Early hominins in north-west Europe: a punctuated long chronology?

Article

Accepted Version

Hosfield, R. ORCID: https://orcid.org/0000-0001-6357-2805 and Cole, J. (2018) Early hominins in north-west Europe: a punctuated long chronology? Quaternary Science Reviews, 190. pp. 148-160. ISSN 0277-3791 doi: 10.1016/j.quascirev.2018.04.026 Available at https://centaur.reading.ac.uk/69498/

To link to this article DOI: http://dx.doi.org/10.1016/j.quascirev.2018.04.026

Publisher: Elsevier

Title: Early hominins in north-west Europe: a punctuated long chronology?

Authors & Affiliations: Rob Hosfield[1] and James Cole[2]

1. Department of Archaeology, School of Archaeology, Geography & Environmental Science, University of Reading, Whiteknights, Reading, RG6 6AB, United Kingdom. E-mail: r.hosfield@reading.ac.uk. ORCID ID: 0000-0001-6357-2805
2. School of Environment and Technology, University of Brighton, Cockcroft Building, Lewes Road, Brighton, BN2 4GJ, United Kingdom. E-mail: j.n.cole@brighton.ac.uk. ORCID ID: 0000-0002-7009-5303

Corresponding author: Rob Hosfield

Corresponding author address: Department of Archaeology, School of Archaeology, Geography & Environmental Science, University of Reading, Whiteknights, Reading, RG6 6AB, United Kingdom.

Telephone: +44 (0)118 378 7632; e-mail: r.hosfield@reading.ac.uk

Keywords: Lower Palaeolithic; Middle Pleistocene; Europe; punctuated long chronology; life history; behavioural plasticity; palaeoenvironment

Abstract

In light of changing views regarding the identity and evolutionary positions of Europe's Lower Palaeolithic hominins, a re-consideration of the hominin occupation of North-West Europe from *c*. 1 million years ago (mya) to *c*. 400 thousand years ago (kya) is timely. A change in the scale and character of the overall European Palaeolithic record around *c*. 800-600 kya has been well documented and argued over since the mid-1990s. Hominin expansion into the European north-west, potentially from southern Europe, Africa or south-western Asia, has been linked to the introduction of a new lithic technology in the form of the biface. We evaluate three potential drivers for this northern range expansion: changing palaeo-climatic conditions, the emergence of an essentially modern human life history, and greater hominin behavioural plasticity. Our evaluation suggests no major changes in these three factors during the *c*. 800-600 kya period other than enhanced behavioural plasticity suggested by the appearance of the biface. We offer here a model of hominin occupation for north-west Europe termed the 'punctuated long chronology' and suggest that the major changes in the European Lower Palaeolithic record that occur at a species wide level may post-date, rather than precede, the Anglian Glaciation (marine isotope stage (MIS) 12).

Highlights

- European Lower Palaeolithic includes key shift in hominin distribution.
- Shift from below 45° north to broader range including higher latitudes.
- Changes in palaeoenvironmental conditions or hominin life history not key factors.
- Increasingly plastic behaviour may have enabled hominin range expansion.

1. Introduction

The hominin occupation of North-West Europe is a complex and important story for understanding hominin abilities to adapt to novel environments and the implementation of the plastic behaviours that were first developed on the savannahs of Africa and Eurasia (Dennell, 2003; Dennell and

Roebroeks, 2005; Grove, 2011; Potts, 2013). North-West Europe is important due to the unique challenges that faced hominins within the higher latitude belt in terms of that region's distinctive flora, fauna and seasonality. The earliest hominin occupation of Europe has traditionally been seen through the long, short, and modified short chronologies (Carbonell et al., 1996; Dennell and Roebroeks, 1996; Dennell, 2003; Roebroeks and van Kolfshoten, 1994; Table 1), recently enriched through the Eurasian perspective (Dennell, 2004).

Model	**Long Chronology (Carbonell et al., 1996)**	**Short Chronology (Roebroeks and van Kolfshoten, 1994)**		**Modified Short Chronology (Dennell and Roebroeks, 1996)**
Summary	Europe occupied in the Early Pleistocene, and in some cases before *c*. 1.5 mya	"No undisputable proof for human occupation of Europe prior to about 500,000 years ago" (Roebroeks and van Kolfshoten, 1994: 500)		"Hominids might have occasionally moved into southern Europe well before 500,000 years ago, as and when conditions permitted" (Dennell and Roebroeks, 1996: 540)
Evidence				
Timeframe	**Before 780,000 years ago (pan-Europe)**	**Before 500,000 years ago (pan-Europe)**	**After 500,000 years ago (pan-Europe)**	**Before 780,000 years ago (Southern Europe)**
Archaeological signature	Small assemblages (typically 10s and 100s of artefacts)	Small series of isolated pieces selected from a natural pebble background	Large collections from excavated knapping floors with conjoinable material	Small assemblages (typically 10s and 100s of artefacts)
Context	Cave(?) and open-air sites (pan-Europe)	Disturbed secondary contexts	Primary context sites (fine-grained matrix)	Cave(?) and open-air sites (Iberia)
Assemblage character	Flake and pebble tools	Contested 'primitive' assemblages	Uncontested Acheulean and non-Acheulean	Flake and pebble tools

			industries	
Human Remains	Occasional	No human remains	Human remains common	Occasional

Table 1: Summarising the long, short and modified short chronologies, as originally proposed (Carbonell et al., 1996; Dennell and Roebroeks, 1996; Gamble, 1999; Roebroeks and van Kolfshoten, 1994).

The long and short chronologies have been hampered by the resolution and scale of the archaeological record and uncertainty whether evidence for hominin presence and absence in North-West Europe prior to 800 kya is a genuine behavioural pattern or the result of research and/or taphonomic bias (Roebroeks and van Kolfshoten, 1994). However, discoveries at a number of sites including Dmanisi, Georgia (Lordkipanidze et al., 2007); Orce and Atapuerca, Spain (Carbonell et al., 2005; Carbonell et al., 1995; Toro-Moyano et al., 2013); Pirro Nord, Italy (Arzarello et al., 2007); Pont-de-Lavaud and Lunery-Rosières, France (Despriée et al., 2011); and Happisburgh III, UK (Ashton et al., 2014; Parfitt et al., 2010) have been instrumental in challenging the notion of a hominin absence in Europe pre-800 kya. Happisburgh III has also challenged the notion of early hominin intolerance for harsh climatic conditions. There are however, still clear arguments to be made in regards to the sustainable nature of early forays substantially above the 45°N mark (MacDonald et al., 2012).

A related question concerns the increasingly complex role of *Homo antecessor* in the earliest human occupation of north-west Europe. It is *Homo antecessor* that has been put forward as one of the contenders for the pre-800 kya human presence at Happisburgh III (Ashton et al., 2014). Although their fossil evidence is limited to the Iberian Peninsula, it is possible that a series of short-lived dispersal events by this species above 45°N may have been the cause of the sparse archaeological record in Europe before 800 kya.

The pace and rhythms of early hominin dispersal in Europe are therefore varied and challenging to decipher. What is clear however is that hominin development must have occurred in conjunction with changes in climate and environment. It is the understanding of the specific climatic and environmental challenges to hominin survival in north-west Europe, and potential solutions to those challenges, which forms the focus of this paper.

2. How to survive Pleistocene North West Europe

Delays in the occupation of northern Eurasia, above *c*. 45°N, after the initial dispersals or range expansions of *H. erectus* (*s. lato*) beyond Africa, suggest that a sustained presence in the north presented significant new challenges to Lower Palaeolithic hominins. Modern ethnographic, ecological and climatological studies would suggest that those challenges were principally increased seasonality, lower mean temperatures, contrasting oceanic and continental zones, reduced plant food resources, and more dispersed and clustered animal food resources (Gamble, 1986; Hosfield, 2016; Kelly, 1995; Roebroeks, 2001, 2006). How might these challenges be met? The 'solutions' can be grouped into two broad categories: firstly, increased animal food contributions to the diet, with implications for the reliability of foraging strategies, the sizes of territories and the knowledge required of landscapes and resources, hominin mobility, social group organisation, and technology. Secondly, enhanced insulation, which can be cultural (encompassing some or all of pyrotechnology, whether managed or opportunistic, 'clothing' or other forms of body covering, and shelter) and/or physiological (e.g. elevated BMR [basal metabolic rate], increased muscle mass, body hairs, elevated brown adipose tissue levels; but *cf*. Aiello and Wheeler, 1995; Aiello and Wheeler, 2003).

These 'solutions' can be most easily described as changing hominin behaviours (i.e. increasingly efficient dietary and insulation strategies). Yet our clearest material insights into hominin behaviour (the lithic record) shows relatively little evidence for major changes across the duration of the Lower Palaeolithic (Klein, 2000), and while Acheulean technology may be absent from the repertoire of the earliest Europeans, it already had a long history in Africa and western Asia by the time of those first dispersals into the Mediterranean. We therefore propose three other potential forms of change which may also be key factors in the pre-/post-800kya settlement patterns in northern Eurasia (Table 2), and ~~will~~ explore these within a European framework: (i) changes in the palaeoclimate and palaeoenvironmental context; (ii) changes in hominin life history; and (iii) changes in behavioural plasticity.

Period	**Chronology**	**Sites**
Later Early Pleistocene	*c*. 1.3–0.78mya	Happisburgh III, Lunery-Rosières, Pont-de-Lavaud
Early Middle Pleistocene	*c*. 0.78–0.5mya	Abbeville, Boxgrove, Happisburgh I, High Lodge, Kärlich G, La Genetière, La Noira, Miesenheim, Pakefield, Warren Hill
Later Middle Pleistocene	*c*. 0.5–0.3mya	Beeches Pit, Bilzingsleben, Clacton, Hoxne, Schöningen, Soucy, Swanscombe,

Table 2: Key chronological phases and selected northern European sites (after Ashton, 2015).

2.1 The palaeoenvironmental context

To what extent may changing palaeoclimatic and palaeoenvironmental conditions underpin the changes in scale in the northern European settlement record? Such arguments have been widely explored. Turner (1992) emphasised the changing large carnivore guild around 500kya and the gradual emergence of the 'mammoth steppe' after MIS 12 (Guthrie, 1990), linked to the changing length of glacial/interglacial cycles during the Mid-Pleistocene Transition (Head and Gibbard, 2005). However, many of these models have tended to primarily emphasise long-term trends. While these are undoubtedly important, the emphasis in this paper is upon the daily, seasonal and yearly challenges to hominins: e.g. low winter temperatures, the degree of seasonality, short-term climatic shifts (e.g. on decadal scales), the diversity or homogeneity of habitats at a local scale, and the condition and availability of plant and animal foods across the seasons. These are increasingly well understood through micro-fauna (e.g. Coope, 2006a), palynology, and the multi-disciplinary investigations of key sites (Bigga et al., 2015; García and Arsuaga, 2011; Parfitt et al., 2010; Parfitt et al., 2005; Rodríguez et al., 2011; Urban and Bigga, 2015), enabling us to consider the nature of the hominin life experience 'on the ground'. We are taking this approach not least because while the MIS record emphasises the increasing stability, length, marked oscillations and decreasing temperature of European glacial/interglacial cycles during the Middle Pleistocene, intra-site records reveal that stability is less apparent at the sub-stage scale (Ashton et al., 2008a; Urban and Bigga, 2015) and may also have been less apparent at the scale of a hominin lifetime too. The key question is can we see clear evidence for a shift in hominin environments across the *c*. 800-600kya boundary that might favour a more sustained northern presence?

2.2 Changes in hominin life history

Changing life history may be a second key factor. The current European fossil record suggests an apparent species contrast pre- and post-800-600kya, with *H. antecessor* (Carbonell et al., 1995) replaced by *H. heidelbergensis* (Stringer, 2012) across the chronological division. It may well also be significant that the Sima de los Huesos fossils, dating to *c*. 430kya, are now argued to be early Neanderthals, or closely related to the latter's ancestors (Meyer et al., 2016b). Why might life history be significant? The modern human life history stages (childhood, juvenile, adolescence, adulthood) are associated with the unusual collection of traits which characterise humans: prolonged gestation, growth and maturation, extremely short inter-birth intervals, helpless newborns, a short period of breastfeeding/early weaning, extended offspring dependency, an adolescence growth-spurt, delayed reproduction, and the menopause (Bogin and Smith, 1996; Schwartz, 2012).

Of particular importance to the occupation of the north may be the emphasis in the human model of early weaning: this strategy places infants at risk, as they are unskilled at finding appropriate foods (of sufficient high quality to fuel brain growth, but also suitable for small, deciduous teeth), are essentially defenceless, and can be competing with other adults (Aiello and Key, 2002; Kennedy, 2003). It therefore has notable dietary strategy implications, but it also has significant implications for infant care. Since early weaning is associated with shorter inter-birth intervals, other forms of childcare are required for the 'weanlings', in order to avoid excessive DEE (daily energy expenditure) loads on the large-bodied and large-brained *Homo* females (i.e. normal DEE + gestation/lactation + nursing of ‘weanlings’; Aiello and Key, 2002). This alloparenting can come from grandmothers (e.g. Hawkes et al., 1998) or older siblings, or in the form of increased male provisioning.

As noted above, a change to a fully modern life history would therefore bring costs, but the addition of an adolescence stage can also bring specific opportunities to improve selective fitness. In a broader context, extended growth development would enable socialisation – learning the ‘rules’ of social life (e.g. hierarchies of food access, recognising the moods and emotions of individuals), made complicated both by larger communities, as predicted by neocortex size and the social brain hypothesis (e.g. Gamble et al., 2014), and perhaps also by periods of individuals’ absences, arising from dispersed resource distributions and social fission-fusion in the seasonal mid- and high-latitudes (Couzin and Laidre, 2009). Kennedy (2003) has argued that adolescence would enable youngsters who were close to maturity to observe and participate in the social, sexual and infant-care practices that are critical to success in adulthood. Bogin and Smith (1996) have similarly emphasised adolescence as a period when parenting skills could be practiced, perhaps resulting in the greater survival of their own offspring later in life. MacDonald (2007) has stressed the knowledge demands of a hunting life, from animal behaviour and their signs, to animal-animal and animal-plant relationships, to the topography, vegetation and seasonality of the environment. Foraging for plant resources, while stationary, would also require a diverse set of ecological knowledge. Adolescence would offer an opportunity to develop much of this base-line knowledge, and the associated skills – not least because the nature and content of learning will vary with age, as both the mind and the body develops (MacDonald, 2007). Thus a modern human model of life history might produce sub-adults and adults with the skills and knowledge to meet the social, ecological and technological challenges of the north.

We can discuss life history and its evolution amongst extinct hominins (Fig. 1) because of the evidence for strong correlations between a range of life history traits: brain size, body size, age at sexual maturity, age at first birth, gestational length, lifespan, and dental development (Kennedy, 2003). The critical question from a European Lower Palaeolithic perspective would therefore seem to be: can we detect any evidence for adolescence in particular, and a truly human model of growth and development in the hominins of the late Early Pleistocene and early Middle Pleistocene?

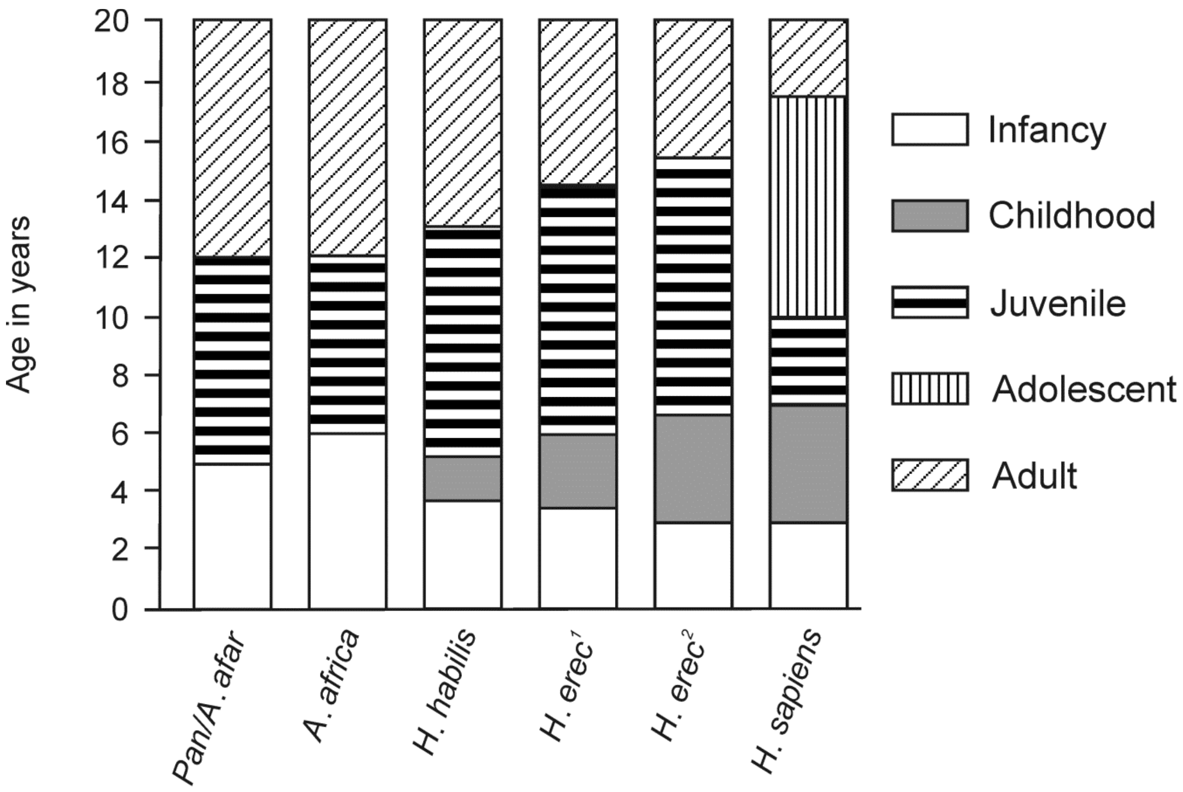

Fig. 1: Inferred life history stages for selected hominin species (Bogin, 1999: fig. 4.9). H. erec.^{1} = early *H. erectus* (adult brain sizes of 850-900cc); H. erec.^{2} = late *H. ~~omo~~ erectus* (adult brain sizes upto 1100cc); A. afar = *A. afarensis*; A. Africa = *A. africanus*.

2.3 Changes in behavioural plasticity

In addition to hominin genotypic adaptations to the north-west European palaeoclimatic and palaeoenvironmental conditions (although some traditionally considered “cold-adapted” hominin traits have recently been questioned (e.g. Rae et al., 2011) hominin range expansion must also have been characterised by phenotypic adaptations to external factors. Archaeologically speaking it is the phenotypic adaptations of behaviour that are the most visible indicators of behavioural plasticity.

It has been suggested for some time that organisms that are both mobile and long-lived are less likely to adapt to local conditions through the selection of genetically based traits (Potts, 1998, 2013; van Schaik, 2013). In effect, the suggestion is therefore that when such organisms encounter variable climatic conditions they are more likely to adapt to those conditions at a phenotypic level rather than a genotypic one (van Schaik, 2013). However, it would also appear that the plastic behavioural strategy may fail if local environments change too rapidly (Van Buskirk, 2012; van Schaik, 2013). This in turn suggests that behavioural plasticity can only carry a species so far in its effectiveness in negotiating novel or rapidly changing environments.

Another important aspect to consider in regards to behavioural plasticity are the links to cognitive capacity and brain size (van Schaik, 2013). From a primate perspective behavioural plasticity derives from learning through mental mechanisms linked to varying degrees of cognitive complexity (Shettleworth, 2010). These processes have been tightly linked to brain size and therefore suggest that behavioural plasticity should be included in the costs of supporting larger brains (van Schaik, 2013). Therefore, it follows that the degree of behavioural plasticity present within an organism may correspondingly be limited by overall brain size. Within the hominin fossil record it has been suggested previously that there are recognisable step changes in hominin brain size (Maslin et al., 2014; McNabb and Cole, 2015; Shultz et al., 2012; Fig. 2) at *c*. 1.8mya, 1mya, 400–200kya, and 100kya, which punctuate periods of stasis in hominin brain expansion. Shultz et al. (2012) further highlight that the increase in hominin brain size *c*. 400–200 kya may be as a result of migrating hominin species into Eurasia as the step changes are not mirrored in Africa. However, from Figure 2 it could be cautiously suggested (based on the limited sample available) that there may also be an increase in hominin brain size within *Homo heidelbergensis* *c*. 800–600 kya.

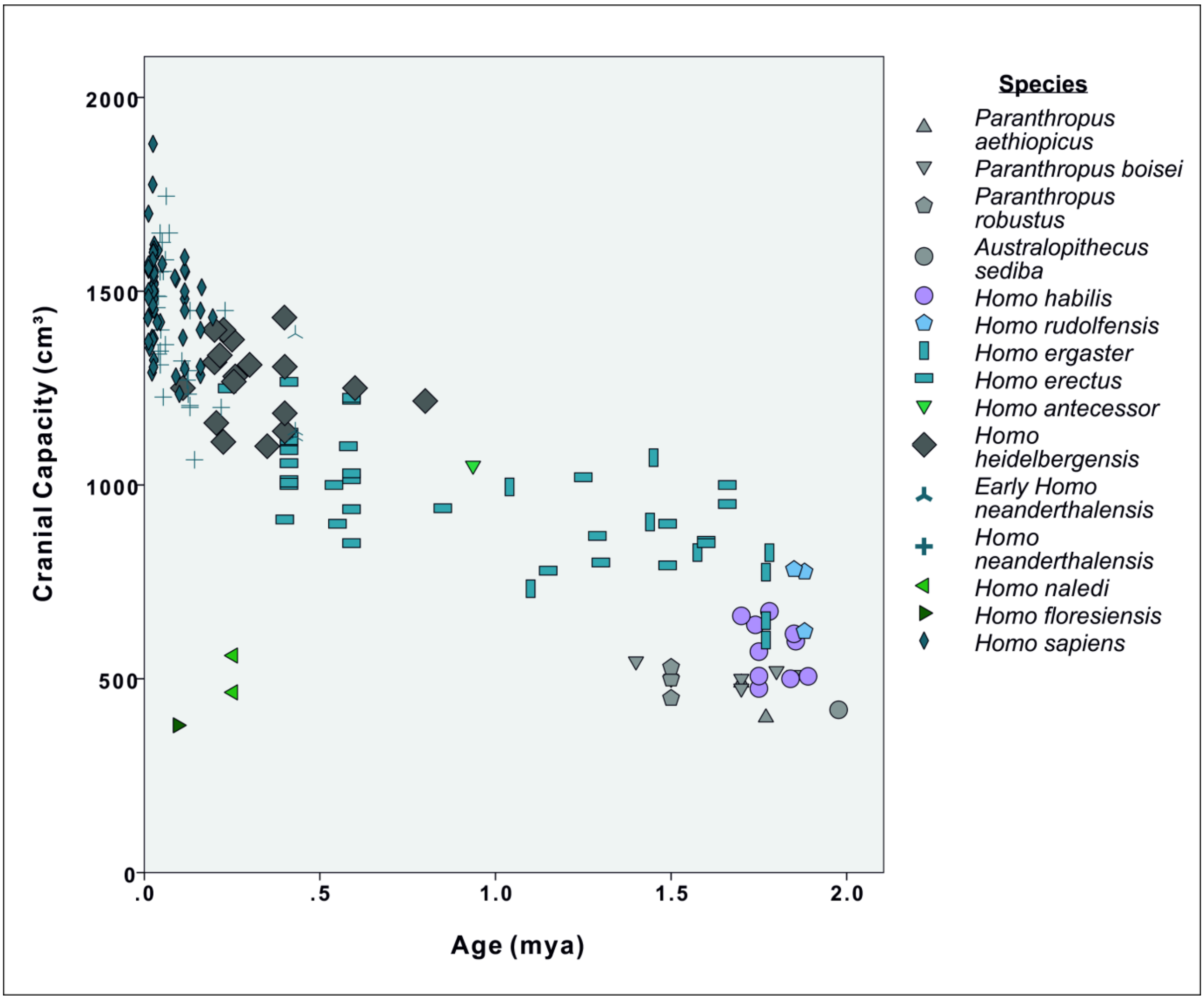

Fig. 2: ~~Showing h~~Hominin cranial volumes (cm^3) ~~at a~~over the last 2myr ~~a (A) and 1mya (B) scale. The fossil specimens and species are divided by location~~ (data after Berger et al., 2015; Brown et al., 2004; Shultz et al., 2012; Thackeray, 2015).

Indeed, if behavioural plasticity and brain size are linked then there is a possibility that a more sustained hominin presence in north-west Europe may require a threshold level of both plasticity and brain size. Therefore, examining the fossil and behavioural signatures of Pleistocene hominin activity in north-west Europe against the context of changing environmental conditions should provide some insight as to the degree of plasticity present, and whether an increase in behavioural plasticity coinciding with an increase in brain size is significant enough of an advantage to lead to a more sustained hominin presence after *c*. 600kya.

3. Discussion

Following the three broad themes presented above, we will now examine and review the evidence for each.

3.1 Palaeoenvironment

Kahlke et al. (2011) argue that 1.2–0.9mya (the late Early Pleistocene) was a period of less uniform climate cycles, varying in both duration and intensity. These climate cycles would have been associated with new mammal communities, increasing varieties of habitats, large riverine systems, and relatively mild and humid conditions, especially in the Mediterranean and the west. As Kahlke et al. (2011) have previously argued, these conditions seemingly favoured the expanding occupation of the Mediterranean zone at sites such as Barranco León and Fuentenueva-3 (Orce), Sima del Elefante (TE9), Pont-de-Lavaud, Lunery-Rosières, Le Vallonnet III (although the character of the lithic assemblage has been strongly critiqued; Roebroeks and van Kolfshoten, 1994) and Monte Poggiolo (Leroy et al., 2011), while dispersal into the north was restricted to favourable interglacials of low seasonality and high habitat diversity, for example at Happisburgh III (Parfitt et al., 2010). By contrast, the period after 0.9mya was increasingly controlled by 100kyr periodicity, with longer and relatively stable climatic intervals, progressive temperature decline and increasing aridity, marked oscillations between highly contrasting landscapes, greater seasonality, and increasingly specialized mammal communities (Kahlke et al., 2011: 1389). These changes ~~become~~ became especially marked after *c*. 500kya (Berger and Loutre, 1991; Lisiecki and Raymo, 2005). Perhaps critically from the perspective of hominin distribution and dispersal, these changes were accompanied by regional shifts in characteristic habitat types (Table 3).

Region	Prevailing habitats (inferred from large mammal communities)		
Apennine Peninsula	High variety of open / forested habitats	Open woodland / steppe	
Iberian Peninsula	Open savannah / lightly forested habitats	Open woodland, tree savannah / steppe	
Western Europe	High variety of open / forested habitats	Woodland / steppe	Variety of open to forested habitats
Northwest Europe	Woodland	Woodland with open patches / mixed habitats	Steppe / woodland
Central Europe	High variety of open / forested habitats	Steppe / woodland with open patches	Steppe-tundra / woodland
Eastern Europe	High variety of forest steppe / open steppe habitats	Open steppe / forest steppe	Steppe-tundra / woodland
Chronology (mya)	1.2 1.0	0.8 0.6	0.4

Table 3: Prevailing habitat characteristics in Europe over the last 1.2mya (re-drawn after Kahlke et al., 2011: Fig. 6).

What might these regional differences have meant in terms of hominin life on the ground? Can we see any evidence of significant change over time? Offering a northern Iberian perspective from Atapuerca, Rodríguez et al. (Rodríguez et al., 2011) have argued for an absence of harsh conditions across the long time-span of the Sima del Elefante, Gran Dolina, and Galería sites. This was based on a wide range of evidence: small vertebrates (amphibians, squamates and small mammals), large mammals, and vegetation (Table 4). Rodríguez et al. (2011) conclude that these prevalent temperate conditions may be associated with a continuous early hominin presence prior to *c*. 0.5mya, and perhaps reflect a *H. antecessor* preference for warmer, less variable conditions (see also Agustí et al., 2009).

So what changes in terms of hominin habitats? The answer from south-western Europe, using Atapuerca as a case study, may be not much. Rodríguez et al.'s (2011) admittedly tentative environmental reconstructions (Table 4) suggest little change between the Early and Middle Pleistocene, while Garcia & Arsuaga's (2011) analysis of the Sima de los Huesos evidence suggests a savannah-like open woodland, dating to *c*. 430kya on the basis of the most recent dating (Arnold et al., 2014). But what is the view from the north?

Evidence	**Key Patterns (Early & Middle Pleistocene)**	
Small vertebrates	• Significant woodland component in herpetofauna • Small mammals suggest moist, open habitats	
Large mammals	• All of temperate affinity • None unequivocally indicating cold or arid environments	
Vegetation	• Continuous presence of Mediterranean taxa & mesic trees • One possible cold steppe landscape phase	
Palaeotemperature (amphibian & squamate assemblages)	• Always warmer than Burgos today • “Cold”/“warm” period differences of only *c.* 2°C	
Annual precipitation	• 750mm (dry)–1049mm (humid), compared to *c.* 570mm in present	
Environment types	**Early Pleistocene** • Mediterranean open woodland • Open woodland and steppe • Open arid (?) • Open woodland and moist meadows • Temperate open woodlands and meadows with lagoons	**Middle Pleistocene** • Humid temperate open woodland • Mediterranean open woodland • Moist meadows with scattered trees • Open woodland and meadows • Steppe

Table 4: Inferred environments at Atapuerca in the Early and Middle Pleistocene (after Rodríguez et al., 2011: table 9).

There is evidence of a tolerance of cooler conditions as a whole (e.g. Hosfield, 2011: table 6), gained from palaeotemperature estimates and environmental descriptors from a range of key northern sites with evidence of hominin activity. These offer a valuable perspective on possible changes in hominin tolerances and/or preferences in northern Europe across the *c*. 800-600kya 'boundary' (Table 5). Summer and winter palaeo-temperatures reveal no major changes across the boundary as a whole, although there is perhaps some evidence for slightly harsher conditions in the MIS 13/15 sites, in contrast to the MIS 11 sites and Pakefield. This might be significant, and slightly counter-intuitive, as MIS 13 sees a marked increase in the number and size of sites across northern Europe (e.g. examples in Tables 5 & 6, plus Warren Hill, Highlands Farm, Valdoe, Kent's Cavern, Abbeville, Miesenheim, and Kärlich G; see also Ashton, 2015).

Site	**T_{min} (°C)**	**T_{max} (°C)**	**Evidence[1]**	**Age (MIS)**	**Source**
Early Pleistocene					
Happisburgh III (Bed E)	-3 – 0	+16 – +18	Coleoptera	Late 25 or late 21	(Ashton and Lewis, 2012; Parfitt et al., 2010)
Early Middle Pleistocene					
Pakefield (Bed Cii–Ciii)	-6 – +4	+17 – +23	Coleoptera	17 or later 19	(Ashton and Lewis, 2012; Coope, 2006b)
Boxgrove (Unit 4c & Freshwater Silt Bed ≈ Units 4b & 4c)	-4 – +4	+15 – +20	Ostracods (MOTR) & Herpetofauna (MCR)	13	(Ashton and Lewis, 2012; Holman, 1999; Holmes et al., 2010)

Happisburgh I (Organic Mud)	-11 – -3	+12 – +15	Coleoptera	13?	(Ashton and Lewis, 2012; Coope, 2006b)
High Lodge (Bed C1)	-4 – +1	+15 – +16	Coleoptera	13?	(Coope, 2006b)
Waverley Wood (Channel 2, Organic Mud)	-	+10 – +15	Coleoptera	13 or 15	(Coope, 2006b; Shotton et al., 1993)
Brooksby (Redland's Brooksby Channel)	-10 – +2	+15 – +16	Coleoptera	13 or 15	(Coope, 2006b)
Later Middle Pleistocene					
Barnham (Unit 5c; HoII)	-	+17 – +18	Herpetofauna	11c	(Holman, 1998)
Hoxne (Stratum D~~[5]~~; HoIIIa~~[6]~~)	-10 – +6	+15 – +19	Coleoptera	11c	(Ashton et al., 2008a; Coope, 1993)
Bilzingsleben II	-0.5 – +3	+20 – +25	Mollusca & ostracods[2]	11	(Mania, 1995; Mania and Mania, 2003)
Schöningen 13 II-4	-4 – -1	+16	Mollusca & ostracods	9	(Urban and Bigga, 2015)
Present Day Comparisons					

East Anglia (present day)[3]	-0.7 – +6.9	+14.2 – +18.0	-	-	-
Bilzingsleben (present day)[4]	-3.3 – +2.0	+12.4 – +22.7	-	-	-

Table 5: Winter and summer temperature estimates for Early and Middle Pleistocene British and German sites (with selected present day equivalents for reference). [1]Sensitivity tests on coleoptera-based MCR procedures suggest that winter temperature estimates are usually too warm (Pettitt and White, 2012: 35). [2]The specific source of the palaeo-temperature estimates is not stated, but the fauna includes molluscs and ostracods; [3]East Anglian data based on Met Office annual mean seasonal temperatures (1910–2016; http://www.metoffice.gov.uk/pub/data/weather/uk/climate/datasets/Tmean/date/East_Anglia.txt); [4]Bilzingsleben data based on Deutscher Wetterdienst (German Weather Service) monthly mean January and July temperatures (1951–2017; Erfurt-Weimar station; https://www.dwd.de/DE/leistungen/klimadatendeutschland/klarchivtagmonat.html)

Site	**Palaeoenvironmental description**	**Age (MIS)**	**Source**
Early Pleistocene			
Pont-de-Lavaud	Closed deciduous forest; warm, wet climate	30	(Messager et al., 2011)
Happisburgh III (Unit C)	Cool temperate; heathland & coniferous forest	Late 25 or late 21	(Ashton and Lewis, 2012)
Happisburgh III (Units D & E)	Cool temperate; dominated by coniferous forest	Late 25 or late 21	(Ashton and Lewis, 2012)

Early Middle Pleistocene			
Pakefield (Units Aiv–Ciii)	Mediterranean-type climate; marshy ground with reed-beds & alder carr, surrounded by deciduous forest	17 or later 19	(Ashton and Lewis, 2012)
Happisburgh I (Organic Mud–Organic Silt Sand)	Cool climate; marshy edge of slow-flowing river, with surrounding coniferous forest	13?	(Ashton and Lewis, 2012)
High Lodge (Units B2–C2)	Cool-temperate climate; marshy ponds, heath & grassland on river floodplain, surrounded by pine & spruce forest	13?	(Ashton and Lewis, 2012)
Boxgrove (Unit 4b)	Coastal mudflats, with occasional drying out & spread of grassland	13	(Ashton and Lewis, 2012)
Boxgrove (Unit 4c & Q1B pond deposits)	Temperate climate, with cooler winters than present; grassland, scrub & mixed woodland, with spring-fed pools	13	(Ashton and Lewis, 2012)
Boxgrove (Unit 8)	Interstadial environment	Later 13–early 12	(Ashton and Lewis, 2012)
Boxgrove (Unit 11)	Periglacial, with ameliorations in climate	Later 13–early 12	(Ashton and Lewis, 2012)
Later Middle Pleistocene			
Bilzingsleben II	Fully temperate, with subcontinental influences; mixed oak woodland & shrub associations, alternating with steppe meadows	11	(Mania and Mania, 2003)
Barnham (Unit 5c;	Temperate climate; mix of grassland &	11c	(Ashton and

HoII)	deciduous woodland on edge of slow-flowing river		Lewis, 2012)
Beeches Pit (Unit 4; HoIII)	Fully temperate environment; spring-fed pools with deciduous woodland	11c	(Ashton and Lewis, 2012)
Beeches Pit (Unit 3b; HoIIb–c)	Temperate climate; shallow to stagnant pools with calcareous grassland and surrounding open woodland	11c	(Ashton and Lewis, 2012)
Hoxne (Unit B1)	Cooler temperatures (*cf*. units D & E); probable birch & pine forest; some grassland areas	11a	(Ashton and Lewis, 2012)
Swanscombe (Lower Loam; HoIIb–c)	Grassy floodplain with shallow pools & occasional flooding; mixed oak forest nearby, with hazel & alder	11c	(Ashton and Lewis, 2012)
Schöningen 13 II-4	Mosaic swamp, with reed-like and sedge vegetation; regional context: highly continental dry steppe/open forest; tree taxa dominated by pine & birch	9	(Stahlschmidt et al., 2015; Urban and Bigga, 2015)

Table 6: Palaeoenvironmental reconstructions for Early and Middle Pleistocene British sites and German sites.

The general trend after MIS 13 is towards full or cool-temperate environments, mixing deciduous or coniferous woodland with open grass and/or heathland, and water sources (Table 6). As Bigga et al. (2015) have noted at Schöningen, such environments provide a diverse range of potential plant foods, meeting both nutritional (e.g. vitamin C in pine and birch bark, berries of common bearberry, European elder, raspberry, and leaves of *Ranunculus* and *Chenopodium*) and seasonal needs (Figure

3). Evidence of animal butchery also suggests few changes in preferred prey across the *c*. 800-600kya boundary, or in comparison between northern and southern Europe (Table 7).

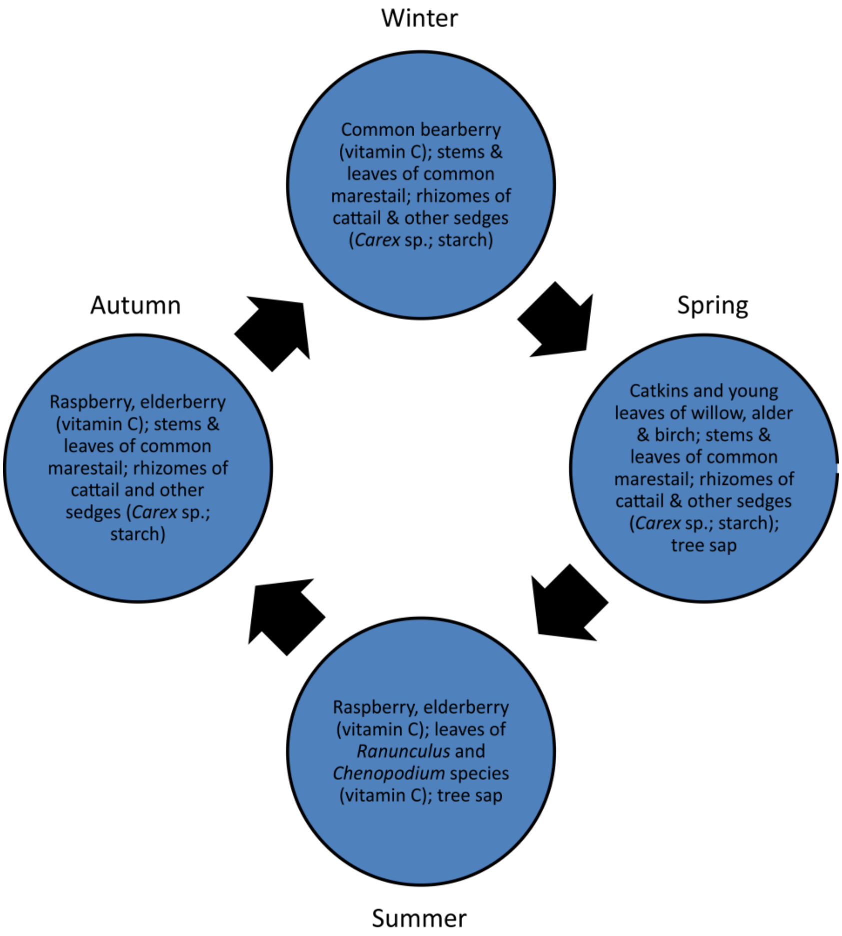

Figure 3: Seasonal variations in selected potential plant food sources identified at Schöningen 13 II-4 (Bigga et al., 2015).

Period	**Species**	**Butchery Evidence**	**Sites**
Early Pleistocene	*Bison* sp. *B. menneri* *B. voigtstedtensis* *C. elaphus* *C. s.l. nestii vallonnetensis*	Defleshing; disarticulation; dismemberment; evisceration; filleting; skinning	Gran Dolina TD6 (Saladié et al., 2011) Sima del Elefante (Huguet et al., 2013)

	Cervid sp. *Cercopithecidae* *Eucladoceros* *Equus sp.* *Hippopotamus* *S. etruscus* *S. hundsheimensis* *U. dolinensis* *V. praeglacialis*		
Early Middle Pleistocene	*Bos* or *Bison* sp. *C. capreolus* *C. elaphus* *E. ferus* *S. hundsheimensis* *U. deningeri*	Cut-marks; defleshing; dismemberment; filleting; marrow bone breakage; skinning	Boxgrove (Bello et al., 2009; Parfitt and Roberts, 1999) Happisburgh I (Ashton et al., 2008b) Westbury (Andrews and Ghaleb, 1999)
Later Middle Pleistocene	*Bos* or *Bison* sp. *C. elaphus* *E. ferus*	Boning; cut-marks; defleshing; dismemberment; filleting; marrow bone breakage; skinning	Barnham (Parfitt, 1998) Schöningen (Van Kolfschoten et al., 2015a; Voormolen, 2008) Hoxne (Stopp, 1993)

Table 7: European sites with butchery evidence.

What is perhaps more noticeable are the conditions at the Early Pleistocene sites of Happisburgh III and Pont-de-Lavaud, and at the MIS 17/19 site of Pakefield. The latter two sites both support a model of temporary northern excursions in line with favourable conditions. As other authors have previously noted (Parfitt et al., 2010), Happisburgh III stands out in the pre-800-600kya record, albeit within a very small sample of early northern sites.

Overall, combining general palaeo-environmental trends and the conditions at hominin sites suggests that the post-800-600kya expansions in the occupation of the north occur at an intuitively odd time – before the favourable MIS 11 interglacial but after the milder conditions of the later Early Pleistocene.

3.2 Life history

Turning away from environmental conditions, can we detect any evidence for childhood and adolescence, and a truly human model of growth and development, in the European Lower Palaeolithic? Of critical importance in beginning to resolve this question for Europe has been the *H. heidelbergensis* and *H. antecessor* fossil material from the Sima de los Huesos and Gran Dolina localities at Atapuerca (Bermúdez de Castro et al., 1997; Carbonell et al., 1995; these analyses pre-dated the recent re-attribution of the Sima de los Huesos material as possible early Neanderthals). Initial analysis of the dental material from TD-6 hominins 1 & 3 and Sima hominin 18 suggested that both European species are similar to modern humans in their dental development, implying both prolonged maturation and new life history stages (childhood and adolescence; Bermúdez de Castro et al., 2003), although *H. antecessor* is not as derived in some respects (e.g. delayed M3 calcification; Bermúdez de Castro et al., 1999). By extension that would also suggest relatively short birth intervals, high rates of postnatal brain growth, extended offspring dependency, marked adolescent growth spurt, and delayed reproductive cycles. Expanded analysis of enamel formation rates for various species of *Homo* also suggested prolonged dental growth in *H. antecessor* and *H.*

heidelbergensis (Ramirez Rozzi and Bermudez de Castro, 2004). Although their mean crown formation times were concluded to be shorter than in Upper Palaeolithic–Mesolithic *H. sapiens* samples, they were slower than those of Neanderthals, whose crown formation was estimated to be 15% quicker than modern humans. The data also suggested only slightly slower growth rates in *H. heidelbergensis* (n=106; 21 individuals) compared to *H. antecessor* (n=8; 4 individuals; *ibid*: fig. 1).

However, these interpretations have been challenged to some extent by Robson and Wood (2008), who have argued that *H. antecessor's* crown formation rates are not modern human-like (although the tooth eruption timings are). They also noted that the crown formation rates of *H. heidelbergensis* are more akin to *H. antecessor* than modern humans, a view supported by Rozzi & Bermudez de Castro's data (2004: fig. 1). Contrasts with *H. sapiens* are also evident in Neanderthals' more rapid dental development patterns (Ramirez Rozzi and Bermudez de Castro, 2004; Smith et al., 2007), although suggested differences between those two species' overall rates of growth have recently been challenged (Rosas et al., 2017). Overall Robson and Wood (2008) conclude that life history shifts are likely to have been piece-meal (with body mass shifts pre-dating dental developments; see also Krovitz et al., 2003), and also that dental development rates and timings do not always correlate well with other life history variables.

These various models and data suggest that European Lower Palaeolithic hominins, whether *H. antecessor* or *H. heidelbergensis*, are likely to have adopted at least a human-like model of reproduction, growth and development, although childhood may not have been as prolonged as in *H. sapiens*. However, it is worth considering whether life history may have become more human-like with *H. heidelbergensis* (i.e. more prolonged maturation and more extended childhood and adolescence stages), given the overlaps in endocranial volume between *H. sapiens*, *H. neanderthalensis* and *H. heidelbergensis*, but not *H. antecessor* (Robson and Wood, 2008: fig. 6), and the delayed M3 calcification and long I2 and C crown formation times in *H. antecessor* (Bermúdez de

Castro et al., 2003; Bermúdez de Castro et al., 1999). As noted above the human life history pattern offers the opportunity to learn skills and experiences that may have been critical in the seasonal latitudes of Europe (e.g. the extended practice argued to be required by prepared platform techniques; Stout et al., 2014). But differences between *H. heidelbergensis* and *H. antecessor* are likely to have been relatively small and it is not immediately obvious as to how and why small extensions in the childhood and adolescence stages, and other associated life-history changes, would facilitate the post-600kya expansion in northern Europe. In many ways, the suggested appearance of an adolescence stage in *H. antecessor*, and perhaps also *H. erectus* (Krovitz et al., 2003; but *cf*. Bogin and Smith, 1996, and Fig. 1) looks more significant, and may well relate to the earlier, first excursions into southern Europe.

3.3 Behavioural plasticity

Within the Lower Palaeolithic record, the biface represents a shift to a multi-functional tool that is easily transportable and adaptable (through resharpening and reworking) to a variety of situations (Moncel et al., 2015). There are a range of additional behavioural and cognitive changes that biface manufacture represents, including indications of greater planning depth, not only in tool production, use and curation, but also a more liberated attitude to landscape use and resource acquisition that potentially underpinned an expansion in group size and more complex group dynamics (Gowlett et al., 2012). Much of these additional bonuses may come from the acquisition of a sustained ability for abstract thought at a species level (Cole, 2015a; Cole, 2015b) contributing to a greater degree of sustained behavioural plasticity as brain sizes increase (Fig. 2). Therefore, tracking the earliest appearance of biface sites in north-west Europe could provide a useful insight into hominin behavioural changes. We follow Ashton (2015) in associating the bifaces of north-west with *Homo heidelbergensis*, as demonstrated at sites such as Boxgrove and Arago (Moncel et al., 2015).

Moncel et al. (2015) have produced an excellent review of biface manufacture in north-west Europe from *c*. 700–600kya which suggests a more extensive biface presence in north-west Europe from 500kya (Table 8).

Age (MIS)	**Contexts**	**Raw Materials**	**Characteristic Biface Morphology**	**Additional Flake Tools**	**Sites**
17-13	Diamicton; fluvial gravel; fluvial sand; fluvial silts; lagoonal silts; palaeosol	Andesite; siliceous; flint; quartzite	Pointed (incl. crude forms); ovate; biface-cleaver; cordiforms	Denticulates; notches; scrapers	Boxgrove (Q1B); Brandon Fields; Happisburgh I; High Lodge (Bed E; Sands & Gravels); La Noira; Maidscross Hill; Warren Hill; Waverley Wood
12-10	Gravel; slope deposit; fluvial sand; fluvial gravel; tufa; pool; colluvial; alluvial	Flint	Pointed (incl. crude forms); backed biface; cleaver; cordiform; ovate; sub-triangular	Denticulates; endscrapers; notches; scrapers; pebble tools; retouched flakes	Cagny-La-Garenne I (Cxb, Cxv, Lg, Lj & Ca assemblages); Cagny-La-Garenne II (13, 14 & J assemblages); Rue De Cagny (Series 3); La Celle; Barnham; Elveden; Beeches Pit; Swanscombe (LMG & UMG); Hoxne (Upper & Lower Industries); Ferme de l'Epinette (MS assemblage); St-Pierre-lès-Elbeuf

Table 8: Summary table of early north-western biface sites, context, raw material, biface form and additional flake tool types (data from Moncel et al., 2015).

When looking at the early biface assemblages of north-west Europe (Table 8) it can be seen that there is a diversity of biface form within the assemblages and the sites tend to cluster around fluvial locations, often at the convergence of ecological zones (Table 6). This is perhaps not surprising as this pattern of hominin site location has been repeated throughout the Old World, probably reflecting the preference of hominins in exploiting a range of resources in the vein of the generalist (Grove, 2011; Potts, 2013). What is interesting is a pattern noticed by Moncel et al. (2015), that the early biface sites in north-west Europe tend to have a relatively low ratio of bifaces to other tools when compared to comparable sites in the Levant or Africa (although there are a few notable exceptions, e.g. Boxgrove). While there are taphonomic complications to this pattern (e.g. variable collecting histories), two potentially key trends have been highlighted (Moncel et al., 2015):

Firstly, the Early Middle Pleistocene sites (MIS 17-13) tend to have not only a range of biface forms made from both core and flake blanks, but they are also characterised by a range of raw material exploitations depending on local availability. This may indicate that the Early Middle Pleistocene biface makers were not locked into a single raw material but flexible enough in cognition and experience to work a range of lithologies when necessary. Alternatively, of course, it may equally suggest a limited ability for planning depth with a more immediate focus on utilising suitable raw materials as they occur in the local landscape. In addition, raw material seems to have differing impacts on the degree of shaping and size of bifaces present between southern British and northern French sites which may go some way to explaining the difference in artefact morphology. However, a common occurrence between these sites are the dual compositions of biface assemblages consisting of thick, crudely pointed bifaces with irregular cutting edges and more comprehensively worked bifaces with regular cutting edges and invasive removals.

Secondly, the late Middle Pleistocene (MIS 12-10) assemblages in contrast seem to be characterised by higher proportions of thinner bifaces with fine retouched edges, although overall shaping is still varied within assemblages. Across the Table 8 sites large flakes could have been produced for blank production, but it would appear that few were. This may in turn reflect the suitability and increasing visibility of good flint sources in the landscape as well as reflect the hominins' ability to read and interpret the landscape around them. Another possible change during the late Middle Pleistocene in Europe (in contrast to the early Middle Pleistocene) is that the biface sites may be supported in the toolkit by a larger range of flake tool types (Table 8), although it is acknowledged that collection biases and varying typological schemes also complicate this interpretation.

Certainly, the patterns of hominin behaviour seen in the early biface sites of north-west Europe are diverse, but they tend to be explained in terms of the differences in local raw material and overall site function even if there are broad similarities in the shaping processes in biface manufacture (Moncel et al., 2015). We would suggest that these differences and similarities in biface shaping are probably more a consequence of local technological and functional decisions rather than cultural factors at this time.

Nonetheless the European biface package would also seem to suggest a range of additional technological developments – although it is not the position here that they are European innovations or that the biface per se enabled northern dispersals. Rather, it is the overall suggested behavioural package that may have facilitated the sustainable tipping point for hominin dispersal into north-west Europe. Preservation records are difficult for non-lithic technologies but there are preserved wooden spears from Clacton *c*. 400 kya (Warren, 1911) and spears and bone tools from Schöningen *c*. 300–337 kya (Richter and Krbetschek, 2015; Van Kolfschoten et al., 2015b). While recent palaeogenetic evidence raises the possibility that these artefacts may be the preserve of a later speciation event (Meyer et al., 2016a), the mosaic character of Middle Pleistocene hominin evolution combined with the Boxgrove puncture wound evidence supports a position that the early biface makers of north-west Europe may have had an extensive lithic and non-lithic tool kit including spears.

In addition, hints of hide processing can be seen in the elaborate scrapers from High Lodge, Warren Hill, Brandon Fields and Maidscross Hill (Moncel et al., 2015) which would presumably indicate a possible use for them as clothing or shelter components. However, direct evidence for such behaviour is sadly lacking. It is also clear that the later biface-making hominins had the controlled use of fire from well-known sites such as Beeches Pit, Ménez Drégan and possibly Aroeira at *c*. 400 kya (Daura et al., 2017; Gowlett, 2006; Molines et al., 2005; Preece et al., 2006). Although some argue that these are isolated instances of controlled fire use in Europe (Roebroeks and Villa, 2011) they are supported by dates for controlled fire use in other parts of Old World since *c*. 800 kya at least (Goren-Inbar et al., 2004).

The biface itself has often been seen to represent something more than just a functional tool with explanations varying from butchery, mechanisms of sexual selection and aesthetic markers to cultural mediators and objects used to negotiate the landscapes and social-scapes of the Acheulean world (Gamble, 1998; Hopkinson and White, 2005; Kohn and Mithen, 1999; Machin et al., 2007; Machin and Mithen, 2004; McPherron, 2000; Porr, 2005; Saragusti et al., 1998; Wenban-Smith, 2004; White, 1998; Wynn, 1995). We agree with aspects of the above and emphasise again that it is not the biface per se that allowed hominins to have a more sustained presence in north-west Europe, but perhaps the full behavioural package that accompanied biface manufacture.

Why then did it take so long for biface makers to enter north-west Europe when there is clearly evidence for these artefacts stretching back to 1.7 million years ago in Africa (Diez-Martin et al., 2015) and first appearing in south-western Asia soon after (Pappu et al., 2011)? We suggest here that not only do you need the biface package (with all the social and technological benefits that includes) but you also need a threshold level of behavioural plasticity that is tied to a brain size of over 1100cm^3 at a sustained species level for hominin populations to persistently survive the difficulties of the European north-west. Since Moncel et al. (2015) and Table 8 demonstrate that bifaces are present in Europe from at least *c*. 700 kya, we suggest that this plasticity package must have been present across the early/late Middle Pleistocene boundary (MIS 13/12).

4. Conclusion

Our interpretation of the palaeoenvironmental (life on the ground) and palaeoanthropological (life history) records from north-western Europe across the *c*. 800-600kya period has struggled to find a clear pattern of changing conditions before and after this 'boundary'. By contrast, the archaeological evidence does highlight the appearance of the biface by *c*. 700kya, although it does not become widespread until MIS 13. The status of this possible behavioural boundary is newly noteworthy in light of the recent palaeo-genetic studies that have pushed back the date of the last common ancestor between modern humans and Neanderthals to *c*. 700 kya (Meyer et al., 2016a). This makes the apparent step-change in the European archaeological record ever more intriguing. Perhaps such changes may simply relate to the appearance of a new species (*H. heidelbergensis?*) able to cope with the rigours of the north-west, although it remains uncertain as to whether such a species is an *in situ* development or a dispersal into Europe from elsewhere.

However, there may be a subtler and more nuanced pattern to the archaeological record, reflecting a multi-phased hominin occupation of north-west Europe, which we dub here the 'punctuated long chronology' (Table 9), which builds on the modified short chronology (Dennell and Roebroeks, 1996). The first phase, contemporary with the pre-1 million year flake and core occupations of the southern European zone exemplified by Dmanisi, Orce and Atapuerca, is characterised by northern absence. Shortly after 1 million years ago there would appear to be small scale, fragmented dispersals of hominins further north into cooler climates such as at Happisburgh III, equipped with a flake and core lithic tool kit. This is succeeded by the appearance of biface-producing hominins between *c*. 700-500kya, possibly originating from regions outside Europe. These biface-makers had a varied lithic and organic tool kit, incorporating the behavioural plasticity package within a broad geographic range, but would still seem to be limited in terms of overall population numbers. This in turn may reflect the continuing challenges of a hominin population adapting to the unique conditions of Pleistocene north-west Europe. We suggest that this second phase of small-scale, biface-making populations, although important, has tended to be over-emphasised in interpretations of the north-west European Palaeolithic record due to the quality of preservation at occasional key sites such as Boxgrove. In contrast, we suggest here that the major behavioural change (the plasticity package) occurs at a species level, leading to demographic growth, during a third phase after MIS 12. This can tentatively be supported by the changing richness, and diversity in tool kits, of the artefactual record (e.g. the terrace archives of the Thames, Solent and Somme; Ashton and Hosfield, 2010; Ashton and Lewis, 2002; Tuffreau and Antoine, 1995) and evidence for cooler climate tolerances (e.g. Hoxne and Cagny-la-Garenne). Perhaps most tantalisingly, such a shift might also map onto the latest palaeogenetic timings for the origins of the early Neanderthals at around *c*. 430kya (Meyer et al., 2016a). Further evidence is certainly need to test this hypothesis, and we suggest an enhanced understanding of the quantities of artefacts at different periods, normalised with reference to sample biases and site taphonomy (e.g. Ashton and Hosfield, 2010; Ashton and Lewis, 2002), as one possible approach.

Phase	**1**	**2**	**3**	**4**
Summary	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 1mya**	**c. 1mya-700kya**	**c. 700-500kya**	**c. 500-300kya**
Archaeological signature	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 10000s of artefacts), with multiple large sites
Context	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, with potential organic tools	Flake and pebble tools, with potential organic tools	Bifaces and flake tools (limited range), with demonstrated	Bifaces and flake tools (expanded range), with demonstrated

			organic tools	organic tools
Human Remains	Very occasional	Occasional	Occasional	Occasional, but with abundant remains at individual sites

Table 9: A punctuated long chronology for the hominin occupation of Europe.

Acknowledgements:

The ideas in this paper benefitted greatly from the AHRC-funded Network meeting "Coping with climate: the legacy of *Homo heidelbergensis*", paper presentations at the Royal Anthropological Institute conference "*Anthropology, Weather and Climate Change*" and the *Palaeolithic-Mesolithic* 2016 meeting at the British Museum: we thank all those who attended and commented on our ideas. We are also grateful for the thoughtful comments provided by the two anonymous reviewers. All remaining ideas and errors are our own.

Funding:

This work was supported by the Arts & Humanities Research Council (grant number: AH/N007514/1).

References:

Agustí, J., Blain, H.A., Cuenca-Bescós, G., Bailon, S., 2009. Climate forcing of first hominid dispersal in Western Europe. Journal of Human Evolution 57, 815-821.

Aiello, L.C., Key, C., 2002. Energetic consequences of being a Homo erectus female. American Journal of Human Biology 14, 551-565.

Aiello, L.C., Wheeler, P., 1995. The expensive tissue hypothesis: the brain and the digestive system in human and primate evolution. Current Anthropology 36, 199 - 221.

Aiello, L.C., Wheeler, P., 2003. Neanderthal Thermoregulation and the Glacial Climate, in: van Andel, T.H., Davies, W. (Eds.), Neanderthals and modern humans in the European landscape during the last glaciation. McDonald Institute for Archaeological Research, Cambridge, pp. 147-166.

Andrews, P., Ghaleb, B., 1999. Taphonomy of the Westbury Cave bone assemblages, in: Andrews, P., Cook, J., Currant, A., Stringer, C.B. (Eds.), Westbury Cave: The Natural History Museum Excavations, 1976–1984. Western Academic & Specialist Press Limited, Bristol, pp. 87–126.

Arnold, L.J., Demuro, M., Parés, J.M., Arsuaga, J.L., Aranburu, A., Bermúdez de Castro, J.M., Carbonell, E., 2014. Luminescence dating and palaeomagnetic age constraint on hominins from Sima de los Huesos, Atapuerca, Spain. Journal of Human Evolution 67, 85-107.

Arzarello, M., Marcolini, F., Pavia, G., Pavia, M., Petronio, C., Petrucci, M., Rook, L., Sardella, R., 2007. Evidence of earliest human occurence in Europe: the site of Pirro Nord (Southern Italy). Naturwissenschaften 94, 107-112.

Ashton, N., Hosfield, R., 2010. Mapping the Human Record in the British Early Palaeolithic: Evidence from the Solent River System. Journal of Quaternary Science 25, 737-753.

Ashton, N., Lewis, S.G., 2002. Deserted Britain: Declining Populations in the British Late Middle Pleistocene. Antiquity 76, 388-396.

Ashton, N., Lewis, S.G., 2012. The environmental contexts of early human occupation of northwest Europe: The British Lower Palaeolithic record. Quaternary International 271, 50-64.

Ashton, N., Lewis, S.G., De Groote, I., Duffy, S.M., Bates, M.R., Bates, R., Hoare, P., Lewis, M., Parfitt, S.A., Peglar, S., Williams, C., Stringer, C., 2014. Hominin Footprints from Early Pleistocene Deposits at Happisburgh, UK. PLoS One 9, e88329.

Ashton, N., Lewis, S.G., Parfitt, S.A., Penkman, K.E., Coope, G.R., 2008a. New evidence for complex climate change in MIS 11 from Hoxne, Suffolk, UK. Quaternary Science Reviews 27, 652-668.

Ashton, N.M., 2015. Ecological niches, technological developments and physical adaptations of early humans in Europe: the handaxe-*heidelbergensis* hypothesis, in: Coward, F., Hosfield, R.T., Pope, M., Wenban-Smith, F.F. (Eds.), Settlement, Society and Cognition in Human Evolution: Landscapes in Mind. Cambridge University Press, Cambridge, pp. 138-153.

Ashton, N.M., Parfitt, S.A., Lewis, S.G., Coope, G.R., Larkin, N., 2008b. Happisburgh Site 1 (TG388307), in: Candy, I., Lee, J.R., Harrison, A.M. (Eds.), The Quaternary of Northern East Anglia Field Guide. Quaternary Research Association, London, pp. 151–156.

Bello, S.M., Parfitt, S.A., Stringer, C.B., 2009. Quantitative micromorphological analyses of cut marks produced by ancient and modern handaxes. Journal of Archaeological Science 36, 1869-1880.

Berger, A., Loutre, M.F., 1991. Insolation values for the climate of the last 10 million years. Quaternary Science Reviews 10, 297-317.

Berger, L.R., Hawks, J., de Ruiter, D.J., Churchill, S.E., Schmid, P., Delezene, L.K., Kivell, T.L., Garvin, H.M., Williams, S.A., DeSilva, J.M., Skinner, M.M., Musiba, C.M., Cameron, N., Holliday, T.W., Harcourt-Smith, W., Ackermann, R.R., Bastir, M., Bogin, B., Bolter, D., Brophy, J., Cofran, Z.D., Congdon, K.A., Deane, A.S., Dembo, M., Drapeau, M., Elliott, M.C., Feuerriegel, E.M., Garcia-Martinez, D., Green, D.J., Gurtov, A., Irish, J.D., Kruger, A., Laird, E.W., Marchi, D., Meyer, M.R., Nalla, S., Negash, E.W., Orr, C.M., Radovčić, D., Schroeder, L., Scott, J.E., Throckmorton, Z., Tocheri, M.W., VanSickle, C., Walker, C.S., Wei, P., Zipfel, B., 2015. Homo naledi, a new species of the genus Homo from the Dinaledi Chamber, South Africa. eLIFE, 4:e09560.

Bermúdez de Castro, J.M., Arsuaga, J.L., Carbonell, E., Rosas, A., Martinez, I., Mosquera, M., 1997. A hominid from the Lower Pleistocene of Atapuerca: possible ancestor to Neanderthals and Modern Humans. Science 276, 1392–1395.

Bermúdez de Castro, J.M., Ramirez Rozzi, F.V., Martinon-Torres, M., Sarmiento Perez, S., Rosas, A., 2003. Patterns of dental development in Lower and Middle Pleistocene hominins from Atapuerca (Spain), in: Thompson, J.L., Krovitz, G.E., Nelson, A.J. (Eds.), Patterns of Growth and Development in the Genus *Homo*. Cambridge University Press, Cambridge, pp. 246-270.

Bermúdez de Castro, J.M., Rosas, A., Carbonell, E., Nicolás, M.E., Rodríguez, J., Arsuaga, J.L., 1999. A modern human pattern of dental development in Lower Pleistocene hominids from Atapuerca-TD6 (Spain). Proceedings of the National Academy of Sciences 96, 4210-4213.

Bigga, G., Schoch, W.H., Urban, B., 2015. Paleoenvironment and possibilities of plant exploitation in the Middle Pleistocene of Schöningen (Germany). Insights from botanical macro-remains and pollen. Journal of Human Evolution 89, 92-104.

Bogin, B., 1999. Patterns of Human Growth, 2nd ed. Cambridge University Press, Cambridge.

Bogin, B., Smith, B.H., 1996. Evolution of the human life cycle. American Journal of Human Biology 8, 703-716.

Brown, P., Sutikna, T., Morwood, M.J., Soejono, R.P., Jatmiko, E., Saptomo, E.W., Due, R.A., 2004. A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. Nature 431, 1055-1061.

Carbonell, E., Bermúdez de Castro, J.M., Arsuaga, J.-L., Allue, E., Bastir, M., Benito, A., I, C., Canals, T., Díez, J.C., van der Made, J., Mosquera, M., Ollé, A., Pérez-González, A., Rodríguez, J., Rodriguez, X.P., Rosas, A., Rosell, J., Sala, R., Vallverdú, J., Vergés, J.M., 2005. An Early Pleistocene hominin mandible from Atapuerca-TD6, Spain. Proceedings of the National Academy of Sciences 102, 5674-5678.

Carbonell, E., Bermudez de Castro, J.M., Arsuaga, J.-L., Diez, J.C., Rosas, A., Cuenca-Bescos, G., Sala, R., Mosquera, M., Rodriguez, X.P., 1995. Lower Pleistocene hominids and artifacts from Atapuerca-TD6 (Spain). Science 269, 826-830.

Carbonell, E., Mosquera, M., Rodríguez, X.P., Sala, R., 1996. The first human settlement of Europe. Journal of Anthropological Research 52, 107-114.

Cole, J., 2015a. Examining the Presence of Symmetry within Acheulean Handaxes: A Case Study in the British Palaeolithic. Cambridge Archaeological Journal 24, 713-732.

Cole, J., 2015b. Handaxe Symmetry in the Lower and Middle Palaeolithic: Implications for the Acheulean Gaze in: Coward, F., Hosfield, R., Pope, M., Wenban-Smith, F. (Eds.), Settlement, Society and Cognition in Human Evolution: Landscapes in Mind. Cambridge University Press, Cambridge, pp. 234-257.

Coope, G.R., 1993. Late-Glacial (Anglian) and Late-Temperate (Hoxnian) Coleoptera, in: Singer, R., Gladfelter, B.G., Wymer, J.J. (Eds.), The Lower Palaeolithic Site at Hoxne, England. University Chicago Press, Chicago, pp. 156-162.

Coope, G.R., 2006a. Insect faunas associated with Palaeolithic industries from five sites of pre-Anglian age in central England. Quaternary Science Reviews 25, 1738–1754.

Coope, G.R., 2006b. Insect Faunas Associated with Palaeolithic Industries from Five Sites of Pre-Anglian Age in Central England. Quaternary Science Reviews 25, 1738-1754.

Couzin, I.D., Laidre, M.E., 2009. Fission–fusion populations. Current Biology 19, R633-R635.

Daura, J., Sanz, M., Arsuaga, J.L., Hoffmann, D.L., Quam, R.M., Ortega, M.C., Santos, E., Gómez, S., Rubio, A., Villaescusa, L., Souto, P., Mauricio, J., Rodrigues, F., Ferreira, A., Godinho, P., Trinkaus, E., Zilhão, J., 2017. New Middle Pleistocene hominin cranium from Gruta da Aroeira (Portugal). Proceedings of the National Academy of Sciences 114, 3397-3402.

Dennell, R., Roebroeks, W., 1996. The earliest colonization of Europe: the short chronology revisited. Antiquity 70, 535–542.

Dennell, R.W., 2003. Dispersal and colonisation, long and short chronologies: how continuous is the Early Pleistocene record for hominids outside East Africa? Journal of Human Evolution 45, 421-440.

Dennell, R.W., 2004. Hominid dispersals and Asian biogeography during the Lower and Early Middle Pleistocene, ca. 2.0 - 0.5 mya. Asian Perspectives 43, 205-226.

Dennell, R.W., Roebroeks, W., 2005. Out of Africa: An Asian perspective on early human dispersal from Africa. Nature 438, 1099-1104.

Despriée, J., Voinchet, P., Tissoux, H., Bahain, J.-J., Falguères, C., Courcimault, G., Dépont, J., Moncel, M.-H., Robin, S., Arzarello, M., Sala, R., Marquer, L., Messager, E., Puaud, S., Abdessadok, S., 2011. Lower and Middle Pleistocene human settlements recorded in fluvial deposits of the middle Loire River Basin, Centre Region, France. Quaternary Science Reviews 30, 1474-1485.

Diez-Martin, F., Yustos, P.S., Uribelarrea, D., Baquedano, E., Mark, D.F., Mabulla, A., Fraile, C., Duque, J., Perez-Gonzalez, A., Yravedra, J., Egeland, C.P., Organista, E., Dominguez-Rodrigo, M., 2015. The Origin of the Acheulean: The 1.7 Million-Year-Old Site of FLK West, Olduvai Gorge (Tanzania). Scientific Reports 5, 17839.

Gamble, C., Gowlett, J., Dunbar, R.I.M., 2014. Thinking Big: How the Evolution of Social Life Shaped the Human Mind. Thames & Hudson, London.

Gamble, C.S., 1986. The Palaeolithic Settlement of Europe. Cambridge University Press, Cambridge.

Gamble, C.S., 1998. Handaxes and Palaeolithic Individuals, in: Ashton, N., Healy, F., Pettitt, P. (Eds.), Stone Age Archaeology: Essays in honour of John Wymer. Oxbow Monograph Oxford.

Gamble, C.S., 1999. The Palaeolithic Societies of Europe. Cambridge University Press, Cambridge.

García, N., Arsuaga, J.L., 2011. The Sima de los Huesos (Burgos, northern Spain): palaeoenvironment and habitats of Homo heidelbergensis during the Middle Pleistocene. Quaternary Science Reviews 30, 1413-1419.

Goren-Inbar, N., Alperson, N., Kislev, M.E., Simchoni, O., Melamed, Y., Ben-Nun, A., Werker, E., 2004. Evidence of Hominin Control of Fire at Gesher Benot Ya`aqov, Israel. Science 304, 725–727.

Gowlett, J.A.J., 2006. The Early Settlement of Northern Europe: Fire History in the Context of Climate Change and the Social Brain. C. R. Palevol 5, in press.

Gowlett, J.A.J., Gamble, C.S., Dunbar, R.I.M., 2012. Human Evolution and the Archaeology of the Social Brain. Current Anthropology 53, 693-722.

Grove, M., 2011. Speciation, diversity, and Mode 1 technologies: The impact of variability selection. Journal of Human Evolution 61, 306-319.

Guthrie, R.D., 1990. Frozen Fauna of the Mammoth Steppe. University of Chicago Press, Chicago.

Hawkes, K., O'Connell, J.F., Jones, N.G.B., Alvarez, H., Charnov, E.L., 1998. Grandmothering, menopause, and the evolution of human life histories. Proceedings of the National Academy of Sciences 95, 1336-1339.

Head, M.J., Gibbard, P.L., 2005. Early-Middle Pleistocene transitions: an overview and recommendation for the defining boundary. Geological Society, London, Special Publications 247, 1-18.

Holman, J.A., 1998. The herpetofauna. The interglacial mammalian fauna from Barnham, in: Ashton, N.M., Lewis, S.G., Parfitt, S.A. (Eds.), Excavations at the Lower Palaeolithic Site at East Farm, Barnham, Suffolk 1989–94. The British Museum, London, pp. 101-106.

Holman, J.A., 1999. Herpetofauna, in: Roberts, M.B., Parfitt, S.A. (Eds.), Boxgrove: a Middle Pleistocene hominid site at Eartham Quarry, Boxgrove, West Sussex. English Heritage, London, pp. 181-187.

Holmes, J.A., Atkinson, T., Fiona Darbyshire, D.P., Horne, D.J., Joordens, J., Roberts, M.B., Sinka, K.J., Whittaker, J.E., 2010. Middle Pleistocene climate and hydrological environment at the Boxgrove hominin site (West Sussex, UK) from ostracod records. Quaternary Science Reviews 29, 1515-1527.

Hopkinson, T., White, M.J., 2005. The Acheulean and the handaxe: structure and agency in the Palaeolithic, in: Gamble, C.S., Porr, M. (Eds.), The Hominid Individual in Context: Archaeological investigations of Lower and Middle Palaeolithic landscapes, locales and artefacts. Routledge, London and New York, pp. 13 - 28.

Hosfield, R., 2016. Walking in a Winter Wonderland? Strategies for Early and Middle Pleistocene Survival in Midlatitude Europe. Current Anthropology 57, 653-682.

Hosfield, R.T., 2011. The British Lower Palaeolithic of the early Middle Pleistocene. Quarternary Science Reviews 30, 1486 - 1510.

Huguet, R., Saladié, P., Cáceres, I., Díez, C., Rosell, J., Bennàsar, M., Blasco, R., Esteban-Nadal, M., Gabucio, M.J., Rodríguez-Hidalgo, A., Carbonell, E., 2013. Successful subsistence strategies of the first humans in south-western Europe. Quaternary International 295, 168-182.

Kahlke, R.-D., García, N., Kostopoulos, D.S., Lacombat, F., Lister, A.M., Mazza, P.P.A., Spassov, N., Titov, V.V., 2011. Western Palaearctic palaeoenvironmental conditions during the Early and early Middle Pleistocene inferred from large mammal communities, and implications for hominin dispersal in Europe. Quaternary Science Reviews 30, 1368-1395.

Kelly, R.L., 1995. The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways. Smithsonian Institution Press, Washington.

Kennedy, G.E., 2003. Palaeolithic Grandmothers? Life History Theory and Early Homo. Journal of the Royal Anthropological Institute 9, 549-572.

Klein, R.G., 2000. Archeology and the evolution of human behavior. Evolutionary Anthropology 9, 17-36.

Kohn, M., Mithen, S.J., 1999. Handaxes: products of sexual selection? Antiquity 73, 518-526.

Krovitz, G.E., Thompson, J.L., Nelson, A.J., 2003. Hominid growth and development from australopithecines to Middle Pleistocene *Homo*, in: Thompson, J.L., Krovitz, G.E., Nelson, A.J. (Eds.), Patterns of Growth and Development in the Genus *Homo*. Cambridge University Press, Cambridge, pp. 271-292.

Leroy, S.A.G., Arpe, K., Mikolajewicz, U., 2011. Vegetation context and climatic limits of the Early Pleistocene hominin dispersal in Europe. Quaternary Science Reviews 30, 1448-1463.

Lisiecki, L.E., Raymo, M.E., 2005. A Pliocene-Pleistocene stack of 57 globally distributed benthic δ18O records. Paleoceanography 20.

Lordkipanidze, D., Jashashvili, T., Vekua, A., Ponce de León, M.S., Zollikofer, C.P.E., Rightmire, G.P., Pontzer, H., Ferring, R., Oms, O., Tappen, M., Bukhsianidze, M., Agusti, J., Kahlke, R., Kiladze, G., Martinez-Navarro, B., Mouskhelishvili, A., Nioradze, M., Rook, L., 2007. Postcranial evidence from early Homo from Dmanisi, Georgia. Nature 449, 305-310.

MacDonald, K., 2007. Ecological hypotheses for human brain evolution: evidence for skill and learning processes in the ethnographic literature on hunting, in: Roebroeks, W. (Ed.), Guts and Brains: an integrative approach to the hominin record. Leiden University Press, Leiden, pp. 107-132.

MacDonald, K., Martinón-Torres, M., Dennell, R.W., Bermúdez de Castro, J.M., 2012. Discontinuity in the record for hominin occupation in south-western Europe: Implications for occupation of the middle latitudes of Europe. Quaternary International 271, 84-97.

Machin, A., Hosfield, R.T., Mithen, S.J., 2007. Why are some handaxes symmetrical? Testing the influence of handaxe morphology on butchey effectiveness. Journal of Archaeological Science 34, 883 - 893.

Machin, A., Mithen, S., 2004. Reply to McNabb et al 2004. The large cutting tools from the South African Acheulean and the questions of social traditions. Current Anthropology 45, 653 - 677.

Mania, D., 1995. The earliest occupation of Europe: the Elbe-Saale region (Germany), in: Roebroeks, W., van Kolfschoten, T. (Eds.), The Earliest Occupation of Europe. Proceedings of the European Science Foundation Workshop at Tautavel (France) 1993. Leiden University Press & European Science Foundation, Leiden, pp. 85-102.

Mania, D., Mania, U., 2003. Bilzingsleben — Homo erectus, his culture and his environment. The most important results of research, in: Burdukiewicz, J.M., Ronen, A. (Eds.), Lower Palaeolithic Small Tools In Europe And The Levant. BAR, Oxford, pp. 29-48.

Maslin, M.A., Brierley, C.M., Milner, A.M., Shultz, S., Trauth, M.H., Wilson, K.E., 2014. East African climate pulses and early human evolution. Quaternary Science Reviews 101, 1-17.

McNabb, J., Cole, J., 2015. The mirror cracked: Symmetry and refinement in the Acheulean handaxe. Journal of Archaeological Science: Reports 3, 100-111.

McPherron, S.P., 2000. Handaxes as a measure of the mental capabilities of early hominids. Journal of Archaeological Science 27, 655 - 663.

Messager, E., Lebreton, V., Marquer, L., Russo-Ermolli, E., Orain, R., Renault-Miskovsky, J., Lordkipanidze, D., Despriée, J., Peretto, C., Arzarello, M., 2011. Palaeoenvironments of early hominins in temperate and Mediterranean Eurasia: new palaeobotanical data from Palaeolithic key-sites and synchronous natural sequences. Quaternary Science Reviews 30, 1439-1447.

Meyer, M., Arsuaga, J.-L., de Filippo, C., Nagel, S., Aximu-Petri, A., Nickel, B., Martinez, I., Gracia, A., Bermúdez de Castro, J.M., Carbonell, E., Viola, B., Kelso, J., Prüfer, K., Pääbo, S., 2016a. Nuclear DNA sequences from the Middle Pleistocene Sima de los Huesos hominins. Nature 531, 504-507.

Meyer, M., Arsuaga, J.-L., Filippo, C., Nagel, S., Aximu-Petri, A., Nickel, B., Martinez, I., Gracia, A., de Castro, J.M.B., Carbonell, E., Viola, B., Kelso, J., Prüfer, K., Pääbo, S., 2016b. Nuclear DNA Sequences from the Middle Pleistocene Sima de los Huesos Hominins. Nature 531, 504-507.

Molines, N., Monnier, J.-L., Hinguant, S., Hallegouet, B., 2005. L'Acheuléen de l'ouest de la France: apports du site de Menez Dregan I (Plouhinec, Finistère, France), in: Molines, N., Moncel, M.-H., Monnier, J.-L. (Eds.), Les Premiers Peuplements en Europe. BAR International Series, Oxford, pp. 533-544.

Moncel, M.-H., Ashton, N., Lamotte, A., Tuffreau, A., Cliquet, D., Despriée, J., 2015. The Early Acheulian of north-western Europe. Journal of Anthropological Research 40, 302-331.

Pappu, S., Gunnell, Y., Akhilesh, K., Braucher, R., Taieb, M., Demory, F., Thouveny, N., 2011. Early Pleistocene presence of Acheulian hominins in south India. Science 331, 1596-1599.

Parfitt, S.A., 1998. The interglacial mammalian fauna from Barnham, in: Ashton, N.M., Lewis, S.G., Parfitt, S.A. (Eds.), Excavations at the Lower Palaeolithic Site at East Farm, Barnham, Suffolk 1989–94. British Museum, London, pp. 111–147.

Parfitt, S.A., Ashton, N.M., Lewis, S.G., Abel, R.L., Coope, R., Field, M.H., Gale, R., Hoare, P.G., Larkin, N., Lewis, M.D., Karloukovski, V., Maher, B.A., Peglar, S.M., Preece, R.C., Whittaker, J.E., Stringer, C.B., 2010. Early Pleistocene Human Occupation at the Edge of the Boreal Zone in Northwest Europe. Nature 466, 229-233.

Parfitt, S.A., Barendregt, R.W., Breda, M., Candy, I., Collins, M.J., Coope, G.R., Durbridge, P., Field, M.H., Lee, J.R., Lister, A.M., Mutch, R., Penkman, K.E.H., Preece, R.C., Rose, J., Stringer, C.B., Symmons, R., Whittaker, J.E., Wymer, J.J., Stuart, A.J., 2005. The earliest record of human activity in northern Europe. Nature 438, 1008–1012.

Parfitt, S.A., Roberts, M.B., 1999. Human modification of faunal remains, in: Roberts, M.B., Parfitt, S.A. (Eds.), Boxgrove: A Middle Pleistocene Hominid Site at Eartham Quarry, Boxgrove, West Sussex. English Heritage, London, pp. 398-419.

Pettitt, P., White, M.J., 2012. The British Palaeolithic: Human Societies at the Edge of the Pleistocene World. Routledge, London.

Porr, M., 2005. The making of the biface and the making of the individual, in: Gamble, C.S., Porr, M. (Eds.), The Hominid Individual in Context: Archaeological investigations of Lower and Middle Palaeolithic landscapes, locales and artefacts Routledge, London and New York, pp. 68 - 80.

Potts, R., 1998. Variability selection in hominid evolution. Evolutionary Anthropology 7, 81-96.

Potts, R., 2013. Hominin evolution in settings of strong environmental variability. Quaternary Science Reviews 73, 1-13.

Preece, R.C., Gowlett, J.A.J., Parfitt, S.A., Bridgland, D.R., Lewis, S.G., 2006. Humans in the Hoxnian: Habitat, Context and Fire Use at Beeches Pit, West Stow, Suffolk, UK. Journal of Quaternary Science 21, 485-496.

Rae, T.C., Koppe, T., Stringer, C.B., 2011. The Neanderthal face is not cold adapted. Journal of Human Evolution 60, 234-239.

Ramirez Rozzi, F.V., Bermudez de Castro, J.M., 2004. Surprisingly rapid growth in Neanderthals. Nature 428, 936-939.

Richter, D., Krbetschek, M., 2015. The age of the Lower Paleolithic occupation at Schöningen. Journal of Human Evolution 89, 46-56.

Robson, S.L., Wood, B., 2008. Hominin life history: reconstruction and evolution. Journal of Anatomy 212, 394-425.

Rodríguez, J., Burjachs, F., Cuenca-Bescós, G., García, N., Van der Made, J., Pérez González, A., Blain, H.A., Expósito, I., López-García, J.M., García Antón, M., Allué, E., Cáceres, I., Huguet, R., Mosquera, M., Ollé, A., Rosell, J., Parés, J.M., Rodríguez, X.P., Díez, C., Rofes, J., Sala, R., Saladié, P., Vallverdú, J., Bennasar, M.L., Blasco, R., Bermúdez de Castro, J.M., Carbonell, E., 2011. One million years of cultural evolution in a stable environment at Atapuerca (Burgos, Spain). Quaternary Science Reviews 30, 1396-1412.

Roebroeks, W., 2001. Hominid behaviour and the earliest occupation of Europe: an exploration. Journal of Human Evolution 41, 437-461.

Roebroeks, W., 2006. The human colonisation of Europe: where are we? Journal of Quaternary Science 21, 425–435.

Roebroeks, W., van Kolfshoten, T., 1994. The earliest occupation of Europe: a short chronology. Antiquity 68, 489-503.

Roebroeks, W., Villa, P., 2011. On the earliest evidence for habitual use of fire in Europe. Proceedings of the National Academy of Sciences 108, 5209-5214.

Rosas, A., Ríos, L., Estalrrich, A., Liversidge, H., García-Tabernero, A., Huguet, R., Cardoso, H., Bastir, M., Lalueza-Fox, C., de la Rasilla, M., Dean, C., 2017. The growth pattern of Neandertals, reconstructed from a juvenile skeleton from El Sidrón (Spain). Science 357, 1282-1287.

Saladié, P., Huguet, R., Díez, C., Rodríguez-Hidalgo, A., Cáceres, I., Vallverdú, J., Rosell, J., Bermúdez de Castro, J.M., Carbonell, E., 2011. Carcass transport decisions in *Homo antecessor* subsistence strategies. Journal of Human Evolution 61, 425–446.

Saragusti, I., Sharon, I., Katzenelson, O., Avnir, D., 1998. Quantitative Analysis of the Symmetry of Artefacts: Lower Paleolithic Handaxes. Journal of Archaeological Science 25, 817 - 825.

Schwartz, G.T., 2012. Growth, Development, and Life History throughout the Evolution of Homo. Current Anthropology 53, S395-S408.

Shettleworth, S.J., 2010. Cognition, evolution and behavior, 2nd ed. Oxford Univeristy Press, New York.

Shotton, F.W., Keen, D.H., Coope, G.R., Currant, A.P., Gibbard, P.L., Aalto, M., Peglar, S.M., Robinson, J.E., 1993. The Middle Pleistocene Deposits of Waverley Wood Pit, Warwickshire, England. Journal of Quaternary Science 8, 293-325.

Shultz, S., Nelson, E., Dunbar, R.I.M., 2012. Hominin Cognitive Evolution: Identifying Patterns and Processes in the Fossil and Archaeological Record. Phillosphical Transactions of the Royal Society Series B 367, 2130-2140.

Smith, T.M., Toussaint, M., Reid, D.J., Olejniczak, A.J., Hublin, J.-J., 2007. Rapid dental development in a Middle Paleolithic Belgian Neanderthal. Proceedings of the National Academy of Sciences 104, 20220-20225.

Stahlschmidt, M.C., Miller, C.E., Ligouis, B., Goldberg, P., Berna, F., Urban, B., Conard, N.J., 2015. The depositional environments of Schöningen 13 II-4 and their archaeological implications. Journal of Human Evolution 89, 71-91.

Stopp, M., 1993. Taphonomic analysis of the faunal assemblage, in: Singer, R., Gladfelter, B.G., Wymer, J.J. (Eds.), The Lower Palaeolithic Site at Hoxne, England. University of Chicago Press, Chicago, pp. 139–149.

Stout, D., Apel, J., Commander, J., Roberts, M., 2014. Late Acheulean technology and cognition at Boxgrove, UK. Journal of Archaeological Science 41, 576-590.

Stringer, C., 2012. The Status of Homo heidelbergensis (Schoetensack 1908). Evolutionary Anthropology 21, 101 - 107.

Thackeray, J.F., 2015. Estimating the age and affinities of Homo naledi. South Africa Journal of Science 111, 1-2.

Toro-Moyano, I., Martinez-Navarro, B., Agusti, J., Souday, C., Bermúdez de Castro, J.M., Martinón-Torres, M., Fajardo, B., Duval, M., Falguères, C., Oms, O., Parés, J.M., Anadón, P., Julià, R., García-Aguilar, J.M., Moigne, A.-M., Espigares, M.P., Ros-Montoya, S., Palmqvist, P., 2013. The oldest human fossil in Europe, from Orce (Spain). Journal of Human Evolution 65, 1-9.

Tuffreau, A., Antoine, P., 1995. The earliest occupation of Europe: continental northwestern Europe, in: Roebroeks, W., van Kolfschoten, T. (Eds.), The Earliest Occupation of Europe. University of Leiden & European Science Foundation, Leiden, pp. 147-163.

Turner, A., 1992. Large Carnivores and Earliest European Hominids - Changing Determinants of Resource Availability During the Lower and Middle Pleistocene. Journal of Human Evolution 22, 109-126.

Urban, B., Bigga, G., 2015. Environmental reconstruction and biostratigraphy of late Middle Pleistocene lakeshore deposits at Schöningen. Journal of Human Evolution 89, 57-70.

Van Buskirk, J., 2012. Behavioural plasticity and environmental change, in: Candolin, U., Wong, B. (Eds.), Behavioural responses to a changing world: mechanisms and consequences. Oxford University Press, Oxford, pp. 145-158.

Van Kolfschoten, T., Buhrs, E., Verheijen, I., 2015a. The larger mammal fauna from the Lower Paleolithic Schöningen Spear site and its contribution to hominin subsistence. Journal of Human Evolution 89, 138-153.

Van Kolfschoten, T., Parfitt, S.A., Serangeli, J., Bello, S.M., 2015b. Lower Paleolithic bone tools from the ‘Spear Horizon’ at Schöningen (Germany). Journal of Human Evolution 89, 226-263.

van Schaik, C.P., 2013. The costs and benefits of flexibility as an expression of behavioural plasticity: a primate perspective. Philosophical Transactions of the Royal Society B 368.

Voormolen, B., 2008. Ancient hunters, modern butchers: Schöningen 13II–4, a kill–butchery site dating from the northwest European Lower Palaeolithic. University of Leiden.

Warren, S.H., 1911. On a Palaeolithic (?) Wooden Spear. Quarterly Journal of the Geological Society of London 67, xcix.

Wenban-Smith, F., 2004. Handaxe typology and Lower Palaeolithic cultural development: ficrons, cleavers and two giant handaxes from Cuxton. Lithics 25, 11 - 21.

White, M.J., 1998. Twisted Ovate Bifaces in the British Lower Palaeolithic: Some Observations and Implications, in: Ashton, N., Healy, F., Pettitt, P. (Eds.), Stone Age

Archaeology: Essays in honour of John Wymer. Lithic Studies Society Occasional Paper 6, Oxbow Monograph 12, Oxford, pp. 98-104.

Wynn, T., 1995. Handaxe enigmas. World Archaeology 27, 10 - 23.