Oxford Handbook of Archaeological Theory

Chapter 3.1

BECOMING HUMAN

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Introduction

What makes us human? The definition of humans vis-a-vis other animals is the subject of some of the very earliest philosophical discussion (see e.g. Pellegrin 1986; Serjeantson 2000, 179), and remains a highly sensitive topic with unavoidable social, cultural and political ramifications (Graves-Brown 1993; Corbey and Theunissen 1995, 235; Marks 1997; Drell 2000; papers in Corbey and Roebroeks 2001; Proctor 2003).

Such debates have a significant impact within archaeology. In most archaeological periods, it can be assumed that people in the past shared essentially the same morphological and physiological attributes and cognitive capacities as the archaeologist investigating them. While bodies differ physically and are historically and contextually situated cultural constructs, all humans share a number of physiological, perceptual and cognitive characteristics which in part structure their experience of the world, and this recognition is central to interpretations of the archaeological record.

However, in the very earliest archaeological record of the Palaeolithic no such luxury is available, and here wider cultural notions about what make us human frame debates about the archaeology of human ancestors (e.g. see discussions in Landau 1984, 1992; Corbey and Theunissen 1995; Drell 2000; papers in Corbey and Roebroeks 2001). Archaeological narratives of human evolution are far from value-free, and at times can seem little more than ex-post-facto arguments designed to reinforce cultural assumptions about social, cultural and cognitive progress throughout hominin evolution.

In contrast, it is becoming increasingly clear that different lines of evidence provide conflicting accounts of ‘becoming human’. For example, while palaeoanthropology has tended to stress the biological record of continuity between humans and other animals, archaeology has more usually focused on a material record which – arguably – demonstrates discontinuity. As a result, one of the most pressing problems of Palaeolithic archaeology is how we deal with multiple, overlapping definitions of humanity, and what weight we should give different strands of evidence in attempting to answer the question: what makes us ‘human’?

BIOLOGICAL HUMANS

Genetic definitions

The evolutionary revolution of the last few decades has been our burgeoning understanding of the genetic basis of evolution and speciation. A major finding of this work has been that all extant humans belong to a single species, *Homo sapiens*, and that we are extremely closely related to the African apes. Indeed, we famously share almost 99% of our DNA with the common chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) and only slightly less with the western and eastern gorillas (*Gorilla gorilla* and *Gorilla berengei* respectively; see e.g. Bradley 2008 for references). As a result, chimpanzees at least are now considered part of the family Hominidae (making them 'hominids'), while humans and our ancestors since the last common ancestor we shared with chimpanzees are now distinguished from the other apes only at the tribe level, as 'hominins'.

As well as re-drawing our family tree, DNA sequencing allowed estimation of *how long* the genetic differences between species might have taken to accumulate. Current thinking is that the hominins (our own lineage) diverged from the hominid ancestors of the chimpanzees somewhere between 8-6 million years ago (see e.g. Bradley 2008 for review), and that the last (female) common ancestor of all living *Homo sapiens* – 'mitochondrial Eve' – lived between 280-140,000 years ago, almost certainly in sub-Saharan Africa (Cann *et al.* 1987, 1994; Vigilant *et al.* 1991). As techniques improve, it is also increasingly becoming possible to identify the specific genetic changes that occur on different lineages; several potentially significant mutations which distinguish humans from our living and fossil relatives have already been identified (e.g. Green *et al.* 2010) and include some implicated in modern human language (FOXP2: e.g. Scharff and Petri 2011) and in brain development (see e.g. Bradley 2008; Somel *et al*. 2013 for review).

Such work has already revolutionized our understanding of human evolution, and the potential for genetic anthropology is extremely exciting. However, it is unlikely to give us all the answers. DNA does not survive well in ancient fossil material, and although techniques continue to improve it seems likely that there will always be an upper limit to the age of fossils yielding viable DNA. In any case, genetics can only ever inform on a species' or individual's *genotype*, i.e. on the collection of genes that make up our DNA. However, many different factors also play a significant role in determining how those genes are expressed in an individual's *phenotype* or physiology during their development (Bird 2007).

Even though only c. 1% of our genotype differs from that of the chimpanzee, many of these differences involve regulatory genes, which govern the ways in which other genes are expressed (Gilad *et al.* 2006; Sholtis and Noonan 2010). Even small changes in these parts of the genotype can have big effects, and although there are many striking similarities between ourselves and chimpanzees, we also differ radically in other ways, and some anthropologists have characterized the famous 99% figure as 'the Great Overstatement of molecular anthropology' (Marks 1997, 49). Genetics is probably not the 'magic bullet' that will tell us how we became human.

Morphological definitions

The most immediate evidence for the evolution of modern humans comes of course from the fossil record. However, the fossilization process preserves only the hard tissues – and many living species are difficult or impossible to differentiate from bones and teeth alone (Tattersall 1992, 341; see also Tattersall and Mowbray 2005, 377; Robson and Wood 2008). Even biologists working with extant species disagree over how 'species' should be defined, and such debates become even more problematic when applied to the fossil record (see e.g. Foley 2005; Wood and Lonergan 2008; Wood 2010 for discussion). On an evolutionary timescale, species are not fixed, static and discrete entities characterized by a checklist of discrete traits, but simply temporary configurations in a process of ongoing change, onto which the fossil record provides only very limited and irregular 'snapshots' of a continuum of variation. In addition, because fossil specimens are often poorly preserved and/or dated and limited in number, it is almost impossible to assess the level of variability within species, and thus to tell whether individual specimens are sufficiently different to be assigned to different species (Wood and Lonergan 2008, 367). Palaeoanthropologists rarely agree on how much variation they are prepared to accept in a species; while some prefer to minimize the number of species by 'lumping' fossil specimens together into large, variable groups, others 'split' fossils with only slight differences into separate species (Wood and Lonergan 2008, 368). As a result, many palaeoanthropologists argue that the identification of every specimen to ‘species’ level is of less significance than the general evolutionary trends visible in the fossil record, and what these can tell us about how our ancestors met the challenges of daily life (Wood and Lonergan 2008, 355).

Figure 1 illustrates one version of the taxonomy of our ancestors as currently understood, but also groups these fossils into broader ‘types’ (also known as ‘grades’ or ‘morphs’ (following Wood e.g. 2010, 8902). This ‘lumping taxonomy’ emphasizes distinctive ‘adaptive radiations’ of closely-related groups, each of whom pursued relatively minor elaborations on the same basic strategies of survival using a similar set of physiological and behavioural traits bequeathed them by their common ancestors. On occasion, these ‘experiments’ in strategy, coupled with or selected for by environmental change, produced a more substantial departure from their ancestors’ lifeways in particular local populations. This in turn opened up a new range of opportunities for a new adaptive radiation of populations descended from this first. Over time, the different behavioural strategies adopted by local populations, and the selective pressures of local habitats (coupled with neutral processes such as genetic drift) meant that morphological and behavioural differences between local populations accumulated, and in the absence of substantial gene-flow between them, such groups eventually became genetically distinct species in the classic sense of being unable to interbreed (Mayr 1969). On an evolutionary timescale, however, speciation itself becomes almost epiphenomenal – a consequence, rather than cause, of a groups’ distinctions (Huxley 1942, 389).

<Figure 1>

Crucially, however, the ‘endpoints’ of these processes are never fixed in advance. There was nothing inevitable about our species ‘becoming human’ – hominin evolution is not a corridor which chimpanzees walk into and come out of human (Tooby and Devore 1987, 95). Our ancestors operated solely in the here-and-now, responding to the immediate demands of life using the physiological and behavioural characteristics they had inherited from previous generations. For all kinds of reasons, including blind chance, only some of these lifeways – indeed, ultimately only one – proved successful, and the groups pursuing them survived and persisted where others died out.

The fossil record, then, gives us an essential insight into the changing physiologies of our ancestors. However, for evolutionary *cause,* we must place these developments in context and examine the specific challenges our ancestors faced, and how they met these.

Contexts for hominin evolution

Rather than being essentialist, pre-given (or divinely-ordained; e.g. Linnaeus 1758) discrete biological categories defined by phenotype in isolation, biological species are much better defined by their positioning in ecological *niches* within broader communities of plants and animals (*ecosystems*). If an ecosystem can be thought of as providing a species' *address*, its *niche* can be defined as its *profession* (Odum 1953), and in particular its interactions with other species (e.g. as prey, predator, competitor). The famous phrase 'survival of the fittest' refers not necessarily to the biggest, the fastest, the leanest or meanest, but to those that 'fit' best into their ecosystems (Gould 1998). However, such ecosystems, being dependent on complex combinations of climatic, geologic and topographical factors, are inherently unstable, with even minor changes entraining a cascade of adjustments to the new ecological status quo, including the biological adaptations of species.

Furthermore, ecological interactions occur within as well as between species and between a species and its environment. Because conspecifics must also compete – or indeed cooperate – to find food, mate and reproduce, 'social' interactions are also a potentially very important selective pressure.

As a result, species do not evolve in a simple, linear fashion, and humans are no exception. Rather than a succession of hominin species progressively 'becoming human', the palaeoanthropological record documents a complex, messy process in which individuals adapted in creative and opportunistic ways to the immediate real-world ecosystems of conspecifics, other plant and animal species and the physical environment in which they lived (Foley 1984, 5).

The rest of this chapter will consider how palaeoanthropologists have interpreted the fossil and archaeological records in their evolutionary and ecosystemic contexts, and what this can tell us about how we became human.

SKILFUL APES

Man the toolmaker?

Although tool use has long been considered a defining characteristic of human nature, it is now clear that stone tools are not the earliest distinguishing markers of the hominin lineage: that honour goes instead to bipedalism. Even the very earliest potential hominins (Harrison 2010) seem to have been at least partly adapted to bipedal locomotion, including *Sahelanthropus* (Brunet *et al.* 2002), *Orrorin* (Richmond and Jungers 2008) and *Ardipithecus* (White *et al.* 1994; Haile-Selassie *et al.* 2004). However, it is not until the appearance of the first pre-modern *Homo* species *Homo ergaster* and *H. erectus* around 1.8ma that our ancestors became fully committed to bipedalism, and debate continues over the selective pressures which led to the adoption of bipedalism (see Niemitz 2010 for review and references). Perhaps the most often-cited of these is the observation that bipedalism freed the hands for activities other than locomotion (e.g. Lovejoy 1981) – whether or not this was a significant selective pressure at the time, it certainly *became* significant later, becoming *exapted* for other purposes in allowing hominins to develop a strategy only partially explored by other primates – that of skilled manual action and tool use.

The earliest stone tools currently known date to 2.6mya (Semaw *et al.* 1997), although cut-marks made on bone by tools have been identified much earlier (3.3mya; McPherron *et al.* 2010, though see also Domingúez-Rodrigo et al. 2010). These tools belong to a school of stone tool manufacture in which simple sharp flakes were detached from stone cobbles and used without significant modification, a ‘culture’ known as the ‘Oldowan’ after its first find spot, Olduvai Gorge.

The Oldowan is traditionally associated with the *Homo* lineage (beginning with *Homo habilis*: hence his soubriquet ‘handyman’). However, more recently tools and bones bearing cut marks have been found associated with other hominins: *Australopithecus garhi*

(Asfaw 1999; Heinzelin *et al.* 1999) and *A. afarensis* (McPherron *et al.* 2010), and fossils of one of the megadont archaics *Paranthropus* (aka *Zinjanthropus*) *boisei* were recovered from the same levels as the early stone tools from Olduvai originally attributed to *Homo habilis* (Leakey 1971).

Tool-making, then, is not unique to the genus *Homo*. In fact, it is not unique to hominins, nor even to primates. All great apes (Goodall 1986; van Schaik *et al.* 1996; Breuer *et al.* 2005) and many other animal species (see e.g. references in Berthelet and Chavaillon 1993) habitually use a variety of tools. Some captive great apes have even learned to 'knap' stone and use the sharp edges of struck flakes, producing simple tools comparable to those used by our hominin ancestors (e.g. Wright 1972; Toth *et al.* 1993; Schick *et al.* 1999; Toth and Schick 2009).

Nevertheless, archaeological stone tools remain a valuable source of evidence on human evolution. Not only are they the only direct evidence of hominin behaviour, but tools also preserve the sequence of actions used to make them – and thus potentially inform on the minds that organized those actions. Where the source of raw materials used to make tools can be identified, tools also provide evidence of hominins' movements.

However, a focus on stone tools inevitably gives us only a very biased picture of hominin technology. Some of the most ubiquitous and simple forms of human technology – bags and snares, clothes and containers – remain all but invisible to us, as it is only considerably later, and only in extraordinarily good preservational contexts, that artefacts made from organic materials can be identified.

Typology and technology

The recognition that tool use does not make our ancestors unique has led in recent years to a significant shift in stone tool analysis in recent years, from a focus on conceptual knowledge (*connaissances*), to a consideration instead of skill or know-how (*savoir-faire*) and the sequencing of gestures and material actions (*chaînes opératoires*) involved in tool manufacture and use (Pelegrin *et al.* 1988; Pelegrin 1991; see also Karlin and Julien 1994; Schlanger 1996 for broader discussion of the concept). Such a perspective views the complex ‘cultural’ *typologies* of stone tools which abound in Palaeolithic archaeology as of less evolutionary significance than the long-term trends in *technology* outlined in Table 1.

<Table 1>

Stone tool typologies of the kind drawn up for the Oldowan by Mary Leakey (1971) assume that a hominin knapper deliberately set out to make a specific type of tool to match a pre-existing cognitive concept (the *mental template*). However, more recent re-evaluations have suggested that most Oldowan tools were produced in a rather *ad hoc* fashion by simply splitting open river-cobbles to produce a sharp edge (Toth 1985; see also e.g. Stout 2005; Stout and Chaminade 2007), and that any conceptual ‘mental templates’ were very limited in scope (e.g. Davidson and Noble 1993; Dibble 1995; Andrefsky 2005, 196-7).

However, although our early ancestors may not have been great *designers*, they do seem to have been accomplished *crafters*. Basic fracture mechanics dictates that to successfully detach a flake, a hammerstone must strike the ‘core’ of raw material at an angle of less than 90º. Indeed, modern human knappers typically work with angles of <80º, and these more acute angles are seen even in the earliest Oldowan assemblages (Delagnes and Roche 2005), but not in those produced by even the most accomplished primate knapper to date, the bonobo Kanzi (Toth *et al.* 1993; Schick *et al.* 1999, 822).

Even early stone tools thus suggest that a complex understanding of fracture mechanics had become more adaptive for their hominin makers than among other primates. However, it is possible that other primates are simply less *physically* able at knapping stone, as chimpanzees’ hand and wrist anatomy is primarily adapted for knuckle-walking, making it difficult to achieve the combination of power and precision humans’ more mobile wrists allow (Marzke 1997): rather than use a hammerstone, Kanzi preferred to detach flakes by throwing his ‘core’ at a hard surface, giving him much less control over the knapping process (Boesch and Boesch 1984, 431; Toth and Schick 2009, 298). The adoption of bipedalism among hominins released hand and wrist anatomy from the selective pressures associated with locomotion, allowing for the anatomical adaptations responsible for the increased dexterity reflected in these early tools.

Stone tool manufacture and cognition

Nevertheless, for many archaeologists it is the mode 2 technologies which succeed the Oldowan c. 1.6mya (Table 1) that signify a step-change in hominin technology. Bifacially worked Acheulean tools, known as handaxes, represent complex *chaînes opératoires* (Gowlett 1996, compare figs 16.2 and 16.3) and such high levels of finishing, symmetry and standardization of shape that it is often argued their hominin makers must have been working to genuine mental concepts of the finished product (see e.g. McPherron 2000 for discussion).

The late Acheulean also yields some of the earliest examples of organic artefacts, including wooden clubs from Gesher Benot Ya'Aqov and Kalambo Falls at 780,000bp and 400,000bp (Goren-Inbar *et al.* 1994), spears from Schöningen and Clacton-upon-Sea c. 400,000bp (Thieme 2003; Oakley *et al.* 1977) and 'handaxes' made from elephant bone from Bilzingsleben (Bruhl 2003) and sites in Italy (see e.g. Costa 2010 for discussion). Arguably, however, it is not until the appearance of mode 3 technologies (Table 1) that hominins appreciated the different *qualities* of these raw materials. Mode 3 'prepared core' technologies, as the name implies, require more complex sequences of motor actions than mode 2, implying more forethought and planning ability on the part of their makers (Foley and Lahr 1997, 9). Furthermore, many later mode 3 technologies were designed to form part of composite tools comprising several different kinds of raw material (e.g. stone spear-heads lashed to wooden shafts). Such *integrative* technologies involve multiple, parallel *chaînes opératoires* and require detailed knowledge of the differing properties of each material involved (Barham 2010, 375-6).

The succeeding mode 4 industries are usually associated – in Europe, at least – with modern humans, which has perhaps coloured interpretation of the cognitive skills involved. Certainly the *chaînes opératoires* involved in prismatic blade production require considerable forethought and skill (compare Karlin and Julien 1994, fig 15.1 with Gowlett 1996, figs 16.2 and 16.3). However, the argument that mode 4 marks a new, 'volumetric' way of thinking about raw material and efficiency (Binford 1973, 1979, 1989; Karlin and Julien 1994) is less easy to support (see references in Coward and Gamble 2010, 51).

In any case, interpretation of the level of cognitive skill hominins were capable of solely from their stone tools remains highly problematic. Many factors affect the complexity of stone tool manufacture: for example, the nature and quality of available raw material is a significant constraint on the kinds of tools it is possible to make (see references in McPherron 2000).,Stone tools are likely to provide only a *minimal* picture of hominin abilities. This may explain why the neat progressive scheme presented in Table 1 is in fact much noisier at a smaller scale. For example, some blade-based mode 4 technologies are thought to have been produced by pre-*sapiens* groups, for example the Châtelperronian industries apparently manufactured by Neanderthals in southwestern France and northern Spain. Whether Neanderthals developed these technologies independently (D’Errico *et al.* 1998; Zilhão 2001) or after having seen the technologies of the newly-arrived *Homo sapiens* (Mellars 1996a, 415-6; 1998), the fact that they were able to replicate the tools suggests that, like chimpanzees, Neanderthals and indeed earlier hominin species may have been cognitively *capable* of more ‘advanced’ technologies than those they habitually relied on. Many fully *Homo sapiens* groups’ stone tool repertoires are comparable to those of modes 1 and 2, but these tools form part of highly complex lifeways (e.g. some Aboriginal groups in Australia [Mulvaney 1969; Hayden 1993]). Only by considering the tools themselves in their broader context of use, therefore, can we understand how and why tool behaviours were so successful that they became a defining trait of the hominin lineage (e.g. Gibson 1993, 263-4; Gowlett 1996, 135).

BIG-BRAINED APES

Subsistence and encephalization

Considering stone tools in their broader context points towards a significant difference between the lifeways of hominins and those of other primates. While chimpanzees do hunt and consume small animals (see e.g. McGrew 2010 for review), meat makes up a very small proportion of their diet (Layton and O’Hara 2010, table 5.2), and they rarely use tools during the capture or consumption of animal prey (though see Pruetz and Bertolani 2007). In contrast, even the very earliest stone tools are almost invariably found associated with animal bones, some of which bear cut-marks produced by stone tools, suggesting that hominins habitually used stone tools to exploit carcasses.

However, early hominins are unlikely to have been great hunters. The anatomical location of cut-marks suggests that hominins were probably scavenging kills made by other carnivores (see Klein 1999, 242-248 for discussion and references), using stone tools to reach the fatty and protein-rich marrow and brains other carnivores and scavengers cannot access. Nevertheless, animal protein probably still formed only a small proportion of early hominins' diets. Because plant foods do not survive on early archaeological sites, archaeologists have a very biased picture of hominin diets. However, analysis of fine damage on the edges of the tools reveals that they were used for many different activities, including cutting meat, but also scraping and sawing wood, cutting grass etc. (Keeley 1980). Other potentially significant food resources are also accessible using stone tools, including aquatic and water-edge resources (Braun 2010), underground roots and tubers (Laden and Wrangham 2005) and termite mounds (Backwell and D'Errico 2001).

Indeed, the fossil evidence suggests that dietary adaptations differed among archaic hominins. The skulls of the 'megadont archaics' or paranthropines (see Figure 1) were apparently adapted for applying considerable crushing force via extremely large grinding teeth, implying adaptation to diets comprising hard, tough and fibrous vegetable foods. Analysis of the chemical traces the paranthropines' diets left in their bones, however, suggests that they actually had a very varied diet whenever possible, but that increasing aridity and seasonality across Africa after c. 3ma may have limited their dietary options (Sponheimer *et al.* 2006). In contrast, the megadonts' cousins the transitional hominins *Homo habilis* and *H. rudolfensis* had relatively smaller molars and larger incisors, implying a more varied diet which may have included a more significant component of animal protein and which perhaps left early *Homo* less vulnerable to the climatic downturn. In any case, ultimately the less specialized morphology of the transitional hominins proved more successful, and the paranthropines disappear from the record after around 1.2ma. What may initially have been only a very minor difference in diet thus had significant ramifications.

Big brains and complex behaviours

One of the most remarked-on differences between humans and other primates is the size of our brains: at an average of 1,200cc our brains are surpassed in gross size only by those of elephants and some cetacean species such as dolphins and whales. Although it is often assumed that the size of our brains accounts for our – self-proclaimed – intelligence, there is little consensus over how and why this might be the case. Some researchers do consider absolute brain size the key to the distinctive suite of human cognitive skills (e.g. Deaner *et al.* 2007). However, *H. floresiensis*, with a brain the size of a modern chimpanzee (380-430cm^3; Aiello 2010) as recently as 12,000bp, is associated with evidence for big-game hunting, sophisticated tool use, control of fire and sea crossings (Morwood *et al.* 2004), suggesting that factors other than gross size are important (see e.g. Conroy and Smith 2007).

Many researchers thus favour measures of brain size which correct for the increased motor and sensory demands of larger bodies (such as encephalization quotient [EQ]; see e.g. Barton 2006 for discussion). Others emphasize instead the structural and organizational changes that may have occurred within the brain during hominin evolution (Rilling 2006; see Roth and Dicke 2005 and Sherwood et al. for discussion), although only very gross features of hominin brain structure can be established from moulds of their skulls (endocasts) with any accuracy (Holloway *et al.* 2004).

Nevertheless, gross brain size (Figure 2) remains significant, because the brain is an energetically ‘expensive’ organ which places particular strain on energy budgets. We must consider not simply *why* brains became larger, but *how* this was achieved. Long, slow life histories and ‘co-operative breeding’ (receiving help feeding and caring for offspring from others (e.g. the male parent or older individuals, especially older females who live longer post-reproductive age among humans than other primates (the ‘grandmothering’ hypothesis; Hawkes *et al.* 1998; O’Connell *et al.* 1999; Caspari and Lee 2004) help spread the added costs (Isler and van Schaik 2009). One possibility is that extra energy became available as hominins incorporated foodstuffs requiring less digestive processing, such as meat, into their diets, and potentially also by cooking foodstuff to break down tough tissue before consumption (Carmody and Wrangham 2009) – all of which allowed them to reduce the size and metabolic cost of their digestive system, (Aiello and Wells 2002).

<Figure 2>

Bigger brains also mean more difficult births, especially given the competing demands bipedalism places on the pelvis. To compensate for this, modern human infants are born at an earlier stage of their overall brain growth, and as a result a much greater proportion of human infants' brain growth occurs outside the womb (Desilva and Lesnik 2006), while the individual is interacting with the world. This early developmental experience is hugely important to brain development, structuring the developing connections in the brain, and may perhaps have become adaptive in itself because of the extent to which it facilitates *learning* (Joffe 1997; Kaplan *et al.* 2000; Macdonald 2007; Grove and Coward 2008; Coward and Grove 2012).

Such extended 'human' life histories seemingly only begin to appear among pre-modern *Homo* as both body mass and brain size increase, and perhaps only became established among later groups such as those of *Homo heidelbergensis* and *Homo neanderthalensis* (Grove and Coward 2008; Robson and Wood 2008; Coward and Grove 2012). However, they clearly build on earlier developments such as the adoption of bipedalism by the basal hominins, and the shift towards higher-quality resources attested to by the appearance of stone tools among the archaic hominins.

Colonizing apes

The gradual incorporation of greater proportions of animal protein into the diet may not only have released constraints on brain size. It may also have actively selected for larger brains via its impact on hominins' ecological niches and distribution. Because higher trophic-level foodstuffs are much less abundantly distributed in the landscape, their consumers have larger geographical ranges – and foraging for more patchily distributed resources, or in more variable environments, may also select for 'ecological intelligence' and sophisticated 'mental mapping' skills (see e.g. Milton 1988; Janson and Byrne 2007 for review; though see also Reader and Macdonald 2003). It is notable that, while the distributions of most species are limited to specific habitats, modern humans are a global species, thriving in almost every terrestrial habitat known on Earth.

Increased carnivory may thus have been a significant preadaptation for the expansion of hominin ranges beyond their traditional homelands in Africa. At higher latitudes, seasonality is more pronounced, and resources are ‘patchier’ in both space and time (Kelly 1983; Gamble 1993, 118). Plant foods are also much less diverse, and a preadaptation to meat-eating and the use of fire (although the earliest currently-known known deliberate use of fire dates to only 790,000kbp (Goren-Inbar *et al.* 2004; see Gowlett 2010 for further discussion) may have been what allowed hominins to reach the Caucasus by 1.7mya (*Homo georgicus*; Gabunia and Vekua 1995; Gabunia *et al.* 2000), Pakistan perhaps as early as 1.9 ma (Dennell 2009, 138), the far East by 1.49ma (*Homo erectus*; Morwood *et al.* 2003), and northern Spain by 1.2ma (*Homo antecessor*; Carbonell 2008). Indeed, it seems increasingly likely that even earlier hominins made occasional forays out of Africa, perhaps leaving traces at Dmanisi (Vekua *et al.* 2002), Denisova (Krause *et al*. 2010) and on Flores in Indonesia (Aiello 2010; see also Dennell 2003, 2009 and Antón and Swisher 2004 for further discussion). However, these early ‘pioneer’ visits to northerly climes may not have been successful in the long term (e.g. Carbonell *et al.* 2010), and it is not until the environmental fluctuations of MIS 12 (~500,000bp), and the extinction of many of the large carnivores that would have provided fierce competition for animal protein (Turner 1992), that occupation of high-latitude regions became more widespread, this time by the later pre-moderns *Homo heidelbergensis* and (after ~300,000bp) the Neanderthals.

These northern hominins were at the very least highly competent scavengers. Their handaxes and wooden spears are found associated with the butchered skeletons of large animals (e.g. Callow and Cornford 1986; Goren-Inbar *et al.* 1994; Mellars 1996a; Thieme 1997; Roberts and Parfitt 1999), and isotopic analysis of Neanderthal skeletons from across northern Europe suggests that meat formed a substantial part of their diet (Fizet *et al.* 1995; Richards *et al.* 2000; Bocherens *et al.* 2001; though see also Henry, *et al.* 2011). While most of the raw material these hominins used to make tools is found very close to its source, some travelled up to 200km (Féblot-Augustins 1993; Féblot-Augustins 1997), suggesting range sizes more like those of carnivores than primates (Gamble and Steele 1999), and the skeletons of both species demonstrate distinctive adaptations to long-distance movement (Trinkaus 1993; Trinkaus and Hilton 1996; Stringer *et al.* 1998; though see also Pearson 2000).

Nevertheless, there are arguments that even the Neanderthals were less 'ecologically intelligent' than modern humans. Many modern human foraging groups organise their subsistence activities by logistical *collecting*, moving resource to people: individuals or small groups make logistical forays from longer-term encampments specifically to target specific resources whose scheduling and location is anticipated and planned for in advance. In contrast, it has been argued that Neanderthals were obliged to rely on a generalized *foraging* strategy, moving people to resources by decamping wholesale between resource-rich areas to gather and hunt opportunistically in the immediate vicinity of their camps (Binford 1983, 1996 [1980]; Kelly 1983). However, it is notable that many modern human groups also pursue generalized foraging strategies, or switch between the two according to the structure of their habitats (Binford 1978, 1996 [1980]; Kelly 1983), rather than because of any innate cognitive difference, and opinion remains divided as to how well these characterisations really fit Neanderthal and human subsistence strategies (see e.g. Peterkin 2001, 172 for review).

Clearly a variety of energetic and ecological co-adaptations were required for encephalization to be so adaptive. However, these do not wholly explain *why* bigger brains proved so successful; many species without big brains are capable of complex foraging behaviours (Humphrey 1976; Dunbar 1998, 178; 2003). The missing parts of the puzzle lie in the cooperative groups and social relations which scaffolded encephalization.

SOCIAL APES

Group life has a number of benefits aside from co-operative breeding, including co-operative foraging and increased security from predation. However, group life also involves considerable costs – especially intra-group competition for resources and mating opportunities. One means of balancing these costs and benefits is to maintain smaller-scale coalitions and alliances within the larger group (Dunbar 2003, 170). However, this requires individuals to maintain up-to-date knowledge of the ongoing soap opera of one’s own and others’ relationships, and the ‘Social Brain Hypothesis’ argues that while group size and complexity are themselves adaptive responses to ecological problems, it is primarily the cognitive demands of these relationships, rather than those of subsistence, technology etc. that drove cognitive evolution and encephalization among hominins (Dunbar 1992, 1998; Dunbar and Shultz 2007, 650).

Of course, members of some other species, most notably chimpanzees, maintain complex social relationships (e.g. de Waal 1982). However, unlike humans, chimpanzees show only a limited ability to empathize, i.e. to appreciate how those other individuals’ perceptions, thoughts and feelings may *differ* from their own, and to ‘putting themselves in another’s shoes’, a skill known as ‘Theory of Mind’ (see e.g. Penn and Povinelli 2007; Premack 2007, Kaminski *et al.* 2008).

Linguistic apes

Theory of Mind is a pre-requisite for the complex metaphorical and symbolic languages which are perhaps the most obvious distinguishing characteristic of modern humans.

These languages are not necessarily spoken ones: language is a system for representing and communicating complex concepts via a range of modalities, of which speech is only one, and there is some debate as to whether the two were associated from the first (e.g. Corballis 2010). Nevertheless, modern spoken languages and human vocal anatomy have clearly co-evolved (e.g. Deacon 1997), and the specialized anatomical features of the human vocal tract, torso and brain are commonly used as a proxy for language in the fossil record (Table 2). However, many of the most significant elements of human speech anatomy do not survive directly in the fossil record, and must be reconstructed from other lines of evidence. As a result, interpretations remain hotly contested (see references in Table 2).

<Table 2>

Another avenue of research has focused instead on the development of higher-level components of human language, notably symbolism. In even the most complex communication systems of other animals (e.g. the alarm-calls of vervet monkeys; Seyfarth *et al.* 1980), the movements and sounds which carry meaning are not symbolic – instead they are direct signals of the animal's internal state (its emotion, health etc.) and/or produced only in the direct presence of the thing to which they refer (the *referent*), and are thus *signs* or *indices*, rather than symbols (Deacon 1997, 54-59). In contrast, the basic linguistic elements of modern human language – words – are true *symbols* in that their relationships with their referents are arbitrary and established only by convention (thus the word *chien* works as well as *dog*, *ci* or *hund* as long as everyone in the group is in agreement; Deacon 1997, 59-68; Saussure 2006). This arbitrariness means that words (like any symbol) can be used to refer to things and concepts that are distant in space and time (or, indeed, that do not exist at all, such as pink elephants or unicorns).

To date, the evidence that other animal species can use symbols is limited. Captive primates have been able to learn the arbitrary associations between symbols such as letters, numbers, ideograms and Kanji characters, and their referents (Savage-Rumbaugh and Lewin 1994). However, their vocabularies remain small and their pronouncements limited in scope to very immediate requests, especially for food. Nor do chimpanzees seem able to combine symbols in the way characteristic of modern human languages (Matsuzawa 2010). Words, or symbols more generally, mean little in isolation, but combining them makes it possible to string together almost unlimited variations, and all human languages have grammars specifying how these combinations are made. In contrast, most symbol-using primates' combinations show little sign of any such structure (to date, the longest phrase produced by a chimpanzee [Nim Chimpsky] is: "Give orange me give eat orange me eat orange give me eat orange give me you"; Terrace 1979; Terrace *et al.* 1979).

The hierarchical nature of human syntax, in which sounds are combined into syllables, syllables into morphemes, morphemes into words and words into phrases and sentences, has led some archaeologists to argue that these grammars are extensions of more general systems of hierarchical combination, such as those seen in the manufacture of stone tools, where gestures must be combined in specific, highly constrained ways to achieve the correct result. If the same cognitive skills underpin both, the development of stone tool technology might act as a preadaptation for language and analyses of tools provide insights into its evolution (see e.g. papers in Gibson and Ingold 1993; Stout and Chaminade 2012). However, as yet the extent to which the two might be interdependent remains unclear.

Symbolic apes

Nor is there any agreement on how non-linguistic symbols might be recognized in the archaeological record. A number of kinds of evidence have routinely been used to 'diagnose' symbolism in the archaeological record, most notably evidence of 'art' and burial. However, in many cases it can be difficult to establish whether the claimed 'art' work was in fact created by hominins, and if so, whether it was created deliberately. For example, many apparent 'engravings' or incisions made on bone, wood or stone are likely to be the product of natural taphomomic processes rather than calendars or musical notation (d'Errico *et al.* 1998, 33; 2003, 18-19). Even if proven both anthropogenic and non-utilitarian, such behaviours do not necessarily demonstrate symbolism, and much otherwise suggestive pre-human evidence has fallen foul of these stringent requirements (see e.g. d'Errico *et al.* 2003 for a comprehensive review of the origins of symbolism).

The earliest indisputable evidence for symbolic art occurs in Europe and western Asia after c. 45,000bp, coinciding with the arrival in these regions of modern humans, and this apparent association of biological and cultural novelty has fostered one-stop 'explanations' positing punctuated cognitive developments such as the appearance of language (Mellars 1996b, 390; 2010) and fully 'multi-modal' cognition (Mithen 1996) – often via the fortuitous occurrence of an as yet unspecified genetic mutation (e.g. Klein and Edgar 2002; Klein 2008).

However, *Homo sapiens* as a species evolved much earlier than this; our characteristic anatomy develops gradually among African groups of *Homo heidelbergensis* after 250,000bp (Stringer 2002), and the archaeological evidence from these early African sites strongly suggests that the behaviours that later burst onto the European stage as a single ‘package’ in fact developed in a much more piecemeal fashion over a long period (see e.g. McBrearty and Brooks 2000, fig. 13; Barham 2010; D’Errico *et al.* 1998, for review and references). Furthermore, insights from neuroscience strongly suggest that language, like all complex behaviours, is not a single, discrete capacity but the product of a network of distinct but highly interconnected neurological components and circuits, each with its own semi-independent evolutionary trajectory (see e.g. Uttal 2003 for review of the evidence for language). To make any sense of the multiple, conflicting lines of evidence for the evolution of language and symbolism, we need to consider instead what it was about hominin lifeways that made these abilities and adaptations so useful.

Cultural apes

One clue lies in the observation that language is founded on much more fundamental social skills. Much recent research has highlighted the significance of social cognition in general, and Theory of Mind in particular, in providing the framework or *social scaffolding* (Vygotsky 1978) by which complex skills such as language, stone tool manufacture, hunting proficiency etc. are acquired.

A significant component of other species’ behaviour is also acquired socially, (see e.g. Whiten *et al.* 2007 for review), to the extent that some primates are now argued to have ‘cultures’ comparable to humans’ (e.g. Whiten *et al.* 1999; van Schaik *et al.* 2003). However, while individuals of many primate species are able to *emulate* one another, i.e. to reproduce the physical effects of the actions they observe, non-human primates seem less able to *imitate*, i.e. to infer the *goals* and *intentions* of others (Tomasello 1999). This kind of programme-level imitation requires Theory of Mind (Frith 2008; Knoblich and Sebanz 2008), which is also crucial for teaching, as being able to model others’ understandings allows teachers to actively intervene in and correct others’ actions and behaviours, and to date, true teaching of this kind is only known among humans (Tomasello 1999). In addition, true imitation of this kind allows *cumulative* cultural evolution, in which successive generations encompass and improve on the efforts of the last (Boyd and Richerson 1996; Tomasello 1999).

Mode 1 technologies do not seem to represent a significant extension of the motor repertoires known among primates, and arguably require only action-level emulation to reproduce successfully (Knoblich and Sebanz 2008). However, mode 2 and subsequent technologies involve stages of manufacture which do not produce immediately useful flakes but instead prepare for later stages of manufacture, suggesting that goal-level imitation is necessary to learn these techniques (Knoblich and Sebanz 2008) and that some elements of Theory of Mind may have developed relatively early in hominin evolution.

However, many other factors also affect cultural transmission (Shennan, this volume), and one alternative explanation for the persistence of relatively simple early material cultures is that groups were too small and too unstable, population densities too low, and range sizes too large (Layton and O'Hara 2010, table 5.1) to accumulate and sustain complex skills and knowledge systems (Cullen 1996; Shennan 2001; Powell *et al.* 2009; Premo and Hublin 2009; Premo and Kuhn 2010). In particular, symbols by definition can only exist as part of much wider systems of cultural conventions (Foster 1990, 519), and the dramatic archaeological developments of the European Upper Palaeolithic 'Revolution' may have had less to do with a dramatic leap forward in cognitive ability than with the networking abilities of Upper Palaeolithic populations entering increasingly inhospitable habitats (Knight *et al.* 1995; Cullen 1996a).

Nevertheless, such 'networking' itself requires some quite demanding cognitive skills. Humans are unique among primates in their ability to maintain social relationships with others even during prolonged absences (Rodseth *et al.* 1991, 240). Modern language, with its multiple tenses and referencing of distant people, places and things, certainly plays a significant role in this (Dunbar 2003, 178; see also Mellars 1996a, 390 for discussion and references). However, symbolic language may be secondary here to the mnemonic and metaphorical role of material objects, which 'stand in' for and reference other people and relationships, allowing the 'stretching' of social relations over temporal and geographical scales greater than those encompassed by individual memory – what Gamble has called a 'release from proximity' (Gamble 1996, 1998, 1999; see also Coward and Gamble 2008, 2010).

Regional-scale networks constructed through material practices such as trade and exchange allowed groups access to alternative sets of resources such as food, raw material, marriage partners and new blood – crucially, it also allowed the exchange of *information* about plants, animals, environments and skills, which may have made the difference between life and death in increasingly unstable climatic conditions.

When did this 'release from proximity' occur? One theory places it after 74,000bp, when the eruption of Mt. Toba on Sumatra triggered a global 'volcanic winter' causing severe drought in Africa. Already widely distributed across the continent at low population densities, early *Homo sapiens* reduced in number still further as many local groups died out. In such circumstances, it is argued, the cognitive skills involved in networking became increasing adaptive (see review and references in Ambrose 1998; Jones 2007, Williams *et al.* 2009; Fagan 2010, 94-7).

However, the true impact of the Toba eruption remains the subject of fierce debate (e.g. Balter 2010), and others would argue that the evidence supports a longer, slower and more gradual mosaic evolution of these behaviours. Evidence for increasing scale of social networks has been identified during the initial expansion of hominins out of Africa before 1.8ma (Gamble 1993, 169; 1999, 124), an argument that might be supported by claims that the Acheulean handaxe fulfils some social role relating to visual display or signalling (Kohn and Mithen 1999; McNabb 2007, 2012; Hodgson 2012). Indeed, even the movements of carefully chosen raw material, cores and 'finished' tools into and out of Oldowan sites (Bunn *et al.* 1980; Potts 1993; Schick and Toth 1995, 209-213; Torre *et al.* 2003, 204) could be argued to demonstrate a more developed form of material engagement than anything known among other primates (Coward and Gamble 2008; Coward 2010), suggesting that the abilities most unique to modern humans today in fact became adaptive very early in the process of 'becoming human'.

CONCLUSION

It can be easy to see hominin evolution as a succession of discrete biological 'types', each with its own distinct anatomy and behavioural repertoire. However, the process of becoming human was much more dynamic than this. Our hominin ancestors did not set out to become human, but to do the best they could in any given situation. Sometimes they found new ways of doing things, as a result of externally-driven environmental changes to their worlds, or through their own ingenuity in interacting with the world around them and its various denizens. These new strategies and behaviours in turn selected for certain biological traits; thus, many biological adaptations we see in the fossil record were not a *cause* of behavioural innovation, but a *result*.

Some of the earliest changes in lifeways dissociating the basal hominins from other apes involved bipedalism. Later, archaic hominins learned to strike flakes from cobbles to access hitherto unexploited resources, including the fatty and calorific bone marrow and brains left in carcasses abandoned by carnivores. It was the transitional hominins – succeeding, whether by luck or judgment, where the megadont archaics failed – and especially the early pre-moderns, who capitalised on these new skills. Their protein-rich diets powered expansion of their brains as part of a constellation of biological and social adaptations relating to changes in social life, childhood, development and growth, and increasing sophistication in culturally transmitted technological and subsistence practices.

These developments allowed some groups to expand their ranges beyond African habitats into more seasonal environments from time to time, probably moving in and out of the ‘biotidal zone’ of the Near East many times before colonization of more northerly latitudes became more or less permanent. These were already sophisticated adaptations that allowed pre-moderns across Asia to survive virtually unchanged for hundreds of thousands of years. Meanwhile, in the westernmost parts of their range some of these hominins became increasingly adept tool-makers, hunters and perhaps most importantly, highly sociable, and thrived in even extremely demanding climatic regimes.

This was not a straightforward, inevitable process; at many different times and in many different places different groups failed, moving on or dying out. Even when the diverse biological and behavioural adaptations popping up across Africa after 250,000 bp coalesced into *Homo sapiens,* the world-conquering finale was not inevitable. *Homo sapiens* is ultimately just ‘another unique species’ (Foley 1987). The Mt. Toba eruption may have brought us to the brink of extinction. Ironically, the aftermath of this near-extinction event may have taught us the harsh lessons we needed to become human – and even this was not always enough. When the ice descended at the last glacial maximum, populations across northern Europe fled or died out, not returning until much later, and it remains to be seen whether we will be able to survive the future climatic changes we have ourselves contributed to.

But what does ‘being human’ really mean? *Homo sapiens* has continued to evolve – the adoption of sedentism and domestication of plants and animals involved many biological, cultural, social and perhaps even cognitive changes (Larsen 1995; Watkins 2004a, b; Bocquet-Appel and Bar-Yosef 2008; Renfrew 2008; Coward 2010); others might point to the Enlightenment, or to the Industrial Revolution, as additional points of change. Even today, IQs continue to rise, perhaps because the kinds of intelligence these tests measure are more valued in contemporary western contexts (Neisser 1997; Flynn 2007), and arguments continue to rage over the social, cultural, biological and cognitive implications – positive or negative – of developments in human technology and lifeways, from junk food and video nasties to computer games, the internet and online social networking (e.g. Kurzweil 2006; Greenfield 2008). ‘Becoming human’ is not a simple, discrete event but a process which continues to this day: we are not yet done ‘becoming human’, and only by appreciating the route we have taken this far can we make decisions about where we want to go next.

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Mode	***Name***	***Description***	***First appearance***	***Associated with***
1	Oldowan	Core and flake tools; river cobbles split open to produce sharp edges, battered ‘core’ forms.	2.6mya (but attested to from 3.3mya), Ethiopia	Traditionally the transitional hominins, (especially *H. habilis*, the ‘handyman’) now also the archaic (*afarensis/garhi*)and possibly the archaic megadont hominins (*P. robustus*)
2	Acheulean	Bifacial retouch of large cutting tools (LCTs), especially the handaxe	1.65mya	Pre-modern *Homo* (especially *H. erectus* and *H. heidelbergensis*)
3	Prepared Core Technology (PCT)	Careful preparation of ‘tortoise’ cores to pre-determine the shape of the flake to be removed. Presumed use for hafting to spears.	~300,000yrs	Later pre-modern *Homo* in the Middle Stone Age of Africa; Neanderthals in the Levant and Europe
4	Blade technology	Prismatic blade techniques in which a series of long, narrow flakes (‘blades’) are detached around the circumference of a core, each new detachment using the edge of the previous flake scar as the central ridge of the next	~70,000yrs	Traditionally with *Homo sapiens* after 70,000 years but several blade-based techno-cultures from Middle Palaeolithic contexts are known
5	Microlithic technology	Blades produced as above ‘snapped’ into small, standardised trapeze shapes for use as armatures in composite technologies	~18,000 (a gradual reduction in size over time accelerated following the last glacial maximum ~18,000 yrs bp)	Modern *Homo sapiens*
6	Ground stone	Heady stone pieces such as axeheads laboriously ground smooth		Modern *Homo sapiens*

Table 1. Technological ‘modes’ of stone tool manufacture (after Clark 1968; Foley 1997; Geneste 2010). Each successive mode *adds to*, rather than replaces, the preceding. Note that modes 5 and 6, microlithic and ground stone technologies, appear *after* modern humans and are not therefore considered in depth here.

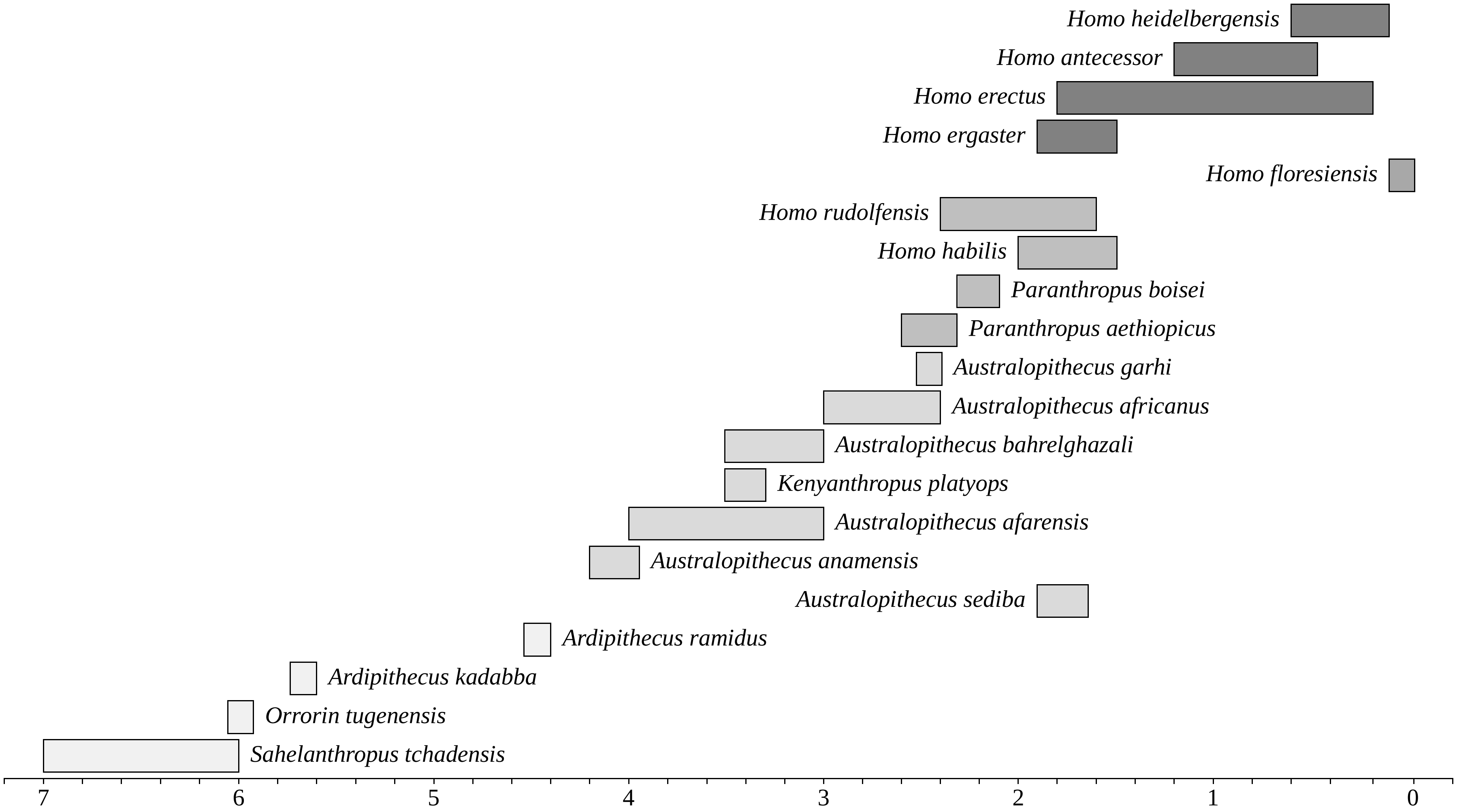
Factor	***Key contributors***	***Theoretical position***
Brain – size of neocortex and subdivisions	Dunbar 1996	Brain (neocortex) size and group size closely correlated among primates; measures of fossil hominins' brain size suggest group sizes significantly above the level of living primates from *H. erectus/ergaster*. Living primates sustain social relations by grooming, but time constraints made this impracticable for modern humans, who use vocal language as amore time- and energy-efficient means of group bonding. Thus increasing encephalization of fossil hominins is a good measure of the extent to which vocal language had supplemented gestural strategies during hominin evolution.
Brain – laterality	Steele 1998, 2000	Human morphological brain asymmetries are conserved hominoid features, but human function asymmetries are derived and may relate to selection for lateralized speech processing. Skeletal adaptations to loading have been argued to suggest an emergence of predominant right-handedness in *Homo ergaster*, and it is clearly present among Neanderthals.
Brain – cranial motor nerves	Kay *et al.* 1998; Degusta *et al.* 1999	Humans have relatively enlarged hypoglossal nerves (as indicated by the size of the hypoglossal canal), suggesting denser motor innervation of the tongue as a speech adaptation, and this enlargement is seen first in Neanderthals and pre-modern *Homo*
	Jungers *et al.* 2003	Corrected for the size of the oral cavity, the hypoglossal nerve of humans is not enlarged relative to those of other apes

	Coward 1999	Humans have a relatively marked enlargement of the mandibular branch of the trigeminal nerve, but not of the facial nerve (as indicated respectively by the sizes of the foramen ovale and of the stylomastoid foramen), suggesting denser motor innervation of the muscles of mastication as a speech adaptation. Traits not yet examined in fossil material.
Oral cavity	Duchin 1990	Chimpanzees cannot articulate because their tongues cannot reach target areas in the oral cavity due to the inclination angles of muscles; however, pre-modern *Homo* (*H. erectus* and Neanderthals) have relatively similar oral cavity morphology to modern humans
Supra-laryngeal vocal tract – larynx	Lieberman, P. 1984 Lieberman, P. *et al.* 1992	The distinctively human lowered larynx creates a pharyngeal cavity that is separate from the buccal cavity (the oral cavity is bounded on the sides by the cheeks); this configuration permits the production of a greater range of vowel sounds (and thus greater generativity in phonological elements of the speech signal). Basicranial flexion is a hard tissue marker of this trait, and is not yet established in Neanderthals
	Houghton 1993 Arensburg 1994	No reason to suppose on the basis of head and neck morphology that Neanderthals had any less linguistic capability than modern humans
	Boë *et al.* 2002	Study of the morphological and acoustic properties of the Neanderthal vocal tract suggests there was no morphological reason why they should not have been able to pronounce all vowel sounds as modern humans do

	Kandler & Martelli in prep.; Martelli *et al.* submitted	Humans and Neanderthals share some derived characteristics of the hyoid bone and hence potentially of laryngeal anatomy, although there may still have been some differences in their pronunciation of different vocal sounds
Supra-laryngeal vocal tract – hyoid	Lieberman, P. 1994; Lieberman, D. E. *et al.* 1998	Analysis of the Kebara hyoid (Neanderthal) cannot be used to reconstruct the fossil's supralaryngeal airway; variations in cranial base flexion do not predict hyoid position in humans or other primates
	Houghton 1993; Arensburg 1994	Kebara hyoid metrically and morphologically within the rand of variation of all recent humans; muscular imprints indicative of the positions of the hyoid bone in relation to the mandible confirmed a low position for the Neanderthal laryngeal vocal tract as among humans, but there is no agreement whether this implies limited speech capabilities for Neanderthals
Pulmonary function	Maclarnon & Hewitt 1999	Modern humans and Neanderthals have an expanded thoracic vertebral canal compared with australopithecines and *Homo ergaster*, suggesting selection for enhanced control of breathing in speech

Table 2. Anatomical markers for the evolution of speech and by extension language (amended from Buckley & Steele 2002, table 4)

Homo sapiens ■
Homo neanderthalensis ▨



'Lumping' taxonomy:

□ Basal hominins
░ Archaic hominins
▒ Megadont archaic hominins
▓ Transitional hominins
▨ Pre-modern Homo
■ Humans

Figure 1. Summary of hominin fossil species and grades known to date (after Wood 2010; Berger *et al.* 2010; Carbonell *et al.* 2008).

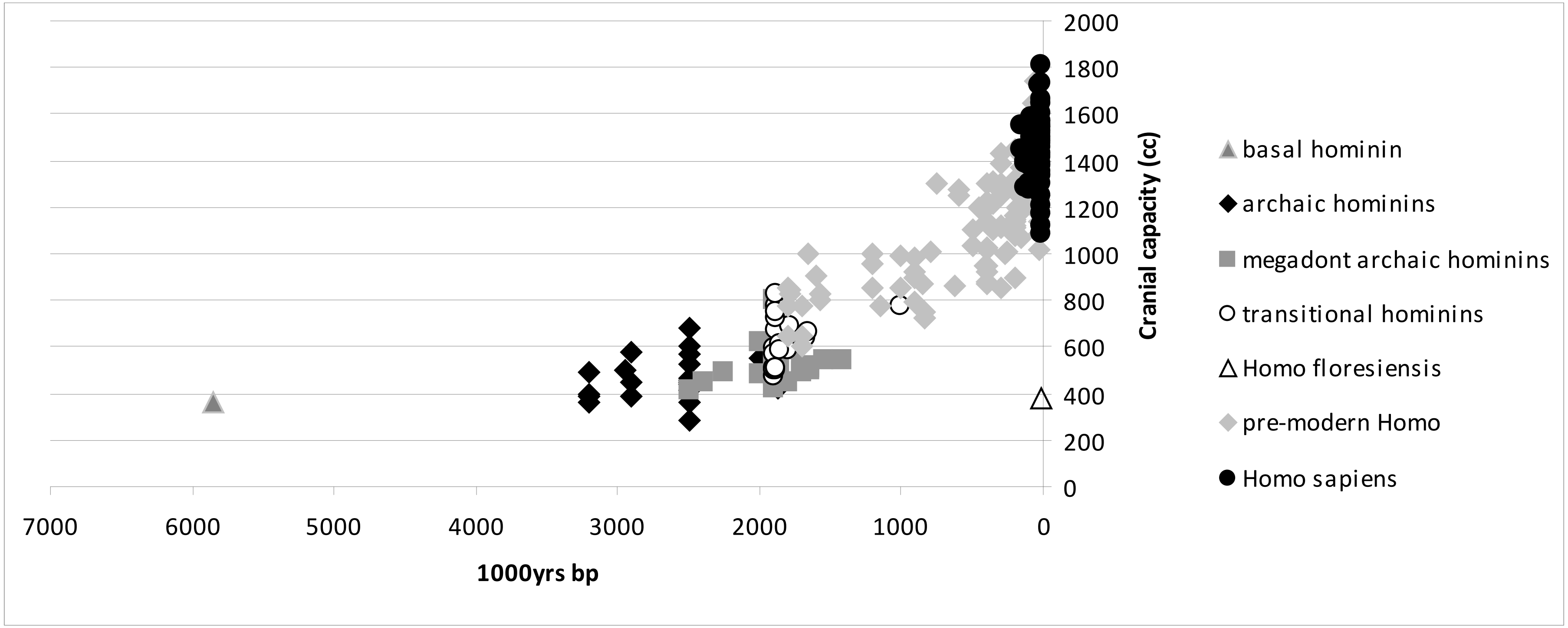


Figure 2. Cranial capacity of fossil hominins over time (data from de Miguel & Henneberg 2001, with additions from Berger *et al.* 2010 and Carbonell *et al.* 2008)