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# Humans as cucinivores: comparisons with other species

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## Abstract

Here we discuss the relations of processed foods, especially cooked foods, in the human diet to digestive tract form and function. The modern consumption of over 70% of foods and beverages in highly refined form favours the diet-related classification of humans as cucinivores, rather than omnivores. Archeological evidence indicates that humans have consumed cooked food for at least 300-400,000 years, and divergence in genes associated with human subpopulations that utilise different foods has been shown to occur over periods of 10-30,000 years. One such divergence is the greater presence of adult lactase persistence in communities that have consumed dairy products, over periods of about 8,000 years, compared to communities not consuming dairy products. We postulate that 300-400,000 years, or 10,000 to 14,000 generations, is sufficient time for food processing to have influenced the form and function of the human digestive tract. It is difficult to determine how long humans have prepared foods in other ways, such as pounding, grinding, drying or fermenting, but this appears to be for at least 20,000 years, which has been sufficient time to influence gene expression for digestive enzymes. Cooking and food processing expands the range of food that can be eaten, extends food availability into lean times and enhances digestibility. Cooking also detoxifies food to some extent, destroys infective agents, decreases eating time and slightly increases the efficiency of assimilation of energy substrates. On the other hand cooking can destroy some nutrients and produce toxic products. The human digestive system is suited to a processed food diet because of its smaller volume, notably smaller colonic volume, relative to the intestines of other species, and because of differences from other primates in dentition and facial muscles that results in lower bite strength. There is no known group of humans that does not consume cooked foods, and the modern diet is dominated by processed foods. We conclude that humans are well adapted as consumers of processed, including cooked, foods.

**Keywords** Digestive physiology; Cooking; Food processing; Digestive enzymes

## Comparisons of digestive strategies

Specialisation of digestive tract structure, physiological properties, bacterial flora, digestive enzymes and nutrient transporters are related to diet across a wide range of species (Stevens and Hume, 1995). Such is the degree of specialisation that species are often confined to a narrow range of diets, modern humans being an exception, as we discuss below. Examples of the restriction that

digestive physiology imposes on diet include ruminant dependence on low protein fibrous plant material, the cat being an obligate carnivore, specialist feeders such as birds and mammals that rely on nectar, and the koala that subsists on an exclusive diet of eucalyptus leaves. These restrictions on food choices are associated with substantial variations in digestive tract anatomy (Fig. 1). They are also reflected in aspects of digestive physiology. For example, cats lack a functional sweet taste receptor for detecting carbohydrate (Li et al., 2005) and, unlike other mammals, the induction of carbohydrases and monosaccharide transporters that occurs with carbohydrate feeding does not occur in cats (Buddington et al., 1991; Kienzle, 1993). Consistent with the lack of sweet taste receptors, cats do not exhibit meaningful behavioural responses to sugars in the diet (Bradshaw et al., 1996). In another example, both the carnivore and ruminant pancreas lacks pancreatic lipase-related protein 2 (PLRP2), an enzyme that degrades plant triglycerides, which is, however, present in non-ruminant herbivores and omnivores (De Caro et al., 2008). Lack of PLRP2 relates to diet, as carnivores do not eat plant triglycerides, and gastric bacteria of ruminants hydrolyse plant triglycerides before they can reach the small intestine. In the absence of cooking and other food preparation strategies, human diet would be more restricted - humans have been able to diversify their diets because of cooking, other food processing techniques, and food storage strategies. Cooking, food processing and food storage have contributed to extending the environmental range of human habitation.

The diversity of solutions to the problems of nutrient assimilation includes that no mammal has evolved to be a universal digester of foraged or hunted food. In the wild, a human could not exist on the diet of a sheep, koala or panda. And a koala or cat could not exist on the diet of these other species. The differences in the diets that animals prefer or are obliged to eat have led to the classification of animals by their dietary specialisation as carnivores, omnivores, herbivores, frugivores and so on. Within these classifications, humans are grouped with the omnivores. However, without being able to prepare and cook foods, some of the major nutrient sources used by humans would be less readily available. The most obvious is grains, which only became a common food source for humans about 10,000 to 30,000 years ago, with the development of grinding to create flour, and the use of cooking. Grains, formerly poorly accessible as food sources, now account for up to 70% of dietary intake in modern societies (Copeland et al., 2009). Because humans rely on cooking and other food preparation and preserving techniques, they should be classified as a species whose dietary specialisation is the consumption of cooked or otherwise prepared foods, that is, as *cucinivores* (Furness et al., 2015).

## History of cooking

Humans have consumed cooked foods for some 300,000–400,000 years, perhaps even longer, and no groups of humans who live without cooking have been recorded (Weaver, 2012; Wrangham and Conklin-Brittain, 2003; Zink et al., 2014). **Cooking is postulated to have shaped human society and human physiology and to have been an important enabler for humans to evolve larger brains, beginning with *H. erectus* about 1.8 to 1.9 million years ago (Wrangham, 2010).** Early hearths indicating that food was cooked 250-400 thousand years bp (before present) include that at Qesem cave in Israel (Shahack-Gross et al., 2014), **Beeches pit in England (Preece et al., 2006) and Bolomer in Spain (Peris et al., 2012).** There is evidence of use of fire at **Qesem cave** for 200,000 to 420,000 years bp. A hearth that has been studied in detail has been dated to 300,000 years bp. It is identified as a cooking hearth that has been repeatedly used by the presence of ash layers that contain charred and calcined bones, microcharcoal, burnt flint, and burnt microscopic clay aggregates. Micro Fourier transform infrared (FTIR) spectroscopic analysis indicates cooking temperatures of about 500 °C. Hearths with evidence of cooking of similar age have been found in Africa, France, Spain, China and Britain (Gowlett and Wrangham, 2013; Peris et al., 2012). **Bone tools (knives, scrapers) with wear patterns indicative of use in butchering were located in the vicinities of the hearths, and burnt bone fragments in the hearths show cut marks.** Burnt artefacts discovered at several sites in Africa suggest controlled use of fire as early as 1.4 to 1.6 million years bp (Gowlett and Wrangham, 2013). Burned seeds, wood, and flint at Gesher Benot Ya‘aqov in Israel suggest the controlled use of fire almost 800,000 years bp (Goren-Inbar et al., 2004). Thus we can conservatively estimate that the regular use of fire for cooking dates back 200,000 to 400,000 years, some 7-14,000 generations.

## Processed food in the human diet

Ways of preparing food and preserving food stocks transform the food so that it is more readily digested. Historically, these include grinding, pounding, fermentation, drying, salting, cooling (natural refrigeration) and burying. In modern times, approximately the last 150 years, other methods have been developed including heat sterilisation, microwaving, mechanical refrigeration, irradiation and vacuum packing. No doubt other methods will appear. **In modern diets, it is calculated that 78% of all food energy intake (939 kcal/day per head) comes from moderately or highly processed foods, much of this being pre-cooked (Poti et al., 2015). This data is for the United States. Percentages of total food purchases in the United States were classified as ready-to-eat (68.1%) or ready-to-heat (15.2%).** Moreover, 80-90% of food that is cooked in modern societies is pre-processed (van Boekel et al., 2010).

Grinding of grain, presumed to be for human consumption, dates to at least 30,000 years bp (Revedin et al., 2010). The evidence comes from the discovery of starch grains in the surfaces of grinding stones dated to this period at three sites in Russia, the Czech Republic and Italy. Similar studies in China indicate grinding of plant starch sources (roots and grains) dating back 19,000 to 23,000 years (Liu et al., 2014). Starch granules in grinding stones in Israel indicate grain processing 23,000 years bp (Snir et al., 2015). In the absence of grinding and cooking, grain starches would not be available as a human food source, because all mammals lack cellulases, and in animals with only hind-gut fermentation, short hind-guts and short hind-gut retention times, such as cats, dogs and humans, cell walls are largely undigested (see below). A strategy of granivorous birds, which also lack cellulases, is to use small stones in the gizzard, which is lined with a tough, cornified epithelium, to grind seeds and make seed starches available to digestive enzymes. Ruminants and hind-gut fermenters solve the problem of digesting plant cells by holding food in capacious gut reservoirs and enlisting cellulolytic, pectinolytic and xylanolytic bacteria that are adapted to breakdown of plant cell walls. In these species, gut bacteria utilise almost all the plant sugars, and glucose must be re-synthesised from bacterially produced short chain fatty acids, primarily propionic acid (Stevens and Hume, 1995). An advantage to foregut fermenters is that these animals can utilise bacterially-produced B vitamins. Coprophagy allows some hind-gut fermenters to obtain this vitamin B and also to increase nutrient gain from re-processing of partly digested plant material. Thus the gastrointestinal tracts of ruminants and hind-gut fermenters are very large, and to gain sufficient energy from food, these animals eat almost continuously while awake, and digest continuously while asleep. By contrast, once humans had secured regular food supplies through agriculture, about 11,000 years ago, food abundance, food storage and the efficiency of digestion of processed food freed time for the development of technology and culture (Diamond, 1997; Zink et al., 2014). It has also been suggested that the absence of a need to spend many hours feeding favoured an increase in brain size (Fonseca-Azevedo and Herculano-Houzel, 2012), and by extrapolation, development of human intelligence and further divergence from other primates. For example, chimpanzees in the wild spend 4–6 hours per day chewing their food, whereas humans typically spend less than 1 hour (Wrangham and Conklin-Brittain, 2003). It is estimated that it takes chimpanzees 4.0 to 11.5 hours to chew small (~4 kg) animal carcasses (Zink et al., 2014).

Fermentation of fruits and grains, for example to form wines and beers, also preserves foods, by producing a milieu in which bacteria and other pathogens cannot thrive (McGovern et al., 2009). The alcohol itself provides an energy source, and levels of B vitamins, produced by yeasts, are increased. It is likely that humans first ate fruits for which fermentation occurred naturally, and it

was later that humans controlled fermentation for their own use and consumption (McGovern et al., 2009). Yeast-based fermentation is also used in bread production, the CO<sub>2</sub> that is produced causing the bread to rise, increasing its digestibility. Foods from fermented milk products date back about 8000-10,000 years (Hayes et al., 2007).

## **Disadvantages of raw foods; advantages and disadvantages of cooking**

In previous millennia, major disadvantages of raw food were the presence of infective organisms (primarily pathogenic bacteria) and products of putrefaction, the difficulty of its preservation and for some foods, difficulties with mastication. Infection is now less of a problem, with the modern understanding of infective agents and how to disable or avoid them. Nevertheless, even if we ignore problems of pathogens and putrefaction, modern humans seem to be less well adapted to the consumption of raw, compared to prepared foods. Modern humans on all-raw diets tend to be underweight (Kwanbunjan et al., 2000) and women consuming an all-raw diet tend to suffer chronic energy shortage and amenorrhea (Koebnick et al., 1999). It has been argued that raw foods are less rewarding than cooked foods in that they demand too much ingestion time for humans to be able to satisfy the demands of the energy hungry brain (Fonseca-Azevedo and Herculano-Houzel, 2012).

### ***Cooking increases net energy gain from food***

Direct studies, although in mice, indicate that cooking food increases the bioavailability of energy from carbohydrate-rich and protein-rich foods (Carmody et al., 2011; Carmody and Wrangham, 2009) and also from lipid-rich foods (Groopman et al., 2015). These authors determined weight gained per energy intake (calculated on the basis of food energy less energy expended in digestion). Mice gained more weight when fed cooked meat compared with raw meat, despite the fact that they ate less cooked meat. The difference was 1 g per 4 days for 36-40 g mice, that is, about 2.5% of body weight (Carmody et al., 2011). Cooking can also increase the availability of some nutrients in foods, for example cooking increases the availability of the vitamin A precursor,  $\beta$ -carotene (van Boekel et al., 2010).

### ***Detoxifying***

In humans, and in mammals in general, gastric acid and proteases kill the majority of bacteria (an exception being *Helicobacter pylori*) in the food. Nevertheless, bacteria and toxins do pass the stomach and can overwhelm intestinal and liver defences. Amongst pathogens that are a danger to human health when orally digested are *Salmonella*, *Staphylococcus* and *Listeria*, each of which is a major public health problem and each of which is killed by high temperature cooking. *Salmonella*

poisoning is most commonly the result of poor storage and inadequate cooking of meats, notably chicken (Juneja et al., 2007), and Listeriosis is a hazard usually associated with consumption of raw milk, although contamination of meat and other foods occurs (Oliver et al., 2009).

### ***Loss of nutrients and disadvantages of cooking***

Some of the major advantages of cooking (extending the range of digestible foods, increasing energy availability, detoxifying and enhancing flavour) are not as necessary for modern societies as they were during earlier phases of human history. This is because food is abundant for many societies, bacteria and other food contaminants can be eliminated by food processing and secure storage, and flavours can be added. Thus some of the disadvantages of cooking come to have greater relative importance. These include loss of nutrients (such as vitamins by degradation or leaching into cooking water), formation of toxic compounds (e.g., acrylamide, furan, acrolein), formation of compounds with negative effects on flavour perception, texture or colour, and formation of advanced glycation end products (Leskova et al., 2006; Uribarri et al., 2010; van Boekel et al., 2010). Advanced glycation end products, produced when proteins and fats are cooked in the presence of sugars at high temperatures, a popular way of preparing fast foods, contribute to diabetes and cardiovascular diseases (Bodiga et al., 2014; Vlassara and Striker, 2013).

### **Human evolutionary rate, was there time for digestive system divergence?**

Can we know whether there is likely to have been evolution of human digestive tract form and function in the time since humans were exposed to cooked food (about 400,000 years bp) and in the 10-30,000 years that humans have used other preparation techniques that improve the digestibility of food and widen food choices? One line of evidence is genetic divergence between species and between groups of humans with different dietary histories.

Clearly there has been considerable evolutionary change since the chimpanzee –human divergence at approximately 6.5 million years bp. Using genetic analysis, it has been estimated that a divergence between Neanderthals and modern humans occurred at 410,000-440,000 years bp (Endicott et al., 2010). This suggests significant evolution of form within the period that humans have been consuming cooked foods. More recent divergences have also been estimated, between the Khoe-San of the Kalahari and Southern Africa and other modern humans at 250,000–300,000 years bp; between African and non-African populations at 100,000 – 120,000 year bp; genetic separation between Europeans and Asians at 100,000 – 120,000 years bp; and between Aboriginal Australians and Eurasians at 62,000 – 75,000 years bp (Scally and Durbin, 2012). Thus, *genetic* differences can be detected within the time period since humans initiated cooking and there would

be time, at least in theory, for evolution of the digestive system during the time that humans have been cucinivores. In fact, analysis of differences between geographically or culturally separated groups of humans indicate that a continuing evolutionary divergence, in which significant differences in the frequencies of occurrence of particular alleles can be detected, occurs over periods of less than 10,000 years (Laland et al., 2010; Scally and Durbin, 2012). In the next section we provide evidence for divergence of digestive processes (see also Table 1).

### ***Evidence for evolutionary divergence of digestive processes***

Expression of lactase, the small intestinal enzyme necessary for the digestion of the major sugar of milk, lactose, disappears soon after weaning in mammals in general, and in the majority of modern humans. Several lines of evidence show that the development of dairy farming, and the consumption of milk and milk products well beyond weaning, which can be dated back for about 8,500 years (Warinner et al., 2014), **correlates with** the selection of genes for the persistence of lactase expression, and thus adult lactose tolerance (Laland et al., 2010; Perry et al., 2015). The lactase persistence (LP) phenotype is determined by alleles in the promotor region of the lactase gene and is inherited as a dominant trait (Swallow, 2003). LP is a common phenotype only in populations with a long history of herding and milk production (Ingram et al., 2009). As an example, the incidence of adult lactase expression is high, up to 75%, in northern European populations that rear cattle and consume cow's milk, and as low as 5% in hunter-gather populations in the same regions (Malmstrom et al., 2010). The lactase persistence allele of some modern human populations is absent in genes isolated from early Neolithic Europeans, 7000-8000 bp (Burger et al., 2007). It is interesting that times to weaning in Neanderthals and in human hunter gatherers were most likely similar, in the order of a year or less (Austin et al., 2013), which is consistent with an absence of lactase persistence in populations that do not consume milk after weaning. **Improved sequencing strategies recently applied to genetic material extracted from 101 individuals, who died 1000 to 3000 years bp, provides data suggesting that adult lactase persistence was present in fewer than 10% of Eurasians 3000 years bp. This implies that positive selection for adult lactose tolerance was more recent than previously thought (Allentoft et al., 2015).**

Salivary amylase gene (*AMY1*) copy number is correlated positively with salivary amylase protein level and individuals from populations with high-starch diets have, on average, more amylase gene copies than those with traditionally low-starch diets. Individuals from populations whose diets include high amounts of starchy foods had a median *AMY1* copy number of 7 and those on traditionally low starch, a median copy number of 5 (Perry et al., 2007). A further comparison has been made between modern humans consuming high starch diets (*AMY1* mean copy number 7.34, s.d. 2.61), Neanderthals, copy number 1.83 and Denisovians (from the Siberian Denis cave,

about 500,000 years bp), copy number 1.76 (Perry et al., 2015). When significant increases in *AMY1* copy number occurred is uncertain, and it may have been prior to the documented utilisation of grain starches at about 20-30,000 years bp (Perry et al., 2015).

Coeliac disease (CD) is a persisting disorder whose symptoms are triggered in genetically susceptible individuals by ingestion of gluteins contained in wheat, rye, oats and barley. If untreated, exposure to cereal gluten causes chronic diarrhea, nausea, vomiting and fatigue in those with CD. In children, CD results in wasting and failure to thrive. Despite the considerable morbidity associated with CD, it is common, with a prevalence of 1-2% in Western societies (Di Sabatino and Corazza, 2009). The fact that it has such a high prevalence, 7-10,000 years after agriculture and cereals were introduced early in the post-Neolithic period, suggest that susceptibility genes for CD may have some positive advantage (Abadie et al., 2011). This is supported by the observation that the prevalence of CD is greater, rather than less, in populations with long histories of cereal consumption, compared with those with historically lower exposure (Lionetti and Catassi, 2014). Recent studies, using genome-wide association analysis, indicate that risk for celiac disease, associated with alleles of *IL12A*, *IL18RAP* and *SH2B3*, has been subject to positive selection because these genes confer protection against infections (Zhernakova et al., 2010). Thus introduction of cereals to the diet has resulted in a shift in CD-associated gene prevalence.

Their dietary history may have influenced humans to maintain an alimentary tract that is substantially smaller than that of other large primates. The total size of the human gastrointestinal tract is about half the size predicted by the relation between gut size and body weight determined for a wide range of other mammalian species (Snodgrass et al., 2009). In humans, the colon represents only 20% of the total volume of the digestive tract, whereas in apes it is about 50% (Milton, 1999, 2003). The sizeable colons of most large-bodied primates permit fermentation of low-quality plant fibres, allowing for extraction of energy in the form of volatile fatty acids (Leonard et al., 2007). Thus humans, having small colons, are relatively poor in utilising uncooked plant fibre. The human large intestine lies somewhere between that of the pig, an omnivore, and the dog, a carnivore capable of consuming an omnivore diet, that, like human, has a reduced cecum and short colon. Evidence for this relationship is that hind gut absorption of short chain fatty acids (SCFA) accounts for 2% of maintenance energy for dogs, 6-9% for human and 10-31% for pigs (Stevens and Hume, 1998). In horses it provides 46% of maintenance energy requirements. The hind gut in pig is 72% of the gastrointestinal tract, compared to 20% in human (Milton and Demment, 1988), which relates well to the relative production and utilisation of SCFA in the two species.

The relatively small size of the human **gastrointestinal tract** may have been influenced by the development of a large, energy hungry brain (Aiello and Wheeler, 1995; Snodgrass et al., 2009). Humans expend an average of 6%–7% of meal energy in digestion, compared to the mammalian average of 13%–16%, because of their use of processed foods (Boback et al., 2007). Thus a smaller digestive tract, combined with greater efficiency of nutrient extraction, allows energy to be utilised elsewhere. However, fossil evidence indicates that the major change in brain size occurred in the period 1.7 to 2.3 million years bp (Schoenemann, 2006). Thus, adaptations that made the digestive system suited to cooked foods and reduced its energy needs probably preceded the regular consumption of cooked food.

The properties of the human muscles of mastication and human dentition results in a lesser bite strength than other large primates (Eng et al., 2013), which is suited to the consumption of prepared foods. However this difference also preceded the time from which we can clearly date cooking and the associated ingestion of foods that are softer than in their raw state (Fig 2). **Nevertheless, there is a trend towards smaller bite area in modern humans when fossil teeth are compared between *Australopithecus*, *Homo habilis* and *Homo sapiens* (Snodgrass et al., 2009).** The smaller gastrointestinal tract of humans requires smaller abdominal and pelvic cavities (Aiello and Wheeler, 1995), which may be an advantage to a mammal that stands erect.

Thus evolutionary divergence of human populations, including diet-induced divergence (see above), took place over periods of 10,000 years or more (Laland et al., 2010; Scally and Durbin, 2012). **Alleles associated with immune responses to pathogens have also changed in human populations over a similar timespan (Barreiro and Quintana-Murci, 2010).** These relatively slow rates of adaptation, compared to the very short periods of major changes in diet, might suggest an inability of humans to adapt adequately to the substantial dietary changes that have occurred in the last 100 years (Carrigan et al., 2015; Lindeberg, 2009). It can be postulated that humans are inadequately equipped for modern diets high in fats, refined carbohydrate, fructose and fermentable carbohydrates that are poorly absorbed in the small intestine. Thus the deleterious effects of modern diets on health, including the rising incidence of liver disease, diabetes and metabolic syndrome (Geiss et al., 2014; Williams et al., 2011), may in part reflect limitations of the human digestive system to quickly adapt. On the other hand the digestive system is sufficiently plastic to adapt to more limited changes in diet, for example the change in gizzard size in response to foods needing more or less grinding for adequate digestion (Svihus, 2011). The gut microbiome also adapts rapidly to changes in diet (David et al., 2014).

Diet-dependent evolutionary changes have been observed in other species, an example is the hummingbird. Birds in general, for example poultry, lack sweet taste receptors. However nectar-

eating hummingbirds have evolved a sweet taste receptor, appropriate to their diet, that is derived from the umami (savory) taste receptor (Baldwin et al., 2014). A curious case of rapid diet-related change in allele frequency in humans is for the frequency of alleles conferring resistance against prion disease (kuru) amongst the Fore linguistic group in New Guinea. Historical studies indicate that endocannibalism, in which brains of relatives were eaten, was practiced by the Fore from the nineteenth century (Mead et al., 2003). This ended in the 1950s. Genetic studies of the Fore people show that the frequency of prion disease resistance genes is highly selected and that a novel prion protein gene variant that confers disease resistance is found exclusively in groups exposed to kuru (Mead et al., 2009).

## ***Conclusions***

Humans have processed food for at least 300,000 years, possibly as long as 800,000 years. This is substantially longer than the time required for genetic divergence of human populations, which is of the order of 10,000 years. Examples of diet-induced divergence in the handling of carbohydrates can be seen in human populations whose diets changed 10,000 to 30,000 years ago. The diets of modern humans are dominated by processed foods. In fact, there is reliance on cooked and processed foods, and preparation that aids digestibility and storage of foods is pervasive. Humans are well adapted to a diet of processed foods, in terms of the size of the digestive system, dentition, gradual genetic adaptation to new food types, and the energy requirements for digestion. It can be argued that humans are advantaged over other species by the adoption of food processing and cooking, which allows them to divert time and energy to other activities and to expand the range of foods that can be effectively digested. The observed evolutionary rates of change in digestive physiology suggest that the human digestive system may be ill-equipped to adapt to substantial changes in diet over periods of only a few generations.

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## **Tables and Figures**

Table 1: Postulated evolutionary changes and divergences in human digestive functions

<b>Digestive feature</b>	<b>Environmental influences</b>	<b>Nature of change</b>	<b>Period of change</b>	<b>References</b>
Enzymes for milk sugars	Cattle herding and adult consumption of milk	Persistence of lactase gene expression in adults	Approx. 8,000 years	(Itan et al., 2010)
Digestion of starches	Increased dietary availability of plant starches (cereal crops, flour production and cooking)	Increased amylase copy numbers	From 20-30,000 years bp	(Perry et al., 2007; Revedin et al., 2010)
Gluten enteropathy	Increased incidence of infective challenge	HLA molecules for combating pathogens that coincidentally interact with gluten	7-10,000 years	(Abadie et al., 2011)
Alcohol metabolism	Consumption of fermented fruit	Induction of liver enzymes	Unknown, but precedes controlled fermentation	(Carrigan et al., 2015; McGovern et al., 2009)
Size of digestive tract	Increased development of brain capacity and associated energy demand, cooking	Reduction in relative size of the digestive tract: preceded cooking and advanced food preparation methods	Beginning perhaps 6.5 my bp, consolidated by cooking, 400,000 years bp	(Aiello and Wheeler, 1995; Milton, 2003)
Dentition and muscles of mastication	Availability of soft foods, cooking	Reduced bite strength compared to apes	Beginning perhaps 6.5 my bp, consolidated by cooking, 400,000 years bp	(Eng et al., 2013)

my bp: million years before present

## Figure descriptions

Figure 1: Relations between diet and digestive tract anatomy. The human digestive tract is relatively small, less than half the size of the pig, an omnivore with similar body size (in the wild, 50-90 kg, which is similar to humans who are not overweight, approx. 70 kg). The dog, a typical carnivore, has a short colon and reduced cecum. The human intestine is also small compared with other hominids, here illustrated by the orangutan. The three herbivores that are illustrated all have capacious intestines with specialised fermentation chambers. The koala, which consumes only eucalypt leaves that are rich in tannins and volatile oils, has an extensive large bowel and reduced small intestine. In proportion to body size, this is the largest cecum plus colon of any mammal. Scales 20 cm, all panels. Reproduced with permission from Stevens and Hume (1995).

Figure 2. Comparison of second molar bite strengths and second molar areas of humans and other primates (logarithmic plot). Bite forces have been calculated from skeletal data and estimates of jaw muscle architecture, and related to actual measurements in modern humans and non-human primates. Note that the human difference from other primates preceded the dates of well documented use of cooking. Where identified, males are plotted as triangles and females as squares. Specimens with unidentified sex are plotted as circles. The regression line does not include *Homo*. **A = Australopithecus; G = Gorilla; H = Homo or Hylobates lar; M = Macaca; P = Pan.** Reproduced with permission from Eng et al. (2013).

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**Human**  
Cucivore:  
small GIT

—

**Pig** Omnivore:  
GIT larger than  
for human

—

**Dog**  
Carnivore:  
small colon

—

**Orangutan**  
Folivore: large  
hindgut

—

**Kangaroo**  
Herbivore:  
non-ruminant foregut  
fermenter

—

**Sheep**  
Herbivore: ruminant  
foregut fermenter

—

**Horse**  
Herbivore: hindgut  
fermenter

—

**Koala** Specialist  
folivore: largest  
mammalian hindgut

—

