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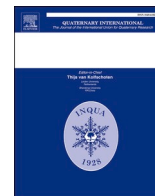
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A contextualised review of genomic evidence for gene flow events between Papuans and Indigenous Australians in Cape York, Queensland

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ABSTRACT

It has long been accepted that the Indigenous groups of Australia's Cape York Peninsula have numerous cultural traits that were adopted from people in New Guinea and/or the Torres Strait Islands after the formation of the Torres Strait around 8000 years ago. However, opinions differ on whether the movement of the traits in question was accompanied by gene flow events. Some argue for a significant amount of gene flow resulting from voyages from New Guinea and the Torres Strait Islands down the east coast of Cape York. Others contend that there was only contact at the northern end of the Cape and that the cultural traits spread through down-the-line transmission. In recent years partnerships between Australian institutions and Indigenous communities in Cape York have led to new genetic research that provides benefits to both parties. We review the currently available genetic data that have the potential to shed light on this issue, concluding that the data are inconsistent with significant gene flow between Indigenous Australians and Papuan people between 8000 years ago and the colonial period. There are indications of gene flow, but it most likely occurred in the Pleistocene rather than the Holocene. As such, the currently available genomic data do not support the hypothesis that the diffusion of cultural traits from New Guinea and/or the Torres Strait Islands into Cape York was accompanied by gene flow. The data suggest instead that the cultural traits most probably spread via down-the-line trade, exchange, and imitation. Our review highlights the gaps in the available genomic information from contemporary and ancestral descendants of Australia's first settlers, and we suggest that researchers adopt a more collaborative approach, involving Indigenous communities and their knowledge in project design, data collection, and dissemination, in future genomic studies in Australia.

1. Introduction

The diffusion of material culture and whether it bears any relationship to the movement of ancient people has long been a source of debate amongst researchers (e.g. Childe, 1925; Smith, 1933). In the last few decades, genomic research has played a crucial role in the investigation of instances of cultural diffusion in the distant past, and whether or not they were associated with significant gene flow, as argued initially by

Ammerman and Cavalli-Sforza (1971), or even large-scale population replacement, as recently documented for the arrival of Bell Beaker pottery in Britain (Olalde et al., 2018). Despite the potential of genomics for untangling these processes, very few such studies have aimed at distinguishing whether demic or cultural diffusion occurred in Australia. Here, we present one of the first attempts to use genomic data in this manner in relation to an important issue in Australian prehistory.

Our study focuses on the peninsula that forms the northeast corner of

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Australia, Cape York. For more than a century, anthropologists and archaeologists have argued that the Indigenous Australians of Cape York have numerous cultural traits that appear to be derived from Near Oceania, specifically New Guinea and/or the Torres Strait Islands (McCarthy, 1977; Rowland, 1987; Barham, 2000). These cultural traits include outrigger canoes, harpoons, barbless bone fishhooks, stone files, multi-pronged spears, and a type of bone projectile point called the 'Muduk point' (McCarthy, 1977; Rowland, 1987). The traits also include a range of myths and rituals often associated with hero cults (Thomson, 1933; Greer et al., 2015). These traditional histories and stories represent a fundamental source of knowledge when it comes to understanding the diffusion of ideas (Thomson, 1933; Greer et al., 2015). Despite the presence of these similarities, we currently have little knowledge about whether people moved to Australia along with these cultural traits.

The spread of cultural traits is thought to have occurred after the inundation of the Torres Plain, which took place around 8000 years ago (Barham, 2000). Authors differ on the precise date. Some argue that it happened after the arrival of Lapita pottery in New Guinea at around 3300 years ago and the Papuan coast at 2900 years ago (McNiven et al., 2011), while others contend that it occurred after the emergence of the so-called Torres Strait Cultural Complex at about 2500 years ago (Barham, 2000). However, there is general agreement that the spread occurred after Australia and New Guinea had become separate land masses.

In contrast to the situation vis-à-vis the timing of the arrival of the traits in the Cape, there is no consensus about how they spread. One hypothesis is that they dispersed as a result of a combination of a) face-to-face contact between Indigenous Australians and Torres Strait Islanders at the top of the Cape, and b) down-the-line cultural transmission among Indigenous Australian groups living in the Cape (Moore, 1978). We will refer to this as the 'Cultural Diffusion Hypothesis'. Another proposal is that the cultural traits were adopted by Cape York Indigenous Australians as a result of contact with seafarers from New Guinea and/or the Torres Strait Islands who undertook long distance journeys to different parts of the Cape to engage in trade and exchange. According to the most recent version of this 'Seafarers Hypothesis', the cultural transmission may also have been accompanied by gene flow or even significant migration (McNiven et al., 2011). The third possibility—adoption via Indigenous Australians travelling to and from New Guinea—is not under consideration because Indigenous Australians are not currently thought to have engaged in long-distance sea travel prior to European colonisation, despite their ancestral great maritime success to settle Sahul 65,000 years ago (Rowland, 2018).

In the present paper, we explore what the currently available genetic data tell us about the Cultural Diffusion Hypothesis and the Seafarers Hypothesis. Given that the latter contends that the adoption of the cultural practices was accompanied by gene flow between Near Oceania and Indigenous Australians, while the Cultural Diffusion Hypothesis does not posit such admixture, genetic data should in theory be able shed light on which of the hypotheses is most likely to be correct. Evidence of gene flow from Near Oceania into Cape York that postdates 8000 years ago but predates the British colonisation of Australia, which began in 1788, would support the Seafarers Hypothesis, whereas a lack of evidence for such gene flow would suggest that the Cultural Diffusion Hypothesis is more likely.

The paper is structured as follows. We begin by describing the Cultural Diffusion Hypothesis and the Seafarers Hypothesis in detail. We then consider which of the two hypotheses is best supported by the available genomic data from modern and ancient Indigenous Australians from Cape York. In the final section of the paper, we outline some potential ways of clarifying the relationships between the inhabitants of Cape York, Torres Strait Islanders, and groups from New Guinea after the formation of the Torres Strait.

1.1. Bridge or barrier?

In his edited volume *Bridge and Barrier*, Walker (1972) concluded that the geologically recent submergence of the Torres Strait around 8000 years ago did not introduce a significant biogeographical barrier between Australia and New Guinea. This view has increasingly gained support from the discovery of significant evidence of material culture in Cape York indicating cultural diffusion from Near Oceania and/or the Torres Strait Islands (Fig. 1; McCarthy, 1977; Rowland, 1987; Barham, 2000). This includes a number of technologies attributable to northern populations, such as dugout and outrigger canoes, harpoons, barbless bone fishhooks and stone files, multi-pronged spears, and bone Muduk points (McCarthy, 1977; Rowland 1987). What remains unclear is whether this diffusion of culture into Australia was associated with any significant population movement.

The two main hypotheses—a) little to no gene flow, or b) extensive gene flow stimulated by northern contact—were considered by Moore (1978). He was critical of the idea that there was significant movement of people from either New Guinea or the Torres Strait Islands along the coastlines of Cape York. While acknowledging a Papuan influence on the mythology, ritual, and technology of Cape York Peninsula, Moore (1978) pointed out that evidence of gene flow was not supported by cranial analyses. Specifically, (Larnach and Macintosh 1970, Macintosh and Larnach, 1973) found that the frequency of Papuan cranial traits declined steadily as one moved southwards from northeastern Australia and concluded that this cline was best explained by internal gene flow. Moore (1978) also found support for his argument in the work of Hale and Tindale (1934), who documented extensive internal exchange systems among Indigenous groups in Cape York. However, Moore (1978) did not discuss the timing, including whether the clinal distribution of cranial traits pre-dated the submergence of the Torres Strait. While the use of non-metric traits and cranial metrics as a mean of measuring the biological distance between populations are still employed today (Wright, 2008; Mallory et al., 2019; Allen et al., 2020), it is worth noting that with more genetic data becoming available we are now able to obtain far higher resolution biological data to reconstruct the biological distance between populations.

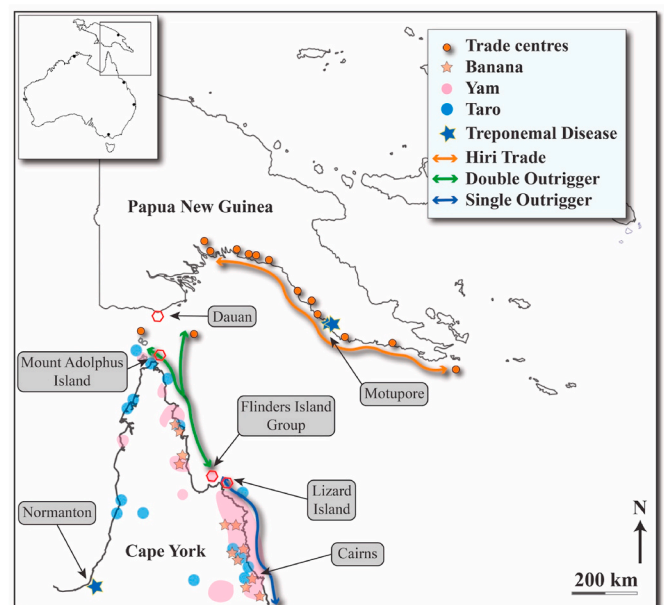


Fig. 1. Overview of cultivars in Cape York and the identification of key trade centres. The extent of outrigger canoe technology along the Australian east coast and known distribution of four-pointed star clubs is also highlighted. The only known cases of syphilis are also identified, with that in Normanton dating to the period of European contact.

In recent years, a significant amount of research has focused on what has been called the Coral Sea Cultural Interaction Sphere (CSCIS) hypothesis. First proposed by McNiven et al. (2004), this hypothesis contends that significant cultural exchange occurred along the south coast of Papua New Guinea, the islands of Torres Strait, and the eastern coast of Cape York. McNiven et al. (2011) has pointed to intriguing archaeological evidence for recent (i.e., post-inundation) cultural contact between groups from Near Oceania and Cape York and suggested that these interactions could have been accompanied by admixture. For instance, the identification of a petroglyph possibly representing a 'lakatoi' crab claw sailing vessel on Dauan Island in the Torres Strait suggests that there may have been some level of contact with Motu traders from the southern coast of Papua New Guinea (Brady, 2006; Richards et al., 2016). Dauan Island is some 200 km west along the Papuan South Coast from the Motu's documented trade network, known as the Hiri. Recent research in Cape York comparing rock art styles in different regions found that examples in the Lizard Island group had greater similarity with that of the Flinders Island group rather than the adjacent mainland Quinkan art (Fig. 4) (Arnold, 2020). It also showed some similarity with art from the Torres Strait (Fig. 1). These observations are consistent with cultural diffusion via the coast.

Likewise, the recent recognition of Lapita pottery on the south coast of Papua New Guinea (McNiven et al., 2011) and in the Torres Strait Islands (Carter, 2004; Wright and Dickinson, 2009) has further expanded knowledge of the range of pottery-making peoples in the Pacific in prehistory. The discovery of large numbers of pottery sherds on Lizard Island at the southern end of the putative CSCIS (Tochilin et al., 2012) is another important indicator of cultural diffusion from the north. Additionally, stone arrangements on Lizard Island share attributes with stone arrangements in the Trobriand Islands and Solomon Islands in the South West Pacific, which also suggests cultural diffusion from the north (Fitzpatrick et al., 2018). These are recent but somewhat controversial discoveries that have significant implications for determining the mechanism for the diffusion of culture, and potentially genes, into Cape York. Rowland (1987) has provided a comprehensive review of the possible advent of external diffusion of material culture into northeast Queensland, something that was possibly associated with a new outrigger canoe technology.

While these cultural traits indicate that contact between the three regions occurred, many unanswered questions remain about the timing and nature of the interactions among the populations. For example, how extensively did the submergence of the land bridge connecting New Guinea and Australia around 8000 years ago impede the diffusion of culture and/or genes across Sahul? The original suggestion by Bowdler (1995) that a significant diffusion event coincided with the arrival of Austronesian-speaking Lapita pottery carrying people in the Pacific 3500 years ago would appear to still be the consensus position. However, Rowland (2018) recently pointed out that diffusion is not necessarily a discrete event, and instead it may have occurred over a long period of time, at irregular intervals, and at a number of different locations in Cape York. Other points of contention include the stimulus for the Lapita colonisation of eastern New Guinea, and the possibility of links with the Hiri Trade. Further south, archaeologists have sought to understand how the emergence of a distinct Torres Strait cultural complex with a strong maritime trade focus sometime after 2500 years ago may have extended the reach of the CSCIS and stimulated cultural change in Cape York (Fig. 1; Rowland, 2018).

1.2. Biological anthropology

As discussed above, McNiven et al. (2011) have suggested that the presence of pottery-producing people in Near Oceania so close to Cape York, raises the possibility that cultural contact in the Cape may have included genetic transfers and perhaps even migration. We note that the limited DNA studies, especially from ancient remains, in Cape York are a major limiting factor when it comes to testing this proposition.

Undoubtedly, the identification of Near Oceania admixture in the genomes of Indigenous Australians from Cape York would provide a clearer understanding of whether direct contact occurred between these populations and the timing of any such event.

The physical anthropologist Aleš Hrdlička (1928) first hypothesized that some of the variations observed in the crania of Australian Aborigines may have resulted from Papuan admixture. Larnach and Macintosh's (1970; Macintosh and Larnach, 1973) later studies of crania from Australia and New Guinea (118 New South Wales, 116 Queensland, and 35 Papua New Guinea individuals) explored this idea, identifying 12 cranial traits that exhibited a north-to-south clinal distribution from Cape York to New South Wales. Larnach and Macintosh (1973: 11) found that their Cape York series of crania was the most similar to their Papua New Guinea series. However, the Papuan crania did not come from one location. They included 17 individuals from the Gulf of Papua, seven from Fife Bay, five from the head of the Sepik River, and six from unrecorded localities. Importantly, subsequent cranio-metric and genomic studies have demonstrated that patterns of diversity within New Guinea are complex (Green 1990; Douglas and Stodder, 2007; Bergström et al., 2017; Pedro et al., 2020) and this diversity cannot be simply linked to linguistic diversity (Douglas and Stodder, 2007). As such, Larnach and Macintosh's finding must be treated with some caution.

1.3. Papuan-Australian gene flow

The significant expansion of contemporary and ancient genomic research in Australia and New Guinea over the last five years has unlocked powerful new data to investigate the question of possible genomic admixture events between these regional populations. Thus far, leading DNA researchers working in the Pacific have focussed primarily on documenting evidence of admixture between modern people and archaic hominins and the timing of colonisation of regions of Oceania. However, there have been several studies that have provided contemporary genomic data from New Guinea, including uniparental mitogenomic (Pedro et al., 2020) and whole genomic data (Bergström et al., 2017), greatly expanding the potential to reconstruct later phases of the region's population history. Unfortunately, similar quality genomic datasets for contemporary Indigenous Australians do not currently exist. From a genomics perspective, Australia remains relatively understudied and for some locations the available evidence is restricted to mitochondrial data only (van Holst Pellekaan, 2013; Malaspinas et al., 2016; Bergström et al., 2016; Nagle et al., 2017; Tobler et al., 2017; Wright et al., 2018; Wasef et al., 2020).

A serious limitation on research moving forward is the issue of who can access and use these data. As an example, the whole modern genomic dataset for Indigenous Australians, which is one of the largest, is currently not publicly shared (Malaspinas et al., 2016; Wright et al., 2018). These restrictions are a point of considerable concern for Indigenous communities and many researchers (Kowal et al., 2017; Wasef et al., 2020) and greatly limit opportunities for engagement with Aboriginal partners. We have been mindful of the ethical imperatives of these establishing these collaborations and have benefited greatly from involvement of local communities. For instance, as part of a recent Australian Research Council-funded project in Cape York, we established an Aboriginal Advisory Committee which was representative of the key communities we worked with on this project. By adopting this approach, Indigenous knowledge and involvement was more directly involved in decision-making as we structured our research, and an Aboriginal liaison officer was employed to support the project. Aboriginal Australian collaborators were involved directly in bioarchaeological fieldwork and analysis, and in helping to interpret the skeletal and DNA results (Adams et al., 2020; Wasef et al., 2020). Together we showed that the complexities of human social life (such as inter-tribal marriage) and the impacts of colonisation on Indigenous Australians meant that even full genome comparisons may not correctly identify an individual's

tribal affiliation (Collard et al., 2019). In addition to new findings the research also illustrated how future research relating to the biology of Indigenous Australians could be undertaken (Wright et al., 2018; Collard et al., 2019; Wasef et al., 2020; Adams et al., 2020).

In addition to the anthropological indications, the evidence from Indigenous Australian biomolecules provides an essential means of testing some of these competing ideas. Our recent research focusing on ancient DNA, modern genomes, and Indigenous knowledge holds the potential to provide some clarity on the questions raised in this paper. However, in line with other evidence, in this paper, we will focus on more details on the genomic admixture signals in the Indigenous Australian genomes available for study.

1.4. Uniparental genomic markers

As ethnographic evidence suggests that most of the proposed seafaring trade between New Guinea and/or the Torres Strait Islands to Cape York would likely have been dominated by males (McNiven et al., 2006), we may hypothesize that a signature from the Y-chromosome uniparental marker of this source population should be present among Indigenous Australians if the cultural diffusion was accompanied by gene flow. However, analysis of Y-chromosome data from 13 Indigenous Australian males estimated the divergence with Papuan populations was nearly 50,100 years ago based on the C haplogroup and around 48,400 years ago based on the K* haplogroup (Bergström et al., 2016). Nonetheless, intriguing evidence for limited subsequent contact comes in the form of the M haplogroup, which is mainly found in New Guinea, Near Oceania, and in less than 1% of Indigenous Australian males, and may represent an admixture event around 10,400 years ago (Bergström et al., 2016). However, in the same study two Indigenous Australian males who carry the M haplogroup had paternal ancestries from the Torres Strait Islands (Mer Island, Torres Strait, Far North Queensland), which Bergström et al. (2017) have argued may represent a very recent introduction into the mainland Australian gene pool at around 9700 years ago, corresponding approximately to the inundation of the land bridge between New Guinea and Australia. Bergström et al. (2017) study did not find evidence for Holocene gene flow or non-genetic influences from Southeast Asia corresponding to the expansion of Lapita pottery producing populations. Other research on contemporary Indigenous Australian males has shown between ~32 and ~70% of Y-chromosome haplotypes are non-Indigenous, reflecting a significant loss of Indigenous Australian Y-chromosome genetic diversity following European contact (Malaspina et al., 2016; Wright et al., 2018). Out of the 44 contemporary male genomes reported in Malaspina et al. (2016), the non-European Y chromosomes included 25 individuals with Australian haplogroups C1b or K2b and three individuals with East or Southeast Asian haplogroups O1a (Birdsville and Weipa) and O2a (Cairns).

Captain Cook's 1770 survey of Australia's east coast initiated over two centuries of profound disruption for Indigenous Australians, including a substantial reduction in population size due to disease and violence. It also initiated an influx of people from other continents who intermarried with each other and with Indigenous Australians. The loss of Indigenous Australian lives and the admixture between Indigenous Australians and European and Asian populations makes the interpretation of modern genomes problematic, particularly in relation to Y chromosome research. Ancient DNA from well-dated archaeological contexts are necessary to reconstruct the comparative baselines for estimating the timing of later external gene flow. However, current sampling of Indigenous Australians is geographically limited, with minimal representation from the possible points of contact that are relevant for the present paper. In fact, Indigenous Australian Y-chromosome genomic data from archaeological contexts is currently available only from our research on the ancient remains of Flinders Island, Cairns, and Mapoon (Fig. 2; Wright et al., 2018; Wasef et al., 2020). This work found that only two haplogroups were present—S1a3a and S1c* (previously known as K2b*). These are considered to be Indigenous

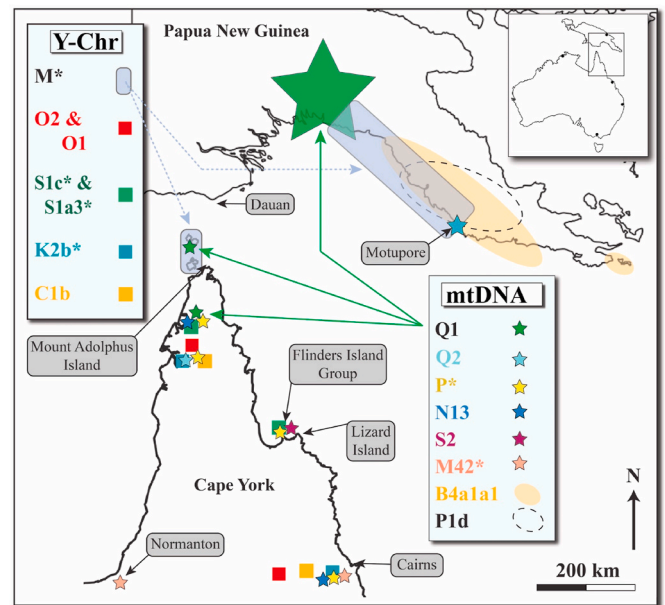


Fig. 2. Mitochondrial and Y-chromosome DNA haplogroups in Cape York and Coastal Papua from ancient and modern genomes. The mitochondrial haplogroups are indicated with a star, while the Y-chromosome haplogroups are indicated by the square sign. The Q1 mitochondrial and the M* Y-chromosome haplotypes are of interest as they might represent a late Pleistocene-early Holocene distribution.

Australian Y-chromosome haplotypes and have yet to be identified in Papuan populations (Fig. 2; Bergström et al., 2017; Wasef et al., 2020). This is not consistent with the idea that the cultural diffusion from New Guinea and/or the Torres Strait Islands to Cape York was accompanied by substantial gene flow.

The availability of a well-established mitochondrial genomic database for both contemporary and ancient Indigenous Australians provides valuable insights into a maternally inherited single locus (van Holst Pellekaan, 2013; Nagle et al., 2017; Tobler et al., 2017; Wright et al., 2018; Wasef et al., 2020). However, for the purposes of understanding gene flow through trade and exchange this database offers a low resolution of understanding in comparison to nuclear and Y chromosome genomic data, as interpretation of admixture and gene flow events from mtDNA represents only one side of the genomic history of Australia's First People. The abundance of mtDNA in the human body means that for the majority of Aboriginal ancestral remains it is quite often the only preserved genomic data that can be recovered. Recent mitogenomic studies of Aboriginal Australians show that they fall within one of the M and N macrohaplogroups and more specifically within one of the haplogroups M, N, S, R, O, P, and Q (Fig. 2; van Holst Pellekaan, 2013; Nagle et al., 2017; Tobler et al., 2017; Wright et al., 2018; Wasef et al., 2020). The most recent analyses have shown that both M and N macrohaplogroup founder types diversified into the present Australian-specific haplogroups shortly after the arrival of the first settlers of Sahul, and thus are present in New Guinea as well (van Holst Pellekaan, 2013; Pedro et al., 2020). Subgroup R (within macrohaplogroup N) is thought to have diversified in Sunda just before the colonisation of Sahul (Tabbada et al., 2010; Delfin et al., 2014), or in northern Sahul (i.e. present-day New Guinea) (Gomes et al., 2015), after which this group further diversified into haplotypes unique to both New Guinea and Australia.

Recent research on the Q mitochondrial haplogroup in Sahul is particularly important for this review. This haplogroup may have originated from M29'Q and diversified into three subclades in highland and coastal New Guinea. Phylogenetic analyses by Pedro et al. (2020) indicated that members of one of these clades introduced the Q1a

haplotype into northern Australia in the postglacial warming period (18,000–10,000 years ago) and that the interaction between northern and southern Sahul stopped before the Holocene. This may have relevance for the patterns observed in the cranial data by [Macintosh and Larnach \(1973\)](#), perhaps indicating that the clinal pattern they identified has an early Holocene/Late Pleistocene antiquity.

Analyses of the mitochondrial haplotype diversity of the 143 ancient and contemporary Aboriginal Australians included in [Wright et al. \(2018\)](#) and the 342 mitogenomes reported in [Wasef et al. \(2020\)](#) showed high levels of genetic diversity and geographic structure. Of the 149 mitogenomes from Queensland, the most common basal haplogroup was P at 59.1% of the total haplotypes observed falling within that classification, followed by S at 24.8%, and M (incorporating M14, M15, both M42a and M42c) at 10.9%. Haplogroups N and O were less common with 2%, while the least common was Q with 1% ([Wasef et al., 2020](#)). Haplogroup Q is of interest because of its estimated age of at least ~37,000 years ago ([Behar et al., 2012](#)) and its relatively high frequency in New Guinea, Timor, and Island Near Oceania ([Friedlaender et al., 2005, 2007](#); [Kayser et al., 2008](#); [Gomes et al., 2015](#)). This haplogroup has three known subclades, Q1, Q2, and Q3, all of which are found in New Guinea/Island Near Oceania, with Q1 and Q3 being additionally present in Timor ([Gomes et al., 2015](#)). Haplogroup Q has been found only in four Indigenous Australians; one was a unique variant within haplogroup Q2, labelled Q2b ([Hudjashov et al., 2007](#)), while the other three reported in [Nagle et al. \(2017\)](#) belonged to Q1. Additionally, two historical hair samples from Mapoon in Queensland belonged to the Q1+16223 haplotype, indicating that ancestors of those individuals are from neighbouring New Guinea or the islands of the Torres Strait ([Wasef et al., 2020](#)). While all of these genomes were collected from Cape York, the three Q individuals were of known Torres Strait Island maternal ancestry. Indigenous Australians are culturally and linguistically distinct from Torres Strait Islanders, but trading and intermarriage between the two populations in the ethnographic period are well documented ([Beckett, 1987](#)).

1.5. Indigenous Australian whole genomes

The limited whole-genome data currently available have provided a number of important insights into the region's population history. It has long been hypothesized that present-day Papuan people and Indigenous Australians were derived from a single founding population and recent genomic studies have narrowed the date of the divergence between Papuan people and Indigenous Australians to around 10,000–32,000 years ago ([Malaspinas et al., 2016](#)). Modern northeastern Indigenous Australians from Cairns and Weipa, as well as an ancient individual from Cairns (PA86), showed 13–15% of Papuan-related ancestry in their genomes, indicating a unidirectional, Pleistocene gene flow from Papuans to Indigenous Australians ([Wright et al., 2018](#)). While individual admixture date inference is bioinformatically possible through new tools such as DATES ([Narasimhan et al., 2019](#)) to estimate the number of generations passed since an admixture event, DNA studies of the Indigenous genomes were not fully used to test the possibility of later Holocene admixture proposed here.

While gene flow from Southeast Asia around 3500 years ago affected the coastal areas of New Guinea ([Bergström et al., 2017](#)), there is currently no genetic evidence for such contact in Australia. East Asian genetic signatures have been found in modern Indigenous Australians, but these appear to have been introduced much more recently and have been attributed to the 19th century gold rush period when people from all around the world travelled to Australia in search of gold ([Malaspinas et al., 2016](#)). None of the ancient genomes obtained thus far from Cape York has an Asian admixture signature, which is consistent with [Malaspinas et al. \(2016\)](#) gold rush hypothesis. Asian genetic signatures introduced to the coast of New Guinea and offshore islands during the mid-Holocene seem to have come from Austronesian groups (Lapita carrying seafarers) ([Bellwood, 2005](#)). While there is no current evidence

for Lapita pottery in Australia, it seems unlikely that Southeast Asian seafarers did not make contact given the size of the Australian landmass. For instance, there is evidence of pre-European colonisation visits from Makassan sea cucumber collectors from Sulawesi (Indonesia) to northern Australia at least since the early 18th century ([Macknight, 1986](#)). Furthermore, the late Holocene arrival of the dingo has in the past been argued to support the possibility of recent admixture with Southeast Asian seafarers ([Ardalan et al., 2012](#); [Oskarsson et al., 2012](#)). Nevertheless, at the moment, there is no genetic evidence to support the hypothesis that there was contact between Lapita carrying people and Indigenous Australians ([Malaspinas et al., 2016](#)).

An expanded genomic dataset from Australia and the Torres Strait Islands holds great potential to provide better resolution in our understanding of northern contact and gene flow into Cape York populations. Moreover, whole genome data will provide a better chronological understanding of late admixture events. However, the expansion in the genomic studies of Indigenous Australian communities needs to be contextualised within ethical sampling practices and Indigenous Australian knowledge and questions ([Collard et al., 2019](#)).

2. Discussion

While limited, the currently available genomic data lack a signature of Austronesian gene flow down the east coast of Cape York that post-dates the flooding of the Torres Strait in the early Holocene around 8000 years ago. The evidence from mtDNA indicates that northern and southern Sahul host different deep-rooted maternal lineages in the age range of more than 50,000 years ago, with gene flow finishing by the time the Torres Strait was submerged. This is potentially supported by the clinal distribution in non-metric traits reported in crania from New Guinea, Cape York, Queensland, and New South Wales. The Y chromosome markers that may be expected within the contemporary populations in Cape York if there was significant interaction between Indigenous Australians and Austronesian seafarers have not yet been detected. However, this position may change with further analyses of ancient genomes from Cape York. Moreover, there is currently a limited understanding of the genetic diversity of the Torres Strait Islands, particularly in relation to Y chromosomes, and this must be remedied if we hope to identify the nature and timing of demographic expansions or interactions in the area.

While there is reasonable genomic and uniparental data currently available from Southern Sahul, we remain unable to demonstrate that there were any late Holocene admixture events. Thus, our current understanding of the timing of gene flow indicates that any morphological similarity between crania from Cape York and New Guinea is not associated with the arrival of people carrying Lapita pottery and their seafaring technology in the later Holocene. This may change with further, targeted analyses of the genomic databases for Indigenous Australians that focus specifically on the movement of people during the last 3500 years in what has been coined 'the Coral Sea Cultural Interaction Sphere'. Furthermore, if we were able to develop an understanding of the genomic history of the people of the Torres Strait, we could more fully investigate the relationship between the people of Cape York and the islands in the last 10,000 years, and perhaps test the assumption that Indigenous Australians did not practice long-distance seafaring. Importantly, this research would enable us to determine the extent to which groups from New Guinea occupied the Torres Strait Islands between 3500 and 3000 years ago, thus providing an indirect mechanism for the flow of genes between New Guinea and Australia ([David 2008](#)).

Despite the current lack of genomic evidence of Late Holocene gene flow between New Guinea and Australia, we remain committed to further investigations exploring this possibility. First, it is clear that Australia was certainly accessible to northern populations who were engaged in long-distance sea trade throughout the Pacific. In more recent times, the well-documented Makassan trade network based in

Indonesia included coastal Arnhem Land of northern Australia (Mulvaney and Kamminga, 1999). This question about the nature and extent of external trade connections fits well into current research being carried out on the complex trade and exchange networks that were operating across Australia without any stimulus from external populations (Mulvaney, 1976; McBryde, 1987).

While genetics no doubt represents a powerful dataset, we also encourage the consideration of other related data to help identify movements and interactions of past populations. For instance, one further aspect of human biology that may provide evidence for external northern contact relates to the introduction of infectious disease, in particular syphilis (*Treponema pallidum*) (Butlin, 1985). This venereal disease (as distinguished from endemic Yaws) leaves significant and diagnostic bony lesions in the cranium, particularly affecting the frontal and the palate in its tertiary stages (Fig. 3; Hackett, 1975). Syphilis is prevalent at Motupore Island, a major Austronesian trading base for the Hiri trade and exchange network in coastal New Guinea (Fig. 1; Stanard, 2008). The severity and location of destructive lesions would suggest that it is more likely syphilis than endemic yaws. The prevalence of both diseases in the prehistory of New Guinea is currently understudied, though early cases of treponemal disease have been documented elsewhere in the Pacific Islands (Pietruszewsky and Douglas, 2012). No evidence of treponemal disease including syphilis that pre-date the arrival of Europeans has been found in Cape York (Webb, 1995) or the Flinders Island group (Adams et al., 2020). We do know of one case in Cape York, but this is dated to the European contact period (Adams et al., 2018). Treponemal disease also appears to have reached regions of northern tropical Australia through contact with Makassan sea cucumber fishermen, though again these examples are relatively recent (Webb, 1995). If Austronesian speaking populations brought syphilis to New Guinea, then its absence from Cape York, along with the absence of Y chromosome data from Austronesians, is a further indicator that there was unlikely to be extensive gene flow from these populations post 8000 years ago.

Strontium (Sr) isotope ratio ($^{87}\text{Sr}/^{86}\text{Sr}$) studies of human teeth from well-dated archaeological contexts are emerging in both New Guinea



Fig. 3. Treponemal disease showing the distinctive nature of bone destruction in frontal of a male individual (M33), Motupore Island (taken from Webb 1995). If significant admixture occurred between traders from Coastal Papua and Cape York, the presence of syphilis may be expected in the latter. There is no evidence for this infectious disease in the prehistoric period for Cape York.



Fig. 4. Cave of ships, Denham Island, Flinders Island group.

and Cape York as a means of understanding trade and mobility. Research at Nebira, inland southern New Guinea, identified that five of the 27 individuals had grown up in a coastal location (Shaw et al., 2011). This indicated that trade and movement between coastal and inland communities was commonplace in the pre-contact period. Further landscape Sr isotope research throughout southern New Guinea is required to establish exactly where they grew up. Adams et al. (2019) also conducted a regional Sr isotope study (isoscape), covering the entirety of Cape York. Results demonstrated a far wider range in landscape $^{87}\text{Sr}/^{86}\text{Sr}$ values when compared to those from New Guinea (Adams et al., 2019). This isoscape has also been used to compare against pre-historic human results from the Flinders Islands of Cape York (Adams et al. under review). Preliminary results of this research suggest a complex story of mobility in the Flinders Island group with two of the five analysed individuals being non-local and likely from mainland Cape York. These burgeoning Sr isotope studies of mobility in Sahul may one day be combined with DNA research to reveal a more nuanced understanding of population dynamics and human mobility in the region.

Investigations employing new statistical methods to analyse cultural traits, such as the studies carried out at Lizard Island indicating possible connections with northern groups based on stone arrangements and rock art (Arnold, 2020), has great potential in the context of Cape York. Our own work on rock art in the Flinders Group of islands has identified large numbers of watercraft images, but these all appear to be of European vessels. In the seven main caves and rock shelters we found no representations of vessels that could indicate earlier contact with northern groups. However, these data may still be useful for exploring the mechanism for down-the-line cultural transmission on the cape. For instance, it is clear from the ethnographic record that movement by sea was a key aspect of the lives of the Indigenous Australians from Flinders Islands (Hale and Tindale, 1934), and recent research has shown that these islands were settled at least 6000 years ago (Wright et al., in press). The new dates undermine the proposition by Beaton (1985) that the island occupation only occurred after outrigger technology was introduced following contact with Near Oceania 2500 years ago. Aboriginal people achieved great maritime success in the initial colonisation of Australia some 65,000 years ago (Bird et al., 2019; Westaway, 2019), and there seems no reason to consider that they had abandoned their ancestral maritime capacities entirely. While these relatively short distance maritime voyages were likely taken by Aboriginal Australians, we still have no evidence that they engaged in the type of long-distance travel necessary to reach New Guinea.

Another means of determining the extent to which Australian populations were in contact with northern groups during the late Holocene

is to examine the movement of cultivars. The recent suggestion of a form of agriculture being adopted in West Torres Strait (Fig. 1; Denham et al., 2009; Williams et al., 2020) highlights a need for new archaeological investigations into East Cape York to understand whether diffusion of ideas and cultivars has occurred from the north, or in fact whether some of these cultivars had an origin in Cape York. In a ground-breaking study by Hynes and Chase (1982) it was suggested that plant communities in Lockhart River on the east coast of Cape York were not merely modified by Aboriginal people but may have in fact been created by them. A pioneering genetic study from northern NSW incorporating traditional owner knowledge (Rossetto et al., 2017) provides a relevant methodological approach to be applied to understand the diffusion of cultivation into, or indeed out of, Cape York. There is no reason to presently dismiss the idea that some of these cultivars may have originated in Australia and moved north from Cape York and into the Torres Strait and beyond. A genetic study of cultivars has great potential to reveal further details of the complexity of movement which we know also incorporated the movement of intangible cultural heritage from Cape York into the Torres Strait (Greer et al., 2015). With the revelation that offshore island occupation predates the arrival of Lapita people in the region, we certainly should be open to the Greer and colleagues' (2015) proposal that movement of plants and other items from Indigenous Australians to Torres Strait Islanders and Papuan people. This represents an important avenue for future research.

A further point for further consideration, which emerged directly from discussions of cultural knowledge with the Cape York Aboriginal Advisory Committee associated with our project, is integrating cultural stories and oral history to help reconstruct ancient trade routes. Shivaree, an ancestral hero from West Cape York who travelled north along the coast to Mabiug Island, is one such example (McConnel, 1936). Certainly, Greer and colleagues' (2015) work has highlighted the high potential of this research to help reconstruct ancient networks of connection between the south and the northern islands of Torres Strait and their relationships to ongoing traditional knowledge that is core to identities and knowledge systems today.

3. Conclusions

Anthropologists and archaeologists have long accepted that a number of the cultural traits of the Indigenous Australians of Cape York were derived from New Guinea and/or the Torres Strait Islands in the period after the formation of the Torres Strait around 8000 years ago. However, opinions differ as to whether the movement of the traits in question was accompanied by gene flow. Some argue for a significant amount of gene flow resulting from voyages from New Guinea and Torres Strait down the east coast of Cape York. Others contend that there was only contact at the northern end of the Cape and that the cultural traits spread via down-the-line transmission. We reviewed the currently available genetic data that have the potential to shed light on this issue.

Analyses of the available genomic data of the Indigenous Australian uniparental and whole genomes have shown no detectable signature of Austronesian gene flow along the east coast of Cape York in the last 3000 years. The current evidence, therefore, supports the Cultural Diffusion Hypothesis. It is perhaps time to start considering that the diffusion of culture along the east coast of Cape York may have largely been facilitated by Aboriginal seafarers in a dynamic socio-cultural space where overlapping zones of interaction occurred. These regions had their own culture that tied local residents to the land, but equally accommodated visitors that came and went for trade and exchange.

Ancient DNA holds enormous potential to unlock many of these secrets from Australia's complex Aboriginal past and provide a deeper understanding of the patterns of diffusion between New Guinea, the Torres Strait Islands, and Cape York, as well as the internal dynamics of diffusion within Cape York. The potential for reconstructing these ancient interactions from these data has already been highlighted using the ethnohistoric record (Greer et al., 2015) and in limited isotopic

(Adams et al., 2020) and genomic research (Wasef et al., 2020). Combining genomic and isotopic methodologies, with careful consideration of archaeological data, ethnohistoric/ethnographic accounts, and, importantly, Aboriginal cultural knowledge and traditions, will provide a powerful way forward for understanding the mechanisms of cultural diffusion in this region of the world. While our genomic research has been, in most cases, initiated in partnership with Indigenous communities to answer questions of relevance to both researchers and Aboriginal communities (Wright et al., 2018; Wasef et al., 2020), a complicating factor will continue to be the poor DNA preservation in the ancestral remains of Indigenous people in tropical contexts – hence the minimal ancient genomes available to date and their bias toward uniparental mitochondrial genomic information. The results reported here reflect the need to expand genomic research on late Holocene human movement and admixture between the Cape York, Torres Strait Islands, and Papuan populations. This, of course, will depend on the establishment of strong collaborative research partnerships, foremost with the Traditional Owners and Indigenous custodians who trust us with investigating the ancestral remains of their past.

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CRediT authorship contribution statement

Sally Wasef: Conceptualization, Formal analysis, Writing - original draft, preparation, Writing - review & editing. **Gabriel Wrobel:** Writing - original draft, preparation, Writing - review & editing. **Nathan Wright:** Research and illustration of maps, Writing - review & editing. **Joanne L. Wright:** Writing - review & editing. **Shaun Adams:** Field work, Writing - original draft, preparation, Writing - review & editing. **Jason Kariwiga:** Writing - original draft, preparation, Writing - review & editing. **Matthew Leavesley:** Writing - review & editing. **Mark Collard:** Conceptualization, Writing - review & editing. **Michael C. Westaway:** Field work, consultation and permission from Aboriginal communities, Conceptualization, and research group management, Writing - original draft, preparation, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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