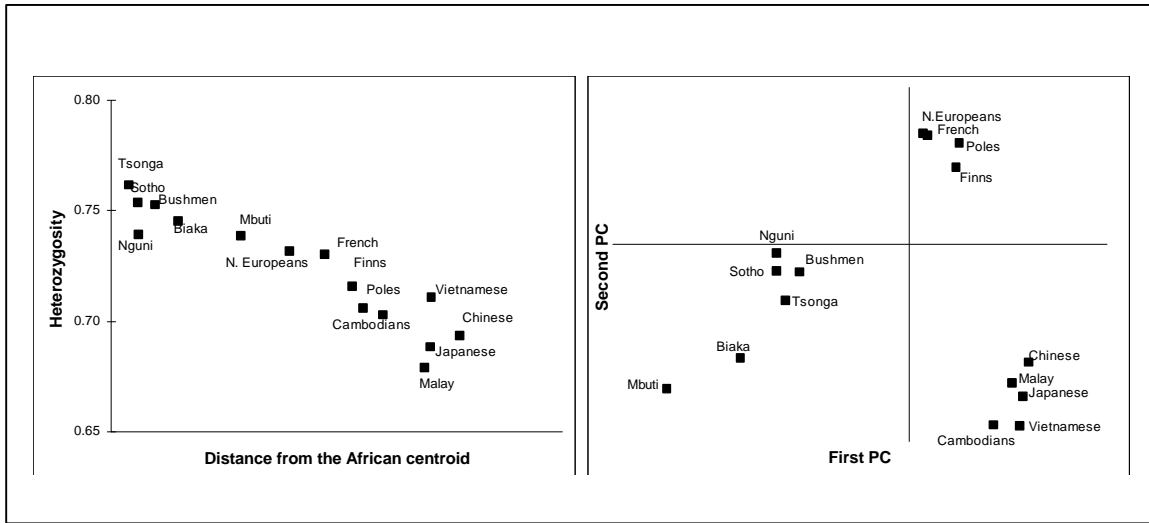


Figure 1. Jorde lab data. The left panel plots heterozygosity (y axis) against genetic distance from Africa (x axis) on the basis of 60 polymorphic microsatellite loci. The right panel shows principal coordinates of genetic distance among populations (Jorde et al. 1995).

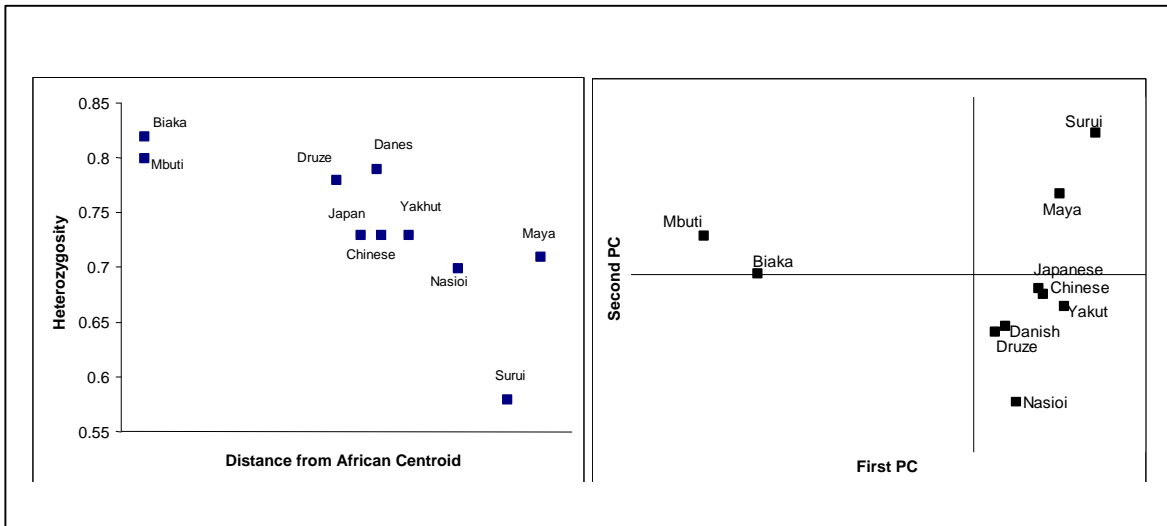


Figure 2. Kidd lab data. The left panel plots heterozygosity (y axis) against genetic distance from Africa (x axis) on the basis of 92 polymorphic microsatellite loci. The right panel shows principal coordinates of genetic distance among populations (Calafell et al. 1997).

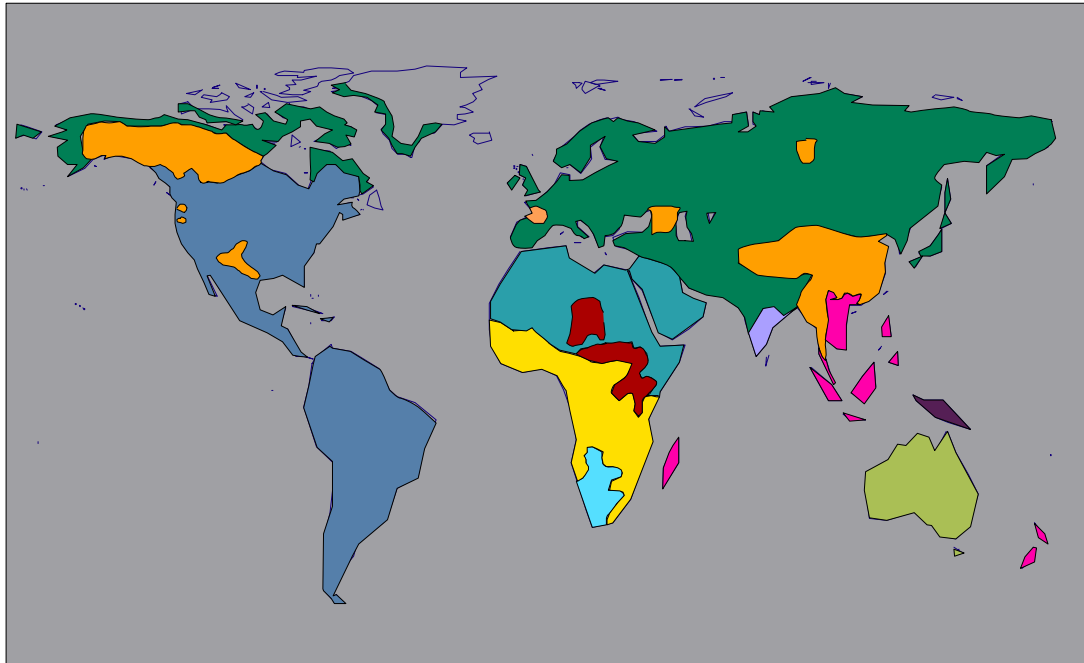


Figure 3. The ten world language macro-families described in Ruhlen (1994).