Crossing borders

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The title of this paper is a tribute to David Penny's ability to cross borders: biology, mathematics, philosophy of science, history ... and the list goes on. The unknown for most people is exciting but fraught with fears. David it seems, is fearless; the unknown for him is the place to search for, until the territory is mapped, and then new unknown areas beckon. David has some good tools in his backpack to assist in his travels: curiosity, enthusiasm, intelligence, and an incredible stamina.

Crossing discipline borders

It was 1988 and David was teaching part of a 300-level paper, *Biogeography, Biosystematics and Evolution*. His lectures wove together the threads of a diverging education system in which each level offers a narrower focus. It was at that moment that I saw my disparate clusters of knowledge converge again.

The following year, I knocked nervously on David's door. I told him I was interested in doing research on primate or human origins. David immediately suggested I look at the ψη-globin gene in the primates. On his desk he had a printout of an alignment of the *ψη*-globin gene (Miyamoto 1987) for the human, chimpanzee, gorilla, orang-utan and rhesus. Beside the over-10 000-base-pair-alignment was a photocopy of *The Temple of Nature* by Erasmus Darwin, Charles Darwin's grandfather. Erasmus's extended poem was about the origin of life and origin of society.

Say Muse! how rose from elemental strife
Organic forms, and kindled into life;
Darwin (1803) *p. 9*

Then David proceeded to remove Charles Darwin's *Voyage of the Beagle* from the shelf. He read some of Darwin's observations from the five-year-long voyage that were later instrumental in his theory of natural selection. David also mentioned Alfred Russel Wallace, who independently developed a theory of natural selection. Wallace did not have the same luck as Darwin in as much as Darwin received most of the credit for the theory, and Wallace's four-year-long adventure in the Amazon ended with his entire collection of specimens being lost when a fire broke out on the boat heading back to England. David mentioned the poets Wordsworth, Coleridge, as well as Charles Lyell's *Principles of Geology* that influenced Darwin strongly.

In these few minutes David had crossed many borders, across time and discipline, and placed evolutionary theory in context with the time. This was a taste of things to come.

The ψη-globin gene is a pseudogene and therefore supposedly accumulates substitutions in a random fashion (neutral). We found, however, that the nucleotide changes were not independent. The substitution rates were affected by the surrounding bases and were especially high adjacent to repeats and between inverted repeats. Insertion and deletion events were associated with adjacent runs and repeats. The longer and more perfect the repeat or run was, the greater the chance of an insertion/deletion event.

As for resolving the 'trichotomy' (see Figure 1), most support was for the Human–Chimpanzee clade. Today the trichotomy is considered resolved, with humans and chimpanzees closer to each other than the gorilla (Ruvolo *et al.* 1994). Ideas from this Honours thesis evolved (Watson 1989). David and I, together with Simon Easteal (Watson *et al.* 2001), proposed a new classification for human and non-human great apes (see Figure 1), whereby humans, chimpanzees and gorillas are all within the same genus *Homo*.

I learnt from David to identify what was fascinating, what the question was, and to figure out a way to investigate it, without looking at all the barriers. I think this is the most important lesson I have learnt. Although it is not a guaranteed formula for success, as some of my adventures were to demonstrate.

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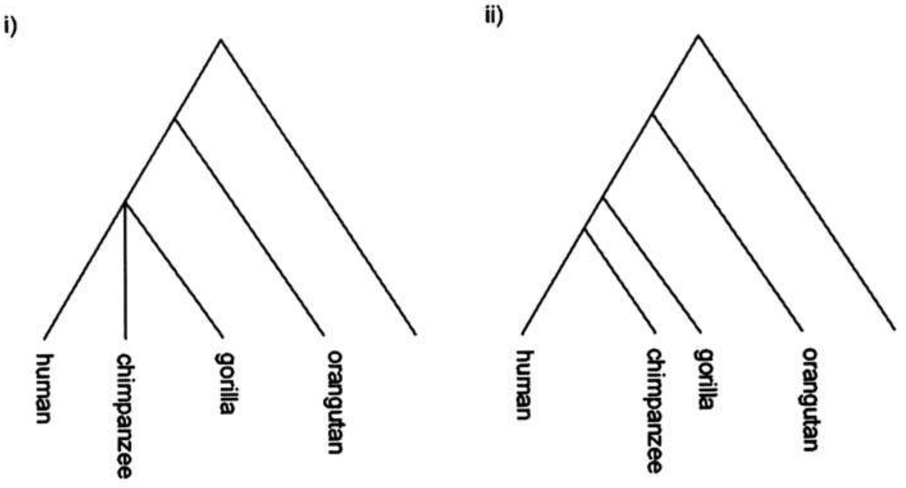

iii)

Existing Classification (Eisenberg, 1981)

Superfamily Hominoidea
Family Hominidae
Genus *Homo*
Family Pongidae
Genus *Pongo*
Genus *Gorilla*
Genus *Pan*

iv)

Proposed Classification (Watson et. al. 2001)

Family Hominidae
Subfamily Homininae
Genus *Pongo*
Pongo pygmaeus
Genus *Homo*
Homo sapiens **(human)**
Homo niger **(chimpanzee)**
Homo gorilla **(gorilla)**

Figure 1. Humans and non-human great apes

i) Tree representing the 'trichotomy', where it was difficult to resolve the branching order of the human, chimpanzee, and gorilla.

ii) Tree for the human, chimpanzee, and gorilla (widespread support for this tree)

iii) One of the standard existing classifications of the great apes and humans (Eisenberg 1981)

iv) Proposed classification (Watson **et al.** ***2001), grouping humans, chimpanzees, and gorillas together in the same genus*** **Homo. Homo troglodytes** ***is a preoccupied name (a secondary homonym); the next available name for the chimpanzee is*** **Homo niger.** ***In 1812, Geoffroy St Hilaire proposed the name*** **Troglodytes niger** ***for the chimpanzee.***

Crossing African borders

A Commonwealth Scholarship and a desire for adventure, took me to Nigeria to study gorillas. I had read a report which mentioned evidence of an, up until then, unknown gorilla population on the Cameroon–Nigerian border. My aim was to conduct a survey, and in addition collect hair from the gorilla's night nests, for later analysis in Allan Wilson's lab in Berkeley. Unfortunately, I never obtained permission to work in the park, and my scholarship proved to be a limiting factor (it is difficult to live and do research on one dollar a day). During this time I was living on the campus of the University of Ibadan, with about 20 000 students from all over Nigeria. It was like the United Nations, Nigeria being a land with over five hundred ethnic groups and corresponding languages. I wondered if the language relationships between the groups reflected their genetic histories.

David was positive when I approached him with this idea. He even arranged that I could work in Svante Pääbo's laboratory at the University of Munich.

For nine months I travelled through Africa collecting blood and hair samples from about 500 people (see Figure 2) and 1000 cattle*. Back in Germany, I sequenced the mitochondrial (DNA) mtDNA control region and compared the African sequences to published mtDNA sequences from around the world. The root of the tree was in Africa, further supporting the Out-of-Africa hypothesis (Watson & Penny 2003). Not only did the African sequences show higher diversity than any other continent, the East African sequences were particularly diverse, and the Turkana people from Northern Kenya was the group showing the highest diversity (see Figure 3). On average the difference between two Turkana people was higher than between any two people from anywhere else in the world. Different mitochondrial haplogroups showed distinctive expansion events (Watson 1996). These population expansions may have been associated with cultural innovations (Watson *et al.* 1997). One such expansion event in Africa was the haplogroup known as L3, which represents approximately one-quarter of all African sequences and practically all of the sequences outside of Africa.

Investigation of the initial question – the degree of correspondence between language and genetics – showed that each ethnic group showed a composite of different haplotypes. These haplotypes were shared with other groups, and this demonstrated fluidity over ethnic borders (and thereby linguistic borders). mtDNA sequences are inherited from the mother and therefore reflect the female history. So this fluidity may partially reflect patrilocal patterns, where it is the women that move to their husband's group.

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*These cattle samples have never been analysed and are available to an interested researcher. Almost all samples have an accompanying photo.

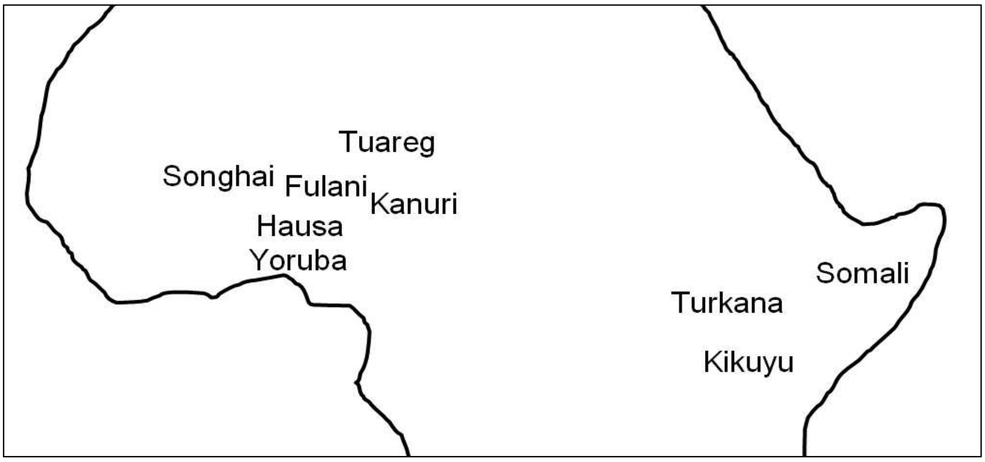

Figure 2. Nine African ethnic groups from East and West Africa.

Of the 24 ethnic groups sampled, 9 groups were sequenced for the mtDNA control region. Tuareg, Hausa, and Somali represent the Afroasiatic language family; Songhai, Kanuri, and Turkana represent the Nilo-Saharan language family; and Fulani, Yoruba, and Kikuyu represent the Niger-Kordofanian language family.

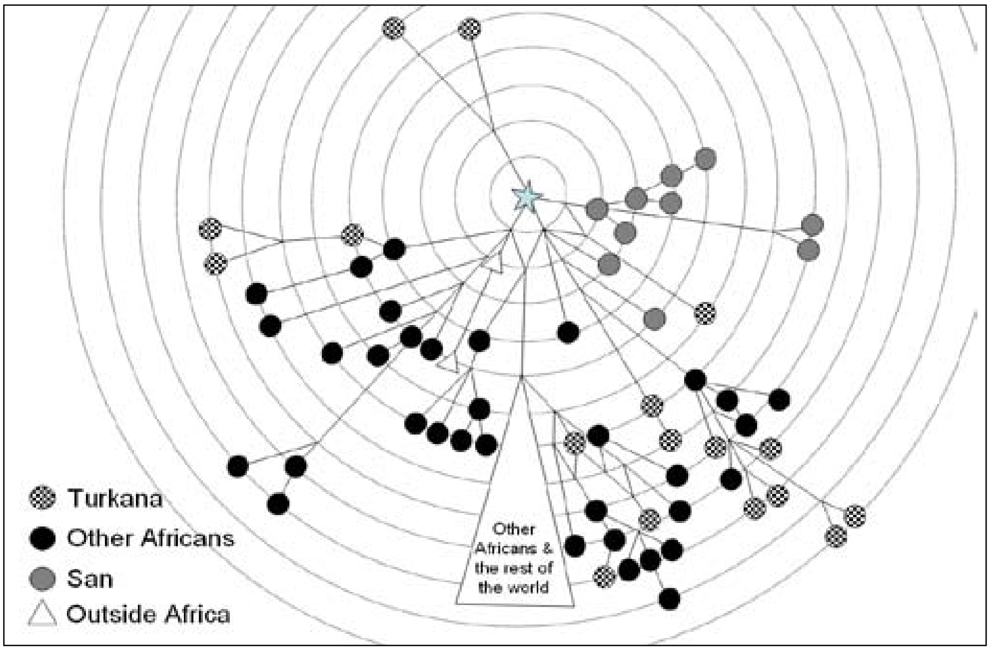

Figure 3a. Network from the combined Vigilant* et al. *(1991) and Watson* et al. *(1997) datasets.

The Turkana are spread throughout the network. 15 of the 36 Turkana mtDNA sequences occur within the L3 cluster represented by the large triangle. This cluster is found in Africa, but more remarkably is where all the sequences from populations outside Africa are found (the exception being 2 Australopapuans, represented by the small triangles). The star represents the root of the network.

David's footprint

David has built up a large extended academic family, with a network that extends beyond New Zealand's borders. Even at the Swedish Museum of Natural History, many of the scientists know of David and one has also collaborated with him.

David's contribution to science has been so extensive, that only in the future will we understand the degree to which he has moved science forward. His impact has not only been the science and resulting publications, but equally importantly his mentorship. David fosters a creative environment, where he attracts people from diverse disciplines, ages, and countries. With an open mind he encourages everyone to see the possibilities, and teaches us all to be alert, curious, and not scared of crossing borders.

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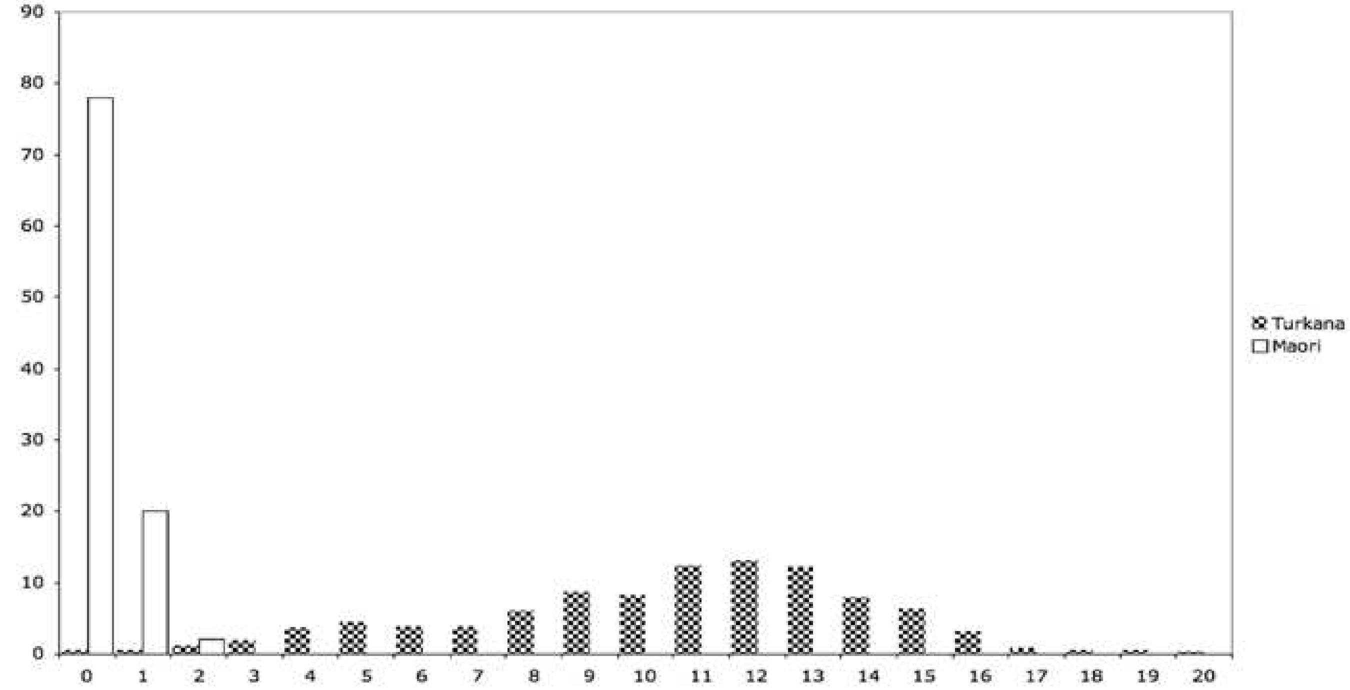

Figure 3b. Pairwise distribution of different peoples based on mtDNA control region.

The pairwise distribution (Y axis, % of pairs; X axis, number of differences between pairs) compares sequences from individuals within the groups for the Māori and the Turkana. The mean varies from 0.65 for the Māori to 10.51 for the Turkana, with intermediate values of 7.01 for Asians, and 8.92 for Africans.

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