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Aspects of human physical and behavioural evolution during the last 1 million years

JULIA GALWAY-WITHAM,[1] JAMES COLE[2] and CHRIS STRINGER[1]
[1]Centre for Human Evolution Research (CHER), Department of Earth Sciences, Natural History Museum, London, UK
[2]School of Environment and Technology, University of Brighton, Brighton, UK

ABSTRACT: This paper reviews some of the main advances in our understanding of human evolution over the last 1 million years, presenting a holistic overview of a field defined by interdisciplinary approaches to studying the origins of our species. We begin by briefly summarizing the climatic context across the Old World for the last 1 million years before directly addressing the fossil and archaeological records. The main themes in this work explore (i) recent discoveries in the fossil record over the last 15 years, such as *Homo naledi* and *Homo floresiensis*; (ii) the implications of palaeogenetics for understanding the evolutionary history of, and relationships between, Neanderthals, Denisovans and *Homo sapiens*; (iii) the interplay between physiology and metabolic demand, landscape use, and behavioural adaptations in the evolution of morphological and behavioural innovation; and (iv) recent advances in archaeological understanding for the behavioural record, in particular that of the Neanderthals. This paper seeks to provide a broad-scale, holistic perspective of our current understanding of human evolution for the last 1 Ma, providing a reference point for researchers that can be built upon as new discoveries continue to develop the landscapes of human evolution.
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Introduction

At the beginning of this century, the basic pattern of human evolution in the Old World over the last 500 000 years seemed relatively clear for the researchers who accepted that our species, *Homo sapiens*, had a recent African origin. The archaic species *Homo heidelbergensis* was widespread, then splitting into two descendant lineages about 400 ka, before subsequently disappearing from the fossil record. 'Archaic' is a descriptive term used here to indicate most members of the genus *Homo* and their common traits, such as a long, low braincase, and strong continuous browridge. Contrasted with *H. sapiens* and its 'modern' traits, such as a globular braincase, lack of a browridge, a chin and a narrow pelvis. Those descendants gradually evolved into *Homo neanderthalensis* in western Eurasia, and *H. sapiens* in Africa (Stringer, 2002). The oldest recognizable members of the descendant lineages were perhaps the Swanscombe skull (UK, about 400 ka – a possible Neanderthal ancestor) and the Omo Kibish 1 skeleton (Ethiopia, then estimated age > 130 ka – an early *H. sapiens*) (Stringer, 2002). Genetic data from extant humans suggested that *H. sapiens* had dispersed from Africa about 55 ka, reached Australia by about 45 ka, and by 30 ka had replaced the Neanderthals across Eurasia with minimal or no interbreeding (Hudjashov *et al.*, 2007; Oppenheimer, 2009; Soares *et al.*, 2009). Archaic populations of uncertain affinities existed in China, represented by fossils such as Dali and Maba, with unknown last appearance dates, while *Homo erectus* possibly persisted in Java (Indonesia) until about 45 ka, roughly coincident with the spread of *H. sapiens* in the region (Stringer, 2002). In terms of range, it was thought that only *H. sapiens*, using ocean-going watercraft, had the capacity to spread eastwards beyond the biogeographical

*Correspondence: Julia Galway-Witham or James Cole, as above.
E-mail: j.galway-witham@nhm.ac.uk; j.n.cole@brighton.ac.uk

barrier in Southeast Asia known as the Wallace Line (Stringer, 2002). The last 40 years have seen the rise of numerous theories about the physical requirements for hominins to disperse into Europe and Asia (e.g. Klein, 2009), and the characteristic morphologies of Neanderthals and *H. sapiens* were primarily summarized as adaptations to the environments in which they evolved, with each species being either cold- or heat-adapted, respectively (e.g. Trinkaus, 1981). While the pattern of physical evolution seemed comparatively straightforward until the early 2000s, there was much debate on the topic of human behavioural complexity. The epitome of early arguments was encapsulated within the human revolution model (Mellars and Stringer, 1989), which saw a sudden appearance of modern human behavioural packages in Europe from ~40 ka, directly corresponding to the arrival of *H. sapiens* in the region.

Within the last 15 years, the discovery of multiple new hominin taxa, as well as new studies of known taxa, have changed the landscape of palaeoanthropological research (Galway-Witham and Stringer, 2018), and signal how much we have yet to understand about human evolution during the last 1 million years. It is becoming increasingly evident that for every adaptive morphology, there are several potential adaptive pathways (Churchill, 2006), and while the development of energetic proxies, through analyses of body form, climate and behavioural indicators, are helping to tease apart these potential causes, relating form and function continues to be difficult. However, the discovery of new fossil sites in unexpected locations and time periods is encouraging us to look more closely at our implicit assumptions. In 2000, McBrearty and Brooks posed a counterposition to the human revolution model that put forward a gradual and much earlier assembling of the modern human behavioural package in Africa beginning ~300–250 ka. Such behaviours included blade and microlith technology, bone tools, increased geographical range,
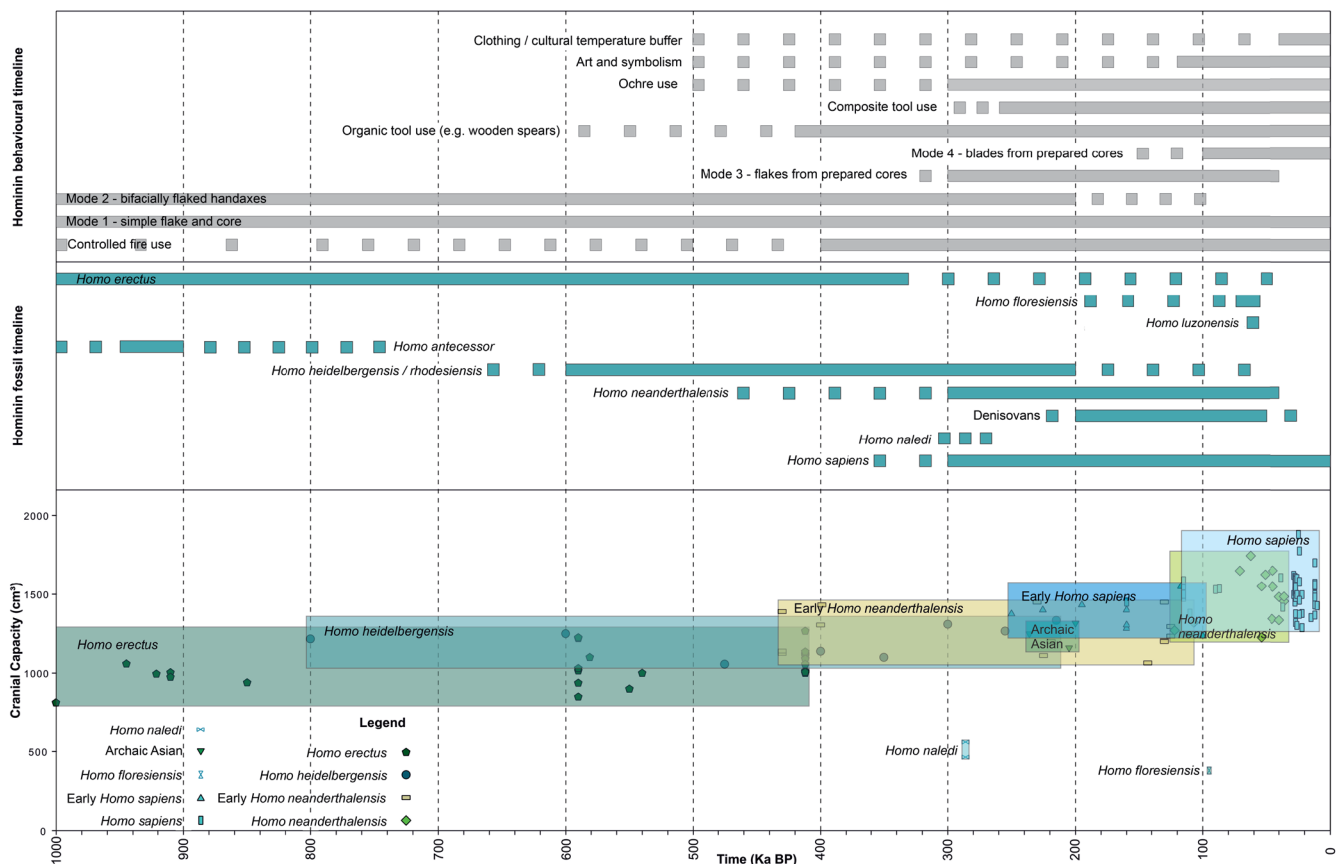
specialized hunting, the use of aquatic resources, long-distance trade, systematic processing and use of pigment, art and decoration (McBrearty and Brooks, 2000; also see Stringer, 2011, p. 115 for a refined list with useful examples). The next 7 years or so of research saw a healthy debate between these positions, culminating in an agenda-setting interdisciplinary rethink of the human revolution (Mellars et al., 2007), which started to suggest and acknowledge that the archaeological record was more complicated and surprising than had previously been recognized.
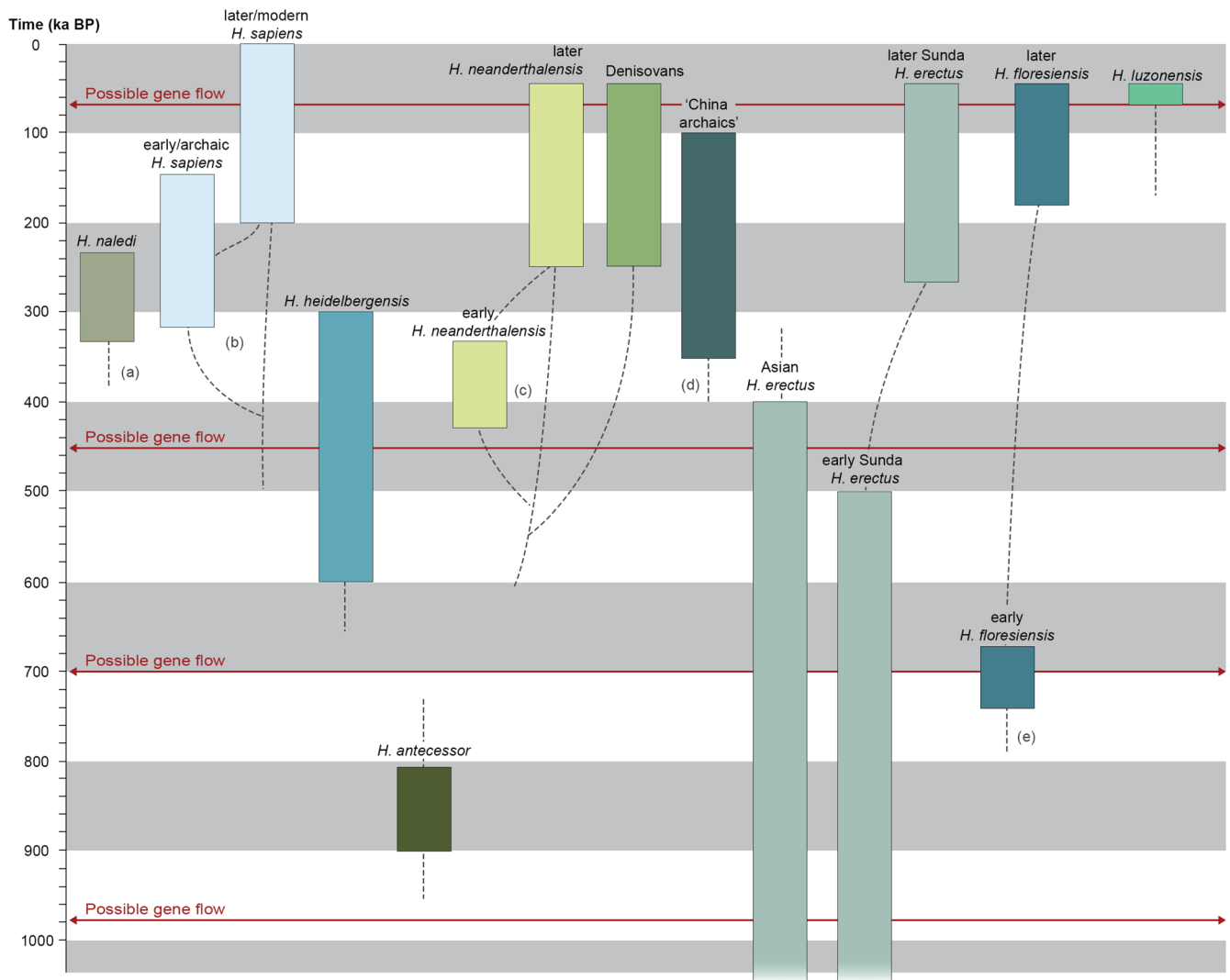
Although it would need a book-length treatment to do justice to all the new data, the following review seeks to summarize some of the most striking new finds in palaeoanthropology and palaeolithic archaeology, bringing together the behavioural and physical evidence, and outlining some of the many remaining questions in understanding the last 1 million years of human evolution. Inevitably there are gaps in this review and we have tried to direct the reader to further resources where appropriate. We have chosen to highlight the complementary nature of the fossil and archaeological evidence by including a summary of new research relating to hominin energetics, sandwiched between the more explicit discussions of these preserved records. Figure 1 illustrates a hominin fossil timeline for the last 1 million years that will be followed through this paper. In addition, information on hominin cranial capacity and the timings of key behavioural traits are illustrated here. Figure 2 depicts what we consider to be the most probable phylogenetic associations between taxa, and Fig. 3 is a map of the Old World showing the location of sites mentioned in this paper.

Climatic context

The potential impact of climate change on the development of evolutionary innovations and dispersals for hominins is well referenced and consistent with ecological theory (e.g. Gamble et al., 2004; James and Petraglia, 2005; Potts and Teague, 2010). Recent studies, however, have been looking at the more nuanced question of how and in what way climate may have changed, moving beyond the more traditional view that implicitly described a climate as either fixed or stable over a given period (Potts, 2013). In particular, this may involve an attempt to find longitudinal trends in temperature change (e.g. Petit et al., 1999; Lambert et al., 2008), aridity and precipitation (e.g. deMenocal, 1995, 2004, 2011), and overall climatic variability (e.g. Potts, 1996, 1998, 2012), and to correlate these trends with notable instances of evolutionary change (Potts, 2013; Shultz and Maslin, 2013; Grove, 2014; Maslin et al., 2014, 2015; Levin, 2015; Trauth et al., 2015; Carotenuto et al., 2016; Burke et al., 2017; Owen et al., 2018; Buck et al., 2018).

Analyses of oxygen isotope data indicate that the Earth experienced an overall cooling over the last few million years, including within the last 1 million years (Sosdian and Rosenthal, 2009). Between ~1 Ma and 700 ka a period of extreme climatic variability appears to have coincided with the formation of large lakes in East Africa (Potts, 2013), and around this time (~940–870 ka) North Africa and eastern Europe were also subjected to increased aridification and climatic variability (Muttoni et al., 2010). This has led some authors to hypothesize about the potential role of climate change as a catalyst for the dispersal of

Figure 1. Timeline illustrating key behavioural traits, hominin fossils and endocranial volume (data from S1) during the last million years. For the behavioural traits and fossils, the solid line represents more certain date ranges, while the segmented lines represent more ambiguous data points that extend beyond the range of established dates. The spacing of the horizontal segmented lines relates to the relative certainty of the associated dates. The fossil timeline does not include any phylogenetic inference. The coloured boxes represent endocranial volume ranges to illustrate areas of overlap in inferred brain size between taxa. Although we have used cited dates in relation to fossils, we do not necessarily agree with all of them. [Color figure can be viewed at wileyonlinelibrary.com]

Figure 2. Schematic diagram of the inferred age ranges of hominin lineages during the last million years. Colours reflect species designations as commonly referenced in the literature. For some species, there is potential for this taxon to encompass more than one 'lineage', e.g. *H. erectus*. Dotted lines indicate our conservative phylogenetic associations of lineages. (a) The evolutionary history of *H. naledi* remains particularly enigmatic, confounded by its unexpected combination of traits that makes it difficult to establish whether the species diverged early on in the evolution of the genus *Homo*, or split off from another lineage more recently. (b) The taxon designated *H. sapiens* may have evolved as a single lineage, where earlier specimens ~300 ka eventually evolved into the more derived specimens after 200 ka. However, the overlapping time periods of these evolving lineages presents an alternative evolution, where these earlier morphs represent a divergent sister lineage that perhaps did not contribute to the morphology of *H. sapiens* today. (c) Neanderthals also present two alternative evolutionary narratives; early Neanderthals could be the earlier members of the lineage that ultimately led to the classic Neanderthal morphology of the later Pleistocene, or it may represent a side branch of the lineage that diverged from the common ancestor with Denisovans. (d) The phylogenetic affinities of specimens designated here as 'China archaics' remains unspecified, until the phylogenetic status (i.e. derived versus ancestral) designation of traits shared with *H. erectus*, *H. heidelbergensis*, *H. neanderthalensis* and *H. sapiens* has been better established, and until we hopefully have a better idea of the morphology of the Denisovans. (e) *H. floresiensis* may be a descendant of *H. erectus* that dwarfed on the island of Flores, or alternatively it evolved from an even deeper, pre-*erectus* divergence. Here we remain agnostic, although the recently announced *H. luzonensis* (Détroit *et al.*, 2019) may add to this debate. Evidence indicates that there was gene flow (red lines) at various times throughout the last 1 million years, although the rate and frequency of this is still being established. [Color figure can be viewed at wileyonlinelibrary.com]

large African mammals into southern Europe, including hominins (Muttoni *et al.*, 2011; Abbate and Sagri, 2012). A similar period of potentially favourable climatic conditions has also been identified between 600 and 100 ka, and may have also permitted hominin dispersals out of Africa (Abbate and Sagri, 2012).

The Early Pleistocene and Middle Pleistocene are separated by the Middle Pleistocene Transition (MPT), which occurred between ~922 and ~640 ka (Dennell *et al.*, 2011). The Middle Pleistocene is characterized as a series of six ~ 100-ka periods of dominant or extreme cold in higher latitudes, punctuated by short periods of warmer interglacials (Dennell *et al.*, 2011). Broadly, mild interglacial periods have been associated with indications of hominin habitation (Bermúdez de Castro and Martinón-Torres, 2013), and according to some researchers, the climate of southwest Asia throughout the Pleistocene may have been consistently suitable for hominin habitation (Hughes *et al.*, 2007).

Across the glacial/interglacial cycles, average aridity was generally increasing in the approach to the Last Glacial Maximum (26.5–~20 ka), and areas such as the Thar Desert would have been intermittently inhospitable (James and Petraglia, 2005). Equally, however, there were periods, notably 130–118, 106–94 and 89–73 ka (MIS 5) and 59–47 ka (MIS 3) when classically inhospitable areas such as the Sahara and the Arabian Desert were more highly vegetated due to increased monsoonal activity (deMenocal and Stringer, 2016). And within the larger orbitally controlled long-term climatic fluctuations there were also many short and sharp millennial-scale oscillations (Cohen and Gibbard, 2019). These are best known within the palaeoclimate records of the last 120 ka, and although still largely undetected, may also have been significant in controlling human population numbers and movements in earlier periods.

Figure 3. (A) Map of Europe, Asia and Africa, with the sites mentioned within the text indicated. (B) Expanded view of Europe to show the distribution of sites therein.

'The muddle in the middle'

This was archaeologist Glynn Isaac's 1975 description of what was known (or, perhaps more accurately, what was not known) about human evolution during the Middle Pleistocene (~130–780 ka) (Isaac, 1975). Despite many more finds, better dating and the growing impact of ancient DNA (aDNA) studies, Isaac's characterization still rings true more than 40 years later. Part of the problem concerns how many human species should be recognized during this period, with workers such as Stringer (2012a, 2012b) and Rightmire (1998, 2008) arguing for a widely diagnosed and widespread species *H. heidelbergensis* in Eurasia and Africa, which then split to give rise to the daughter species *H. neanderthalensis* and *H. sapiens*, in the same two regions. Others have stressed the idiosyncratic nature of the Mauer mandible, the type specimen of *H. heidelbergensis*, and some consider the name 'H. rhodesiensis' (given to the Broken Hill cranium in 1921) more appropriate for the species that putatively represented the last common ancestor (LCA) (Balter, 2014). Yet others favour *heidelbergensis* as part of a European lineage of time-successive species leading to the Neanderthals, with 'rhodesiensis' forming part of an African equivalent leading to modern humans. The latter view implies a deeper division and a more ancient LCA for the Neanderthals and modern humans, linked with claims that the species *H. antecessor*, named in 1997 for fossil material from the Gran Dolina locality at Atapuerca, Spain, and now dated to ~850 ka, is closer to the morphology of the LCA instead (Bermúdez de Castro *et al.*, 2004).

That last view is gathering renewed support, based on suggestions that the small and retracted middle of the face of *antecessor* is morphologically like that of *H. sapiens*, and reinforced by studies showing the *sapiens*-like facial growth of the immature type specimen of *antecessor* (Lacruz *et al.*, 2013). In addition, some genetic data from members of the Neanderthal and *H. sapiens* clades are now being interpreted as indicating an older LCA for these lineages — ~550–765 ka (Meyer *et al.*, 2016) vs ~503–565 ka (Hajdinjak *et al.*, 2018). And a recent study of dental evolutionary rates has suggested an even earlier divergence of > 800 ka (Gómez-Robles, 2019). It may well be that within the Middle Pleistocene there are at least two distinct facial forms, a more gracile one that is primitive but also *sapiens*-like (found, for example, in *H. antecessor* in Spain, Nanjing in China, and Jebel Irhoud in Morocco), and a more derived one, with a relatively taller and more inflated cheek region (e.g. Petralona in Greece, Sima de los Huesos, Atapuerca, in Spain, and Broken Hill in Zambia) (Stringer, 2016; Lacruz *et al.*, 2019).

There are also further data on the early evolution of the lineages of *H. neanderthalensis* and *H. sapiens*. The large fossil sample from the Sima de los Huesos in Atapuerca can now be firmly placed in the Neanderthal clade through cranial and dental morphology, facial growth patterns, and genomic DNA, and has been dated from associated sediments to ~430 ka (Arsuaga *et al.*, 2014; Lacruz, 2015; Meyer *et al.*, 2016). A possible equivalent on the *sapiens* lineage, although younger in age, has now been established from the Jebel Irhoud site in Morocco. Old and new fossil finds, with associated Middle Stone Age archaeology, have been dated to ~315 ka (Richter *et al.*, 2017), although there has been no recovery of aDNA. The cranial morphology is primarily primitive, although the dentition, mandible and browridges are argued to show *sapiens*-like features (Hublin *et al.*, 2017). Later and more definite members of the modern human lineage have been confirmed in the form of the Omo Kibish 1 skeleton (Ethiopia), now more soundly dated to ~195 ka (McDougall *et al.*, 2005; Aubert *et al.*, 2012; Brown *et al.*, 2012), and three individuals, also from Ethiopia, discovered at Herto and dated to ~160 ka (White *et al.*, 2003; McCarthy and Lucas, 2014). Lastly, part of a *H. sapiens* upper jaw from Misliya, Israel, has been dated to ~180 ka, demonstrating that the *sapiens* lineage already extended beyond the African continent before the end of the Middle Pleistocene (Hershkovitz *et al.*, 2018). Recently, an even earlier (>200 ka) record of H. sapiens has been claimed from a partial cranium discovered in Apidima Cave, Greece (Harvati *et al.,* 2019).

Homo floresiensis

The biogeographical patterning of archaic humans as restricted to the west of the Wallace Line received a major challenge in 2004 with the publication of a diminutive archaic skeleton (LB1) from Liang Bua cave on the Indonesian island of Flores,

some 500 km to the East of Java, which was assigned to a new human species, *H. floresiensis*. This skeleton and the associated finds of artefacts were initially dated to < 20 ka, and the population concerned was argued to have undergone a process of island dwarfing (Brown *et al.*, 2004; Morwood *et al.*, 2004). The LB1 skeleton displayed archaic or idiosyncratic features such as a very small endocranial volume (~420 ml), a buttressed lower jaw, a wide flaring pelvis, an upper body seemingly adapted to climbing, primitive wrist bones, relatively short legs, and large, flat feet. By contrast, the face was retracted under the braincase in a more modern fashion, and the teeth were similar in size to those of *H. sapiens*, albeit with some unusual traits. These claims soon provoked heated arguments, however, with critics particularly troubled by the ape-sized brain capacity and an estimated stature of only ~1.05 m. It was argued that the small cranial and body size of the skeleton indicated pathology rather than evolutionary change, with a range of syndromes known in *H. sapiens* such as Down syndrome, Laron syndrome and Cretinism advanced as the agent, operating on an anatomically modern rather than an archaic human (e.g. Jacob *et al.*, 2006; Hershkovitz *et al.*, 2007). However, none of these syndromes convincingly duplicates the entire morphology of the Liang Bua skeleton, and numerous additional finds attributed to *H. floresiensis* have been excavated from even earlier deposits in Liang Bua, all equally indicative of a small body, and including another archaic-looking mandible and further wrist bones with a primitive morphology (Brown and Maeda, 2009; Jungers *et al.*, 2009; Morwood and Jungers, 2009).

More extensive excavations and further dating work now place the main skeleton at ~60 ka, with associated archaeology and more fragmentary archaic fossils spanning a period between about 50 and 190 ka (Sutikna *et al.*, 2016a). The presence of a succeeding population of modern humans may be indicated by teeth dated to ~46 ka (Sutikna *et al.*, 2016b). Moreover, additional excavations at open-air sites in the So'a Basin on Flores have revealed archaeology stretching back to at least 1 million years, and the presence of a small fragmentary jawbone and isolated teeth at ~700 ka, perhaps documenting an ancestral population for *H. floresiensis* (Brumm *et al.*, 2010; Brumm *et al.*, 2016; van den Bergh *et al.*, 2016).

Although the claims that *H. floresiensis* represents a pathological form of *H. sapiens* are now generally disregarded, there is evidence of some developmental abnormalities in the LB1 cranium such as increased asymmetry, plagiocephaly (an unusually flattened top to the braincase), and teeth that are rotated in their sockets (Kaifu *et al.*, 2009, 2015). Whether these are evidence that the LB1 individual was an archaic human with pathologies or a member of an isolated and inbred population with a high mutational load is still unclear. Even disregarding the claims of pathological abnormalities, *H. floresiensis* remains a highly controversial species. Some expert opinion still supports the view that this species represents an island-dwarfed descendant of *H. erectus*, perhaps derived from Javanese populations to the west (e.g. Falk *et al.*, 2009; Kaifu, 2017). However, others have increasingly favoured a more primitive origin, either from a smaller-brained and smaller-bodied form of *erectus*, like that known from Dmanisi (Georgia) at about 1.8 Ma, or from an even more primitive species, such as *Homo habilis* or an australopith (Brown and Maeda, 2009; Jungers *et al.*, 2009; Morwood and Jungers, 2009; Argue *et al.*, 2017). This possibility was used by Dennell and Roebroeks (2005) to argue that a pre-human species could have been the first hominin to emerge from Africa, rather than *H. erectus*, and that it was represented by a long-lived descendant lineage,

surviving in a remote isolation on the island of Flores for over 1 million years. These arguments will continue with the addition of *H. luzonensis* to the fossil record (Détroit *et al.*, 2019; Tocheri, 2019).

How the Flores lineage first arrived on the island is also unclear. Could sea-going boats have been developed by early humans more than 1 Ma, and used to reach the islands of Wallacea, long before *H. sapiens* achieved that feat? Or could ancient tsunamis in this tectonically active region have torn off strips of coastal vegetation, complete with their ancient human inhabitants, which later drifted hundreds of kilometres to islands like Flores (Smith et al., 2001)? Currents in the region today and as reconstructed during the Pleistocene predominantly run from the north towards Flores and its neighbouring islands, suggesting that an origin from somewhere like Sulawesi is actually more likely than from Java (Morwood and van Oosterzee, 2007).

Homo naledi and the African fossil record

An equally challenging discovery was made in 2013 and published from 2015 onwards, but this time it came from a region that was supposedly well explored for its hominin fossil record – the 'Cradle of Humankind' in South Africa. Exploration and subsequent excavations have uncovered over 1500 fossils representing at least 18 individuals, showing a unique blend of primitive and derived anatomical features (Berger *et al.*, 2015; Hawks *et al.*, 2017). The crania had very small endocranial volumes in the range ~400–610 ml, a highly projecting face, relatively small teeth set in gracile jaws, and a skeleton displaying primitive shoulders and pelvis, human-like hands (apart from the highly curved digits) and feet, and unique details in the morphology of the femur and thumb. The finds were assigned to a new species *H. naledi*, and had accumulated in chambers deep within the Rising Star cave system. The team studying the material proposed that the fossils had been intentionally deposited in remote chambers far into the dark zone of the cave, controversially implying that *H. naledi* potentially engaged in ritual disposal of its dead (Dirks *et al.*, 2015; Stringer, 2015). Moreover, study of the inferred brain shape in several *naledi* fossils indicates a small but humanly structured brain (Holloway *et al.*, 2018), leading some workers to further infer sophisticated behaviours for the species. In 2017, age estimates for the first group of fossils discovered were published, using U-series, luminescence and electron spin resonance methods, centring on values around 285 ka (Dirks *et al.*, 2017). This is a remarkably young age estimate for material showing morphologies previously known in fossils at least 1 million years older, and that raises questions about how such a primitive species could have survived in southern Africa when other, supposedly more derived, humans were also present. The survival of *H. floresiensis* and *H. luzonensis* could reasonably be attributed to their island isolation, without competing human species, but how had *naledi* been able to persist for so long with its essentially ape-sized brain and elements of primitive morphology? The evolutionary history of *naledi* is completely unknown at present, raising the possibility that other fossil material in Africa may represent this lineage, and that its behaviour is already recorded in the archaeological record of southern Africa, but currently unrecognized (Stringer, 2015; Berger *et al.*, 2017). Moreover, its phylogenetic position as basal or more derived among *Homo* is difficult to establish, given its disparate combination of traits (Dembo *et al.*, 2016; Figure 2).

Thus, in the last few years, it has become apparent that the pattern of recent human evolution in Africa was not the

straightforward story of a gradual emergence of the morphology characterizing extant *H. sapiens* – skeletal traits such as a globular braincase, small or non-existent browridges, a chin on the lower jaw, a narrow pelvis, etc. Instead, it seems likely that at least three human species existed across the African continent at ~300 ka. The lineage of *H. sapiens* was present, considering Jebel Irhoud at a date of ~315 ka, but the evolution of modern humans within Africa was complex and probably 'multiregional' (Scerri *et al.*, 2018a). In addition, as we have seen, the newly discovered and primitive species *H. naledi* still persisted in southern Africa. And in Central Africa, there is evidence from ongoing chronological studies of the material from the Broken Hill site in Zambia that the archaic species *H. heidelbergensis* (as explained earlier, sometimes alternatively called '*H. rhodesiensis*') probably also persisted around 300 ka (as it may have done in Europe and Asia too) (Balzeau *et al.*, 2017). Moreover, there is genetic evidence of at least one archaic ghost lineage persisting in Africa, which was responsible for introgressed DNA in extant sub-Saharan Africans (Hsieh *et al.*, 2016). Such introgression may be reflected in the relatively archaic morphology of late Pleistocene fossils such as the Iwo Eleru cranium from Nigeria (Harvati *et al.*, 2011; Stojanowski, 2014).

The impact of aDNA from Neanderthals and Denisovans

As we have discussed, new fossil discoveries have highlighted the complexity of recent human evolution, revealing unsuspected lineages in areas that were poorly known from their fossil record (Flores, Luzon), as well as in areas that were supposedly well known (South Africa). Genetic data have certainly also added to the complexity of recent human evolution, as well as identifying another new lineage – the Denisovans. The first traces of DNA from any ancient humans were portions of the mitochondrial DNA (mtDNA) genome, recovered from 1997 onwards, confirming that the Neanderthals were a distinct evolutionary lineage from all extant humans, diverging over 300 ka (Krings *et al.*, 1997). By 2010, methods had advanced so far and fast that whole Neanderthal genomes could be reconstructed, and to the surprise of many, comparisons with recent human genomes suggested that extant populations that traced their origins outside of Africa contained evidence of ancient interbreeding with Neanderthals, at a level of around 2% of their genomes (Green *et al.*, 2010). Examining larger Neanderthal-derived DNA segments in early modern human fossils suggests that this interbreeding predominantly occurred between 50 and 60 ka, most likely in western Asia (Nielsen *et al.*, 2017). Most Neanderthal DNA appears to have been rapidly selected away, but some of it appears to be expressed physically today, for example in traits linked with the skin and hair, the immune system, hypercoagulation and certain personality disorders (McCoy *et al.*, 2017). In addition to the Sima de los Huesos early Neanderthal material discussed already, at least seven other Neanderthal fossils from Spain to Siberia and ranging in date from ~40 to 120 ka have now had their genomes sequenced, showing a low population variation and small effective population size compared with groups of modern humans spread across comparable areas today (Nielsen *et al.*, 2017; Hajdinjak *et al.*, 2018).

In 2010, a fragment of a fossilized finger bone from Denisova Cave in Siberia was analysed for aDNA, also with surprising results. mtDNA from the fossil showed that it represented a lineage distinct from both Neanderthals and modern humans (Krause *et al.*, 2010), and shortly thereafter the

whole genome of this 'Denisovan' was reconstructed, suggesting it was from a population that diverged from the Neanderthal lineage at about 400 ka, after the Neanderthal lineage diverged from that of modern humans (Reich *et al.*, 2010). Three further fossils (all teeth) from Denisova Cave have since yielded comparable aDNA, indicating that the Denisovans occupied the region for over 100 000 years, and that their population variation and effective population size was intermediate between the smaller values of Neanderthals and the larger values of regional groups of humans today (Sawyer *et al.*, 2015; Stringer and Barnes, 2015). There were further surprises when comparisons were made with extant genomes, since those of many native Australasians contain some 5% of Denisovan-like DNA, as well as around 2% of Neanderthal DNA (Sankararaman *et al.*, 2016; Vernot *et al.*, 2016). The DNA traces in native Australasians are not identical with those found in the Siberian Denisovans, and recent research indicates that there were at least three separate and varied Denisovan-like sources of introgression, one of which lived in the same biogeographical zone as *H. floresiensis* and *H. luzonensis* (Jacobs *et al.*, 2019a). Populations in southern Asia contain smaller traces of comparable Denisovan-like DNA, while those in eastern Asia contain traces more similar to the actual Denisova Cave genomes (Browning *et al.*, 2018). Specific Denisovan-like genes linked with high-altitude adaptation and storage of fats have been recognized in Tibetans and Inuit, respectively (Huerta-Sánchez *et al.*, 2014; Racimo *et al.*, 2017). Recent research suggests that the apparent effects of archaic introgression may also be evident in the unusual morphology of late Pleistocene fossils from Dushan Cave, China (Liao *et al.*, 2019), and a primitive-looking mandible from Xiahe has provided the first physical evidence of a Denisovan in China, based on its large and complex molars and proteomic affinities with the material from Denisova Cave (Chen *et al.*, 2019).

DNA analyses of *Homo sapiens*

Unfortunately, scientists have not yet been able to recover aDNA from African fossils older than about ~15 ka (Van de Loosdrecht *et al.*, 2018), nor from *H. sapiens* fossils older than about 45 ka in Eurasia. However, thousands of modern human genomes have now been sequenced, and these allow extrapolations about the evolutionary history of our species, supported by a growing number of genomes from Eurasian fossils younger than 45 ka. Regional diversification of *H. sapiens* appears to have begun in Africa at least 200 ka (Schlebusch *et al.*, 2017), while the main exit of our species from Africa is calibrated at ~60 ka, with colonization of Australia at ~50 ka, Europe at ~40 ka and the Americas at ~15 ka (Nielsen *et al.*, 2017). However, there are growing indications from fossil and archaeological discoveries in eastern Asia and Australasia that there must have been dispersals of *H. sapiens* into those regions before 60 ka (Liu *et al.*, 2015; Bae *et al.*, 2017; Clarkson *et al.*, 2017; Westaway *et al.*, 2017), which presumably means that earlier migratory pulses from Africa either died out or were largely overprinted by the significant dispersal at ~60 ka. Whether other archaic humans beyond Neanderthals, Denisovans, *H. floresiensis* and *H. luzonensis* still persisted when *H. sapiens* began its dispersal from Africa is still unclear. Archaic humans were evidently still in China at ~100 ka (Li *et al.*, 2017) and perhaps much later (Liao *et al.*, 2019), but how such populations related to Neanderthals, Denisovans or *H. erectus* is currently unclear. And it is also now unclear whether late *erectus* populations represented by samples such as those from

Ngandong and Sambungmacan in Java (Indonesia) might have survived into the last 60 ka (Indriati *et al.*, 2011).

Trends in postcranial morphology

Most of what we know about hominin evolution over the last 1 million years is primarily derived from analyses of cranial remains, including teeth. For postcrania, it can be difficult to assign these fossils to specific taxa, as they may not have any associated cranial remains, or taxa do not have any known postcranial fossils with which to compare it. Consequently, we are limited in the generalizations about temporal and geographical changes for species over the last 1 Ma that we can make. From the available evidence, it does seem that most of the morphological differences between the large-bodied archaic species and *H. sapiens* relate to differences in the cranium. The postcranial variation that has been observed primarily relates to differences in hindlimb robusticity, notably in the thickness of the cortical bone and the marked muscle attachments indicating increased muscularity (Klein, 2009; but see Pearson and Lieberman, 2004; Trinkaus *et al.*, 2016). If we were to plot the available postcrania of all hominins along axes representing size and shape, most data points associated with later *Homo* would converge, and the anatomies of earlier hominins would be more widely distributed (Will *et al.*, 2017). In other words, the morphology of later *Homo* is generally less variable than other taxa, and, on the whole, they are larger-bodied (Holliday, 2015) and taller than earlier hominins (Will *et al.*, 2017).

There are two notable exceptions that do not conform to this trend. *Homo naledi* has been estimated to reach the diminutive adult height of only ~1.46 m, and weighed between 40 and 56 kg (Berger *et al.*, 2015), which, relative to *H. heidelbergensis* (estimated at the upper range for males to have been ~1.8 m tall, and weighing 90 kg; Gallagher, 2013), is very small indeed, and rather closer in size to hominins such as *H. habilis* or *H. rudolfensis* (Gallagher, 2013). *H. floresiensis* was apparently even smaller, estimated to reach an adult height of ~1 m (Brown *et al.*, 2004), and weighing only ~28 kg (Jungers *et al.*, 2016). Dated to ~285 and ~60 ka, respectively, these two species were possibly sympatric with other hominins, including *H. sapiens*. Putting aside questions about their taxonomic assignments, at a minimum, these small-bodied and small-brained species represent a distinct adaptive pathway for hominins during the Pleistocene. Their non-conformity to the trend of increased body size, stature and brain size over time are significant in adding to the pattern of complexity of morphs during the last 1 Ma (Will *et al.*, 2017). Both species signal a different kind of energetic and locomotive strategy than their larger counterparts, and *H. floresiensis* in particular challenges long-held notions about the physiological prerequisites for hominin species to colonize non-African environments.

Changes in energy expenditure

The implication of a trend in increasing body size over the last 1 Ma would have meant that the daily energetic expenditure of these hominins would have correspondingly increased (Froehle and Churchill, 2009). The many physiological factors that influence energy expenditure, such as weight, nutrition and health, however, are difficult to measure from the fossil record directly (Heyes and MacDonald, 2015; Vidal-Cordasco *et al.*, 2017). Therefore, relatively good proxies have been developed (e.g. Cordain *et al.*, 1998; Pontzer *et al.*, 2009),

which can assist in assessing whether specific gaits, such as walking or running, would have been more or less efficient in transferring energy in a given species (Pontzer, 2017a). Fully 'modern' locomotor endurance appears to have emerged ~1 Ma (Pontzer, 2017a), and, broadly, studies of body form proxies (e.g. the ponderal index – and index by which mass can be estimated from stature) indicate that later *Homo* generally follow the predictions laid out by Bergmann's rule, in which dispersal to higher latitudes created a selective pressure for thermoregulatory adaptations (Will *et al.*, 2017). Although Neanderthals have also been alternatively hypothesized to have been well suited to exert high muscular force (Churchill, 2006), there are difficulties in establishing what combination of factors may have influenced their physiology.

While Neanderthals were able to find successful adaptive strategies for the harsh climates of Pleistocene Europe, these were energetically expensive (Churchill, 2014). Compared to *H. sapiens*, Neanderthals may have needed to ingest between 100 and 350 more calories per day (Froehle and Churchill, 2009). Some authors have suggested that for particularly large and robust hominins, such as Neanderthals, the increased demand for energy to maintain metabolic processes would have put them more at risk in environments with fewer available calories (Froehle and Churchill, 2009). During periods of low resource availability, Neanderthals may also not have had surplus energy to allocate to reproduction, putting putatively small populations (Nielsen *et al.*, 2017; Hajdinjak *et al.*, 2018) at even greater risk of collapse (Pontzer, 2017b).

In addition to physiology, environmental factors influence a species' energetic demands, and these can include variability of the terrain and the density of resources, caloric or otherwise. The distances that hominins transported resources have been reconstructed to have increased by 10 × between 3.6 and 1.8 Ma, correlating with the increased carrying capacity of *H. erectus* over earlier hominins (Wang *et al.*, 2003). Combined with the relatively longer lower limbs of *H. erectus* and other later hominins, which have been reconstructed as energetically more efficient over long distances, resource availability may have continued to play an important role in hominin evolution over the last 1 Ma. Evidence for high degrees of food availability for secondary carnivores was found at Atapuerca, which would have meant relatively low competition between hominins and the other occupants of the carnivore guild (Rodríguez-Gómez *et al.*, 2013). It seems likely that this space in the niche assisted *H. antecessor* and any of its descendants in establishing a foothold in the early Pleistocene of Europe. The shift to a more meat-rich diet in later *Homo* has been well represented in the literature and movement across trophic levels influences how required resources are transported, and over what distances (Kuhn *et al.*, 2016). Additionally, carrying was possibly a significant factor in the later evolution of the genus *Homo*, as upper limb length was recently found to more strongly correlate with energy expenditure during catchment and transport of raw materials than lower limb length (Vidal-Cordasco *et al.*, 2017).

Given the diversity of environments occupied by later species of *Homo* within the last million years, these hominins have been repeatedly suggested to have been differentially adapted to their respective environments (e.g. Holliday, 1998; Stock, 2006). Modern populations in northern latitudes tend to have higher basal metabolic rates than lower latitude populations (Snodgrass and Leonard, 2009), and Neanderthals appear to have had smaller ranges in the Levant, compared to Upper Palaeolithic *H. sapiens*, and preferentially lived in environments with diverse elevations in the Mediterranean woodlands (Henry *et al.*, 2017). This may be due to the relative

abundance of resources in these areas that compensates for the comparatively smaller range sizes (Henry *et al.*, 2017). *Homo sapiens*, by contrast, appear to have been less restricted in the landscapes in which they could inhabit (Henry *et al.*, 2017), including colder latitudes than those observed for the Neanderthals (Froehle and Churchill, 2009).

Although *H. sapiens* appears to have been able to occupy colder environments than Neanderthals, Neanderthals have been frequently referred to as a clearly cold-adapted species (e.g. Churchill, 1998; Steegmann *et al.*, 2002), with *H. sapiens* evolving instead for dissipating heat in warmer climates (Ruff, 1994). In particular, it is Neanderthals' large noses which have been suggested to have been beneficial by conditioning cold or dry air before it enters their torso (Wroe *et al.*, 2018). According to Aiello and Wheeler (2003), however, the Neanderthal morphology was not significantly better adapted to colder climates than *H. sapiens*, and they would have therefore required significant cultural buffering (fire, clothing, shelter) and greater metabolic heat production to survive the harsh conditions of a glacial winter in Pleistocene Europe. Instead, Churchill (2006) believes that given the high metabolic heat output and cultural buffering that was probably available to Neanderthals, the capacious chests of Neanderthals probably contributed comparatively little to their heat conservation. Instead, it is more likely that the distinctive Neanderthal thorax morphology related more to heat *production*, rather than *conservation*. Complementary to this are the results of a recent study by Naya *et al.* (2016), who assert that the evolution of the costly large brains of later *Homo* species could have been selectively driven by a decrease in global temperatures due to the increased endothermic properties of larger internal organs.

Alternatively, the Neanderthal nasal morphology could equally have served to accommodate increased respiratory demands (Wroe *et al.*, 2018). The capacious nasal cavities of Neanderthals and modern humans were seemingly more adept at conditioning air than those of *H. heidelbergensis*, and Neanderthals were able to move a greater volume of air through their nasal pathway than either *H. sapiens* or *H. heidelbergensis* (Wroe *et al.*, 2018; see also de Azevedo *et al.*, 2017). Additionally, reconstructions of the Neanderthal thorax indicate that they would have had a slightly increased respiratory capacity relative to modern humans (Gómez-Olivencia *et al.*, 2018). This is in line with indications that Neanderthals in particular had high respiratory requirements due to their large body mass and energetically costly food procurement strategies (Wroe *et al.*, 2018).

For *H. naledi*, *H. floresiensis* and *H. luzonensis*, these species are only known from single sites in South Africa, Indonesia and the Philippines, respectively, if we remain cautious about whether the earlier So'a Basin record does represent *H. floresiensis*. From this limited biogeographical information, it is difficult to estimate how any of these species may have been able to exploit their environments, although it is worth noting that they were in areas that were adjacent to, or possibly overlapping with, the ranges of *H. sapiens* during some time periods. Therefore, it seems reasonable to assume that the smaller-bodied *H. naledi*, *H. floresiensis* and *H. luzonensis* may have occupied niches distinct from the larger *H. sapiens*. In the case of *H. floresiensis*, it has been suggested that its exceptionally small body size allowed for higher population numbers on the island of Flores than would have been possible for a larger-bodied species of hominin (Dennell *et al.*, 2014), which could explain why the *H. floresiensis* lineage was able to occupy Flores since ~700 ka (Sutikna *et al.*, 2016a).

Technological buffering and optimization

The technologies developed by later *Homo* were not only facilitated by the evolution of a large brain, but were also necessary to procure the energetic resources required to support it (Cofran and DeSilva, 2015). Later species of *Homo* are particularly interesting ecologically as they created both an adaptive environment and the selective pressures within it (Downey and Lende, 2012). This interaction between niche construction and physical adaptation was an important selective pressure in their evolution (Potts, 2012), and increasingly researchers are emphasizing this interplay between behaviour, physiology and anatomy as a positive feedback system (Antón and Snodgrass, 2012). Given this interplay, it is therefore difficult to extricate cultural parameters from physical adaptations, as both were instrumental in the energetic strategies of hominin species during the Pleistocene.

One such adaptation is the move towards an increasingly meat-rich diet in later species of *Homo*. It has been suggested that the barrel-shaped thorax of Neanderthals evolved to accommodate the necessary increase in liver size and urinary system size for a species that may have been reliant on a diet of up to 85% animal fat during glacial winters (Ben-Dor *et al.*, 2016). This complements the theory discussed earlier that Neanderthal morphologies were adapted to encourage heat production, as studies have indicated that a high protein diet considerably increases heat production from metabolism (Snodgrass and Leonard, 2009). However, in spite of Neanderthals' frequent reconstruction as almost exclusively reliant on meat as a primary food source, recent studies using the analysis of dental calculus have found that Neanderthals also consistently incorporated plants into their diet and this may have been an integral part of a species-wide niche (Power *et al.*, 2018).

The procurement of fuel for fires can incur very high energetic costs, particularly in sparsely forested areas, and therefore the potential benefits of fire would need to outweigh these costs (Henry *et al.*, 2018), as has been suggested for the introduction of cooking during the last million years (Carmody *et al.*, 2011; Fonseca-Azevedo and Herculano-Houzel, 2012). However, body mass was not found to be a significant constraint in encephalization, but instead was more influenced by foraging efficacy (Cornélio *et al.*, 2016). In fact, hominins were probably able to obtain the requisite number of calories for encephalization through the consumption of raw, rather than cooked, meats (Cornélio *et al.*, 2016). The amount of cooked meat that would be required to counteract the effect of potentially costly fuel procurement was extremely high, indicating that creating fire may not have been a consistently beneficial strategy (Henry *et al.*, 2018).

Another consideration is how much clothing might have been required by hominins across their respective ranges. This topic is intriguing as the causal relationships between clothing and physiological adaptations to improve heat conservation are unknown, and clothing does not tend to be preserved in the archaeological record. For *H. sapiens*, the use of clothing is substantiated by the occurrence of bone needles across their ranges, with the earliest evidence of a bone needle dated to 37–40 ka (Golovanova *et al.*, 2010), and bone awls that may have been used for piercing material are known from Blombos Cave as early as 76–71 ka (Henshilwood *et al.*, 2001). Some researchers have inferred that clothing may have been utilized from about 72 ± 42 ka (Kittler *et al.*, 2003), as it is around then that human head and body lice are reconstructed to have diverged phylogenetically, with the suggestion that the introduction of clothing provided a new environment for body lice to adapt to (d'Errico *et al.*, 2018). Other evidence for *H. sapiens* includes remains of sewn material at the middle

Upper Palaeolithic site of Sunghir in Russia (Trinkaus and Buzhilova, 2012), as well as changes in the foot morphology associated with habitual footwear use, which appears in the fossil record as early as ~40 ka in modern humans (Trinkaus and Shang, 2008). However, the extent to which this was also required for Neanderthals across their range is not yet clear (Collard *et al.*, 2016). Proxies such as faunal remains at hominin sites can give an indication as to what type of clothing Neanderthals may have made. One such study concluded that *H. sapiens* developed more complex clothing than Neanderthals, the latter of which produced comparatively simple garments likened to fur capes (Collard *et al.*, 2016; see Gilligan, 2007, 2018 for more information on simple and complex clothing).

Another approach to establishing whether Neanderthals would have required the same degree of clothing as *H. sapiens* was by modelling the climatic conditions of the species' respective sites (Wales, 2012). *Homo sapiens* were apparently consistently living in areas that would have required ~10% more of their body to be covered than Neanderthals (80–90% body coverage, compared to 70–80%; Wales, 2012). This corroborates the results found by Collard *et al.* (2016), in which a fur cape would have been sufficient, and therefore the tailored clothing of *H. sapiens* was not necessary (Wales, 2012). In addition, to mitigate the likelihood of encountering frostbite and hypothermia, clothing could also have extended the times of the day in which hominins may have been able to forage and hunt, as well as the geographical areas into which they could have ranged. These in turn may have increased foraging yields, thereby supplementing the available energetic resources for somatic or reproductive efforts (Collard *et al.*, 2016). It seems likely that the tailored clothing of *H. sapiens* was a behavioural innovation that was necessitated by their being physiologically less well adapted to cold weather, with less insulating muscle (Gilligan, 2007; Froehle and Churchill, 2009).

Archaeological perspectives on hominin behaviour

As has been discussed above, we have seen the biological and genetic results of *H. sapiens* interacting with the Neanderthals, Denisovans and possibly other archaic human species in Africa (Reich *et al.*, 2010; Meyer *et al.*, 2015, 2016; Hsieh *et al.*, 2016). However, the nature of these interactions is still unclear with regard to how similar or different these human species were at a behavioural level. The answer to this question will inevitably be bounded by degrees of comparison (conscious or not) between distinct human species and our own. Although far from ideal, the implicit use of comparisons of past human species against us results in benchmarks of 'humanness' where we see other hominins as more or less like ourselves. The human revolution debates mentioned above encapsulated these positions well, although several researchers (e.g. Klein and Steele, 2013) argued that modern human behaviour had a punctuated development in Africa at ~50 ka, spreading rapidly from there. It would now seem to be clear that the origins of complex modern human behaviours associated with *H. sapiens* originated as an older, more gradual behavioural package in Africa and was carried with dispersing populations as they moved across the globe (Stringer, 2011; McBrearty, 2013; Scerri *et al.*, 2018a). However, questions still remain concerning how other human species such as the Neanderthals or Denisovans relate to our species at a biological and behavioural level. The answer is important because independent behavioural similarity could

suggest that these other human species should be considered as 'modern' as we are, on a cultural and cognitive level, while fully acknowledging their biological distinctness. In contrast, divergence in the archaeological record would reinforce a biological, behavioural and cognitive difference between us and the other human species with which we shared the Pleistocene world.

One of the most significant changes in our understanding of *H. sapiens* and Neanderthal interactions, at least in Europe, stems from the technological revolution in radiocarbon dating arising from ultrafiltration (Higham *et al.*, 2006), which has allowed a more accurate chronology to be established for the physical extinction of Neanderthals in relation to the arrival of *H. sapiens* in Europe. Older chronologies, based on previous radiocarbon dating methods, had suggested that there may have been as much as ~10 ka coexistence between Neanderthals and *H. sapiens* in Europe, between 40 and 30 ka (e.g. Zilhão and d'Errico, 1999; Zilhão, 2006). However, using ultrafiltration, Wood *et al.* (2013) suggested that this chronological framework may be wrong by as much as ~10 ka, with regard to the Iberian Peninsula. This dating refinement has made a considerable contribution to the framing of when Neanderthals may have been displaced by *H. sapiens* populations in Europe, which it is now widely accepted to have occurred by ~39 ka. This date is further supported through a recent re-examination of one of the oldest *H. sapiens* fossil fragments from Europe, the KC4 maxilla from Kent's Cavern (UK) dated to ~40 ka (Proctor *et al.*, 2017). Previous age estimates of the KC4 maxilla (Higham *et al.*, 2011) suggested there could have been a ~5000-year period between ~45 and 40 ka in which *H. sapiens* and Neanderthals may have overlapped in Europe. Suggestions of a comparably early modern presence at Cavallo (Italy) and Willendorf (Austria) have also been challenged recently (Zilhão *et al.*, 2015; Teyssandier and Zilhão, 2018), although there is another recent claim of a similarly early modern human presence recorded at Bajondillo Cave in southern Spain (Cortés-Sánchez *et al.*, 2019). *Homo sapiens* and Neanderthal interactions may have had considerably greater longevity in the Near East from ~120 ka (Hovers, 2006) and probably even older (Hershkovitz *et al.*, 2018). The results from the recent reanalysis of two fossilized human crania from Apidima Cave, southern Greece (Harvati *et al.*, 2019) would seem to support this longevity with a potential *H. sapiens* population present ~210 ka being superseded by a Neanderthal population by ~170 ka. Apidima would therefore seem to support multiple dispersals of *H. sapiens* out of Africa, some of which were perhaps more successful than others in terms of their longevity, but not all seem to have resulted in biological interactions with indigenous human species. There is not enough scope here to review the entire Old World archaeological record from ~1 Ma, so much of the following discussion emphasizes advances in knowledge in relation to *H. sapiens* and Neanderthal interactions, as this is the knowledge sphere where some of the most recent research has been focused. The broader Old World context from ~1 Ma to 300 ka will also be briefly summarized below.

Behavioural complexity in non-*Homo sapiens* species

Plotkin (2011, p. 457) states that '(c)ulture is not just the expression of different forms of knowledge within social groups, it is that which causally gives rise to human variation and diversity of culture'. Against this definition it can be seen that demonstrable cultural variation helps to frame our understanding of what it means to be human. We often have little difficulty in accepting cultural variation within and between *H. sapiens* groups, resulting from different traditions

of social learning and group experiences – see for example the numerous stone tool industries assigned to identifying the presence of *H. sapiens* populations such as the Aurignacian, Howiesons Poort and Aterian. However, it is often harder to accept the presence of genuine cultural variation in other species of human or even non-human primates.

Much work has been done on demonstrating that non-human primates have behavioural differences in their approach to similar tasks between groups of the same species – these have been often described as proof of primate culture (e.g. McGrew, 1998; Whiten *et al.*, 1999; van Schaik *et al.*, 2003). While there is certainly clear evidence of primate behavioural diversity (and complexity), Gruber *et al.* (2015) make a good point that although primates may have cultural diversity, they may not be consciously aware of that diversity. This must therefore form a key difference in non-human primate culture vs human culture – we are explicitly aware of our cultural diversity, and use it to define and recognize differences between groups.

Within the context of this paper, our understanding of the Pleistocene archaeological record of the last ~1 Ma has developed exponentially over the last decade. For north-west Europe the mapping of hominin dispersals relies heavily on the presence of distinct technological tool types (typically flake & core and Acheulean bifaces pre-300 ka, and prepared core levallois post-300 ka for non-*H. sapiens* species) that contribute to identifying models of occupation centred on the Long (Carbonell *et al.*, 1996), Short (Roebroeks and van Kolfschoten, 1994), Modified Short (Dennell and Roebroeks, 1996) and Punctuated Long Chronologies (Hosfield and Cole, 2018) (Table 1).

From Table 1, it can be seen that hominin presence in Europe from ~1.8 Ma (if the neighbouring site of Dmanisi is counted) to ~700 ka is represented by a fragmentary and seemingly limited or intermittent flake and core industry. There would seem to be more sites below 45° longitude (Dennell and Roebroeks, 1996; Dennell, 2003) with the occasional, and ultimately unsuccessful, foray north of the 45° line as represented by sites such as Happisburgh III (Parfitt *et al.*, 2010) and Pakefield (Parfitt *et al.*, 2005). It is not entirely clear which hominin species may be responsible for the early flake and core European assemblages from ~1 Ma; current evidence would suggest *H. antecessor* as a likely originator (Bermúdez de Castro *et al.*, 1997; Ashton *et al.*, 2014). After ~700 ka, a new technology appears in Europe, the Acheulean biface. The Acheulean has a punctuated presence, until after ~524 ka (Marine Isotope Stage [MIS] 13) when there seems to be a more extensive and sustained signal in terms of site and assemblage size, presumably reflecting increased population thresholds (Moncel *et al.*, 2015). Hosfield and Cole (2018) suggest that the sustained demographic increase after ~500 ka is related to a major species-level physiological change towards a minimum brain size of ~1100 cm³ that facilitated an increase in cognitive plasticity that drove behavioural changes towards a suite of complex behaviours (termed the plasticity package), including the production of Acheulean bifaces.

The appearance of Acheulean bifaces in Europe therefore seems to indicate the presence of a hominin that was more able to cope with the palaeoenvironmental rigours of north-west Europe (e.g. increased seasonality and greater temperature ranges). It is not the biface *per se* that facilitated the sustained presence in north-west Europe, but the full behavioural package that accompanied biface manufacture (e.g. hide processing [Moncel *et al.*, 2015], bone and wooden tools [Warren, 1911; Richter and Krbetschek, 2015; Van Kolfschoten *et al.*, 2015], and controlled use of fire [Molines *et al.*, 2005; Gowlett, 2006; Preece *et al.*, 2006]) at a species

level. However, it is not clear whether this is due to the presence of a new species, such as *H. heidelbergensis*, representing an *in situ* development or a dispersal into Europe from elsewhere (Hosfield and Cole, 2018).

Furthermore, the European Palaeolithic record is complicated by indicators of cultural diversity within the European Middle Pleistocene related to *H. heidelbergensis* or early Neanderthals. Such markers include the twisted ovates of Britain in MIS 11, representing a distinct lithic tradition from the continent (White, 1998), or the presence of distinct flake and core assemblages (e.g. the Clactonian) appearing within the same MIS 11 interglacial landscapes as Acheulean handaxe makers (McNabb, 1992; Wenban-Smith, 1998, 2013; White, 2000, 2015; Wenban-Smith *et al.*, 2006; Ashton *et al.*, 2016). The deep time and often palimpsestual and secondary context nature of these older assemblages make it difficult for researchers to get to grips with the subtleties of the behavioural record and it is not clear whether these local variations reflect cultural diversity within a single species or distinct behaviours across hominin species.

The Palaeolithic record of Eurasia has seen an increased level of attention over the last decade. Stand out finds from the Arabian Peninsula include identifying the presence of *H. sapiens* by 85 ka (Groucutt *et al.*, 2018) and the first stratified Acheulean site from the region (Scerri *et al.*, 2018b) demonstrating hominin presence from at least ~243 to 190 ka. Useful reviews include Groucutt and Petraglia (2012, and references therein) where it is clear that the Arabian Palaeolithic holds a rich and as yet relatively unexplored resource that will continue to deliver surprises in the field of human evolution.

The Asian Pleistocene record has also benefited from increased visibility in a long tradition of research over the last decade and a half with hominin presence now confirmed ~2 Ma from sites such as Shangchen and Majuangou (China), Riwat (Pakistan) and Mojokerto (Indonesia) (Dennell and Roebroeks, 2005; Zhu *et al.*, 2018). However, the < 1 Ma Palaeolithic record of east and south-east Asia has historically been dominated by the hypothesis put forward by Movius (1948) that there were two monolithic technological blocks: the Acheulean found in Africa, Western Europe, South-West and south Asia and unstandardized flake and cores found in East and South-East Asia. Robin Dennell has already written several papers effectively dismantling the Movius argument and demonstrating that it is no longer an appropriate framework for the Asian Palaeolithic (Dennell, 2014, 2016); there is no need to go over those arguments here. However, the impact of the Movius position has been to focus much Early Palaeolithic research in East and South-East Asia on demonstrating the presence of bifaces. There are now several studies that clearly demonstrate that Acheulean bifaces are present on the far side of the Movius Line (e.g. Brumm and Moore, 2012; Li *et al.*, 2014; Wang *et al.*, 2014). In addition, the lack of suitable lithic raw materials for handaxe manufacture to the east of the Movius Line has often been suggested to explain why there are fewer handaxe sites (Corvinus, 2004; Lycett and Norton, 2010; Brumm and Moore, 2012). A recent discovery of a bone handaxe from Gele Mountain in Chongqing dated to ~170 ka (Wei *et al.*, 2017) and a bone pick from Renzidong Cave, Anhui (Zhang *et al.*, 2000), offer an intriguing possibility as to how eastern hominins may have adapted and maintained their knapping abilities across different raw materials. Bone handaxes are also known from European, African and Middle East contexts through the Lower Palaeolithic (see Zutovski and Barkai, 2016 and references therein) and although the Chinese examples may be relatively young, it seems likely that more

Table 1. Summary of the Long, Short, Modified Short and Punctuated Long Chronologies as originally proposed for the Palaeolithic occupation of Europe. Modified after tables 1 and 9 of Hosfield and Cole (2018).

Model	Long Chronology (Carbonell et al., 1996)	Short Chronology (Roebroeks and van Kolfschoten, 1994)		Modified Short Chronology (Dennell and Roebroeks, 1996)	Punctuated Long Chronology (Hosfield and Cole, 2018)			
Summary	Europe occupied in the Early Pleistocene, and in some cases before ~1.5 Ma	'No undisputable proof for human occupation of Europe prior to 500 ka' (Roebroeks and van Kolfschoten, 1994, p. 500)		'Hominids might have occasionally moved into southern Europe well before 500 ka, as and when conditions permitted' (Dennell and Roebroeks, 1996, p. 540)	Only Southern Europe occupied	Continued occupation of Southern Europe, with small-scale fragmented dispersals into northern Europe (e.g. Happisburgh III)	Continued occupation of southern and northern Europe. Emerging behavioural plasticity package (possibly originating from outside Europe), but limited overall population numbers, especially in the north	Full behavioural plasticity package and expanded population numbers across Europe
Timeframe	Before 780 ka (pan-Europe)	Before 500 ka (pan-Europe)	After 500 ka (pan-Europe)	Before 780 ka (Southern Europe)	Before 1 Ma	~1 Ma – 700 ka	~700–500 ka	~500–300 ka
Archaeological signature	Small assemblages (typically 10s and 100s of artefacts)	Small series of isolated pieces selected from natural pebbles	Large collections from excavated knapping floors with conjoinable material	Small assemblages (typically 10s and 100s of artefacts)	Small assemblages (typically 10s and 100s of artefacts)	Small assemblages (typically 10s and 100s of artefacts)	Larger individual assemblages (100s and 1000s of artefacts)	Large assemblages (1000s and 10 000s of artefacts), with multiple large sites
Context	Cave (?) and open-air sites (pan-Europe)	Disturbed secondary contexts	Primary context sites (fine-grained matrix)	Cave (?) and open-air sites (Iberia)	Cave (?) and open-air sites	Cave (?) and open-air sites	Cave and open-air sites	Cave and open-air sites
Assemblage character	Flake and pebble tools	Contested 'primitive' assemblages	Uncontested Acheulean and non-Acheulean industries	Flake and pebble tools	Flake and pebble tools, with potential organic tools	Flake and pebble tools, with potential organic tools	Bifaces and flake tools (limited range), with demonstrated organic tools	Bifaces and flake tools (expanded range), with demonstrated organic tools
Human remains	Occasional	No human remains	Human remains common	Occasional	Very occasional	Occasional	Occasional	Occasional, but with abundant remains at individual sites

bone handaxes may emerge in the future, if preservation circumstances allow.

Dennell (2016) effectively demonstrated that the East Asian fossil and Palaeolithic record was not the isolated back-water put forward by Movius, but is complex and probably the outcome of 'autochthonous' and 'allochthonous' developments. The presence of the Denisovans and enigmatic archaic hominins from China (e.g. Dali and Jinniushan) would suggest that hominin populations that may have dispersed into East Asia during windows of climatic opportunity and extending their ranges in both a latitudinal and longitudinal axis across Asia (Dennell, 2004, 2016) were also then able to successfully survive and adapt to local conditions, including colder and more arid regions. Furthermore, the Asian Early Palaeolithic record should now be seen as an extension of the African and European records, with open-air and cave sites with Acheulean biface and non-biface flake and core assemblages present. However, it is not clear whether the overall lower density of sites in this region is due to taphonomic issues, research bias or a genuine behavioural signal. During the Middle Pleistocene, mainland South-East Asia appears to have been inhabited by such low population numbers as to leave little trace of their presence; by contrast, the Upper Pleistocene shows hominins to be using simple flaked assemblages that appear contemporary with the post-Acheulean Middle Palaeolithic and early microlithic assemblages from western and south-western Asia, with no apparent clarity on why these prepared-core technologies are not found more extensively further east (Dennell, 2016).

The African Stone Age is traditionally framed through the Early, Middle and Later Stone Ages (Table 2) and has received no less attention than Europe and Eurasia in terms of advances in knowledge over the last decade.

The Early Stone Age includes the early flake and core assemblages (Lomekwian and Oldowan) and Acheulean or bifaces assemblages. Multiple hominin species are probably responsible for the production of these early industries especially given that the Lomekwian (Harmand et al., 2015) has extended flake and core stone tool use beyond known examples of the genus Homo to ~3.3 Ma. The Acheulean assemblages for the moment seem to be more securely associated with H. erectus and H. heidelbergensis within Africa, although there are outlying exceptions to this general rule (e.g. Clark et al., 2003; McBrearty, 2003; White et al., 2003). The Middle Stone Age is a rather more complicated technological complex to pin down. Although largely recognized and defined as a Levallois prepared core technology, the longevity of the label also includes blade and microlith production from volumetric cores from ~120 ka. In addition, there is increasing recognition of regional typological variability within the Early Middle Stone Age (~300–130 ka) that may or may not be associated with manufacture of the artefacts by different hominin species

(such as late H. heidelbergensis), an increasing range of H. sapiens (e.g. Herto), or expressions of distinct cultural identities and learning practice within a single species. The Later Stone Age is typically associated with H. sapiens and often associated with microlith production within established regionally distinct typologies that seem to reflect cultural variation.

One of the most significant developments in the last decade in terms of understanding the African Middle Stone Age was the extension of the origins of our own species back to ~315 ka at Jebel Irhoud (Richter et al., 2017) alongside Middle Stone Age artefacts, sparking questions as to the origins of the technology from single or multiple sources. As alluded to previously, Scerri et al. (2018a) frame a timely and useful discussion in which they suggest that our species may have evolved within a network of interlinked groups across the African continent, fluctuating between periods of greater or lesser connectivity. If this is indeed the case, then the pattern of greater cultural variability, at least within the Middle and Later Stone Ages (e.g. Dusseldorp et al., 2013 for a useful review of the South African perspective), could be explained as a factor of social fission and fusion, but at a much greater scale than previously appreciated. Indeed, this network may even extend beyond our own species if the archaic ghost lineage introgression seen within sub-Saharan Africans (Stringer, 2011; Hsieh et al., 2016) is considered as a biological marker of such interactions. Certainly, the presence of H. naledi between ~335 and 236 ka (Dirks et al., 2017) and H. heidelbergensis in the form of Broken Hill 1 dated to ~300 ka (Balzeau et al., 2017) clearly indicate that other hominin species coexisted within Africa alongside evolving H. sapiens for a long period. The implication of hominin interbreeding on the interpretation of the archaeological record has yet to be fully understood in terms of the framing of regional and global typologies and no doubt the next decade of African Palaeolithic research will be as exciting, frustrating and confusing as the last.

Updating Neanderthal behaviour

The knowledge base relating to Neanderthals has increased exponentially over the last decade, and it is worth spending some time here considering the implications of how we should be engaging with and interpreting degrees of complexity within Neanderthal behaviour. Villa and Roebroeks (2014) produced a useful review, so our discussion here will update and offer a big picture perspective to focus on key advances in knowledge that have impacted our perceptions of our human relatives. However, as much of the following discussions will focus on Neanderthals and their interactions with H. sapiens, we do need to present a brief discussion incorporating transitional industries.

Table 2. Broad overview of the African Stone Age sequence. Adapted after Dusseldorp et al. (2013: table 1).

Early Stone Age (~3.3 Ma – ~200 ka)	Hand-held tools, initial stages represented by simple struck flakes, core and pebble tools (Lomekwian and Oldowan), followed by bifacially shaped handaxes, cleavers and picks (Acheulean).
Middle Stone Age (~300–~20 ka)	Levallois prepared core technology (unifacially and bifacially retouched points) but also includes blade production and microliths from volumetric cores. Evidence for hafted tools, bone points, exploitation of marine shells for ornamentation, engraved ochre nodules and ostrich eggshells, grindstones. Increasing variability between assemblages through time.
Later Stone Age (< ~40 ka)	Variability between assemblages with micro- and macro-lithics. Hafted stone and bone tools, borers, grindstones, grooved stones, ostrich eggshell beads, ornamentation, fishing equipment, rock art and ceramics towards final phases.

Transitional industries

The production of lithic blades is predominantly seen as a characteristic of the Upper Palaeolithic in western and central Eurasia, and the Middle to Later Stone Age in Africa. Johnson and McBrearty (2010) reported the discovery of deliberate blade production from the Kapthurin Formation dated to c. 500 ka, extending the range of blade production by ~150 ka into the Early Stone Age. Nonetheless, blades are primarily a feature of mode 4 technology (Clark, 1961; and see below) and while there are many regional variations in the typology of the technology (such as the Aurignacian in Europe), most have traditionally been largely associated with the presence of *H. sapiens*. However, the temporal extension of the Kapthurin blades (Johnson and McBrearty, 2010) and other ancient bladed traditions, such as the Amudian of the Acheulo-Yabrudian Complex (Barkai *et al.*, 2005), suggests that the association of the technology type to a specific species (i.e. *H. sapiens*) is no longer reliable and local technological chronologies will be increasingly important in framing our understanding of the archaeological record going forward (see below). Within the context of this paper however, a technological scheme of terminology that reflects broad changes across a global scale would still be useful. A heuristic to which many researchers may be familiar (but not necessarily agree) that facilitates such a broad classification system is Clark's (1961) technological modes (Table 3; Fig. 1).

The modes are a rather blunt and simplified classification describing the basic manufacturing procedures and broad stone tool outputs while ignoring any organic artefacts. In addition, there are continuities between the technological modes and time divisions that Table 3 and Figure 1 do not illustrate (Gamble, 2013). However, the modes do demonstrate that broadly through time, methods of lithic artefact production become more complex, leading to greater control in knapping techniques and raw material utilization (Foley and Lahr, 2003). One of us (Cole, 2019) has attempted to update the use of Clark's technological modes to include the increased range of behaviours seen in the archaeological record (e.g. stone tools, organic artefacts, ornamentation) and map these to hominin species and cognitive complexity. In addition, Shea (2013) has produced a thoughtful and useful review of Clark's modes and put forward his own more detailed and nuanced scheme (modes A–I). Such approaches may provide useful starting points for the development of a new framework for the 21st-century appreciation of the Palaeolithic record. As has already been demonstrated in this review, the archaeological, fossil and genetic records are now so complex and increasingly intertwined that old typologically based scaffolds are becoming less relevant to structuring our understanding of the Pleistocene record. However, as the purpose of this paper is to set the framework of understanding from the last decade of research, we will proceed within the limitations of the current models.

In Europe, the presence of the Aurignacian (mode 4 blade[let] technology) has been used to track and date the spread of *H. sapiens* across the region (e.g. see Dinnis *et al.*, 2019 for discussions centred on Eastern Europe and an important recognition of bladelet production, rather than blades, within a refined regional chronology for Kostenki) feeding into debates on the disappearance of Neanderthal populations by ~39 ka (Wood *et al.*, 2013). Of particular relevance here are the presence of much debated 'transitional' industries such as the Châtelperronian (France and northern Spain) (Churchill and Smith, 2000) and the Uluzzian (Italy and Greece) (Douka *et al.*, 2014), which seemingly contain elements of bladed and Mousterian (mode 3/4) technologies, and are key in understanding the chronology and nature of the cultural and genetic interactions between the last Neanderthals in Europe and the earliest *H. sapiens* (Welker *et al.*, 2016). The Châtelperronian has had an especially turbulent interpretive history with several arguments for a Neanderthal or *H. sapiens* origin. One site in particular, the Grotte du Renne at Arcy-sur-Cure (France), has played an important role when it comes to understanding the Châtelperronian debate. The Châtelperronian artefacts, lithics and decorative pendants from this site are stratigraphically related to Neanderthal hominin remains (Hublin *et al.*, 1996; Bailey *et al.*, 2009). Explanations for Neanderthal associations are well known and rehearsed in the broader literature including acculturation by *H. sapiens*, independent innovation of the pendants by Neanderthals, to movement of artefacts or hominin remains within the stratigraphic sequence (White, 2001; Bar-Yosef and Bordes, 2010; Higham *et al.*, 2010; Hublin *et al.*, 2012; Hublin, 2015). Thankfully, Welker *et al.* (2016) have provided some clarification that the Châtelperronian artefacts from the Grotte du Renne are linked to the Neanderthals, using biomolecular and chronological analysis with a date of ~43–40 ka. These results corroborate earlier claims by Hublin *et al.* (2012), who also suggest a correlation at Saint-Césaire (France) between Neanderthals and the Châtelperronian, and therefore the bladed technologies found within the transitional industry. However, what remains unclear is whether this is a truly independent innovation or a result of *H. sapiens* acculturation. Results from Canaule II (France) and Arcy-sur-Cure suggest that the Châtelperronian layers are distinct from the Mousterian and Aurignacian layers and are therefore a unique entity, innovation or example of cultural succession, rather than the result of a mix of Middle and Upper Palaeolithic traditions (Bachellerie *et al.*, 2007; Villa and Roebroeks, 2014; Rocca *et al.*, 2017), although Ruebens *et al.* (2015) provide interesting discussions on the emergence of the Châtelperronian out of the Mousterian tradition. Gravina *et al.* (2018) further demonstrate through a detailed taphonomic, spatial and typo-technological reassessment of the Neanderthal skeletal layers from Saint-Césaire that there is no reliable evidence for a Neanderthal Châtelperronian at the site. It would therefore seem that there is still uncertainty as to the true nature of the Châtelperronian in Europe, as well as its authorship. Future research will no doubt help to further clarify the position of the Châtelperronian and whether it is even a genuine behavioural expression or not, but at the time of writing it is perhaps up to individual researchers to decide where they fall on this issue.

The interpretation of transitional industries in terms of assigning them to a specific hominin becomes even more complicated when looking at the Uluzzian from Italy and Greece. The Uluzzian was traditionally linked to the Neanderthals when first described (e.g. Palma, 1989) but has also

Table 3. Modes of stone technology. Adapted after Gamble (2013: box 2.3).

Mode	Description	African convention	European convention	First appearance datum (FAD)
1	Simple flake and core (e.g. Lomekwian and Oldowan)	Early Stone Age	Lower Palaeolithic	~3.3–~2.6 Ma
2	Bifacially flaked hand axes, cleavers and picks (e.g. Acheulean)	Early Stone Age	Lower Palaeolithic	~1.7–1.4 Ma
3	Flakes from prepared cores (e.g. Levallois, Victoria West)	Middle Palaeolithic	Middle Stone Age	~315 ka
4	Blades from prepared cores (e.g. Aurignacian)	Later Stone Age	Upper Palaeolithic	~120–~50 ka
5	Microlithic components of composite artefacts	Later Stone Age	Mesolithic	< 12 ka

been associated with *H. sapiens* remains (Benazzi *et al.*, 2011), and a refined chronology cautiously suggests the independent innovation of this 'transitional' looking industry by *H. sapiens* without a Neanderthal influence (Douka *et al.*, 2014), although Zilhão *et al.* (2015) provide arguments against. The picture that is starting to emerge is that we potentially have two populations of human species (Neanderthals and *H. sapiens*) that have different lithic traditions (the Mousterian and the Aurignacian) but that are also capable of seemingly independently innovating so-called 'transitional' industries that appear, to the modern eye at least, to combine elements of the Mousterian and Aurignacian together. If the transitional industries are indeed truly independent innovations by two human species, then the blended similarities are hard to explain unless the two human species have broadly similar biology, behavioural tendencies and cognitive constructions.

The picture is convoluted further by the fact that the makers of other transitional industries from north-western, central and south-eastern Europe and Russia, such as the Lincombian–Ranisian–Jerzmanowician (LRJ), Bohunician, Bachokirian, Szeletian and Streleskayan remain unknown (Dinnis *et al.*, 2019). They could feasibly be made by late Neanderthals or *H. sapiens* (Flas, 2011; Villa and Roebroeks, 2014; Hublin, 2015). In addition, the appearance in Siberia of early burin-core and laminar reductions (typically seen as part of the *H. sapiens* toolkit) at ~43 ka from sites such as Kara-Bom and Denisova Cave further confuses the record of hominin presence as the makers are again unknown, but could conceivably be *H. sapiens*, Neanderthal or Denisovan (Zwyns *et al.*, 2012; Douka *et al.*, 2019; Jacobs *et al.*, 2019b).

Therefore, while the transitional industries are undoubtedly important for understanding the nature of the *H. sapiens* dispersal and the complexity of the behavioural patterns of indigenous human species, we still know so little about the context, timing and creation of many of them that we must exercise a large degree of caution in their use (Villa and Roebroeks, 2014). We should therefore turn to the broader context of behaviour for non-*H. sapiens* species and see whether it is possible to track parallel evidence for cultural and cognitive complexity.

The broader behavioural context

There have been several recent studies that convincingly suggest that the Neanderthals of the late Middle Palaeolithic (~115–39 ka) had a developed sense of distinct cultural identities expressed through the lithic record (Ruebens, 2013, 2014). The distinct cultural groups are the Mousterian of Acheulean Tradition (MTA) for south-west France and north-west into Britain, representing a Mousterian tradition dominated by handaxe manufacture, including the British regional version of the Bout Coupé (White and Jacobi, 2002); the second identified group was the Keilmessergruppen (KMG) from central and eastern Europe, dominated by backed and leaf-shaped bifacial tools; and the third group identified was the Mousterian with Bifacial Tools (MBT) geographically located between the MTA and KMG groups through Belgium and northern France and characterized by a variety of bifacial tools. The studies conclude that the differing typologies of artefacts cannot be accounted for as reflecting raw material or function, but rather the MTA and KMG were two distinct cultural traditions in which the specific concept of bifaces was passed down through the generations. The MBT is interpreted as a border zone where highly mobile Neanderthal groups of the MTA and KMG seem to have interacted. These studies therefore support the notion of distinct regionalized cultural

behaviour among late Neanderthal groups in Western Europe as defined through the lithic record.

There are indications from other behavioural practices of the Neanderthals that may also suggest the presence of distinct cultural groups. One of these avenues of research revolves around the treatment of the dead. Despite controversy over whether Neanderthals buried their dead (e.g. Gargett, 1999), it has now been generally accepted that Neanderthals (or at least some of them) engaged in mortuary practices (Pettitt, 2010). Furthermore, the Neanderthal treatment of the dead seems to be geographically and temporally variable, where practices range from non-burial; caching of body parts; inhumation without grave goods – perhaps utilizing natural features; deliberate burial with grave goods; and skeletal defleshing, through space (evidence has been found in western, central and eastern Europe as well as the Near East) and time (~115–40 ka; Pettitt, 2002, 2010).

However, Neanderthals did not just bury their dead, they also engaged in other forms of mortuary treatment of the remains such as cannibalism (Cole, 2017b; Saladié and Rodríguez-Hidalgo, 2017). What is of further interest is that even within the acts of cannibalism, there may well be a range of motivations with interpretations ranging from survival cannibalism (Rosas *et al.*, 2006; Defleur and Desclaux, 2019) to nutritional cannibalism (as part of the diet) (Barroso and de Lumley, 2006; Maureille *et al.*, 2007; Rougier *et al.*, 2016; Rodríguez *et al.*, 2019). The case of Troisième caverne of Goyet (Belgium) (~45.5–40.5 ka; Rougier *et al.*, 2016) is additionally intriguing due to the processing of the Neanderthal carcasses and the production of bone tools from the Neanderthal remains, which were used as soft hammers to knap stone tools. Rougier *et al.* (2016) also point out that the cannibalistic treatment of the Neanderthal remains at this site seems to be different to the post-mortem treatment of Neanderthal remains at other sites in the region, which are either non-existent (Walou Cave and Trou de l'Abîme – Belgium), possible burial (Feldhofer – Germany) or active burial (Spy – Belgium). From isotope analyses it would appear that the consumed from Goyet had a foreign origin (so possible exocannibalism) and were perhaps slaughtered by the local inhabitants, presumably another group of Neanderthals or possibly even an unknown group of *H. sapiens* (Wißing *et al.*, 2019). There have been previous arguments that even when acts of cannibalism have been assigned to survival or nutritional labels, that there may well be social or cultural motivations that contribute to and underpin the consumptive act (Cole, 2017b). Therefore, there is a great deal of behavioural complexity surrounding the Neanderthal treatment of the dead in both time and space. At the time of writing, the only other species that seems to have an equally diverse range of motivations and post-mortem treatment of human bodies is our own (but see van Leeuwen *et al.*, 2017 for an example of chimpanzee practice).

McBrearty and Brooks (2000) highlight that systematic ochre use is a key component of what may be considered modern human behaviour. d'Errico *et al.* (2010) and d'Errico and Stringer (2011) conducted useful reviews of Neanderthal and *H. sapiens* pigment use, which highlighted more than 40 Middle Palaeolithic sites from MIS 6 to 3 or ~160–30 ka, some with vast quantities such as 450 pieces (250 of which show use) from Pech de l'Azé I (France) (see also Villa and Roebroeks, 2014: S1). In addition, Roebroeks *et al.* (2012) have shown that Neanderthals may well have been exploiting haematite at Maastricht-Belvédère (the Netherlands) from ~250 to 200 ka. In which case, the Neanderthal exploitation of ochres and pigments would seem to match in time the exploitation of such resources in the African record (Barham,

1998, 2002). The reasons for ochre or pigment use has been much debated ranging from medicinal, as a preservative in hide processing, an adhesive in composite tool-making and social signalling (Velo, 1984; Minzoni-Déroche et al., 1995; Callahan, 1999; Barham, 2002; Barham, 2010; Kuhn et al., 2007). However, it is interesting to note that from the ethnographic record, the use of pigments has always had a primary use in social signalling rather than the signalling arising as a secondary purpose (Knight et al., 1995; Barham, 2002). This would certainly seem to be the case at Cioarei-Boroşteni Cave (Romania) dated to ~47 ka, where a geode has been deliberately painted with red ochre (the authors suggest for some symbolic meaning) and where ochre preparation containers have been suggested from the upper components of stalagmites (Cârciumaru et al., 2015). This behaviour apparently dates before the arrival of H. sapiens in the region and therefore, if symbolic, could suggest that Neanderthals were an independently symbolic species before the arrival of H. sapiens in Europe (and see below).

One of the major markers of modern human behaviour still remains the ability to produce art. Currently, the earliest evidence for engraving comes from the H. erectus site of Trinil, ~540–430 ka (Joordens et al., 2015), where a geometric engraving has been carved into a freshwater mussel shell. Although a lone instance (so far), the act of engraving has some intriguing implications for the origins of deliberate pattern production in non-H. sapiens species. Cave art and rock art are still seen to be the benchmarks of art production, where it was previously thought that the earliest evidence for such behaviour came from north-west Europe ~40–35 ka (see references in Pike et al., 2012; García-Diez et al., 2013), although recent research from Sulawesi (Indonesia) and Borneo has shown that rock art is also present in the South-East Asia from at least ~40 ka (Aubert et al., 2014, 2018b) with evidence of ochre use from Madjedbebe Rockshelter in Australia from ~65 ka (Clarkson et al., 2017). This would suggest, therefore, that the H. sapiens behavioural package including rock art may well have originated in Africa and then spread across the globe with the dispersing populations. For the Neanderthals, however, their ability to produce rock art remains more controversial. Pike et al. (2012) had previously dated Iberian rock art and while most of their samples fell within the H. sapiens presence in Europe (< 41.5 ka), the oldest components of the El Castillo Cave frieze, the red discs at ~40.8 ka (as a minimum), could have potentially been related to either Neanderthals or H. sapiens. In addition, Rodríguez-Vidal et al. (2014) have reported a Neanderthal geometric engraving from Gorham's Cave (Gibraltar) dated to > 39 ka. Recently, Hoffmann et al. (2018a) may have pushed back the origins of cave art in Iberia by another ~20 ka, long before the presence of H. sapiens in Europe. If accepted, this new dating evidence would certainly suggest that Neanderthals were capable of producing painted cave art, and we may now need to re-evaluate other cave art sites in terms of their authorship. However, this is an ongoing debated topic with responses to the Hoffmann et al. (2018a) paper coming from Aubert et al. (2018a) and Slimak et al. (2018) advising caution in accepting the older dates followed by rebuttal papers (Hoffmann et al., 2018c). As with the Châtelperronian debate, at the time of writing, individual researchers will need to decide for themselves where they fall on this issue.

Even if the older cave art dates are accepted, it would seem that Neanderthal cave art was a relatively rare behavioural expression of symbolism, presumably because Neanderthals had a preference for other symbolic outlets that better suited their cultural frameworks, such as personal and body adornment. Interestingly, there is yet to be any evidence for Neanderthal figurative art with the oldest H. sapiens examples (e.g. the Venus of Hohle Fels) dating to ~40 ka (Conard, 2009), which may further highlight differences between the two species' cultural frameworks for symbolic expression and construction.

By contrast, the evidence for Neanderthal jewellery and personal adornment manufacture has grown in recent years. Radovčić et al. (2015) have suggested that Neanderthals modified the claws of white-tailed eagles at the site of Krapina (Croatia) for use as jewellery dated to at least 130 ka, while additional uses of raptor claws for presumably symbolic purposes come from Combe-Grenal (France) at ~90 ka and Les Fieux (France) at ~60–40 ka (Morin and Laroulandie, 2012). The Neanderthals seemed to have had a clear fascination with certain predatory birds such as raptors, corvids and vultures as well as other birds like wood pigeon and Alpine chough as feather exploitation for symbolic purposes (presumably linked to adornment of people or objects) has been reported from Fumane (Italy) at ~44 ka and Gibraltar (Peresani et al., 2011; Finlayson et al., 2012). In addition, Zilhão et al. (2010) report the use of perforated (~43 ka) marine shells that must have been transported ~60 km from Antón rockshelter and pigment-stained marine shells from Aviones Cave in the Iberian Peninsula. As the authors readily admit, the Antón assemblage falls within the range of possible overlap with H. sapiens presence in the region. However, recent work on the Aviones assemblage places it beyond the presence of H. sapiens in Iberia at ~115–120 ka (Hoffmann et al., 2018b) and therefore suggests that Neanderthals were independently using pigments and shells for decoration and ornamentation. Further evidence for such complicated Neanderthal behaviour comes again from Fumane Cave (~47–45 ka), where a fossil marine shell was brought to the site from over 100 km away and seems to have been covered in red ochre possibly for personal adornment (Peresani et al., 2013). From the highlighted examples presented here, it is clear that the Neanderthals were apparently cognitively and behaviourally capable of producing personal adornments for at least as long as H. sapiens populations in Africa and the Near East (d'Errico et al., 2001, 2005; Parkington et al., 2005; Vanhaereny et al., 2006; Bouzouggar et al., 2007; Kuhn et al., 2007; Botha, 2008; Henshilwood et al., 2009; d'Errico and Stringer, 2011). They may have done so in technologically different ways to H. sapiens adornment, but the end result must have been the same: to produce a social message about the wearer that was read and understood by a wider community. For such messages to be successfully transmitted within and between hominin groups, it follows that the makers must have had a clear capacity for language and symbolism.

As Villa and Roebroeks (2014) suggest, there is little in the Neanderthal behavioural package that differs significantly from the African Middle Stone Age (associated with H. sapiens) where we have no problem accepting a capacity for language for those populations. There have been many arguments regarding the Neanderthal capacity for language that we do not need to reiterate here (but see Johansson, 2015 for a useful review). However, recent work has suggested that there would seem to be biological support for the Neanderthal ability for speech from D'Anastasio et al. (2013) arising from a new study of the Kebara 2 (Israel) Neanderthal hyoid bone. In addition, from a social and cognitive perspective, Neanderthals were potentially capable of grammatical language (Gowlett et al., 2012; Gamble et al., 2014), further supported by their symbolic material culture production discussed above. Therefore, we should probably consider Neanderthals as a hominin species that had complex communication systems, including the

capacity for speech, but we acknowledge here that the exact mechanisms would, of course, be different to those of *H. sapiens.*

Additional indications from the Neanderthals regarding complex behavioural practices come from the structuring of space in Bruniquel Cave (France) dated to ~176 ka (Jaubert *et al.,* 2016), where Neanderthals seem to have arranged broken stalagmites in ovals (we do not yet know why), along with multiple traces of fire ~336 m from the cave entrance. This would certainly seem to suggest that Neanderthals had an ability to control fire and used it to explore deep caves. In addition, intriguing evidence from Molodova I (Ukraine) dated to ~44 ka suggests that Neanderthals may have been constructing shelters from mammoth remains as well as exploiting the animals for food (Demay *et al.,* 2012). Tacking back to the lithic technology of the Neanderthal tool package, Levallois, a type of mode 3 prepared core technology, is about versatility and adaptability of raw material exploitation and composite tool production (Scott, 2011; Scott *et al.,* 2011; Scott and Ashton, 2011). With Levallois technology, specialized lithic points (and other flake variants such as radial and laminar flakes) can be made for hafting and the creation of stone-tipped spears. In addition, we have good evidence for the Neanderthal creation and use of pitch as a binding agent in composite tool production (Wragg Sykes et al., 2015; Roebroeks and Soressi, 2016). Using composite tools, certain cognitive thresholds must have been crossed by the creating species (Barham, 2010). These include a transition to a third order of intentionality at a minimum and certainly a fourth-order minimum once symbolic artefacts are manufactured (Cole, 2017a). This would put the Neanderthals at a comparative cognitive level to *H. sapiens* at this time. As well as Neanderthals being acknowledged as expert big-game hunters who are also able to exploit a wide range of smaller terrestrial, avian and aquatic resources (e.g. see Hardy and Moncel, 2011; Villa and Roebroeks, 2014), Neanderthals also had the ability to exploit a variety of flora (Shipley and Kindscher, 2016) even to the point that they may have managed pain using plants (Weyrich *et al.,* 2017). Therefore, pulling these diverse evidentiary threads together suggests that Neanderthal subsistence strategies were varied and adaptable to the range of habitats in which they resided, long before they encountered *H. sapiens* populations. Yet, available genetic data suggest that Neanderthals achieved this with low population numbers and low genetic diversity, compared with *H. sapiens* (Reher *et al.,* 2019).

Concluding thoughts

The topics discussed herein are some of those that we feel have catalysed new thinking about how human evolution progressed. These developments are either in the form of new discoveries themselves, or in the re-analysis of old data via new techniques. The discoveries of *H. floresiensis, H. luzonensis,* Denisovans and *H. naledi* in the last 15 years should remind us that the fossil record of humans is still very patchy – Africa has Palaeolithic tools across virtually its whole landscape as a witness to (at times) widespread human occupation, yet palaeontological evidence has been recovered from < 10% of the area of that continent. The percentage coverage for Asia and South-East Asia is even lower in places, highlighting the missing data of the deeper evolutionary history of each of those four new discoveries, and no doubt of other extinct lineages still to be revealed. On a behavioural level, the archaeological record continues to provide a wealth of surprises. While there are certainly biological differences between Neanderthals and *H. sapiens,* the behavioural gap has narrowed to a point where there seems to be little difference between the two, even at the point when Neanderthals were becoming physically extinct.

In some cases, these advances are throwing new light on long-contentious topics, making clear that now, more than ever, we need to offer up new solutions to these existing theoretical problems. The inadequacy of the biological species concept, for example, has been well recognized for palaeontology. But until the rise of ancient genomics, the potential for a hominin hybrid had yet to be realized. Several instances of known introgression later, we are now faced with having to choose between the wealth of alternative species concepts, the difficulty of which is compounded by the reality of having a range of morphological evidence for which we do not have any aDNA, and a collection of genetic data for which we have little or no morphological information. The best solution to this problem will differ depending on who is asked, and teasing apart the relative merits of each approach goes beyond the scope of this paper. However, whatever the stance, we have passed the threshold of phylogenetic complexity where we can hope that new fossils will organically elucidate the existing record's evolutionary relationships, and at minimum we will need to get better at specifying our naming conventions with respect to the amount of variation we think is necessary or sufficient when describing new species. One of the most interesting questions for current researchers is whether *H. sapiens* populations recognized the Neanderthals (and presumably the Denisovans, although we know almost nothing about Denisovan material culture production) with their personal adornments, distinct complex cultural structures between groups, variable mortuary practices, structured use of space, composite tool technologies and specialized hunting strategies as fellow humans at a cultural level, albeit of a different biological type to them? To mate successfully there should be a degree of biological recognition of sameness, but what about a cultural recognition of similarity? Increasingly, as highlighted here, evidence would seem to suggest that the behavioural gap between Neanderthals and *H. sapiens* is closing (some may even consider it closed) and future discoveries within this sphere are eagerly awaited. Additionally, the known cultural complexity of Neanderthals is continuing to increase, with multiple occurrences of putative symbolic behaviour predating the arrival of *H. sapiens* in Europe, although that statement is now tempered by the recent claim that *H. sapiens* was already in Greece by ~210 ka (Harvati *et al.,* 2019). Our understanding of these complex human behaviours and their origins requires more information from sites outside of Europe and species beyond the Neanderthals. Hopefully, future research in this area will add to an already rich and complex picture.

As the resolution of our various reconstructions of hominin evolution increases, the potential for equifinality (that an end state can be met by multiple different routes) to confound our understanding of causal relationships is brought into greater relief. Aspects of this have been discussed throughout the paper, such as in the various adaptive theories used to explain the Neanderthals' large nasal cavities. Crucially, it is becoming clear with this debate, as with many others, that these scenarios have historically been routinely presented as false dichotomies. Increasingly, research is revealing that the factors influencing morphological and behavioural innovations are complex and that some combination of multiple scenarios may best approximate the truth.

Supporting information

Additional supporting information can be found in the online version of this article.

Abbreviations. aDNA, ancient DNA; LCA, last common ancestor; LRJ, Lincombian–Ranisian–Jerzmanowician; MBT, Mousterian with Bifacial Tools; MIS, Marine Isotope Stage; MPT, Middle Pleistocene Transition; mtDNA, mitochondrial DNA.

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