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Analysis of the Evolution of the Hominin Jaw & Dentition

Matthew Koelbel

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Matthew Koelbel

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Brooke Haiar, Ph.D.

Takashi Maie, Ph.D.

Nancy E Cowden

Nancy Cowden, Ph.D .

ABSTRACT

The food an organism consumes impacts the evolution of its dentition and facial morphology. As the teeth of early hominins are often some of the only parts of the skeleton to be fossilized, their morphological changes throughout time are better documented and understood than many other body parts. A literature review of articles focusing on the evolution of the dentition and mandibular morphology of members of the tribe Homininae was conducted. We deduced the ways in which tool use and cooking directly affected the teeth of hominins from the late Pleistocene to Pliocene from this information. The tangible ways that changing dietary patterns acted as selective forces throughout the course of hominin evolution are discussed.

INTRODUCTION

In order to study a species which has no living specimens, scientists must rely completely upon fossilized remains. As intense pressure under sediment is most often what leads to fossilization, what best lends a part of a plant or animal to this process is how hard it is. The expected result of this would be that the hardest parts of an organism would be the most abundant in the fossil record, and this is certainly the case with the teeth of hominids. Teeth, whose enamel contains the highest concentration of hydroxyapatite in the body, are the hardest part of mammals and, in many cases, the only remaining material an individual leaves behind in the fossil record (Scott & Turner 1997). Because teeth are frequently present in deposits of mammalian remains, paleoanthropologists have a relative abundance of dental material from many specimens to study and, consequently, more is known about the evolutionary history of teeth than other body parts.

Besides this fortunate side-effect of their physical properties, teeth are considerably useful in themselves. For example, the approximate age at death, sex, diet, geographic ancestry, diseases and malnourishment, signs of the mouth having been used as a tool, and body mass are all things that paleontologists can learn about a specimen from teeth (Price & Knudson 2018). Analysis of an animal's dentition is arguably one of the most efficient ways to study an extinct species of interest. For this reason, we looked at the dentition and jaw apparatus of selected hominins, which are members of a tribe of bipedal apes, past and present, with humans comprising the only living members. We attempted to explore the selection pressures that acted on the evolution of these structures throughout the Pliocene and Pleistocene, i.e., 5.3 Ma (million years ago) to 12 ka (thousand years ago).

Dentition Definitions

The 32 teeth of an adult hominin can be separated into four categories based on their morphology, or size and shape. These are the incisors, cuspids (also known as canines, but referred to as cuspids for the remainder of this review), premolars (also known as bicuspids but referred to as premolars for the remainder of this review), and molars (Jheon et al. 2013). Because the human jaw apparatus is symmetric, the teeth can be separated further based on whether they sit on the right or left side of the mouth. They can also be described by the bone in which they are situated: maxillary (also known as upper, but referred to as maxillary for the remainder of this review) if in the top part of the mouth, and mandibular (also known as lower, but referred to as mandibular for the remainder of this review) if connected to the bottom jaw. In this way, the mouth can be divided both horizontally and vertically in hominins, with each quadrant containing only eight teeth.

Because hominins have two incisors, one cuspid, two bicuspids, and three molars in each dental quadrant, their dental pattern is often abbreviated as: 2.1.2.3 in the literature (Kumar & Dhanari 2018). For ease of communication, each tooth has been labeled with three character addresses based on its position and type. The first character is “R” or “L” for right or left. The second is “I” for incisor, “C” for cuspid, “P” for premolar, or “M” for molar. The last character is a number, which can either be “1” for first, “2” for second, or “3” for third. The number takes the form of a superscript if the tooth is maxillary, a subscript if it is mandibular. For example, RM^3 would be spoken as “upper-right, third molar,” or “right-maxillary, third molar” (Xing et al. 2015). When referring to the incisors, the first ones are called “central,” while the second are called “lateral.” Therefore, LI_1 would be described as “lower left central incisor,” while RI^2 would be described as “upper right lateral incisor” (Xing et al. 2015).

Here, it should be noted that the teeth can be divided further into two categories based on which side of an imaginary line between the cuspids and premolars they are positioned. As can be seen in Fig. 1, all the teeth in front of this line (incisors and cuspids) are called "anterior," while all teeth behind it (premolars and molars) are "posterior" (Groves & Napier 2019).

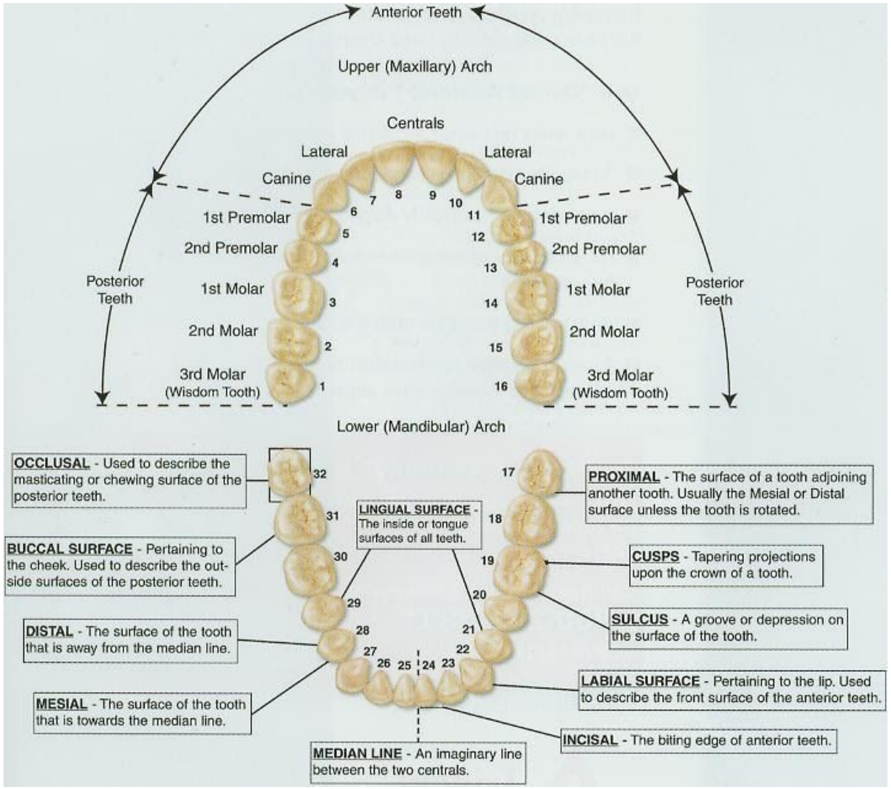


Figure 1. The teeth of *Homo sapiens*, labeled with the American System of dental notation, with each tooth's type and location described (www.napervilledentist.com).

Because teeth are not uniformly shaped, and their features vary systematically depending on what direction that part of the tooth is facing, specific words are used when describing their various surfaces. The midline, an imaginary line between the central incisors, is used as a reference point for two such terms (Foster 2019). The side of a tooth farther from the midline is called "distal" (also known as lateral). The side closer is called "mesial" (also known as medial) The side of a tooth that faces towards the outside of the body is called "facial." In the anterior teeth, it is more specifically the "labial" surface, in posterior teeth the "buccal" surface (Foster

2019). On the opposite, inner side, which faces the oral cavity, the tooth's surface is called "lingual." It does not matter here whether the tooth is anterior or posterior; lingual applies to all teeth. "Incisal" is a term used only for anterior teeth, and refers to their biting edge. Therefore, the incisal surfaces come into contact when the jaws are shut. The synonymy for this part of a posterior tooth is the "occlusal" surface.

The four groups of teeth evolved their shape because of the evolutionary history of mammals. Because it was advantageous for those teeth at the front of the mouth to be used for cutting off bits of flesh of meat or fruit, selection resulted in their showing incisor type morphology (Foster 2019). The cuspids, or canines, having a single point, look the most similar to how all teeth would have appeared before heterodonty, the trait of having differently shaped teeth, appeared. Because they are situated at the corners of the mouth, farthest from the temporomandibular joint (TMJ), which acts as the jaw's fulcrum, they are the fastest moving teeth in the hominin mouth and are used to grasp and tear food (Bergqvist 2003). The bicuspids, whose function is to partly crush food, are posterior to the cupids. The molars have the most cusps and surface area of all the teeth and are used to crush and grind down food before it is transported to the esophagus (Foster 2019). Because they do the majority of work in mastication, molars show the greatest degree of diet-related differences among species (Bergqvist 2003).

Hominins

In the mid-eighteenth century, Carl Linnaeus worked to formalize the system of binomial nomenclature. This is a system where every organism can be referred to by a general (genus) and specific (species) epithet. In writing, these names are formatted in italics with the first letter of the genus capitalized and the specific epithet completely lower-case. Latin grammar is used for suffixes, though the roots can come from any language. However, Carl Linnaeus lived before the concept of evolution was understood, and he and many other scientists of the time subscribed to the immutability of organisms; they believed that animals and plants were unchanging, and once discovered, no new species would arise and have to be named (Anderson 2015). Today, we recognize that species evolve, but we still use binomial nomenclature that predates the concept of evolution when we talk and think about fossil organisms whose evolutionary relationships are poorly understood, and this creates problems. For example, two predominant ideas exist on what exactly a genus is. One is the evolutionary systematic interpretation, which posits that a genus is a group of species of common ancestry that occupies an adaptive zone occupied by no species of another genus (Wood & Collard 1999). This essentially means that all species in a genus fill an ecological niche that no member of another genus fulfills. Here, a genus may be monophyletic or paraphyletic. A monophylum is a group of organisms that includes an ancestor and all of its descendants, while a paraphylum is a group of organisms that all share the same ancestor, but does not include every descendent of said ancestor. Therefore, some descendents of the last common ancestor (LCA) must be excluded for a group to be paraphyletic. The leading alternative viewpoint is the cladistic definition of a species, which focuses more on the relationships between species than their role in the ecosystem. It posits that a genus is a group of species more closely related to one another than to a species of another genus (Wood & Collard 1999). The situation for the genus *Homo* is not made any better by the fact that those trying to define it belong to it as well. Fortunately, though, some very broad consensus exists among the majority of the paleoanthropological community, which serves as a starting point for defining the genus. *Homo* was named and described in 1758 by Linnaeus in his 10th edition of *Systema Naturœ* (Collard & Wood 2007). At this point, modern humans were the only members of the genus, but six years later William King called a fossil discovered in Germany *Homo neanderthalensis*, adding the first fossil taxon to the genus. As more and more fossils have been discovered, changes to the definition of *Homo* have been made in an ad hoc fashion.

The defining features that allow us to distinguish members within a genus from those without are called apomorphies. An apomorphy is a heritable, genetically based physical or behavioral trait a group of organisms evolves that distinguishes them from their ancestors (Kitching et al. 1998). As a rule, a single species is designated as the type specimen of a genus. This means that all other species in the genus are compared to that select specimen of a species, and are included in the genus only if they are found to be more similar to it than the type specimen of another genus (Wood & Collard 1999). For the genus in question, the type specimen happens to be *Homo sapiens*. Currently there are four apomorphies for *Homo*, although not everyone agrees on their significance, and there are problems with each one (Wood & Collard 1999). One of these apomorphies is having a cranial capacity of at least 600 cc, but a problem with brain size is that its significance has been brought into question. Linguistic ability is another, but using endocranial casts to ascertain a hominin's use of language is obviously difficult with current technology. Furthermore, the area of the brain that produces language happens to not be as localized as was once thought, and casts created from models that have been rectified from crushed and warped fossils are of questionable utility. Precision grip with an opposable thumb is another apomorphy of *Homo*, but this too is difficult to deduce from fossil evidence. The fourth trait is the ability to manufacture stone tools, but it has been found that the earliest stone tools date to 2.6 Ma and could have been produced by paranthropiths, hominins of an entirely different genus (Wood & Collard 1999). Nevertheless, with these guiding criteria most of the species currently included in *Homo* are found to be adequately placed. This includes

H. sapiens, *H. neanderthalensis*, *H. erectus*, *H. ergaster*, and *H. heidelbergensis*. There are two other species of *Homo* that are often referred to in the literature: *Homo habilis* and *Homo rudolfensis*. However, by many metrics, such as strategies of maintaining homeostasis, gathering food, and producing offspring, fossils attributed to *H. rudolfensis* and *H. habilis* have been found to be more similar to australopiths, an older extinct group, than to modern humans. Due to these reasons, this paper will not consider *Homo habilis* or *Homo rudolfensis* to be members of the genus *Homo*.

Detailed exploration of the dental morphology of the widely accepted species of *Homo* will help us understand how the teeth changed in response to shifting selection pressures over time. We will explore the morphology of each species below, in chronological order of appearance in the fossil record.

Homo erectus

The first fossils now attributed to *H. erectus* were discovered in the 1890's by the Dutch paleoanthropologist Eugene Dubois on the island of Java in the East Indies (Schwartz & Tattersall 2015). The fossil specimens lived from 1.8 Ma-100 ka, during the Pleistocene Epoch (Antón 2003). Dubois named his find *Pithecanthropus erectus* because the assemblage contained a skullcap that was both ape-like (*pithec*) and human-like (*anthrop*), as well as a femur which indicated an upright posture (Birdsell 1972). The skullcap in the assemblage made this the first discovery of a fossil species whose cranial cavity was larger than living great apes but smaller than humans. Some viewed the specimen as an intermediate stage of hominid between humans and apes, while others speculated it represented a diseased, aberrant human (Tattersall 2007). In the late 1920's, a site in China produced many similar fossils, which were referred to as

Sinanthropus pekinensis. After similarities of the fossil assemblages from China and Indonesia were confirmed, both were reclassified under the name *H. erectus* in the 1950s (Antón 2003). Since then a diverse array of fossils from other regions have been included under *H. erectus*, and it has been recognized as a species of high morphological diversity.

Some apomorphies of *Homo erectus* include a smaller neurocranium, a lower vault, broader base, and more complicated roots on their premolars (Collard & Wood 2007). Their supraorbital torus is also continuous. They have thick supraorbital tori, their postorbital region flares laterally; it just barely has a midline keel but does have shallow bilateral depressions (Fig. 2). Its braincase's lateral walls are short and tilt inward. Their nuchal angle, which relates to the neck, is short. The femora of *H. erectus* were very robust and platymeric (flat). The Javan specimens are all similar in these ways and are part of the same Asian hominid clade.

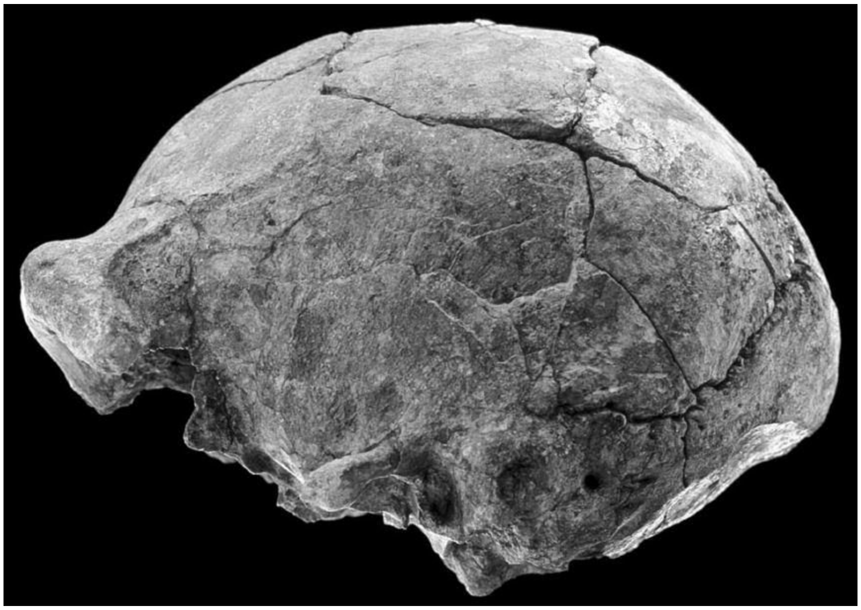


Figure 2. Lateral profile of *H. erectus* skull (with only the frontal, temporal parietal and occipital bones) from Daka, Ethiopian Rift (Gilbert & Asfaw 2008).

During the second half of the 20th century, workers believed that human evolution occurred in a line that culminated with the modern species. *Homo erectus* became a catchall for many fossils of varying morphology. Historically, anything from the early Middle Pleistocene in Africa is labelled as *H. erectus*. The Pleistocene was a period of short term climatic oscillations, and it is possible that *H. erectus* fossils are morphologically variable because they are a single species with huge variation or represent multiple speciations that branched out.

In 1975 paleoanthropologists Colin Groves and Vratislav Mazák excavated a mandible in Kenya which was deemed different enough from *H. erectus* to be named *Homo ergaster* (Groves & Mazák 1975). This species, often referred to as "African *H. erectus*," was considered to exhibit morphology slightly more similar to that of *H. sapiens* than fossils traditionally grouped with *H. erectus* (Bräuer & Mbua 1992). However, it is now evident to many researchers that *Homo erectus* and *H. ergaster* both represent a somewhat cohesive group within Hominidae. Because of this, we will treat them as the same group, referred to as *H. erectus*.

In summary, the teeth of *H. erectus* are distinguishable from other species in the genus by having the following characteristics. Compared to non-hominin apes, *H. erectus* tooth roots developed first before the teeth erupted, as opposed to simultaneously. This developmental schedule is followed by all later hominins, and indicates a prolonged childhood. *H. erectus* incisors were similar in size to those of Australopiths while their molars had thinner enamel than Australopiths (Ungar 2004; Dean & Cole 2013). The anterior teeth of early African and Central Asian *Homo erectus* specimens are buccolingually narrow (Antón 2003). Most African specimens rarely have accessory cusp complexes, while the Georgian *H. erectus* do have them, as well as wider molars. Chinese specimens tend to have smaller anterior teeth than those of Indonesia, which have a greater occlusal area (Antón 2003).

Homo heidelbergensis

The first fossil now attributed to *H. heidelbergensis* was discovered by mine workers in Mauer, Germany in 1907, who discovered the mandible of a primitive young adult. This jaw was described by Otto Schoetensack as *Homo heidelbergensis*, after the nearby city of Heidelberg (Mounier et al. 2009). The species lived from 800-200 ka, the middle Pleistocene, and have been found in Africa and Europe (Wood & Collard 1999). Due to the lack of similar fossils discovered in Eurasia during the 20th century, *H. heidelbergensis* was largely forgotten after the initial discovery of the Mauer jaw.

Some apomorphies of *H. heidelbergensis* include the jaw having a high mandibular thickness, a ramus with a long anteroposterior length, no chin, and a receding symphyseal axis (Mounier et al. 2009). The mandibular symphysis is the fused area of the symmetric dentary bones. *H. heidelbergensis* have smaller brains than modern humans, a more robust braincase, rounded supraorbital ridge, and a thicker occipital bone (Fig. 3).

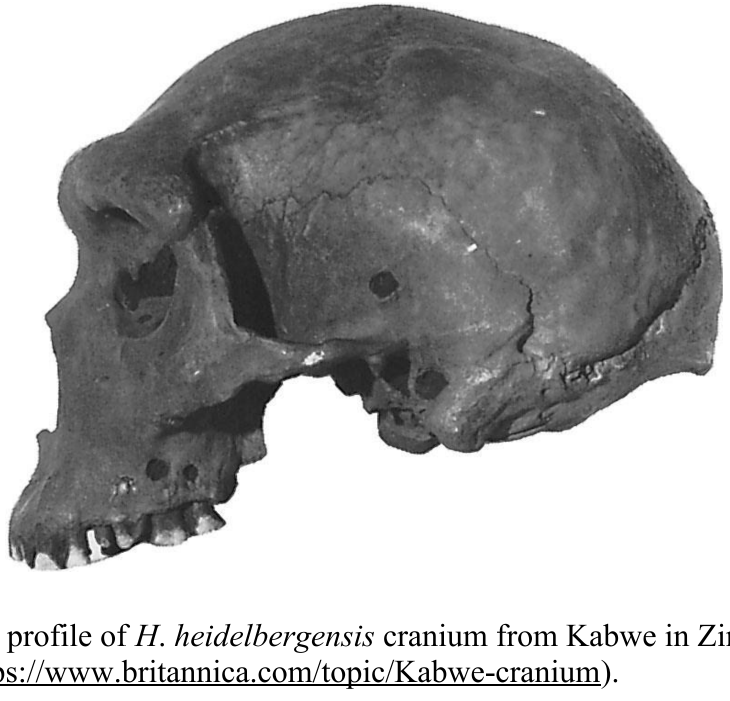


Figure 3. Lateral profile of *H. heidelbergensis* cranium from Kabwe in Zimbabwe, formerly Broken Hill (https://www.britannica.com/topic/Kabwe-cranium).

Homo heidelbergensis' long bones are thicker and more robust than those of modern humans. Their dentary is more primitive than *H. neanderthalensis* (Collard & Wood 2007). Enamel rates indicate that *H. heidelbergensis* had a more humanlike development schedule (Collard & Wood 2007).

No evidence exists that the posture or gait of *H. heidelbergensis* was different from *H. sapiens* (Wood & Collard 1999).

They had wide retromolar gaps, the area in between the M_3 and the ramus; their gonia were shortened, and their mental foramen that the trigeminal nerve branch that innervates lower teeth, are situated more posteriorly (Mounier et al. 2009).

It is very difficult to distinguish the teeth of *H. heidelbergensis* from those of other species of *Homo*, but there are a few characters that stand out. One such trait is that the M^1 of *H. heidelbergensis* shows an enlargement of the hypocone and a reduction of the metacone (Quam et al. 2009). In general, their teeth were larger than earlier species such as *H. erectus*, but larger then later ones, such as *H. sapiens*. Some *H. heidelbergensis* mandibles possess a retromolar gap (Dorey, 2019).

Homo neanderthalensis

The first specimen of *H. neanderthalensis* was discovered in 1856, in Prussia, modern Germany. Neanderthals were the first extinct species to be placed in the genus *Homo* (Collard & Wood 2007). Less derived Neanderthals first appear 300 ka in the fossil record, though classic Neanderthals lived from about 130 to 35 ka all over Western Eurasia, from Gibraltar to Uzbekistan (Stringer & Andrews 2005). It should be noted that less definitive Neanderthal fossils have been dated as far back as 400 ka (Harvati 2007). Many of them lived in caves, which is part of the reason we have so many fossils from this species. Although the first Neanderthal fossil was discovered in 1856, it was not until 1864 that the English geologist William King classified *H. neanderthalensis* as a separate species from *H. sapiens* (Collard & Wood 2007).

The physical traits that dictate Neanderthals being their own species appear less pronounced at first and became more exaggerated as the Pleistocene epoch progressed. The earliest Neanderthal specimens are known from about 600 ka in Spain. Neanderthal traits become a little stronger in fossils 150 ka around the turn of the Middle to Late Pleistocene. The classic Neanderthals, those with the most derived features, appear in the Late Pleistocene, around 70-30 ka (Fig. 4).

Figure 4. Profile and frontal view of a classical Neanderthal cranium (Harvati 2007).

These traits include having a larger brain and larger nose than modern humans, double-arched supraorbital ridge, and a more anteriorly-pulled face (Fig. 5) (Stringer & Andrews 2005). In addition to these cranial features, Neanderthals were shorter and stockier than modern humans, with much thicker long bones (Stringer & Andrews 2005).

As for their teeth, west Eurasian dental features that are particularly prevalent among *H. neanderthalensis* include more buccal concavity on the maxillary canines, taurodontism (when the molars are elongated vertically and the roots are forced to shorten), and bigger hypocones on M^1s that protrude away from the root of the tooth (Xing et al. 2015). Overall, their teeth were larger than *H. sapiens*. Neanderthals also had a retromolar gap, which is a space between the third and final molars and the ascending ramus, the more vertical part of the jaw which branches out and articulates with the cranium. Their mental foramen is below the M_1, as opposed to behind the premolars like in modern humans. Their gonion, the angle where the ramus meets the body of the mandible, is rounded.

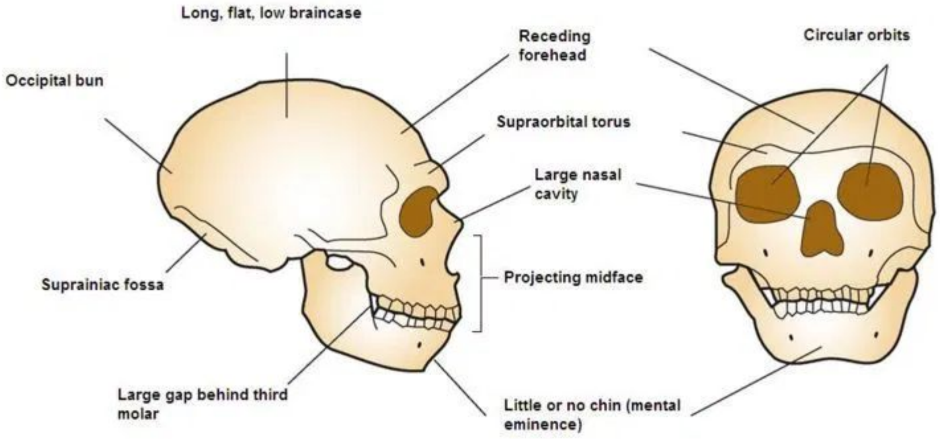


Figure 5. Profile and anterior view diagram of diagnostic *H. neanderthalensis* features (Kamrani 2007).

Another defining feature is that the coronoid process of *H. neanderthalensis* is higher than their condyloid process, giving them an asymmetrical mandibular notch, similar to *H. sapiens* but unlike other earlier hominins (Fig. 5). Their mandibular notch is also shallow. They also have deep pterygoid fossae (Harvati 2007). Although these are very Neanderthal-like traits, it is often the case that any European population from that time can exhibit them, though they may be more rare in non-Neanderthal populations (Xing et al. 2015). This can make it difficult to differentiate the two at times. Overall, the teeth of *H. neanderthalensis* were larger than those of *H. sapiens*, and were set in a more robust jaw (Dorey 2019).

Homo naledi

Homo naledi is a species that is represented by fossils that have been exclusively found in Gauteng, South Africa, discovered in 2013 (Berger et al. 2015). The age of the fossils may be anywhere from 335 to 246 ka.

While the hands, wrists, feet, and lower limbs of *H. naledi* are humanlike, the proximal femur, torso, shoulders and pelvis are more like that of an australopith (Berger et al. 2015).

The maxillary incisors, mandibular incisors, and canines overlap in size with *Paranthropus*. *H. naledi*'s mandible is more gracile than that of *Paranthropus*, specifically in its symphysis and corpus. The mandibular symphysis is more vertically inclined. The buccal side of the mandibular molars are narrow, and postcanine teeth are smaller than those of australopiths and Paranthropus. Both I^1s lack a median lingual ridge, but they do have a broad and uninflated, lingual cervical prominence. The buccal grooves on P^1 and P^2 are weakly developed (Berger et al. 2015). *H. naledi* does have an isolated, small Carabelli's cusp on the upper molar; this is an additional tubercle on M^1 (Fig 6).

Figure 6. Photograph of the M^1 of a modern *H. sapiens*, with the cusp of Carabelli encircled (https://supernumeraryteeth.com/cusp-of-carabelli/).

The lower molars have small protostylids, which are a type of paramolar cusp. Both the maxillary teeth and mandibular teeth are smaller than those of *Australopithecus sediba*, and its mandibular molars specifically are buccally narrow. On its I^2, *H. naledi's* lingual mesial and distal marginal ridges do not merge onto the central prominence. The paracone (anterior cusp) and protocone (centrally located cusp) on the P^3 are of equal size. Furthermore, the molars' lingual cusps lie at the occlusobuccal margin, while the buccal cusps are more lingually relative to the occlusobuccal margin (Berger et al. 2015). Although the features of the mandibles are a mosaic of human and chimp-like traits, the eruption sequence of teeth is more human-like. For example, the M_2 of *H. naledi* erupted very late in development, which has previously only been known in modern humans. Even *H. neanderthalensis* had a more primitive eruption sequence (Cofran & Walker 2017).

The roots of *H. naledi*'s molars have more primitive features. The size of their teeth are quite similar to *H. sapiens*, in that they are smaller than earlier hominins such as *H. erectus*. *H. naledi*'s molar crowns are small, similar to *H. sapiens*, although their incisors are more similar in size to those of *Australopithecus*. Overall, *H. naledi* teeth are higher crowned and more resistant to wear than the teeth of Paranthropiths and Australopiths (Dorey 2019).

Homo floresiensis

The first fossils now attributed to *H. floresiensis* were discovered in 2003, in Liang Bua cave in Indonesia by Mike Morwood (Henneberg, Eckhardt & Schofield 2011). The earliest horizon that associated artifacts have been found in date to 190 ka, and the most recent horizon has now been pushed back to 60 ka at the latest. *H. floresiensis* have only been found in Liang Bua on the island of Flores, from where they get their name (Stringer & Andrews 2005).

Some apomorphies of *H. floresiensis* include having a cranial capacity of about 417 cc and standing about a meter tall (Collard & Wood 2007). From their bones it appears *H. floresiensis* had an australopith-like gait, but from the cranial remains (Fig. 7) it is clear that they should be included in the genus *Homo*, perhaps descended from a population of *H. erectus* that underwent island dwarfing in isolation (Stringer & Andrews 2005).

The dentition of *H. floresiensis* is more similar to *H. erectus* found on Java than *Homo habilis* or *Homo erectus* (Kaifu et al. 2015). Some of their defining traits include a developed crown on the P^2, which also has a transverse crest. Their alveolar arcade is moderately wide, and the lingual cusp on P_1 is distally positioned (Kaifu et al. 2015).

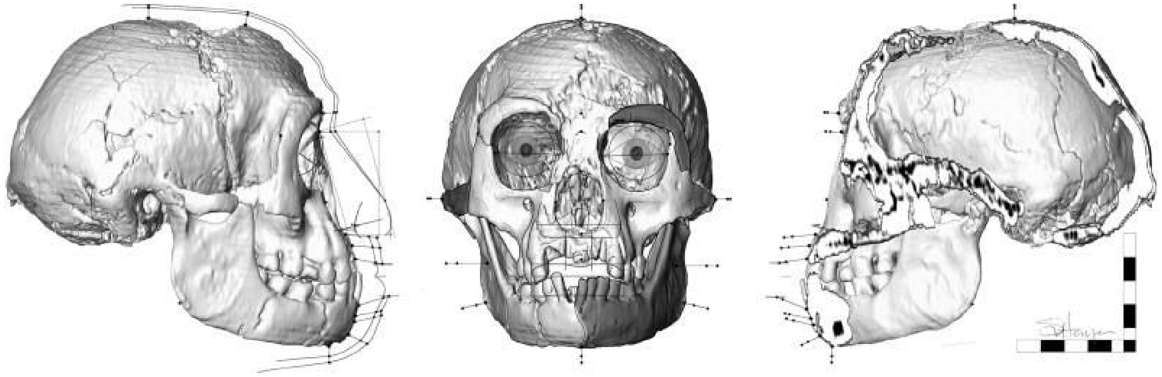


Figure 7. Lateral and profile views of *Homo floresiensis* skull found in Indonesia (Hayes et al. 2013).

Many scientists argue that including *H. floresiensis* in *Homo* will push the genus to have a huge range of cranial capacity, which has historically been used as an apomorphy for *Homo*. Wood & Collard (2007) think *H. floresiensis* should be assigned to another genus because their gait, brain size, and limbs are so different from *H. sapiens*.

Homo sapiens

Anatomically modern humans inhabit every continent save Antarctica, and have existed in their current form for approximately the last 200 ka (Stringer & Andrews 2005). In 1758, Carl Linnaeus named our species *Homo sapiens,* meaning “wise earthly being.” He used himself as the lectotype, or type specimen, for describing the species (Anderson 2015).

Some apomorphies of the jaw of *H. sapiens* include the styloid process being extremely laterally positioned, the plane of the occipital bone that is very high and narrow, and the presence of a chin (Tattersall & Schwartz 2008). For complete tables of the measurements of H. sapiens teeth, see Appendix A.

When examining teeth for mandibular incisors, the centrals are slightly smaller than the laterals (Hohmann & Hielscher 2014). Their lingual surfaces are slightly concave, which is necessary for them to function properly, and they have straight and leveled edges. It is difficult to distinguish between left and right lateral and central incisors. The lingual surfaces of the incisors have less pronounced dental tubercle (Hohmann & Hielscher 2014). Two sides of the canine meet at its cutting edge: the distal side, which is longer and recedes steeply, and the shorter mesial side.

The premolars have a variety of distinguishing characteristics. The medial ridge on the P^1 are more distally placed, mesiobuccal cusp ridges are longer, and the cervical margin is curved apically. A P^1 has an oval-shaped occlusal surface with its buccal cusps being higher and more angular than its more-rounded lingual cusps. The groove formation has the appearance of a broad letter H (Hohmann & Hielscher 2014). P^2 are smaller and more symmetrical than the first, upper premolars although their cusps are similar in size to the first. Its buccal surface is smaller than that of the first, upper premolar but with less pronounced angles. P^2's occlusal surface is more symmetric than P^1 but with essentially the same features. The outline of the lower premolars is more circular than the upper ones, and while the P^1 and P^2 are similar, great differences exist between P_1 and P_2. The buccal surface for the first lower premolar is actually pretty similar to the lower canine. The tip of the cusp is rounded, and they have a prominent central ridge. There is only a slightly developed lingual cusp; the lingual surface is narrow and small. As for the occlusal surface of this tooth, the lingual cusp is smaller and more truncated than the buccal one. The P_2 has a more horizontal occlusal surface when compared to the first one. Its buccal surface is reminiscent of a broad canine tooth, as it has a cusp ridge and rounded point. Its lingual surcade is shorter and has a transverse complexity. The occlusal surface of P_2 has cusps, cusp crest-ridges, marginal ridges, and grooves. The groove formation of this surface has a Y-shape.

The molars of *H. sapiens* have numerous apomorphies and morphological diversity within the species. The first upper molar has a longitudinal groove, which gives it the appearance of being two premolars fused together. The occlusal border has a ridge-shaped cusp form, with the distal cusp being lower and less pronounced than the mesial one. Its cervical grooves are less developed. The lingual surface is smaller than its buccal surface, and its longitudinal groove is displaced distally. Both cusps bulge inward toward the occlusal surface. The first, upper molar also happens to have an additional, low-lying cusp named the cusp of Carabelli, which lies on the mesial part of the lingual surface. The four main cusps are all on the occlusal surface, and are all different sizes (Hohmann & Hielscher 2014). The two buccal cusps are more angular and for shearing while the two palatal ones are more rounded and used for crushing. The mesiolingual cusp is the largest, with the mesiobuccal smaller than that, the distobuccal smaller than that, and the distolingual being the smallest. M^2 is very similar to M^1, except for its lingual surface being less developed, and it has no cusp of Carabelli. In order to more easily visualize the relation of the different sides of a tooth, see Fig. 8.

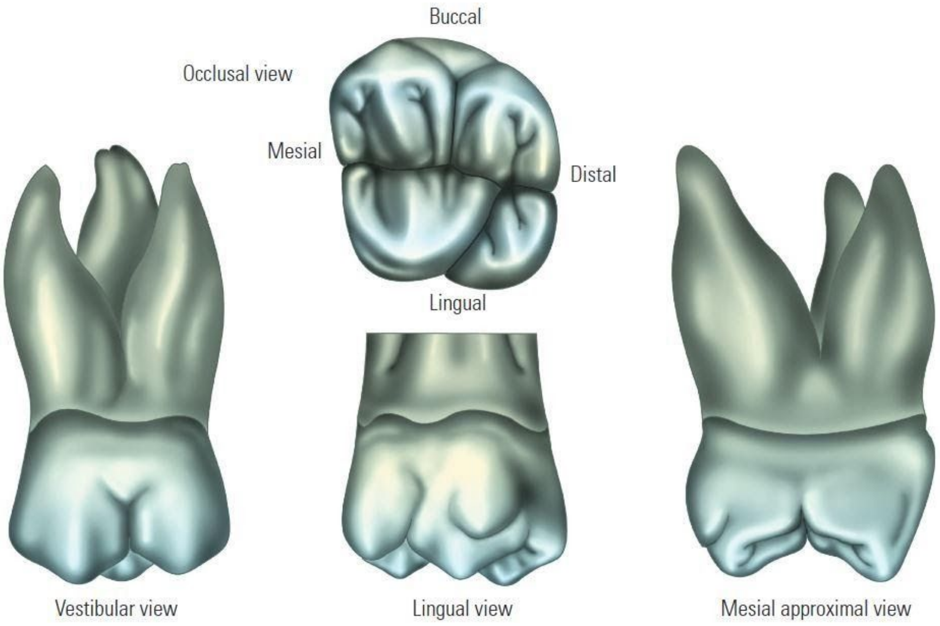


Figure 8. The labeled sides of an upper-left, first molar (Hohmann & Hielscher 2014).

The lingual surface of M^2 tapers sharply to the cervix (the section of the tooth that is closest to the gum, but still above the root). The occlusal surface is sufficiently similar to that part of M^1. M^3 comes in different forms, sometimes having all four cusps, and sometimes being only a single peg (Hohmann & Hielscher 2014). M_1 normally has a crown with five cusps: three lingual and two buccal. Its periodontium, which is the bone tissue that surrounds and supports the tooth, is quite well developed, and the tooth has an overall lingual inclination. Its three buccal cusps all have longitudinal grooves, and its lingual surface is also divided by a longitudinal groove. The mesiolingual cusp is larger than the mesiobuccal, which is larger than the distolingual, which is larger than the centrobuccal, with the distobuccal being the smallest cusp on the M_1. M_2 has only four cusps and is slightly smaller than M_1, and its cusps are, for the most part, equally sized with a symmetrical layout. As for the M_3, there is much variability among individual *H. sapiens*, and I will not list average measurements because it can take the form of a three, five, or six-cusped tooth. It is normally a little smaller than M_2 (Hohmann & Hielscher 2014).

After birth, the two parts of the mandible fuse to become a single bone (Betts et al. 2013). The margin where the body and ramus meet is called the angle of the mandible. Each side of the mandible has two upward bony projections, the anterior of which is called the coronoid process, and the posterior is called the condylar process (Fig. 9).

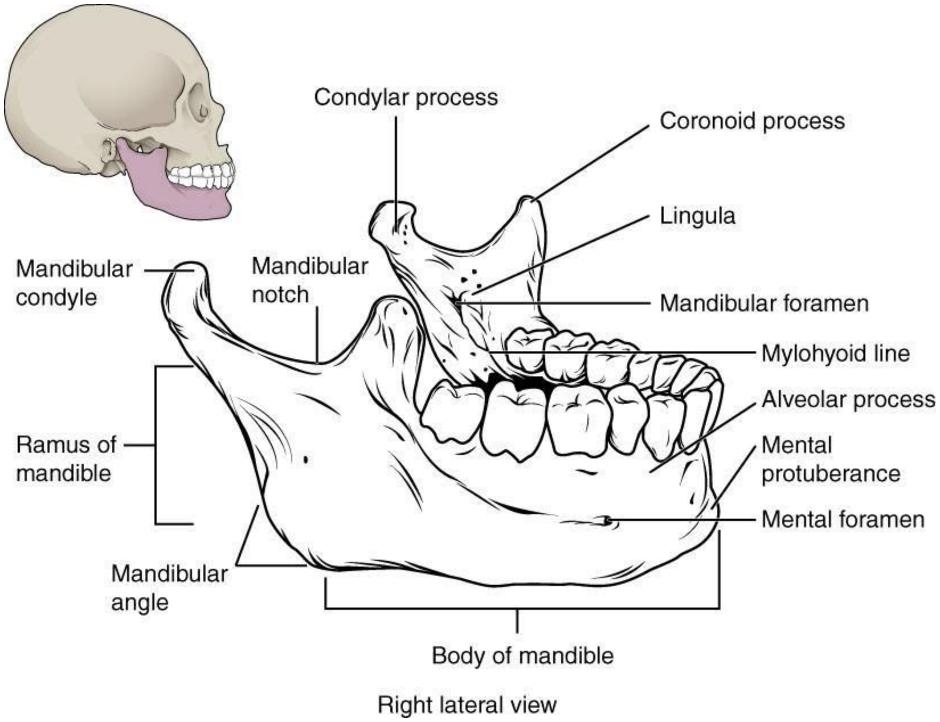


Figure 9. Diagram of a *H. sapiens* mandible (Betts et al. 2013).

One feature that distinguishes the mandible of *H. sapiens* is the mental protuberance. This is the chin, which is a projection of bone that comes out of the inferior margin of the jaw (Betts et al. 2013).

When compared to other hominins we have reviewed, the teeth of *H. sapiens* are at their smallest. The canines, especially, are small, nonprojecting, and formed very much like incisors. The incisors themselves are also much smaller (Dorey 2019). Another apomorphy of *H. sapiens* is that their P_1 have two equal sized cusps, making them bicuspids. A retromolar gap in *H. sapiens* is very rare (Dorey 2019).

Effect of Cooking on Hominin Teeth

Although *H. erectus* and later hominins may have been able to control fire as early as 800 ka, satisfactory evidence does not exist for their wide-spread use of fire to cook food (Stringer & Andrews 2005). The current evidence suggests that only *H. sapiens* used cooking in a way that could have feasibly exerted an evolutionary pressure on their teeth.

A circle of scorched stones, called a hearth, is widely accepted as indisputable evidence for fire controlled by *H. sapiens*. Remnants of charred bone are not necessarily indicative of purposeful cooking because this artifact can be generated naturally. Likewise, a single site of a hearth is not satisfactory evidence because the whole of the species would need to be cooking food for there to be a uniform selective pressure for evolution. While clear evidence for hearths first shows up 250 ka, it appears that 125 ka may be the most conservative estimate for widespread, consistent use of cooking with fire (Pennisi 1999).

As has been stated previously in this review, hominins that existed before the advent of cooking have larger molars with more surface area, more robust jaws and larger premolars. These include fossils attributed to species such as *H. erectus*, *H. heidelbergensis*, and *H. neanderthalensis* (Antón 2003; Harvati 2007; Dorey 2019). Because these species were not able to consistently cook their food before mastication, there would have been an evolutionary pressure on their jaws and teeth to remain larger and more robust in order to exert the pressure required for breaking down uncooked, unprocessed foods (Pennisi 1999).

Cooking has a considerable impact on food and how easily mastication can be carried out. Cooking meat stiffens its muscle fibers, which reduces the amount of energy that dissipates when the meat is fractured (Zink & Lieberman 2016). As for plants, heat degrades polysaccharides and weakens intercellular bonds, making the plant tissue softer (Zink &

Lieberman, 2016). In these ways, cooking reduces the amount of force required to adequately chew food before it can be transported to the esophagus.

With these processes being regularly used to manipulate the physical properties of food consumed by *H. sapiens*, the pressure to build large teeth and jaws, which in itself is energetically taxing, would have been relieved. This could have allowed for the decrease in size in the posterior dentition that we see in modern *H. sapiens* (Emes, Aybar & Yalcin 2011). However, the decrease in the size of *H. sapiens* dentition seen over time appears to be a gradual change, and there may not have been a strong selective pressure from any one tactic of food preparation during the Pliocene and Pleistocene (Gómez-Robles et al. 2017; Ungar 2002). A decrease in the size of the posterior teeth, cusp size, and a decrease in the build of the jaw, resulting in a more gracile mandible, were all changes that occurred in hominin species over time. These trends are found to begin even before the evolution of the tribe Hominini, when looking at the greater pattern of evolution among the Australopiths and Paranthropiths (Birdsell 1972; Dorey 2019). There were very likely other selection pressures that also guided the trajectory of the dentition of *H. sapiens* during the Pliocene and Pleistocene (Gomez-Robles et al. 2017). *H. sapiens* posterior teeth, dated to as much as 300 ka have been found in Europe with similar morphology and dimensions that the species exhibits today. With the evidence we have now for the earliest wide-spread use of controlled fire, a strong connection between cooking and the evolution of the jaws and teeth cannot be made (Gómez-Robles 2017; Evans et al. 2016).

***Homo sapiens* Teeth Today**

Weston Price was a Canadian dentist who traveled around the globe in the 1930's to study the relationship between diet and dental health (Larabell 2017). In search of a control group to use as a comparison to patients with dental ailments, Price photographed people from numerous cultures to visually record the condition of their dentition (Fig 10). He found that groups of people who consumed harder, tougher foods, which he referred to as “native foods” had wide, symmetrical dental arcades, a lack of tooth crowding, excessively worn-down teeth, and rates of dental caries per tooth that often remained below 1% (Price, 1939). However, populations that ate softer foods, which he referred to as “imported” or “western foods,” suffered from malocclusion, tooth crowding, toothaches, and rates of caries of around 25%, though their teeth were considerably unworn (Price 1939).

Figure 10. (a) Four photographs of Melenisians whose diet consisted of native food which required more mastication. (b) Four photographs of Melenisians whose diet consisted of imported, western food which was both calorie-dense and softer (Price 1939).

Most of the communities that Price studied represented static populations in terms of dietary pattern, that is, either whole communities consuming either native foods or western foods. However, the Native Alaskans surveyed offered him a dynamic view which shows how quickly the transformation took place, and suggests that the development of the jaw related maladies may be correlated with the diets of those individuals. At the time of Price's survey, colonization of the Arctic was underway in the form of the introduction of Western schools and Catholic missions. This gave some individuals (youth living near commerce ports) access to "Western" food, while others (parents of the youth) chose to keep eating traditional "Native" food (Price 1939). Again, it was those who ate the imported softer foods that developed maladies and whose teeth went largely unworn, while those living in the same settlements who stuck to traditional, harder foods were without these ailments. Price's work *Nutrition and Physical Degeneration* was published well before the rigorous standards of scientific study prevalent today were commonplace. Although his findings can not be taken as robust evidence for the effect of an organism's diet on its skeletal and dental development, his book nudged the concept into the scientific conversation and made people aware of such a possibility.

In 1982, scientists performed a study on South *Saimiri sciureus* to explore this relationship in a more controlled setting. Here, researchers compared dental casts made on 43 *S. sciureus* that had been raised on varying diets. A group of 22 of the squirrel monkeys were captured from the wild, who had matured consuming their naturally tough foods. Another group of 17 monkeys were raised in a laboratory setting raised on artificially soft foods (Corruccini & Beecher 1982). To each group, 2 monkeys were added that had been raised in the laboratory and closely monitored throughout their life; the 2 individuals added to the "hard diet" group were raised on biscuits, while the 2 monkeys added to the "soft diet" group were raised on the same type of biscuit but consumed it only after it had been saturated in water, making it softer. Stone dental casts were made of the mouths of all subjects at the end of the experimental period, and sent to other researchers to study and measure them in a double blind fashion (Corruccini & Beecher 1982). The *S. sciureus* from the soft diet group produced casts which demonstrated mesially narrow and elongated maxillary arches, malaligned premolar rows, crowded and rotated incisors, and a higher tooth displacement count (Fig. 11). Subjects from the hard diet group had significantly larger mediolateral arch breadth, and a higher palate, which was measured as the distance from the occlusal surface of M^3 to the palatine bone (Corruccini & Beecher 1982).

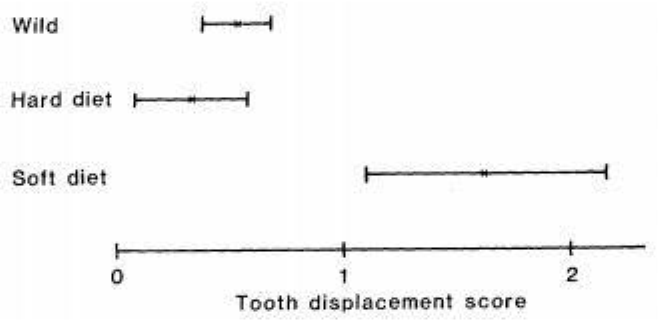
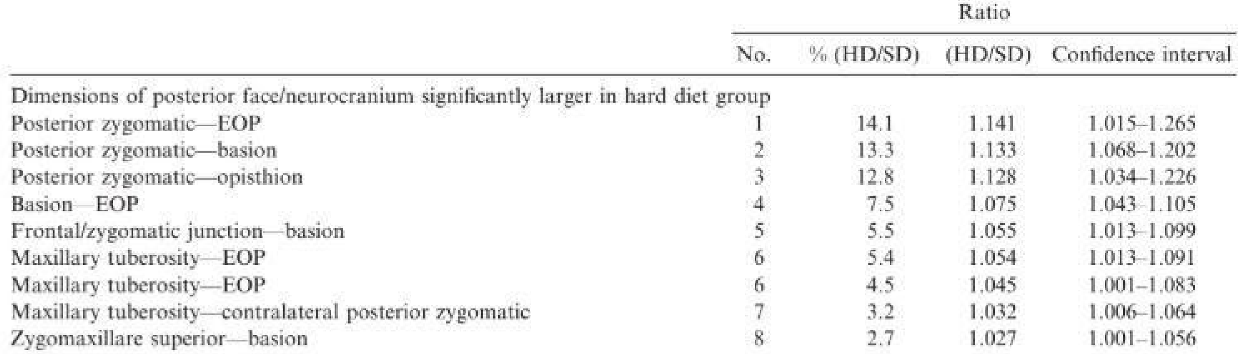


Figure 11. Mean tooth displacement scores with 95% confidence intervals of *S. sciureus* raised on varying diets.

A more recent experiment on this phenomenon was performed by paleoanthropologist Daniel Lieberman and others in 2004. This time *Procavia capensis* were used, a mammal with a retrognathic face. This feature, meaning that the molars of the mammal are situated behind the eye orbits, makes the cranium and mastication musculature of the Rock hyrax more analogous hominins than most extant non-human primates available for research (Lieberman et al. 2004). In this study, all subjects were fed uniform servings of sweet potato, apple, kale, and rabbit chow, though the preparation of the food differed between the two groups. The food was dehydrated for the “hard diet” group to make it tougher; for the “soft diet” group the vegetables were microwaved and the rabbit chow was saturated in water (Lieberman et al. 2004). Additionally, some *P. capensis* had FRA-1-11 rosette strain gauges surgically implanted onto different areas of their face ro collect data as those individuals masticated the different foodstuffs. Unsurprisingly, the data show that the duration of time required to masticate the harder foods is longer than for softer foods, and the magnitude of force required to masticate the harder foods was greater than that needed for softer foods (Lieberman et al. 2004). The subjects were half a year old when the study commenced, and after 98 days the experiment was concluded. Interlandmark dimensions were taken from the craniums of the subjects (Table 1), and show that subjects in the hard diet group experienced greater physical development, such as a greater contralateral zygomatic arch distance, a both taller and wider rostrom, and more anteroposterior growth between the zygomatic arch and the maxilla (Lieberman et al. 2004). Additionally, the corpus of the mandible of specimens from the hard diet group was on average 15% taller and 14 % thicker than the mandible of Rock hyraxes raised on soft foods. In all cases, the areas of greater bone growth in the hard diet group corresponded to the planes of deformation generated during mastication, suggesting that the additional ossification was a response to counteract the greater stresses placed on those areas when chewing tougher foods (Lieberman et al. 2004).

Table 1. Differences in cranial dimensions between hard and soft diet groups of *P. capensis*.



		Ratio		
	No.	% (HD/SD)	(HD/SD)	Confidence interval
Dimensions of posterior face/neurocranium significantly larger in hard diet group				
Posterior zygomatic—EOP	1	14.1	1.141	1.015–1.265
Posterior zygomatic—basion	2	13.3	1.133	1.068–1.202
Posterior zygomatic—opisthion	3	12.8	1.128	1.034–1.226
Basion—EOP	4	7.5	1.075	1.043–1.105
Frontal/zygomatic junction—basion	5	5.5	1.055	1.013–1.099
Maxillary tuberosity—EOP	6	5.4	1.054	1.013–1.091
Maxillary tuberosity—EOP	6	4.5	1.045	1.001–1.083
Maxillary tuberosity—contralateral posterior zygomatic	7	3.2	1.032	1.006–1.064
Zygomaxillare superior—basion	8	2.7	1.027	1.001–1.056

The experiments on *S. sciureus* and *P. capensis* demonstrate that harder foods require more muscular effort in order to masticate, and that such additional stress is placed particularly on the bones of the cranium most closely involved with mastication, such as the maxillae and the mandible. It is known that bones which experience more stress and deformation from muscular forces respond to those stresses by stimulating more ossification and attaining a larger size (Avin et al. 2015). These experiments suggest that mammals whose diet consists of harder, tougher foods experience greater growth in the skull and exhibit fewer cases of dental maladies. However, this phenomenon is not proven to be a direct causal relationship, and more experiments would be needed to substantiate the relationship between the consistency of diet and proper or abnormal dental development.

***Homo sapiens* Teeth Tomorrow**

It is clear that the foods many *H. sapiens* consume today do not require the same time and effort in mastication to be digested as the foods which the species has historically consumed. The many modern diseases such as malocclusion and tooth crowding may be a result of this, as the mandible and maxillae do not grow to a larger size because they do not have as much force exerted on them during development. However, this is only an inference, as no scientific investigation has been carried out to directly test such a hypothesis. Because the size of the teeth are independent of the amount of force placed on them during an individual's development, this results in many living specimens of *H. sapiens* ending up with jaws too small for their complete set of dentition to fit well (Price 1939). I predict that if a population of *H. sapiens* goes completely without orthodontic intervention for a sustained period of time, then those softer foods should exert enough selective pressure on that population to result in an adaptation that could align the morphology of the jaw and dentition to suit such food. However, it should be remembered that in many areas, surgically removing the M_3 and M^3 and using other orthodontic measures such as braces are utilized to correct malocclusion in individuals. However, the resulting physical state is not a genuine phenotype, and cannot be passed genetically to offspring; the problem must be fixed with each generation. For this reason it is difficult to predict how the teeth of *H. sapiens* will look in the distant evolutionary future.

CONCLUSION

When reviewing the size and shape of mandibles and teeth of fossil hominins from the Pliocene to the present, a number of trends make themselves evident. These include a decrease in the size and overall robustness of the mandible, a shortening of the height of cusps on the postcanine teeth, as well as a decrease in size of the molar teeth. By studying primates who existed before and are likely ancestral to the tribe Hominini, such as Australopiths, it is clear that these evolutionary trends began even before *Homo* appeared. The morphology of the face and dentition of *H. sapiens* alive today can also be seen as a continuation of this trend that has been present in our lineage for millions of years. Any attempt to ascribe technological innovations like meat butchery with stone flakes or cooking with fire as an evolutionary force on this changing morphology is difficult, due to the fragmentary nature of such evidence, and the nature of artifacts necessary to support such a claim.

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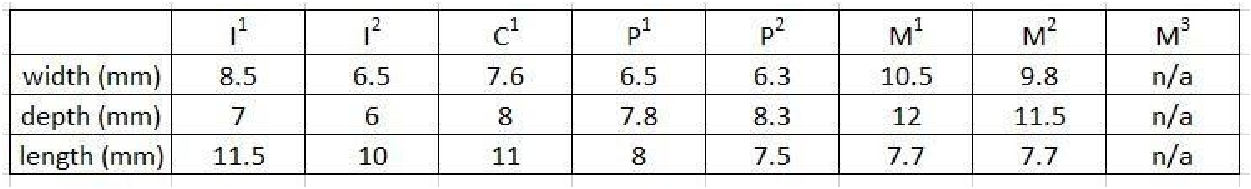
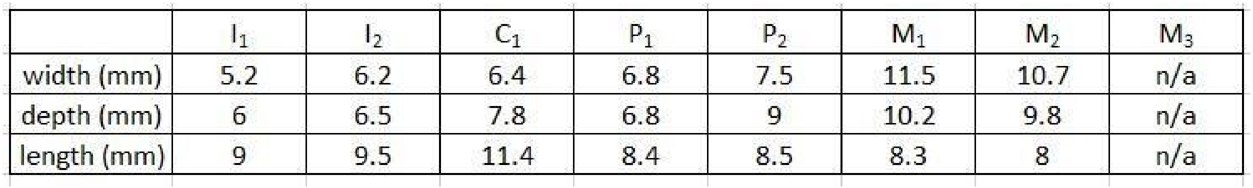
APPENDIX

Table 1. Average maxillary dimensions for *H. sapiens* (Hohmann & Hielscher 2014)



	I^1	I^2	C^1	P^1	P^2	M^1	M^2	M^3
width (mm)	8.5	6.5	7.6	6.5	6.3	10.5	9.8	n/a
depth (mm)	7	6	8	7.8	8.3	12	11.5	n/a
length (mm)	11.5	10	11	8	7.5	7.7	7.7	n/a

Table 2. Average mandibular dimensions for *H. sapiens* (Hohmann & Hielscher 2014)



	I_1	I_2	C_1	P_1	P_2	M_1	M_2	M_3
width (mm)	5.2	6.2	6.4	6.8	7.5	11.5	10.7	n/a
depth (mm)	6	6.5	7.8	6.8	9	10.2	9.8	n/a
length (mm)	9	9.5	11.4	8.4	8.5	8.3	8	n/a