# A different paradigm for the initial colonisation of Sahul

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## ABSTRACT

*The questions of when and how humans reached Sahul, the Pleistocene continent of Australia and New Guinea, has remained a central issue of Australian archaeology since its development as an academic discipline in the mid-twentieth century. Modelling this event has persistently appealed to minimal assumptions – the simplest watercraft, the shortest routes, the smallest viable colonising groups. This paper argues that Australian archaeology can no longer ignore the way our understanding of this initial colonisation is being reshaped by current genomic research. It reviews this evidence and concludes that a colonising wave of hundreds or perhaps low thousands of people was involved. If correct, it suggests that we need to rethink our models, modify or discard the minimalist assumptions that have so far driven them and consider how this different paradigm affects our understanding of early settlement in Sahul.*

**Keywords:** colonisation, genomics, isolation, mitochondrial DNA, Sahul, Wallacea

## RÉSUMÉ

*La question de savoir quand et comment les hommes ont atteint Sahul, le continent pléistocène regroupant l'Australie et la Nouvelle-Guinée, persiste comme une problématique centrale de l'archéologie australienne depuis son essor en tant que discipline universitaire au milieu du vingtième siècle. La modélisation de cet événement s'est appuyée de façon récurrente sur des présupposés minimalistes, impliquant les moyens de navigation les plus simples, les routes les plus courtes, les groupes de colonisation viable les plus restreints. Ce papier soutient que l'archéologie australienne ne peut plus ignorer combien notre compréhension de ce peuplement initial se trouve aujourd'hui redéfinie par la recherche génomique en cours. Il passe en revue les données et conclut que plusieurs centaines ou quelques milliers de personnes ont participé à cette vague de peuplement. Si cette hypothèse est correcte, elle implique que nous repensions nos modèles, que nous modifiions ou abandonnions les présupposés minimalistes qui ont jusqu'à présent défini ceux-ci et que nous analysions comment ce nouveau paradigme influence notre compréhension du premier peuplement de Sahul.*

**Mots-clés:** ADN mitochondrial, colonisation, génomique, isolement, Sahul, Wallacea

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> We must not be obsessed with the route to Australia involving the shortest water crossings.
> Rhys Jones (1968: 190)

## INTRODUCTION

Together and independently over the last four decades we argued questions of initial Sahul colonisation with our friend John Beaton, even after his career moved away from archaeology. He had more than a passing interest in this wide subject (e.g. Beaton 1985, 1991, 1995). Beaton loved the notion of thinking outside the square, and we offer here some different ideas on Sahul colonisation as a mark of respect to our late colleague.

This paper argues that recent genetic studies can be interpreted to show that the initial human colonisation of Sahul involved many hundreds and possibly thousands of individuals, probably within a time period shorter than one millennium. A similar conclusion has been recently reached by Bradshaw *et al.* (2019) based on a different approach to ours. If we are both correct, the demographic scope of this colonisation indicates that the process was more complex than previously allowed and the existing explanatory models are in need of revision. Whole genome studies are

too few to apply to this question and thus we appeal mostly to recent work on mitochondrial DNA (mtDNA), currently the best understood and reported segment of the genome, but we also refer to data and results developed from Y-chromosome studies. Our working assumption is that the haplogroup diversification we identify occurred prior to arrival in Sahul. Aspects of this assumption are contested by some geneticists, and thus we develop arguments to support our position. We review genetic data from Wallacea that can be read to suggest that Sahul may have been isolated from the west during last glacial maximum (LGM) low sea levels. We propose a possible explanation, that depletion of coastal and fringing reef resources during periods of low sea level inhibited transit along the Sunda/Sahul arc.

In inferring human behaviour from archaeological data, it is prudent to create minimalist models of that behaviour because such models usually demand the fewest assumptions to infill the gaps in the material evidence, such as those reflecting human motives, objectives, cooperation, information sharing, and so on. There is a general if uneven correlation between the minimalism of such scenarios and the time depth involved. This partly reflects greater evidence gaps for the deep past, but also an earlier, sometimes lingering view that early anatomically modern humans (AMH) were restricted in their ability to solve new problems. Some still choose to view long-term history in social evolutionary stages, from savagery to civilisation, if you will, where the associated capabilities of Pleistocene hunter–gatherers were implicitly inferior to ours.

Minimalist modelling is no more apparent in Sahul archaeology than in discussions of Sahul's initial colonisation. Ever since Grafton Elliot Smith argued in 1914 that the proposed antiquity of the Talgai cranium showed that Sahul's first colonists were also the world's earliest sailors, periodic examinations and reconstructions of this seaborne colonisation have mostly appealed to the simplest explanations, particularly in respect of the sea as a barrier. It is thus useful to consider the development and nature of Sahul colonisation models.

## HISTORICAL BACKGROUND

The rise in professional archaeology in Australia from the 1960s onwards led to speculation on various aspects of the initial human arrival in Sahul. Despite Jones' insightful 1968 admonition, the dominant early theme was that accidental crossings at times of lower sea levels that provided potentially shorter inter-island distances were to be favoured (Hallam 1977: 130; Jones 1979: 449, 1989: 753-6; Mulvaney 1975: 144; White & O'Connell 1982: 46). Calaby's (1976: 23-4) whimsical proposition of a pregnant woman on a log being the Aboriginal Eve touched on two further themes subsequently much developed, those of minimal sea transport and the minimum number and age/sex composition of a viable colonising population. An early contributor here, demographer Norma McArthur (1976) and McArthur *et al.* (1976) glimpsed the future

when she and colleagues reported computer simulations of demographic viability, suggesting that while Australia might statistically have been populated by one man and two women of reproductive age, the overwhelming probability was high failure rates for small colonising groups. Another emergent theme, that rising sea levels reduced the availability of land and forced eastwards movement (Thiel 1987) had already been countered a decade earlier by Dunn and Dunn (1977) who showed that Sunda, when the sea was at 100 m below present levels, possessed less than 50% of the present length of coastline. One consequence of this idea, developed first by Chappell and Thom (1977) and elaborated by Chappell (1993) and Terrell (2004), was the idea that higher sea stands promote the development of productive littoral zones, including reefs, lagoons, estuaries and swamps. This suggested that movement might best have been undertaken during these higher stands and offered a counter to the minimalist lower sea levels argument.

A third minimalist theme concerned routes. Birdsell (1977) became and continues to be a perennial reference for this, although his paper was concerned with other things as well, watercraft capabilities and a preference for lower sea levels among them. Irwin's (1991, 1992) perceptive elaboration of Birdsell's ideas, especially questions of intervisibility, allowed us (e.g. Allen & O'Connell 2008: 37-8, 43) to advocate the probable primacy of Birdsell's northern route into the Bird's Head of New Guinea, even though many Australian researchers then and now favour the southern route through Timor, freeing them from considering the New Guinea evidence. Throughout, models and interpretations of the data on routes, including ours, remained minimal.

This summarises some salient points elaborated elsewhere both by us (Allen & O'Connell 2008; O'Connell & Allen 2012; O'Connell *et al.* 2010) and others (e.g. Anderson 2000; O'Connor 2010; O'Connor & Veth 2000). What these and other summary papers (e.g. Davidson & Noble 1992) also tried to address were what factors might have led to this diaspora and how it might have been achieved. Working from the available archaeological evidence in Wallacea and using aspects of optimal foraging theory (OFT) (see also Anderson 1981, 2009), we proposed a model for this colonisation that might be tested in the expanding archaeological record. This involved the primacy of reef/littoral resources, especially shellfish, as both a major subsistence target for expanding AMH groups moving through Wallacea and also an impetus for movement into pristine coastal environments as the most attractive resources diminished in occupied areas. The model grew from the ethnographies of tropical coastal hunter–gatherers (Bird & Bliege Bird 1997; Meehan 1982) and available archaeological evidence (Gosden & Robertson 1991; Leavesley & Allen 1998; see also Codding *et al.* 2014) and the knowledge that people moving east through Wallacea increasingly encountered islands with diminishing land faunas before reaching Sahul. We recognised the simplicity of this model, given the variability of the Wallacean islands in terms of sizes and concomitant

availability and sustainability of food sources, but saw that it offered an alternative to untestable explanations like human curiosity. While the littoral model has drawn some criticism (e.g. Anderson 2018) it has been largely adopted by others (e.g. Kealy *et al.* 2016; Norman *et al.* 2018; O'Connor *et al.* 2017).

Inevitably discussions of colonisation became linked to questions of the chronology of first arrival. Our earliest summary (O'Connell & Allen 1998) promoted our view of a short chronology linked to purposeful colonisation. Colleagues favouring the longer 60 ka chronology (O'Connor & Veth 2000: 103-5; Chappell 2000) pointed to the disparity between this age for Australian sites and then current dates, up to 30 ky younger, for Island South East Asia and Melanesia. They took this to indicate a more random colonisation of Sahul, an argument also seen to favour the Timor route (O'Connor 2007). While the chronology of Sahul colonisation remains important, we see no arguable cause-and-effect nexus between when Sahul colonisation first occurred and AMH ability to achieve it (cf. Davidson & Noble 1992). If we exclude the extreme age claimed for Madjedbebe (Clarkson *et al.* 2017) the increasing consensus of available evidence currently puts this event in the range 47–51 ka. Despite some suggestions (e.g. Cooper & Stringer 2013; Jacobs *et al.* 2019; Teixeira & Cooper 2019), there is so far no serious challenge to the proposition that the colonisation of Sahul was only achieved by *Homo sapiens* and never by archaic humans. However a radical extension of this time frame, perhaps to 80+ ka on the published Madjedbebe evidence, would call this view into question (but see critical assessment of Madjedbebe claims in O'Connell *et al.* 2018).

### WHERE ARE WE NOW?

A survey of recent literature mostly indicates a continuation of the same or similar themes using better maps and marine charts and more powerful computing and modelling programs.

Anderson (2018) elaborates a theme he has previously developed (e.g. Anderson 2000, 2010) where the availability of warm seas and large diameter bamboos and many island targets in Wallacea made marine mobility easy. We do not see how the coalition of these factors might necessarily force early maritime migration in the region, although they certainly facilitated it. Our argument that serial depletion of high-ranked resources propelled AMH through Wallacea is not challenged by easy mobility. Nonetheless Anderson offers compelling evidence for the primacy of bamboo rafts as watercraft, which required limited tools and technical skill to construct. Such vessels might keep 50–100 individuals seaborne almost indefinitely. We do not subscribe to Anderson's further view that we need not consider other than drift voyages with no means of steerage on such craft, where the question is what might motivate 100 modern humans to build and board a raft without any control over an eventual landfall?

At the same time Anderson (2018: 225) questions our serial depletion model by arguing for high skill in marine and terrestrial food acquisition by the earliest colonisers, suggesting that for such people local shellfish depletion would not force migration. Certainly the wide range of terrestrial foods referenced at Niah Cave (Piper & Rabett 2017) indicates that AMH had such terrestrial skills prior to leaving Sunda. Even east of Wallace's Line, where the variety of terrestrial prey diminished, tropical Pleistocene hunter–gatherers certainly targeted terrestrial foods such as the fruit bat on New Ireland (Leavesley 2004). However, in a recent summary O'Connor *et al.* (2017) have reviewed Pleistocene dietary remains in sites from Sunda to Sahul and noted an unusual distinction between archaic human and AMH deposits across Wallacea, where archaic human sites reflect no dependence on littoral/marine resources and AMH sites show the opposite:

> All records indicate that *H. sapiens* that moved through the islands east of Huxley's Line were able to do so as a result of ecological flexibility and innovation, which allowed them to successfully subsist on the most depauperate of islands through the exploitation of almost purely marine resources. (O'Connor *et al.* 2017: S578)

Shellfish, and especially species from fringing reefs, form the most consistent aspect of these assemblages although none of the sites reviewed apparently relate directly to the initial colonisation. OFT suggests that in these circumstances larger species of shellfish, such as *Tridacna spp.* (Bird & Bliege Bird 1997; Codding *et al.* 2014; O'Connell *et al.* 2010) would have been frequently exploited high-ranked resources because of low search time and easy processing. When such resources are depleted, OFT suggests that the predator either adds lower ranked prey to its diet or moves to a new location where the higher ranked resources are more common. Moving to pristine shell beds was an obvious strategy, particularly in the eastern islands of Wallacea where terrestrial resources may have consisted only of reptiles, rats and bats.

Despite the argument that higher sea stands support the most food-productive littoral zones, the idea that lower sea levels may have facilitated onward movement between islands has had a recent resurgence for various reasons, none of which should be accepted uncritically. For example, Norman *et al.* (2018) begin with the premise that AMH had reached Sahul between 60 and 70 ka, at which time low sea levels enlarged islands and reduced distances between them. Here the argument is predicated on the Madjedbebe dates; the lower sea levels of this period require an accommodation to fit the dates rather than offering an explanation for human transit. These authors apply an intervisibility analysis ("bi-directional macro-viewshed analyses") and test the results against various simulations involving, for example, push-pull factors and ocean currents. They conclude that their model predicts that entries into Sahul via both of Birdsell's northern and southern routes were "almost certain". Although the discussion is obscure, these authors flag "the potential for temporally phased migrations into

Sahul through the north-west shelf and the Bird's Head" which we take to mean that they favour an earlier entry into north Australia from Timor. This is *post hoc* justification.

Bird *et al.* (2018) are concerned mainly with routes and develop an argument that the southern route would have provided the best corridor for first colonists with "savannah-adapted skills" as a basis for supporting initial arrival into north Australia from Timor. They work within a wider time framework for this event, between 70 and 47 ka, to cover the long and short chronologies. They note that sea levels, the major determinant of the relevant palaeogeography and palaeoenvironments, fluctuated c.10 m during this time, with the greatest dry land exposure and shortest island crossings coinciding with the claimed date of 65 ± 5 ka for Madjedbebe. Accepting a conservative drop of sea level to −75 m and using intervisibility and drift modelling, Bird *et al.* propose that the Sahul Banks, between north-western Australia and Roti-Timor were both visible and feasible AMH habitats in terms of available food and water and thus add support to the viability of Birdsell's southern route. At the same time, these authors do not deny the probability of the northern route being used, nor the possibility that it provided AMH access to Sahul equally as early as the Timor route. Much depends on the claimed viability of the Sahul Banks for human sustenance, argued by Bird *et al.* on modern analogies with an island in the Pacific, another in the Indian Ocean and nearby Ashmore Reef. The reliability of these comparisons is worth further examination.

De Deckker *et al.* (2019) suggest on evidence from a new deep-sea core that the climate cooling of MIS 4 between 71 and 59 ka was more extreme than currently believed and was a major glacial period in the Southern Hemisphere. They argue that glacial conditions peaked at 65 ka at which time sea levels were lowered by 100 m and sea surface temperature dropped 5°C. Leaving aside the diminishing of Anderson's warmer seas and other environmental effects − perhaps including a more limited distribution of bamboo at this time − these authors uncritically accept the coincidence of the central age of this stadial interval and the nominated age for Madjedbebe, without acknowledging the uncertainties of this comparison or noting previous criticisms made of the Madjedbebe evidence (e.g. O'Connell *et al.* 2018).

Three further papers by Kealy *et al.* (2016, 2017, 2018) remain more centrally concerned with routes that are determined by island intervisibility. The 2016 paper is part review but also draws attention to c.100 submerged Wallacean islands that may have been exposed depending on Pleistocene sea levels, arguing that lowest sea level points are less important than understanding the total seascape during the relevant colonisation period. The 2017 paper develops this theme by offering five palaeogeographical constructions of sea levels and uplift rates at 5000-year intervals between 65 and 45 ka. These data are then used to construct intervisibility models that indicate a visual pathway from Timor to north-west Australia before 62 ka and after 47 ka but not between. Instead, as Irwin showed in 1992, Kealy *et al.* (2017: 69)

conclude that on the basis of intervisibility Birdsell's northern route was "the more likely route for initial colonization". The 2018 paper elaborates these themes further, taking 70 ka as a proxy for the time of the highest sea level and 65 ka as a proxy for the lowest sea level during an assumed colonisation period of 70 to 40 ka. Using least-cost pathway models (see Kealy *et al.* 2018: 63 for explanation), these authors conclude, contra Norman *et al.* (2018) and Bird *et al.* (2018) that their models result in "overwhelming support" for initial entry via the northern route, whether one considers the highest or lowest sea-stands in the relevant period. Of minor importance here, some details of these papers will need adjustment if the sea levels during the MIS 4 glacial period argued by De Deckker *et al.* (2019) are correct.

In reviewing these papers, we cannot escape the conclusion that current research on this subject is discovering more and more about less and less. Birdsell had arrived at many of the current conclusions in 1977 using only the data available to him at that time, as did Irwin in 1992. More elaborate data bases and computing might provide more "robust" evidence for the same conclusions, but if they only reinforce what we already know, is this a significant advance? When arguments revolve around whether intervisibility is to be measured from a reconstructed sea level, or 10 m above that sea level or from the highest available mountain, has research become pedantry?

At the same time, many of these papers now touch the edges of important new conclusions. Evidence from Wallacea and Sahul has slowly accumulated to judge the cognitive, technological and artistic skills of late Pleistocene AMH (see Bird *et al.* 2018: 437 for a summary and references therein). The idea that both of Birdsell's routes were viable at roughly contemporaneous times seems an inevitable conclusion from the multiple papers dealing with this aspect. Kealy *et al.* (2016: 170) elaborate this idea by proposing that AMH movements in Wallacea are better seen as "a radiation of island colonisation" than direct west-to-east movement. We agree. Various lines of evidence, especially the genetics reviewed here and elsewhere, indicate higher numbers of first colonists than earlier minimalist models required. For most archaeologists accidental colonisation of Wallacea and Sahul by AMH is no longer seriously considered (but cf. Bird *et al.* 2019).

## GENOMIC DATA DEMAND THE ATTENTION OF ARCHAEOLOGISTS

Molecular anthropology has had an increasing impact on archaeological practice worldwide since the publication of the highly influential paper on mitochondrial DNA and human evolution by Cann *et al.* (1987). Analyses of progressively larger samples of DNA have enhanced understanding of genetic diversity in living populations, including those of New Guinea and Australia.

Improvements in protocols for the treatment of ancient DNA have helped alleviate contamination problems and now provide more precise estimates of mutation rates in the Late Pleistocene, fundamental to estimating the antiquity of indigenous Sahul genetic lineages. Opportunities for more comprehensive integration with archaeological findings are steadily increasing. Nevertheless and similar to the acceptance of radiometric dating techniques that are not completely understood by archaeologists, so far local archaeologists have been content to cherry-pick interpretations of genomic analyses that coincide with their arguments. Broader consideration of the results of genetic analyses is essential to appreciate their implications for understanding the process of Sahul colonisation. The necessary comprehensive review is beyond the scope of this discussion, but reference to recent work on mtDNA indicates some of the more important insights to be gained from this research. Y-chromosome data show parallel patterns, with deeply rooted Sahul-specific haplogroups C and K diverging from the most closely related non-Sahul lineages c.54 ka and dividing into Australia- and New Guinea-specific lineages c.48–53 ka (Bergström *et al.* 2016).

Geneticists have known for more than a decade that the first AMH populations colonising Sahul included representatives of all three Eurasian mtDNA macrohaplogroups, now called M, N and R (Huoponen *et al.* 2001; Ingman & Gyllensten 2003; van Holst Pellekaan *et al.* 2006). Estimates of the minimum *effective* founder population sizes (the numbers of reproductive-age women) required to insure the post-arrival persistence of each of these groups have led to further estimates of the minimum total (a.k.a. census) populations of which they were a part. Initially the census estimates were in the scores of individuals for each macrohaplogroup (O'Connell *et al.* 2010) and in the hundreds for all three combined (O'Connell & Allen 2012). Developing more accurate figures has required identifying a more complete inventory of indigenous Australia–New Guinea mtDNA lineages, determining their respective ages relative to the date of initial Sahul colonisation, and inferring whether they are likely to have evolved either offshore before colonisation or after their ancestors arrived on the continent. Evidence of their presence outside Australia–New Guinea may point to an exotic origin, since indications of back-flow from Sahul remain limited. Nonetheless, this possibility complicates the inference, as do the further possibilities that evidence of their presence in Sunda or Wallacea prior to Sahul colonisation may have disappeared over time, or that some colonising mtDNA haplogroups have since disappeared within Sahul.

In two recent studies of whole genome and control region mitochondrial diversity in samples obtained from hundreds of living Aborigines in many parts of Australia, Nagle *et al.* (2017a, 2017b) identified at least three common haplogroups – M42, $S^N$ and $P^R$ – together with M15, M16, $O^N$ and N13. All are highly diversified, implying long-term presence on the continent. Tobler *et al.* (2017) reporting on a different but still relatively large whole mitogenome

dataset developed from hair samples collected in the last century from living Aborigines, most of Arnhem Land and South Australian origin, found at least five well-defined haplogroups – M16, M42, $S^N$, $O^N$ and $P^R$, again mostly highly diversified. Over a decade ago, Friedlaender *et al.* (2005, 2007) and Merriwether *et al.* (2005) published on more than a thousand whole mitogenome and control region sequences, mainly from Island Melanesia, most assigned to haplogroups $Q^M$ and $P^R$ but with a notable few placed in M27-29. Haplogroups $Q^M$ and $P^R$ were again highly diversified, with most of those in $P^R$ (P1-2, 3b, 4) representing haplotypes not found in Australia (see also Tommaseo-Ponsetta *et al.* 2013).

Precise estimates of the ages of these various haplogroups (i.e. their respective "times to most recent common ancestors", or TMRCAs) vary depending on the sources and numbers of individual haplotypes included in analyses and on the estimated inclusion (mutation) rate for characteristic genetic markers (Table 1). Two rates cited in recent literature are important here: one based on phylogenetic comparisons (Soares *et al.* 2009); the other on analyses of ten ^{14}C-dated Late Pleistocene *H. sapiens* skeletons distributed across Eurasia (Fu *et al.* 2013). The rates are similar but both Nagle *et al.* and Tobler *et al.* consider the Fu *et al.* rate to be more accurate. Relying on that rate, Tobler *et al.* estimate median TMRCAs for five haplogroups in the range 43–48 ka, though with 20–30 ky error bars (95% CI) associated with each (Table 1). Given those estimates, inspection of the basal splits shown in their overall phylogeny (Tobler *et al.* 2017: fig. 1) leads Tobler *et al.* to suggest that those the splits between three older sets of Sahul haplogroups representing each of the main Eurasian lineages (M16 and M42 within M; O, S and N13 in N; P within R) took place c.50 ka. Assuming that the median dates listed in Table 1 are relatively precise, that estimated ages for the older splits are accurate, and that initial colonisation took place somewhere in the range 47–51 ka (Allen & O'Connell 2014; Veth *et al.* 2017], then as many as six pre-Sahul mitochondrial haplogroups may have been represented among the founders (Tobler *et al.* 2017).

Nagle *et al.* (2017a, 2017b) offer a more comprehensive set of TMRCA estimates based on both the Fu *et al.* and Soares *et al.* replacement rates, including at least one estimate >50 ka for six lineages but again with wide error bars (Table 1). Early estimates listed here for basal P along with the presence of P9-10 haplotypes in the Philippines are seen by some (e.g. Larruga *et al.* 2017) to indicate an offshore origin for earliest Sahul representatives of this haplogroup. Others prefer an intra-Sahul emergence based on similar estimated time depths for P9-10 versus Australian P subtypes (Nagle *et al.* 2017a, 2017b; John Mitchell pers. comm. 2019), though this begs the question of its presence in the Philippines. Comparably grounded calculations are unavailable for Melanesian haplogroups P1-2, 3b and 4, Q and M27-29 reported by Merriwether *et al.* (2005) and Friedlaender *et al.* (2007) but their published mutation counts and phylogenies suggest that

Table 1.    Estimated time to most recent common ancestor (TMRCA) (median, 95% CI calibrated in ka) for selected mtDNA haplogroups. Data and analyses were reported in three sources (Nagle *et al.* 2017a, b; Tobler *et al.* 2017). TRCMA estimates were based on calibrated mutation rates reported either by Fu *et al.* (2013) or Soares *et al.* (2009). Columns 1–2, 3–5 and 6–7 in the bottom third of the table list haplogroups reported in one of the three data sources and related TRCMA estimates derived via one or the other calibration. Thus, for example, Tobler *et al.*, using the Fu *et al.* calibration, estimated the TRCMA for haplogroup M42 at 45.7 (35.4–56.6) ka. Note that haplogroups were similarly but not identically defined across all data sources. TMRCA estimates were based on different haplotype samples reported in each data source; hence differences in those estimates are not unexpected. Note also some complexity in labelling: M42a'c includes M42a and M42c; P5 is derived from P; P11 is a relabelled version of P4b (see Tobler *et al.* and Nagel *et al.* for details).

| Tobler *et al.* (2017) | | Nagle *et al.* (2017a) | | | Nagle *et al.* (2017b) | |
|---|---|---|---|---|---|---|
| **Calibration** | **Fu *et al.* (2013)** | | | **Fu *et al.* (2013)** | **Soares *et al.* (2009)** | | **Soares *et al.* (2009)** |
| | | M42a'c | 53 (42–66) | 50 (39–62) | | |
| M42 | 45.7 (35.4–56.6) | M42a | 36 (27–46) | 39 (31–47) | M42a | 55.2 ± 16.7 |
| | | Q | 44 (34–55) | 53 (37–68) | Q | 53.1 ± 12.9 |
| S | 47.2 (36.9–58.6) | S | 51 (40–64) | 49 (39–59) | S* | 49.5 ± 10.2 |
| O | 42.5 (31.6–61.3) | O | 37 (25–50) | 43 (28–59) | O | 39.5 ± 13.4 |
| | | P | 60 (50–73) | 62 (54–70) | P* | 57.4 ± 11.7 |
| P4b | 45.7 (36.1–56.1) | P11 | 50 (39–62) | 39 (29–48) | P4b | 48.4 ± 15.5 |
| P5 | 43.8 (33.6–55.9) | P5 | 31 (23-41) | 28 (18-39) | | |

Labelled groups are similarly but not identically defined across all published sources. TMRCA estimates are based on different haplotype samples; hence differences in those estimates are not unexpected. M42a'c includes M42a and M42c; P5 is derived from P; P11 is a relabelled version of P4b.

TMRCAs for some of these may also be >50 ka. Our reading of Cooper (section on 'Genetics' in O'Connell *et al.* 2018) leads us to suggest that as many as 9–10 haplogroups may have been present among the Australian founders. Based on the Friedlaender *et al.* and Merriwether *et al.* findings, we would add perhaps two to three among the earliest arrivals in New Guinea.

Despite the obvious and important uncertainties in all of this and the possibility that some founding lineages disappeared after arriving in Sahul, the number of mtDNA haplogroups represented among the colonisers must have been at least four (M, N, R and P), five if we include Q whose status is less clear, and possibly as many as a dozen or more overall. Assuming, as above, that each haplogroup was represented by an effective population numbering in the tens and a census population numbering in the scores, the colonising meta-wave might have been in the low thousands. Relying on essentially the same genetic data, Bird *et al.* (2018: 437) make this point explicitly. It is repeated by Kealy *et al.* (2018: 63). Notions of significant transport capacity – watercraft capable of holding scores of passengers and of maintaining technically aided headway in contrary currents – are reinforced.

The crucial question at this point is whether the descendent haplogroups of M, N and R had diversified before arrival in Sahul or after. Bergström *et al.* (2016) advocate a single founder group settling what is now Australia and New Guinea, but one that separated soon after arrival. As just proposed, we consider that the data can equally be read to imply haplogroup diversification prior to arrival in Sahul. Both the projected time constraints between an initial arrival date of c.50 ka and the estimated TMRCAs for the haplogroups listed in Table 1, and their geographical distributions, about to be reviewed, lead us to this view.

Superimposed on these data is one further element of complexity. Stone tools and human fossils show that pre-AMH hominin populations had crossed into western Wallacea (Philippines, Sulawesi, Flores) more than a million years ago and persisted there until the arrival of modern humans (Brumm *et al.* 2010; Ingicco *et al.* 2018; Sutikna *et al.* 2016; van den Bergh *et al.* 2016). Recent genetic analyses indicate the presence of at least three archaic groups in these populations – Denisovans and two less well-known entities labeled EH (extinct hominins) 1 and 2 (Teixeira & Cooper 2019). Resource competition with incoming AMH seems likely and if AMH populations were larger, their technologies more complex and their subsistence economies more broadly based, as the available evidence suggests, then rapid displacement of the indigenous archaics would have been inevitable. Genetic data suggest it was accompanied by significant archaic-AMH introgression: evidence of interbreeding between AMH, Denisovans, EH1 and to a lesser extent EH2 is present in modern human genomes throughout Wallacea, New Guinea and Australia (Teixeira & Cooper 2019: fig. 2). The parallels between this process and the displacement of Neandertals by AMH in western Eurasia slightly later in time are striking. The opportunity for comparative analysis, beyond us here, is obvious.

**FURTHER INFERENCES FROM GENOMICS**

Although at this stage problematic, the distribution of indigenous mtDNA haplogroups across modern

Figure 1. Wallacea and adjacent parts of Sunda and Sahul, showing locations mentioned in text and land exposed by –60 and –120 m sea level falls relative to modern. Dotted line shows A. R. Wallace's phenotypic division of "Malayans" and "Papuans" (after Bellwood 2017).
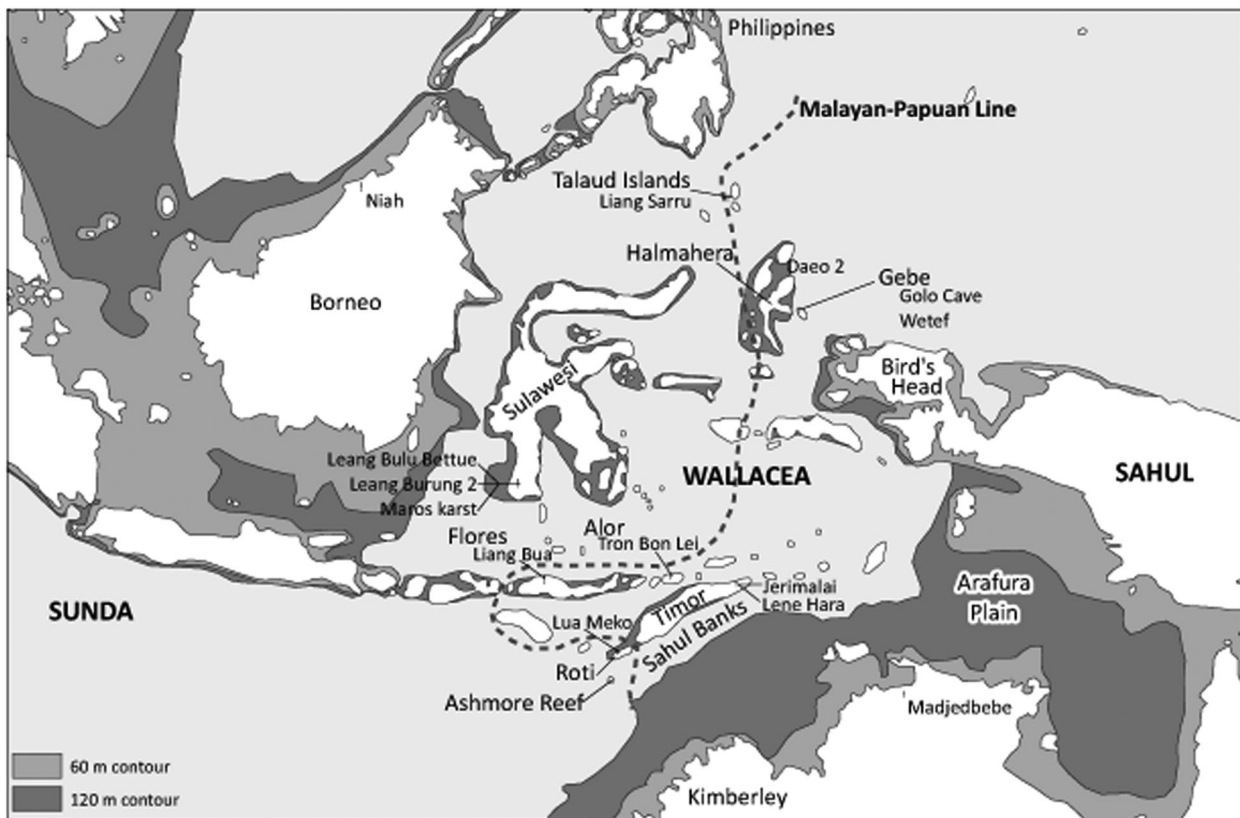


Australia–New Guinea offers hints about landing points on Sahul. Three contiguous locations suggest themselves. The New Guinea Bird's Head would allow colonisers to move either east along the north coast of Sahul or south onto the eustatically exposed Arafura Plain. Colonisers might also have landed on the Arafura Plain itself, then moved eastwards to the east coast and south into the woodlands underlain by the Great Artesian Basin, connecting with the Murray–Darling Basins and the south coast of Australia. Landing on the Arafura Plain or further south in the Kimberley region would also allow access south along the west coast and deep into the interior via rivers such as the Ashburton, Fortescue and Gascoyne.

Although both Australian Aborigines and New Guineans share the founding mtDNA macrohaplogroups M, N and R, distinct north-south differences are apparent. For example, from R, the deep subclade P is found in Australia and New Guinea as haplogroups P3a and P11 in the south and P3b and P4 in the north. Similarly, within M, a characteristic variant nucleotide position, 13500, is widespread in New Guinea and island Melanesia but has only a single cited presence in Australia (Hudjashov *et al.* 2007) that may be a product of recent history (Nagle *et al.* 2017a, 2017b). The Y-chromosome data indicate similar deep time splits. On a more regional basis, the prevalence of mtDNA haplogroups $Q^M$, M27 and New Guinea-specific subsets of $P^R$ in the Highlands and further east in island Melanesia as well as

their absence in the continental south point to the arrival of these groups on the Bird's Head. Relatively high numbers of haplogroup $O^N$ along the west Australian coast suggest a landing in the Kimberley, possibly via Timor. The prevalence of haplogroups M42, $S^N$ and Australia-specific $P^R$ across most of Australia but not northern New Guinea fits best with arrival on the Arafura Plain. No single line of advance across Wallacea nor any single landing point on the Sahul shore is indicated. Instead a spatially complex wave, internally structured along mitochondrial and other genetic lines, is strongly implied. At the moment, such patterns offer a possible line of inquiry that might one day find resonance in the archaeological record or in other aspects of the genetics. It is intriguing that the cultural divisions between Australian Aborigines and New Guineans may have had their origin in the earliest Pleistocene settlement patterns rather than the formation of the Torres Strait. Certainly, the central New Guinea cordillera and the wet forests of southern New Guinea would have provided a formidable barrier between people moving along the northern New Guinea coast and those who moved south. That division appears to be reflected in these haplogroup data.

This raises the question of the arrival period(s) for founding haplogroups. Did they land in Sahul close in time or spaced out over millennia? Current research is silent on this issue, partly because at this stage the archaeological

record cannot resolve it. Without human skeletal remains, haplogroup identities are not reflected in that record, though if they were, increasing precision in radiocarbon results might provide intriguing insights. Moore (2001) showed that smaller populations were at risk of extinction within a millennium, especially if they were isolated from other groups. Larger founding census populations located close enough to exchange mates would enhance the prospects for small group survival. On this basis, nearly simultaneous, geographically proximate arrivals at different points along the Sahul shore are implied. If further apart in time and space, such landings were less likely to result in individual group survival.

This reasoning has further implications for conditions in Sunda source zones. A push eastward across Wallacea implies significant population increase and associated resource depletion in those areas. Though data pertinent to the latter point are extremely limited, the use of high-cost plant foods such as *Pangium* and *Alocasia* (Barton & Paz 2007) at 40–48 ka at Niah Cave is consistent with such depletion. On population increase, Atkinson *et al.* (2008) appealed to mtDNA variation and used coalescent theory – loosely like considering evolution in reverse – to estimate past growth phases in populations across Eurasia, Australia and into the Americas following AMH exit from Africa. They found that southern Asia shows "the earliest and most pronounced population expansion outside Africa, with a 5-fold increase in population size estimated by 52 kya" (Atkinson *et al.* 2008: 470). Though the date and scale of this particular increase is now subject to adjustment in light of more recent estimates of mtDNA mutation rates, if substantiated it would indicate a powerful push factor for movement into Sunda and across Wallacea.

## WAS SAHUL ISOLATED FROM THE REST OF THE WORLD DURING THE LGM?

Genetic research in the first decade of this century supported a two-stage model of AMH population movement across the Sunda/Sahul arc, the first involving the initial dispersal of AMH, the second the Holocene spread of Austronesian speakers eastward across the region and out into the Pacific. On the basis of recent surveys of Y-chromosome and mtDNA haplogroups in Wallacea scholars now propose a four-stage spread, the first involving the pioneering AMH dispersal and a second Pleistocene dispersal (sometimes called the "early train" model), this latter roughly placed in the range from 40 to 10 ka. Some authors (e.g. Karafet *et al.* 2010) suggest that this dispersal may have occurred after the LGM, timing that would be consistent with inferences above about post-LGM increases in littoral resource availability. Stage one is marked by the derivatives of mtDNA and Y-chromosome haplogroups reviewed above, while the second is marked by mitochondrial haplogroups B4, B5, D and E and Y-chromosome haplogroups O-M119*, O-M95*, O-P203 and O-M122 that swamped lineages associated with initial

AMH dispersal across the region (Gomes *et al.* 2015; Hudjashov *et al.* 2017; Jinam *et al.* 2012; Karafet *et al.* 2010; Tumonggor *et al.* 2013). We assume that individuals represented by the recently reported late Pleistocene human skeletal remains from Alor (Samper Carro *et al.* 2019) were descendants of one or the other of these incoming groups.

The second stage population spread resulted in a strong division in the genetic make-up of east and west Wallacea with the east genetically reflecting the original founding stage unaltered by the second stage influx. It is unclear whether this means the second stage did not penetrate the eastern Wallacean islands or whether this could reflect back flow from Sahul. The boundary between the two genetic zones coincides with A. R. Wallace's phenotypic division of "Malayans" and "Papuans", a line running south between Sulawesi and Maluku and then west of Flores (Figure 1) (Wallace 1869: vol. 2, chap. 40). This should not be confused with Wallace's biogeographical divide known as the Wallace Line, or other Wallacean divisions such as Weber's Line or Lydekker's Line. Cox (2017: 111) underlines the genetic importance of this divide, suggesting people on opposite sides of Wallacea exhibit amongst the largest differences in genetic diversity anywhere: "Differences of this magnitude have only been observed elsewhere when imposed by major geographical barriers such as the Himalayas or the Sahara Desert. . . . . . [C]urrent interpretations favour restricted mobility of hunter–gatherer populations during the Pleistocene".

Why might AMH mobility be apparently unrestricted at 50 ka, but restricted at the terminal Pleistocene? One plausible hypothesis is that falling sea levels inhibited previous levels of AMH mobility. Terrell (2004) suggested that during periods of low sea level the north coast of New Guinea may have become uninhabitable as reefs, lagoons, floodplains and swamps were replaced by dry land, rocky coasts and entrenched rivers, and that New Guinea may have therefore been isolated during the terminal Pleistocene. We believe this argument should be extended more generally to steep rocky coasts in Sahul and the Wallacean islands.

In general terms and following the sea level curve proposed by Lambeck and Chappell (2001), sea levels at 50 ka were between −40 and −50 m relative to present levels. Subsequently sea levels fluctuated gradually downwards to c. −80 m between 35 and 31 ka, after which they descended rapidly towards a low stand of −120 m. Lambeck *et al.* (2014) using data from several different world locations suggest a rapid fall of 40 m in <2000 years, between 31 and 29 ka. Recent fossil reef drilling data from two locations on the shelf edge of the Great Barrier Reef (GBR) indicate a second plunge towards the full extent of the LGM that occurred at 22 ka (Webster *et al.* 2018; Yokoyama *et al.* 2018). The oldest reef in this part of the GBR (Reef 1) died from subaerial exposure, an event constrained by dates of 35.6 ± 0.3 ka and 34.3 ± 0.3 ka. Reef 2 began to grow after the 40 m plunge at 27 ka, but died when subaerially exposed between 22.11 ± 0.23 ka

and $21.87 \pm 0.24$ ka, the point at which the sea fell a further 20 m in a second 1–2 millennia period.

From c.21 ka to c.17 ka modelling of global sea levels suggests that they dropped further to between –125 and –130 m and slowly rose to –120 m at c.17 ka, after which sea levels rose rapidly with deglaciation. Given that these large episodic sea level falls occurred during such relatively limited time periods, change may have been noticeable within human lifetimes; even if not, the overall environmental effects must have been dramatic.

Accepting the subsistence dependence on coastlines and reefs argued earlier, it is especially pertinent to ask what occurred with fringing reefs during the sea level descent towards the LGM. There is a vast literature on the evolution of tropical coral reefs and especially the GBR, but much of it relates to periods when postglacial rising seas provided appropriate conditions for fringing reef systems to grow and expand. Coming to terms with the opposite proposition, that fringing reefs shrank in size or disappeared in periods of sharp sea level decline, confronts not only a much smaller research literature but also the wider problem that factors affecting reef evolution may be highly island- or area-specific. Apart from changes to reef accommodation space during changing sea levels, reef growth is affected by sea surface temperature, tectonic subsistence or uplift, the steepness of marine slopes, water turbidity/light and the production levels of $CaCO_3$ among other factors (Montaggioni 2005). Various researchers point to the inhibiting factors for reef development during periods of declining sea level (e.g. Abbey *et al.* 2011: 75; Gischler *et al.* 2013: 1463; Camoin *et al.* 2001; Webster *et al.* 1998, 2018: 339). The GBR research referred to above showed that Reef 2 began to grow as low sea levels stabilised in the LGM between $27.35 \pm 0.14$ ka and $27.34 \pm 0.07$ ka. "At this time the GBR formed a very narrow and ephemeral reef system" (Webster *et al.* 2018: 428). As a generality, whether fringing reefs grew during periods of descending sea levels appears to depend on both the speed of sea level descent and the steepness of underwater slopes. Since inter-island distances in Wallacea were not significantly increased when sea levels descended to –120 m (Irwin 1992: 22), this implies that the submarine topography of many Wallacean islands involves steep slopes not conducive to reef growth in times of falling sea levels. In addition, fringing reefs will preferentially accrete vertically (Kennedy & Woodroffe 2002) and die when exposed subaerially as sea levels drop. Depending on their morphologies, a common predicted palaeo-shoreline would be raised coralline cliffs, not unlike present-day *makatea* islands found in the Pacific (although there created by uplift) that would offer both difficult landings and poor foraging locations.

Testing the hypothesis of drastically reduced mobility coinciding with sea level decline remains difficult. A simplistic proposition might be that if true, Wallacean island sites should reflect human depopulation especially during the LGM. The archaeological record indicates that some sequences indicate abandonment but in others occupation occurs immediately at and around the LGM. To take a few examples reviewed by O'Connor *et al.* (2017), Liang Sarru in the Talaud Islands was occupied at 35–30 ka, then at 21–17 ka and not again until the Holocene (Ono *et al.* 2009). A large suite of dates from Golo Cave and Wetef Shelter on Gebe Island in the Maluku Islands suggest initial occupation of both sites c.36 ka, continuing to c.26 ka and then abandonment until the terminal Pleistocene/Holocene (Bellwood *et al.* 1998, 2019: table 1.1). Daeo 2 on Morotai in Halmahera was first occupied between 16.8 and 15.9 ka (Bellwood 2019: table 1.1) during the rapid post-LGM sea rise. O'Connor (2007: fig. 3) reports a calibrated date of c.42 ka for basal deposits for Jerimalai shelter on Timor, 50 cm below a date of c.14 ka. It is unclear whether the shallow deposits between these dates represent continuous occupation, but with an average accretion rate of <2 cm/1000 yr, possibly not. Also on Timor, Lene Hara cave is now shown to be of the same antiquity as Jerimalai (O'Connor *et al.* 2010) but appears to be abandoned from c.30 ka until the last several thousand years (O'Connor *et al.* 2002). Similar but slightly younger ages have been proposed for cave art in the Maros karsts of Sulawesi (Aubert *et al.* 2014). Tron Bon Lei shelter on Alor Island in the Lesser Sunda Islands was occupied from c.21 to 18 ka then not again until the early Holocene (Samper Carro *et al.* 2016). Three sites on Roti Island have yielded 13 $^{14}$C dates of which one from Lua Meko cave was c.24 ka, while the remainder were Holocene (Mahirta 2009). An Optically-Stimulated Luminescence (OSL) date from basal sand 10 cm below the Pleistocene date for Lua Meko provided a "tentative" age of c.29 ka. The author notes reduced deposition during or after the LGM during which time human occupation was much more infrequent or absent.

Although it needs remembering that available data sit above current high sea levels, implying much must now be submerged, few other islands in Wallacea have yet revealed any evidence of Pleistocene occupation by AMH. Even allowing for the sample to be unrepresentative it is interesting that no site ages have yet been reported that overlap the range of 47–51 ka demonstrated for Sahul. Any extension of the colonising date for Sahul to 65 ka or older increases this dichotomy. Here we note but pass by the tantalising possibility that the re-excavation of Leang Burung 2 on Sulawesi (Brumm *et al.* 2018) and the on-going excavation at the less-disturbed and nearby Leang Bulu Bettue (Brumm *et al.* 2017) might provide such evidence, given that deep-trench excavations at neither of these sites have reached bedrock below cultural deposits spanning 50 to 40 ka; see also the continuing work at Liang Bua on Flores (Sutikna *et al.* 2016, 2018; Morley *et al.* 2017). Presently, and excepting the Timor sites, most Pleistocene sites in Wallacea only become archaeologically visible at a time when sea levels descended towards –60 m and beyond. It is tempting to link occupation after 35 ka and especially those sites dating around the LGM with the observation by O'Connor *et al.* (2017) that lowered sea levels connected small island archipelagos into larger landmasses that provided more subsistence

viability for human occupation. If this correlation holds it might imply that terminal Pleistocene humans remaining in Wallacea were adapting the strandlooper strategy of the earliest colonists to one where falling sea levels reduced both reef area and high-ranked reef resources, requiring these people to extend the food quest to include a wider range of lower ranked resources. For example, it may be telling that Golo Cave contains mostly small shell species (Peter Bellwood pers. comm. 2019). Are all Wallacean sites younger than 35 ka the same?

Under this hypothesis, it appears possible that the marine "highway" that facilitated AMH entry into Sahul became less productive and less accessible by c.35 ka and increasingly difficult into the LGM. Might Sahul have been effectively isolated by this changed ecology for unknown millennia until rising sea levels again linked it to Wallacea? Might the Wallacean archaeology from these periods be reflecting remnant populations adapting to this massive environmental shift? These ideas are in step with the proposition that high sea levels facilitated both AMH occupation in, and transit through Wallacea towards Sahul (Chappell 1993; Chappell & Thom 1977; Terrell 2004). They pose questions to others like Clarkson *et al.* (2017), Norman *et al.* (2018) and De Deckker *et al.* (2019) who favour low sea level transit at c.65 ka. Such ecologically driven isolation would also explain the Wallacean/Sahul genetic disjunction.

## CONCLUSION

Advances in genetics, and in our case advances in Sahul-specific mtDNA in particular, lead us to conclude that the colonisation of Sahul involved at least hundreds and possibly more people who arrived within a time frame sufficiently limited to permit and promote the continuing growth of founder populations that quickly spread through the continent. This model builds on previous discussions of various factors affecting successful colonisation (e.g. Allen & O'Connell 2008; O'Connell & Allen 2012, 2015; O'Connell *et al.* 2010).

As noted earlier, our present argument is predicated upon our assumption that the haplogroup mutations we identify mostly occurred prior to, rather than after humans arrived in Sahul; this is currently a contested idea (e.g. see Bergström *et al.* 2016; Nagle *et al.* 2017a, 2017b). We have promoted our position based on (1) that the earliest AMH arrivals included representatives of all three Eurasian mtDNA macrohaplogroups, M, N and R; (2) that evidence of the presence of P9-10 haplotypes in the Philippines and Sahul is best explained as pre-Sahul divergence. This allows the possibility that more external matches will be located; (3) that despite the wide error ranges, TMRCA estimates approach and surpass the most likely date of human arrival in Sahul; and (4) the current distribution of indigenous mtDNA haplogroups across Sahul suggests different arrival points on the Pleistocene continent.

While this paper was in preparation, Bradshaw *et al.* (2019) reported a similar conclusion to ours. Based on an entirely different modelling procedure, these authors proposed a census founding population of 1300 to 1550 people arriving at a single point in time or within a period of about 700 to 900 years. A similar founding population of 1000 to 2000 people was previously proposed by Williams (2013).

If these models prove accurate, the demographic scale of this colonisation was such that the process must have been far more complex than has so far been acknowledged. However, researchers coming from an archaeological base have been content to refine old paradigms that do not confront the complexities implied by such founding numbers. Minimalist constructions that were once appropriate need revisions that accommodate these new models. In particular, secondary arguments, such as privileging low sea levels to support the long settlement chronology, should be avoided. We are reminded that several decades ago, claimed dates of c.46 ka for the disappearance of the megafauna caused colleagues to switch from favouring the long colonisation chronology for the short one, in order to preserve the concept of blitzkrieg.

We have offered here further data and argument about why we are sceptical of the low sea level argument. In the same way that our discipline has assessed accidental colonisation to be so unlikely that most no longer consider it, we should also move on from the sea level debate and abandon the argument about routes. There is now consensus in the literature that all routes were possible and choosing the primacy of one over another seems only to depend on which variables are stressed. Given our proposed demographic model, we think that Birdsell's west-to-east migration routes, that have served us so well until now, might better be replaced by considering a general eastwards-moving human progression that occupied most or all of the useful islands of Wallacea in turn (Kealy *et al.* 2016), eventually to access Sahul at various locations.

Lastly, the discipline should now be integrating palaeoenvironmental, archaeological and genetic data that lead to the recognition and formulation of the next-generation set of problems. As a start, we would include among them (1) refining the number of first-wave colonising groups arrived in Sahul; (2) refining the time period over which these mitochondrial populations arrived; (3) identifying the distribution of their respective landfalls and patterns of dispersal across the continent; (4) determining the sizes, internal complexity and subsistence economies of their respective SE Asian source populations, being factors that framed the "push" for movement into and across Wallacea; (5) exploring Wallacean Pleistocene histories against the backdrop of significant sea level change; and (6) considering the effects of potential isolation for Sahul populations through the LGM.

Brian Codding, Murray Cox, Iain Davidson, Kristen Hawkes, Lisa Matisoo-Smith, John Mitchell, Nano Nagle, Christophe Sand, Steven Simms, Ray Tobler, Jody Webster, Peter White and Alan Williams. Shannon Arnold-Boomgarden drew the map.

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