Review

Ancient DNA and the human settlement of the Pacific: A review

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ABSTRACT

The Pacific region provides unique opportunities to study human evolution including through analyses of ancient DNA. While some of the earliest studies involving ancient DNA from skeletal remains focused on Pacific samples, in the following 25 years, several factors meant that little aDNA research, particularly research focused on human populations, has emerged. This paper briefly presents the genetic evidence for population origins, reviews what ancient DNA work has been undertaken to address human history and evolution in the Pacific region, and argues that the future is bright but research requires a collaborative approach between academic disciplines but also with local communities.

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Introduction

The Pacific region plays a key role in understanding human evolution and human migrations as it was both the endpoint of one of the earliest 'Out of Africa' migrations, with the arrival of humans in Australia and New Guinea some 50,000 years ago, and the location of the last major human migration, resulting in the colonization of the islands of East Polynesia, which occurred in the last 1000 years. The relative isolation of the Pacific region, with its many island environments, has also been an important, though sometimes over-emphasized, factor in the history of the region and one which again makes the Pacific region particularly valuable for evolutionary studies. Most recently, the identification in some modern Pacific populations of ancient admixture with Denisovans (Reich et al., 2011) also highlights the importance of the region for understanding ancient hominin population histories and their interactions with modern human populations moving out of Africa and through Asia.

While the Pacific played a very early role in studies of modern human variation in general and even in ancient DNA (aDNA) studies, there has not been a significant amount of ancient DNA research in the region to date. This is related to two main factors: the ethical issues and concerns of indigenous communities regarding scientific analyses of both ancient and modern human samples and the environmental characteristics, namely the heat and humidity, of the region, which are not conducive to aDNA preservation (Smith et al., 2003).

Pacific populations and questions regarding their origins and relationships to each other and to other non-Pacific populations have been topics of much scientific interest since Europeans first arrived in the region. Unfortunately, this fascination resulted in a range of questionable activities undertaken in the name of science. Collecting large numbers of anatomical specimens of indigenous peoples, living and dead, for biological studies was commonplace (Douglas and Ballard, 2008). As a result of these behaviours and their connections with the colonial powers in the region, the relationship between Western science and indigenous communities in Australia and the Pacific has often been one of fear and mistrust (Durie, 2004). Thus population studies in the region have been, until recently, limited to the analyses of curated samples collected prior to the concerns of indigenous communities that were raised publically, particularly in response to the Human Genome Diversity Project (Resnik, 1999).

Background: the history of human occupation of the Pacific region

As fully modern human populations moved out of Africa around 55–65 kya (thousands of years ago) (Soares et al., 2012) and along the southern coast of Asia, sea levels were much lower than they are today, so those first colonists into the greater Pacific region would have been able to walk through most of what is now Island Southeast Asia. Upon reaching what is now Java and Borneo, however, they would have encountered their first major water barrier (see Fig. 1). Even at lowest sea levels (around 25 kya at −135 m) the deep water trenches of Wallacea would have

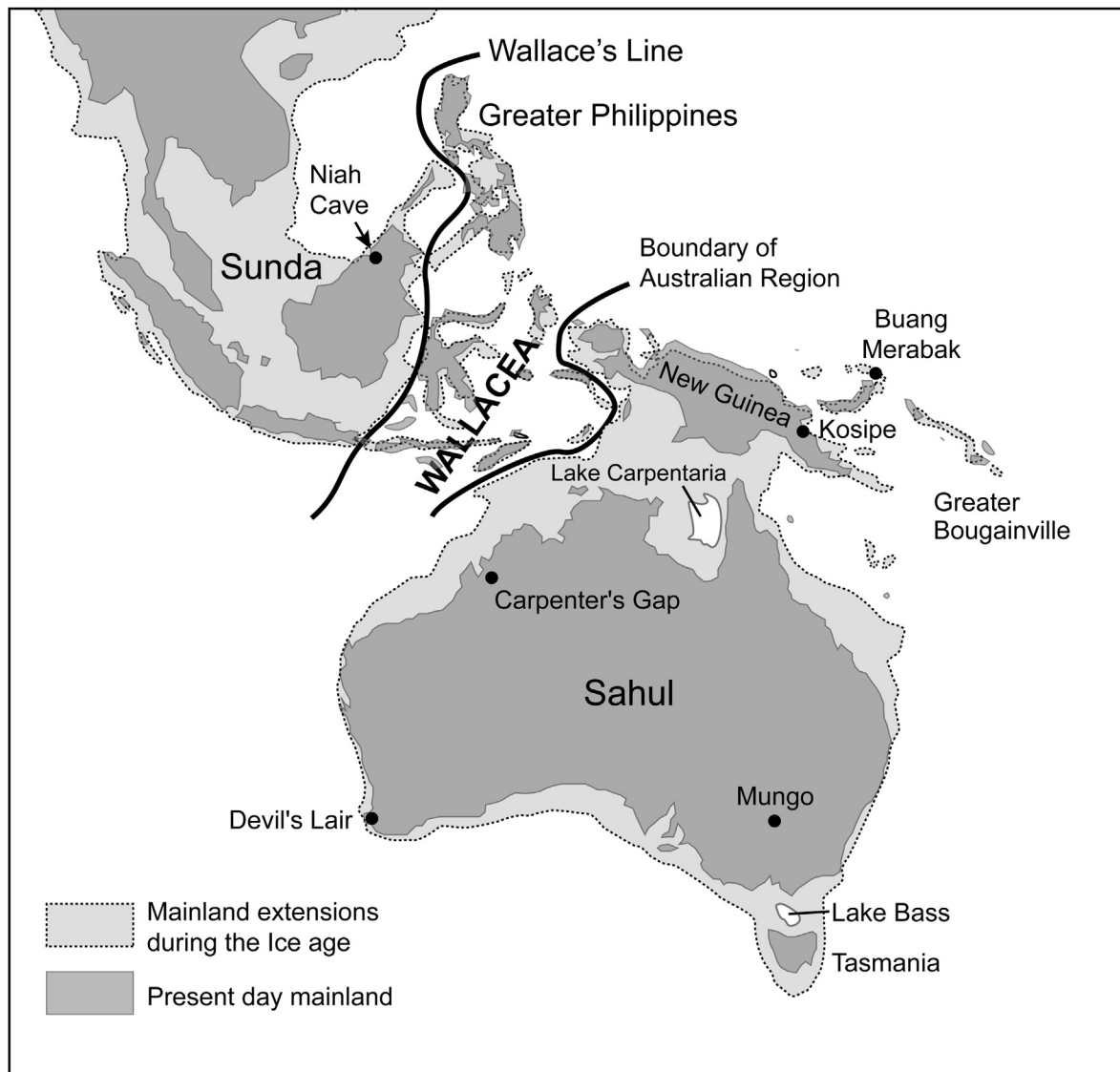E-mail address: matisoo-smith@otago.ac.nz.

Figure 1. Map of the ancient (Pleistocene) landmasses of Sunda and Sahul and the biogeographic region of Wallacea, with some of the early (>40,000 years BP) archaeological sites in the region. Map by Vivian Ward.

impeded further migration by foot (see http://sahultime.monash. edu.au/explore.html). Yet people did cross the boundary from Sunda into Sahul, arriving in New Guinea and reaching the highlands around 50,000 years before present (BP) (Summerhayes et al., 2010a). This would have required crossing minimum water gaps of 70 km, indicating the ability to construct some form of watercraft.

The earliest archaeological evidence for human occupation of Australia, which was until around 11,000 years ago joined to New Guinea, dates to around 45,000 BP (O'Connell and Allen, 2004). Sites that date to between 40,000 and 45,000 years BP are found across the continent, suggesting that the first arrivals quickly dispersed across the landscape, most likely following and utilizing the rich resources of the coastline and inland waterways. Human occupation of the islands of New Britain and New Ireland, lying north of New Guinea and which were not part of the Sahul landmass, dates to about the same period, around 40,000 years BP (Leavesley et al., 2002). By 30,000 years ago people had reached Buka, the northernmost island in the Solomon Island chain (Wickler and Spriggs, 1988). The greater Solomon Islands represent the most eastern expansion of this early period of occupation.

Environmental factors including the extreme mountains and valleys of New Guinea, the relative isolation of major islands, and the vastness of Australia resulted in isolation of these small hunter-gatherer groups, which, combined with the deep history of the region, likely led to the significant genetic and linguistic variation that is still seen today (Friedlaender et al., 2008; van Holst Pellekaan, 2013). This region of early, Pleistocene human occupation is generally referred to as Near Oceania, to delineate it from the rest of the Pacific, which was settled much more recently and is referred to as Remote Oceania (Green, 1991).

The settlement of Remote Oceania, which encompasses all of the islands from the Reef/Santa Cruz Islands in the southeast Solomon Islands through to the extremes of the Polynesian Triangle and Micronesia, has a much shorter colonization history. The earliest archaeological sites in Remote Oceania date to around 3000 years BP (Petchey et al., 2014) and are associated with the Lapita Cultural Complex, though slightly earlier dates have been suggested (Rainbird, 1994) for initial settlement of the Mariana Islands, in Western Micronesia, which currently have no evidence of Lapita occupation. The earliest Lapita sites are found in the St. Matthias

Islands in the Bismarck Archipelago and date to around 3350–3500 years BP (Kirch, 2001; Summerhayes et al., 2010b). They are identified by the unique red-slipped, dentate stamped pottery along with a range of other artifacts, the appearance of new domesticated plants and animals, and the earliest village settlements in the region, with stilt-structures built out over the reefs. It is generally accepted that the appearance of Lapita sites in Oceania is associated with the Neolithic population expansions from Southeast Asia into the islands and the subsequent spread of the Austronesian languages through Island Southeast Asia and into the Pacific. While there is no obvious single source location that can be identified as the likely origin of the Lapita culture, based on archaeological data, linguistic evidence suggests that Taiwan is the origin of the Austronesian languages and therefore the likely origin of the Lapita culture is postulated to be somewhere between Taiwan and the Bismarck Archipelago (Blust, 1996). This has led to much debate about the origins of the Lapita culture and even more debate about the origins of the people who are associated with the spread of Lapita.

Lapita sites extend eastwards as far as Samoa and Tonga, on the edge of the Polynesian Triangle, covering a distance of some 4000 km. While no Lapita pottery has been found in Micronesia, the settlement of the Caroline and Marshall Islands are thought to be associated with Lapita derived populations in the central Pacific (Vanuatu or the Solomon Islands) (Kirch, 2000). Lapita sites in Samoa and Tonga date to about 2850 years BP (Burley et al., 2012), the settlement of the rest of the Polynesian Triangle, however, did not occur until approximately 1500–2000 years later. Lapita style pottery disappears in Samoa and Tonga within a few hundred years and is replaced by Polynesian plainware. By the time further expansion eastwards resumed, around 1200 years BP (Wilmshurst et al., 2011), pottery had been abandoned in Samoa and Tonga and was not introduced to the rest of Polynesia (though a few sherds have been found in the Marquesas and the Cook Islands) (Kirch, 2000). The final phase of Pacific settlement and of human colonization world-wide was marked by the arrival of humans on the islands marking the apices of the Polynesian Triangle, with

settlement of Hawai'i by 1000–1200 years BP and Rapa Nui/Easter Island and Aotearoa/New Zealand around 750–800 BP years (Wilmshurst et al., 2011) (Fig. 2).

Genetic evidence for Pacific origins and settlement history

This general picture of Pacific settlement has developed over the last 30 years as modern archaeological research methods were applied in the region as part of major international research programs (Allen, 1984; Sand, 1997; Kirch, 2001). Genetic and, in particular, molecular research has also contributed to our understanding of human origins and migrations in the area. For instance, the discovery, dating and distribution of Lapita sites in the Pacific made it clear that the origins of Polynesian peoples were to be found, not in America as proposed by the Norwegian explorer Thor Heyerdahl (Heyerdahl, 1952), but to the west in Near Oceania and Island Southeast Asia. However, it was not until the mid 1980s that biologists could refute this American origin suggestion based on ABO or other blood protein data (Simmons, 1962). The discovery of high rates of globin gene mutations in Polynesians, which could only have been inherited from populations in Near Oceania, provided the first conclusive biological evidence of Oceanic origins for Polynesians (Hill et al., 1987). This was followed quickly by the evidence of a particular mitochondrial DNA motif that linked Polynesian origins with Island Southeast Asia (Melton et al., 1995; Redd et al., 1995).

By the late 1980s, the archaeological and biological evidence for human settlement of the Pacific fit well with the linguistic evidence of two major colonization events. The very early, Pleistocene settlement of Near Oceania began 30–50,000 years ago by the ancestors of today's 'Papuan' peoples and the Australian Aboriginals. The genetic signatures of these early human migrations into Near Oceania are the numerous, regionally specific mitochondrial DNA (mtDNA) and Y chromosome haplotypes that are found in Australia and New Guinea. These include lineages belonging to mtDNA haplogroups M, O, P and S in Australia (van Holst Pellekaan et al., 2006; van Holst Pellekaan, 2013), and P, Q and some unique
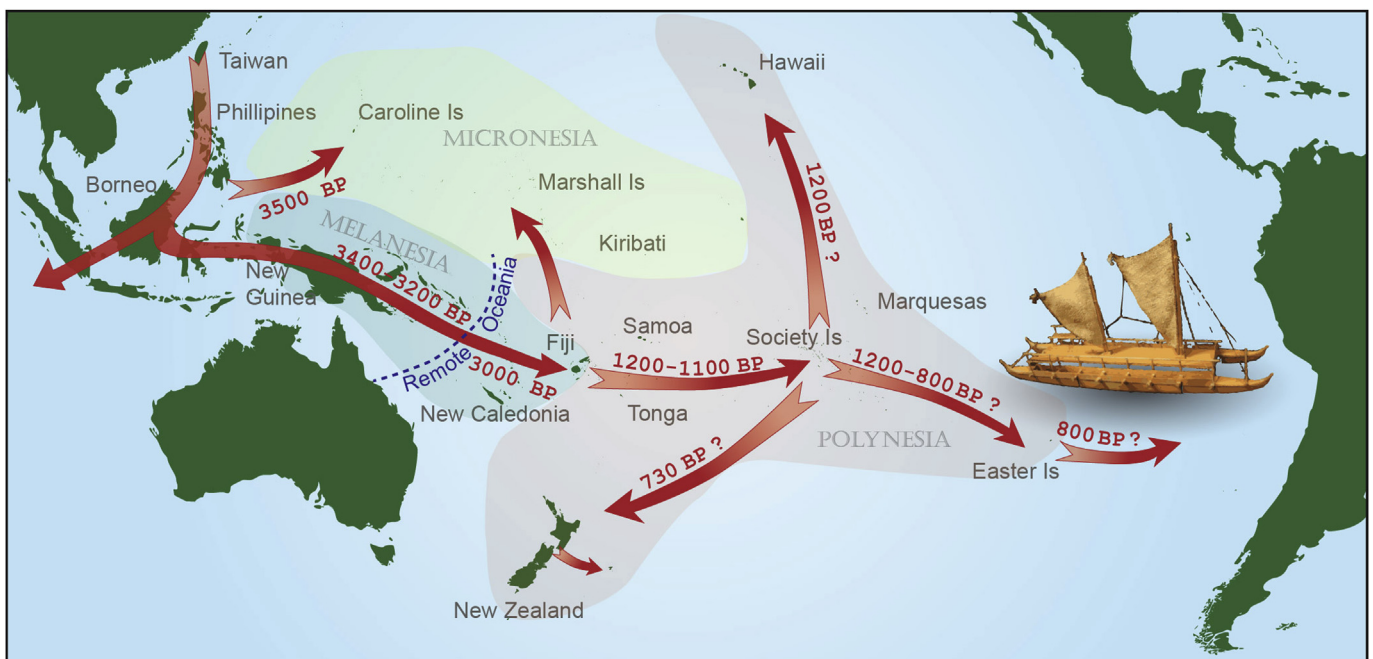

Figure 2. Map of Near and Remote Oceania, with colonization trajectories and dates indicated. Map by Ceridwen Fraser.

branches of M (specifically M27, M28 and M29) in New Guinea and Near Oceania (Merriwether et al., 2005; Friedlaender et al., 2005, 2007), and Y chromosomes belonging primarily to the K, M and C clades (Scheinfeldt et al., 2006; Kayser, 2010; van Holst Pellekaan, 2013).

According to what has become the orthodox model of Pacific settlement (Kirch, 2000), this early wave of migration was followed by the arrival of the second 'wave' involving Neolithic, Austronesian speaking 'Lapita people' and beginning around 3500 years BP. The Lapita culture and presumably the peoples who carried it originated in Island Southeast Asia and moved relatively quickly through Near Oceania, interacting and exchanging genes with the indigenous inhabitants there, before they colonized Remote Oceania.

Linguistically and culturally, these Lapita peoples are seen as the immediate ancestors of the Polynesians (Kirch and Green, 2001). The accumulating biological data in the early and mid 1990s also supported this view of ultimate Southeast Asian, and more specifically, Taiwanese origins for Polynesians, and presumably their more immediate Lapita ancestors. In particular, a combination of mtDNA mutations was identified, with the characteristic single nucleotide polymorphisms (SNPs) at nucleotide positions 16217, 16247 and 16261 and the nine base pair (bp) deletion in the COII/tRNA^{Lys} intergenic region, the combination of which defined the B4a1a1a haplogroup (note: Phylotree build 16 (http://www.phylotree.org/) has resulted in a major revision of the B4a1a1 and derived haplogroups). This haplogroup was found at high frequency throughout the Pacific, but particularly in Polynesia, where its distribution has been described as near ubiquitous and thus it became referred to as the Polynesian motif (PM) (Hagelberg and Clegg, 1993; Melton et al., 1995; Redd et al., 1995). The ancestral haplogroup, B4a1a, is clearly of Asian origin and is found in Taiwan and throughout Island Southeast Asia and the western Pacific, and this was seen initially as supporting an 'Out of Taiwan model for Polynesian origins' (Trejaut et al., 2005; Friedlaender et al., 2007). However, more recently, the immediate origin and age of B4a1a1a is a topic of much debate (Tabbada et al., 2010; Soares et al., 2011). The B4a1a1a haplogroup is not present in Taiwan or the Philippines and, based on analyses of complete mtDNA genomes, Soares et al. (2011) argue that the Polynesian motif and its immediate ancestral lineages (B4a1a1) evolved within the Bismarck Archipelago some 6000–8000 years ago, several thousand years before the appearance of the Lapita cultural complex in that same location. There is much debate, however, regarding the reliability of estimates of coalescence dates, and it is possible that the haplogroup was present at low frequency in Island Southeast Asia prior to Austronesian expansion and was subsequently spread causing an increased frequency as a result of that expansion into Near and Remote Oceania. (Note that build 16 of phylotree, released in February 2014, has, based on a recent publication [Duggan and Stoneking, 2013], declared that the mutation defining B4a1a1a, 16249G, is no longer a reliable defining mutation for the haplogroup and thus the nomenclature for this haplogroup and derived subgroups has been updated).

While the mtDNA suggested a primarily Island Southeast Asian origin for Austronesian-speaking populations, analyses of Y chromosome variation in the Pacific tells of a much more complex history of population origins and interactions. The Y chromosomes belonging to haplogroups K, M, S and C are generally restricted to Oceanic populations and are generally believed to have originated in Near Oceania during the Pleistocene period of human occupation. Pacific populations also carry Y chromosomes belonging to the O branch, which is widespread in Asia and likely these were brought into the Pacific during the Holocene, presumably as part of the Austronesian expansion (Kayser, 2010). Austronesian speaking populations in both Near and Remote Oceania, even those with near fixation of Asian derived mtDNA lineages show significant levels of Near Oceanic derived Y chromosomes (Kayser et al., 2000, 2006; Kayser, 2010). Even in Polynesia over 60% of the Y chromosomes are of Oceanic origin, with the predominant type being C2a-M208. It has been suggested that this contradiction between predominantly Asian derived mtDNA and Y chromosomes of Near Oceanic origin in Remote Oceanic populations is an indication of the Lapita societies having a matrilineal descent structure and matrilocal residence patterns (Hage and Marck, 2003). Recently, a study of Y chromosome variation in Tongans and Samoans has identified a high frequency of the Asian derived O3a2c-P164 Y chromosome haplotype, reaching levels as high as 53% in Tonga. This haplotype was also found in the Ami indigenous peoples of Taiwan, providing the first direct link between Taiwan and Polynesia (Mirabal et al., 2012). Unfortunately, to date, few other populations in Island Southeast Asia and the Pacific have been assayed for the P164 marker, and it is possible that many more of the Pacific Y chromosomes that are on the O3 branch may also carry this marker.

It should be noted that, in general, Polynesian populations are not well represented in most genetic analyses of Pacific populations. When we look at the few Polynesian populations that have been sampled (see for example Fig. 1 in Kayser et al., 2006) there is quite some variation in Asian versus Near Oceanic derived Y chromosomes, which may reflect sampling bias. Another process that might create quite disparate patterns of Y chromosome variation across the Pacific was the removal of men from many of the islands in the Pacific by historic slave traders 'recruiting' labour for the Peruvian guano mines or Australian sugar plantations (Corris, 1968; Bennett, 1976; Maude, 1981; Kirch and Rallu, 2007; Matisoo-Smith, 2012). In some instances, such as on the atolls of Tokelau, as much as 48% of the population, including almost all able-bodied men were 'recruited' and taken, with few if any ever returning (Green and Green, 2007). Another issue with interpreting the variation we see in the Pacific is that of ascertainment bias. Because Pacific populations in general have not been subjected to large population studies, it might be expected that future full sequencing of Pacific Y chromosomes will identify new, Pacific specific markers that will allow us to further assess the history of male migration in the region in a way that complete mitogenome sequencing is providing further, fine-grained evidence of maternal relationships within and between Pacific populations (Duggan et al., 2014).

Increasingly, genome-wide studies are being employed to overcome some of the limitations of the single-locus mitochondrial and Y chromosome analyses. To date, the results of the genome wide studies undertaken in the Pacific provide a similar picture of population origins and admixture shown by the mitochondrial and Y chromosome studies. Analyses using the Pan-Asian SNP dataset indicate an East Asian derived population migration moving through eastern Indonesia towards New Guinea around 4000 years BP, which corresponds with the Austronesian expansion (Xu et al., 2012). Asian admixture within New Guinea only occurs at low frequency and only along the coast and through the islands of the Bismarck Archipelago, where it is always less than 20%; and again, sex-biased admixture was identified with Asian-derived markers on the X chromosome being much greater than across the genome generally (Friedlaender et al., 2008). Asian ancestry of Polynesian populations is calculated at approximately 87% and 13% Near Oceanic (Wollstein et al., 2010). It has been suggested that perhaps a later, post-Lapita and more directly Asian derived migration may have stimulated the final population expansion into Central and East Polynesia from Samoa (Addison and Matisoo-Smith, 2010) and this might account for the strong Asian genetic component in

East Polynesian populations. Further whole genome studies on a wider selection of Polynesian populations and analyses of ancient DNA will be useful for testing this hypothesis and many others including assessing issues of population replacement, identifying particular genes under selection or to address the issue of the impact of the introduction of infectious diseases as a result of initial European contact.

Despite the acceptance of this general model of Island Southeast Asian origins for Polynesians and their Lapita ancestors, questions still remained: How was the Polynesian Triangle itself settled? What were the immediate origins of the New Zealand Maori or the people of Rapanui? How much interaction was there between the Lapita peoples in western Remote Oceania with the Papuan populations of Near Oceania? Where was the homeland of the Lapita peoples and their culture? Ancient DNA provides a unique opportunity to address many of these questions but requires a multi-disciplinary approach and collaboration and engagement with local communities. We might also be able to further engage with and encourage Pacific communities to participate in whole genome studies (both ancient and modern) to begin to address questions about how Pacific populations might have adapted genetically to the range of Pacific environments and specific challenges. These approaches could help us better understand why Pacific communities today suffer from higher than normal rates of particular diseases such as diabetes, gout and other metabolic disorders (Hancock et al., 2008; Phipps-Green et al., 2010; Buckley, 2011).

The commensal model and aDNA

In response to these questions and constrained by the ethical and political issues of collecting DNA or tissue samples from either ancient or modern indigenous populations in the Pacific, a new approach to studying human migration patterns was developed. What became known as the commensal approach focused on genetic analyses of the plants and animals that people transported in their colonizing canoes (Matisoo-Smith, 1994). Many of these introduced species cannot self disperse and therefore had to be introduced by humans. The animals introduced by Lapita were said to include the dog, pig, chicken and the Pacific rat (*Rattus exulans*). These animal remains often appear in the archaeological sites across the Pacific, and in relatively large numbers compared with human remains. It was also believed that there was limited mtDNA variation in human populations in the Pacific, particularly Polynesia, yet there was a chance of significantly more variation in the commensal animals, which might allow for the identification of the specific origins of the colonizing canoes of locations like New Zealand and Easter Island.

The first animal to be investigated in this commensal model approach was the Pacific rat, *R. exulans*. This small rat was a known food item throughout the Pacific region. Its natural distribution is Island Southeast Asia (Tate, 1935) and recently the island of Flores has been suggested as a likely homeland (Thomson et al., 2014a). *R. exulans* remains are found in the earliest archaeological deposits and middens throughout Polynesia and most of Remote Oceania. It is a separate species from the later introduced European rats, and cannot interbreed and generally does not co-exist with them in European vessels. Therefore, it was argued that the *R. exulans* populations found on Pacific islands today should be the direct descendants of those introduced by the original Pacific colonists and thus tracing the origins of the rat populations would identify the origins of the canoes that transported them (Matisoo-Smith, 1994). The model was applied and analyses of mtDNA variation in Polynesian populations identified multiple origins of rats to both Hawai'i and New Zealand and indicated that there were two major spheres of interaction within the Polynesian Triangle, a northern

and a southern sphere, both interacting and most likely originating in Central East Polynesia (the Cook Islands and the Society Islands) (Matisoo-Smith et al., 1998).

Ancient DNA analyses of archaeological remains of *R. exulans* indicated that there was indeed continuity between ancient and modern populations on most islands (Matisoo-Smith, 2002), and therefore both ancient and modern mtDNA data could be combined and were useful in addressing the question of population origins. The approach was then applied beyond Polynesia to address the questions regarding the links between Polynesia, Lapita, and *R. exulans* populations in Near Oceania and Island Southeast Asia (Matisoo-Smith and Robins, 2004). Interestingly, archaeological evidence suggests that *R. exulans* was not present in Taiwan, the postulated homeland of the Austronesian languages and, by association, also possibly of the Lapita culture. This evidence suggested that at least this one component of the Lapita cultural complex had to have been picked up and incorporated elsewhere prior to its introduction to the Pacific. The mtDNA data from the rats also indicated that there were several distinct populations and likely interaction spheres across Island Southeast Asia and the Pacific, two of which were found on the Pacific islands.

Ancient DNA analyses were then applied to the other Pacific commensal animals. Analyses of ancient pig mtDNA indicate that only a single lineage was introduced to the Pacific, and that lineage could be traced back to the coast of Vietnam (Larson et al., 2007). Ancient DNA analyses of archaeological dog remains from the Pacific indicate at least two mtDNA lineages were introduced, both of which are distinct from the introduction of dogs/dingoes to Australia and New Guinea (Savolainen et al., 2004). The earliest evidence of dog bones in the Pacific region comes from Australia, where dingo remains date to about 3500 years BP (Milham and Thomson, 1976). Interestingly, however, when the archaeological evidence for dog remains in Lapita sites was investigated, there was little to no evidence for dog bones in early contexts. While dog bone does appear in reasonable numbers in archaeological sites in the Pacific that date from about 2000 years BP onwards, dog bone has never been identified in pre-European archaeological sites in Vanuatu or New Caledonia. This evidence suggests that perhaps dogs were not part of, or certainly not a significant part of, the Lapita cultural complex (Matisoo-Smith, 2007). It also raises some interesting questions regarding the introduction of dogs to Polynesia. Dog bone appears in many early sites in Central and East Polynesia (though dogs were not introduced prehistorically to Easter Island) but how did those dogs get to Polynesia, and from where, given that they did not appear to pass through New Caledonia or Vanuatu?

The last of the four major commensal animals of Pacific peoples to be studied using aDNA was the chicken (Storey et al., 2007). Chicken bones are found in the earliest Lapita sites in both Near and Remote Oceania and many of these have been made available for aDNA analyses as have chicken bones from sites across Polynesia (note chickens were not introduced to New Zealand during pre-history). While the chicken mtDNA data also indicated at least two distinct lineages of chickens were introduced to the Pacific, what was perhaps most surprising was that chicken bones were found in pre-Columbian archaeological sites from a coastal site, El Arenal, in Chile. Chickens were believed to have been introduced to the Americas by early European sailors, but the archaeological context, direct radiocarbon dates and isotope studies on three bones all confirm their pre-Columbian context (Storey et al., 2008). The mtDNA sequences from these chicken bones were identical to those obtained from chicken bones in early Pacific sites (Storey et al., 2007, 2010). While some have suggested that the DNA sequences obtained from the Chilean bones were the result of contaminated reagents or other sources (Gongora et al., 2008; Thomson et al.,

2014b), responses to all of the issues raised have been addressed and the alternative interpretations questioned; we still argue that the evidence for pre-Columbian Polynesian contact with the Americas is sound (Storey and Matisoo-Smith, 2014). Further research has shown the archaeological evidence and radiocarbon dates, combined with the isotope data, which indicate that the diet of the chickens was likely to be totally terrestrial (and thus the radiocarbon dates do not need to be adjusted for marine effect) still indicate a pre-Columbian introduction (calibrated ages at 2 standard deviations fall between AD 1304 and 1450) regardless of the DNA data (Storey et al., 2013a; Beavan, 2014). Given that the dates for East Polynesian settlement all fall around AD 1300 (Wilmshurst et al., 2011), this is exactly when Polynesians, who were known to be transporting chickens and who were already sailing in an eastward direction towards the South American coast, would most likely have had their eastward migration halted by contact with South America. If Polynesians were not the people who first introduced chickens to the Americas some 100 years prior to the earliest evidence of European arrival, then we will have to seriously reconsider our understanding of American prehistory allowing for Asian or some other contact for which there is yet any archaeological, linguistic or other evidence. While it may be considered controversial, there is some archaeological and linguistic evidence, other than the chicken bones, indicating likely Polynesian contact with the Americas (see Jones and Klar, 2005 and Klar and Jones, 2005 for discussions on the linguistic and archaeological evidence for Polynesian style sewn plank canoes in the Americas).

The El Arenal chicken bones are not the only evidence for Polynesian contact with the Americas. During searches of museum collections to attempt to find other commensal animal bones, we encountered archaeological collections of human remains from Isla Mocha, a small island located approximately 30 km off the coast of south central Chile, about 100 km south of the site of El Arenal. Many of the crania and some of the postcranial remains from the island had characteristic morphological features associated with Polynesian populations. This 'Polynesian phenotype' includes features such as tall stature, overall robusticity, a pentagonal cranium when viewed from behind, mandibles with a broad, vertical ramus and convex curved mandibular body resulting in a 'rocker' motion when placed on a flat surface, and an oval fovea capitis on the head of the femur (Houghton, 1977, 1996). Craniometric analyses of these skulls suggest that the population is admixed with some crania clustering with South American populations and others with Polynesian and Pacific populations (Matisoo-Smith and Ramirez, 2010). Ancient DNA analyses, including attempts at whole genome sequencing, are currently being undertaken on these samples to identify if there is any genetic evidence of Polynesian ancestry.

The first recognized and perhaps strongest evidence for Polynesian contact with the Americas is the presence of the sweet potato (Ipomoea batatas), a South American plant, in pre-European archaeological contexts throughout Polynesia (Hather and Kirch, 1991; Ladefoged et al., 2005). Perhaps more telling of actual person-to-person contact is the Polynesian term for the plant, kumara (or similar derivatives), which is remarkably similar to and the predicted Polynesianization of the Quechuan name for the sweet potato, cumar (Scaglion, 2005). This use of a South American name for the plant indicates that there was direct contact and communication between peoples of the two regions and that the plant was not naturally dispersed into Polynesia, which has been indicated, using computer simulations, to be a possibility (Montenegro et al., 2008). If, as we have argued (Jones et al., 2011), it was Polynesians who made that contact in South America and returned with the sweet potato, it is not surprising that they would have chosen to bring the kumara (as opposed to other

South American plants such as corn) with them on their return voyage to Polynesia, given their experience and familiarity with other tuber crops such as taro and yam.

Unfortunately, kumara and other plant remains are rarely preserved in archaeological contexts in the Pacific, and when they are, such as in the case of the charred remains recovered from the Cook Islands (Hather and Kirch, 1991) the samples are in poor condition and aDNA is not obtainable. Historic and linguistic evidence indicate that there were likely at least two later, independent introductions of sweet potatoes to the Pacific region. The Spanish galleons were known to have transported the Meso-American varieties of camote to the Philippines from Mexico around AD 1500 and Portuguese traders introduced a third variety, batata, to Indonesia in the sixteenth century from the Caribbean and Central America. These varieties have since been transported around the Pacific region and in many places were likely to have hybridized with or replaced the originally introduced South American varieties (Yen, 1998), making it difficult to use modern genetic variation to trace the early history of the plants.

Recently, however, researchers have obtained DNA from early European herbarium samples of numerous varieties of sweet potato from across the Pacific and South and Central America (Roullier et al., 2013). As was suggested by historical and linguistic evidence (Yen, 1974; Green, 2005), they found evidence of multiple introductions of the sweet potato to the Pacific from several source regions. The first introduction, which was revealed by both chloroplast and nuclear microsatellite DNA markers recovered from very early herbarium samples (seventeenth to early twentieth century collections) came from the region around Ecuador/Peru. Included in these early samples were specimens that were collected by Joseph Banks and Daniel Solander in Tahiti and New Zealand during Cook's first voyage into the Pacific in 1769. While the Tahitian samples appear to represent a single clone, the New Zealand sample represents a totally different variety and thus Polynesians must have brought back a number of different types of plants if there was only one contact event, or they made multiple contacts with South America prior to European arrival. The recent herbarium analyses also confirmed the tripartite hypothesis, showing that samples collected from Island Southeast Asia, Madagascar, New Guinea and other western Pacific islands were not of the South American, kumara, variety, but were from the more northern sources and thus were most likely dispersed into the western Pacific from Island Southeast Asia after European contact there.

Other commensal plant species have also been the subject of genetic analyses to assess what the observed variation might suggest about their origins and implications for Pacific prehistory. These include the Polynesian Ti plant (Cordyline fruticosa) (Hinkle, 2007), paper mulberry (Broussonetia papyrifera) (Seelenfreund et al., 2010), taro (Matthews, 1990, 1996), and bottle gourd (Lagenaria siceraria) (Clarke et al., 2006; Kistler et al., 2014), but all are complicated by analyses of modern specimens and historic reintroductions. There is the possibility, however, for herbarium analyses or, in the case of the gourd and the paper mulberry, for aDNA analyses of museum artifacts or archaeological remains (Erickson et al., 2005; Moncada et al., 2013; Kistler et al., 2014).

The commensal species that travel directly on or in humans also provide exciting opportunities for tracking human migrations in the Pacific. Studies of the bacterium Helicobacter pylori (H. pylori), which is found in the stomachs of nearly half of the human population, indicate that it has been spreading across the globe with humans since the Out of Africa migrations. While normally considered harmless to most people carrying it, it has been associated with increased risk of certain types of stomach cancer and ulcers in many. Once obtained, the bacterium stays in the stomach

for life, and its rapid rate of mutation makes it ideal for tracking human migrations (Falush et al., 2003). Four major populations of *H. pylori* have been identified, two in Africa, one in East Asia and one in Europe. The East Asian strain is further subdivided into at least four sub-types: hspAmerind, hspEast Asia, hspSahul and hspMaori. The hspSahul types were identified in Australian aborigines and New Guinea Highland populations, where hspMaori was identified in Taiwanese aboriginals, in the Philippines, through Melanesia and in Polynesians from Tonga, Samoa, and New Zealand, indicating that it was probably spread with Austronesian expansion (Moodley et al., 2009). Unfortunately, sampling for *H. pylori* generally involves taking a stomach biopsy, but no doubt improved methods of DNA analysis will allow for detection in saliva or other fluids more easily obtained. Other bacteria or viruses such as the JC virus have also been used to trace population migrations in the Pacific, but researchers have not yet sampled enough populations to add further to the story of human migration (Takasaka et al., 2004; Storey et al., 2013b).

Another exciting development, which has not yet been applied to Pacific populations, is the analysis of DNA obtained from ancient calculus or dental plaque adhering to teeth (Adler et al., 2013; Metcalf et al., 2014). These analyses can provide a wealth of information regarding the health, diet and other aspects of ancient individuals and will also no doubt prove to be useful in tracing population origins, interactions and adaptations.

Ancient human DNA studies in the Pacific

In the 20 years since the commensal model was applied to studies of Pacific migrations and origins, attitudes of both scientists and indigenous communities and their leaders have begun to change. Pacific peoples are becoming more familiar with genetic studies, the methods employed and their rights as participants and collaborators in proposed research projects (Marshall, 2012; Tupara, 2012). Researchers and their funders and overseeing institutions realize that they have responsibilities to involve Pacific peoples and their views in their research projects as opposed to seeing them purely as samples (Wilcox et al., 2008). As a result, there has been a much more positive relationship in research addressing issues such as population origins and migrations, and communities are now participating in research involving human samples, both ancient and modern. In many cases, in our experience, the research questions and the projects themselves are being driven by or have been undertaken at the request of the indigenous communities (Knapp et al., 2012).

As mentioned earlier, some of the earliest studies involving aDNA obtained from archaeological skeletal remains utilized samples from the Pacific region (Hagelberg and Clegg, 1991, 1993; Hagelberg et al., 1994). These studies focused on the presence or absence of the 9 bp deletion in Polynesian and other Pacific samples. The identification of the 9 bp deletion in pre-European Polynesian remains was presented as proof that the DNA was authentic as the deletion is to be expected only in individuals, like Polynesians, of East Asian descent. In their 1993 paper, Hagelberg and Clegg tested East Polynesian samples including ancient samples, aged between 700 and 200 years old, from Hawai'i, New Zealand, the Chatham Islands and the Society Islands; one 300 year old archaeological sample from Tonga, in West Polynesia; and 10 samples associated with Lapita archaeological sites in New Britain, Vanuatu, Fiji, Tonga, and Samoa all dated to between 2700 years BP and 1700 years BP. The goal of the study was to assess the relationships between Lapita peoples and Polynesians. Of particular significance was the fact that while all of the East Polynesian samples and the 300 year old Tongan bone possessed the 9 bp deletion and some even possessed the three point mutations

defining the Polynesian motif, the Lapita associated samples did not. This was taken as evidence that "the earliest inhabitants of the central Pacific (Fiji, Tonga and Samoa) may have originated in Melanesia. If this was indeed the case it implies that the Lapita culture was carried from its Melanesian homeland into the Pacific by indigenous inhabitants of island Melanesia rather than by Austronesian-speaking migrants from Southeast Asia who settled the region en route to the eastern Pacific" (Hagelberg and Clegg, 1993:168). While the possibility of indigenous Melanesian origins for both the Lapita culture and at least admixed origins for the people who transported the Lapita culture had been suggested by several archaeologists, this result caused significant discussion and debate amongst Pacific prehistorians. Like many early aDNA studies, those of Hagelberg and Clegg (1993) were undertaken prior to the development of the now recognized and stringent aDNA contamination protocols (Cooper and Poinar, 2000). While the presence of the 9 bp deletion in conjunction with the Polynesian motif could be presented as evidence of authentic Polynesian DNA, the lack of the 9 bp deletion is what would be expected if the amplified DNA was the result of contamination from the lab or from the non-Polynesian researchers who had handled the bones in the various studies conducted on the bones prior to their aDNA analyses. Unfortunately, the results have never been replicated and our attempts to obtain aDNA from Lapita associated skeletal remains from sites across the Pacific have been unsuccessful. We have also seen that in the Pacific, even the archaeological samples that are less than 800 years old, can have an average fragment length of only about 70 bp or less due to degradation (Knapp et al., 2012) and thus the amplification of fragments of endogenous DNA of 120 bp and 228 bp in material several thousands of years old using traditional PCR methods is unlikely. The development of 'next generation sequencing' technologies, and the ability to now sequence very short segments of degraded aDNA may allow for recovery of at least mitochondrial sequences from Lapita associated human remains in the near future.

Ancient and modern DNA in Polynesians from the Gambier Islands

One of the first studies to publish aDNA using modern methods for the control of contamination and specifically designed aDNA laboratories involved analyses of both ancient and extant mtDNA from the Gambier Islands (Deguilloux et al., 2011). This study not only provided much needed information about modern mtDNA variation in East Polynesia, but presented data obtained from archaeological human remains dated to between the fourteenth and seventeenth centuries from the nearby islands of Temoe. Five of the seven aDNA samples provided hypervariable region (HVR) sequences. For the modern population, analysis of genealogical information allowed for the identification of 17 unrelated lines of descent in the Mangarevan population and samples were collected and HVR I and II and the COII/tRNA^{Lys} intergenic region were sequenced from these 17 representatives.

All of the ancient and modern sequences fell into two major lineages. The majority (15/17) of the modern samples had haplotypes that included the so called 'Polynesian motif' or Hg B4a1a1a (Trejaut et al., 2005). Similarly, six of the ancient samples also were identified as having the B4a1a1a defining mutations. The remaining samples (2/17 modern samples and 1/7 ancient) had mutations that define the Q1 haplogroup, which is of Near Oceanic origin, but had been found previously to be at low frequency across Remote Oceania and as far east as Samoa and the Cook Islands (Friedlaender et al., 2005; Kayser et al., 2006). These results extended the distribution of haplogroup Q1 eastwards and, for the first time, provided evidence that it was introduced to Polynesia prior to European arrival in the region, and most likely as part of the

founding population of the Gambier Archipelago. This study also presented the first replicated aDNA sequence data of archaeological human remains in the Pacific and demonstrated continuity between ancient and modern populations in East Polynesia.

Nineteenth century Solomon Islanders

A similar study, looking at the population continuity but more specifically focused on the impact of European contact in the Solomon Islands, was undertaken on nineteenth century hair and tooth samples found in the Duckworth Collection at the University of Cambridge (Ricaut et al., 2010). The samples were collected by Lieutenant Somerville during the British Royal Cartographic survey of the New Georgia group in the Western Solomons in 1893 and 1894. Hair samples were collected by Somerville from living people while tooth samples were taken from nearby ancestor shrines and thus their age is unknown. A total of 21 samples were analysed, consisting of teeth from 13 individuals and hair shafts (no roots) from eight individuals. Samples were sequenced for the HVS-I and the 9 bp deletion. Strict protocols to both reduce the likelihood of contamination and to identify any possible contamination were employed and all lab work was carried out in specialized aDNA facilities.

A total of 17 of the 21 samples provided mtDNA sequence that allowed haplogroups to be assigned. The majority of samples (12/17) provided DNA sequences that define haplogroup B4a or its derived subgroup B4a1a1. One sample was identified as B4, one as Q1 and three samples belonged to M27, one of which was defined as M27c. Haplogroup M27 is ancient, over 30,000 years old, and is thought to have evolved in Bougainville in the north of the Solomon Island chain but is found today in both New Britain and New Ireland, in the Bismarck Archipelago (Friedlaender et al., 2007). The haplogroups present and their frequencies are remarkably similar to the makeup of modern western Solomon Islanders. This result indicates that the significant depopulation associated with the introduction of European diseases, which occurred in many islands of Melanesia in late nineteenth and early twentieth century (Spriggs, 1997) did not appear to have a major impact on the mtDNA makeup of the population of the western Solomons (Ricaut et al., 2010). Similar continuity studies involving ancient and modern population studies will no doubt provide us with important information for reconstructing population histories in the Pacific, where depopulation due to disease and 'blackbirding' or the forced removal of many Pacific Islanders for labour in South America or Australia may have had devastating consequences for island populations and modern genetic diversity observed today (Corris, 1968; Bennett, 1976; Maude, 1981; Kirch and Rallu, 2007).

The first New Zealanders: Wairau Bar

The advent of next generation sequencing technology is opening up important opportunities for aDNA analyses in the Pacific, where DNA degradation has proven to be a major obstacle for standard polymerase chain reaction (PCR) methods. These technological developments coincided in New Zealand with a request by a Maori tribe for repatriation and reburial of human remains recovered from the archaeological site of Wairau Bar, located at the northern tip of the South Island of New Zealand. The site is a large village site, and is securely dated to 1285–1300 AD, making it one of the oldest sites in the country and one of the few with numerous burials (Higham et al., 1999; Brooks et al., 2009). The presence of large numbers of moa (Aves: Dinornithiformes) bones and eggshells indicate that the site was most likely occupied within a generation or two of initial human colonization of New Zealand, as the large, flightless birds were driven to extinction within 100 years of the arrival of Polynesians (Holdaway and Jacomb, 2000). The rich archaeological assemblage of distinctive archaic East Polynesian artifacts, many of which were found with the burials, may indeed suggest that the site represents a founding settlement from an East Polynesian homeland (Davidson et al., 2011).

Excavations at the site of Wairau Bar began in the 1940s and continued through the 1960s. As a result of these excavations, 42 individual burials were recovered and, along with numerous artifacts, were deposited in the Canterbury Museum and held in their permanent collections until 2009 when repatriation was requested by Te Runanga a Rangitane o Wairau (Rangitane), the tribal group who hold guardianship status over the Wairau Bar site. As part of an agreement between the Canterbury Museum, Rangitane and the University of Otago, full biological assessment and ancient DNA analyses were conducted on the burials prior to their re-interment at the site (Buckley et al., 2010; Knapp et al., 2012).

From a total of 19 burials deemed possible candidates for aDNA recovery (based on physical examination of the skeletal and dental material), we were able to obtain complete mtDNA genomes from two individuals (burials 1 and 2.1) and nearly complete mtDNA genomes from two others (burials 16a and 18). Burials 1 and 16a could be assigned unambiguously to mtDNA haplogroup B4a1a1a3, which had previously been identified in a modern Maori population from the east coast of the North Island of New Zealand (Benton et al., 2012). Burial 2.1 could be assigned to haplogroup B4a1a1a with two unique mutations at nucleotide positions 4917 and 8790. Burial 18 could only be identified as belonging to haplogroup B4a1a1 as identifying downstream markers were not sufficiently well covered (Knapp et al., 2012).

The analyses of the Wairau Bar burials represented the first complete mitochondrial genome sequences from any ancient samples in the Pacific. They showed that there was significant mtDNA variation in the first colonists of New Zealand, which was unexpected given previous studies of mtDNA variation in Maori that focused exclusively on variation in the HVR (Murray-McIntosh et al., 1998; Whyte et al., 2005). This has implications for calculations of the likely numbers of founding females but perhaps more importantly, these results, along with those of Benton et al. (2012) on complete mitochondrial genome sequences in modern Maori, demonstrate the need for further complete mitochondrial sequencing in the Pacific region. From these studies alone it appears that we have significantly underestimated the mtDNA diversity in Polynesia and the population histories within the Polynesian Triangle may be more complex than initially thought. It is hoped that this study also demonstrates the importance and the potential of working with indigenous descent communities for further aDNA studies in the Pacific. The potential for moving beyond mtDNA to whole genome or other multi-locus analyses of ancient remains is also exciting as these are likely to provide significant data to help us better understand human history and adaptation in the Pacific.

A 100 year old Australian Aboriginal genome

In addition to being used to sequence complete ancient mitochondrial genomes in the Pacific, next generation sequencing technologies have also recently resulted in the sequencing of a complete genome from a 100 year old lock of hair collected from a young Australian Aboriginal man in the early 1920s and stored in the Duckworth Laboratory Collections at the University of Cambridge (Rasmussen et al., 2011). This man's mtDNA belongs to a previously unidentified sub-group of haplogroup O and his Y chromosome was assigned to the K M0256* macro-haplogroup, both of which are consistent with what we might expect based on the limited available studies of contemporary Australian

Aboriginal populations (van Holst Pellekaan, 2013). Analyses indicated that this man carried a similar amount of Neanderthal DNA to most modern non-African populations and he also shared several alleles with the Denisovan genome. The divergence estimates indicate that the ancestors of Australian Aboriginals split from ancestral Eurasian populations between 75,000 and 62,000 years BP, which was separate from a later dispersal into Asia that gave rise to most modern East Asian populations. Further, the authors argue that the data suggest that Australian Aboriginal populations were isolated from all other populations, with the possible exception of Highlanders of New Guinea, for the last 15,000 to 30,000 years. A slightly more recent genome-wide SNP study on modern Aboriginal populations (Pugach et al., 2013), however, identified evidence of gene flow between India or Indian derived populations and Australian Aboriginals at some point in the mid to late Holocene, significantly before European contact. There was no evidence for similar contact in New Guinea Highland populations or in 11 populations sampled in Island Southeast Asia. It was noted, however, given that the samples studied came from the Northern Territories of Australia, further analyses of a more geographically diverse population of Aboriginal Australians was needed to further elucidate the broader impact of that contact.

With the increasing number of ancient genomes being produced, we might hope that we can start applying these methods to Pacific samples. We are currently starting to develop genome sequencing for analyses of some of our ancient Chilean samples that show phenotypic evidence of Polynesian admixture (Matisoo-Smith and Ramirez, 2010). To date, these individuals have produced mtDNA genomes that belong to Native American haplogroups, but if the Polynesian voyagers who made contact with South America were men, as we might expect if they were traders or explorers, we would not see any evidence of Polynesian mtDNA unless we found the remains of those voyagers.

Nineteenth century Botocudo Indians in Brazil — evidence of Polynesian admixture?

Interestingly, a recent publication described finding the Polynesian motif in mtDNA of nineteenth century skeletal remains from the Botocudo Indians of Brazil (Gonçalves et al., 2013). Unfortunately, the researchers did not initially sequence the entire mtDNA genome or the necessary SNPs to identify the Madagascar specific haplogroup that also contains the Polynesian motif (Razafindrazaka et al., 2010). If Gonçalves et al. (2013) had those data they could have confirmed what they rightly suggest is a likely explanation: that rather than Polynesians being present in Brazil, the remains represent individuals who were the descendants of Malagasy slaves who were brought to Brazil in the nineteenth century and who were known to have worked with the Botocudo on plantations (Razafindrazaka et al., 2010). This study, once again, highlights the importance of obtaining complete mitochondrial genome sequences from Pacific populations if we are going to understand and reconstruct population origins and interactions.

The most recent publication on the Botocudo remains reports full genome sequences from two of the skulls from the museum collection (Bot 15 and Bot 17) that indicate full Polynesian ancestry and thus reject the possible Madagascar connection (Malaspinas et al., 2014). The samples were radiocarbon dated to sometime between 1452–1510 AD and 1579–1620 AD for Bot 15 and between 1419 and 1477 AD for Bot 17. These dates indicate that the skulls were unlikely to represent the remains of living individuals picked up in Polynesia during periods of Pacific slave trade, because that was not fully established until after 1760 AD. They could, however, have been skeletal remains that were picked up in Polynesia by some early European voyager and which were subsequently

incorrectly labelled and catalogued into the Botocudo collections held in the Museu Nacional in Rio de Janeiro. No doubt further research, including isotope analyses on this collection will address these issues and shed further light on possible Polynesian contacts with the Americas.

Conclusion

While the Pacific region has a relatively long history in the short lifetime of aDNA studies, the potential for its contribution to studies of human evolution and population history is perhaps just being realized. The development of new and improved methods of aDNA extraction and constant improvements in sequencing technologies mean that many of the technical limitations researchers faced in the past are no longer impediments for aDNA studies in the Pacific. The significantly reduced costs of whole genome analyses will allow us to move beyond the single locus focus that has dominated both ancient and modern studies of Pacific populations. Genome wide data may identify a huge new array of markers to not only tease apart ancestry and population history, but also to better understand and possibly treat the health issues that disproportionately affect Pacific populations today. The potential of applying these new genomic methods to ancient remains is most exciting. Perhaps more important, however, is the fact that indigenous communities are becoming increasingly aware of the potential issues that can be addressed with aDNA and are actively engaging with researchers in DNA studies to address questions of mutual interest. In addition to working with local communities, biologists and others focusing on aDNA analyses need to work closely with researchers from other disciplines, particularly archaeology, anthropology and linguistics to take full advantage of all information available for the interpretation of results. These collaborative approaches integrating both ancient and modern genetic variation will only benefit our understanding of the history and prehistory of this vast region known as the Pacific and of the evolution and dispersal of our species.

Acknowledgements

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