



# Control of Fire in the Paleolithic: Evaluating the Cooking Hypothesis

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“Control of fire in the Paleolithic: evaluating the cooking hypothesis”

Short title: “The cooking hypothesis”

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**Abstract)**

Except when accessing global markets of domesticated food species, *Homo sapiens* is biologically committed to a cooked diet. Since cooked diets have large physiological and behavioral consequences a critical question for understanding human evolution is when the adaptive obligation to use fire developed.

Archaeological evidence of fire use is scarce prior to ~400 ka, which suggests to some that the commitment to fire must have arisen in the mid-Pleistocene or later.

However weak jaws and small teeth make all proposals for a raw diet of early Pleistocene *Homo* problematic. Furthermore the mid-Pleistocene anatomical changes seem too small to explain the substantial impact expected from the development of cooking. Here I explore these and other problems. At the present time no solution is satisfactory, but this does not mean the problem should be ignored.

(133 words)

In this paper I consider the current status of the cooking hypothesis. I use 'cooking' to mean the processing of food with heat. The cooking hypothesis posits that control of fire leads to such a large increase in energy acquisition, and reduces the physical challenges of eating food so greatly, that the evolution of an obligation to incorporate cooked food in the diet should be recognizable by evidence of novel digestive adaptations and increased energy use; and that the only time in the fossil record when the appropriate changes are seen is the early Lower Paleolithic (Parker et al. 2016; Wrangham 2006; Wrangham and Carmody 2010; Wrangham et al. 1999).

The evidence for Lower Paleolithic control of fire has been increasing in the last decade (Alperson-Afil 2008; Bosinski 2006; Berna et al. 2012; Walker et al. 2016). Nevertheless numerous archaeological sites prior to the Upper Paleolithic challenge the cooking hypothesis because they find no evidence for the control of fire. European Lower Paleolithic sites such as Dmanisi, Atapuerca, La Caune d'Arago and Boxgrove represent in total a screening of thousands of unburned bones but no burnt bones (Gowlett and Wrangham 2013). Even in the Middle Paleolithic many Neanderthal sites have no fire evidence (Sandgathe et al. 2011a, b). Outside Europe the few cases where preservation conditions allow long sequences also offer puzzles. Tabun and Qesem caves lie near the Mediterranean coast about 100 km apart. In Tabun cave fire use was "regular or habitual" by 350-320 ka but burnt flints were scarce or absent during at least 50 ka of prior occupations (Shimelmitz et al. 2014). In Qesem, by contrast, the evidence of fire use is impressive back to 420 ka (Barkai et al., in press).

One interpretation of such cases is that absence of evidence really is evidence of absence. The implication is that populations of *Homo* occupied Europe during the Lower Paleolithic and later without the systematic control of fire, surviving on raw food for hundreds of thousands of years (Roebroeks and Villa 2011; Shimelmitz et al. 2014). Alternatively the archaeological visibility of fire may vary too much to allow the history of its control to be confidently reconstructed. For example Boxgrove was a damp shoreline site that might have been unsuitable for locating fire. Changes in the style of fire use over time could have biased preservation. Middle Paleolithic fire-sites might have been larger, or more permanent, or sited more often in caves than in earlier times (Gowlett and Wrangham 2013). For these reasons the debate over the meaning of *Homo* sites that lack any evidence of fire is unresolved, and I will not discuss it here.

I consider instead some conceptual and empirical challenges arising from the assumption that cooked food did not become obligatory until the mid-Pleistocene. The evolution of *H. erectus* is often discussed without mentioning the control of fire (e.g. Anton and Snodgrass 2012; Hrdy 2009; Isler and van Schaik 2012; Potts 2012). The implication is that either a later time can be confidently found for the origin of obligatory fire use, or fire control has only small effects on human adaptation, or both. But those implications are rarely considered carefully. I suggest that they are wrong.

Here, therefore, I assess the difficulty of understanding a date later than the origin of *H. erectus* for when cooking might have become obligatory. In the first section I review the current status of the cooking hypothesis. I then consider

some difficulties that follow from the assumption that *H. erectus* could not cook. Finally I consider problems for the cooking hypothesis.

### **(1) Current status of the cooking hypothesis.**

#### *1. Adaptation to cooked diets.*

The cooking hypothesis starts with the claim that unlike other animals *H. sapiens* has evolved an obligation to include cooked food in the diet, such that we cannot live without it. The idea has been intimated for at least half a century (Brace 1995; Coon 1962; Symons 1998) and directly supported more recently (Wrangham and Conklin-Brittain 2003).

Key evidence comes from research on raw-foodists, i.e. people who live for long periods on all-raw diets. Raw-foodist groups typically live in industrial societies on store-bought foods. Even though raw-foodists take little exercise compared to hunter-gatherers and have fewer disease challenges, on average they experience chronic energy shortage (leading to low BMI). In the only study of reproductive performance incompetent or absent ovulation left more than 50% of women on an all-raw diet unable to reproduce (Koebnick et al. 1999).

These physiological detriments are striking because the diet eaten by raw-foodists is extremely high quality compared to any known hunter-gatherer diet (if it was eaten raw). Most of the raw-foodists' diet is rich in digestible energy and low in structural fiber because it comes from domesticated species. Furthermore raw-foodists typically process the food extensively by non-thermal means (such as by blending) and (in spite of their supposed adherence to raw) often use heat

to lightly cook (up to around 114°F). In addition raw-foodists experience no important seasonal energy shortages (because they buy from globally connected markets) (Wrangham 2009).

Low meat intake does not account for the problems faced by raw-foodists. No relationship has been found for raw-foodists between BMI and the amount of meat eaten (Koebnick et al. 1999). Unlike meat-eating raw-foodists, vegetarians eating cooked diets thrive. They have high BMI and excellent ovarian function (Barr 1999, Rosell et al. 2005).

Cooking is thus more important than meat for human welfare. On the basis of contemporary evidence dogs *Canis familiaris* are the only nonhuman species that might be adapted to cooked food given that their pancreatic amylases are adapted to a high-starch diet (Axelsson et al. 2013; Reiter et al. 2016). However, it is unknown whether the relationship between dogs and cooked food is obligatory. Possibly dogs are merely able to take advantage of a cooked diet, and can survive without it if needed (as dingoes *Canis dingo* do, Whitehouse 1977). So with the possible exception of some domesticated species, *H. sapiens* is unique among living species by being evolutionarily restricted to diets that contain a substantial proportion of cooked food (Wrangham and Carmody 2010).

## 2. How does cooked food benefit consumer physiology?

Evidence of BMI reduction and reproductive problems among raw-foodists

indicates that cooked food provides higher net energy gain than raw food. Feeding experiments with mice support this prediction for all three major macronutrients, i.e. long-chain carbohydrates, proteins and (plant) lipids (Carmody et al. 2011; Groopman et al. 2015). On raw diets (sweet potato tuber, meat or peanuts) mice typically lose weight, whereas on cooked diets they maintain weight.

One reason is that digestibility is increased. With regard to starch, ileostomy experiments with five domesticated plants (oats, wheat, plantain, green banana, potatoes) eaten by humans indicate that cooking raises starch digestibility in the small intestine by amounts that vary across foods from 28% to 109%. On the conventional assumption that due to fermentation by the microbiome 50% of starch energy is recovered from the colon, the median increase in net energy gained is 30.2% (Carmody and Wrangham 2009).

Schnorr et al. (2015) and Henry (in press) noted that the effects of cooking in human evolution are best studied in wild plants roasted on open fires rather than in domesticated plants cooked with contemporary methods. They assessed the energetic impact of brief roasting times (average 8.7 minutes) on four species of tuber eaten by Hadza. Three of the species were normally cooked and one was normally eaten raw. Schnorr et al. (2015) found that such cooking led to much variation in *in vitro* starch digestibility both within and between species. In two species cooking led to a 10% increase in glucose availability, whereas in the species typically eaten raw (*Ipomoea transvaalensis*), glucose absorption fell after roasting. Schnorr et al. (2015) concluded that starch gelatinization is not



necessarily a route by which cooking increases net energy gain. Instead, after finding that brief periods of roasting made tubers much easier to chew, they suggested that cooking could increase net energy gain by making chewing more efficient. Cooking also makes tubers easier to peel, which Henry (in press) suggested was its main benefit. Such experiments are promising but as Schnorr et al. (2015) noted, they are at an early stage since they have considered only glucose, have not taken account of variation in quality within food species, and rely on *in vitro* measures of digestibility.

Other energy benefits of cooking have been less well quantified. They include a reduced cost of digestion (snakes: Boback et al. 2007; rats: Carmody 2012), shorter and less vigorous chewing times (humans: Zink et al. 2014), increased chewing efficiency (Dominy et al. 2008), and reduced investment in immune defences when meat is eaten (Carmody and Wrangham 2009; Carmody et al. 2016). In addition, cooked food is more quickly digested than raw food, which means that if extra food is available the total rate of energy acquisition per day can be higher.

In the case of plant lipids, a principal mechanism by which cooking increases digestibility concerns the common way in which they are stored in oil-seeds. Oil-seed lipids are stored in oil-bodies surrounded by proteins called oleosins that present a hydrophobic interior surface and a hydrophilic exterior. Cooking denatures the oleosins and thereby makes the lipids available for faster digestion (Groopman et al. 2015).

No tests of the effects of cooking on energy gain have yet been conducted

with animal lipids, which are mostly stored as droplets inside adipocytes or other cells. The lipid droplets of vertebrates and insects are coated with proteins of the perilipin family (Arrese and Soulages 2010; Brasaemle 2007). The effect of heat on denaturation of perilipins appears to be unknown. The physical effect of heating solid fats to liquid forms or thin layers could be important in promoting release of lipids from adipocytes. Furthermore the thinning of fats into oils could facilitate more rapid digestion given that digestive lipases are active only at oil-water interfaces, where they depend for their effectiveness on lipids presenting a high surface area (Lentle and Janssen 2011). How much such effects matter is unknown. There are numerous ethnographic reports of eating raw animal fat (Ben-Dor et al. 2016). Variation in fat type could be important. It might be more beneficial to cook lipids that have high melting points.

The uncertainty about effects on animal-sourced lipids as well as limited experimental study for all macronutrients mean that the energetic impact of cooking is not well quantified. Progress in solving this problem will be slowed by numerous sources of variation, including the physical states of the diet, such as whether it is eaten cold or hot, blended or whole, mixed or pure, and fresh or fermented. However, even though the energy gain from eating food cooked is poorly known there are clear indications that the amount is large enough to have major fitness consequences. The figure of 30.2% increase for starch may well be on the low side because it is derived solely from considering digestibility, excluding reduced costs of digestion, increased food safety and reduced time digesting. Effects of cooking a starch-rich food appear broadly similar to those for

cooking protein-rich food (meat) and lipid-rich food (nuts) (Groopman et al. 2015). Thus a 30% gain in energy seems a reasonable starting-point for considering the impact of cooking.

Much smaller increases in energy have large fitness effects in the wild. When chimpanzees of the Kanyawara community in Kibale National Park, Uganda, were able to eat 5% more fruit in their diet than usual (thanks to improved fruit availability) they experienced a 4-month reduction in waiting time to conception (Emery Thompson and Wrangham 2008). Numerous similar examples in large nonhuman primates indicate that even modest increases in net energy gain have substantial positive effects on fitness. The estimated 30% impact of cooking on calorie is therefore comparatively massive. It is also exceptional because compared to many changes in diet (e.g. addition of fat-rich meat) it works both during periods of food scarcity and during periods of abundance.

### 3. *Could H. sapiens live without cooked food in the wild?*

No human populations are known to live without cooking, but might it be possible? L. Glowacki (pers comm) observed that unmarried Nyangatom men in cattle camps in southwestern Ethiopia sometimes spend several weeks or a few months living solely on raw blood and milk. While this diet leaves the men thin, it raises the question of whether African populations of *H. sapiens* might have been able to survive on a diet that was sufficiently focused on equivalently fat-rich and/or easily chewed raw wild foods, such as oil-seeds, marrow, brains or guts.

In African habitats seasonal variation is a problem for both oil-seeds and marrow (Speth 2010). Oil-seeds can be vanishingly scarce, while the fat content of herbivore marrow declines from more than 90% dry weight at the best time of year to 2-3% at the worst (late dry and early wet seasons: Dunham and Murray 1982, Lupo 1998). So oil-seeds and marrow are unreliable sources of energy year-round (Speth 2010).

However brain fats are never depleted, remaining around 50-60% dry weight all year (Carlson and Kingston 2007; Stiner 1994). So conceivably a sufficient abundance of brains could give modern humans the basis for surviving as wild raw-foodists during food-scarce seasons. How much brain would be required is therefore an interesting question. If the diet needs to be ~50% fat (i.e. for an animal-based diet, Speth 2010), and brains are roughly 50% fat, then a near-exclusive diet of brains might be predicted. Availability of other foods rich in fats or easily digested carbohydrates would lessen the reliance on brains.

Intestines, especially of ungulates, could also represent an important item of diet partly because semi-digested chyme would provide an easily accessed source of energy. Furthermore they are readily eaten by Hadza (Buck et al. 2016).

In sum, there is no evidence of modern *H. sapiens* populations surviving on raw foods, but possible diets allowing earlier *H. sapiens* to have lived without fire require easily chewed and/or fat-rich foods, of which brains and guts are the most plausible. But these scenarios are speculative. Despite cooking their main meals, even well-adapted Arctic populations living on high-fat diets suffer

extreme food shortages (Balikci 1989, Hardy et al. 2015). It is doubtful that they would survive if they were forced to eat all their food raw.

#### 4. *Why does H. sapiens find it so difficult to thrive on raw foods?*

The inferred inability of *H. sapiens* to survive on raw wild diets is explicable by a series of adaptations that have apparently promoted efficiency in processing easily digested foods at the expense of being able to process relatively indigestible foods. The best-known adaptations are the diminution of the human mouth, jaw muscles, jaw, incisors, molars, stomach, cecum and colon compared to those of nonhuman primates (Martin et al. 1985; Perry et al. 2015; Ungar 2012; Wrangham 2009). Overall, Aiello and Wheeler (1995) estimated that the human gut is 60% of the expected size for a primate. Note that Hladik et al. (1999) presented data to claim that the human gut was the same size as expected in a non-human primate of the same body size. However their data were solely for absorptive mucosa, i.e. the small intestine. In humans the small intestine is indeed the size expected by body mass, whereas the big reductions are in the cecum and colon (Martin et al. 1985). These reductions appear to be responsible for humans having a relatively small intake of dry weight of food per day compared to nonhuman primates (Barton 1992), and being relatively poor at digesting long-chain carbohydrates (Milton and Demment 1988). Presumably the reductions could not have evolved until consumers had consistent (year-long) access to appropriately calorie-dense, easily chewed and easily digested foods.

Numerous parallel adaptations to cooked food can be expected in

physiological traits, such as in digestive enzymes. A leading candidate is the amylase system, which has been putatively associated with increased consumption of starch (Perry et al. 2007), specifically cooked starch (Hardy et al. 2015). Compared to chimpanzees and bonobos, humans have been found to have a three or more times increase in copy number of the salivary amylase gene *AMY1*, which appears responsible for levels of salivary amylase protein being at least three times as high as in *Pan* (Perry et al. 2007). No increase in salivary amylase copy number compared to *Pan* was found for Neanderthals or Denisovans (Perry et al. 2015). In theory this could mean that adaptation to cooked diets occurred in the *Homo* lineage after the splits from Neanderthals and Denisovans. However only one individual has been characterized for each of the latter species; and it is not known whether duplication of amylase is associated with increased starch consumption (Carpenter et al. 2015). Even if it were, whether the amylase difference between *Pan* and *H. sapiens* is associated with cooking, or only with an increase in the starch component of the diet, is unknown (Perry et al. 2015). More information is therefore needed to make the amylase system informative about the history of cooking.

A different approach to investigating physiological adaptations to cooking uses gene expression. Carmody et al. (2016) found that genes expressed in the livers of mice eating cooked food have been under positive selection in *Homo sapiens*, Neandertals and Denisovans. The cooking-related genes were associated with lipid-related metabolic processes on meat diets, and with carbohydrate-metabolic processes on tuber diets. While this research has not

identified a specific cooking-related phenotype it suggests that human adaptation to a cooked diet occurred prior to the evolution of Neandertals and Denisovans, i.e. before 550 – 765 ka (Prüfer et al. 2014). However similar cautions apply as to the amylase studies.

The question arises as to why Neandertals would have had “cooking genes”, given evidence that they sometimes lived without using fire (Henry in press). One possibility is that Neandertals cooked sufficiently often to maintain their genetic adaptation. Another is that the genes were retained from a cooking-dependent ancestor, despite a low frequency of cooking.

#### 5. *What diet type shaped the digestive anatomy of H. erectus?*

The evidence of predictable high energy gain from eating foods cooked is helpful because the evolution of *Homo erectus* was marked by an increase in total energy expenditure (e.g. Anton and Snodgrass 2012). Importantly, there is no subsequent time in human evolution when a marked increase in energy use has been suggested. Since cooking is strongly associated with an increase in energy gain, it is therefore predicted to have been adopted by *H. erectus* (Wrangham 2006). Paleoanthropologists routinely attribute increased energy use by *H. erectus* to increased reliance on animal source foods (e.g. Zink and Lieberman 2016). However contemporary evidence indicates that cooking has much greater impact on energy gain than meat, as shown by the robust performance of vegetarians eating cooked food compared to meat-eating raw-foodists (See above, (1) 1. *Adaptation to cooked diets*).

Changes in *H. erectus* anatomy are critical for reconstructing diet. *H. erectus* digestive anatomy is known from teeth and jaws, and inferred from rib-cage and pelvis. *H. erectus* incisors and molars were markedly smaller than in *H. habilis*, especially the third molar (Ungar 2012). Their jaws were similar in absolute size to *H. habilis* (Anton and Snodgrass 2012), which means that in relationship to body mass the jaw of *H. erectus* was relatively small (Wood and Collard 1999: body mass estimates: australopithecines 36-44 kg, *H. habilis* 34 kg, *H. erectus* 57 kg).

Aiello and Wheeler (1995) proposed that *H. erectus* also experienced a major reduction in the size of the gut, based on a reconstruction by Schmid (1983) of the rib-cage of *H. erectus* as being barrel-shaped compared to more bell-shaped in australopithecines and living great apes: the flared shape is thought to allow a large intestinal capacity below the ribs. In addition the pelvis was seen as relatively narrow compared to earlier hominins, suggesting a small intestinal floor supporting what was therefore considered to be a relatively small gut compared to prior species. These points supported the idea that *H. erectus* acquired a small gut at about the same time as getting smaller teeth, mouth and jaws.

However subsequent analysis has changed the reconstruction of the *H. erectus* pelvis, because *H. sapiens* now appears to be the only species of *Homo* with a reduced pelvis compared to australopithecines (Holliday 2012). This means either that the size of the pelvis is less informative about the volume of the gut than Aiello and Wheeler (1995) suggested, or that the *Homo* gut



remained large until the evolution of *H. sapiens*. For the moment I assume the former conclusion, i.e. the pelvis is not well correlated with gut size (see (3) 3).

The idea that these changes to the jaws, teeth and guts were the result of a dietary improvement is universal, and the leading candidate diet has long been increased animal source foods, especially high-fat meat and marrow. However the animal-food idea faces a major difficulty. Dietary adaptations must be relevant not only to preferred foods but also to fallback foods, i.e. those eaten during periods of food scarcity. Such fallback periods occur frequently, approximately every year, regardless of habitat: they are found even in rainforests for great apes (Marshall and Wrangham 2007), and are well documented for African dry-country hunter-gatherers (Speth 2010).

So the difficulty is to understand what an importantly carnivorous *H. erectus* would have eaten during the inevitable periods when animal products were inadequate. Presumably *H. erectus* incorporated some plant matter in their diets just as recent hunter-gatherers do. But unlike hunter-gatherers, if *H. erectus* did not control fire they would have had to eat their plants raw. Since neither molars nor guts indicate an ability for *H. erectus* to utilize raw plants high in structural fiber, this makes no sense. Either a solution must be found to this problem, or *H. erectus* had to cook. Two non-cooking solutions are worth considering.

First, the reduced digestive system could have been made possible by a commitment to fat-eating as implied by Ben-Dor et al. (2011). As discussed for *H. sapiens*, prey brains would have been one of the few sources of fat in fallback

seasons for *H. erectus*. This hypothesis should eventually be testable by the fossil record.

Second, *H. erectus* might have physically processed plants (likely underground or underwater storage organs, USOs) prior to consumption in ways that allowed teeth to be functional despite being small, and/or that allowed fermentation to occur without a large colon. Zink et al. (2014) and Zink and Lieberman (2016) proposed this scenario after showing that mechanical tenderization decreased the toughness of tubers by 42%.

Against the proposed importance of physical processing, however, mechanical tenderization has limited benefits to judge from the fact that raw-foodists suffer energy deficiencies despite using electrical blenders to produce smoothies. Furthermore no ethnographic or primate models seem to be known of physically processing a food for consumption raw. Contemporary foragers sometimes use techniques such as hammering (to extract an edible seed), but the seed itself is not smashed unless it is due to be cooked. These arguments mean that *H. erectus* was unlikely to have been able to live off raw plant foods even if they were mashed. Accordingly even if *H. erectus* had an ape-sized gut the puzzle remains of why teeth, jaws, jaw muscles and mouth size became reduced.

#### 6. *Did H. erectus have the cognitive ability to cook?*

Warneken and Rosati (2015) have shown that chimpanzees have the cognitive ability to understand the transformative effects of cooking, and sufficient

inhibition to carry food to a cooker rather than eat it unripe. This indicates that *H. erectus*, with a presumably greater understanding of cause-effect relationships and more inhibitory ability, was plausibly able to cook.

### *7. Use of honey.*

The symbiotic relationship between humans and greater honeyguide birds, *Indicator indicator* has been proposed to depend on a long evolutionary history of controlling fire (Crittenden 2011; Marlowe et al. 2014; Wrangham 2011). Honeyguides are genetically adapted to leading humans towards *Apis mellifera* bee-hives, from which humans extract honey-comb. Humans benefit by finding honey more quickly, while honeyguides benefit by feeding on otherwise unattainable products (Spottiswoode et al. 2016). African hunter-gatherers use smoke to quell the bees' defensive response, suggesting an ancient control of fire. However this proposal has been weakened by Kraft and Venkatamaran's (2015) finding that some populations of honey-collectors use plant volatiles rather than smoke to control bees. So collecting *Apis* honey in the Paleolithic might not have depended on controlling fire.

## ***(2) Problems in understanding adaptations of H. erectus if they were limited to raw food.***

### *1. Scavenging on raw food would be difficult except for marrow or brains.*

Eating of meat and marrow is evidenced back to 2.5 million years ago (de Heinzelin et al. 1999), and arguably to 3.3 million years ago (McPherron et al.

2010, but see Domínguez-Rodrigo and Alcalá 2016). However only by 1.8 million years ago do hominin sites indicate regular butchering of large animals (Potts 2012). This suggests that *H. erectus* was the first species to rely extensively on access to animal foods, and raises the question of how they escaped a high risk of disease from pathogens (Ragir et al. 2000). One answer would be a focus on eating marrow, which has a low bacterial load as a result of being protected inside bone (Smith et al. 2015). Brains are probably similarly safe.

Nevertheless cut-marks show that edible meat portions were also commonly removed. Careful attention paid by the butchers to identifying dangerously infected sections of meat would have helped reduce the dangers of eating raw wild meat, but cooking would still have been a safer strategy (Smith et al. 2015).

## *2. Hunting effort would be mysterious (time would be constrained if food is raw)*

Although exploitation of meat and marrow can lead to high gains, nowadays those foods are not dependable as a source of calories for tropical hunter-gatherers because the amount of animal food obtained on any given day is often inadequate (Speth 2010). This suggests that the same would have been true in the Lower Paleolithic. Accordingly individuals who invested in trying to hunt or find carcasses would sometimes fail, and would therefore need to have an alternative source of food that day. The problem is easily solved in modern humans: when an entire group runs short of animal products, they are able to eat starchy plant foods that are consumable quickly because they have been

cooked. Plant foods are generally less satisfying than animal foods, but their merit is that they are more easily obtained and are therefore relatively predictable. However, the value of plant foods depends on their being cooked, not only because cooked plants provide more energy than raw plants but also because they can be eaten much faster (perhaps in 10-20% of the time needed for raw plants, Organ et al. 2011). Without access to cooked food, failed hunters would need many hours to chew and digest plant foods that would provide their daily energy requirements. This means that a significant increase in the amount of meat eaten, as occurred most clearly with *H. erectus*, depended on having cooked food as a substitute food resource on days when no animal source foods were obtained (Wrangham 2009).

### *3. Brain size increase in H. erectus would be challenging to understand*

Aiello and Wheeler (1995) recognized two major rises in human brain size (cf. Rightmire 2004). First was around 2 million years ago, including *H. habilis/rudolfensis* and *H. ergaster*, which they attributed to increased meat-eating. Second was in the latter half of the Middle Pleistocene. They suggested that cooked food could have been an important factor in the second rise.

If the mid-Pleistocene increase in cranial capacity was due to hominin exploitation of cooked food, the fact that cooked food increases energy gain by 30% or more should be recognizable in other changes also. But in the Mid-Pleistocene there are no other significant signals of improved dietary quality, nor any marked decline in tooth size that would be expected to accompany an

increasingly tender diet produced by cooking. This makes the idea of cooked food being introduced at that time problematic.

Fonseca-Azevedo and Herculano-Houzel (2012) drew attention to a second difficulty with postulating that the positive influence of cooked food on brain size was not achieved until the mid-Pleistocene (i.e. with *H. heidelbergensis*). Based on extrapolation from living primates they calculated the metabolic cost of servicing bodies and brains of hominin species. Noting that a combination of large body and large brain is a difficult challenge because of the high maintenance costs of both, they found that if *H. erectus* ate only raw food they would be required to chew for as many hours per day as a gorilla, i.e. up to 8 hours or more. Their calculation seems to be an under-estimate since it assumes that digestive effectiveness was as high in *H. erectus* as in gorillas, which seems unlikely given the smaller teeth (and possibly smaller gut) of *H. erectus*. The demand of exceptionally high foraging time (which would necessarily be associated with high resting time to allow digestion to occur) appears to be impossible for a species that supposedly had high travel distances (cf. Organ et al. 2011).

Fonseca-Azevedo and Herculano-Houzel (2012) concluded that *H. erectus* and subsequent species needed to eat cooked food in order to obtain enough calories per day to satisfy the combination of larger bodies and larger brains without spending all day chewing.

The major alternative is that *Homo* (starting presumably with *H. habilis*) fuelled their larger brains thanks to a diet that included more raw meat and fat

products of animals than before (Leonard et al. 2007). This is premised on animal foods being more energetically efficient than plant foods. In favor of this explanation, among carnivores a diet richer in vertebrate animals is correlated with increased relative brain size (Swanson et al. 2012). Against it, allometric variation in carnivore brain size is explained principally by between-family differences (Finarelli and Flynn 2009). Within families, the most striking variation in eating vertebrates is found in the Ursidae, from the vegetarian giant panda *Ailuropoda melanoleuca* to the vertebrate-eating polar bear *Ursus maritimus*. If meat products are important for brain growth, polar bears should have relatively large brains. But although larger bear species eat more vertebrates, the slope of brain volume on body mass is the same in bears as in basal Carnivora. So bears have larger brains than other carnivores without any evidence that a diet incorporating more meat influences this relationship (Finarelli and Flynn 2009).

If cooked food explains the rise in brain size in *H. erectus*, what explains the later, mid-Pleistocene, grade shift in brain size (Rightmire 2004)? One possibility is that developments in hunting ability led to increased procurement of fat-rich prime adults, compared to weakened, fat-depleted, prey (Stiner et al. 2009). The interesting problem that remains is how sufficient dietary fat could be maintained during seasons of food scarcity.

#### *4. Running would not be favored without the use of fire*

Endurance running is a unique human ability compared to other primates. Bramble and Lieberman (2004) argue that it is made possible by various

anatomical adaptations in *H. sapiens* that occur also in *H. erectus* but not earlier, including features that promote stabilization of head and trunk, and energy storage and shock absorption in the foot. Their proposals have been criticized on the basis that australopithecines may have had the same adaptations, allowing them to be equally effective endurance runners (Pontzer 2012).

Physiological adaptations for endurance running include increased ability to lose heat compared to apes, such as longer legs in relation to body mass (Pontzer 2012). Loss of body hair would make a particularly important contribution to the ability to lose heat. In support of an early loss of body hair (and the associated evolution of pubic hair), the human pubic louse *Pthirus pubis* diverged an estimated 1.84-5.61 ma from its closest living relative (*P. gorillae*, the gorilla louse) (Reed et al. 2007).

However a critical function of body hair is to retain heat during sleep, which means that sufficient reduction of body hair to allow endurance running would seem to depend on a system of heat maintenance during sleep other than an insulating layer of hair.

Clothes are one possibility, but parasite evidence indicates clothes were adopted relatively late. Thus clothing appears to have been responsible for a functional split between head lice and body lice (both *Pediculus humanus*), which are estimated to have been genetically separated since 83-170 ka (Perry 2014), long after the evidence for endurance running.

Other than clothing the obvious way for a species with reduced body hair to keep warm at night is to use fire (Wrangham 2009). This suggests that



endurance running could not have occurred without the loss of body hair made possible by the control of fire.

In sum, endurance running presumably depended on the loss of an insulating layer of hair, and therefore on non-insulated humans being able to warm themselves at night by a fire. The evidence for Lower Paleolithic endurance running therefore suggests that fire was controlled by then.

##### *5. Sleeping on the ground would not be favored without the use of fire*

The adaptations of *H. erectus* to terrestrial locomotion include reduced climbing ability. Having an essentially modern frame with long legs, *H. erectus* cannot be expected to have been able to climb into trees every night to make a bed of leaves and twigs in the way that most great apes do. They therefore presumably slept on the ground (Coolidge and Wynn 2006). Gorillas regularly sleep on the ground, and so do chimpanzees in some populations, but only where predators are not a serious risk (Koops et al. 2007). Terrestrial sleeping for humans in a predator-rich savanna, by contrast, can be expected to be very dangerous. Even today people in lion-rich environments are most vulnerable to predation shortly after dark (Packer et al. 2011). Accordingly the reduction of climbing adaptations that occur with *H. erectus* appears to signal the simultaneous evolution of a method of achieving safety at night. Control of fire is the obvious possibility since it is the principal method used by modern humans sleeping in the kinds of habitats occupied by *H. erectus* (Wrangham and Carmody 2010).

Shipman (2009) objected to this proposal by noting that antelopes sleep on the ground without fire. However antelope sleep less than humans (Richard Estes, personal communication). Smaller species tend to hide at night, e.g. under bushes. Larger species avoid cover and prefer to be in the open. Although no detail is known about sleeping patterns of African ungulates they certainly do not have long periods of relaxed sleep. Even domesticated ungulates sleep briefly: according to Elgar et al. (1988, 1990) total sleep time per 24 hours is less for artiodactyls (mean 5.3 h) and perissodactyls (4.8 h) than in 10 other orders of mammals, including primates (10.3 h). In relation to body mass domesticated ungulates also have the shortest cycle of REM sleep and slow-wave sleep of 9 orders of mammals, whereas primates have the longest. Short REM cycles in ungulates fit with the observation by Richard Estes (personal communication) that wildebeest (*Connochaetes taurinus*) sleep deeply for only a few minutes at a time. In general, species in riskier environments have less REM sleep (Lesku et al. 2006).

Thus ungulates sleep little compared to humans, enabling them to be relatively vigilant, and they sprint faster. Yet their mortality from predation is clearly much higher than in humans. Among Kalahari foragers, data collected by Polly Wiessner indicated that predation risk on humans is sharply higher when sleeping without fire than when fire is present (Wrangham and Carmody 2010).

In short, the pattern of sleep by large herbivores is not an argument against the claim that *H. erectus* would have been very vulnerable if they slept on the ground unprotected by fire or some alternative system. The proposal that *H.*

*erectus* did not control fire therefore demands a novel explanation of their defenses at night, such as the evolution of an ungulate-like pattern of sleep, a surprisingly good ability to sprint, and/or the building of effective fences.

### **(3) Problems for the cooking hypothesis**

#### *1. Why were population densities so low?*

Cooking presumably increased both the range of foods that could be eaten and the total energy gained from those foods. Yet although *Homo* achieved a wide geographical distribution around the time of *H. erectus* it appears to have been a relatively unsuccessful genus in terms of its population densities and total numbers, at least intermittently. Later, Neanderthals were in small, widely dispersed groups, and *H. sapiens* experienced a severe bottleneck around 70,000 years ago. How do we reconcile the benefits of cooked food with the poor ecological success of *Homo* prior to agriculture?

One possibility is that by adapting to forego the ability to eat fiber-rich foods (such as raw leaves, stems and USOs), *Homo* boxed themselves into requiring even higher-quality foods than before. Such foods would be animal products and low-toxin, low-lignin plants containing high concentrations of sugar or starch. The acquisition of adaptations to take maximal advantage of cooked may thus have been a Faustian pact in which the benefit of high-quality foods was set against the loss of ability to digest foods on which other hominoids (such as chimpanzees and orangutans) can readily survive.

#### *2. Why was H. habilis intermediate?*

There is increasing evidence that the evolution of *H. erectus* was not a single “Adamic” event (Hublin 2015) but a “fuzzy transition” occurring in a complex series of shifts (Anton & Snodgrass 2012; Anton et al. 2014). This means that whatever the dietary change responsible for *H. erectus*, its impact took time to be felt; and geographical variation suggests that the process happened erratically in space.

Thus the conclusion that *H. erectus* was the first obligatory cook leads to the expectation that species prior to *H. erectus* would not show indications of being adapted to cooked food. In line with this prediction, *H. habilis* has a similar postcanine crown size to *A. africanus*, and a similarly robust jaw in relation to body mass (Wood and Collard 1999, Eng et al. 2013).

However there are at least two problems that the cooking hypothesis must deal with. First, based on one specimen (OH13) Eng et al. (2013) modeled *H. habilis* as producing only a low maximum bite-force, in line with later *Homo* and different from the higher bite forces of *Australopithecus* (and contemporary great apes). This result came from *H. habilis* having a relatively small second molar. Eng et al. (2013) therefore suggested that *H. habilis* might be adapted to foods that had been mechanically processed to reduce their toughness or other physical challenges. In support, dental microwear studies indicate that *Australopithecus* ate tougher foods than *H. habilis* (Ungar and Scott 2009; Villmoare et al. 2015). Thus a potential solution to *H. habilis* having a craniofacial structure that is to some extent intermediate between *Australopithecus* and subsequent *Homo* is that a period of mechanical processing preceded cooking.

While this makes sense given that stone tools that could cut and pound food were available long before *Homo erectus*, it also raises the possibility that the reduced craniofacial robusticity of *H. erectus* reflects a continuation of the same process (Zink and Lieberman 2016). According to this idea mechanical, non-thermal processing became even more important and/or effective in *H. erectus* than in *H. habilis*, and accounts for the small teeth (a reduction of ca. 25% in size), shorter face and more lightly built jaw.

The second challenge has a similar implication of being able to explain *H. erectus* biology on the basis of adaptations begun in *H. habilis*. Before “Homologization” of the jaw and teeth, brain size in *H. habilis* had risen from the australopithecine level of 385-571 cc to 510-750 cc (Anton et al. 2014; Spoor et al. 2015). Whether this was due to increased animal foods in the diet, non-thermal processing or some other change, the increase in diet quality that is indicated by the rising brain size in *H. habilis* could have been continued and caused the changes seen in *H. erectus*.

A solution offered by the cooking hypothesis is that prior to the obligatory adaptation to cooking indicated for *H. erectus*, *H. habilis* used fire intermittently. As a result they were able to regularly eat relatively tender food (as indicated by microwear, Ungar 2012) and gain sufficient extra energy to promote an increase in brain size. However because they could not guarantee having access to cooked food, they retained dental and digestive adaptations that allowed them to effectively chew plant foods when animal foods were scarce.

Despite these problems for the idea of a single shift encompassing diverse

features of *Homo* simultaneously, it is often concluded that habilines had a faster life-history than *H. erectus* (e.g. “non-erectus early *Homo* was smaller and developed more quickly than *H. erectus*”, Anton and Snodgrass 2012: S487). A slower life-history could imply earlier weaning and more dependence of juveniles on adults for food (Thompson and Nelson 2011). Early weaning is clearly hard to reconcile with a raw diet unless it predictably included such elusive foods as brain and fat-rich marrow. Unfortunately although these arguments are intriguing, they are premature given that it remains unclear how different the life-history of *H. erectus* was from its antecedents (Schwartz 2012).

### *3. There may have been important variation in gut size within post-habiline Homo.*

The idea that the inferred small gut size and observed small molar size of *H. erectus* are only explicable by a cooked diet is challenged by the observation that there is more difference in gut size among species of *Homo* than previously appreciated. This raises the possibility that the intestinal volume (including the colon) could have been so much larger in earlier *Homo* than in *H. sapiens* that *H. erectus* was capable of surviving on a raw diet. How much larger can only be guessed, but the idea raises the possibility that the colon was sufficiently large for foods to be retained and well fermented. Ben-Dor et al. (2016) have similarly suggested that the digestive anatomy of Neandertals differed significantly from that of *H. sapiens* by being relatively large. If this meant that they were able to live on raw diets, the fact that some Neandertal sites were apparently occupied

without fire would be more easily explicable (Sandgathe et al. 2011a, b; Henry in press). An improved understanding of the relationship between trunk morphology and digestive anatomy would be useful in establishing the potential for different species of *Homo* to exploit different diets.

#### *4. Biological evidence for late adaptation to fire.*

Several recent results challenge the prediction that fire was controlled by species as early as *H. erectus*. Chisholm et al. (2016) concluded that the evolution of tuberculosis (TB) in *Homo* was a consequence of living with fire, and that it likely happened between 6 and 70 ka. While analysis of dental calculus shows evidence of smoke inhalation between 300 and 400 ka at Qesem (Hardy et al. 2015), at Atapuerca at 1.2 ma it indicates consumption of raw foods and a lack of exposure to fire (Hardy et al. 2016). Hubbard et al. (2016) found an allele conferring protection against smoke toxins in *H. sapiens* that was absent in four Neandertals and Denisovans, suggesting adaptation to fire by at least 550 ka (Prüfer et al. 2014).

#### ***Closing Remarks.***

The cooking hypothesis is sometimes treated as if the fossil evidence of an improved and more easily chewed diet at the origin of *H. erectus* is its only significant source of support (e.g. Armelagos 2014, p. 1333: “The link to changes in morphology that are claimed to be related to cooking are confounded by the evidence for the control of fire”). Given the contrary archaeological evidence,

such a perspective can easily relegate a dependence on cooking and the control of fire to a later time in human evolution. The implication is that compared to other changes responsible for *H. erectus* the evolution of cooking and the control of fire have had relatively little impact on behavior and adaptation. This kind of thinking presumably explains why some recent papers considering the origin of *H. erectus* and the reasons for its higher-quality diet, larger body and larger brain have omitted any consideration of the cooking hypothesis (Anton and Snodgrass 2012, Potts 2012).

In fact, however, the evidence of increased dietary quality in the early Lower Paleolithic is only one of several sources of support for the cooking hypothesis, as discussed above. Furthermore the emergence of *H. erectus* is not adequately accounted for by an increased frequency of meat-eating. Thus while the cooking hypothesis may be wrong, it cannot fairly be dismissed by ignoring it.

Accordingly two questions must be answered before the time for the control of fire is assigned to the mid-Pleistocene. First, how could *H. erectus* use increased energy, reduce its chewing efficiency and sleep safely on the ground without fire? Second, how could a cooked diet have been introduced to a raw-foodist mid-Pleistocene *Homo* without having major effects on its evolutionary biology? Satisfactory answers to these questions will do much to resolve the tension between archaeological and biological evidence.

The results should be rewarding. The control of fire and the emergence of cooking had numerous effects on human biology and behavior, including cognition and cooperation (Attwell et al. 2015; Burton 2009; Dunbar and Gowlett



2014; Gintis et al. 2015; Wiessner 2014; Wrangham 2009). A better understanding of when the process started will have wide-ranging implications for human biological and social evolution.

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