> “Because of our evolutionary history, we can adapt and acclimatize to a wide variety of foods, provided that adequate nutritional requirements are met.”

Evolution of the human diet[1]

Amanda G. Henry, Leipzig

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We humans have evolved from an ape-like ancestor who lived in small groups in restricted African rain forest environments to a massively successful species, with over 7 billion members who have colonized nearly every habitat on every continent. This success is due in part to our unique diet, and how that diet has changed over the course of our evolutionary history.

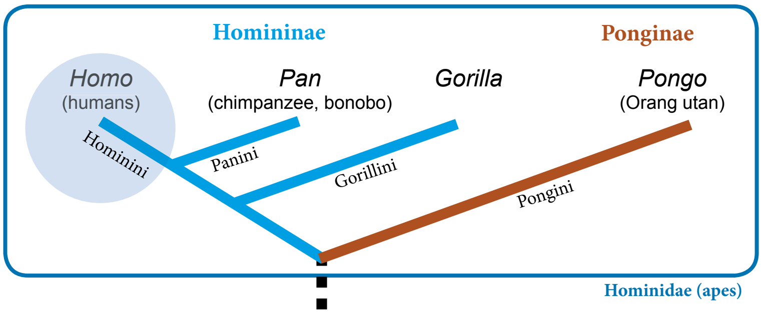
Introduction

The diets of living humans differ vastly from those of our closest living relatives, chimpanzees *(Pan troglodytes)* and bonobos *(Pan paniscus)*. Both of these ape species live in rain forest to open woodland environments in central and western Africa. They eat primarily fruits, nuts, and leaves, with occasional meat from insects and small mammals [1]. In contrast, the average living human acquires roughly half of their calories from domesticated cereals, with nearly 10% of calories coming from meat and animal fats, and roughly 10% coming from fruits, vegetables, and nuts [2]. There is considerable dietary variation from country to country and even from population to population.[2] How and when did this dietary shift occur?

To understand the diets of present-day humans, we must first grasp the diets of our ancestors, dating back to the earliest hominin (◆ Figure 1). Hominins comprise those species – all now extinct – who were more closely related to us than to other living apes (◆ Box 1).
Reconstructing hominin diets is a challenging task, and relies on several different lines of evidence from archaeological[3] and paleoanthropological[4] studies. Much of the **archaeological** evidence of diet comes from the tools used to acquire and process foods, and from the preserved remains of the food itself, including cut-marked bones, charred plant seeds, and plant microremains (i. e. microscopic remnants of plants that preserve unique morphologies that identify the plant from which they came).
Some tools can suggest a specific dietary function, like arrowheads used for hunting or grindstones for making flour. However, many tools can be used for processing a variety of foods (e.g., a knife can cut meat or vegetables), and specialized tools appear only relatively late in human history. The remains of food can also be a problematic record of diet, because they are only preserved in certain archaeological settings, and so are often missing from the record.
Paleoanthropological methods for reconstructing diet focus on the record preserved in the skeletal material of the hominins themselves.

BOX 1: THE HOMINIDAE-FAMILY

The Hominidae-family is divided in the Homininae-subfamily (with the genera *Homo*, *Pan*, and *Gorilla*) and the Ponginae-subfamily (represented by *Orang utan*). Within the Homininae the tribus Hominini includes the species *Homo* with its ancestors but not the common ancestors of *Homo* and *Pan*.



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[2] In Germany about 25% of food energy (En%) are coming from cereals, 19 En% from milk, dairy products and eggs, 12 En% from meat and 9 En% from vegetables, fruits and starch-containing tubers (www.nationalgeographic.com/what-the-world-eats/).
[3] The aim of archaeological studies is to reconstruct the human behavior and culture using artifacts of ancient humans.
[4] The aim of paleoanthropological studies is to reconstruct the shape and physical appearance of the human body, allowing conclusions on adaptive processes and behavior.

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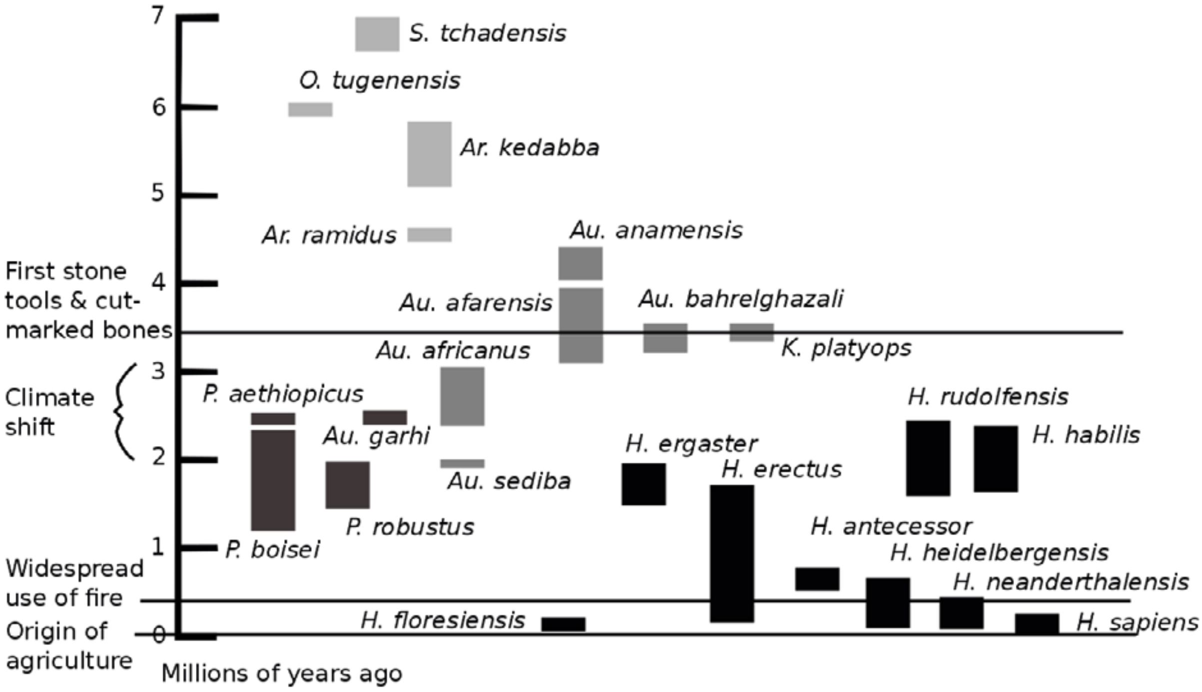

Fig 1: **The hominin family tree** [own depiction]
Each species is indicated by a bar that represents how long that species existed, at least as known from the fossil record. Modern humans *(Homo sapiens)* have lived for a relatively short period of time. Major dietary shifts are indicated on the left of the time scale.

- First, the **morphology of the masticatory system**, specifically the teeth and the skull, can provide clues about the kinds of foods an individual was physically capable of eating (i. e. what kinds of force they could create while chewing to break into hard or tough foods).
- Second, the consumed foods can leave a record preserved in the **wear patterns** present on the surface of teeth. At the micro-, meso- and macroscopic scale, these wear patterns provide information about the texture of the food (i. e. was it hard or soft, tough or brittle), or about how the teeth moved against each other during chewing.
- Finally, analysis of the **relative proportions of certain stable isotopes** of nitrogen, carbon, and some other elements can provide some dietary information. The stable carbon system indicate what percentage of the diet came from closed, forested environments, versus that from open, grassland environments. This system works best in environments where certain kinds of grasses grow, as in much of Africa. In European systems, the carbon system can indicate the amount of fish versus terrestrial foods in the diet. The nitrogen system is in some ways more simple, in that it indicates where an animal falls on the food chain, for example, as an herbivore (eating plants), primary carnivore (eating herbivores) or secondary carnivore (eating carnivores). The nitrogen system can only be used on specimens with good protein preservation in their bones, which is limited to individuals living in the last 50 k years.

Overall, each of these methods has benefits and drawbacks, and are therefore best used in combination for reconstructing the diets of our hominin ancestors.

Main taxa of hominin ancestors

The first groups of hominins to consider are those species closest to the split between the hominin group and the lineage that led to modern-day chimpanzees (◆ Figure 1, ◆ Box 1). These early specimens, dating to roughly between 8 and 4.5 My, are likely but not certainly ancestors of living humans [3].

The four main taxa, *Sahelanthropus tchadensis*, *Orrorin tugenensis*, *Ardipithecus kadabba* and *Ardipithecus ramidus*, are represented by a handful of fossils at a few sites around eastern and western Africa. They have never been found with associated stone tools or cut-marked bones. The dietary information we can gather from these early putative hominins comes primarily from their physical features. They had small molars with thin to moderate enamel, which is associated with low bite forces and suggests a diet of soft fruits [4–6]. Those that have been examined for stable carbon isotopes have signals suggesting consumption of resources from closed forest environments [7]. Finally, many signals in their post-cranial anatomy, including their long arms and long curved toes, suggest that these species spent a considerable amount of time in the trees [5, 8].

All of these traits are very similar to what we see in modern-day chimpanzees, and suggest that there had not yet been a significant dietary shift.

Archaic hominins of east and southern Africa – significant change in the body form

Not until about 4.5 Ma do we see a significant change in the body form of the hominin species. The archaic hominins, comprised of *Australopithecus anamensis*, *Australopithecus africanus*, *Australopithecus afarensis*, *Australopithecus bahrelghazali*, *Australopithecus sediba* and *Kenyanthropus platyops*, lived in east and southern Africa until about 2 Ma, and represent the first species who were clear bipeds – that is, they may have still spent considerable time in the trees, but had committed adaptations for bipedal locomotion [9, 10]. Reconstructions of the habitats in which they lived suggest that several of these species spent most of their time in open, grassy habitats [11].

Other aspects of their morphologies are different from that of the apes, including larger molars with thicker enamel, suggesting a diet of harder foods [7, 9]. It is also in this time period that we see the first, albeit controversial, evidence for cut-marked bones and early stone tools. The earliest cut-marked bones, dating to c. 3.4 Ma, are associated with the east African *Astralopithecus afarensis* ("Lucy"), and have so far been found in small numbers only at one site [12]. The earliest putative stone tools likewise come from east Africa, dating to 3.3 Ma [13]. The bones are direct, and the tools indirect, evidence for the consumption of animal meat and marrow. Furthermore, the bones come from larger-bodied savanna ungulates, which represents a major shift from the kinds of small game hunted by chimpanzees.

However, with the evidence at hand it is impossible to say how regularly early hominins consumed animal foods or what percentage of the diet was comprised of meat. It may have been a very rare behavior.

In summary, the archaic hominins are the first group for which we see clear signs of a diet different from that of chimpanzees and bonobos, with adaptations for harder foods from non-forested habitats and a potential increase in the reliance on meat.

Climate change enhanced selective pressure

A major climate change occurred between 3 and 2 Ma in Africa, leading to the drying out of the subtropical regions, a significant decrease in forest cover, and increased patchiness of habitats [14]. This environmental shift put selective pressure on early hominins, and likely led to the speciation events that occurred between 2.5 and 2 Ma. There was an increase in the number of hominins co-existing on African landscapes, and a diversification of morphologies, particularly those related to food consumption. From the archaic


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Due to a climate change between 3 and 2 Ma in Africa with a severe drought, a change from forested habitats to open grassland occurred with great influence on the development of our ancestors who were previously more adapted to the woodlands.

hominin form, which has a relatively large jaw and thick enamel, two main variants appear.

One variant is known colloquially as the „robust" group, and is represented by *Paranthropus robustus, Paranthropus aethiopicus, Paranthropus boisei and Australopithecus garhi*. These species all share a hyper-developed masticatory system, with massive jaws and teeth, hyper-thick enamel, and other features that suggest they were evolved to create tremendous bite force [15]. Some have argued this was in order to access very hard nuts, tubers, or possibly for repetitive chewing of grass or grass seeds [16].

The other main variant includes the earliest representatives of our genus: *Homo*. These specimens of early *Homo* retain the thick enamel of the archaic hominins, but have relatively smaller jaws and teeth. Some authors have interpreted this to mean that *Homo* had developed the capability to pre-process their food outside of the mouth, such as with cooking or grinding [17]. This preprocessing reduced the selective pressure for larger teeth. Another suggestion is that early *Homo* species focused more heavily on animal foods, which are generally softer and tougher than the hard vegetal foods that were the supposed mainstay of the robusts. This likewise would have reduced the need for such large, flat and thick teeth, and would have promoted the development of the smaller, sharper teeth seen in *Homo* [18].

The underlying cause of this morphological difference is unclear. Comparing the stable carbon values of the archaic hominins, robusts, and early *Homo*, we see first that there is significant dietary variation within and between species [7]: Individuals of *Australopithecus africanus*, a southern African archaic hominin, show a broad range of values, indicating that they ate foods from very closed forest to very open grassland. The southern African robust form, *Paranthropus robustus*, has nearly as broad a range of carbon values, with fewer individuals from very open habitats. Most early *Homo* specimens overlap with *Paranthropus robustus*.

This contrasts sharply with the data from *Paranthropus boisei*, the east African robust species, which cluster strongly in the open grassland end of the spectrum. These carbon data suggest that though the robust forms share strikingly similar morphologies, they may have consumed quite different foods, with the eastern species focusing perhaps on grass seeds or underground storage organs from open habitats. Overall, different species behaved quite differently. Finally, cut-marked bones are found at increasing frequency at archaeological sites during this time period, and suggest an increased reliance on animal foods [19]. However, with so many species occupying nearly the same habitats, it can be impossible to discern which of the hominins were consuming meat. During this time stone tool technology also becomes more widespread, but again it is impossible to identify the species responsible for creating and using these tools. In summary, the period from roughly 3 to 2 Ma represents a major evolutionary shift in the hominin lineage. This period can be described as an adaptive radiation of hominins, in which different species appeared and evolved to make use of a variety of newly appearing niches on the African landscape. Animal foods, and an increased reliance on non-forested and even open grassland habitats become increasingly important, reflecting the drying environments.

Homo erectus – the first obligate biped

A major shift in body form, habits, and lifestyle occurred roughly 1.9 Ma with the appearance of *Homo erectus*. This is the first species of hominin who left Africa and colonized a variety of habitats in eastern Europe and central and south-east Asia [20]. It is also the first obligate biped - that is, its body was fully evolved for walking and particularly for running [21]. Both of these changes would have required and been facilitated by changes to the diet.

> **Energy for long distance endurance running requires a high-quality food resource. That food resource must have been flexible and not restricted to any one kind of environment since *H. erectus* is found in a variety of habitats.**

In spite of this lack of evidence, several theories have been proposed for what this high-quality food might have been. Some have argued that *H. erectus* consumed more meat than its predecessors, and may have been the first successful hunter of large game [22]. Others have suggested a reliance on plant underground storage organs could have provided more calories in the form of carbohydrates [23]. Still others have proposed that cooking was the only way in which food could be transformed to be more calorie rich [24].

None of these theories have been possible to test, since the faunal record cannot provide evidence for the quantity of meat consumed, plant remains are usually poorly preserved, and there is no credible evidence for consistent control of fire prior to roughly 400 ka [25].

In summary, *H. erectus* was likely able to gain more energy from its environment, which allowed it to expand out of Africa, but whether certain food types or processing methods were the key is still highly debated.

Neanderthals in Europe, and early modern humans in Africa

African and non-African populations continued to evolve, eventually resulting in Neanderthals in Europe, and early modern humans *(Homo sapiens)* in Africa. Between 100 and 30 ka, early modern humans migrated into the Near East and Europe, interbreeding with but also replacing Neanderthal populations. Many authors have proposed that dietary differences between Neanderthals and early modern humans may have contributed to the disappearance of the former [26, 27].

Neanderthals are the oldest group for which we have evidence from nitrogen isotopes, and these suggest a diet consisting overwhelmingly of meat protein [28]. Faunal remains show that Neanderthals were capable hunters who made use of a wide variety of large game available in their environment, though generally avoiding small game like rabbits, birds and fish [29]. They did consume some amount of plant foods as evidenced by plant microremains and dental wear, but the ratio of plants to meat remains unclear [30, 31]. Cooking was likely part of the Neanderthal suite of behaviors [25].

Some researchers point to evidence that European early modern humans ate a wider variety of species, including small, fast and hard-to-catch animals as evidence that they were more capable of acquiring food from the landscape [26]. Recent studies have refuted this, suggesting instead that there was no one single „Neanderthal“ or „modern human“ diet; instead both groups tailored their diet to the foods available in the local environment [32].

Several prehistoric cave-paintings give evidence that our ancestors came into contact with large animals like mammoth, bear or bison as shown in this drawing in the Chauvet cave in France.

Agriculture and growth of population

This pattern, of human groups adapting their diets to the environment, continues until roughly 10 ka, when a major shift in subsistence and in population structure occurred with the increased use of, and eventual domestication of rich seed-bearing grasses [33]. Population estimates based on genetic data suggest that modern humans experienced a severe bottleneck 40-20 ka, and only recovered between 15 and 10 ka. Since that point, population sizes have been closely tied with advances in domestication. This is a feedback system, in which increasing food stability and sedentism led to increased birth rates [34], and larger numbers of individuals required the acquisition of more calories per unit land, leading to pressure for use of agriculture. Major shifts in agricultural production such as the industrialization and planning that began in the 1700s and 1800s, led to dramatic increases in population sizes [35].

Gaining control over our food supply has been the key factor in enabling human success around the world and our immense population of today.

What about ‹Paleolithic› diet?

However, it has recently been asked whether our success as a species and particularly our reliance on domesticated food has come at the cost of the health of the individual. Increasingly, we see evidence that our health is compromised by our diets, leading to obesity, heart disease and diabetes [36, 37]. Some authors have proposed that there has not been sufficient time for us to adapt to an agricultural diet, and instead we should return to a diet like that


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Farming and using cereals together with sedentism lead to a strong growth of population.

of our ancestors [38]. There are several arguments against this line of reasoning.

1. First, there is no single ‚Paleolithic' diet. As reviewed above, we hominins have had many different diets over the last 7 Ma with a lower and higher proportion of meet and other foods. Even focusing only on early modern humans in the last 40 ka, groups living in different areas had widely different diets that reflected the foods available in their environment. One could therefore be oriented towards many different „primal" diets: from mainly plant- and fruit-based foods originating from forests up to more plant seeds and tubers from open grass landscapes, and meat of smaller and larger animals.
2. Second, even a diet that avoids the ‚problematic' agricultural foods like cereals, beans, dairy and starchy tubers still relies on domesticated plant and animals that have significantly different nutritional characteristics from their wild ancestors [39].
3. Finally, there is ample evidence that we have adapted to our diet of domesticated foods. One excellent example is the lactase persistence gene, which allows adults to digest milk.

The ability to digest milk evolved independently twice in the human lineage within the last 10ka, once in Europe and once in northern Africa [40]. Clearly milk provided such an advantage to those who could eat it as adults that the selection pressure was very high.

There is still clear evidence, however, that our health has been compromised by our diets. Rather than the consumption of domesticated food, it is likely that the way these foods are processed plays a key role in the etiology of many so-called ‚diseases of affluence'. The processing of food including:

- turning seeds into oils
- thickening these oils by hydrogenation
- making flours, starch and modified starch from carbohydrate rich foods
- creating various forms of sugar
- and chemically treating food prior to consumption

has been strongly linked with disease [41]. These processes remove vitamins and fiber, and instead provide many „empty calories" – that is, an abundance of energy with no additional benefits.

Furthermore, the sterilization of our food and heavy use of antibiotics in ourselves and in our foods have consequences for our health, because these behaviors alter the communities of commensal gut bacteria [42]. Interestingly, many of the diet-related health problems - heart disease, diabetes, obesity - negatively affect the health of the individual at a somewhat advanced age, but often do not affect the ability of that individual to reproduce.

"Rather than the consumption of domesticated food, it is likely that the way these foods are processed plays a key role in the etiology of many so-called ‚diseases of affluence'."

The long-term success of a species does not necessarily require that individuals live to ripe old age. Our modern industrialized diet may promote our ability to produce offspring by providing an abundance of calories, while at the same time risking our own long-term survival.

Conclusion

Because of our evolutionary history, we have evolved to tolerate and even thrive on a wide variety of diets, reflecting the wide variety of habitats and social systems that humans used prior to globalization. Domestication and industrialization of our foods have enabled us to support even greater numbers of humans, even while potentially challenging the health of individuals. There is no single healthy diet, instead, we can adapt and acclimatize to a wide variety of foods, provided that adequate nutritional requirements are met.

Amanda G. Henry
Plant Foods in Hominin Dietary Ecology Research Group
Max Planck Institute for Evolutionary Anthropology
Deutscher Platz 6
04107 Leipzig
E-Mail: amanda_henry@eva.mpg.de

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