Chapter 10
Australia and Oceania

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Abstract We review the evidence for the settlement of Australia and Oceania focusing on population history prior to the arrival of Europeans. Topics discussed include archaic admixture in the ancestors of Aboriginal Australians and New Guinea Highlanders and gene flow from India to Australia. We review in detail the dual-migration history of Near Oceania and the subsequent colonisation of Remote Oceania, the evidence for contact between South America and Polynesia, and make special reference to the population of Santa Cruz.

Keywords Population genetics · Demographic history · Oceania · Australia · Austronesian expansion · Archaic admixture

10.1 Geography and Ecology of Australia and Oceania

During periods of lower seas levels, such as during glacial maxima, much of Island Southeast Asia was contiguous with mainland Asia forming a continent known as Sunda. Across the Wallace Line, the island of New Guinea, Australia and Tasmania were similarly connected forming a continent known as Sahul. It is during this period of lower sea levels that the first anatomically modern humans are believed to have reached Australia and New Guinea. Though the presence of Sunda and Sahul would have reduced water crossings, it is clear that some form of boating or rafting would have been necessary as the Wallace Line was never closed. This in turn implies that the settlement of Sahul was intentional and directed, not passive (Fig. 10.1).

Despite their historical connection, Australia has a very distinct geology and ecology compared to New Guinea. Many of these differences are driven by their difference in latitude. While New Guinea is largely tropical, Australia spans more than 30° of latitude, is comparatively flat and has large areas of desert and rock

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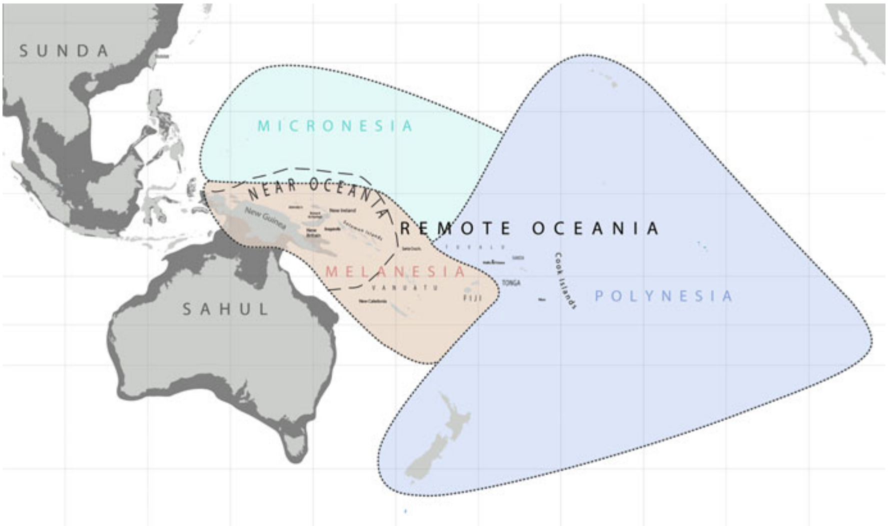

Fig. 10.1 Map indicating relative positions of Melanesia, Micronesian and Polynesia with respect to Near and Remote Oceania. Last glacial maximum boundaries of the former continents of Sunda and Sahul are indicated in dark grey. Used with permission from Duggan (2014)

(White and O'Connell 1982). There are large areas covered in grasslands and forest, though rainforests are minimal and geographically restricted, and overall rainfall is quite low and highly seasonal (White and O'Connell 1982). From the perspective of biodiversity, Australia is best known for its unique assortment of faunal species; the sharp contrast and diversity were first noted by Alfred Russell Wallace, with marsupial species, such as the kangaroo, and monotremes found almost exclusively in Australia and New Guinea.

While boundaries such as Melanesia, Polynesia and Micronesia may be more familiar, they fail to capture cohesive groups biologically, archaeologically or linguistically (Kirch 2000). These terms are increasingly replaced with Near Oceania and Remote Oceania which do reflect a shared history, both archaeologically and biologically (Green 1991) (Fig. 10.1). Near Oceania includes the island of New Guinea and surrounding islands such as those of the Bismarck Archipelago and the Solomon Islands Archipelago, extending to the islands of Makira (San Cristobal) and Santa Ana. In practical terms, this boundary represents the points beyond which islands are no longer inter-visible and it becomes necessary to complete longer crossings of open water. This likely proved to be a technological impediment as superior water craft and navigational skills would be crucial to cross beyond Near Oceania into Remote Oceania. Many of the islands in Near Oceania are quite large and topographically varied, consisting of distinct coastal regions, interior mountain ranges and rain forests. During the periods of lower sea levels these islands remained separate from Sahul; however, much of the Solomon Islands Archipelago was connected as a single larger island called Greater Bougainville or Greater Bukida

(Kirch 2000; Spriggs 1997; Walter and Sheppard 2009). With their larger size, heterogeneous landscapes and plentiful microhabitats, Near Oceanian islands generally support a larger and more varied fauna, including several endemic mammal species, and also present more arable land providing opportunities for multiple subsistence patterns (White and O'Connell 1982). Remote Oceania, in contrast, is composed of clusters of smaller islands mostly of volcanic origin or coral atolls. Beyond those previously included in the grouping of Polynesia and Micronesia, Remote Oceania also includes the islands of Santa Cruz and the Reef Islands, Vanuatu, New Caledonia and Fiji. The geology and topography of Remote Oceania result in less varied habitats and the large expanses of open water necessary to travel between islands leads to a sharp reduction in faunal diversity (Kirch 2000). There are no endemic mammals in Remote Oceania, though some have colonised the islands either as passive stowaways or as intentional introductions by humans; these islands tend to have few crops and their populations are much more dependent on the sea for sustenance.

10.2 Australia

Archaeological evidence suggests that Sahul was settled by about 45,000 years ago (kya) with sites in both Australia and New Guinea dating to this time frame and suggesting the possibility of a single migration into Sahul (O'Connell and Allen 2004; Summerhayes et al. 2010). Genetic evidence suggests that the initial inhabitants of Sahul were descended from an early Out-of-Africa migration which likely followed a southern route to Sahul and that this migration was separate from that which gave rise to modern Asian populations (Rasmussen et al. 2011; Pugach et al. 2013; Reich et al. 2011; Wollstein et al. 2010). Furthermore, with a notable exception detailed below, the populations descended from these early settlers of Sahul probably remained isolated from all other populations for 15,000–30,000 years (ky) (Rasmussen et al. 2011).

Genetic research into the history of contemporary Aboriginal Australian populations has been hampered, in part, by a deep distrust of medical and academic researchers due to a historical sense of exploitation (van Holst Pellekaan 2000). In the DNA era of molecular anthropology, there have been several studies involving mitochondrial DNA (mtDNA) and some Y-chromosome polymorphisms; however, samples sizes have often been small and population coverage unfortunately low. These studies have shown that there are limited mtDNA lineages present amongst Aboriginal Australians; some of these appear to be unique to Australia (such as haplogroups O and S), whereas others (such as haplogroups P and Q) form deep branches that are shared with New Guinea Highlanders (Ingman and Gyllensten 2003; van Holst Pellekaan et al. 1998, 2006; Huoponen et al. 2001; Redd and Stoneking 1999; Hudjashov et al. 2007). Notably, Aboriginal Australian mtDNA and Y-chromosome lineages comprise some of the deepest rooting lineages found outside of Africa, once more reinforcing the early Southern route hypothesis, and suggesting that these are among the oldest continuous populations found outside of Africa (Hudjashov et al. 2007; van Holst Pellekaan et al. 2006; Kayser et al. 2001, 2006). However, within the past few years, there have been several significant contributions to the study of Aboriginal Australian population history employing whole-genome methods. Rasmussen et al. (2011) published the first whole-genome sequence of an Aboriginal Australian, analysing a museum specimen of hair collected approximately 100 years previously; this hair was clearly collected well after the first European settlement of Australia in 1788 but pre-dates most recent admixture with Europeans. Despite its relatively young age, this hair sample suffered from many problems associated with ancient DNA, such as short fragment lengths and deamination at the ends of each fragment (Rasmussen et al. 2011; Pääbo et al. 2004); however, genome coverage of 6.4X was achieved nevertheless. The mtDNA and Y-chromosome haplogroups for the sample were consistent with lineages already found in Australia, suggesting that there were no issues with contamination despite being a heavily handled museum specimen, and also providing some preliminary indication that there was no recent European admixture in this individual (Rasmussen et al. 2011).

In a Principle Components Analysis (PCA) comparison with populations from across the globe, the ancient Aboriginal Australian genome clustered with samples from the Highlands of Papua New Guinea, further supporting their shared ancestry, and was in next closest proximity with a population from Bougainville (an island politically part of Papua New Guinea but geographically part of the Solomon Islands archipelago), and the Aeta, a ‘Negrito’ population from the Philippines (Rasmussen et al. 2011). These findings are further supported by an ADMIXTURE analysis in which the Aboriginal Australian genome is best represented as having primarily near equal Highland New Guinea and Bougainville-like ancestries (Rasmussen et al. 2011).

With respect to population history, one of the more interesting results from Rasmussen et al. (2011) is the estimation of population split times calculated from linkage disequilibrium and allele frequencies between pairs of populations. With their method of estimation, Rasmussen et al. (2011) concluded that the ancestors of Aboriginal Australians and New Guinea Highlanders have been largely separated from Eurasian populations since 62–75 kya (with some cases of admixture described below), while European and Asian populations split only 25–38 kya.

The Aboriginal Australian genome paper was further augmented by the publication of genotyping results from 12 modern Aboriginal Australians (Pugach et al. 2013). Apart from a greater sample size, the genotyping study also benefitted from a greater array of Asian and Southeast Asian populations for comparison. An earlier study had a similar design but was more limited in terms of insights into Aboriginal Australian history, as almost all of the Aboriginal Australians included were known to have recent, mostly European, admixture and in fact had on average only 64% Aboriginal Australian ancestry (McEvoy et al. 2010). Pugach et al. (2013) confirmed the shared ancestry of Aboriginal Australians and New Guinea Highlanders, and moreover showed that the Mamanwa, a ‘Negrito’ group from the Philippines—similar to the Aeta mentioned above—were equally related to both Aboriginal

Australians and New Guinea Highlanders, suggesting they had once been part of the same early Southern route population and that the Mamanwa split from this group before the separation of Australian Aboriginals and New Guinea Highlanders (Pugach et al. 2013). Curiously, in an examination of linkage disequilibrium patterns, it was observed that the patterns of linkage disequilibrium in the Mamanwa suggested that they had undergone a rather recent bottleneck and the New Guinea Highlanders a more ancient bottleneck (Pugach et al. 2013). The presence of an ancient bottleneck in New Guinea Highlanders but absent in the Mamanwa suggested that this bottleneck occurred after the split of the Mamanwa lineage from New Guinea Highlanders and Aboriginal Australians. The absence of evidence for such a bottleneck in Aboriginal Australians suggests that either they were not affected by the same event as the New Guinea Highlanders, i.e. the bottleneck in New Guinea Highlanders occurred after the split from Aboriginal Australians, or that there was less isolation in Aboriginal Australian populations compared to New Guinea Highlanders (Pugach et al. 2013).

Indeed, it seems Aboriginal Australians were not as isolated as New Guinea Highlanders and instead, around 4230 years ago, received an influx of genes from a population most closely related to present-day Dravidian speakers in Southern India (Pugach et al. 2013). This finding was confirmed through several different analyses, including PCA, ADMIXTURE and TreeMix analyses, which are all calculated under different algorithms and methods and yet all demonstrated clear signs of admixture between Aboriginal Australians and southern Indians (Pugach et al. 2013). The TreeMix analysis estimated the amount of gene flow from India to represent approximately 11% of the Aboriginal Australian genome (Pugach et al. 2013) (Fig. 10.2). This finding, while surprising, has further support. At approximately the same time as this admixture is estimated to have occurred, several changes take place in the Australian archaeological record: the stone tool technology changes, as does the manner in which plants are processed, and the dingo makes its first appearance (Pugach et al. 2013 and references therewithin). Beyond archaeological evidence, there had been genetic hints of this admixture event as well; the authors of the ancient Aboriginal Australian genome study (Rasmussen et al. 2011) noted a tiny component of Indian ancestry in their ADMIXTURE analyses as well but dismissed it as an artefact where no appropriate ancestral population was provided to the algorithm (understandably so when working with a single representative sample). And previous studies on both mtDNA and Y-chromosome variation in Australia found closer than expected affinities between Aboriginal Australians and the Indian subcontinent (Redd and Stoneking 1999; Redd et al. 2002).

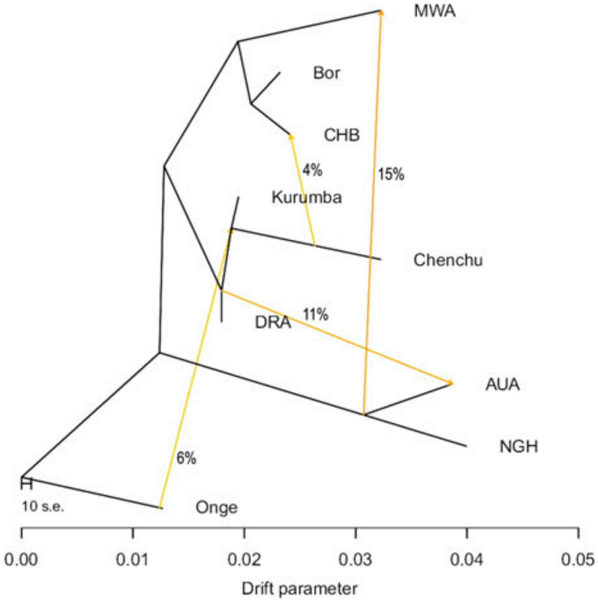

Fig. 10.2 TreeMix analysis of population relationships. Percentages indicate the contribution from source to recipient populations. Modified with permission from Pugach et al. (2013)

10.3 Oceania

10.3.1 Near Oceania in the Pleistocene

Many of the early archaeological sites in New Guinea are found in the southeast of the island. The oldest sites date to approximately 45 kya; however, there are sites of a similar age found on the islands of New Britain and New Ireland in the Bismarck Archipelago, suggesting that there was further rapid and intentional movement across the strait which separates the islands from New Guinea (Summerhayes et al. 2010; Leavesley et al. 2002; Leavesley and Chappell 2004; Groube et al. 1986). These populations also managed to spread at least as far as Buka, at the northernmost tip of the Solomon Islands Archipelago, and Manus in the Admiralty Islands by 28 and 12 kya, respectively (Wickler and Spriggs 1988; Fredericksen et al. 1993) (Fig. 10.3). Curiously, despite ample evidence of settlement in Buka and given the contiguous nature of Greater Bougainville including Buka, there are no other archaeological sites of similar antiquity in the Solomon Islands. The only other evidence of human habitation in the Solomon Islands prior to the arrival of the Austronesian expansion, to be discussed in Sect. 10.3.2, is a site on the island of Guadalcanal dated to approximately 6 kya (Roe 1993).

Much of the existing genetic evidence from Near Oceania comes from uniparental markers which seem to indicate that, despite a common ancestry, the early settlers formed populations which were largely isolated. From the maternal perspective, these older populations are characterised by autochthonous haplogroups such as Q, P, M27, M28 and M29, some of which show extreme geographic specificity

Fig. 10.3 Map indicating relative location of populations referred to in the text

(Friedlaender et al. 2005, 2007; Merriwether et al. 2005; Duggan et al. 2014). Studies of mtDNA indicate that autochthonous haplogroups are often exclusive to particular populations or regions. Moreover, specific sequences (haplotypes) within these haplogroups are rarely shared between populations and are frequently defined by multiple mutations, suggesting prolonged periods of separation have allowed drift to occur (Friedlaender et al. 2007; Duggan et al. 2014). Frequencies of these haplogroups are higher in New Guinea, particularly in the Highlands which appear to have been largely unaffected by the Austronesian expansion, as well as the Bismarck Archipelago and Bougainville, in keeping with archaeological data which suggests that these areas have deeper settlement histories (Friedlaender et al. 2005, 2007; Merriwether et al. 2005; van Oven et al. 2014; Duggan et al. 2014). Even within the island of New Guinea there are large differences observed between populations in the highlands and the coast, attributable to the effect of the Austronesian expansion on coastal regions (Stoneking et al. 1990; Redd et al. 1995; Redd and Stoneking 1999; Kayser et al. 2006; van Oven et al. 2014; Ingman and Gyllensten 2003; Tommaseo-Ponzetta et al. 2002).

While many populations show a strong impact of the Austronesian migrants in the maternal line, discussed further in Sect. 10.3.2, Y-chromosome haplogroups throughout Near and Remote Oceania are generally dominated by those of Near Oceanian origin (Delfin et al. 2012; Scheinfeldt et al. 2006; Kayser et al. 2000, 2001, 2003, 2006, 2008a; van Oven et al. 2014; Hagelberg et al. 1999). Y-chromosome studies to date have been primarily based on SNP or STR typing and thus cannot offer the same level of resolution as most whole mtDNA genome sequence studies. However, it has been observed that Y-chromosome diversity is particularly low in the highlands of New Guinea, while in Remote Oceania, where a single mtDNA haplogroup of Asian origin reaches near fixation, the Y-chromosome diversity is considerably higher and Near Oceanian haplogroups are found at, on average, 66% frequency (Kayser et al. 2003, 2006; Mona et al. 2007; Hagelberg et al. 1999). These differences have been largely attributed to cultural practices and the customs of patrilocality and potentially polygyny in Papuan societies, versus a probably matrilocal residence pattern in Austronesian societies (Feil 1987; Jordan et al. 2009).

To date, studies of genome-wide data in Near and Remote Oceania are limited. One study of autosomal STR variation suggested that populations are genetically distinct and that population differentiation is driven less by linguistic classification than by island size and topographical complexity (Friedlaender et al. 2008). However, differentiation can also be observed between groups in the same geographic regions which are separated by languages, as has been observed in the Southern Highlands of Papua New Guinea between Huli and Mendi-Kewa speaking populations (Wollstein et al. 2010). We will discuss genome-wide data in more detail in Sect. 10.3.3.

10.3.2 The Austronesian Expansion and the Colonisation of Remote Oceania

Around 3.5 kya, more than 40 ky after the initial Papuan settlement, a new cultural complex appears in the Near Oceanian archaeological record (Specht and Gosden 1997; Summerhayes 2001). First identified in the Bismarck Archipelago and synonymous with a particular style of pottery, the Lapita Cultural Complex is believed to have arrived with migrants whose ancestors left Taiwan approximately 5 kya and travelled throughout ISEA before reaching Near Oceania (Kirch 2010; Ko et al. 2014; Gray et al. 2009). The migrants who arrived in the Bismarck Archipelago are believed to have spoken Proto-Oceanic, a language which soon after began to diversify and spread and is the ancestral language of all Austronesian languages spoken in Near and Remote Oceania (with some exceptions in Micronesia) (Lewis et al. 2013; Gray et al. 2009). Compared to the Pleistocene settlers of Near Oceania, the Austronesian migrants are thought to have had better sailing technology which allowed them to spread more rapidly and also cross larger distances over water. Indeed, the Austronesian expansion colonised Remote Oceania, and potentially much of the Solomon Islands, within approximately 2.5 kya (Kirch 2010; Wilmshurst et al. 2011).

The Austronesian expansion is closely associated with a particular mtDNA lineage—the B4a1a1 lineage—which reaches near fixation in Remote Oceania (Melton et al. 1995; Redd et al. 1995; Kayser et al. 2006; Hagelberg et al. 1999; Duggan et al. 2014). The B4a1a1 lineage is found in high frequencies in almost all Near Oceanian populations, even Papuan speaking populations, with the exception of New Guinea Highland populations and some populations in the Bismarck Archipelago (Kayser et al. 2006, 2008a; Delfin et al. 2012; van Oven et al. 2014; Duggan et al. 2014; Friedlaender et al. 2007). A particular mutation on the B4a1a1 lineages, an A→G transition at position 16,247, became known as the 'Polynesian motif' due to its extreme frequency in Remote Oceania and was synonymous with the Austronesian spread in Oceania (Melton et al. 1995). Reconstructed time estimates for the first appearance of this mutation have generated the suggestion that it was in fact present in Near Oceania prior to the arrival of the Lapita cultural complex (Soares et al. 2011). However, the estimates for haplogroup ages have large confidence intervals and these intervals do include the archaeological time estimate for the arrival of Lapita in Near Oceania (Soares et al. 2011; Specht and Gosden 1997). Also, the transition known as the 'Polynesian motif' has been found to be unstable; the derived allele appears to have arisen only a single time but has undergone multiple independent back mutations on multiple lineages and was found to have elevated levels of heteroplasmy, which likely confounds any attempt to date the lineage (Duggan and Stoneking 2013). Following the documentation of the instability of the derived 16,247 allele, the phylogeny of the B4a1a1 lineage underwent major revisions and the diagnostic mutations for many haplogroups were modified (PhyloTree Build 16, van Oven and Kayser 2009). The rapid expansion of Austronesians throughout Oceania is evident in the B4a1a1 lineage, where there is remarkably little diversity in haplogroups between populations. Identical whole mtDNA haplotypes can be observed between populations separated by thousands of kilometres (Duggan et al. 2014). This extensive sharing and the low observed haplogroup diversity leads to two conclusions: first, Austronesian women admixed extensively with existing Near Oceanian populations and second, the people involved in the Austronesian expansion through Oceania were small in number and/or very closely related. Their movement throughout Oceania occurred so rapidly and recently that mutations did not have time to develop on their lineage during the expansion nor have the populations been settled long enough for drift to occur.

While Austronesian mtDNA is clearly dominated by the B4a1a1 lineage, there is no single dominant Austronesian Y-chromosome lineage, though there may be population- or island-specific dominance of a given lineage (Hurles et al. 2002; Kayser et al. 2000, 2006; Scheinfeldt et al. 2006; Hagelberg et al. 1999; Delfin et al. 2012). In fact, the presence of Austronesian Y-chromosomes in Oceania is not nearly as extreme as is the case with Austronesian mtDNA. Approximately 94% of Remote Oceanian mtDNAs belong to the single B4a1a1 lineage while approximately 65% of Remote Oceanian Y-chromosomes are of Near Oceanian origin and belong to multiple lineages (Kayser et al. 2006). Thus, while the settlement of Remote Oceania was clearly achieved by Austronesian peoples with Lapita cultural practices and Oceanic languages, Near Oceanian men were undoubtedly involved as well. As methods for the study and phylogenetic resolution of Y-chromosomes become more advanced, it will become possible to conduct studies of male-mediated diversity and origin similar to those which are currently achieved with whole mtDNA genomes (Karafet et al. 2014; Lippold et al. 2014). These developments should shed further light on the paternal history of Oceania and may illuminate additional patterns of diversity or gene flow.

10.3.3 Duality of Oceanian Heritage

Uniparental markers provide ample evidence for dual-ancestry in Oceanian populations, however, given their unique inheritance patterns and lack of recombination, it can prove difficult to estimate time since admixture and accurate individual ancestry proportions from mtDNA and Y-chromosome data. Genome-wide data are a much richer source of information on ancestry and admixture and while data is still sparse, the existing genome-wide studies of Oceanian populations have already provided great insights.

Studying populations primarily from Northern Island Melanesia and analysing insertion/deletion polymorphisms and STR variation, Friedlaender et al. (2008) concluded that Oceanian populations did have heritage from both Papuan and Asian sources but that the Austronesian signal was very low and present almost exclusively in Austronesian-speaking populations. This work is notable for its extensive sampling in the Bismarck Archipelago and Bougainville. The findings of higher genome-wide Papuan ancestry validate earlier mtDNA and Y-chromosome work in the area and corroborate with archaeological evidence which decisively points to early and prolonged Papuan settlement in the area prior to the arrival of the Austronesian expansion (Scheinfeldt et al. 2006; Friedlaender et al. 2007, 2008; Summerhayes 2007).

The other two genome-wide studies focused on the ancestry of Polynesian populations. In a study of STR variation, it was concluded that Polynesians carry, on average, 79% Austronesian and 21% Papuan ancestry (Kayser et al. 2008b). A later study working with genome-wide SNP data and accounting for ascertainment bias in the SNP selection, adjusted this figure to 87% Austronesian and 13% Papuan ancestry (Wollstein et al. 2010). Both of these estimates suggest a greater proportion of Austronesian than Papuan ancestry but not to the same extreme as observed in mtDNA data, further validating the value of genome-wide ancestry assessments (Kayser et al. 2006). In addition to investigating Polynesian ancestry, Wollstein et al. (2010) concluded that Fiji represented a population which had undergone an additional admixture event with Near Oceania. Fijian ancestry was estimated to be approximately 65% Polynesian and 35% Papuan (Wollstein et al. 2010). The initial admixture event between Austronesians and Papuans to produce the Polynesian ancestry was estimated to have occurred approximately 3 kya, which is very close to the estimate of 3.4 kya for the arrival of Austronesians in Near Oceania from archaeological records, while the second admixture between the ancestors of Fijians and Near Oceanians to produce a modern Fijian ancestry occurred sometime after the ancestors of Polynesians had already left Fiji (Wollstein et al. 2010).

10.3.4 *Evidence for Contact Between South America and Polynesia*

The two ancestral components, Near Oceanian and Austronesian, are well supported archaeologically, linguistically and biologically; however, there has been considerable speculation of contact between Remote Oceanian populations and South American populations. Such hypotheses originated to account for the presence of sweet potato (Roullier et al. 2013) and bottle gourds (Green 2000) from South America in Oceania. New research has demonstrated that the population of Rapa Nui (Easter Island), while predominantly Polynesian, have signatures of ancestry from both Native Americans and Europeans in their genomes (Moreno-Mayar et al. 2014). These signals were absent from other Polynesian samples examined and while the Native American proportion was, on average, less than the European proportion of the Rapa Nui genome (8% and 16%, respectively), the Native American component was composed of shorter tracts of inheritance and was more evenly distributed across the population suggesting that it reflected an older admixture event that the European proportion (Moreno-Mayar et al. 2014). The Native American admixture was estimated to have occurred between AD 1280–1425, well before the first European contact with Rapa Nui in AD 1722, and the European admixture was estimated to have occurred between AD 1850–1870, contemporary with European mediated slave trade in the Pacific (Moreno-Mayar et al. 2014 and references therewithin). This genomic signature has two possible explanations: South Americans sailed to Rapa Nui and intermixed with the local population; or Polynesians sailed to South America and then returned to Rapa Nui either carrying with them individuals of South American ancestry or the products of gene flow in South America. While the second scenario involves sailing greater distances, the feat of settling all the Pacific islands is formidable and there is no reason to believe that the Austronesian Expansion should have stopped there; the coast of South America is closer to Rapa Nui than either New Zealand or the Hawai'ian Islands, the other two points of the Polynesian Triangle. Further evidence for Polynesian contact with South America may come by way of Brazil. Two skulls associated with the Botocudo population from the Museu Nacional of Brazil were found to be of Polynesian origin (Malaspinas et al. 2014). While radio isotopes were unable to unequivocally confirm that the skulls pre-dated European contact with Polynesia, they do suggest that these two Polynesian individuals made their way not only to South America, but also either across the Andes or around the Cape to eastern Brazil (Malaspinas et al. 2014).

10.3.5 *The Unique History of Santa Cruz*

Santa Cruz occupies a distinctive position in the history of Oceania. It is part of a group of islands located beyond the boundary of Remote Oceania, approximately 400 km past the main chain of the Solomon Islands. Archaeological evidence suggests that Santa Cruz was colonised 3 kya by Lapita people who engaged in obsidian trade with populations from New Britain in the Bismarck Archipelago over a period of several hundred years (Sheppard et al. 2015). Curiously, it appears that the people voyaging between New Britain and Santa Cruz did so directly, 'leapfrogging' over the rest of the Solomon Islands, which lacks evidence of any contemporary Lapita settlements (Sheppard and Walter 2006). Linguistically, the languages of the Temotu family found in Santa Cruz and the nearby Reef Islands also have a unique history. Once believed to be the easternmost Papuan languages, they are now recognised as part of the Oceanic family of Austronesian though they are more distantly related to other Oceanic languages and are thought to have separated from the rest of the Oceanic family soon after the diversification of Proto-Oceanic (Ross and Næss 2007).

Curiously, the mtDNA and Y-chromosome lineages found in Santa Cruz contrast greatly with the rest of Remote Oceania. Available genetic data on Santa Cruz is restricted to mtDNA and the Y-chromosome, but nonetheless these exhibit interesting patterns. Despite an archaeological record which suggests no pre-Lapita settlement, the mtDNA and Y-chromosome composition of Santa Cruz has a greater proportion of Near Oceanian ancestry than any other population in Remote Oceania (Delfin et al. 2012; Duggan et al. 2014; Friedlaender et al. 2002). In fact, the proportion of Near Oceanian ancestry in Santa Cruz is greater than that of many Near Oceanian populations, particularly with regard to mtDNA ancestry (Fig. 10.4) (Delfin et al. 2012; Duggan et al. 2014). Furthermore, this Near Oceanian ancestry is present as multiple haplotypes within diverse haplogroups, which suggests that this elevated Near Oceanian component is not the result of a recent bottleneck or population replacement (Duggan et al. 2014). There are several possible explanations for this observation, all detailed in Delfin et al. (2012). One of the possibilities is that there was in fact a pre-Austronesian settlement of Santa Cruz; this scenario was recently tested by comparing empirical mtDNA data from Santa Cruz and New Britain to simulated data for a variety of settlement histories. The results suggested that a time depth of greater than 3 kya for the settlement of Santa Cruz was possible, but did not completely exclude the possibility of a Lapita-age colonisation (Duggan et al. 2014).

The apparent disconnect between archaeology, genetics and linguistics in Santa Cruz also calls into question the progression of settlement into Remote Oceania. The mtDNA genetic profile of Santa Cruz is strikingly different from other Remote Oceanian populations (Duggan et al. 2014); this makes it unlikely that it was a seed population for the colonisation of islands further to the east. Archaeology suggests that Vanuatu and New Caledonia were settled by Lapita people at approximately the same time as Santa Cruz (Walter and Sheppard 2009; Sheppard and Walter 2006). Comparable datasets from these regions could clarify whether their composition is similar to Santa Cruz or, if they are different in comparison with Santa Cruz, could they possibly be the seed populations for Remote Oceanian populations. If Vanuatu and New Caledonia do appear more similar to other Remote Oceanian populations, it could further proposed model for the settlement of Santa Cruz whereby it was first colonised by Lapita people but incurred extensive gene

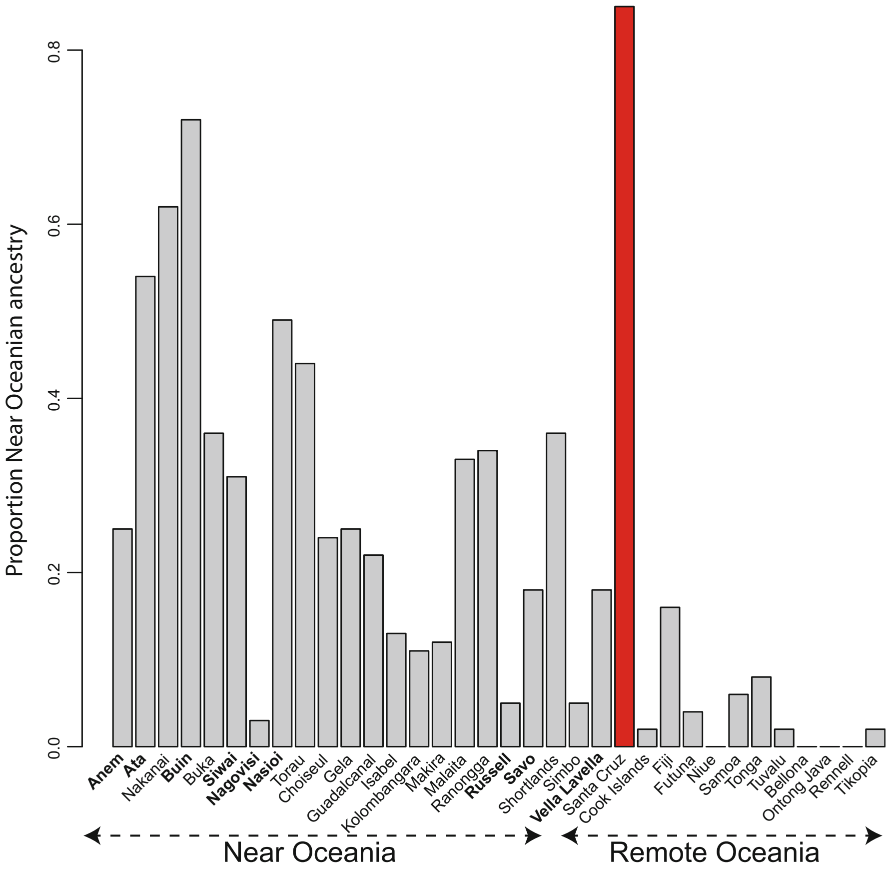

Fig. 10.4 Relative proportion of Near Oceanian ancestry, based on mtDNA data. Papuan speaking populations are identified in bold, the extreme Near Oceanian ancestry of Santa Cruz is highlighted in red. Data source: Duggan et al. (2014), supplemental Table 2

flow and possible secondary settlement during the obsidian trade (Delfin et al. 2012). Additionally, genome-wide data could elucidate the genetic history of Santa Cruz with greater precision in determining ancestry composition and dating the time of admixture events(s).

10.4 Archaic Admixture in Australia and Oceania

Thus far, we have only discussed the ancestry of Australia and Oceania as they relate to modern human populations. Ancient DNA—in particular, admixture signals from archaic hominins—is another source of ancestry information. All modern human populations outside of Africa received a small portion of their genome, 1–2% on average, from Neanderthals (Green et al. 2010; Prüfer et al. 2014). However, when a second archaic hominin more closely related to Neanderthals than humans, 'Denisovans', was identified, evidence of introgression between modern humans and Denisovans was found only in New Guinea Highlanders and Bougainvilleans (Reich et al. 2010). In a follow-up study, 33 Asian and Oceanian populations were screened for evidence of Denisovan admixture with genome-wide SNP data (Reich et al. 2011). This work concluded that there was evidence of admixture in New Guinea Highlanders, Aboriginal Australians, Fijians, Polynesians, populations from the Nusa Tenggaras and Moluccas in eastern Indonesia, and the Mamanwa 'Negrito' group and Manobo populations of the Philippines (Reich et al. 2011) (Fig. 10.5). New Guinea Highlanders and Aboriginal Australians have approximately the same amount of Denisovan ancestry, consistent again with their origin from a common ancestral population. The average Denisovan ancestry in Mamanwa is only about one half of that present in New Guinea Highlanders and Aboriginal Australians. However, this ancestry is best modelled whereby a common ancestral population of New Guinea Highlanders, Aboriginal Australians and Mamanwa incurs gene flow from a Denisovan population, and subsequent to the split of Mamanwa from the ancestral population of New Guinea Highlanders and Aboriginal Australians, the Mamanwa incur significant admixture with one or more groups not carrying any Denisovan ancestry (Reich et al. 2011). Furthermore, the Denisovan ancestry of the Fijian, Polynesian and Indonesian populations from the Nusa Tenggaras and Moluccas is derived from a more recent admixture event between incoming Austronesian populations and existing Papuan populations (Reich et al. 2011; Xu et al. 2012). Denisovan ancestry was also found in the ancient Aboriginal Australian genome sequence (Rasmussen et al. 2011), albeit at slightly lower levels than previously estimated in New Guinea Highlanders (Reich et al. 2010).

10.5 Conclusions

In summary, existing genetic data suggest a very dynamic history of population migration and admixture within Australia and Oceania. Descendants of an initial early migration out of Africa, the ancestral population of Aboriginal Australians, New Guinea Highlanders and the Philippine Mamanwa admixed with Denisovans, an archaic hominin population. This ancestral population then split and each division incurred separate and unique admixture events: the Mamanwa with one or more groups related to modern Han populations, Aboriginal Australians with a population from the Indian subcontinent, and with the exception of some populations isolated in the Highlands of New Guinea, almost all Papuan populations experienced significant gene flow with Austronesian migrants.

Through the study of modern populations, it is possible to discern how modern populations are unique but also deeply related to each other. Many of these discoveries have happened only recently due to technological improvements in obtaining genetic data and in statistical modelling and methodology. Recent work on Southeast

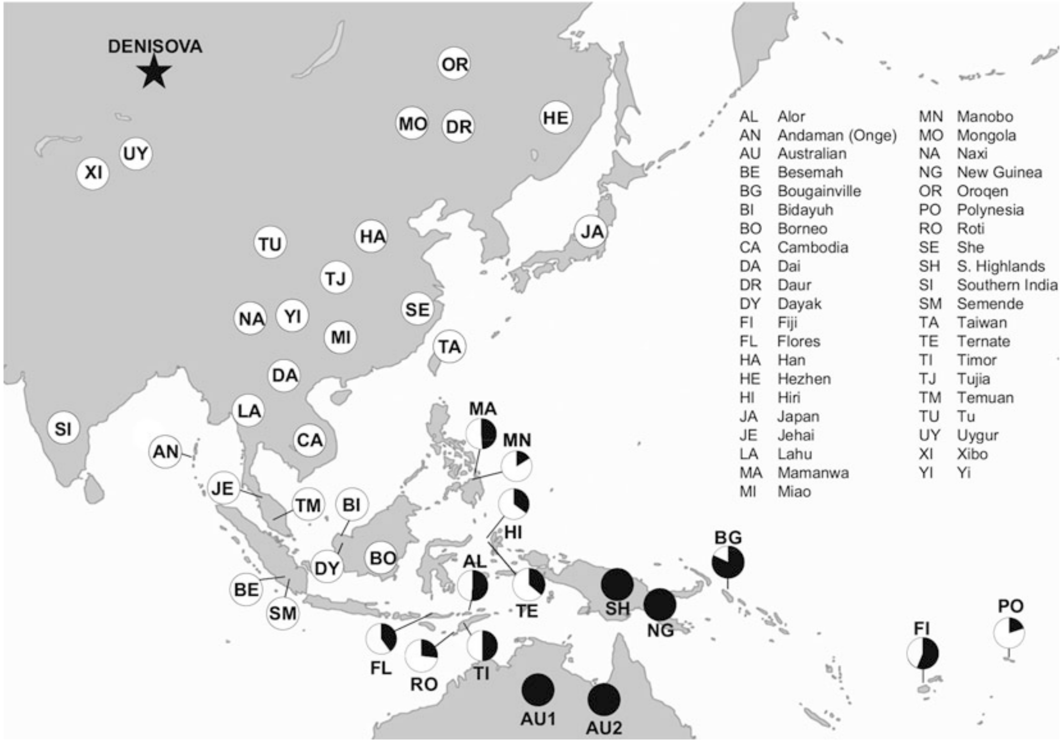

Fig. 10.5 Denisovan ancestry as a fraction of that found in New Guineans. Used with permission from Reich et al. (2011)

Asian populations identifies the potential of yet another admixture or population expansion event which has not been previously detected through archaeology or linguistics (Lipson et al. 2014). Despite sound linguistic reconstructions (Gray et al. 2009), the genetic origin of the Austronesian expansion in Taiwan was only recently confirmed thanks to the discovery of an 8000 year old skeleton ancestral to Taiwanese aboriginal populations, and sophisticated modelling which identified an entry into Taiwan at approximately 6 kya and departure of the Austronesian expansion from Taiwan around 4 kya (Ko et al. 2014). Future work in Oceania should shed light on additional population migrations and interactions as well. We are particularly hopeful that as technologies continue to improve, additional results from ancient DNA, such as the recent study of ancient Maori (Knapp et al. 2012), as well as genome-wide studies of large numbers of SNPs or even whole-genome sequencing will investigate areas of Near Oceania such as the Solomon Islands (comparatively under-studied and curiously bereft of archaeological sites), as well as non-Polynesian populations in Remote Oceania (i.e. Vanuatu and Near Caledonia). These populations will be of particular interest and may provide answers to lingering questions as to the settlement and provenance of some Oceanian populations.

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