An Invited Perspective by Murray Cox

Although often unrecognized, molecular anthropology has a surprisingly long pedigree in Island Southeast Asia. Just five years after Hirsfeld and Hirsfeld (1919) performed the first population genetic analysis of human blood groups (in the global mix of soldiers fighting in Europe during the First World War), the first studies of blood group diversity across Island Southeast Asia were being published (Bais and Verhoef 1924; Heydon and Murphy 1924). In this respect, the founding of molecular anthropology was contemporary with the first major work of modern social anthropology (Malinowski 1922), which similarly benefited from the stimulating environment of Island Southeast Asia and the Pacific region in the 1910s and 1920s.

A century later, research on the molecular diversity of Island Southeast Asia is nearly unrecognizable in all but its aim: to reconstruct the history of the region’s peoples using inherited genetic characters. Early work on blood groups, both the familiar ABO system and more esoteric blood proteins such as Duffy and hemoglobin, provided relatively little definitive insight into population prehistory. The key exception was a consistently observed distinction, albeit often blurred, between populations in Melanesia versus those in Island Southeast Asia and Polynesia (Cavalli-Sforza et al. 1994; Mourant et al. 1976), a feature of Pacific genetic diversity that is still important for understanding the prehistory of this region today.

Molecular anthropology really came into its own during the late 1980s and early 1990s when new molecular techniques, particularly the Polymerase Chain Reaction (PCR), first allowed researchers to observe small DNA changes directly. Sex-specific markers, especially on the maternally inherited mitochondrial DNA (mtDNA) and the paternally inherited Y chromosome, gave us our first estimates of the times and movements of prehistoric groups in the Pacific region (Kayser 2010). Today, ongoing success in automation and miniaturization is allowing geneticists to analyze whole genome sequences – the entire DNA complement of an individual – at community, regional, and global scales. This “genomic” research, which will dominate molecular anthropology for the foreseeable future (Stoneking and Krause 2011), promises to reveal the biological history of peoples in the Indo-Pacific region with ever-increasing precision. Indeed, genome sequences are the ultimate genetic data – at least for the purposes of reconstructing the human past – and any stories that remain untold after the genomic era will necessarily have been lost to the depths of time. Genomic data are even being obtained from ancient DNA, which promises to reveal the biology not of people living today, but of their ancestors.
(Pickrell and Reich 2014). While ancient mtDNA sequences have been reported from the Solomon Islands and New Zealand (Knapp et al. 2012; Ricaut et al. 2010), the first nuclear markers are just appearing and promise great insight into the region’s prehistory (Matisoo-Smith 2015).

Genetic evidence from around the world supports the view that modern humans arose in Africa, dispersing from there around 50 kya to settle Europe and Asia. Although there is some contention around timing and whether there was one or multiple waves (Rasmussen et al. 2011), there is general agreement that the first inhabitants of the Pacific world were the ancestors of today’s Papuans and indigenous Australians. Dating of early archaeological sites indicates that these first travelers probably arrived in, and spread across, Island Southeast Asia within just a few thousand years (O’Connell and Allen 2004). Uniparental genetic markers are consistent with this view: some of the earliest mtDNA lineages to branch off the M and N super-haplogroups (the major trunks of the mtDNA tree that chronicle our species’ rapid expansion out of Africa) are found today in Papuans, indigenous Australians, and some Island Melanesian populations (Ingman and Gyllensten 2003). These very early mtDNA lineages, which include M17a, M47, M73, N21, N22, R21, R22, and R23 (Figure 4.6), are typically rare, but widely dispersed (Tumonggor et al. 2013).

As the first and least legible writing on what has since become a well-used palimpsest, very little is known genetically about these first arrivals. Nevertheless, we see their presence on the Y chromosome as well. Haplogroups C and K, with their downstream branches M and S, similarly highlight a rapid movement out of Africa, followed by a radiation within Island Southeast Asia (Karafet et al. 2015). In contrast to mtDNA, many of these early male lineages reach appreciable frequencies in Island Southeast Asia today, likely reflecting secondary expansions later in the Pleistocene, well after the initial settlement period. Genome-level sequencing promises to improve the resolution of the Y chromosome tree, thereby providing an even more detailed reconstruction of past population movements (Poznik et al. 2013; Karmin et al. 2015).

The African exodus caused anatomically modern humans to encounter and interact with pre-existing archaic hominin populations across Eurasia. For a long time, it was thought that modern humans simply replaced these ancient groups, but growing evidence shows that all non-African individuals derive a small proportion of their genome from Neanderthals (typically 2–4%; Sankararaman et al. 2014). Island Southeast Asians, especially in Wallacea, carry an additional contribution from Denisovans (Krause et al. 2010; Reich et al. 2011), an equally ancient sister group to Neanderthals, otherwise known only from their DNA (Meyer et al. 2012). Morphological evidence for Denisovans is extremely limited, originally comprising just one bone from the tip of a pinkie finger. But with them, for the first time, the genome of an early human species was identified before its skeletal morphology.
Figure 4.6  Approximate migration tracks of mtDNA and Y-chromosome haplogroups into and through Island Southeast Asia in three time bands during the past 50,000 years. The lowest map represents the haplogroups most closely associated with Austronesian speakers.
Because regions of Denisovan DNA are closely linked with markers of Papuan ancestry in Island Southeast Asian individuals, this contact likely occurred during, or very soon after, the expansion from Africa (Cooper and Stringer 2013; Veeramah and Hammer 2014). Intriguingly, genetic contributions from much older hominins have also been detected in modern humans (Hu et al. 2014), possibly hinting at additional contact with *Homo erectus* or *H. floresiensis*. The absence of genome sequences for these older species hinders accurate provenancing of these genetic contributions. Nevertheless, the human genome is increasingly viewed as a mosaic formed from repeated admixture events with other human-like species (and therefore broadly mimicking the species history of other primates such as baboons; Ackermann et al. 2014).

Modern humans may retain these archaic lineages for a reason. For instance, the gene variant that allows modern Tibetans to survive high altitudes in the Himalayas likely derives from archaic humans (in this case, Denisovans) (Huerta-Sanchez et al. 2014), as do key variants in the immune system genes of many Eurasian groups (Abi-Rached et al. 2011). In all likelihood, we owe much more to our sister species than has historically been admitted. Whether genes from archaic hominins provide some biological advantage to modern Pacific peoples remains completely unexplored.

Although the first movements of modern humans into Island Southeast Asia set the stage, the late Pleistocene also saw numerous arrivals and migrations within the region. This contrasts with the occasional portrayal of this period as a long hiatus before the distinctive events of the Holocene. While the perception of stasis is not true, the disruptive processes of the Neolithic now make it challenging to reconstruct population history during the late Pleistocene with any accuracy. Certainly, some founder lineages began to diversify during this period. On the mtDNA, many haplogroups that are common and widespread today (such as B4a, B4b, B4c, B4c1b3, B5a, B5b, B5b1, D, and E) arose between 10 and 40 kya (Soares et al. 2008; Tumonggor et al. 2013). As these lineages vary considerably in diversity (and hence, probably their age) and exhibit quite different geographical distributions, it is unlikely that any single demic event explains their presence in Island Southeast Asia. These lineages often occur as key components of modern populations in Peninsular Malaysia, particularly semi-isolated Negrito communities (Jinam et al. 2012). It therefore seems likely that they reflect repeated population movements from mainland Asia, possibly of hunter-gatherers (such as the Hoabinhians) who lived along the now-submerged river systems that once ran out from mainland Asia between the modern islands of Sumatra, Java, and Borneo.

Although these genetic lineages cannot be linked in any convincing way with specific archaeological assemblages, Pleistocene population movements are also seen on the Y chromosome. Several major subclades of haplogroup O, such as O-M119, O-M95, O-P203, and O-M122, arose between 8 and 35 kya (Karafet et al. 2010; Trejaut et al. 2014). A key feature of Island Southeast Asia, which probably dates to this time, is an exceptionally strong east–west divide in genetic
diversity. Broadly following Wallace’s (1962) biogeographical line, although shifted slightly east in agreement with his lesser-known phenotypic division between “Malayan” and “Polynesian” (also glossed by Wallace as “Papuan”) races (see Figure 5.1), people living across this boundary exhibit one of the largest differences in genetic diversity observed anywhere in the world. Haplogroups C-M38*, M-P34, and S-M254 account for more than half of Y chromosomes in the east and yet are nearly absent in the west. Conversely, haplogroup O lineages O-P203, O-M95*, and O-M119* exceed a frequency of 60% in the west but are markedly less common in the east (<10%; Karafet et al. 2010). Similar patterns are seen in the mtDNA (Tumonggor et al. 2013). Differences of this magnitude have only been observed elsewhere when imposed by major geographic barriers such as the Himalayas or the Sahara Desert. Clearly, no comparable geographic barriers occur in Island Southeast Asia and alternative explanations are necessary. Since Holocene lineages cut across this division, current interpretations favor restricted mobility of hunter-gatherer populations during the Pleistocene. However, like most genetic features that seem best attributed to the Pleistocene period, there is less clarity around how or why these patterns arose.

The genetic events of the Holocene are less ambiguous, simply because they are more recent and have not yet been overwritten. This period is characterized by major dispersals: some ultimately from mainland Asia and possibly attributed to the spread of agricultural populations (Bellwood 2005); others within and between island chains in Island Southeast Asia and perhaps more likely caused by alternative farming and maritime activities (Bulbeck 2008). At least some of these dispersals are also thought to account for the widespread, indeed nearly complete, spread of Austronesian languages across Island Southeast Asia, as well as the first long-distance migrations out into the remote islands of the Pacific (Kayser 2010).

On the mtDNA, lineages M7b3, E1a1a, M7c3c, and Y2 saw major expansions at this time. Perhaps around 20% of these dispersals may reflect movements from Taiwan (Brandão et al. 2016), the favored source location of Austronesian languages, while others may better reflect movements within and between other island groups (such as the Philippines and eastern Indonesia; Tumonggor et al. 2013). Networks representing relationships between lineages are frequently inconclusive about directions of dispersal during the Holocene. When movements are rapid, insufficient time elapses for a step-wise series of mutations to develop, and this characteristic seems to hold for many lineages that arose within, or entered into, Island Southeast Asia during the Holocene. However, many Island Southeast Asian populations do show signs of population growth and expansion at this time, reflected in summary statistics such as Fu’s Fs and Tajima’s D, and also in the “star-like” phylogenies of many mtDNA lineages.

Perhaps the most famous mtDNA lineage is the Polynesian motif (B4a1a1a1) and related forms. Although originally thought to have spread from Taiwan (Hertzberg et al. 1989) and thus providing a direct analogue for the dispersal of Austronesian languages, this lineage is now known to possess an unusual
geographical distribution and its history remains surprisingly unclear (Cox 2005; Richards et al. 1998). The Polynesian motif itself is found only at low frequency in eastern Indonesia (2.3%; Cox 2005), although it reaches as high as 7.4% on Timor (Tumonggor et al. 2014). The lineage occurs no further west than Bali (0.4%; Tumonggor et al. 2013) and is absent from the Philippines (Tabbada et al. 2010), but is the dominant mitochondrial lineage across the islands of Oceania (Duggan et al. 2014). The contemporary view is that the Polynesian motif arose about 6000 years ago, perhaps in the Bismarck Archipelago (east of New Guinea), from where it dispersed more widely as part of later population movements (Soares et al. 2011). Curiously, a variant of the Polynesian motif is exceptionally common on Madagascar (13–50%; Razafindrazaka et al. 2010), an island off the east coast of Africa that was settled during the mid-first millennium AD from western Indonesian sources (Cox et al. 2012).

The Polynesian motif may once have been more common in western Indonesia than it is today, as suggested by genome-wide markers that increasingly place the Asian source of Malagasy in Borneo (Kusuma, Brucato et al. 2016), with likely genetic connections to sea nomad populations (Kusuma et al. 2015). However, an inclusive framework that describes the full distribution of this unusual mtDNA lineage still appears to be lacking; it clearly describes the major population movement from Near to Remote Oceania (Duggan et al. 2014), although a direct upstream connection with population dispersals from Taiwan as part of the Austronesian expansion seems increasingly unlikely (Soares et al. 2016).

Holocene dispersals are also recorded on the Y chromosome. The broad distributions of haplogroup O-P201 and probably O-M110 and O-P203 likely date to this time. Tellingly, these lineages are found on both sides of Wallace’s line, as would be expected if they were carried by rapidly dispersing communities with a strong maritime tradition. Hundreds of thousands of genetic markers spread across the genome are now providing important new insights into possible dispersal routes. All populations in Island Southeast Asia harbor genomic ancestry that is closer to aboriginal Taiwanese (Formosans) than mainland Asian groups (Lipson et al. 2014). Although genome-scale data are still sparse – some populations are politically indisposed to sampling, while others that are critical for reconstructing Island Southeast Asian prehistory have simply not been studied – this evidence provides convincing statistical support that Taiwan played an instrumental role in Holocene dispersals across Island Southeast Asia.

Even more importantly, a team led by David Reich has obtained the first genomic markers from any ancient tropical Pacific remains. More than 144,000 genome-wide markers were screened on ancient DNA extracted from three ~3000-year-old skeletons at the Early Lapita site of Teouma in Vanuatu (Petchey et al. 2014; Skoglund et al. 2016). Crucially, these individuals carry no Papuan variants, but instead closely match part of the genetic profile of indigenous Taiwanese,
such as the Ami and Atayal, as well as populations from the northern Philippines, such as the Kankanaey, that are plausibly descended from the first phase of the Austronesian expansion. Unlike all present-day Oceanians who carry at least 25% Papuan genomic markers, it seems that the Early Lapita settlers reached unoccupied parts of Remote Oceania with minimal admixture along the way, consistent with morphological evidence (Valentin et al. 2016). Thus in both cases of farming dispersals elucidated by ancient DNA – the Austronesian expansion into the Pacific and the spread of Neolithic farmers in Europe – the first migrants did not mix substantially with the people they encountered, and extensive admixture occurred only after a substantial time delay.

This mixing of populations, following the initial dispersal, produced many of the genetic patterns that characterize the region today. For instance, Lipson et al. (2014) identified a second Asian substratum that links western Indonesian populations with Austroasiatic-speaking groups on the Asian mainland. One possibility is that there was once a substantial Austroasiatic presence in Island Southeast Asia, since linguistically erased. Perhaps more likely, non-Austroasiatic-speaking groups may have moved into western Indonesia during the late Pleistocene, with Austroasiatic languages spreading across Mainland Southeast Asia at a later date. Alternately, Austronesian speakers may have interacted with groups in mainland Southeast Asia before expanding into western Indonesia. It follows that Asian movements into Island Southeast Asia during the Holocene may have been two pronged: a western route from the mainland to Sumatra, Java, and Borneo; and a second north-to-south route through Taiwan, the Philippines, and eastern Indonesia. These preliminary results again provide an exciting glimpse of what genome-scale data promise to reveal.

After groups with Asian ancestry spread through Island Southeast Asia during the Holocene, they interacted extensively with earlier Australo-Papuan communities (Friedlaender et al. 2008). At approximately the same time, there were movements westward from New Guinea, bringing the Trans-New Guinea Papuan languages to eastern Indonesia, as well as new agricultural crops such as bananas (Denham and Donohue 2009). Today, almost all Island Southeast Asian and Pacific individuals carry genomic markers of both ancestries. Western Indonesian populations reach nearly 100% Asian ancestry, which drops to zero in many highland New Guinea groups (Cox et al. 2010). Yet surprisingly this change from Asian to Papuan ancestry is not gradual, but instead appears as a sharp transition over a relatively small region of eastern Indonesia. The cause of this rapid shift in ancestry proportions remains unclear, but may be associated with social change following the Austronesian expansion and/or a switch in subsistence practices. Markers from across the genome date the start of this admixture process with considerable certainty to 4000 years ago (Xu et al. 2012). Additional contributions may possibly have reached Island Southeast Asia at this time from India (Pugach et al. 2013), with more definite contacts occurring later.
during the Historic era (Kusuma, Cox et al. 2016). These findings firmly place the admixed nature of Island Southeast Asian peoples within the suite of genetic, linguistic, and cultural changes that so radically altered this region during the mid- to late Holocene.

It is worth noting that movements during the Pleistocene and Holocene are also reflected in genetic systems beyond our own. As we move, so too do the species we carry along with us — willingly or not. Studies of genetic diversity in pigs highlight two movements into Island Southeast Asia: one from Taiwan to the Philippines and colonial-era Micronesia; and a second along the chain of islands linking Sumatra to Timor and then out via New Guinea to Remote Oceania (Larson et al. 2007). Similar stories are told by the movements of chickens (Thomson et al. 2014), rats (Matisoo-Smith and Robins 2004), the paper mulberry (Chang et al. 2015), and other commensal plants and animals. The human pathogen *Helicobacter pylori*, which lives (mostly asymptptomatically) in the stomachs of many people, is represented by two main genetic types in the Indo-Pacific region: the first reflecting very early movements from Africa; the other a more recent dispersal from Asia (Falush et al. 2003) and thus potentially associated with the Austronesian expansion. Given the extent of microbial diversity — our bodies play host to more bacterial cells than human cells — our microbial companions may well provide a largely untapped resource for reconstructing prehistoric movements and contact.

While genetic data have traditionally aimed to inform the route and timing of human population movements, they are now also providing unexpected insight into social processes. Some social actions, especially marriage practices that in turn affect the number and distribution of offspring, leave long-term echoes in the genetic record. Proportions of Asian ancestry in eastern Indonesian populations (e.g., Flores, Sumba, and Timor) vary across regions of the genome (Kayser et al. 2008). Asian ancestry averages 89% on the mtDNA (which is only passed down the female line), 69% on the X chromosome (which spends two-thirds of its time in women and one-third in men), 59% on the autosomes (equal time in men and women), and 13% on the Y chromosome (only passed down the male line) (Lansing et al. 2011). This progression suggests that men and women experienced different social pressures. In particular, higher Asian ancestry in female-associated genomic markers hints that the Austronesian expansion was favorably biased towards Asian women.

This genetic pattern might be explained by the existence of matrilocal “house societies” during the Austronesian expansion (Lansing et al. 2011). As communities spread, women sometimes accepted husbands from neighboring indigenous communities. Under matrilocal residence, the children of such marriages would inherit their father’s Papuan Y chromosome, their mother’s Asian mtDNA, and presumably also spoke her Austronesian language, given that mothers play an especially influential role in passing language to their children.
Even if marriage with Papuan men was rare, there was ample time for a pronounced sex bias to develop. For instance, models in which only 2% of marriages occur with Papuan men are sufficient to predict the sex bias observed across all four genetic systems, while simultaneously accounting for the widespread replacement of indigenous tongues by Austronesian languages.

Of course, it is crucial to recall that we are viewing these genetic patterns some 4000 years after the events that initially triggered them. Consequently, they represent the outcome of that first expansion phase, together with the effects of processes that occurred over the next four millennia. Polynesians today have substantially more Asian ancestry (~80%) than individuals in eastern Indonesia (50–60%). The settlement of Remote Oceania was enacted by individuals who still mostly derived from expanding Asian groups, but subsequently moved into uninhabited territory where their genetic profile essentially became fixed. In contrast, higher Papuan ancestry in eastern Indonesia likely reflects additional admixture with Papuan groups long after the initial contact period. The Austronesian expansion, for all practical purposes, is a process that is still ongoing.

Other social behaviors can also affect genetic patterns. We can tell that male dominance – where men pass social status and hence fecundity to their sons – has historically been uncommon in Island Southeast Asia (Lansing et al. 2008). However, a fairly frequent switch from matrilocal residence, where husbands move to the village of their wives, to patrilocal residence, where brides move to the village of their husbands, has been influential (Jordan et al. 2009). In matrilocals, men move widely between communities, while women stay at home. The converse holds for patrilocal societies, which are common across Island Southeast Asia today. In predominantly patrilocal regions, mtDNA lineages tend to exhibit broader geographical distributions than Y chromosome lineages, consistent with the greater expected dispersal of women than men (Tumonggor et al. 2013). However, in the princedom of Wehali on Timor, where the ancestral state of matrilocal residence has been retained, the opposite genetic pattern is seen (Tumonggor et al. 2014).

To date, genetic data have largely been treated as a silent observer of human history. Indeed, most of the markers discussed above have no physical or physiological effect and provide nothing more than a record of the past. Nevertheless, our genetic inheritance influences both what we look like and how we act, and there is increasing interest in identifying how history has shaped our genes and how they in turn have shaped us. In the 1960s, James Neel proposed that prolonged voyaging might select for individuals whose gene variants allow them to survive cycles of feast and famine. He called this the “thrifty” genotype (Neel 1962). Although soon afterwards gene frequencies were found to vary between different populations in the expected manner (such as Gm blood group types between Austronesian- and non-Austronesian-speaking
populations in Papua New Guinea; Giles et al. 1965), technologies at the time could not determine whether these differences were caused by selection or history. Genomic data now provide a framework to revisit this question. A variant of the \textit{PPARGC1A} gene, found in 70\% of Polynesians but absent in New Guinea, regulates fat usage, raises susceptibility to diabetes, and may help explain the different prevalence of type II diabetes in Polynesians and neighboring populations (Myles et al. 2007). Other selected gene variants target alternative mechanisms of energy metabolism and may explain the large body mass of Polynesians (Kimura et al. 2008). Fifty years after Neel raised his hypothesis, genetic data are beginning to more firmly support the thrifty genotype, highlighting characters that were once advantageous but now find themselves maladapted in the modern world.

Yet other genes hint at alternative pressure points for selection. The blond hair seen in many Melanesian children has been linked to a single DNA change (Kenny et al. 2012). More influentially, gene variants that confer resistance to malaria, such as the molecular basis of Southeast Asian ovalocytosis (SAO), are associated with Austronesian languages, but are not found in Taiwan and instead appear to have been selected within expanding Austronesian communities in the lower tropical latitudes (Wilder et al. 2009). Similarly, the very frequent Ge negativity genes that occur in coastal areas of New Guinea protect against malaria and have experienced strong selection pressure (Maier et al. 2003). Austronesian and Papuan groups were also infected with different strains of the hepatitis B virus (Locarnini et al. 2013; Paraskiews et al. 2013) and likely evolved different host resistance variants to counter them. Indeed, elevated Papuan ancestry may have been driven in part by selection. Children of mixed marriages likely gained the benefits of both worlds – receiving the cultural repertoires of both parents and a suite of genetic variants that may have favored survival during voyaging and protected against local diseases. Genetic data cannot speak to the social pressures that such children may or may not have faced, but from the perspective of biology, they may have had an evolutionary advantage.

Other gene variants (Pickrell et al. 2009; Sabeti et al. 2007), or changes in the way that existing gene variants are regulated (Martin et al. 2014), were almost certainly favored during the movements of Pacific peoples, and this promises to be a major focus of research in coming years. As well as being a goal in itself, reconstructing population history is increasingly perceived as necessary to infer which genes are under selection, as demographic processes (such as bottlenecks) can mimic patterns caused by selection. As amply shown above, human population genetics is increasingly illuminating facets of human prehistory that lie outside its traditional purview. Given the growth of this field over the past 20 years, there is every reason to believe that molecular anthropology will continue to influence and challenge our understanding of the prehistory of Island Southeast Asia for quite some time to come.
1. The term “Australo-Papuan” is often rendered “Australo-Melanesian” in other publications, but I hesitate to use this term since the islands of Melanesia as well as parts of coastal New Guinea have witnessed lots of population admixture during the Holocene. The most unmixed Papuan populations in a genetic sense exist today in the interior highlands of New Guinea and all speak Papuan languages.

2. The term “phylogenetic” refers to genetic inheritance through time, with evolutionary modifications occurring in populations due to mutation, selection, and various types of genetic drift, especially small population founder effects in small and relatively isolated islands. The term “phenotypic” refers to physical expression – body features, hair form, skin pigmentation, and so forth. Hence, phenotype is a reflection of both inherited genotype and the impacts of environmental factors following conception.

3. For strong arguments to the effect that the oldest Levantine examples of *Homo sapiens*, at more than 90 kya, were ancestral to those groups who moved east into India and Southeast Asia, eventually Australia, see Schillaci 2008; Boivin et al. 2013; Reyes-Centeno et al. 2014. See also Kuhlwilm et al. 2016 for possible admixture around 100 kya between early Levantine modern humans and Neanderthals. For genetic evidence against early Levantine survival into modern populations see Fu et al. 2014.

4. Kaifu and Fujita 2012 discuss the modern human mandible fragment from Zhirendong in Guangxi but advise caution on the suggested date of 100 kya. The presence of a few human teeth in the Punung Cave fauna from Java (Storm and de Vos 2006) has led to suggestions that modern humans could have been present there as early as the last interglacial, but the context of these finds leaves much to be desired (Storm et al. 2013:362). The new announcement that human teeth found in Fuyan Cave in Hunan in China date to 80 kya (Liu et al. 2015) is therefore of interest. Three new genomics papers (Pagani et al. 2016; Mallick et al. 2016; Timmermann and Friedrich 2016) suggest that early modern humans might indeed have left Africa between 120,000 and 70,000 years ago. This is still an area of great uncertainty.

5. The Niah Deep Skull has recently been compared to a Negrito or a modern Iban according to a new analysis of 18 cranial variables (Curnoe et al. 2016), and a very short femur found nearby suggests a stature of only 135 cm. Since the Deep Skull can hardly be a modern Iban (assuming that the uranium series date is correct), then it becomes possible that some aspects of Negrito stature and cranial shape were already becoming differentiated in the Borneo rainforest environment from within the basal *Homo sapiens* population of Island Southeast Asia by 37 kya.


10. For Niah see von Koenigswald 1952. Statements exist to the effect that the Niah early Holocene squatting burials were from a “Mongolid” population (Lloyd-Smith 2012:53), but no convincing statistical evidence is presented. However, see Krigbaum and Manser
2005 for a suggestion of Polynesian and Australian affinities. Bulbeck 2015 notes that the teeth of the Niah Neolithic burials differ in both size and shape from the Paleolithic sample.

13. Song is Javanese for cave, equivalent to gua or liang in Malay and Bahasa Indonesia.
17. The authors of the craniometric analysis express sincere gratitude to the following for permission to access comparative dental specimens: Wang Daw-Hwan (AST); Chris Stringer, Margaret Clegg, Robert Kruszynski (BMNH); Robert Foley, Jay Stock, Maggie Bellati (CAM); Nguyen Viet (CSPH); Rachanie Thosarat, Sahawat Naemma, Amphan Kijingam, Suphot Phommanodch (FAD); Nguyen Giang Hai, Nguyen Lan Cuong, Nguyen Kim Thuy (IAH); Le Chi Huong, Nguyen Tam (KHPM); Bui Phat Diem, Vuong Thu Hong (LAPM); Philippe Menneceier (MHO); Wilfredo Ronquillo (NMP); John de Vos (NNML); Tsai Hsi-Kue (NTW); Zhang Chi (PKU); Korakot Boonlop (SAC); Michael Pietrusewsky (UHW); Denise Donlon (USYD); Gen Suwa (UTK); Bernardo Arriaza, Vicki Cassman (UNLV); Charles Higham, Nancy Tayles (University of Otago); Bui Chi Hoang (Southern Institute of Social Sciences, Ho Chi Minh City) and Hsiao-chun Hung (Australian National University). The study was supported in part by JSPS KAKENHI Grants No. 20520666 and No. 23247040.
18. In this book these cultures are referred to as Para-Neolithic.
20. Denisovans are named after Denisova Cave in Russian Siberia, where the remains of these archaic hominins were first identified (Krause et al. 2010). Denisovans share a common origin with Neanderthals but are as divergent from Neanderthals as from modern humans. Denisovans and Neanderthals appear to have lived in partly overlapping territories and genetic evidence suggests that Denisovans and modern humans also interacted and intermarried.
21. In Human Biology 85(1), 2013, see the papers by Stock, Bulbeck, Jinam, Tommaseo (for New Guinea), and McAllister (for Queensland). All agree on independent origins for short stature.

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