

Paleontology Series

Biogeography and evolution of the genus *Homo*

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The debate about the origins of modern humans has traditionally focussed on two contrasting views. Multi-regional evolution proposes that present-day populations worldwide are the descendants of *in situ* evolution after an initial dispersal of *Homo erectus* from Africa during the Lower Pleistocene. The alternative, Out-of-Africa 2, proposes that all present-day populations are descended from a recent common ancestor that lived in East Africa ~150 000 years ago, the population of which replaced all regional populations. The weight of the evidence is now in favour of Out-of-Africa 2, and discussion is now dominated by the causes of the dispersal of modern humans out of Africa and the outcome of contact with other populations. Fresh approaches, from disciplines hitherto peripheral to the debate, such as evolutionary ecology, and new discoveries are challenging established views, particularly the prevalent idea that biologically superior modern humans were the cause of the demise of all other populations of *Homo* worldwide. Climate-driven ecological change has been, as with many other taxa, the driving force in the geographical range dynamics of the genus *Homo*.

Our changing view of the genus *Homo*

Here, I present a current picture of the evolution of the genus *Homo*, focussing on the major geographical range expansions, contractions and extinctions throughout its two-million-year history. Modern humans were the most recent in a sequence of geographically expanding populations and new evidence [1–3] is showing that they overlapped in time with other populations of *Homo* in Asia and Europe, challenging the established view that behaviourally superior modern humans caused the extinction of congeners when they met [3].

Flores and the diversity of Homo in The Pleistocene

The discovery of a small hominin, *Homo floresiensis*, on the island of Flores, Indonesia, was an unexpected find for the palaeo-anthropological community [1]. The Flores hominin, whose status is debated, is very small and might be a unique example of island dwarfism in the

genus. It might also be related to an early-arriving *H. erectus* in south-east Asia that subsequently evolved in isolation. The dating of the specimen at 18 thousand years ago (ka) has shown, contrary to established thinking, that modern humans, *Homo sapiens*, only very recently became the sole representatives of the genus on the planet. The discovery has strengthened indications that the late survival of archaic hominins might be a feature of tropical and warm temperate regions of the Old World. In 1996, Carl Swisher III and colleagues reported the late survival (27 ± 2 – 53.3 ± 4 ka) of *Homo erectus* in Central Java [2] and, in Europe, increasing archaeological and dating evidence indicates that Neanderthals survived in southern and Atlantic refugia as recently as 28 ka [3]. These discoveries offer strong support for the argument that modern humans did not carry a massive advantage that caused the rapid extinction of other populations of *Homo* when they met, a view that I develop here.

Early hominin dispersals from tropical Africa

Dispersals of *Homo* from tropical Africa have been a regular feature since the emergence of the genus 1.9 million years ago (mya). The earliest well dated dispersals show that the behavioural attributes ascribed to modern humans were not a prerequisite to dispersal from tropical Africa.

The earliest representative of the genus, *H. erectus*, is found in tropical East Africa 1.9 mya [4] (Box 1). It is a large hominin, also described as *Homo ergaster* [4,5], which was adapted to a fully terrestrial way of life. A rapid dispersal out of tropical areas followed the emergence of this African *H. erectus* (Box 2), judging by the presence of hominins, attributable to this species, in Dmanisi (the Republic of Georgia in eastern Europe) at 42°N in the Caucasus by 1.7 mya [6].

First colonization of eastern Asia

The available evidence strongly indicates an early establishment of populations of *H. erectus* in tropical south-east Asia that persisted for the following 1.7 mya [7] (Box 1). Ar^{40}/Ar^{39} dating of a volcanic layer from which an *H. erectus* cranium was derived in Mojokerto, Java, indicates an early presence at 1.8 ± 0.04 mya [8,9]. The early dates are supported by work in Bapang, Central Java, which has produced numerous specimens of *H. erectus* (time range: 1.51 ± 0.08 mya to 1.02 ± 0.06 mya) [10]. The recent

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Box 2. Biogeography of the genus *Homo*

Figure 1a details the initial distribution of *Homo erectus*, with the geographical area covered by fossils and archaeological sites older than 1 ma shown in pink. There is a large area of southern Asia that is notable for the absence of evidence. Possible dispersal routes of *erectus* between Africa and East Asia are shown by arrows. The colonization of Europe might have commenced ~ 1.2 ma, judging from stone tool evidence from Orce in south-east Spain [15] but it is not known whether these populations, and later ones in Atapuerca (Spain) and Ceprano (Italy), arrived from either the east (via the Middle East) or the south (across the Strait of Gibraltar). Numbers indicate earliest dates currently available for the earliest fossils or archaeological occupation horizons (see main text).

Figures 1a–d detail the dispersal of modern humans based on genetic marker evidence [28–30,54], with black circles indicating the approximate areas of dispersal. A recent study of variation at 377 autosomal loci in 52 worldwide populations suggests that the effective population size of the ancestral African population, whose descendants colonized the world, was only 700 [55]. This population lived in sub-Saharan Africa some time between 141.7 ± 5.7 and 71.2 ± 4.4 ka. The divergence of the Eurasian population from the ancestral African population is in the temporal range of ~ 127.4 and 37.8 ka [55]. Work on Y-Chromosome markers has provided a picture of when and how this population dispersed across Eurasia ~ 45 ka [29,30]. Although it is

difficult to correlate genetic and archaeological data, the early entry into Europe via the Middle East ~ 45 – 40 ka could correspond to the arrival of modern humans with the earliest Upper Palaeolithic technology (the Aurignacian). The second entry, at 30 ka, could correspond with the arrival of modern humans with a new portable technology, for use with long-range projectiles (the Gravettian). In this scenario, the Gravettian would be associated with the exploitation of the mammoth steppe fauna and the eastward expansion of this fauna in response to increasing cold and aridity during between 35 and 20 ka [56].

In Figure 1b, the dispersal of modern humans in Africa and the Middle East between 130 and 70 ka is shown in pink. Coastal dispersal, pre-50 ka, via the Horn of Africa reaching Australia by 50 ka [27] and subsequent expansion north and into North America is shown in green. This event might have been followed closely by a second wave that reached East Asia [29,30]. In Figure 1c, pink arrows indicate dispersal into the Levant from north-east Africa (black circle) at 45 ka and subsequent expansion into Europe, India, Central Asia and north-east Asia. A subsequent lineage (not indicated) reached New Guinea but not Australia. In Figure 1d, the dispersal of central Asian populations westwards into Europe at 30 ka is indicated by pink arrows, and north-eastwards towards Siberia at 20 ka by blue arrows; this population dispersed further into North America shortly afterwards [29,30].

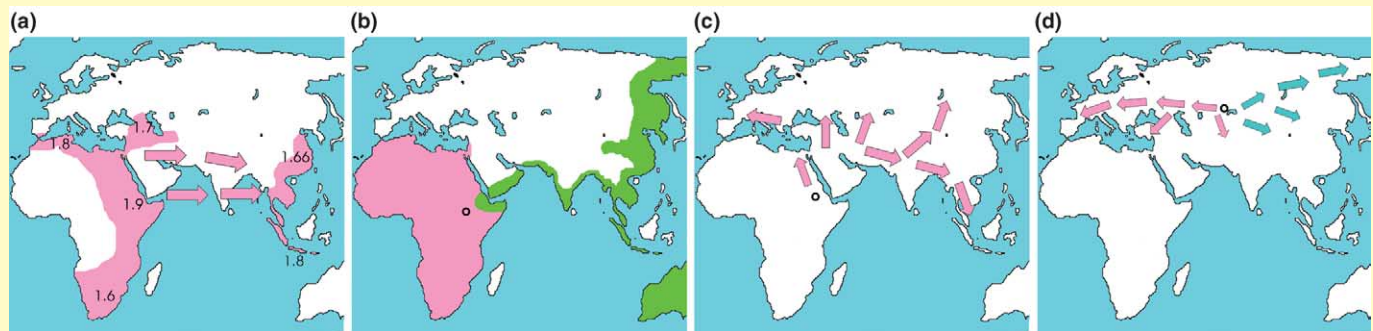


Figure 1.

evolutionary trajectory from African *H. erectus* to *H. sapiens* by 600 ka [14,17,18]. Four hundred thousand years later, we observe the first anatomically modern humans, confirmed by the latest dating of fossils from Omo in Ethiopia, at 195 ± 5 ka [19].

Another lineage, leading to the Neanderthals, evolved in Europe and western Asia while *H. erectus* persisted in the Far East (Box 1). The early stages of the Neanderthal lineage are evident in the specimens from the Sima de los Huesos, Atapuerca (Spain), dated at ~ 300 ka [20]. The retrieval of mitochondrial DNA (mtDNA) sequences from five Neanderthal specimens from widely separated parts of the geographical range, in Germany, Croatia, Russia and northern Spain [21–24], has strengthened the view that they were a lineage that was separate from the ancestors of modern humans; the time of the last common ancestor of Neanderthals and modern humans has been estimated from genetic divergence rates to be ~ 465 ka (these estimates have large errors, 317–741 ka, but give a helpful indication of the time of the lineage split) [21–23]. This evidence suggests that Neanderthals (in Europe and western Asia) and modern humans (in Africa) evolved in allopatry some time after 0.5 mya (Box 1).

Early dispersals of anatomically modern humans

The recently published dates for the first anatomically modern humans (195 ± 5 ka [19]) indicate that they were restricted to tropical Africa for up to 80 ka before the first dispersal into the Levant. This suggests that species attributes, such as large brains and complex behaviour, were not the trigger for this dispersal.

By 125 ka, anatomically modern humans are found throughout Africa. They crossed the Sahara and are present in the Middle East sites of Qafzeh and Skhul, between 120 and 80 ka (Box 2). However, this early expansion did not result in the colonization of Europe [25]. Dispersal eastwards, keeping within the tropical belt, again seems to have been easier for these people as they tracked environments, such as tropical grasslands with mammalian herbivores, with which they were familiar. An arrival in Australia by 50 ka marks the earliest occupation of the continent by *Homo* and is supported by dates of 40 ± 2 ka for modern human burials in Lake Mungo, south-eastern Australia [26].

One view that has gathered recent support is that this early dispersal followed a coastal route (Box 2) as proposed by Lahr and Foley 11 years ago [27]. In 1999, Quintana-Murci and colleagues [28] provided genetic evidence for an

exit from Africa into southern Asia via the Horn of Africa. They showed that the Asian mitochondrial haplogroup M (which occurs in high frequency in India) separated from its eastern African counterpart over 50 ka. The haplogroup is rare in the Levant but occurs in high frequency in the southern Arabian Peninsula. Further support for a coastal dispersal to Australia comes from the Y chromosome that is used to track male lineages [29,30]. The presence of humans in coastal areas of north-east Africa has been confirmed by the discovery of early Middle Stone Age artefacts in an emerged reef terrace on the Red Sea coast of Eritrea [31]. Using U-Th mass spectrometry techniques on fossil corals, it has been possible to age the artefacts to around 125 ka [31].

Later dispersals of anatomically modern humans

Later dispersals of modern humans (Box 2) might have been, at least in part, into vacant territory previously occupied by earlier modern humans given that those that had reached the Levant 120 ka, for example, left no subsequent trace [17]. In other areas, modern humans encountered other hominins, such as the Neanderthals. Much of the recent debate has centred on whether species biology or ecological factors were responsible for these range expansions.

According to those who support a saltationist perspective of the origins of anatomical (~195 ka) and behavioural (~50 ka) modernity [32], modern humans appeared rather suddenly in Africa and so modernity is their exclusivity. That a significant behavioural shift enabled modern humans to exploit resources more efficiently and expand geographically out of Africa is central to this argument [17]. The alternative, that climate-forced ecological change opened a window of opportunity for a small African population to disperse across the Sahara, tracking open grassland habitats and mammalian herbivores, is coming to the fore [3].

The exploitation of coastal resources is, for some, considered to have been crucial in opening the way for the later dispersals of anatomically modern humans [33]. These authors argue that anatomically modern humans only spread into Eurasia after 50 ka, even though they had been in Africa for at least 100 ka before this time. According to this view, it was only when the African moderns developed an advantage that made them behaviourally, as well as anatomically, modern that they were able to disperse and outcompete other humans (Box 2). There is, in reality, no convincing evidence to show such sudden behavioural change. In any case, this idea of use of coastal resources after 50 ka is inconsistent with the first known coastal dispersal that, allowing for an arrival in Australia by 50 ka, must have occurred some time before 50 ka [28] and the clear evidence of much earlier coastal exploitation, in the Middle Stone Age (MSA) 125 ka [31].

The behavioural shift is attributed to a genetically based neurological change [34], but no evidence of such a change yet exists. There are clear flaws in the way in which data, offered in support of more efficient subsistence strategies after 50 ka, are currently interpreted [35–37]. The claim of improved energy extraction efficiency in an

African population at 50 ka [33,34] is therefore on thin ground. There are further reasons for questioning the point of view that there was a significant genetically based behavioural shift around 50 ka. For example, evidence of a rapid technological transition from the MSA to the Late Stone Age (LSA) at 50 ka in Africa is limited. At Enkapune Ya Muto, in the Kenyan central Rift Valley, the LSA is thought to have begun before 46 ka [38], but direct evidence of a consequent LSA population expansion, as predicted by the behavioural-shift model [33,34], is lacking.

In South Africa, where much of the comparative MSA and LSA work has been done [17,33,34], there are no sites corresponding to the period of the beginning of the LSA. Most South African LSA sites are post-20 ka [37] and cannot be used to make a direct comparison of a transition at 50 ka. Yet comparisons of subsistence behaviour are based on MSA sites that are older than 60 ka and LSA sites that are younger than 20 ka. At Die Kelders Cave 1 in South Africa, for example, the MSA chronology spans 71–57 ka and the LSA levels accumulated 2–1.5 ka and were dominated by sheep [34]. In Europe, the equivalent comparison would be between Neanderthals and Roman shepherds.

When we place the origin of behavioural modernity will depend on what we consider modernity to be. In a seminal paper, McBrearty and Brooks [37] characterized modern human behaviour by the capacity for: (i) abstract thinking; (ii) planning depth; (iii) behavioural, economic and technological innovativeness; and (iv) symbolic behaviour as materially reflected by, for example, paintings and ornaments. In a detailed analysis of the African evidence, the authors convincingly showed that all the elements of modern behaviour accumulated over 200 ka and did not suddenly appear together. Instead, the elements originated in locations that were widely separated in space and time. Apparent leaps in the northern and southern tips of Africa, as indeed in the European ‘cul-de-sac’, merely reflect a discontinuous archaeological record. Since their research was published, evidence in support of modern behaviour has increased further. Most recently, d’Errico *et al.* [39] provided convincing evidence of symbolic behaviour, in the form of perforated shells, in the MSA levels at Blombos Cave, South Africa, ~75 ka.

There is, therefore, no solid evidence of a sudden behavioural change in modern humans at 50 ka and the reasons for the geographical expansion must be sought elsewhere. Instead, the expansion is closely linked with the climatic events of the Last Glacial Cycle (125–18 ka), which includes the coldest and most unstable moments of the entire Pleistocene [3]. The consequent opening up of ecological routes into Eurasia for an African human population adapted to the exploitation of large mammalian herbivores on open plains coincides with this expansion (Box 2).

Modern humans versus Neanderthals

The question of behavioural modernity also lies at the heart of the discussion of the outcome of modern human–Neanderthal contact (Box 3). Increasingly, the view that Neanderthals were intelligent, although different, from modern humans, is gaining support [3].

Box 3. The Neanderthals and climate change

Climate change, which opened and closed ecological and physical barriers, is correlated closely with human demography and biogeography [3,27,57]. The Neanderthals occupied regions that are currently represented by Mediterranean bioclimates. Temperate bioclimates were occupied during milder episodes but the mammal-rich mammoth steppe was never exploited (Figure 1). They survived until 28 ka in isolated refugia [3] and thus would have shared parts of Europe with the newly arrived modern humans for up to 15 ka.

The anatomically robust Neanderthals have been viewed for a long time as hominins that were adapted to the cold conditions of glacial Europe [58] and this has coloured our understanding of their biogeography [3]. The alternative view, that the Neanderthals were severely affected by the conditions of glacial Europe, contracting their range to southern refugia and only dispersing northwards during warm intervals [3,59], is now receiving considerable support. During 2004, research was published by a multidisciplinary team that analysed archaeological, palaeontological and climatic data for Europe during Oxygen Isotope Stage 3 (OIS 3) between 65 and 25 ka [56]. The period studied coincided with that of the Neanderthal extinction and the arrival of modern humans. The evidence highlighted climate as a major factor in determining the range dynamics of the Neanderthals, who retreated to refugia during cold episodes in a similar manner to many other species [60]. Experimental work by Aiello and Wheeler has now demonstrated that Neanderthal body size, shape and proportions conferred no significant thermoregulatory advantage [61].

Neanderthal locomotion was energetically costly [62] and thus unsuited to open environments. Cultural responses were insufficient to deal with the encroaching steppe when climate cooled [3]. However, the gracile morphology of modern humans, linked to endurance running in open environments [63], enabled the exploitation of the mammoth steppe at 40 ka [3].

The traditional view, that the Neanderthals went extinct because of the arrival of modern humans [17], is now under serious challenge [3]. Instead, climate change is seen, through ecological changes in resources, as the key to the fragmentation of the Neanderthal population during OIS 3, a time when Europe experienced intense and abrupt climatic and environmental variability [56,64–66]. The impact of climate on the Neanderthal extinction is, nevertheless, still hotly contested [67,68]. The modern humans that colonized Europe during the Late Pleistocene were also forced into southern refugia during the Last Glacial Maximum, 20 ka. Those that survived repopulated Europe as the climate improved [69].

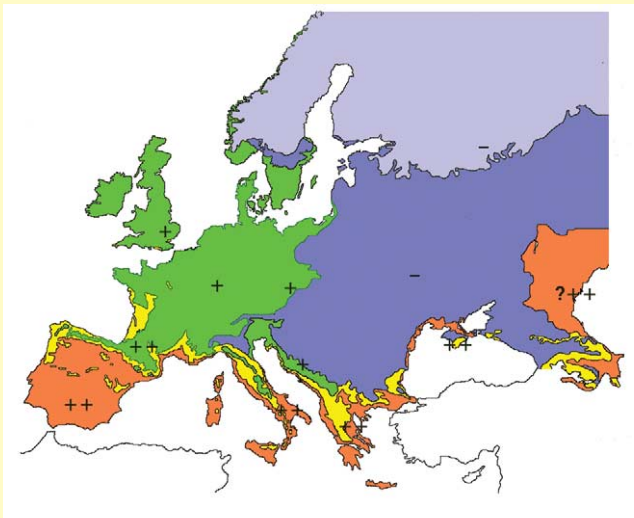


Figure 1. The distribution of Neanderthals in relation to bioclimate. Orange, Mediterranean; yellow, sub-Mediterranean; green, temperate oceanic; dark blue, temperate continental; pale blue, boreal. ++, permanently occupied; + occupied during mild periods; - never occupied. Adapted with permission from [3].

Language is seen by some as a crucial element of the package of behavioural attributes that make up modern humans and distinguishes them from the Neanderthals [40]. Support for the connection between spoken language and modern humans has recently been provided by the estimated fixation time of the *FOXP2* gene, which is involved in speech and language, to some time within the past 200 ka [41]. Using archaeological evidence and computer simulations, Marwick [42] identified the first appearance of exchange networks that required a communication system in the form of human language to 130 ka in Africa, although protolanguage might have existed as far back as 1 mya [42]. Parallel processes might have therefore driven analogous language evolution in other hominins, including the Neanderthals.

The extraction of DNA from Neanderthal fossils [21–24] and the comparison of this DNA with that of present-day and Upper Palaeolithic modern humans [43] indicates that Neanderthal genes have not contributed to the current gene pool [44]. In a study using computerized fossil reconstruction and geometric morphometrics, Ponce de León and Zollikofer showed that characteristic differences in cranial and mandibular shape between Neanderthals and modern humans were deep rooted and arose early during development, possibly prenatally, and were maintained throughout postnatal ontogeny [45]. Currat and Excoffier [46] have modelled the range expansion of modern humans into Europe and the nature of the possible contact with Neanderthals. They concluded that the absence of Neanderthal mtDNA sequences in modern Europeans today was compatible with a maximum of 120 admixture events between Neanderthals and modern humans during the 12 ka of their coexistence and that maximum interbreeding rates of the two populations should have been <0.1%. This result is consistent with the ecological evidence that indicates differences in habitat exploitation between Neanderthals (heterogeneous vegetation mosaics) and modern humans (open plains habitats) in Europe [3]. It also casts doubt on the validity of claims that a burial excavated in Lagar Velho, Portugal, reveals Neanderthal-modern human genetic admixture [47].

However, the question of cultural information transfer between Neanderthals and modern humans remains open. The presence of stone tool technology that appears transitional between the Middle Palaeolithic industries of the Neanderthals and those of modern humans during the Upper Palaeolithic in Western Europe at a time of potential contact has been hotly debated in recent years [48–50]. Some defend that Neanderthals acquired new ways of making tools from modern humans, implying contact occurred [48]. Others defend the view that Neanderthals developed the new technologies, and entered the Upper Palaeolithic independently [49,50]. Either way, the Neanderthals were capable of behaviour that is attributed to modern humans.

Towards a comprehensive theory of human evolution

It is unlikely that the genus *Homo* would have evolved as it did in the absence of the climatic vicissitudes of the Pleistocene. Modern humans would not have evolved into

generalists that were capable of resolving unpredictable and rapid small-scale environmental change through complex social and cultural behaviour [3]. Our evolution should be seen in terms of niche evolution [51] that enabled our ancestors to disperse into new habitats and climates, and to persist in unpredictable environments. When modern humans met other hominins, the outcome was not always clear. The colonization of the world by modern humans had more to do with contingency than with any obvious biological advantage [3].

The study of human evolution has been largely shaped by the discovery of new fossils, such as Flores, but it has lacked rigour in theoretical development. The time is now right, given recent advances described here, for the development of a comprehensive theory of human evolution with a solid foundation in evolutionary ecology. An ecological approach, aided by the high-resolution study of climate change, phylogeography and computer modelling of populations, will be central to our understanding of the evolution of our genus.

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