The Human Genetic History of Oceania: Near and Remote Views of Dispersal

Review

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The human history of Oceania is unique in the way that it encompasses both the first out-of-Africa expansion of modern humans to New Guinea and Australia as well as the last regional human occupation of Polynesia. Other anthropological peculiarities of Oceania include features like the extraordinarily rich linguistic diversity especially of New Guinea with about 1,000 often very distinct languages, the independent and early development of agriculture in the highlands of New Guinea about 10,000 years ago, or the long-term isolation of the entire region from the outside world, which lasted as long as until the 1930s for most of the interior of New Guinea. This review will provide an overview on the genetic aspects of human population history of Oceania and how some of the anthropological peculiarities are reflected in human genetic data. Due to current data availability it will mostly focus on insights from sex-specifically inherited mitochondrial DNA and Y-chromosomal DNA, whereas more genome-wide autosomal DNA data are soon expected to add additional details or may correct views obtained from these two, albeit highly complex, genetic loci.

Introduction

The definition of Oceania differs according to source. Historically, Oceania is divided into Melanesia (Greek for 'black islands'), i.e. New Guinea and the surrounding islands as well as the Solomons, New Caledonia, Vanuatu, Fiji; Polynesia (Greek for many islands), i.e. islands roughly in a triangle with its corners at Hawaii, Easter Island and New Zealand; and Micronesia (Greek for small islands), i.e. islands north of northern Island Melanesia and northwest of Polynesia. However, the term Melanesia (and, albeit less so, Micronesia) often is criticized when not strictly referring to the geographic region because its inhabitants do not represent one (e.g. cultural) entity, whereas the historically termed Polynesians have been shown to represent a homogeneous group of people. Hence, a different classification of Oceania into a western part termed Near Oceania and an eastern part called Remote Oceania has been introduced [1] also to take into account inter-island distances — small distances between islands make them easier to reach in Near Oceania while large distances make them difficult to reach in Remote Oceania, which has important consequences for the human settlement history. Near Oceania comprises mainland New Guinea with surrounding islands such as the Bismarcks, up to the main Solomon Islands in the east, whereas Remote Oceania includes all islands further eastward, i.e. Vanuatu, New Caledonia, Fiji, as well as Micronesia and Polynesia. Historically, Australia is not considered part of Oceania,

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and is sometimes referred to as Australasia together with New Zealand (sometimes also with New Guinea); for the purpose of this review I will include Australia as well.

In a simple model, the human history of Oceania before European contacts can be characterized by two major periods of population expansions into the area — early movements of people into Sahul (the former continent comprising New Guinea and Australia) during the Pleistocene, and then a much later period of human migration(s) in the mid-Holocene finally reaching Remote Oceania; both episodes will be discussed in separate sections. Although the human history of Oceania is expected to be more complex than implied by this simple two-phase settlement model [2], most currently available genetic data have been employed under such a scenario.

Pleistocene Occupation of Oceania: Into Sahul

According to archaeological evidence, New Guinea and Australia were settled by anatomically modern humans very early in human history; sites from around 50 thousand years ago (kya) are known from Australia [3], and of around 40 kya from New Guinea [4], although the exact timing is still debated [5]. It often is assumed that the occupation of Sahul represents the results of the first exodus episode of modern humans out of Africa [6,7]. The time period of at least 40 kya of potentially shared contacts between New Guinea and Australia, until both regions became separated by rising sea levels about 8 kya, might seem to suggest that the human occupation of Sahul stems from a common origin. This view may be supported by a number of at least superficially similar phenotypic traits, such as their exterior appearance, between these two populations. However, many of these traits are expected to be influenced by selective processes that can be of independent origin in different geographic regions while resulting in similar phenotypic outcomes because of similar environmental factors to which people genetically adapted. However, population-based mitochondrial DNA (mtDNA) studies, mostly based on the non-coding control region, either found no similarities between Aborigines from New Guinea and Australia (Figure 1), and distant positioning of both groups in phylogenetic analyses, or they revealed that, although most of the mtDNA variation differs between both regions (Figure 1), some very few Australians clustered closer to New Guineans than to any other worldwide samples [8–10]. Similar results were obtained from more recent studies using whole mtDNA genomes [11,12]. However, one study based on complete mtDNA genomes and using lineage-based (but not population-based) phylogenetic analyses argued for a single founder group having settled in Australia and New Guinea about 50 kya [13]. Studies on the non-recombining part of the Y-chromosome (NRY) revealed that no major lineages are shared between Australia and New Guinea [14–16] (Figure 2). Moreover, the major Australian NRY lineage (C-DYS390.1del/M347) is not only restricted to but also appears highly frequent across Australia [13,14,17,18]. Together with low diversity of lineage-associated Y-chromosomal short tandem repeat (Y-STR) haplotypes, this lineage

Figure 1. Distribution of mitochondrial DNA (mtDNA) lineages in human populations across Oceania.

Only those lineages currently known from Oceania are shown together with their frequencies in East Asia and Southeast Asia (excluding eastern Indonesian islands). Lineages are defined by one or several slowly evolving single nucleotide polymorphisms (also referred to as haplogroups). Assumed geographic origins are indicated as follows: AS, Asian origin; EI, eastern Indonesia origin, haplogroups with assumed affiliation to the expansion of Austronesian speakers (Aus) are indicated separately; NG, New Guinean (Near Oceania) origin, haplogroups with subregional northern Island Melanesian (NIM) origin are indicated separately; Au, Australian origin. Population data are grouped according to geographic subregions with sample size provided in brackets and language group affiliations indicated by one asterisk for only or mostly Austronesian-speakers, and two asterisks for only or mostly non-Austronesian (Papuan) speakers. Data are taken from the literature as follows: for East Asia, Southeast Asia, West and Central Polynesia [16], for the Admiralty Islands [43], for North and Northwest Australia [9,10,13], for Southeast Australia [10], for Papua New Guinea (PNG) inland and coast/Island, the Bismarcks, and Fiji [16,34], for Southwest New Guinea (SWNG) [34,85], and for Bougainville,

the Solomon Islands, Santa Cruz, Vanuatu, and New Caledonia [34]. Notably, the M15 mtDNA haplogroup was called M13 by Hudjashov *et al*. [13], who seem to have overlooked that this label was used before for another branch of the mtDNA phylogeny; M7c3c refers to the previously called M7c1c haplogroup but was updated based on complete mtDNA genome information, for details on mtDNA phylogeny, including haplogroup nomenclature, see PhyloTree (http://www.phylotree.org) [86].
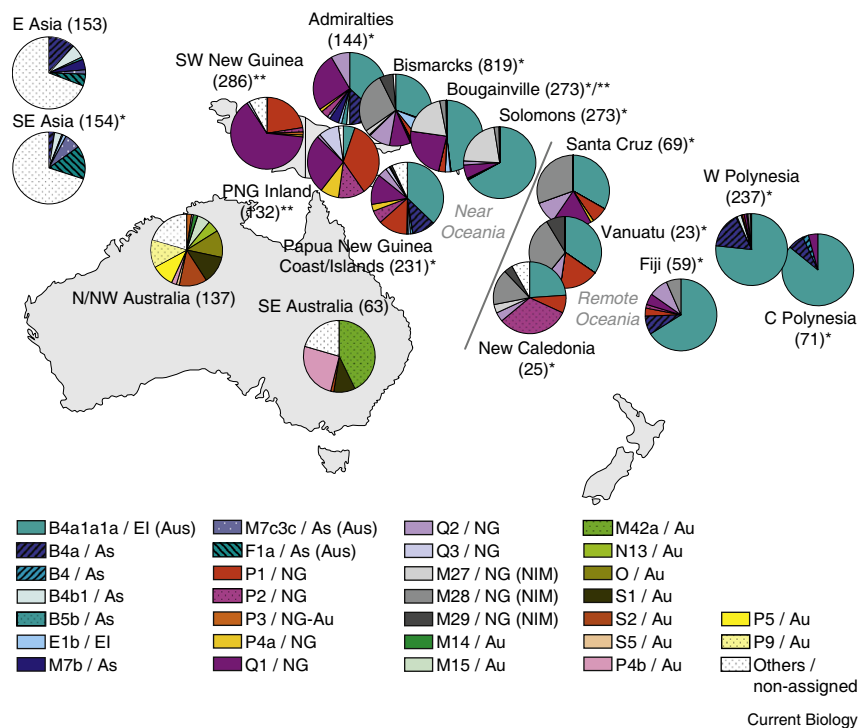
provides evidence for a somewhat recent founder or bottleneck event in the Australian history as well as subsequent population expansion [14]. This may be in line with archaeological data indicating a mid-Holocene 'intensification' — beginning about 4 kya new tool types occur, many sites were occupied for the first time, whereas other sites show a higher density of materials [19]. However, the reduced Australian NRY diversity contrasts sharply with strong mtDNA heterogeneity [11,12], implying that the assumed founder/bottleneck event and subsequent population expansion concerned mainly males. Hence, overall, most NRY and mtDNA studies either failed to establish the degree of genetic relationship expected under the common-origin hypothesis, or, alternatively, suggest that if a common ancestry did exist, it must have been well before the entry into Sahul about 50 kya. Notably, also linguists failed so far to detect similarities between the many languages spoken by Australian and New Guinean Aborigines [20]. Currently available autosomal DNA data from single locus (such as α-globin genes or HLA genes) studies have been used to support both a common-origin hypothesis as well as a different-origin model [21–23].

One of the reasons for the uncertainty about the joined *versus* distinct history of New Guineans and Australians, if not the most important one, may be that the assumed shared history goes very far back in time (more than 50 kya). It can be expected that because of such depth of time, elements (genetic, anthropological or linguistic) that were shared initially may have diverged significantly due to long-term isolation. However, this does not necessarily mean that some parts of the human genome may not still carry such

hypothetically joined signatures that may be identifiable by future large-scale sequencing or genotyping studies. For instance, a recent study on whole mtDNA sequences identified a potential link between Australia and India [24]; however, this particular lineage has not been found in New Guinea or Island Melanesia so far. Perhaps, our current genetic knowledge is too much biased by the limited number of genetic loci studied so far (note that NRY and mtDNA are just two loci due to the absence of recombination) and when data on more autosomal loci will become available the current view may change. Support for shared ancestry may come not only from studies on Alu insertion/deletion polymorphisms, which found similarities between Australians and New Guineans in a worldwide context [25,26], but also from a recent study employing genetic diversity of *Helicobacter pylori*. This human bacterial parasite was shown earlier to be useful for indirectly tracing human migration history [27], and revealed considerable similarities between such bacteria of Australians and New Guineans [28].

There are several NRY [14–16,29–32] as well as mtDNA lineages [16,33–35] with an assumed origin in Near Oceania (Figures 1 and 2). They are most frequent in regional non-Austronesian (also referred to as Papuan) speakers, who are thought to be the descendents of the initial human occupation of New Guinea during the Pleistocene (Figures 1 and 2). So far, these lineages were found absent (or nearly so) from Southeast Asia (or further to the west) (Figures 1 and 2), with the exception of some eastern Indonesian islands [36], where Papuan-speakers are also found. In very rare cases some of these mtDNA lineages (e.g. P, Q) were also observed westward of the eastern Indonesian islands

Figure 2. Distribution of Y-chromosomal (NRY) lineages in human populations across Oceania.

Only those lineages currently known from Oceania are shown together with their frequencies in East Asia and Southeast Asia (excluding eastern Indonesian islands). Lineages are defined by one or several slowly evolving single nucleotide polymorphisms (also referred to as haplogroups). Assumed geographic origins are indicated as follows: AS, Asian origin, haplogroups with assumed affiliation to the expansion of Austronesian speakers (Aus) are indicated separately; NG, New Guinean (Near Oceania) origin, haplogroups with subregional northern Island Melanesian (NIM) origin or those with affiliation to the expansion of Trans-New-Guinea (TNG) speakers are indicated separately; RO, Remote Oceania origin; Au, Australian origin; EuAs, Eurasian origin. Population data are grouped according to geographic subregions with sample size provided in brackets and language group affiliations indicated by one asterisk for only or mostly Austronesian-speakers, and two asterisks for only or mostly non-Austronesian (Papuan) speakers. Data are taken from the literature as follows: for East Asia, Southeast Asia, West and Central Polynesia, Papua New Guinea (PNG) inland and coast/islands, Fiji, and Southwest New Guinea (SWNG) [16,43], for the Admiralty Islands [43], for Australia [14,16], for Northwest New Guinea [31], for the Bismarcks [16,30], for Bougainville [30], for Vanuatu [56], and for the Solomon Islands [55]. The white-striped lineages have not been fully resolved because of missing sub-lineage marker genotyping and are hence not fully comparable with their non-striped counterparts (but included for orientation purpose only). For details on NRY phylogeny, including haplogroup nomenclature, see [87].

but not further west than Borneo thus far [2]. Hence, there currently is no convincing direct human genetic evidence to prove an initial occupation of New Guinea from Asia (i.e. Sunda) under the 'southern-route' dispersal hypothesis [7,37]. Notably, although the Niah cave on Borneo and the Tabon cave on Palawan (Philippines) have provided dates similar to the oldest ones from New Guinea [38–41], there are currently no archaeological sites possibly associated with modern humans in Southeast Asia that revealed dates older than the earliest sites from Australia. Whereas future archaeological work may reveal such earlier sites, the genetic situation may be explained by the fact that most of Island Southeast Asia has been re-populated recently by Austronesian-speaking migrants, who either displaced the initial populations or mixed with them (see next section). Another explanation may be that the genetic markers currently known from New Guinea arose only locally and after the initial occupation of the region. Although the currently available methods are far from delivering reliable dates, this seems to be true for all NRY lineages of assumed New Guinean origin ([31], but see [30]). However, the situation appears to be more complex for mtDNA as there are some lineages that seem to be as old as the initial occupation of Sahul (such as P) [13,34], whereas others appear similarly old but seem restricted to northern Island Melanesia and are rare in mainland New Guinea (such as M27) [34,42], and again others (such as Q1, Q3, M28, M29) seem considerably younger [13,34]. However, there indeed is indirect genetic evidence for an occupation of New Guinea from the west as provided by the phylogenetic background of the NRY/mtDNA

lineages with assumed New Guinean origin. All such NRY lineages belong to two ancient branches of the human NRY phylogeny characterized by the derived state of either the single nucleotide polymorphisms (SNPs) M9 or M130 (synonym RPS4Y) [43]. Both lineages are assumed to have arisen outside of Africa either in Asia or in ancestors prior to their move into Asia. The same holds true for mtDNA lineages with assumed New Guinean origin such as P being derived from R existing in Asia, and Q being derived from M existing in Asia (but with different sublineages) [44]. Based on such phylogenetic analyses of mtDNA lineages some authors have argued in favor of the southern route dispersal hypothesis [45,46]. Recently, more than 50,000 autosomal SNPs were analyzed in a large number of East and Southeast Asian individuals and populations, and the authors interpret the pattern of genetic diversity observed as supporting a single wave expansion into Asia via a southern route [47]. Future studies will reveal if this scenario is in agreement with genome-wide diversity in Oceania.

There is one sub-region of Near Oceania, namely the Bismarck Archipelago of northern Island Melanesia, that currently is the genetically most studied part of Oceania. Extensive NRY [30,43] and mtDNA [33–35,43] studies have revealed a fascinatingly rich genetic diversity of these islands going back perhaps to the first settlement of the region assumed at least for some mtDNA lineages in agreement with archaeological data [48]. Some lineages with high frequency and an assumed origin in the Bismarcks have been identified, such as M27, M28, M29 for mtDNA (Figure 1) as well as K-P79, K-P117, M1-M104/P22 for NRY (Figure 2),

that are not only rare in the New Guinea mainland but were even found further east with implications for the settlement history of Remote Oceania (see below) [30,34]. Furthermore, genome-wide analysis of nearly 900 autosomal STRs and insertion–deletion polymorphisms has been added recently, showing that genetic clusters of populations can be identified within and between the major northern Melanesian islands that appear distinct from mainland New Guineans [49]. Based on this dataset it also has been shown that linguistic and genetic exchange in the Bismarcks have erased any evidence of a splitting and isolation process that might have occurred early in the settlement history of this region, with the exception of some groups from the interior of New Britain [50].

Most of the regional human genetic work has focused so far on differentiating aspects of early settlements from recent ones such as the influence of the Austronesian expansion. A notable exception is a study [15] that contrasted NRY and mtDNA variation in parts of West New Guinea that lack Austronesian-speaking groups, which found evidence for a reduced unbiased NRY, but not mtDNA, diversity. Such discrepancy between paternally and maternally inherited genetic diversity can be explained by cultural effects such as patrilocality (sons stay in the village they were born in and daughters move to their husband's family), polygyny (some men have children with multiple wives and others have none) or male-biased warfare, all of which are common traits in New Guinea Aborigines that were preserved until recently, at least in the western part of the island.

The distinct genetic diversity, at least with respect to NRY and mtDNA in Near Oceania as outlined above, is accompanied by a distinct and very rich linguistic diversity with about 800 non-Austronesian (or Papuan) languages and additionally hundreds of Austronesian languages [20]. Linguists are still discussing the relationships of the regional non-Austronesian languages [51] and so far, there is only limited knowledge about the affinities between genetic and linguistic diversity within the non-Austronesian speakers of Near Oceania. One example is a recent study [31] proposing that two NRY lineages (M1-P34 and S-M254; Figure 2) may have been distributed around New Guinea and neighboring eastern Indonesian islands by the expansion of Trans-New Guinea speakers starting about 6–7 kya (perhaps 10 kya). It has been suggested that the spread of Trans-New Guinea speakers was associated with the spread of agri/horticulture [52], which locally arose about 10 kya in the highlands of what is now Papua New Guinea [53].

Archaeological data suggest that the initial occupation of Oceania during the Pleistocene only reached as far as Near Oceania with respective sites from mainland New Guinea, the Bismarck Archipelago as well as Buka Island of the northern Solomons [4,48], but there is no archaeological evidence that any island in Remote Oceania was reached before 3.2 kya [54]. Hence, archaeological evidence shows that the biogeographic boundary separating Near from Remote Oceania seemed to have served also as a border for human migration for many thousands of years, most likely because of large inter-island distances together with the lack of appropriate boat technology at the time. However, although data for islands close to the Near–Remote Oceania border are still poorly sampled for mtDNA [34] (Figure 1) and for NRY, and also lack the necessary NRY marker resolution [55,56] (Figure 2), it seems that the same lineages that are present in Remote Oceania also exist in Near Oceania albeit with quite some frequency differences.

Mid-Holocene Occupation of Oceania: Through Near Oceania into Remote Oceania
Archaeological data have shown that certain parts of Near Oceania, in particular Island Melanesia, but much less so coastal mainland New Guinea, have received a second human expansion wave of pottery-making farmers, fishermen and seafarers during the Neolithic. Subsequently, these migrants expanded for the first time in human history into Remote Oceania. This expansion is assumed to have started about 5.5 kya in Taiwan, with its ultimate roots somewhere in southern China, and distributed pottery and other tools to the Philippines and further south to island Southeast Asia arriving about 3.4 kya in the Bismarck Archipelago of northern Island Melanesia [57,58]. Today it is often believed that these Neolithic migrants spoke Austronesian languages [59]. Austronesian languages are currently widespread all over Southeast Asia, part of northern and eastern mainland New Guinea, parts of Island Melanesia, up to Micronesia and Polynesia (even in Madagascar) and trace back to an ultimate proto-Austronesian language spoken most likely in Taiwan [60]. A recent Bayesian analysis of lexical data revealed a Taiwanese origin of the Austronesian languages about 5.2 kya, as well as a tree structure in almost perfect agreement with geographic distance from Taiwan up to eastern Polynesia [61]. In the Bismarck Archipelago these people are assumed to have developed the characteristic elements of the Lapita cultural complex, including the distinctively decorated pottery, as well as the Proto-Oceanic language. Lapita cultural elements were further distributed eastwards into western Polynesia, while various Oceanic languages diversified. Notably, this migration wave, for the first time in human history, crossed the biogeographic boundary between Near and Remote Oceania about 3.2 kya [62,63]. This scenario has been summarized as the 'out-of-Taiwan' model of Austronesian expansion [58].

Several mtDNA [2,34,64–67] (Figure 1) and NRY [14,29,43,68] (Figure 2) lineages have been identified in Oceania that are of assumed East Asian origin. Some of them remain poorly studied in Oceania thus far, and for some the molecular dates are not entirely in agreement with the archaeological and linguistic evidence of the timing of the Austronesian expansion so that it is difficult thus far to conclude who brought them to Oceania [2,34,64,69]. Currently, the most convincing genetic markers for the Austronesian expansion are B4a1a1a (the so-called 'Polynesian motif'), M7c3c (formerly referred to as M7c1c), and F1a for mtDNA (Figure 1), as well as O-M110, O-M119, and O-M324 for NRY (Figure 2). However, more population data and improved molecular dating methods may specify more East Asian lineages as genetic markers of the Austronesian expansion into Oceania. Often, lineages of East Asian origins, including those assigned to the Austronesian expansion, appear in Oceania at higher frequencies in Austronesian-speaking groups living in some coastal regions of New Guinea, some parts of Island Melanesia, and in Polynesia compared to non-Austronesian speaking ones from the interior of mainland New Guinea and from parts of Island Melanesia (Figures 1 and 2). Often, they are absent from non-Austronesian-speaking groups living distant from Austronesian-speaking ones in Near Oceania, e.g. in the interior of New Guinea (Figures 1 and 2). However, the

distribution of East Asian NRY/mtDNA lineages, including those affiliated with the Austronesian expansion, appear highly non-uniform across Austronesian-speaking groups of New Guinea and Island Melanesia for reasons not quite understood so far. For example, the Bird's Head region of northwest New Guinea harbors most Austronesian-speakers of West New Guinea but NRY lineages of assumed Austronesian origin were only observed at very low frequency (2.5%) [31] (Figure 2). Similarly low frequencies of these Austronesian NRY lineages were observed in New Britain, New Ireland and Bougainville (less than 10%) (Figure 2) and almost exclusively in Austronesian-speaking groups [30]; notably, the frequency of mtDNA lineages associated with the Austronesian expansion was found in around 30% of the same samples [42] (Figure 1). In contrast, the neighboring Austronesian-speaking Admiralty Islanders harbor about 18% Austronesian NRY (Figure 2) and about 60% Austronesian mtDNA lineages [43] (Figure 1), and even higher frequencies of Austronesian NRY lineages (38%) were found on the Trobriand Islands east of New Guinea [14]. A recent study [49] on hundreds of autosomal markers in northern Island Melanesia revealed a signature of Asian genetic ancestry of less than 20% in less than half of the Austronesian-speaking groups; notably, such an Asian signature was lacking from regional non-Austronesian speaking groups.

Genetic studies have revealed another fascinating aspect of human history in Oceania. It has been shown that the vast majority of mtDNAs in Polynesia (e.g. 96%) are of Asian origin, whereas only a very small fraction of Polynesian mtDNA (e.g. 3%) can be traced back to New Guinea [16] (Figure 1), and similar estimates were reached by earlier studies [65–67]. In contrast, about two-thirds of Polynesian Y-chromosomes (62%) can be traced back to New Guinea, whereas about one-third (33%) are of Asian origin [16] (Figure 2). Such sex-specific discrepancy in the geographic origin of genetic diversity was also found in parts of northern Island Melanesia such as the Admiralty Islands, although with higher frequencies of NRY and mtDNA lineages of New Guinean origins [43]. The dual-mixed genetic ancestry of Polynesians as derived from sex-specific DNA markers has recently been confirmed by hundreds of autosomal STRs. It was estimated that 79% of the Polynesian autosomal genome is of Asian origin, whereas 21% is of New Guinean ancestry [70], and almost identical estimates were obtained from analyzing 500,000 autosomal SNPs [71]. Notably, also earlier autosomal data (α-globin genes) indicated that New Guinea must have played a considerable role in the genetic history of Polynesia [72].

Taking together the human genetic, linguistic and archaeological evidence suggests a scenario along the following lines: pre-Proto-Oceanic speaking migrants from East Asia started to expand most likely from Taiwan about 5.5 kya, and via parts of Southeast Asia arrived in northern Island Melanesia about 3.4 kya, where they genetically mixed with local people while developing the elements of the Lapita cultural complex as well as the Proto-Oceanic language. This genetic admixture scenario involved mostly women of Asian origin and local men, as indicated by the contrasting ancestry picture of NRY and mtDNA data. Moreover, the total number of Austronesian women taking part in the admixture process must have been considerably larger than the total number of local men to explain the higher Asian relative to New Guinean components as revealed in the genome-wide autosomal studies [73]. Such sex-biased genetic admixture

may have been triggered by the structure of the Proto-Oceanic [74], and also earlier Austronesian societies [75], which were matrilocal in residence — daughters stay in the village they were born in and sons move to their wives' family — and matrilinear in descent — clan affiliation is inherited from the mothers side [75,76]. The larger total number of women relative to the total number of men that took part in the initial admixture process may have been supported by polygyny, which was until recently widespread among non-Austronesian communities in New Guinea [77,78]. The female-driven cultural features in the pre-Polynesian society may also be the reason for the co-ancestry of languages and mtDNA, but not NRY DNA, in contemporary Polynesians, which indicates a female-based inheritance of the Oceanic languages in Polynesian history. Finally, the mixed genetic heritage was then distributed eastward together with Lapita artifacts via parts of Island Melanesia, crossing the Near–Remote Oceania border into western Polynesia in the relatively short time of a few hundred years, with subsequent spread into all over Polynesia, while Oceanic languages diversified. This scenario has been summarized previously as the 'slow boat (from Asia)' model of Polynesian origin [68] to specifically acknowledge the genetic evidence for a considerable mixing between people of Asian and New Guinean ancestry before the occupation of Remote Oceania.

That the initial population mixing occurred in northern Island Melanesia, the homeland of Oceanic languages and the direct home of the Lapita cultural complex, is supported by a number of lineages that originated from the Bismarck Archipelago of northern Island Melanesia [30], but were also observed (albeit less frequently) in Remote Oceania, such as M27, M28, M29 for mtDNA (Figure 1) and K-P117, K-P79, M1-M104 for NRY (Figure 2) [30,34,43]. In fact, almost all lineages observed in Remote Oceania were also found in the Bismarcks — although the major lineages did not originate there (Figures 1 and 2) — which would be in line with the hypothesis developed from archaeological and linguistic data that northern Island Melanesia was the intermediate source of the human occupation of the Pacific [43]. However, more genetic work, including genome-wide autosomal data, is needed to fully establish this scenario from the genetic perspective.

Genetic evidence from the maternal side for the origin of the Austronesian expansion from Taiwan, the homeland of all Austronesian languages and of some material culture such as pottery which later developed into the full Lapita style in the Bismarcks, into Oceania is provided so far by the so-called 'Polynesian motif' (B4a1a1a), which represents the most frequent Asian mtDNA lineage in Polynesia [16,65], as well as some other mtDNA lineages that are less frequent in Oceania, such as M7c3c and F1a [2] (Figure 1). The full Polynesian sequence motif most likely originated in eastern Indonesia but can be traced back to Taiwan via its precursor motif [64,65,67,79] (for an alternative view, see [2,69]). From the paternal genetic side, such evidence is provided by NRY lineage O-M110 representing the most common Asian type of Y-chromosome in Island Melanesia (Figure 2) and showing its highest frequency as well as highest associated Y-STR diversity in Taiwan [43]. However, this lineage has so far only been observed in Remote Oceania in a single western Polynesian man and a single Fijian man and perhaps got lost by genetic drift in most of Remote Oceania (Figure 2). Moreover, the major Asian NRY lineage in Polynesia

(O-M324; Figure 2) does not show a specific Taiwanese origin, but instead a more general East Asian origin [43]. The recently published autosomal study [49] showed primary affinities of Austronesian-speaking Polynesians and Micronesians with Taiwanese Aborigines and only secondary ones with other East Asians, and weaker suggestions of links with New Guineans. Additional genetic evidence for the Taiwanese origin of the Austronesian expansion was recently provided from *H. pylori* where a distinct subpopulation of bacteria was detected in Austronesian-speaking individuals of Taiwan, the Philippines, New Guinea and Polynesia with highest frequency and highest associated genetic diversity in Taiwan and a phylogenetic tree in agreement with a migration from Taiwan via the Philippines and New Guinea to Polynesia [28].

Several other models for the Austronesian expansion and the origin of Polynesians have been formulated, such as the 'express train to Polynesia' model [80], the 'entangled bank' model [81], or the 'slow boat to Melanesia' model [69]; however, they all disagree with parts of the existing genetic, linguistic or archaeological evidence. Remarkably, the 'triple-I' model proposed for the emergence of Lapita in Island Melanesia [82] may come close to the 'slow boat from Asia' model summarized above, as it covers intrusions (i.e. East Asian elements such as genetic ones), integrations (i.e. local New Guinean elements such as genetic ones), as well as innovations (although not yet identified in the genetic data). Finally, there is no convincing human genetic evidence for an occupation of Polynesia from South America, as suggested by Thor Heyerdahl [83]; although Native American NRY/mtDNAs have been very rarely observed in Polynesians [66,84], this has been best explained as the genetic impact of a 19th century Peruvian slave trade in Polynesia, but not as signatures of the initial settlement of the region [84].

Conclusions and Outlook

To summarize, most currently available genetic data either support the idea of an independent migration into New Guinea and Australia, or suggest that if humans of both groups indeed share a common ancestry, it must date well before the entry into Sahul. Notably, this current view may be biased as most genetic evidence so far comes from only two loci (mtDNA and NRY). Although archaeological data show that the first occupation of Sahul during the Pleistocene did not reach Remote Oceania, almost all genetic lineages of Remote Oceania are also found in Near Oceania, albeit in different frequencies and some are of Near Oceania origin whereas others came from Asia. A sex-biased genetic admixture scenario in northern Island Melanesia between more incoming women from East Asia (including Taiwan) and less local New Guinean males with subsequent expansion into Remote Oceania has been suggested to explain the genetic findings ('slow boat from Asia' model). The observation of strong Asian genetic signatures in people of Remote Oceania, as well as the suggestion for a special role of northern Island Melanesia in the genetic history of Remote Oceania, are in line with archaeological and linguistic evidence of a mid-Holocene Austronesian expansion from East Asia (most likely Taiwan) via parts of Island Southeast Asia into northern Island Melanesia and subsequently into Remote Oceania. On the other hand, clear evidence for New Guinean signatures all over Remote Oceania, and for considerable and sex-biased admixture between people of East Asian and New Guinean ancestry before the occupation of Remote Oceania, have been provided by genetic studies. Hence, with Oceania it can be exemplified that human genetic data are useful for confirming ideas about human origins and migration history derived from disciplines such as archaeology and linguistics, but in addition are also able to provide new insights not necessarily detectable from other data for various reasons.

There are still many regions of Oceania that lack good knowledge of NRY and mtDNA diversity; these should be studied in the future to better understand the uniparental genetic history of all of Oceania. Also needed are improvements of the statistical tools for mtDNA/NRY data analysis, particularly more accurate methods for inferring demographic parameters, including time estimates. But clearly one of the biggest limitations in the current genetic understanding of the human population history of Oceania (similar to many other world regions at this moment) is the small number of genetic loci investigated. Hence, it will be very important to focus in the coming future on genome-wide human genetic diversity in Oceania either via parallel microarray-based SNP genotyping or via massive parallel DNA sequencing using next-generation technologies. Going along with the advent of genome-wide datasets, we will need appropriate statistical methods, including simulation approaches, to extract demographic parameters from such highly complex data sets. Furthermore, it will be fascinating to see how other aspects of human history in Oceania that lie beyond demographic parameters may be retrievable from such genome-wide (and other genetic) data, such as human adaptation history, a relatively new field that has just started to be applied to Oceania [71]. Perhaps with those data and suitable statistical analyses in hand we will be able to understand the genetic processes that have shaped the particular phenotypes of the people in Oceania, such as resistance to parasites and diseases (e.g. towards malaria in coastal New Guinea and Island Melanesia), or adaptations to climate and other factors such as nutrition (e.g. extremely small stature in some groups of the New Guinea highlands), or potential adaptation processes that might have taken place during the initial long sea voyages to reach the Polynesian islands (e.g. food shortage that may have resulted in the high frequency of obesity and obesity-related diseases in contemporary Polynesians). Perhaps by virtue of such studies we will one day be able to explain the peculiar internal and external features of the diverse peoples living in Oceania since ancient and more recent times, which have fascinated and continue to fascinate anthropologists and lay people alike.

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