PERSPECTIVE



# When did *Homo sapiens* first reach Southeast Asia and Sahul?

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Anatomically modern humans (*Homo sapiens*, AMH) began spreading across Eurasia from Africa and adjacent Southwest Asia about 50,000–55,000 years ago (*ca.* 50–55 ka). Some have argued that human genetic, fossil, and archaeological data indicate one or more prior dispersals, possibly as early as 120 ka. A recently reported age estimate of 65 ka for Madjedbebe, an archaeological site in northern Sahul (Pleistocene Australia–New Guinea), if correct, offers what might be the strongest support yet presented for a pre–55-ka African AMH exodus. We review evidence for AMH arrival on an arc spanning South China through Sahul and then evaluate data from Madjedbebe. We find that an age estimate of >50 ka for this site is unlikely to be valid. While AMH may have moved far beyond Africa well before 50–55 ka, data from the region of interest offered in support of this idea are not compelling.

Homo sapiens | anatomically modern humans | Late Pleistocene | Madjedbebe | Sahul

Fossil data suggest that the modern human lineage appeared in Africa by 300 ka (1). There is broad but not universal agreement that near-modern or modern humans were confined to Africa and nearby parts of Southwest Asia until ca. 50–55 ka. After that time, so the argument goes, anatomically modern humans (AMH) spread rapidly across Eurasia, displacing and occasionally interbreeding with Neandertals and other archaic humans and colonizing large areas (Sahul and northem Siberia; later the Americas and Oceania) that no hominin had occupied before (2, 3). This process is sometimes called the "single-wave" model of AMH dispersal beyond Africa.

Over the past decade or so, some analysts have suggested a more complex series of events beginning well before 50-55 ka (see refs. 4 and 5 for review), an argument grounded on archaeological evidence from South Asia, fossil remains from East and Southeast Asia, and genetic data from southern Eurasia and Australia.

Advocates envision a stepwise spread in at least two stages, the first across southern Eurasia and another much later into higher latitudes, including Europe.

Late Pleistocene dispersal from Africa, at one time an issue, is now rarely questioned, but resolving its details in time and space is essential to explaining it. The recently reported 65-ka age estimate for the northern Australian site of Madjedbebe (6) might be an important contribution to this discussion. If the proposed ages and connections with artifacts are as reported, they would represent the most compelling body of evidence yet offered for an AMH expansion out of Africa >50–55 ka. The early age proposed for this site was quickly accepted by some commentators (7) but disputed by others (8). Here we consider the issues, attending especially to Southeast Asia and areas further south and east, where critical fossil, archaeological, and genetic data, as well as reports on Madjedbebe, have emerged in the past decade.

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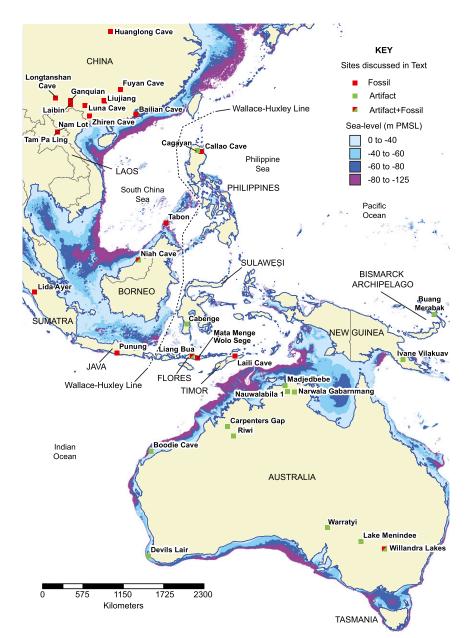


Fig. 1. Map of the SCS arc showing the locations of all fossil and archaeological sites mentioned in the text and of the WHL between Sunda and western Wallacea.

# Setting

The area of interest extends from South China south and east through mainland Southeast Asia, the Malay Archipelago, and Australia–New Guinea (Fig. 1). We refer to it here as the "South China–Sahul (SCS) arc." It has had a complex environmental history over the last several million years, mainly due to changes in earth's orbital geometry and their impact on climate and sea level. Here we focus on the earlier part of the last glacial cycle (40–130 ka), the time period bracketing the first definite and most of the earliest purported evidence for AMH in the region.

During the Last Interglacial (115–130 ka), sea levels were 6–10 m higher than at present (9, 10), but landform configurations were broadly similar to those of today (11). Thereafter, sea levels fluctuated irregularly, ultimately falling to the Last Glacial Maximum low, minus 120 m, at 20 ka. Drops of 40 m or more exposed large, now submerged areas of the Sunda and Sahul shelves, in the former case joining Sumatra,

Borneo, and Java as part of a broad peninsula extending south and east of the present Southeast Asian mainland and in the latter creating dry land connections between Australia, New Guinea, and Tasmania (12, 13). The islands of Wallacea, the vast archipelago between Sunda and Sahul, remained unconnected with either, forming the barrier between the Oriental and Australian biogeographical provinces originally recognized by Alfred Russel Wallace (14). No large-bodied terrestrial mammal managed a complete, demographically successful transit of this threshold before the arrival of AMHs.

#### **Fossil Evidence for AMH Presence**

Four species of *Homo* are identified in the region of interest. Definitive characteristics include aspects of body size, skeletal robusticity, and cranial anatomy (*SI Appendix, SI.1.1*). *Homo erectus*, African-derived and the earliest definite representative of

the genus, may have been present on Java by 1.5 Ma (15) and possibly persisted there and in Southeast Asia more broadly until the Late Pleistocene arrival of AMH (compare refs. 16 and 17). By 1.0 Ma, H. erectus had reached Flores, where it likely gave rise to the insular dwarf Homo floresiensis (18, 19). Assuming current landform configurations (past tectonic activity not having been a complicating factor), passage on the shortest route from Sunda to Flores required two open ocean crossings, the longer ca. 20 km, both complicated by the strong north-south Indonesian Throughflow current. An alternative model suggests travel via the Philippines and Sulawasi, a route that required several crossings (one >80 km) but that may have been facilitated by that same north-south current (20). Regardless of the route taken, transit is thought to have been accidental (21). Archaic Homo sapiens, distinguished by brain sizes within the modern human range but otherwise broadly similar to late H. erectus, was present in southern China and southwards from 100-400 ka or later and may have included representatives of the lineage defined on genomic grounds as Denisovan (22). Denisovan genes have been detected at low levels in living human populations in South Asia and the Pacific and at relatively high levels in Australo-Melanesians.

Seventeen sites in the area and time frame of interest have yielded human remains classified by at least some analysts as anatomically modern (*SI Appendix, SI.1.2* provides details). Nine of these sites are in southern China; eight are further south and east. As published so far, 9 of the 17 sites have provided only teeth, and seven of these sites produced only one or two teeth. One site has produced a full skeleton; five have yielded isolated crania, mandibles, or fragments thereof; two sites have provided single postcranial elements. Estimated fossil ages range from 36 to 220 ka; most fall in the interval 40–120 ka. Most age estimates are based on U-series analyses of flowstones said to bracket human remains. Several have been made from analyses of the remains themselves. Other dating techniques employed include <sup>14</sup>C, electron spin resonance, luminescence, and faunal correlations.

Taken as presented in initial reports, these data suggest an AMH presence in southern China as early as 120 ka, in Wallacea by 50–70 ka, and in Sahul by 40 ka. A more critical perspective, based on comments by various reviewers, would eliminate specimens from six sites (Callao, Longtanshan, Luna, Nam Lot, Punung, and Zhiren) because of uncertainty about their identification as anatomically modern, those from another four sites (Fuyan, Huanglong, Laibin, and Liujiang) based on questionable relationships between fossils and dated sediments, and those from two sites (Bailian and Ganqian) because of limited information on fossil taxonomy, dating, and depositional context (SI Appendix, SI.1.2).

Additional concerns pertain to the reliability of age estimates based on analyses of the fossils themselves. Those for four specimens [Tam Pà Ling (TPL) 1 and 2, Callao, and Tabon] are derived from U-series determinations. These measure the ratio of uranium to thorium in the sample of interest, the assumption being that the only variable affecting this relationship is the decay rate of uranium to thorium. This often works well for dating flowstone but is questionable with bone, which may lose or take up uranium from surrounding sediments after burial, making it difficult to establish a baseline uranium content. The issue is especially important in the case of TPL 1 (Laos), a set of cranial and other elements characterized as "essentially modern" *H. sapiens* (23–25). These remains were redeposited from another location into sediments dated by luminescence at 40–50 ka. The remains themselves were U-series dated at 63.6 ± 6 ka but with questions

about the reliability of the estimate (*SI Appendix, SI.1.2.2*). Age estimates for Callao (Luzon) and Tabon (Palawan) can be challenged on similar grounds. Ambiguity in the taxonomic assignment of the Callao metatarsal adds further uncertainty.

The two teeth from Lida Ayer (also called "Lida Ajer," Sumatra), indirectly dated at 63–73 ka (*SI Appendix*, *SI.1.2.5*), represent what might be the best case for a >50-ka AMH presence in the region of interest (26). They are said to have been recovered in the 1880s (27) but were not identified as human until the 1940s (28). Their assignment to *H. sapiens* appears solid, as does the dating of site sediments. Their original stratigraphic positions were established by reference to Dubois' century-old field notes. The question is whether that placement is accurate. The passage of time between recovery and stratigraphic assessment and their lack of discoloration relative to other teeth thought to have been retrieved from the same sediments (figure 3 in ref. 26) have prompted guarded skepticism about their estimated ages (29). Direct dating of the teeth might resolve the issue.

The only remains from well-dated contexts confidently assigned to *H. sapiens* are those from Niah (Borneo) and Willandra (Australia), placed at *ca.* 40 ka. TPL 1, definitely anatomically modern, could date to about 40–50 ka. Fossil evidence for an earlier AMH presence anywhere in the region is questionable (*SI Appendix, SI.1.3*).

# Archaeology

The archaeological record for the SCS arc begins late in the Early Pleistocene. Sites with relatively well-dated stone tool assemblages include Ngebung (Java), ca. 800 ka (30), and Mata Menge and Wolo Sege (Flores), 880 ka and 1.0 Ma, respectively (18, 31). Lithics at Talepu (Sulawesi) have an estimated age of ca. 200 ka (32). Less certainly dated are assemblages at Cabenge (Sulawesi) (33) and Cagayan (Luzon) (34), estimated at 700–900 ka. If accurate, the suggested ages for Cabenge and Cagayan, combined with those from Flores, indicate an early, surprisingly widespread human presence in western Wallacea, east of the Wallace–Huxley Line (WHL). Seafaring capability might be inferred, but the lack of evidence for passage further east until much later suggests accidental transit, the pattern known for other large mammals over the last several million years (35).

The regional record remains limited and qualitatively unchanged until the mid-Late Pleistocene (35-38). After 50 ka, it is radically altered by the arrival of anatomically modern humans. At or shortly after this date, archaeological remains attributable to AMH appear widely across the SCS arc: at Niah Cave (Borneo) by 48-50 ka (39), throughout Sahul by 46-50 ka, and at Buang Merabak (New Ireland) by 44 ka (40). New data from Liang Bua (Flores) are said to mark the replacement of long-resident H. floresiensis by AMH. H. floresiensis persisted there until 50-60 ka (41). Two teeth, claimed to be anatomically modern, are dated ca. 46 ka (42), but further information on these is lacking. Following new excavations, Morley et al. (38) propose AMH presence by 41 ka based on evidence for the controlled use of fire. The gap between 50 ka and 41-46 ka coincides with the earliest claimed date for AMH elsewhere in Wallacea, ca. 44 ka at Laili Cave (Timor-Leste) (43).

The overall speed and spatial extent of this spread point to deliberate migration enabled by developments in seafaring. Even at lower sea levels, Wallacea still presented a major impediment to west–east movement. The overall distance between the exposed Sunda and Sahul shelves measured 1,000–1,500 km. Island hopping on any of the more direct routes through it required

multiple crossings, including one >70 km (44). As noted above, strong north–south ocean currents complicated passage on some of these routes. Travel east of Sahul as far as New Ireland required additional sea crossings, including one >50 km. Passage beyond the Bismarck Archipelago was apparently delayed by about 15 ky, probably because of the increased interisland distances involved. Even so, crossing to the northern Solomon Islands, ≥140 km distant from the nearest departure point on the Bismarck Archipelago, was accomplished by 34 ka (45, 46). Paddle- or sail-powered rafts or canoes capable of maintaining headway in contrary currents are clearly implied, as are complex planning and organizational skills (47). Simulation studies suggest that in vessels of this type crossings in the 50–100-km range might have required as many as 4–7 days (44).

Data on the intracontinental occupation of Sahul add further perspective on the pace of this process. At the time of colonization, the exposed landmass covered more than 11 million km². Its southern limits were 3,500–5,000 km distant from landing points on its northwest coast, further if considering movement along the coast. The diversity of habitats occupied in the process is striking (Fig. 1): high-altitude tropical forest-grassland (Ivane), subtropical savanna (Nawarla Gabarnmang, Riwi, and Carpenter's Gap), semiarid woodland and grassland (Boodie, Warratyi, and Menindee), and temperate forest (Devils Lair) (48). Subarctic Tasmania was occupied by 40 ka, soon after a dry land connection was established across Bass Strait (12, 49).

Except in the tropical north (50), terrestrial floras throughout this region were unfamiliar to arriving migrants, and marsupial faunas were almost entirely so. Novel food acquisition and processing technologies were likely required. They are definitely indicated in island settings (Timor, New Ireland), where fishing gear and remains of pelagic taxa (tuna) are reported in archaeological deposits dated 40–42 ka (51, 52). The use of fire in habitat management and in processing toxic plant foods, evident in at least one location occupied by AMH at about this time in Sunda (53, 54), was probably practiced in Sahul as well (55). The ecological impacts of early colonists, especially their role in the extinction of Pleistocene megafauna, remain contentious (56, 57).

In addition to these indications of adaptive capability, the regional record also shows evidence of symbolic behavior typical of anatomically modern humans but unusual, if not entirely absent, among earlier hominins. Rock art is dated as early as 40 ka on Sulawesi (58); personal ornaments appear on Timor by 38–42 ka (59); red-stained human cranial parts, possibly employed as paint vessels, are reported in Borneo at 41 ka (60); and mortuary rituals including cremation and anointment of the dead with ochre are known in Australia by 40–42 ka (61).

Overall, these are clear indications of modern behaviors. There is no solid evidence anywhere on the SCS arc of comparable behaviors >50 ka.

#### Genetics

Genomic data from living and ancient populations provide an increasingly detailed view of the timing of AMH emergence from Africa, its geographic spread, and introgression with archaic humans (62). Genomic assessment of Late Pleistocene fossils that have been dated directly has created a well-constrained chronology for emerging genetic histories (62, 63). Importantly, the calibrated ancient genomic data offer both timelines and measures of mutation rates that are independent of archaeological chronologies.

Molecular clock studies of mitochondrial, Y chromosome, and genomic data suggest that the ancestors of living AMH populations moved out of Africa into Southwest Asia ca. 50–60 ka (62). However, molecular date estimates vary depending on the rate calibrations used, and confidence intervals can be large. Ideally, rates should be calibrated with measures that are close to the time period under comparison rather than by extrapolation from divergences deep in time (human vs. chimpanzee) or from short-term (pedigree) measures (64). Fortunately, interbreeding events with both Neandertals and Denisovans have generated a distinct set of markers which provide a more temporally constrained view and allow AMH population movements beyond Africa to be traced and dated (62, 65–68).

The first and most significant pulse of introgressed Neandertal DNA left a genetic contribution that now comprises around 2-2.6% of the genome in all global human populations outside Africa (66, 67). The universal nature of this signal indicates that the initial Neandertal interbreeding occurred in a small AMH population that had left Africa but before its spread to form descendent populations across Eurasia (62, 65, 66, 68, 69). The precise timing of the initial interbreeding event, which presumably occurred in Southwest Asia, can be calculated through the highly resolved genome sequence from the radiocarbondated Siberian H. sapiens Ust'Ishim femur (43.2-46.9 cal BP, 95% CI) (70). The introgressed Neandertal signal is present in large blocks in the Ust'Ishim genome due to the limited number of recombination events after the interbreeding. The length of these blocks shows that the initial AMH-Neandertal interbreeding occurred 232-430 generations earlier, at most 50-55 ka (70, 71), providing a maximum date for the founding of modern global non-African populations. If earlier non-African AMH populations existed, they left no detectable genetic traces in modern populations.

Slightly higher proportions of Neandertal DNA in modern eastern Eurasian populations indicate subsequent introgression events involving closely related Neandertal groups as AMH moved through Asia and Europe (67, 68, 71). Similarly, multiple interbreeding events with Denisovans are recorded as AMH moved through eastern Eurasia (67). The earliest occurred as the ancestors of Sahul populations and Philippines Mamanwa transited Southeast Asia around 50 ka and involved Denisovans distantly related to the Altai population. Subsequent isolation in Australia and New Guinea preserved a relatively high level of Denisovan genetic component (4-6%) (72). A later introgression from a similar Denisovan source population left trace amounts in modern South Asian genomes and was followed by interbreeding between a Denisovan group closely related to the Altai population and the ancestors of modern East Asians (67). The relative lengths of the Neandertal and Denisovan introgressed genetic fragments can be used to date the event leading to the Denisovan genomic signals in Sahul populations (72). The Ust'Ishimcalibrated 50-55 ka date for Neandertal interbreeding suggests the ancestral Sahul populations mixed with Denisovans around 45–49 ka, consistent with molecular clock estimates from genomic studies (73).

These findings cannot be reconciled with a 65-ka date for Madjedbebe unless that date represents a cryptic earlier population movement that has left no identifiable trace in modern Australo-Melanesians, meaning that the former were not the ancestors of modern Aboriginal populations. Currently there are no ancient genomic data from Southeast Asia before the Holocene; the only reports of potentially deeper genetic signals within

modern Sahul populations are from Melanesian lineages (74). These appear to be erroneous and probably relate to issues with genomic phasing and inefficient removal of Denisovan content (65, 67), since evidence of such ghost populations has not been recognized in subsequent studies of modern Sahul and related populations (62, 73, 75). Indeed, appropriately calibrated molecular clock studies of mitochondrial, Y chromosome, and nuclear DNA all converge on Sahul colonization around or slightly after 50 ka (73, 76), in close accord with the estimates for Denisovan interbreeding and a wide range of Sahul archaeological data (40), with the notable exception of Madjedbebe. In short, a range of molecular clock estimates and archaeological data suggest the initial colonization of Sahul by AMH occurred around 48–50 ka, matching estimates for an out-of-Africa movement 50–55 ka (62).

Surveys of mitochondrial diversity in modern Sahul populations allow estimates of the minimum size of the colonizing population. A conservative approach suggests that the ancestors of at least 9 or 10 separate lineages (S/O, N, R, P5, P8, P11, M42, M16, M, and possibly Q) were present among the founders (76, 77). If each lineage was represented by four or five founder females (a family group of mother/sister/daughters), this would equate to 36-50 females. This estimate is conservative: Any founder females who failed to have female children would not pass on their mitochondrial lineage, while some related family groups would share the same mitochondrial lineages. Estimates of 10-20 females per mitochondrial lineage in colonizing populations (78) would suggest 90-200 females (46). Assuming a colonizing party had a 1:1 female-to-male ratio, the inferred minimum founding population is >72-400 individuals but probably many more (79). Clearly, this represents a deliberate colonization process. It reinforces inferences about the use of paddle- or sail-powered watercraft large enough to carry both passengers and the supplies needed to sustain them on multiday voyages (44).

#### Madjedbebe

Data reported most recently from this site were recovered mainly from a  $20\text{-m}^2$  excavation that reached a maximum depth of 3.4 m (SI Appendix, SI.2.1 and ref. 6). The first occupation is said to be indicated by a band of >10,000 artifacts, referred to as "phase 2," located 1.90--2.60 cm below modern ground surface. Contents include flaked stone tools, edge-ground axes, seed-grinding implements, unifacial points assumed to be projectile armatures, ground ochres, and fragments of reflective sheet mica. Bayesian modeling of 18 optically stimulated luminescence (OSL) estimates on sand grains from within the band suggest an age range of  $52.7 \pm (2.4, 4.3)$  to  $65.0 \pm (3.7, 5.7)$  ka. Excavators explicitly favor the earliest age (see below). Features characterized as a "hearth" and a "pit," both presumed to be anthropogenic, are taken to show that sediments and their contents have not been disrupted since initial deposition.

In the context of Sahul and the wider region, these ages are anomalous. The earliest falls 15–20 ky before dates on the eight next-oldest archaeological sites on the continent (Fig. 2). It exceeds unambiguous evidence for the use of symbols anywhere on the SCS arc by >20 ky. With one apparent exception (85), it exceeds the earliest age estimate for edge-ground axes in Sahul by 30 ky and in Eurasia by 27–35 ky (83, 86, 87). It precedes nearly all evidence for unifacial points and intensive seed processing in Sahul by 60 ky (88, 89). These mismatches demand critical review, not the unquestioned acceptance and attempts at accommodation they have received from some (84, 90).

Support for the 65-ka age estimate is based partly on the notion that the established post-50-ka continental chronology reflects the limits of radiocarbon analysis, which some commentators suggest cannot produce reliable dates >40 ka (90). Appeal to other techniques, notably luminescence analysis, is seen by these critics as essential to the production of accurate dates beyond this "barrier." This ignores developments in <sup>14</sup>C sample treatment and calibration that push the applicable range of the technique to 50 ka (91–93). It also ignores the fact that paired <sup>14</sup>C and luminescence applications on materials from several Sahul sites have produced essentially identical age estimates in the range of 40-49 ka (82, 94). In the nearly three decades since the first luminescence-based archaeological age estimates of >50 ka for Sahul sites were published, only three—Madjedbebe, Nauwalabila, and the WLH 3 H. sapiens interment—have been placed beyond this threshold (6, 95-97). Ages >50 ka for the latter two have now been discounted (98), leaving Madjedbebe as the only remaining candidate despite intensive search throughout Australia since 1990 for similarly old sites.

Intrasite issues raise further concerns about the archaeological significance of a 65-ka age estimate. Some suggest that statistical uncertainties allow for chronological overlap with other, well-documented early Sahul sites (99). This interpretation does not account for most of the dating anomalies noted above. It also depends on accepting the youngest proffered age for Madjedbebe phase 2 (48.4–55.1 ka) and disregarding excavators' claims for initial occupation "around 65 ka" or "conservatively 59.3 ka" (ref. 6, p. 309).

An age estimate in this range might have been supported by an infinite (>50 ka) result from analysis of charcoal encountered in phase 2 deposits. Clarkson et al. (6, 100) say that efforts to obtain such an assessment were frustrated when a sample of this material failed to survive pretreatment, even though it was preserved well enough to allow taxonomic identification. Note, however, that Bird et al. (101) reported a calibrated <sup>14</sup>C date of 12.8–13.0 ka (ANUA-9915) on charcoal collected from phase 2 deposits (-2.54 cm) sampled during 1989 excavations at the site. This finding shows that datable carbon is recoverable from these depths and that the results of analysis are inconsistent with the OSL-based archaeological chronology. However, in a detailed account of the 1989 excavations, Clarkson et al. dismiss the charcoal that provided this age as "intrusive," the sample "possibly [having] fallen or blown in during excavation." (102, p. 5). They do not tell how sample-recovery procedures might have allowed this to happen or how it might have escaped notice at the time, nor do they mention the date in their subsequent 2017 report.

Confidence in the 2017 report is further undercut by the fact that while stratigraphically lower phase 1 deposits are said to be sterile or to contain few artifacts, published supplementary data show that they yielded hundreds of stone tools dated via OSL at 65.4–87.4 ka. This is the basis for suggestions in the popular press that the site was first occupied 80 ka. It is not clear why Clarkson et al. (6) accepted the phase 2 artifact/date associations but rejected those for underlying deposits on grounds that they represent postdepositional "settling." In a more recent comment, Clarkson et al. (100) continue to maintain that phase 1 artifacts most likely represent the result of postdepositional displacement but also allow that they might represent occupation >65 ka.

These observations together with other points elaborated in SI Appendix prompt us to consider alternate explanations for the

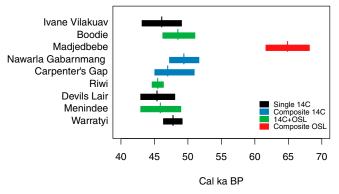


Fig. 2. Radiometric ages for the eight oldest securely dated archaeological sites in Sahul vs. Madjedbebe phase 2 (40, 80–84).

Madjedbebe data. The site is situated in a regionally extensive sand sheet. Substrates of this kind in tropical environments with pronounced wet and dry seasons are subject to a variety of postdepositional disturbances, including rain-splash erosion, subsurface eluviation, creep, and, most notably, bioturbation by termites. All can be observed at or near Madjedbebe today. Clarkson et al. (6) acknowledge but dismiss them as insignificant with respect to buried sediments, but the dilemma is that many of these processes leave little visible trace in Pleistocene sand deposits. In particular, abandoned termite galleries collapse and disappear. An exception is dripline erosion, which is an obvious explanation for the purported anthropogenic "pit" (better described as a "gutter") in phase 2 and for the proliferation of artifacts and natural rocks throughout the sequence at this depth at the front of the site (SI Appendix, SI.2.3).

Extensive geomorphological literature (SI Appendix, SI.2.2) indicates that all these processes facilitate the downward movement of rocks, including artifacts, into deeper sand deposits that will yield radiometric (OSL) ages older than the artifacts they contain. Unambiguous demonstration of their effect on sediments at Nauwalabila (98) led to the abandonment of claims for human occupation >50 ka at that location, once commonly cited but now rarely mentioned in reference to Sahul colonization. We contend that Madjedbebe deposits were also disturbed in this fashion and that this explains the age discrepancies in the data outlined above and reviewed in SI Appendix. The anomalous content of the phase 2 assemblage, the 12.8- to 13.0-ka <sup>14</sup>C date reported at phase 2 depth by Bird et al. (101) and the hundreds of artifacts from phase 1, accepted (with minor reservations) by Clarkson et al. (6, 100) as products of vertical displacement, are consistent with this contention.

If we are correct, Madjedbebe cannot be promoted as proof of an AMH presence in Southeast Asia and Sahul >50 ka. Currently this site is the single data point arguing for the possibility of AMH east of the WHL before 50 ka. Minimally, substantiation of this antiquity would require evidence from another site in Sahul situated in a more secure geomorphic setting.

## **Discussion**

Representatives of genus *Homo* spread from Africa across large parts of Europe and Asia at least three times in the last two million years: as *H. erectus/ergaster* 1.8–2.0 Ma, as *H. heidelbergensis* 0.5–0.7 Ma, and as *H. sapiens* (AMH) 50–55 ka. Evidence of other, similar events in that same broad time frame would not be surprising (103). Our concern here is with the 50- to 55-ka event and

the possibility that AMH ventured far beyond Africa before that time.

Advocates of early dispersal envision movement across southern Asia in one or more waves sometime in the period 60–120 ka (4, 5, 104–106). The bases for these arguments include:

- Stone tool assemblages from South and Southwest Asia dated to 60–120 ka and attributed to African-derived AMH (107).
- Human remains from South China and Southeast Asia assigned to AMH, dated in the range 60–120 ka (SI Appendix, SI.1.2).
- Mitochondrial DNA data interpreted as indicating a relatively early separation (>60 ka) of lineages ancestral to modern Australo-Melanesians from those leading to most Eurasians (108).

All these points are problematic. The first has been discussed at length elsewhere (109–112) but with no definite conclusion. The recent report of an intermediate phalanx from the Arabian Nefud, dated 86–95 ka and assigned to *H. sapiens* (113), is consistent with the earlier Levantine evidence of AMH in the region, but it does not resolve the question of a presence further east at this time or before. Arguments in favor of this possibility rely on analyses of lithic assemblage characteristics, but, as advocates themselves concede, "stone tools are a poor indicator of the species of the hominin that made them" (ref. 114, p. 16). Nothing certain about movements of AMH beyond Arabia >50 ka has emerged from this work.

Our review challenges the other two points and adds archaeological information relevant to the overall issue as it plays out on the SCS arc. Discussion of human fossils in this region dated 50-120 ka is complicated by potentially confusing taxonomic terminology and the small, fragmentary nature of the sample that limits the potential of the data to identify species. Arguments that it offers evidence of AMH arrival require a clear picture of the Late Pleistocene morphological characteristics of East and Southeast Asian H. erectus and archaic H. sapiens as distinct from those of AMH; however, thorough review (115) has shown that a clear picture is not yet available. It also requires unambiguous control on the ages of fossils in question, but that too is often absent. It is not surprising that some of the strongest proponents of an AMH dispersal >50-55 ka qualify their arguments by questioning aspects of data quality and reliability across the skeletal sample (4). It may be that some human remains on the SCS arc do indeed represent evidence of AMH in the region >50-55 ka, but the data available so far do not provide firm support for that idea.

With respect to genetics, the well-constrained timing of recent Neandertal introgression places an upper limit of *ca*. 55 ka on the origin of all modern non-African *H. sapiens* populations (62, 70). Genetics-based inferences about earlier Sahul colonization dates (108) are no longer viable. Denisovan introgression with the ancestors of Sahul populations occurred later, *ca*. 45–49 ka. Appropriately calibrated molecular clock studies of Sahul genetic diversity all point to a colonization date of *ca*. 50 ka (73, 76, 77), consistent with comprehensive reviews of available archaeological data cited in Fig. 2. A Madjedbebe archaeological age of 65 ka, if confirmed, would represent a group that did not contribute genetically to modern indigenous Australia–New Guinea populations.

Madjedbebe apart, there is little archaeological evidence of human presence on the SCS arc >50 ka, and what there is—simple core and flake stone tools—shows formal artifact and assemblage-level continuity from well before 120 ka (37). The obvious break in the regional sequence falls at or after 50 ka, marked by data from

Sahul, Wallacea, Southeast Asia, and further afield in the East Asian mainland and Japan (35, 38, 40, 116). That break is associated with the appearance of clear indications of modern human behavior. Salient aspects include the rapid crossing of Wallacea, the widespread, similarly rapid occupation of Sahul, and the use of material symbols.

Madjedbebe offers no unambiguous evidence that changes this interpretation. Our reconsideration of site geomorphology suggests an alternative explanation for its formation, namely that the content of the phase 2 assemblage and its association with sediments dated 65 ka are products of postdepositional processes operating on younger archaeological remains. These are the same factors that disrupted artifact distributions at Nauwalabila, a sand-sheet rock shelter, 65 km south of Madjedbebe. There, the presence of stone tools mixed in a rubble layer at the base of the deposit strongly suggests postdepositional settling and comingling. Seven calibrated <sup>14</sup>C dates on charcoal, 7.7-10.8 ka, retrieved from sediments 228–301 cm below the surface, bracketed by OSL age estimates of 48-67 ka reinforce that suggestion (98, 101). These observations do not eliminate the possibility that the Madjedbebe phase 2 artifact assemblage dates to 65 ka, but they do cast serious doubt on that notion. An argument in support of it requires substantial archaeological evidence from other, more secure geomorphological contexts elsewhere in Sahul. No such evidence is yet on offer.

We conclude that the case for an AMH expansion across the SCS arc >50 ka remains weak. More compelling evidence from the human fossil record, identification of genetic signals of a >50-ka Sahul population, or support from a well-dated archaeological site in Sahul would change this picture. However, it would also raise questions about the adaptive advantages over regional archaic populations enjoyed by the newly arriving groups, about their disadvantages relative to AMH arriving post-50 ka, and about the ecological and demographic circumstances surrounding both processes. How did those groups manage to displace those archaic populations, and how were they in turn so thoroughly pushed aside by still later arriving AMH? No answer to either question has been offered by proponents of an AMH presence on the arc >50-ka.

Our review points to significant changes in human morphology, genetic makeup, and behavior along the SCS arc beginning 45–50 ka. This parallels dates for analogous changes in the Late Pleistocene record of other parts of the Eastern Hemisphere, notably the movement of AMH into southern and eastern Europe, represented by the Initial Upper Paleolithic, at or shortly before the beginning of Greenland Interstadial 12 (ca. 47 ka) (117–119). Data from Sahul reflect marine voyaging and pelagic fishing capabilities as well as the capacity to adapt quickly to unfamiliar terrestrial foraging opportunities. Evidence from Europe shows something similar in the development of relatively complex Early Upper Paleolithic subsistence and settlement technologies, the achievement of unprecedentedly high population densities, and the persistent occupation of challenging, high-latitude habitats (3). This hemisphere-wide shift in behavior, a unitary if regionally diverse phenomenon marked most clearly in the Sahul and European sequences post-50 ka, is unmistakable.

As others have noted (120), increased interest over the last decade in the possibility of AMH expansion eastward from Africa in the interval 60–120 ka has drawn attention away from the 50- to 55-ka event. While evidence from the SCS arc seen to support this notion is intriguing, our review shows that it is not compelling. At the same time, this review also highlights significant, perhaps unexpected details of the increasingly well-documented regional record, especially from Wallacea and Sahul, as well as parallels in behavior that become apparent at about the same time in western Eurasia and elsewhere across the Old World.

Something important happened in human evolutionary history at or just before 50 ka. The interesting questions are why, and why then.

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- 1 Hublin J-J, et al. (2017) New fossils from Jebel Irhoud, Morocco and the pan-African origin of Homo sapiens. Nature 546:289–292.
- 2 Klein RG (2009) The Human Career: Human Biological and Cultural Origins (Univ of Chicago Press, Chicago), 3rd Ed.
- 3 Hoffecker J (2017) Modern Humans: Their African Origin and Global Dispersal (Columbia Univ Press, New York).
- **4** Groucutt HS, et al. (2015) Rethinking the dispersal of *Homo sapiens* out of Africa. Evol Anthropol 24:149–164.
- **5** Bae CJ, Douka K, Petraglia MD (2017) On the origin of modern humans: Asian perspectives. *Science* 358:eaai9067.
- 6 Clarkson C, et al. (2017) Human occupation of northern Australia by 65,000 years ago. Nature 547:306-310.
- 7 Veth P (2017) Breaking through the radiocarbon barrier: Madjedbebe and the new chronology for Aboriginal occupation of Australia. Aust Archaeol 83:165–167.
- 8 Allen J (2017) Yes, Virginia, there is a Santa Claus; He just doesn't bring presents to children who don't believe in him. Aust Archaeol 83:163–165.
- **9** Grant KM, et al. (2014) Sea-level variability over five glacial cycles. *Nat Commun* 5:5076.
- **10** Rohling EJ, et al. (2017) Differences between the last two glacial maxima and implications for ice-sheet, δ<sup>18</sup>O, and sea-level reconstructions. *Quat Sci Rev* 176:1–28.
- 11 Murray-Wallace CD, Woodroffe CV (2014) Quaternary Sea-Level Changes: A Global Perspective (Cambridge Univ Press, Cambridge, UK).
- 12 Lambeck K, Chappell J (2001) Sea level change through the last glacial cycle. Science 292:679–686.
- 13 Williams AN, et al. (2018) Sea-level change and demography during the last glacial termination and early Holocene across the Australian continent. Quat Sci Rev 182:144–154.
- 14 Wallace AR (1863) On the physical geography of the Malay Archipelago. Royal Geographical Society 7:205–212.
- 15 Larick R, et al. (2001) Early Pleistocene 40 Ar/39 Ar ages for Bapang formation hominins, central Jawa, Indonesia. Proc Natl Acad Sci USA 98:4866–4871.
- **16** Yokoyama Y, Falguères C, Sémah F, Jacob T, Grün R (2008) Gamma-ray spectrometric dating of late *Homo erectus* skulls from Ngandong and Sambungmacan, central Java, Indonesia. *J Hum Evol* 55:274–277.
- 17 Indriati E, et al. (2011) The age of the 20 meter Solo river terrace, Java, Indonesia and the survival of Homo erectus in Asia. PLoS One 6:e21562.
- 18 Brumm A, et al. (2010) Hominins on Flores, Indonesia, by one million years ago. Nature 464:748–752.
- 19 van den Bergh GD, et al. (2016) Homo floresiensis-like fossils from the early Middle Pleistocene of Flores. Nature 534:245–248.
- 20 Morwood M, van Oosterzee P (2007) Discovery of the Hobbit: The Scientific Breakthrough that Changed the Face of Human History (Random House Australia, Sydney).

- 22 Cooper A, Stringer CB (2013) Paleontology. Did the Denisovans cross Wallace's line? Science 342:321-323.
- 23 Demeter F, et al. (2012) Anatomically modern human in Southeast Asia (Laos) by 46 ka. Proc Natl Acad Sci USA 109:14375–14380.
- 24 Demeter F, et al. (2017) Early modern humans from Tam Pà Ling, Laos: Fossil review and perspectives. Curr Anthropol 58:S527-S538.
- 25 Shackelford L, et al. (2018) Additional evidence for early modern human morphological diversity in Southeast Asia at Tam Pà Ling, Laos. Quat Int 466:93-106.
- 26 Westaway KE, et al. (2017) An early modern human presence in Sumatra 73,000-63,000 years ago. Nature 548:322-325.
- 27 Dubois E (1891) Voorlopig bericht omtrent het onderzoek naar de Pleistocene en Tertiaire vertebraten-fauna van Sumatra en Java, gedurende het jaar 1890. Nat Tijdschr Ned Indië 51:93–100.
- 28 Hooijer D (1948) Prehistoric teeth of man and of the orang-utan from central Sumatra, with notes on the fossil orang-utan from Java and Southern China. Zool Meded 29:175–301.
- 29 Hawks J (2018) Lida Ajer, early modern human remains in island Southeast Asia. January 7, 2018. Available at johnhawks.net/. Accessed March 31, 2018.
- 30 Falguères C, et al. (2016) Geochronology of early human settlements in Java: What is at stake? Quat Int 416:5-11.
- 31 O'Sullivan PB, et al. (2001) Archaeological implications of the geology and chronology of the Soa Basin, Flores, Indonesia. Geology 29:607-610.
- 32 van den Bergh GD, et al. (2016) Earliest hominin occupation of Sulawesi, Indonesia. Nature 529:208-211.
- **33** Aziz F, et al. (2009) Excavations at Tangi Talo, central Flores, Indonesia. *Palaeontology and Archaeology of the Soa Basin, Central Flores, Indonesia*, eds Aziz F, et al. (Indonesian Geological Survey Institute, Bandung, Indonesia), pp 41–58.
- 34 Ingicco T, et al. (2018) Earliest known hominin activity in the Philippines by 709 thousand years ago. Nature 557:233-237.
- 35 Bellwood P (2017) First Islanders: Prehistory and Human Migration in Island Southeast Asia (Wiley Blackwell, Oxford).
- 36 Rabett R (2012) Human Adaptation in the Asian Paleolithic: Hominin Dispersal and Behavior During the Late Quaternary (Cambridge Univ Press, Cambridge, UK).
- 37 Moore MW (2013) Simple stone flaking in Australasia: Patterns and implications. Quat Int 285:140-149.
- **38** Morley MW, et al. (2017) Initial micromorphological results from Liang Bua, Flores (Indonesia): Site formation processes and hominin activities at the type locality of *Homo floresiensis*. J Archaeol Sci 77:125–142.
- **39** Barker G, et al. (2007) The 'human revolution' in lowland tropical Southeast Asia: The antiquity and behavior of anatomically modern humans at Niah Cave (Sarawak, Borneo). J Hum Evol 52:243–261.
- **40** O'Connell JF, Allen J (2015) The process, biotic impact, and global implications of the human colonization of Sahul about 47,000 years ago. J Archaeol Sci 56:73–84
- 41 Sutikna T, et al. (2016) Revised stratigraphy and chronology for Homo floresiensis at Liang Bua in Indonesia. Nature 532:366-369.
- 42 Callaway E (2016) Human remains found in hobbit cave. Nature, 10.1038/nature.2016.20656.
- 43 Hawkins S, et al. (2016) Oldest human occupation of Wallacea at Laili Cave, Timor-Leste, shows broad spectrum foraging responses to Late Pleistocene environments. Quat Sci Rev 171:58–72.
- **44** Bird MI, et al. (2018) Palaeogeography and voyage modelling indicates early human colonisation of Australia was likely from Timor-Roti. *Quat Sci Rev* 191:431–439.
- 45 Wickler S, Spriggs M (1988) Pleistocene human occupation of the Solomon Islands. Antiquity 62:703-706.
- **46** O'Connell JF, Allen J, Hawkes K (2010) Pleistocene Sahul and the origins of seafaring. The Global Origins and Development of Seafaring, eds Anderson A, et al. (McDonald Institute for Archaeological Research, Cambridge, UK), pp 57–68.
- 47 Davidson I, Noble W (1992) Why the first colonisation of the Australian region is the earliest evidence of modern human behavior. Archaeol Ocean 27:113–119.
- 48 O'Connell JF, Allen J (2012) The restaurant at the end of the universe: Modeling the colonisation of Sahul. Aust Archaeol 74:5-17.
- 49 Allen J, Cosgrove R, Garvey J (2016) Optimality models and the food quest in Pleistocene Tasmania. J Anthropol Archaeol 44:208-215.
- 50 Golson J (1971) Australian Aboriginal food plants: Some ecological and culture-historical implications. Aboriginal Man and Environment in Australia, eds Mulvaney DJ, Golson J (Australian National Univ Press, Canberra, Australia), pp 196–238.
- 51 Leavesley MG (2004) Trees to the sky: Prehistoric hunting in New Ireland, Papua New Guinea. PhD dissertation (Australian National Univ, Canberra, Australia).
- 52 O'Connor S, Ono R, Clarkson C (2011) Pelagic fishing at 42,000 years before the present and the maritime skills of modern humans. Science 334:1117–1121.
- 53 Hunt CO, Gilbertson DD, Rushworth G (2012) A 50,000-year record of late Pleistocene tropical vegetation and human impact in lowland Borneo. Quat Sci Rev 37:61–80.
- 54 Barton H, Paz V, Carlos AJ (2017) Plant food remains from the Niah Caves: Macroscopic and microscopic approaches. Archaeological Investigations in the Niah Caves, Sarawak, eds Barker G, Farr L (McDonald Institute for Archaeological Research, Cambridge, UK), pp 455–468.
- 55 Summerhayes G, Ford A (2014) Late Pleistocene colonisation and adaptation in New Guinea: Implications for modelling modern human behavior. Southern Asia, Australia and the Search for Human Origins, eds Dennell R, Porr M (Cambridge Univ Press, Cambridge, UK), pp 213–228.
- 56 Wroe S, et al. (2013) Climate change frames debate over the extinction of megafauna in Sahul (Pleistocene Australia-New Guinea). Proc Natl Acad Sci USA 110:8777–8781.
- 57 Saltré F, et al. (2016) Climate change not to blame for late Quaternary megafauna extinctions in Australia. Nat Commun 7:10511.
- 58 Aubert M, Brumm A, Taçon PSC (2017) The timing and nature of human colonization of Southeast Asia in the late Pleistocene: A rock art perspective. Curr Anthropol 58:S553–S566.
- 59 Langley MC, O'Connor S, Piotto E (2016) 42,000-year-old worked and pigment-stained Nautilus shell from Jerimalai (Timor-Leste): Evidence for an early coastal adaptation in ISEA. J Hum Evol 97:1–16.
- **60** Pyatt FB, Barker GW, Rabett RJ, Szabo K, Wilson B (2010) Analytical examination of animal remains from Borneo: The painting of bone and shell. *J Arch Sci* 37:2102–2105.
- 61 Bowler JM, et al. (2003) New ages for human occupation and climatic change at Lake Mungo, Australia. Nature 421:837–840.
- 62 Skoglund P, Mathieson I (2018) Ancient human genomics: The first decade. Annu Rev Genomics Hum Genet 19.
- 63 Fu Q, et al. (2013) A revised timescale for human evolution based on ancient mitochondrial genomes. Curr Biol 23:553-559.
- 64 Ho SYW, et al. (2011) Time-dependent rates of molecular evolution. Mol Ecol 20:3087-3101.
- 65 Lipson M, Reich D (2017) A working model of the deep relationships of diverse modern human genetic lineages outside of Africa. Mol Biol Evol 34:889–902.
- 66 Prüfer K, et al. (2017) A high-coverage Neandertal genome from Vindija Cave, Croatia. Science 358:655-658.
- 67 Browning SR, Browning BL, Zhou Y, Tucci S, Akey JM (2018) Analysis of human sequence data reveals two pulses of Archaic Denisovan admixture. *Cell* 173:53–61.e9.
- **68** Villanea FA, Schraiber J (2018) Spectrum of Neandertal introgression across modern-day humans indicates multiple episodes of human-Neandertal interbreeding. bioRxiv:10.1101/343087. Preprint, posted June 11, 2018.
- 69 Sankararaman S, et al. (2014) The genomic landscape of Neanderthal ancestry in present-day humans. Nature 507:354–357.
- 70 Fu Q, et al. (2014) Genome sequence of a 45,000-year-old modern human from western Siberia. Nature 514:445–449.
- 71 Moorjani P, et al. (2016) A genetic method for dating ancient genomes provides a direct estimate of human generation interval in the last 45,000 years. *Proc Natl Acad Sci USA* 113:5652–5657.
- 72 Reich D, et al. (2010) Genetic history of an archaic hominin group from Denisova Cave in Siberia. Nature 468:1053–1060.
- 73 Malaspinas A-S, et al. (2016) A genomic history of Aboriginal Australia. Nature 538:207–214.
- 74 Pagani L, et al. (2016) Genomic analyses inform on migration events during the peopling of Eurasia. Nature 538:238–242.

- 75 Mallick S, et al. (2016) The Simons Genome Diversity Project: 300 genomes from 142 diverse populations. Nature 538:201-206.
- 76 Tobler R, et al. (2017) Aboriginal mitogenomes reveal 50,000 years of regionalism in Australia. Nature 544:180-184.
- 77 Nagle N, et al.; Genographic Consortium (2017) Aboriginal Australian mitochondrial genome variation—An increased understanding of population antiquity and diversity. Sci Rep 7:43041.
- 78 Moore JH (2001) Evaluating five models of human colonization. Am Anthropol 103:395-408.
- **79** Williams AN (2013) A new population curve for prehistoric Australia. *Proc Biol Sci* 280:20130486.
- 80 Hamm G, et al. (2016) Cultural innovation and megafauna interaction in the early settlement of arid Australia. Nature 539:280-283.
- **81** Wood R, et al. (2016) Towards an accurate and precise chronology for the colonization of Australia: The example of Riwi, Kimberley, Western Australia. *PLoS One* 11:e0160123.
- 82 Veth P, et al. (2017) Early human occupation of a maritime desert, Barrow Island, North-West Australia. Quat Sci Rev 168:19-29.
- 83 Delannoy J-J, et al. (2017) Engineers of the Arnhem Land Plateau: Evidence for the origins and transformation of sheltered spaces at Nawarla Gabarnmang. The Archaeology of Rock Art in Western Arnhem Land, Australia, Terra Australis, eds David B, et al. (ANU Press, Canberra, Australia), Vol 47, pp 197–244.
- **84** Maloney T, O'Connor S, Wood R, Aplin K, Balme J (2018) Carpenter's Gap 1: A 47,000 year old record of indigenous adaptation and innovation. *Quat Sci Rev* 191:204–228.
- **85** Hiscock P, O'Conner S, Balme J, Maloney T (2016) World's earliest ground-edge axe production coincides with human colonisation of Australia. *Aust Archaeol* 82:1–11.
- **86** Geneste J-M, David B, Plisson H, Delannoy J-J, Petchy F (2012) The origins of ground-edge axes: New findings from Nawarla Gabarnmang, Arnhem Land (Australia) and global implications for the evolution of fully modern humans. *Camb Archaeol J* 22:1–17.
- 87 Takashi T (2012) MIS 3 edge-ground axes and the arrival of the first Homo sapiens in the Japanese archipelago. Quat Int 248:70-78.
- 88 Smith M (2013) The Archaeology of Australia's Deserts (Cambridge Univ Press, Cambridge, UK).
- 89 Zeanah DW, Codding B, Bliege Bird R, Bird D (2017) Mosaics of fire and water: The co-emergence of anthropogenic landscapes and intensive seed exploitation in the Australian arid zone. Aust Archaeol 83:2–19.
- 90 Marean CW (2017) Archaeology: Early signs of human presence in Australia. Nature 547:285–287.
- 91 Bird MI, et al. (1999) Radiocarbon dating of 'old' charcoal using a wet oxidation-stepped combustion procedure. Radiocarbon 41:127–140.
- 92 Fifield LK, et al. (2001) Radiocarbon dating of the human occupation of Australia prior to 40 ka B.P.-successes and pitfalls. Radiocarbon 43:1139–1145.
- 93 Reimer P, et al. (2013) IntCal13 and Marine13 radiocarbon age calibration curves, 0-50,000 years cal. BP. Radiocarbon 55:1869-1887.
- 94 Allen J, O'Connell JF (2014) Both half right: Updating the evidence for dating first human arrivals in Sahul. Aust Archaeol 79:86-109.
- 95 Roberts RG, Jones R, Smith MA (1990) Thermoluminescence dating of a 50,000-year-old occupation site in northern Australia. Nature 345:153-156.
- 96 Roberts RG, et al. (1994) The human colonisation of Australia: Optical dates of 53,000 and 60,000 bracket human arrival at Deaf Adder Gorge, Northern Territory. Quat Sci Rev 13:575–583.
- 97 Thorne A, et al. (1999) Australia's oldest human remains: Age of the Lake Mungo 3 skeleton. J Hum Evol 36:591–612.
- **98** Allen J, O'Connell JF (2003) The long and the short of it: Archaeological approaches to determining when humans first colonised Australia and New Guinea. *Aust Archaeol* 57:5–19.
- 99 Dortch J, Malaspinas A-S (2017) Madjedbebe and genomic histories of Aboriginal Australia. Aust Archaeol 83:174–177.
- 100 Clarkson CC, et al. (2018) Reply to comments on Clarkson et al. (2017) 'Human occupation of northern Australia by 65,000 years ago.' Aust Archaeol 84:84–89.
- **101** Bird MI, et al. (2002) Radiocarbon analysis of the early archaeological site of Nauwalabila 1, Arnhem land, Australia: Implications for sample suitability and stratigraphic integrity. *Quat Sci Rev* 21:1061–1075.
- **102** Clarkson C, et al. (2015) The archaeology, chronology and stratigraphy of Madjedbebe (Malakunanja II): A site in northern Australia with early occupation. *J Hum Evol* 83:46–64.
- 103 Lahr M, Foley R (1994) Multiple dispersals and modern human origins. Evol Anth 3:48-60.
- 104 Oppenheimer S (2012) A single southern exit of modern humans from Africa: Before or after Toba? Quat Int 258:88–99.
- **105** Reyes-Centeno H, et al. (2014) Genomic and cranial phenotype data support multiple modern human dispersals from Africa and a southern route into Asia. *Proc Natl Acad Sci USA* 111:7248–7253.
- 106 Rabett RJ (2018) The success of failed Homo sapiens dispersals out of Africa and into Asia. Nat Ecol Evol 2:212–219.
- 107 Petraglia MD, Haslam M, Fuller DQ, Boivin N, Clarkson C (2010) Out of Africa: New hypotheses and evidence for the dispersal of *Homo sapiens* along the Indian Ocean rim. *Ann Hum Biol* 37:288–311.
- 108 Rasmussen M, et al. (2011) An Aboriginal Australian genome reveals separate human dispersals into Asia. Science 334:94–98.
- 109 Armitage SJ, et al. (2011) The southern route "out of Africa": Evidence for an early expansion of modern humans into Arabia. Science 331:453-456.
- 110 Clarkson CC, Jones S, Harris C (2012) Continuity and change in the lithic industries of the Jurreru Valley, India, before and after the Toba eruption. Quat Int 258:165–179.
- 111 Mellars P, Gori KC, Carr M, Soares PA, Richards MB (2013) Genetic and archaeological perspectives on the initial modern human colonization of southern Asia. Proc Natl Acad Sci USA 110:10699–10704.
- 112 Usik VI, Rose JI, Hilbert YH, Van Peer P, Marks AE (2013) Nubian Complex reduction strategies in Dhofar, southern Oman. Quat Int 300:244–266.
- 113 Groucutt HS, et al. (2018) Homo sapiens in Arabia by 85,000 years ago. Nat Ecol Evol 2:800-809.
- 114 Dennell R, Petraglia M (2012) The dispersal of Homo sapiens across southern Asia: How early, how often, how complex? Quat Sci Rev 47:15–22.
- 115 Dennell R (2014) Smoke and mirrors: The fossil record of Homo sapiens between Arabia and Australia. Southern Asia, Australia and the Search for Human Origins, eds Dennell R, Porr M (Cambridge Univ Press, Cambridge, UK), pp 33–50.
- 116 Bae CJ (2017) Late Pleistocene human evolution in eastern Asia: Behavioral perspectives. Curr Anthropol 58(Suppl 17):S373-S382.
- 117 Müller UC, et al. (2011) The role of climate in the spread of modern humans into Europe. Quat Sci Rev 30:273–279.
- 118 Rasmussen SQ, et al. (2014) A stratigraphic framework for abrupt climatic changes during the last glacial period based on three synchronized Greenland ice-core records: Refining and extending the INTIMATE event stratigraphy. Quat Sci Rev 106:14–28.
- 119 Hublin J-J (2015) The modern human colonization of western Eurasia: When and where? Quat Sci Rev 118:194-210.
- **120** Kaifu Y, Izuho M, Goebel T (2015) Modern human dispersal and behavior in Paleolithic Asia: Summary and discussion. *Emergence and Diversity of Modern Human Behavior in Paleolithic Asia*, eds Kaifu Y, et al. (Texas A&M Univ Press, College Station, TX), pp 535–566.