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# David Penny: Man on the edge

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When asked to become involved in this celebration of David Penny's 70<sup>th</sup> year I had to think back to the first time I met David. I believe it was in 1992 at a conference honouring the late Allan Wilson. I was a very green graduate student in the Anthropology Department at the University of Auckland – just beginning to engage with both molecular biology and phylogenetics. Allen Rodrigo and I presented a paper there on how we might test and generate various models of Pacific prehistory using phylogenetic methods. Since that first meeting, David and I have been in contact regarding our mutual interest not only in better understanding the human settlement of the Pacific but in the application of molecular methods to anthropological studies in general. We have co-authored two papers, co-supervised students and I am proud to say have become colleagues. As investigators in the Allan Wilson Centre for Molecular Ecology and Evolution, one of the seven Centres of Research Excellence established in 2002, we have worked together on a major programme on Pacific settlement and prehistory; I hope this collaboration continues for many more years to come. Here I will review David's general contribution to anthropology over the years and specifically his work on Pacific settlement – where David so aptly suggested that we really are 'On the Edge of the Knowable' (Hurles *et al.* 2003).

## Use of commensal animals for tracking migration

Though I first met David in 1992, I first really worked with him during the later stages of my PhD. I was interested in using genetic variation to track Pacific settlement. I knew from earlier work (Hill & Serjeantson 1989; Matisoo-Smith 1990) that there was unlikely to be enough genetic variation within Polynesian populations to identify the specific pathways their ancestors travelled as they colonised the Polynesian triangle. It was unlikely that we could, for example, identify the specific islands of origin of the colonising canoes that eventually landed in New Zealand. So I had to think of another way to address the issue. I realised, through several conversations with my friend

and colleague Mere Roberts, that there might be another way to address the issue of Māori origins. Mere explained to me that Māori had brought a number of plants and animals with them when they settled New Zealand. We realised that these animals might serve as a proxy for the humans that transported them. If we could undertake DNA analyses of animals that could not naturally self-disperse, but relied exclusively on humans for transport, we could possibly reconstruct the human migration pathways through Polynesia. We might then identify Hawaiki or the homeland/homelands of the various colonising canoes and the immediate origins of the Māori.

While the human occupation of New Zealand occurred as recently as 1200 AD, people have been in the Pacific for over 40 000 years. The first people to arrive in the region were part of one of the first 'Out of Africa' migrations. Sometime around 60 000 years ago, during a period when sea levels were much lower than today, they most likely followed the coastline through southern Asia, along the landmass of Sunda (what is now Island Southeast Asia) and crossed the water gap of Wallacea to eventually reach the ancient continent of Sahul (made up of what is now New Guinea, Australia and Tasmania). Soon after arrival, they began to explore the island environment of Near Oceania, voyaging out to the Bismarck Archipelago and reaching as far east as the Solomon Islands by 30 000 years ago (O'Connell & Allen 2004). These early populations did not, however, venture beyond the Solomon Island chain into what is now often referred to as Remote Oceania (See Figure 1). To continue to move eastward beyond the main Solomon Islands to the Reef or Santa Cruz Islands requires people to venture out of the region of inter-island visibility and sail out of sight of land. This apparently presented a psychological or technological barrier for these early human populations in Near Oceania (Irwin 1992).

The Lapita colonists were the first humans to arrive on the islands of Remote Oceania. Archaeological evidence suggests that these colonists moved from the Bismarck Archipelago



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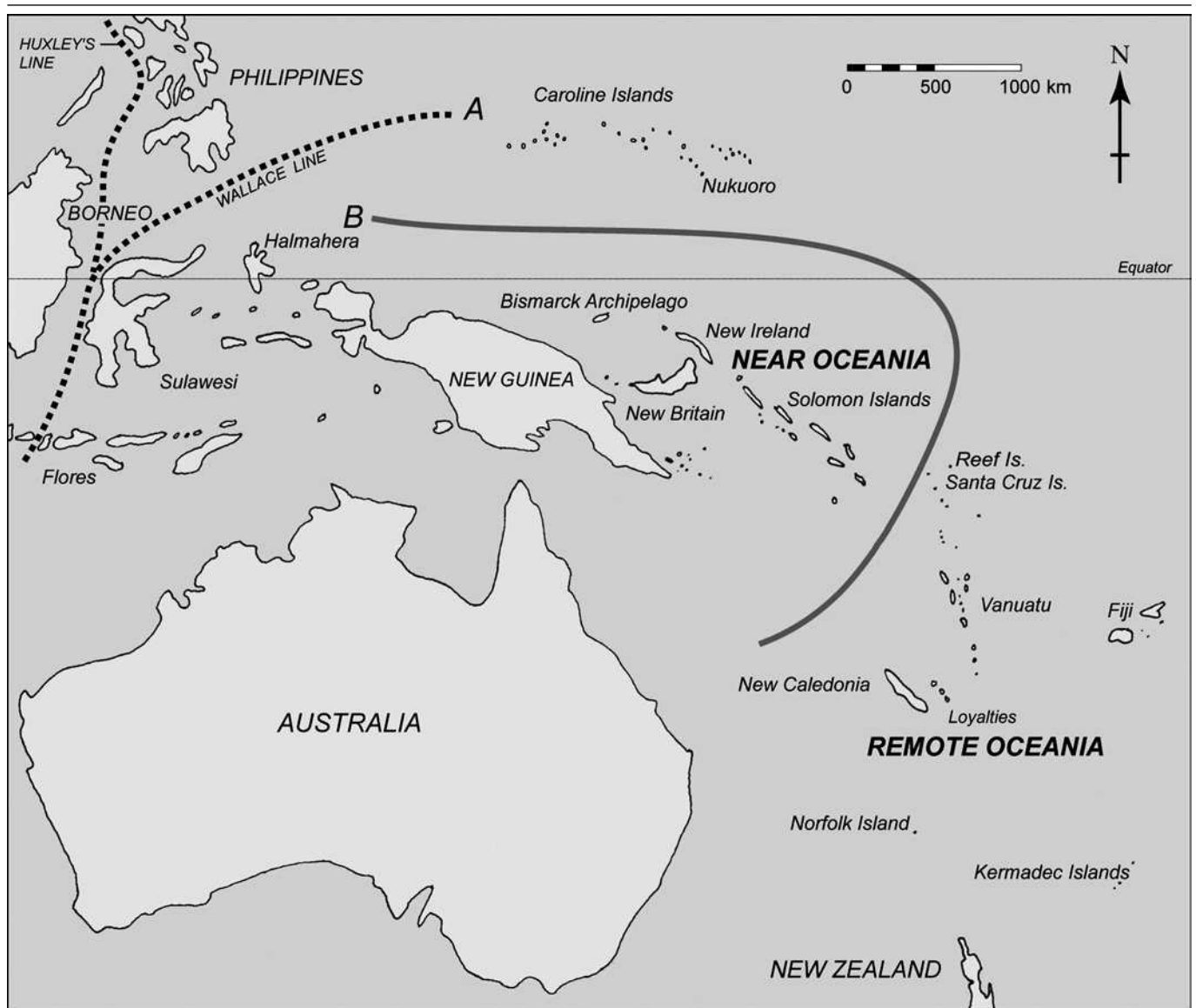


Figure 1. Map of the Western Pacific showing Wallace's Line (A) and the line delineating Near and Remote Oceania (B).

(where the oldest Lapita sites are found) out into the previously uninhabited islands of Remote Oceania sometime around 3000 years ago. Lapita sites appear at about that time from the Reef Santa Cruz Islands through Vanuatu, New Caledonia, Fiji, Tonga, and Samoa. The Lapita people are believed by most prehistorians to be the ancestors of the Polynesians. Like the Polynesians, the Lapita peoples carried with them their familiar and important food items and introduced these to the pristine island environments they settled. The animals that were introduced by Lapita peoples to Remote Oceania included the dog, the pig, the chicken, and the Pacific rat (*Rattus exulans*). Not all of the animals were successfully introduced to all of the islands. Though all four commensal animals were present in East Polynesia, only two animals were successfully introduced by Māori to New Zealand – the Pacific rat, also known as kiore, and the dog. Māori either didn't bring pigs or chickens with them, or for some reason they were introduced but never successfully established. Since the dogs introduced by Māori belong to the same species as the dogs introduced by later European voyagers and colonists, they have interbred to the point that it would be very difficult to find or identify pure 'Polynesian' dogs today. The kiore on the other hand does not belong to the same species as

the rats introduced by Europeans – and does not interbreed with *Rattus rattus* or *Rattus norvegicus*. Therefore the kiore found on Pacific islands today should be the direct descendants of those introduced by Māori and other Polynesian and Lapita peoples. So, based on those early conversations with Mere Roberts regarding the commensal nature of kiore and their transport to New Zealand in the colonising canoes, I decided to undertake a mitochondrial DNA (mtDNA) analysis of Polynesian populations of *Rattus exulans* for my PhD.

Once I had collected my tissue samples of rats from throughout the Polynesian Triangle and extracted and amplified the control region of the mt genome, I thought that I had done the hard part. I had tackled fieldwork in remote locations, learned about DNA extraction and mastered the polymerase chain reaction technique (PCR) – all new experiences for me. I thought the analysis should be a piece of cake, but I was wrong. I had my data, but I had no real idea what to do with it. I started attending the many meetings being run by David's group in Palmerston North. These meetings were supposed to help take the uninitiated and introduce them to phylogenetics. There were numerous lectures by David and colleagues about new methods they were

developing and we were given tutorials on new programmes. These were all very exciting and useful meetings (though I have to admit that I only ever followed a tiny fraction of the lectures and I still have no idea what the Hadamard conjugation really does or realised the true significance of a Lento Plot). At these meetings I kept hearing the mathematicians talking about theoretical trees with only four taxa – I had 130. They all talked about lovely clean sequence data; mine were messy with lots of indels (insertions and deletions of single bases) and ambiguous sites. I knew that I needed help and David was the man.

I then spent several months involving multiple visits to Palmerston North trying to get David to help me with the analysis of my messy rat data. There was no doubt that he was interested in the topic: he had just published a paper with Ros Murray McIntosh in which, based on the mtDNA diversity found within New Zealand Māori, they estimated the number of women who would have been in the colonising canoes (Murray-McIntosh *et al.* 1998). I just had to compete for his time with all of his other projects and the numerous students he was helping! Finally we found a window of opportunity and David was able to look at what I had done and tweek it here and there, applying his new technique – nearest neighbour bootstrap – to show that there was a consistent signal in my messy rat mtDNA data. We found that the commensal model did work. The patterns observed did indicate specific connections between islands in Central East Polynesia and New Zealand (see Figure 2). We published our results in 1998 (Matisoo-Smith *et al.* 1998).

## Human genetics markers

Over the next 10 years, more and more genetic data began to accumulate for human populations in the Pacific. Many of the studies were focused on identifying the origins of the Polynesians and their Lapita ancestors. Early studies of mitochondrial DNA variation in the Pacific (Hertzberg *et al.* 1989; Ballinger *et al.* 1992) identified a particular marker found at very high frequency in Pacific populations. This non-deleterious mutation, in which one copy of a 9 base-pairs repeat sequence in region V of the mitochondrial genome is deleted (known as the 9 bp deletion), is believed to have originated in East Asia and is therefore a general marker of Asian-derived populations. It is the defining mutation of mitochondrial DNA haplogroup B, which is found throughout the Pacific, but is also found in the Americas and as far west as Madagascar. There are, however, some sub-lineages of Haplogroup B that are found exclusively in the Pacific. In particular, researchers identified three point mutations (single base mutations) found in the control region of the mtDNA genome. This combination of mutations became known as the ‘Polynesian motif’ owing to its near-ubiquitous distribution throughout the Polynesian triangle (Melton *et al.* 1995; Redd *et al.* 1995). It is also found at similar high frequencies in many populations across the Pacific, particularly in coastal populations in Island Melanesia. This recognition led some to suggest that it should be called the ‘Austronesian motif’ or even the ‘Oceanic motif’ linking this genetic marker to particular linguistic groups. However, more recent, fine-grained analyses have shown that there is limited correlation between linguistic and genetic variation in Island Melanesia (Friedlaender *et al.* 2008; Hunley *et al.* 2008).

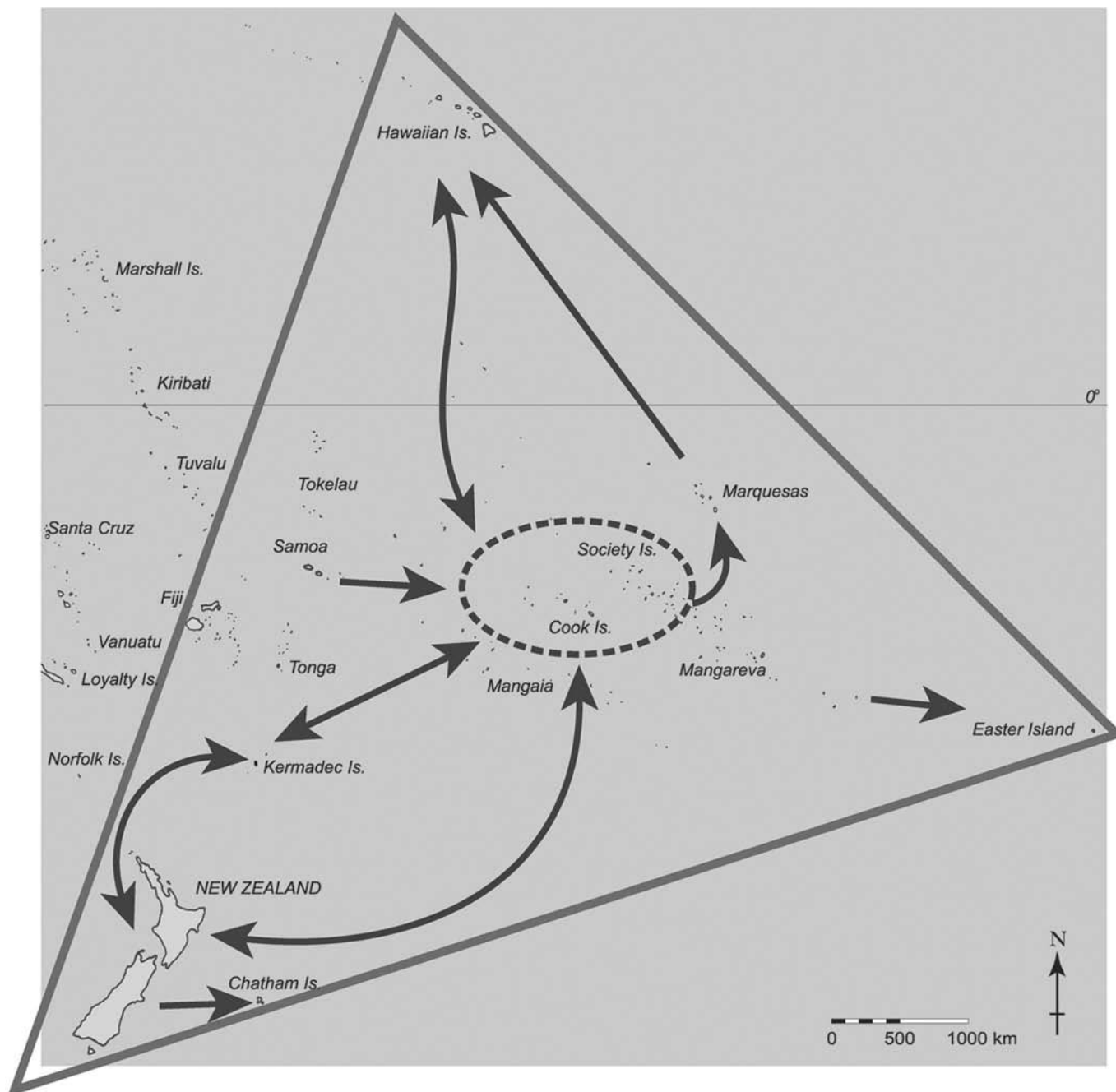
During this period, David and others of us working on the problem realised that the issue of identifying Polynesian

origins required two things – better data and a multidisciplinary approach. The accumulating mtDNA data continued to suggest a limited amount of variation in Polynesia, with the main lineages (those belonging to mitochondrial Haplogroup B) being traced back to East Asia and this led to a number of papers in which geneticists argued that the data supported an ‘Out of Taiwan’ model for Polynesian origins. During this time, however, researchers found a new tool they could apply to population origin studies – Y chromosome variation. Where mtDNA is of course inherited maternally, variation identified on the Y chromosome provides the history of the male line, and Y chromosome studies in the Pacific told a very different story from the mtDNA. Rather than looking like a mainly-Asian derived population, Polynesian Y chromosome studies showed that there was much more input from Near Oceania (Hurles *et al.* 2003; Kayser *et al.* 2006).

David also continued to push for better data. He realised that our interpretations were being hindered by the fact that, generally, researchers were only looking at control-region variation (and the 9 bp deletion). He began to push for the study of complete mitochondrial genomes. In 2006, David’s group not only produced 19 new complete mitochondrial DNA sequences of Pacific populations, but also applied another new method they developed (Holland *et al.* 2005) to the analyses of these new sequences and all others available to address the question of Pacific population origins (Pierson *et al.* 2006). They showed that, unlike the short control-region sequences, analyses of the complete mitochondrial genomes clearly indicated that Polynesians were derived from mixed populations with both Near Oceanic and Asian origins. We have also extended our studies of *Rattus exulans* and other *Rattus* species from Island Southeast Asia and the Pacific to include complete mitochondrial genomes in order to address issues about rodent evolution and dispersal (Robins *et al.* 2007, 2008).

## Commensal plants

The commensal approach has also been extended with exciting research on genetic variation in Pacific plants by David’s student Andrew Clarke. Andrew has been applying the commensal approach to studies of the sweet potato, or kumara, and the bottle gourd, or huē as it is known in Māori (Clarke *et al.* 2006). These plants were present in New Zealand and East Polynesia prior to the arrival of the European voyagers, but unlike most of the other commensals did not come from the west with the Lapita voyagers. They were introduced to Polynesia from the Americas. Ever since the work of Thor Heyerdahl, people have been intrigued about the possibility of contacts between Polynesia and the Americas. Did Native Americans voyage out on balsa wood rafts to the islands of Polynesia? Or was it Polynesians who continued on their eastward trajectory until the Pacific Ocean ran out? Another recent study from the Wilson Centre, focused on ancient DNA of Pacific chickens (Storey *et al.* 2007, 2008), has finally put Heyerdahl’s ideas of native Americans coming to Polynesia to rest. Both radiocarbon and ancient DNA analyses of archaeological chicken bones found in a pre-Columbian site on the coast of south central Chile, at a site called El Arenal, show that it was Polynesians who made the first contact with South America. Sometime around or before 1400 AD, they apparently introduced their Pacific chickens to the native populations of Chile and, after cruising up the coast on the Pacific current, they reached northern Peru or Ecuador,



**Figure 2.** Map of the Polynesian triangle showing interaction spheres identified by analyses of mitochondrial DNA variation in Polynesian *Rattus exulans* populations. The area defined by the dotted line identifies a homeland region for East Polynesian populations of *Rattus exulans*.

the region where sweet potatoes grew. Being already familiar with tubers (taro and yams), they undoubtedly recognised the potential for taking the kumara and possibly bottle gourds back with them into central east Polynesia where they were distributed throughout the Polynesian triangle. It was not long after that that Europeans arrived in the Pacific, and the rest, as they say, is history.

As many involved in New Zealand science may know, David Penny has just stepped down as Research Director of the Allan Wilson Centre. The Wilson Centre was, of course, named after one of New Zealand's most outstanding biologists, a man many would consider to be the father of molecular anthropology. Allan Wilson, who died in 1991, was shortlisted for the Nobel Prize and is the only New Zealander to ever receive a MacArthur genius award. Like Allan Wilson, David Penny is a man with vision; a scientist ready to push the boundaries of science and

technology and ask the big questions. Also like Allan, he has produced a huge number of highly successful students and has stimulated those students and his colleagues to cross academic boundaries. He has been a mentor to many, a major contributor to the international scientific community and a great representative of New Zealand science. He is truly a national treasure.

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