Austronesian prehistory and Polynesian genetics: A molecular view of human migration across the Pacific

Stephen J. Marshall,¹ Adele L. H. Whyte,¹ J. Frances Hamilton,² and Geoffrey K. Chambers¹

¹Victoria University of Wellington, PO Box 600, Wellington, New Zealand

²Intellectual Property Office of New Zealand, PO Box 30-687, Lower Hutt, New Zealand

The migration into and settlement of remote Oceania by the modern Polynesian and Māori peoples is a major achievement, which has been the subject of extensive research and scholarship. The routes taken by the Austronesian peoples and the origins of the migrations are subject to ongoing debate. We present a range of findings from molecular genetic studies of Polynesian and New Zealand Māori populations and a 'synthetic total evidence theory' that we suggest can account for key elements of the migrations.

This paper is based on a paper presented at the International Symposium on the Dispersal of Austronesians and the Ethnogenesis of the People in the Indonesian Archipelago (Chambers 2005)

Introduction

The Austronesian people occupying the Pacific regions of Melanesia, Micronesia, and Polynesia (Figure 1) have achieved remarkable success in populating one of the largest areas on earth. Their skills in conducting this migration through dangerous waters are regarded with universal respect, particularly given the simple, organic, technologies they used and their dependence on cultural traditions and skills descending verbally through a rich oral tradition. The migration and expansion through the Pacific has generated the abundant cultural and linguistic diversity that forms the principle sources of evidence upon which modern historical reconstructions are based. These



Stephen Marshall is a Senior Lecturer at Victoria University of Wellington with wide interests in molecular biology, computer science and e-learning. His PhD research under Geoff Chambers's supervision established the presence of the 'Oriental' alcohol dehydrogenase variant in the New Zealand Maori and Polynesian populations and demonstrated its protective role against the development of alcoholism in the Maori population. For correspondence, Stephen may be contacted at stephen.marshall@vuw.ac.nz

Adele Whyte, a Tupapa Putaiao scholar of Ngati Kahungungu and Ngati Hawea descent, is currently studying as a PhD student at Victoria University of Wellington. Her Masters research under Geoff Chambers's supervision has established that the Māori population that settled New Zealand was large, numbering approximately 190 females, suggesting that the process was planned and deliberate. Adele is also involved in the Victoria University of Wellington's Awhina mentoring programme for Māori science students. Her current research is on the genomics of environmental toxicology in shellfish and is supported by ESR and Ngati Kahungungu lwi Incorporated.





Frances Hamilton qualified BSc Hons at Victoria University, where she went on to complete a doctorate in 1994. While finalising her PhD thesis, she commenced a career as a forensic scientist at the Institute of Environmental Science and Research Ltd (ESR), a role she continued until 2001. During her latter years at ESR she worked at the DNA Databank, helping to make the Crime Sample database a successful result-producing entity for the New Zealand Police. She left ESR to join the Intellectual Property Office of New Zealand, where she is currently a Patent Examiner.

Geoffrey Chambers is Reader in Cell and Molecular Biology in the School of Biological Sciences at Victoria University. Dr Chambers runs a set of extremely wide-ranging research projects, covering everything from albumins, albatrosses and alcoholism to alpine plants and Austronesians and that is just things starting with an 'A'. These projects are gathered into three programme areas; human evolution and health, conservation biology, and microsatellite biology. His laboratory has produced many distinguished graduates over the past twenty years including his present co-authors.



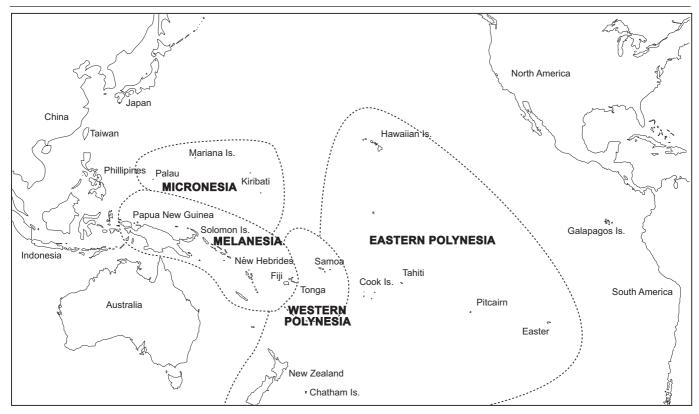


Figure 1. Oceania and nearby regions (after Kirch 2000).

new scientific theories contain implicit genetic hypotheses that can be tested with modern molecular biological techniques.

This review focuses on work undertaken in New Zealand, at Victoria University of Wellington under the direction of Dr Geoff Chambers, but it is but one part of a wider international body of scholarship aimed at better understanding the evolution of humans under the challenges of migrating through the vast but empty Pacific (Cann 2001; Cann & Lum 2004; Cavali-Sforza 2000; Gibbons 2001; Hurles *et al.* 2003a; Jobling *et al.* 2004; Kirch 2000). A number of pseudo-competing theories have been proposed to account for the voyaging history of Austronesians. These theories are presented briefly below. We believe that key evidence from the majority of existing theories can be drawn together into a synthetic total evidence account supported by oral tradition, linguistics, archaeology, and DNA.

Models of migration

It is generally accepted that the Austronesian populations of Oceania can be divided into at least two groups. The first of these was an ancient Papuan-speaking group who moved south from Asia between 40 000 and 70 000 years before present (ybp). These were the ancestors of Australian Aborigines and Melanesians including, for example, the Highland Tribes of Papua New Guinea (Ingman & Gyllenstein 2003). In response to rising sea levels, some of these peoples became separated and dispersed throughout the Bismarck Archipelago by 33 000 ybp and the Northern Solomons by 29 000 ybp. The second group consisted of Austronesian-speaking peoples who first occupied the island of Taiwan around 6000–5000 ybp and southeast Asia and parts of Indonesia by 4000 ybp (Handoko *et al.* 2001).

This more recent expansion of Austronesian-speaking peoples and subsequent partial or total displacement of the older Papuan-speaking people and cultures resulted in the marked differentiation in coastal and highland populations still apparent in Papua New Guinea/Irian Jaya (Bellwood 1997, 1998; Kirch 2000; Spriggs 2003). These processes are associated with the rise of the Lapita culture identified through extensive archaeological remains (Kirch 1997) and which spread from New Caledonia to Vanuatu, Tonga, and Fiji through a process of ongoing dispersal until around 2800 ybp (Burley & Dickinson, 2001).

After a period of comparative stability (Pawley & Ross 1993), additional migrations were undertaken around 1800–1400 ybp to settle central Polynesia, including the Cook Islands and Marquesas, followed by further dispersal to the Hawaiian islands (1400–1200 ybp), Rapanui (Easter Island, 1400–1000 ybp) and finally Aotearoa (New Zealand) perhaps as recently as 650 ybp.

This high-level overview conceals a significant degree of discussion and theorising as to how the various populations interacted, as well as the geographical locations of the migration origins within the Asian and Oceanic regions. These descriptive and mechanistic theories include Peter Bellwood's (1991) extensively developed account of the migration dubbed the 'Express train to Polynesia' (Diamond 1988) characterised by rapid expansion and relatively little initial interaction, Oppenheimer's (1998) 'Slow Boat', which argues for an island southeast Asian origin (specifically eastern Indonesia), and Terrell's (1988) 'Entangled Bank' in which the future Polynesian voyagers arise by a reticulated process from island Melanesia without significant input from new arrivals coming from the north and west. The 'American Origin' model of Heyerdahl (1953) is no longer regarded as credible. However, it is clear that contact between Oceania and South America has

resulted in the transfer of semi-domesticated food plants (Green 2000).

Also proposed are complex archaeological models incorporating the impact of changes in sea levels (Oppenheimer 1998; Oppenheimer & Richards 2001) and more extensive interaction between migrating and localised populations (Green 2003). Assessing the validity of these proposals remains challenging, and they are subject to debate, especially within archaeological circles. The need to consider multiple lines of evidence from a range of disciplines, particularly our own area of genetics and molecular biology has led to our proposal of a 'synthetic total evidence theory' drawing on this rich and diverse scholarship (Whyte *et al.* 2005; Chambers 2005).

Polynesian and New Zealand Maori genetics

The genetic information contained in human populations is a rich source of data, not least because it contains traces of each historical member of that population. Genetic information can be viewed in different ways to show the impact of reductions in the size of the population due to war, the environment, or the separation imposed by distance, as well as the different impacts on the male and female contributions to the whole. When combined with information from other populations, it can also tell us something of the origins and relationships between peoples in ways that may validate or falsify hypotheses developed from other data sources such as tradition, archaeology, and linguistics.

DNA fingerprints and population bottlenecks

Early work conducted in New Zealand to validate the forensic use of multi- and single-locus DNA fingerprinting technologies (Hamilton 1994; Clark *et al.* 1995) showed relatively low levels of genetic variation in Polynesian subjects compared with Asians or Caucasians (Figure 2).

An even greater reduction is evident in the New Zealand Māori population. This result is consistent with the findings of others (Flint *et al.* 1989) and suggests that during the process of migration some constraint resulted in the loss of diversity, perhaps due to extended periods of small population sizes or founder effects caused by low numbers of people undertaking or surviving migratory voyages (Hurles *et al.* 2003b).

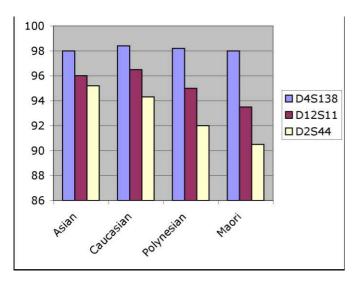


Figure 2: Genetic variation revealed by DNA fingerprinting (Hamilton 1994).

Alcohol metabolism and Asian origins

The restricted genetic diversity of modern Polynesian populations suggests something of the hardships they faced in travelling, but does not tell us anything about the source or path of the journey. Examination of particular gene variants such as those involved in the metabolism of alcohol, which have well known population and location frequency patterns, provides evidence suggesting possible starting points (Table 1). Alcohol dehydrogenase (ADH) and aldehyde dehydrogenase (ALDH) are both essential in the metabolism and detoxication of alcohol, and specific variants (ADH 2-2 and ALDH 2-2) are predominantly found in Asian populations, making them useful indicators of Asian origin of modern Polynesians.

Determination of the frequencies of these variants in modern Polynesian and New Zealand Māori populations (Marshall 1994; Chambers *et al.* 2002) strongly supports an Asian rather than American origin. These data also suggest that common ancestors of the Polynesians can be found amongst the Taiwanese Aboriginal populations, consistent with the 'Taiwanese Homeland' concept of Redd *et al.* (1995), the absence of the ALDH 2-2 variant being readily explained by its relative rarity in the ancestral population, or its subsequent introduction at low levels in the Aboriginal population by intermarriage with the dominant Han Chinese population.

Mitochondrial DNA and the matrilineal migration

Mitchondrial DNA provides another window into population changes as it is inherited maternally and regions of the mitochondrial genome have been sequenced and characterised for a large number of different populations. Among Polynesians there are two common sequence variations, the well-known '9 base pair deletion' and 'Polynesian CGT Motif'. These are found at a high frequency within Polynesian populations, and the decreased diversity of these 'CGT' variant haplotypes in the New Zealand Maori population (Whyte et al. 2005) is consistent with the results discussed above for nuclear DNA variants. Generally, and in line with the DNA fingerprinting results, the Polynesian populations have reduced mitochondrial DNA diversity compared with other groups surveyed (Murray-McIntosh et al. 1998; Penny et al. 2002). This reduction in genetic diversity is also strong evidence of 'founder' effects in the ancestry of modern Polynesian populations.

The variants found in Polynesian mitochondrial DNA, as with the ADH and ALDH results discussed, are consistent with a Taiwanese origin for the modern Polynesian and New Zealand Māori genome (Whyte *et al.* 2005; Trejaut *et al.* 2005), but there is also some evidence that a small amount of exchange occurred with the Melanesian peoples occupying the islands of western Oceania (Merriwether *et al.* 1999; Sykes *et al.* 1995, Cox 2003). This suggests that the modern Melanesian peoples have arisen from a similar introgression of the genepool of ancestral Austronesian-speaking migrants into the resident Papuan-speaking genepool encountered along the way. Thus, in genetic terms, the descriptors 'Melanesian' and 'Polynesian' probably reflect the Papuan and Austronesian ends of a continuum produced by prehistoric (and continuing) intermarriages.

The 'founder' effect sampling process that results in the reduced genetic diversity of the resulting populations also, how-

Table 1. Frequencies of ADH and ALDH gene variants	s (Marshall & Chambers 2005).
--	-------------------------------

Ethnic Group	ADH 2-1	ADH 2-2	ALDH 2-1	ALDH 2–2	
European					
Caucasian	0.89-1.00	0.00-0.11	1.00	0.00	
American					
Indian (N.American)	0.93-1.00	0.00-0.04	0.92-1.00	0.00-0.08	
Indian (S.American)*	1.00	0.00	0.75-1.00	0.00-0.25	
Indian (Ecuador)	n.d.	n.d.	0.56	0.44	
Mayan	0.94	0.05	n.d.	n.d.	
Asian					
Ainu	n.d.	n.d.	0.89	0.11	
Cambodian	0.72	0.28	n.d.	n.d.	
Chinese	0.27-0.38	0.62-0.73	0.69-0.89	0.11-0.31	
Filipino	n.d.	n.d.	0.93	0.07	
Indian	1.00	0.00	0.98-1.00	0.00-0.02	
Indonesian	n.d.	n.d.	0.78	0.22	
Japanese	0.24-0.39	0.61-0.76	0.61-0.87	0.13-0.39	
Korean	0.29	0.71	0.83-0.87	0.13-0.17	
Taiwan (Atayal)	0.09	0.91	0.95	0.05	
Thai	n.d.	n.d.	0.96	0.04	
Vietnamese	n.d.	n.d.	0.66-0.67	0.33-0.34	
Polynesian					
American Samoa	0.84	0.16	1.00	0.00	
Cook Island Maori	0.45	0.55	1.00	0.00	
Hawaii (Oahu)	0.66	0.34	0.98	0.02	
Micronesian	0.78	0.22	n.d.	n.d.	
New Zealand Maori	0.47	0.53	1.00	0.00	
Western Samoa	0.55-0.70	0.30-0.45	0.99	0.01	

ever, allows for an estimation of the size of the migrating populations (Murray-McIntosh *et al.* 1998). Although this work is still limited by the lack of extensive sampling and characterisation of genetic diversity in eastern Polynesia, we have nevertheless been able to use the data presently available to model the effect of different migrating population sizes and population growth curves and use this to gain insights into the historic migrations (Whyte *et al.* 2005) to Aotearoa/New Zealand. This work, together with archeological and paleodemographic data (Brewis *et al.* 1990; Pool 1991), suggests that the best current estimate for the number of females settling Aotearoa/New Zealand is 190 (170–230); with possibly as many as 400 females migrating, depending on how rapid population expansion occurred after arrival.

The true numbers are impossible to pin down exactly, as the estimate is vulnerable to the effects of different models and assumptions. However, our conclusion was that a large population strongly supports oral tradition, arguing for large planned voyages rather than a popular fallacy of 'accidental discovery' by a small number of waka or castaways.

The Y chromosome and patrilineal migration

The mitochondrial genome provides valuable information on the maternal heritage of modern populations, which is complemented by the Y chromosome's information on the paternal genetic heritage. Interestingly, while the mitochondrial story indicates a relatively low proportion of Melanesian admixture, the Y chromosome suggests rather more extensive interaction, with up to three times as much variation coming from Melanesian populations, compared with the mitochondrial DNA results (Underhill *et al.* 2001; Kayser *et al.* 2000, 2003; Hurles *et al.* 2002, 2005). These findings are still supportive of a Taiwanese origin but suggest possible cultural (Hage & Marck 2003) and/or gender-biased geneflow during migration (Devlin *et al.* 2001, Trejaut *et al.* 2005).

Evidence from commensal organisms

A large-scale and organised migration into eastern Polynesia and Aotearoa/New Zealand is also consistent with the wide range of non-native food plants that were brought by the settlers, including taro, yam, bottle gourd, paper mulberry, ti tree, and kumara (Whyte 2002). The South American origin of some species of food plant strongly supports the idea of a Polynesian expedition (Green 2000) followed by rapid dispersal of the agricultural bounty. As well as plants, the Polynesian rat or kiore, a valued food animal, also supports the general picture provided by human genetics (Matisoo-Smith & Robins 2004) as does the lizard *Lipinia noctua* (Austin 1999).

'A synthetic total evidence theory' or genetic account of Māori migration to Aotearoa

Myths are much more than mere stories intended to amuse children; they serve the important role of explaining how we see ourselves and the world we live in. The genetic information we and others have obtained to date represent a sort of modern mythology of an adventurous people who braved a challenging and mysterious ocean. This information, combining the research and scholarship in genetics, linguistics, archaeology, and history allows us to propose a 'synthetic total evidence theory' explaining the process of migration and consequent settlement of Aotearoa/New Zealand.

These people first originated as an Austronesian population within Asia and used Taiwan as a staging post to enter Oceania and move east across the Pacific following a trail through the modern Philippines, Indonesian, Papua New Guinea, and island Melanesia. There may well have been several additional migrations and contributions from different routes. As they travelled, the voyagers interacted with the Papuan-speaking people already present and a small proportion of female and larger proportion of male Melanesians were recruited. Moving from island to island in large outrigger canoes caused genetic bottlenecks in the migrating population, culminating in the reduced diversity found today in eastern Polynesia and New Zealand. At the far extremes of this migration, explorers visited South America and obtained valuable plants for agriculture, and finally, somewhere around 650 ybp, there was a deliberate settlement of Aotearoa/New Zealand.

We will probably never know for certain the exact routes they took and the obstacles they had to overcome, but our growing knowledge illustrates clearly that the settlement of Aotearoa/ New Zealand was a significant, intentional, and well-planned venture. The genetic evidence of bottlenecks and reduced variability indicates something of the hardships that were faced and which Polynesian people (including New Zealand Māori) survived in order to be here today in Oceania. We look forward to results from ongoing linguistic, archaeological, historical, and genetic research in order to better understand and appreciate this achievement.

References

- Austin, C.C. 1999. Lizards took express train to Polynesia. *Nature* 397: 113–114.
- Bellwood, P. 1991. The Austronesian dispersal and the origin of languages. Scientific American 264: 70–75.
- Bellwood, P. 1997. The Austronesian dispersal. *Newsletter of Chinese Ethnology* 36: 1–26.
- Bellwood, P. 1998. Human dispersals and colonizations in prehistory
 the Southeast Asia data and their implications. Pp. 199–205 in:
 Onomoto, K.; P.V. Todias, P.V. (eds), *The Origins and Past of Modern Humans Towards Reconciliation*. World Scientific,
 Singapore.
- Brewis, A.A.; Molloy, M.A.; Sutton, D.G. 1990. Modeling the prehistoric Maori population. *American Journal of Physical Anthropology 81*: 343–356.
- Burley, D.V.; Dickinson, W.R. 2001. Origin and significance of a founding settlement in Polynesia. *Proceedings of the National Academy of Sciences* 98: 11829–11831.
- Cann, R.L. 2001. Genetic clues to dispersal in human populations: Retracing the past from the present. *Science 291*: 1742–1748.
- Cann, R.L.; Lum, J.K. 2004. Dispersal ghosts in Oceania. American Journal of Human Genetics 16: 440-451.
- Cavali-Sforza, L.L. 2000. *Genes, People and Languages*. North Point Press, New York.
- Chambers, G.K. 2005. Polynesian genetics and Austronesian Prehistory. Paper presented at the International Symposium on the Dispersal of Austronesians and the Ethnogenesis of the People in the Indonesian Archipelago, Solo, Indonesia.
- Chambers, G.K.; Marshall, S.J.; Robinson, G.M.; Maguire, S.M.; Newton-Howes, J.; Chong, N.J. 2002. The genetics of alcoholism in Polynesians: Alcohol and aldehyde dehydrogenase genotypes in young men. *Alcoholism Clinical and Experimental Research* 26: 949–955.
- Clark, A.G.; Hamilton, J.F.; Chambers, G.K. 1995. Inference of population subdivision from the VNTR distributions of New Zealanders. *Genetica* 96: 37-49.
- Cox, M.P. 2003. Genetic patterning at Austronesian contact zones. PhD thesis, Department of Biochemistry, Otago University, Dunedin.
- Devlin, B.K.; Roeder, K.; Otto, C.; Tiobech, S.; Byerley, W. 2001. Genome-wide distribution of linkage disequilibrium in the

population of Palau and its implications for gene flow in remote Oceania. *Human Genetics 108*: 521–528.

Diamond, J. 1988. Express train to Polynesia. Nature 336: 307-308.

- Flint, J.; Boyce, A.J.; Martinson, J.J.; Clegg, J.B. 1989. Population bottlenecks in Polynesia revealed by minisatellites. *Human Genetics* 83: 257–263.
- Gibbons, A, 2001. The peopling of the Pacific. *Science 291*: 1735–1737.
- Green, R.C. 2000. A range of disciplines support dual origins for the bottle gourd in the Pacific. *Journal of the Polynesian Society* 109: 191–197.
- Green, R.C. 2003. Pp. 95–120 in: Sand, C. (ed.), Pacific Archaeology: Assessments and Anniversary of the First Lapita Excavation (July 1952). Les Cahiers de l'Archéologie en Nouvelle-Caledonie 15.
- Hage, P.; Marck, J. 2003. Matrilineality and the Melanesian origin of the Polynesian Y chromosomes. *Current Anthropology* 44: S121-S127.
- Hamilton, F. 1994. Multi-locus and single-locus DNA profiling in New Zealand. PhD Thesis, Victoria University of Wellington, New Zealand.
- Handoko, H.Y.; Lum, J.L.; Rismalia, G.; Kartapraja, H.; Sofro, A.S.M.; Marzuki, S. 2001. Length variations in the COIItRNALys intergenic region of mitochondrial DNA in Indonesian populations. *Human Biology* 73: 205–223.
- Heyerdahl, T. 1953. *The Kon-Tiki expedition: By raft across the south seas*. Allen and Unwin, London.
- Hurles, M.E.; Nicolson, J.; Bosh, E.; Renfrew, C.; Sykes, B.C.; Jobling, M.A. 2002. Y chromosomal evidence for the origins of Oceanic-speaking peoples. *Genetics* 63: 1793–1806.
- Hurles, M.E.; Matisoo-Smith, E.; Gray, R.D.; Penny, D. 2003a. Untangling Oceanic settlement: the edge of the knowable. *Trends* in Ecology and Evolution 18: 531–540.
- Hurles, M.E.; Maund, E.; Nicholson, J.; Bosch, E.; Renfrew, C.; Sykes, B.C.; Jobling, M.A. 2003b. Native American Y chromosomes in Polynesia: the genetic impact of the Polynesian slave trade. *American Journal of Human Genetics* 72: 1282–1287.
- Hurles, M.E.; Sykes, B.C.; Jobling, M.A.; Forster, P. 2005. The dual origin of the Malagasy in island Southeast Asia and East Africa: Evidence from maternal and paternal lineages. *American Journal* of Human Genetics 76: 894–901.
- Ingman, M.; Gyllenstein, U. 2003. Mitochondrial genome variation and evolutionary history of Australian and New Guinea aborigines. *Genome Research* 13: 1600–1606.
- Jobling, M.A.; Hurles, M.E.; Tyler-Smith, C. 2004. Human Evolutionary Genetics: Origins, Peoples and Disease. Garland, New York.
- Kayser, M.; Brauer, S.; Weiss, G.; Underhill, P.A.; Roewer, L.; Schiefenhövel, W.; Stoneking, M. 2000. Melanesian origin of Polynesian Y chromosomes. *Current Biology* 10: 1237–1246.
- Kayser, M.; Bauer, S.; Weiss, G.; Schiefenhövel, W.; Underhill, P.;
 Shen, P.; Oefner, P.; Tommaseo-Ponzetta, M.; Stoneking, M. 2003. Reduced Y-chromosome, but not mitochondrial DNA, diversity in human populations from West New Guinea. *American Journal of Human Genetics* 72: 281–302.
- Kirch, P.V. 1997. The Lapita Peoples: Ancestors of the Oceanic World. Blackwood, Oxford.
- Kirch, P.V. 2000. On the Road of the Winds: An Archaeological History of the Pacific Islands before European Contact. University of California Press, Berkeley, CA.
- Marshall, S. 1995. The genetics of human alcohol metabolism. PhD thesis, Victoria University of Wellington, New Zealand.
- Marshall, S.J.; Chambers, G.K. 2005. Genetic aspects of alcohol metabolism: An Overview. Pp. 31–48 in Preedy, V.R.; Watson, R.R. (eds), Comprehensive Handbook of Alcohol Related Pathology. Academic Press, London.
- Matisoo-Smith, E.; Robins, J. 2004. Origins and dispersals of Pacific peoples: Evidence from mtDNA phylogenies of the Pacific rat.

Proceedings of the National Academy of Sciences 101: 9167–9172.

- Merriwether, D.A.; Friedlaender, J.S.; Mediavilla, J.; Mgone, C.; Gentz, F.; Ferrell, R.E. 1999. Mitochondrial DNA variation is an indicator of Austronesian influence in island Melanesia. *American Journal of Physical Anthropology* 110: 243–270.
- Murray-McIntosh, R.P.; Scrimshaw, B.J.; Hatfield, P.J.; Penny, D. 1998. Testing migration patterns and estimating founding population size in Polynesia using human mtDNA sequences. *Proceedings of the National Academy of Sciences 95*: 9047– 9052.
- Oppenheimer, S. 1998. Eden in the East: The Drowned Continent of Southeast Asia. Phoenix, London.
- Oppenheimer, S.; Richards, M. 2001. Fast trains, slow boats, and the ancestry of the Polynesian islanders. *Science Progress* 84: 157–181.
- Pawley, A.; Ross, M. 1993. Austronesian historical linguistics and culture history. *Annual Review of Anthropology 22*: 425–459.
- Penny, D.; Murray-McIntosh, R.; Harrison, G.L. 2002. Estimating the number of females in the founding population of New Zealand: Analysis of mtDNA variation. *Journal of the Polynesian Society 111*: 207–221.
- Pool, D.I. 1991. Te iwi Maori: A New Zealand Population, Past, Present, and Projected. Auckland University Press, Auckland.
- Redd, A.J.; Takezake, N.; Sherry, S.T.; McGarvey, S.T.; Sofro, A.S.M.; Stoneking, M. 1995. Evolutionary history of the COII/ tRNA (lys) intergenic 9 base pair deletion in human mitochondrial

DNAs from the Pacific. *Molecular Biology and Evolution 12*: 604–615.

- Spriggs, M. 2003. Chronology of the Neolithic transition in Southeast Asia and the western Pacific: A view from 2003. *Review of Archaeology 24*: 57–80.
- Sykes., B.; Leiboff, A.; Low-Beer, J.; Tetzner, S.; Richards, M. 1995. the origins of the Polynesians: An interpretation from mitochondrial lineage analysis. *American Journal of Human Genetics 57*: 1463–1475.
- Terrell, J. 1988. History as a family tree, history as an entangled bank: Constructing images and interpretations of prehistory in the South Pacific. Antiquity 62: 642-657.
- Trejaut, J.A.; Kivisild, T.; Loo, J.H.; Lee, C.L.; He, C.L.; Hsu, C.J.; Li, Z.Y.; Lin, M. 2005. Traces of archaic mitochondrial lineages persist in Austronesian-speaking Formosan populations. *PLoS Biology 3*: e247. www.biology.plosjournals.org/perlserv/ ?request=get-document&doi=10.1371/journal.pbio.0030247
- Underhill, P.A.; Passaino, G.; Lin, A.A.; Marzuki, S.; Cavalli-Sforza, L.L.; Chambers, G.K. 2001. Maori origins, Y-chromosome haplotypes, and implications for human history in the Pacific. *Human Mutations* 17: 271–280.
- Whyte, A.L.H. 2002. Human evolution in Polynesia: A molecular biological study. MSc thesis, Victoria University of Wellington, New Zealand.
- Whyte, A.L.H.; Marshall, S.J.; Chambers, G.K. 2005. Human evolution in Polynesia. *Human Biology* 77: 157–177.