

Australopithecus & Ardipithecus Foodways

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SUMMARY

As we move into the story of human evolution, we should acknowledge that previously in this book we have been concentrating on living animals--ones that we can observe in the wild and conduct experiments on in the laboratory. But here on out until we arrive at ourselves, Homo Sapien, we will be concentrating on extinct primates, such as the Australapithicus, that we cannot directly study. Instead we have to be more clever, relying primarily on clues and various forms of reasoning from many different fields of inquiry--sort of like sleuths actually, trying to unravel the story of our own existence from the clues left behind. Fortunately, scientists are quite clever and have developed many different forms of enquiry that allow us to make some reasonable hypothesis about these Australopithecus and their foodways.

HISTORIC OVERVIEW

Australopithecus/Ardipithecus' Place in the Evolutionary Tree

But before considering this, let's first consider how scientists are tending to believe our evolution happened. In these early years, seven or so more millions of years ago, the environment was changing already but still warm; and since warm and moist environments do not preserve fossils well, we may never have fossils during this time. At the moment genetic evidence, in conjunction with what little we have of the fossil record, suggests that somewhere around eight millions years ago, our common ancestor evolved into the Gorilla, then the Chimpanzee, then our line: the Hominidae. Accordingly, towards the end of this stage, a group of Hominids emerged in eastern Africa that may have been part of our direct line: called the Ardipithecus; to date we have identified about four, distinctive versions--all of which are roughly similar.

THE AUSTRALS

Around four millions years ago, another group, called the Australopithecus, emerged in eastern Africa. Whether they evolved directly from one of the Ardipithecus or some other ancestor not yet discovered is not known; but it's likely they were connected in some way because they are so similar. Over the past one hundred years or so, we have collected hundreds of fragments of bones, skulls, teeth and even petrified footprints from this group which has allowed us to reconstruct them way more than the Ardipithecus. For some particular species, we have as many as three hundred fragments of bones and other parts; but with some others, we may just have one or two fossils. In any case, from this both abundant and limited evidence, we have been able to reconstruct them into several different species within the one group.

They are broken down into two categories, called the Gracile, who have both thinner and finer bones and teeth, and the Robustus, otherwise known as Paranthropus, who have more robust bones and teeth.

Within the Graciles, there are many different species, including the Anamnesis, Afarensis, Sediba and the Africanus. It is generally believed that our line of evolution emerged from one of the Graciles. The Robust include the Robustus and the Bosei. But otherwise all these different creatures are quite similar to each other--they were all bipedal. We have ample evidence to believe that the male Austral's, like the Ardi's, were quite similar to the chimps in their size size, though maybe tending towards slightly smaller, with long limbs and dark bodies. and otherwise shared many of the same, physical attributes but with variations in the shapes of their skulls and faces, as well as their teeth and jaws, although these two had many commonalities. Some of them may have shown greater adaptation to bipedalism. Since they are all so similar, I will tend in many cases to deal with them as one group but will at times also deal with them as individual species. With larger strokes, we can sketch what seems to be the predominant thinking on how these creatures evolved--and the nature of their particular foodways, and then concentrate on the various species.

BASICS OF EVOLUTIONARY THEORY

As we noted in the Introduction, evolution typically works this way: one species, say our common ancestor, is living somewhat comfortably in his reasonably stable environment to which he is well-adapted. But when that environment begins to change, he must change as well—that is, he must adapt to his environment: since primates are intelligent enough, they can adapt in part by merely changing their behavior—but only up to an extent. At some point they must actually change their DNA—or at least the expression of that DNA—to survive and that usually involves some change in their morphology. As we will see, we have reason to believe that our initial primates adapted simply by changing their behavior and eventually their morphology. Usually, too, as species adapt and change, they can become separate from their ancestors and even geographically dislocated from them, allowing for even further changes in their evolution. And when environments become even more varied, with many, different ecosystems, we can tend to see even more diversification or radiation of that same species.

As we shall see, this theoretical framework, now quite commonly observed in biology, appears to be what happened to our own species.

In more simpler terms, you can imagine a creature not too different from a chimp living comfortably in the jungle, perched high above his predators, shaded from the sun, swinging through the foliage with his buddies while eating his tender leaves and fruits. He lives in a sort of Garden of Eden. But suddenly parts of that jungle start to disappear and this arboreal species is forced to adapt in part to life on the land, where predators abound, where the food is tougher and harder and perhaps less tasty. Overall, life is harder, perhaps even more violent than before and he must learn to adapt to survive in this changing world.

CHANGES IN CLIMATE & ENVIRONMENT

underlying the evolution of our species and our ever-evolving foodways

About ten millions years ago, all of Africa was carpeted with forests. But when the tectonic plates under Africa began to collide in the eastern part of the continent, they pushed upward to create a rounded mountain range about nine thousand feet high that separates east and west Africa. Soon after that the Great Rift formed—a valley that runs from north to south. On the western side of the mountains, there continued to be jungle even to this day; this is the side where the Chimpanzees and Gorillas and Gibbons evolved and continue to thrive today. But on the other side of this rift around where Ethiopia exists today, another climate emerged that in general was way less jungly and forested; and this is where the Homidae evolved and accordingly where we find most of the fossils of our own line of evolution, along with parts of South Africa.

In other words, we have here the first step in the evolution of any species—a change in the climate. But we have another step as well: when these mountains formed, they served to separate one species from another species, therefore preventing them from interbreeding and

making their own, unique form of evolution to their specific environment more possible. But then we have even another step common in evolution: the formation of many different environments which creates even more diversity amongst species. On the eastern side of the Rift, we do not have one consistent environment, as we are more prone to find on the western side; instead, back then and even now, we have a patchwork of various environments, consisting of forest patches, woodlands, shrublands with precipitous cliffs that dropped off into arid lowlands. In time, grasslands and savannahs developed as well.
(deMenocal, P.B.)

At this same time we have other changes in the climate happening worldwide, which continued to shift eastern Africa towards a drier, more treeless and perhaps cooler environment. All of human evolution took place during either two or three climatic eras. At first was the Pliocene from about 6 to 2.5 million years when temperatures were stable and even warmer by several degrees than they are now. During this time, we see the advent of our evolution--but not necessarily all that much change in our morphology or behavior from Chimpanzee. During the Pleistocene, from about 2.5 millions years ago to 10k years ago, the climate generally became colder and drier; we typically refer to this time period as the Ice Age but the truth is that, during this time, the environment around the world varied greatly during times of increasing glaciers, known as the Glacial Maximum, followed by retreats; during this time, temperatures could vary substantially and quickly. Worldwide, this was generally a time of biological stress when animals and plants constantly struggled to adapt to the changes, following the curve of the glaciers: retreating and advancing into various ecosystems.

During this time, we see that most of our own evolution took place; in other words, we evolved mostly during times of environmental stress, not calm, as you would expect based on our theoretical model, leading some to call humans the Crisis Animal. Finally, about ten thousand years ago, we entered into our own era, the Holocene when temperatures worldwide increased and stabilized at least for the moment, leaving greater parts of the earth open to human habitation. During this time, concomitant to the change in environment, we see another major shift in at least some aspects of our evolution; we started to farm and domesticate more fully and regularly. Or in other words, from the beginning to the present or at least close to the present, our own evolution, especially in relation to foodways, appears to be intricately linked to the change in our environment.

In the end, it is likely this constant adaptation to the changing environment that largely driven and determined much of our own evolution. You can imagine our species as one cast from its jungle into a drier, leaner and meaner world; once safe in the trees, you are preyed upon predators; your rich, succulent fruits increasingly hard to find; at the same time, as you adapt to this changing environment, the environment then changes again, leading to constant hardship and adaptations. At first these adaptation seem morphological but, at some point, it seemed that was not working well enough so nature needed to innovate the greatest technology known to biology: the human brain, which ultimately allowed us to adapt to our environment and our changing foodways, not by changing our morphology or physiology, which might require thousands of years, but merely by changing our thoughts and behaviors in the blink of an eye.

“Scientists have used chemical isotopes in ancient soil to measure prehistoric tree cover -- in effect, shade -- and found that grassy, tree-dotted savannas prevailed at most East African sites where human ancestors and their ape relatives evolved during the past 6 million years...Fossils of early humans and their ancestors and extinct relatives have been found in both wooded and open environments in East Africa. Even 4.3-million-year-old *Ardipithecus* -- which lived in the woods, according to its discoverers -- had a small component of tropical grasses in its diet, Cerling says...Cerling says even sparse woody canopy provided hominins with shade, some foods and refuge from predators.” (University of Utah).

NOTES ON ENVIRONMENTAL CHANGE & AUSTRALOPITHECUS

Defining African Environments --

The landscape of Africa around the time of the early hominins was a mosaic of habitats that quickly transitioned from woodland to bushland to shrubland and then possibly on to grassland all within a small distance. This mosaicism was partly the result of a relatively abundant amount of subterranean water that arose from nearby lakes and rivers, providing enough water to support habitats that would be unexpected for the mean average rainfall, the overall climate, and soil type. Thus, from this surplus of underground water, edaphic (i.e. water-filled) grasslands, woodlands, thicker bushlands, and forests arose in an environment with a mean average rainfall that would have normally only supplied enough water for grasslands or shrublands to grow.

Together all of these varying habitats formed what is now known as the African savanna, with the word ‘savanna’ acting as an umbrella term that encompasses many of the different environments inhabited by the early hominins. Within each habitat, the early hominins would have been faced with distinct food resources. For instance, the woodlands would have been covered by grasses while the bushlands offered fewer grasses and more fruiting and likely edible plant species than the woodlands.

The Major Patterns of Climate Change in Africa --

7 million years ago during the Miocene, the African landscape was composed of forests and deciduous woodlands. Through a series of glacial cooling cycles, one of which spanned from 3.2-2.2 million years ago, and another more swift cooling that was from 2.1 to 1.9 million years ago, Africa experienced major changes leading to a drier and more open landscape. The ultimate result of 10 million years of glacial cycling in Africa has been more dry and open habitats dominating the African landscape that is currently seen today.

Habitats of the Early Hominins --

The earliest E. African Hominins (i.e. *Ardipithecus*)--

The evolutionary story of the hominids may actually begin in the rain forest alongside the hominids' forest-dwelling primate relatives. Tropical forests, dry forests, woodlands, and montane forests with lakes and rivers were supposedly the original habitats of the earliest bipedal hominids during the Miocene and the beginning of the Pliocene from about 5.8 to 4.3

million years ago. The particular species of mammals discovered in the strata with one of the earliest E. African hominins, *Ardipithecus*, also suggests that the earliest hominids lived in fairly closed woodlands or possibly forested environments. Going back even farther to as early as 15 million years ago, some members of the Hominoidea such as *Kenyapithecus* and *Victoriapithecus* were living in the woodlands of East Africa. This has led some scientists to argue that significant steps in our evolutionary past could have occurred in more forested environments.

Habitats of the Hominins from 4.2 - 3.0 million years ago (*A. anamensis*, *A. afarensis*, *Kenyanthropus platyops*, *A. africanus*):

From 4.2 - 3.0 million years ago, hominins began to live in regions characterized more as mosaics where many different types of habitats existed side by side. Closed to open woodlands, bushlands, riverine forests, seasonal floodplains, and in some regions more dry and open landscapes formed part of the overall habitat of these hominins.

In general, the *Australopithecus* species was found in fairly wooded regions with ample water supply. Among the many habitats exploited by *Australopithecus*, the most commonly noted are closed to open woodlands and bushlands, often with edaphic (water-filled) grasslands. These environments appear to have been fairly static, providing *Australopithecus* with a sure habitat without too many unexpected variations. This setup made *Australopithecus* relatively maladapted to a climate and environment in flux, particularly one where an ample water supply did not exist year round. Thus, it has been proposed that the more unstable climate that resulted in the gradual change to drier and more open habitats with more pronounced dry seasons 2.8-2.5 million years ago may have contributed to their eventual extinction.

Habitat of *Australopithecus afarensis*-

A. afarensis is thought to have mainly inhabited woodlands, dry forested environments, and wooded bushlands. That being said, the different sites of *A. afarensis* indicate that this early hominin existed in varied habitats across both time and space. *A. afarensis* appears to have exploited a very wide range of habitats from dry grasslands to more humid and arboreal forests and woodlands. Thus, *A. afarensis* is considered to be a savanna-forest dweller that exploited the more open as well as the more closed habitats. The ability of *A. afarensis* to successfully inhabit so many different types of habitats suggests that this species had a diet based upon foods that could be found in a diverse range of environments.

Environment of *Paranthropus*--

Paranthropus, also known as robust *australopithecus*, was the likely descendant of the gracile *australopithecines*. *Paranthropus* lived in the same environments as the gracile *australopithecines* (*A. afarensis*, *A. africanus* etc.) in addition to habitats that were slightly more open. Wetlands were supposedly present in both the open and more closed regions inhabited by *Paranthropus*, possibly supplying *Paranthropus* with foods that came from the river, lake margins, or edaphic (water-filled) grasslands. Indeed, *Paranthropus* is always found in relative proximity to bodies of water, often with many mammals who are known to have eaten vegetation from these near water environments. It is important to note that *Paranthropus* is not

found in the arid grassland environments that became more widespread in the early middle Pleistocene. Thus, as the habitats changed to become more arid and open throughout the early Pleistocene, it is most likely that Paranthropus was confronted with diminishing resources in this environment it was not accustomed to.

The Chimpanzee as a potential living model for Australopithecus & Ardipithecus:

In any case we will start with our model of the common ancestor, the Chimpanzee. We use this primate as our model for many reasons already mentioned--that is, his great genetic, behavioral and physiological and even dietary similarity to yourself. But as we shall see, the first of the Hominoids, Ardipithecus and Australopithecus, seem quite similar to the Chimpanzee, with the same approximate weight and size and level of encephalization, as well as some similar anatomy; in fact the first Hominoids seem like the same basic model as the Chimpanzee but with some important adaptation. As such, while our common ancestor was not the Chimpanzee, he was most likely similar to him, perhaps even almost the same.

He already has much of the culture of humanity: he lives in groups of about one hundred: the women tend to the children; the men violently protect their territory and occasionally and opportunistically hunt. Since the females leave at puberty for other groups, the males are more closely bonded and, as such, have more political and violent control over the females; but due to only slight sexual dimorphism, the females nonetheless exert some considerable counter-balance over the males and can even play some significant part as to who serves as the Alpha male; and at the same time, the females have their own form hierarchy of leadership designed more to create cohesion and harmony in the group--though at times they too revert to violence. Chimps seem to express all the positive traits of humanity, love of their children, the desire to protect, even empathy and care for each others--and all the worst, including rape and cannibalism and deception and the acquisition of power through force.

Chimpanzees also show considerable intelligence and skill in monitoring their relationships with as many as one hundred other chimps. They also evidently possess considerable skills in understanding their terrain: where their food is located, what time of year it becomes available, as well as what to eat, and what not--some of which are based on cultural traditions. They even possess the ability, like some other animals, to use food medicinally. On top of this, they have been proven to be able to use rudimentary tools to crack nuts, "fish" for insects, unearth tubers and even impale other primates. Additionally the males can use sophisticated and even strategic social behavior to hunt and defend their territory aggressively and even violently.

While Chimpanzees inhabit various ecosystems that provide different foods, they nonetheless seem to make the extra effort to eat the same certain foods--that is, fruits and leaves, with small amounts of animal foods, suggesting, and perhaps even proving, that their basic caloric and nutritional needs are not determined by their environment but their underlying needs. As medium-sized primates, they have middling metabolism and as such, eat diets more refined than Gorillas but less so as compared to the Capuchin. Furthermore, they have digestive systems that seem perfectly designed for handling those types of foods: with larger, acidic stomachs, longer small intestines, and smaller colons as compared to animals that eat more

leaves and grass. In the end they are animals that need considerable amounts of sugars, in the form of glucose and fructose, from fruits which provide fuel for their considerable brain and testicles, as well as some other purposes. Additionally, the fructose and glucose can be converted into fatty acids, if necessary. At the same time, too, Chimps seem to get ample amounts of fatty acids in their diet, from palm fruits, nuts, and some animal foods like termites; generally these fatty acids are a balance of saturated and monounsaturated with plenty of the polyunsaturated Omega 6 and much lower amounts of Omega 3. These fatty acids in turn provide energy for their heart and working, skeletal muscles.

Overall these two sources, ample sugars and fatty acids, provide the best fuel for generating ATP, the energy molecule, in the body. They get additional energy, too, from the ferments. Additionally they ate leaves for protein and other nutrients, such as magnesium, beta carotene and vitamin K. They also target animal foods, such as termites, and the fatty parts of other primates, that provide ample amounts of these fats. At the same time, they eat only about ten percent of their calories from animal foods but while the amount is small, it nonetheless seems essential to their diet, likely for the fats, but also for the protein, as well as possibly some other nutrients, such as Phosphorus or Calcium or others.

SENSING

SMELL

As we have noted earlier, nocturnal primates tend to have a more developed sense of smell but based on what we know of their anatomy, that does not appear to be the case with Austals, so its most likely that they were--or at least most of them--more diurnal like the chimps and most other extant Apes.

LOCOMOTION

Ardipithecus' Locomotion—feet and musculature in legs for climbing trees, walk upright on ground; more primitive pelvis with mix of more human-like and ape-like features that would have supported both walking and climbing; Ardi was an efficient walker, but a less efficient and slower runner.

Author's Notes: "Until now, the fossil record has told us little about when and how the early hominid pelvis evolved. Even 3 to 4 million years ago (when our brains were still only slightly larger than those of chimpanzees), it had already undergone radical transformation. One of the oldest hominid pelvis, that of Australopithecus afarensis (A.L. 288-1; "Lucy"), shows that her species had already evolved virtually all of the fundamental adaptations to bipedality. Even the kinetics of her hip joint were similar to ours. Although the human pelvis was later further reshaped, this was largely the result of our much enlarged birth canal.

Ardipithecus ramidus now unveils how our skeleton became progressively modified for bipedality. Although the foot anatomy of Ar. ramidus shows that it was still climbing trees, on the

ground it walked upright. Its pelvis is a mosaic that, although far from being chimpanzee-like, is still much more primitive than that of Australopithecus.

The gluteal muscles had been repositioned so that *Ar. ramidus* could walk without shifting its center of mass from side to side. This is made clear not only by the shape of its ilium, but by the appearance of a special growth site unique to hominids among all primates (the anterior inferior iliac spine). However, its lower pelvis was still almost entirely ape-like, presumably because it still had massive hindlimb muscles for active climbing.

Changes made in the upper pelvis rendered *Ar. ramidus* an effective upright walker. It could also run, but probably with less speed and efficiency than humans. Running would also have exposed it to injury because it lacked advanced mechanisms such as those that would allow it to decelerate its limbs or modulate collision forces at its heel. Australopithecus, which had given up its grasping foot and abandoned active climbing, had evolved a lower pelvis that allowed it to run and walk for considerable distances.

Ar. ramidus thus illuminates two critical adaptive transitions in human evolution. In the first, from the human-chimp last common ancestor to *Ardipithecus*, modifications produced a mosaic pelvis that was useful for both climbing and upright walking. In the second, from *Ardipithecus* to Australopithecus, modifications produced a pelvis and lower limb that facilitated more effective upright walking and running but that were no longer useful for climbing. Because climbing to feed, nest, and escape predators is vital to all nonhuman primates, both of these transitions would likely have been a response to intense natural selection.” (Lovejoy, Suwa, Spurlock, Asfaw, & White 2009).

“The femur and pelvis of *Ardipithecus ramidus* have characters indicative of both upright bipedal walking and movement in trees. Consequently, bipedality in *Ar. ramidus* was more primitive than in later Australopithecus.” (Lovejoy, Suwa, Spurlock, & White 2009).

FIRST ADAPTATIONS: ARDIPITHECUS

If you remember: when Savannah Chimps encountered an environment in which their food is more scattered, they did not change their diet: they simply expanded their territory and therefore covered more ground to attain their food, changing some of their social behaviors along the way. With the first of our Hominoids, the *Ardipithecus*, we see a similar adaptation but taken to another level--that is, they actually became genetically designed to move more efficiently over the land so they could access more food--that is, they became bipedal, like us, so they could walk upright and cover more territory as well as gain some other advantages as well. Extant apes, like the Chimps and Orangutans, will use bipedalism occasionally sometimes in the trees to extend their reach and sometimes on the ground for the same reason or for better locomotion--but they can maintain that uprightness for only short periods of time. However the *Ardipithecus* was likely the first of the primates to be able to walk upright permanently; indeed, from studying their anatomy, we know that they were designed for it.

Many theories have been proposed about the reasons for this adaptation but one in particular makes the most sense, especially regarding foodways--that is, that bipedalism greatly increased their efficiency of movement which therefore makes more food available to them. Conclusive studies have demonstrated that bipedalism is considerably more efficient than the knuckle-walking of other apes.

Naturally, if they can move over the ground better, they greatly increase their efficiency in relation to foodways, acquiring more calories with less effort (Efficiency theory). As we have already seen, one of the most likely or even assured outcomes of the change of environment millions of years ago is that trees--and therefore ape food--became more scattered. So therefore it makes lots of sense to think that one of the most convenient and best adaptations would be improved locomotion between patches of trees--and therefore increased efficiency.

Other theories, too, have been proposed for this adaptation but instead of thinking of one theory right or wrong, I tend to think of all or some of them as correct, provided that they provide some survival advantage, therefore making nature more likely to select for them. For example, another theory states that bipedalism, by elevating the ape into cooler breezes and temperatures and changing the relationship of its body to the sun, helps him dissipate heat better which, in turn, helps him to move better over the ground. While they are higher off the ground, they can also find food better, as well as detect and avoid predators. Though bipedalism increased efficiency in walking, it likely did not help them run faster or longer. (p. 56, *Origins*, Leakey.)

We can easily imagine how this adaptation happened. At some in the past these creatures were like the Savannah Chimps, expanding their territory to account for more scattered food; but as their food became more scattered, they started losing the equation between calories burned, and calories collected--and as such, they were starting to starve. Back then they already possessed some ability to walk upright, since even the Chimps have this ability; but if one of them had this ability more than the others, he could move more efficiently than the others, access limited food better and avoid predation better, helping him to survive much better. At the same time, he would probably more easily elevate himself to alpha male--thereby increasing his chances for breeding and propagation. Meanwhile his knuckle-walking buddies became increasingly weak and did not even know what was coming when the predators attacked. These selective pressures would have continued until over time all these Apes would have possessed that same, similar skill. In the end you have a species that still feeds and sleeps in the trees but then cautiously, while wide open to predation, heat and sun, moves cautiously and quickly across open ground to the next clump of trees. It is possible that they may stop to feed on the open ground but, given its dangers and given that they may not have yet been physiologically adapted to eating starch, they probably did not.

While other adaptations also happened with *Ardipithecus*, I am nonetheless not going to focus on them anymore, just because we know so little about them, having only limited and scattered fossils. Furthermore, most of their other adaptations continued through to the *Australopithecus*

so from now on, we will concentrate on them, especially since we have way more data about them.

AUSTRALS' LOCOMOTION

Pelvis well suited for bipedal locomotion so could walk or run considerable distances; Important because Australs most likely ranged across a greater span of territory composed of a myriad of environments, each with distinct foods available. Pelvis was also still suitable for movement in trees, although Australs had lost the ape's grasping foot.

Australia's footprints displayed toes in line with the rest of foot as in humans, and in contrast to apes who have a diverging big toe they use for climbing/grasping. Australs had a similar heel to toe gait as modern humans, but had shorter legs leading to a smaller stride.

Australia's hands had fingers less adapted for climbing, with longer and more dexterous thumbs more well suited for manipulating tools.

Luke's note: chimps had consistent jungle environment, defined territory, controlled by rival groups but likely very different for Australs: as we will see, much greater range, harder to defend--but within that territory, more variation in terrain and ecosystems; so we cannot necessarily think that these Austral relied upon one certain ecosystem: they may have moved around between the two: summary of article that reconstructs the habitat

Rebecca's note: Baboons and Australopithecines originated in Africa around the same time after the expansion of the grasslands and were thus likely to have been seeking survival amongst similar environmental changes and ecological challenges. In response, both species appear to have developed strategies that involved the exploitation of a wide array of habitats, making use of a greater range of food sources. Unlike their forest-dwelling primate relatives who typically relied upon solely the forest for food, both australopithecines and baboons evolved to subsist on eclectic diets composed of foods from the dry grasslands as well as the more humid and arboreal forests and woodlands. Thus, both species have come to be characterized as savanna-forest dwellers who most likely roamed in the areas of transition between the open savannas and the forests or woodlands, exploring the savanna but never straying significantly far away from the forest.

So from this limited information, we can make some strong hypotheses about the nature and function of the Australopithecus, or at least some of the specific species. At night they slept in the trees to stay safe from predators and during the day, they probably fed predominantly in the trees because, as we shall see, that is probably where they found their preferred foods. However, since the trees were more widely scattered, they, like the Savannah Chimps and the Ardipithecus, would need to travel from one forest to another.

It is possible and even likely that the Australs, too, would feed more from the ground, like the Baboon, but they also would have been more subject to predation there, so nature may have selected away from this characteristics. And, as we shall see, they may not yet possess some

of the nutritional physiology to eat the most nutrient-dense and powerful foods like seeds and tubers that are typically found closer to the ground.

Instead of breaking into smaller groups like the jungle chimps, the Australs probably stayed together more as one group like the Savannah Chimps, especially when travelling from one forest to another, for two reasons: to avoid becoming lost and separated from each other, and to better avoid predation. Prey living during this time were abundant—giant hyenas, saber-toothed cats, mega sized carnivores and raptors—6 to 10 percent preyed upon—evidence tooth marks upon bones, talon marks, same predation percentages as other primates today. Social skills and intelligence developed in response to avoid predation. Groups main protection in any species—more eyes and ears, more to mob, confuse and scatter. (Washington University in St. Louis 2005).**more info on Australopithecus as prey rather than predator under 'Predation Warning' under 'Social Dynamics'

AUSTRALS' FEET, STRIDE & GAIT

“The Laetoli footprints were most likely made by Australopithecus afarensis, an early human whose fossils were found in the same sediment layer. The entire footprint trail is almost 27 m (88 ft) long and includes impressions of about 70 early human footprints...The early humans that left these prints were bipedal and had big toes in line with the rest of their foot. This means that these early human feet were more human-like than ape-like, as apes have highly divergent big toes that help them climb and grasp materials like a thumb does. The footprints also show that the gait of these early humans was "heel-strike" (the heel of the foot hits first) followed by "toe-off" (the toes push off at the end of the stride)—the way modern humans walk.

The close spacing of the footprints is evidence that the people who left them had a short stride, and therefore probably had short legs. It is not until much later that early humans evolved longer legs, enabling them to walk farther, faster, and cover more territory each day.” (Smithsonian Institution 2016).

Australia's Hands—Longer and more dexterous thumbs more suited for using tools. Fingers less adapted for climbing, yet, the pattern of trabecular (spongy) bone density seen in Australia is similar enough to chimps to suggest that they were still using their hands for climbing. However, there are differences as well. Like the Ardi's, the Australs were also bipedal--and we have already concluded that this adaptation was mostly about more efficient locomotion across the plains, both to find food and avoid predation. As you might expect, we see some tendency away from hands fully developed for climbing; their fingers were still good for climbing but not as good as the chimps; also their thumbs were longer and more dexterous, which suggests they may have been able to manipulate objects, like tools, better than the chimps.

(<http://anthropology.si.edu/humanorigins/faq/Encarta/encarta.htm> Smithsonian National Museum of Natural History) **Luke, link no longer valid and with a little bit of searching on the Smithsonian website did not find a source.

“The high Pan-like trabecular density in *A. africanus* and the Swartkrans hominin metacarpals suggests that the hands of these early hominins may still be used for arboreal locomotion.” (Skinner, M.M. et al. 2015).

New (Sept 2016) research suggests that Lucy, who was an *Australopithecus afarensis*, was killed from a fall, possibly out of a tall tree, adding to the evidence that they spent time in trees, and highlighting the possibility that Australs were not as adept at tree climbing as earlier hominins.

“The Pliocene fossil ‘Lucy’ (*Australopithecus afarensis*) was discovered in the Afar region of Ethiopia in 1974 and is among the oldest and most complete fossil hominin skeletons discovered. Here we propose, on the basis of close study of her skeleton, that her cause of death was a vertical deceleration event or impact following a fall from considerable height that produced compressive and hinge (greenstick) fractures in multiple skeletal elements. Impacts that are so severe as to cause concomitant fractures usually also damage internal organs; together, these injuries are hypothesized to have caused her death. Lucy has been at the centre of a vigorous debate about the role, if any, of arboreal locomotion in early human evolution. It is therefore ironic that her death can be attributed to injuries resulting from a fall, probably out of a tall tree, thus offering unusual evidence for the presence of arborealism in this species.” (Kappelman, J. et al. 2016).

“Lucy likely died about 3.2 million years ago after tumbling 40 feet out of a tree, according to findings published Monday in the journal *Nature*. She hit the ground feet-first traveling 35 miles per hour, while stretching out her arms to break her fall.

John Kappelman, a University of Texas geologist who proposes the new hypothesis, called it ironic that the fossil that fueled debate about the role tree-climbing played in human evolution died falling out of one.” (Norris, Courtney 2016).

Side Note: Lucy was named after a Beatles song...

“That first evening they celebrated at the camp; at some stage during the evening they named fossil AL 288-1 “Lucy”, after the Beatles’ song “Lucy in the Sky with Diamonds”, which was being played loudly and repeatedly on a tape recorder in the camp.[12]” (Wikipedia, The Free Encyclopedia “Lucy (*Australopithecus*).”).

There would have been some major advantages of bipedalism.

Bipedalism allows for energy savings while walking (not running) and would allow for the early hominins to cover a larger daily range.:

“It has been well established that, at maximum running speed, human bipedalism is twice as expensive energetically than estimated for a quadrupedal mammal of the same mass and that human walking is energetically much more efficient than human running. At an average walking speed of 4.5 km/h, human bipedalism is slightly more efficient than is quadrupedalism in the average mammal. Both bipedalism and quadrupedalism are equally as expensive in

chimpanzees, and at average walking speeds the chimpanzee consumes 150% more energy than does a similarly sized quadruped.

This means that if the proto-hominin was energetically equivalent to a modern chimpanzee there would have been considerable energy savings through adoption of bipedalism, particularly if a large proportion of time was spent moving on the ground. Foley (1992) calculated that at the same body mass a bipedal hominin would have been able to travel up to 11 km for the same level of energy expenditure as a chimpanzee would use over a 4-km distance. At a large body size, bipedal hominins were likely to have been more energy efficient than chimpanzees, to the extent that a 53-kg hominin would have been able to travel 14km, while a 57-kg hominin would have been able to travel 13-km. This would have allowed a greater foraging area. The advantage of bipedalism appears to be energy savings at walking speeds, whereas the advantage of relatively long Homo legs would have been the potential for a significantly increased daily range." p. 332-333

"The shift to bipedalism certainly relates to more efficient terrestrial locomotion. Models exploring the costs and benefits of bipedalism suggest that bipedalism is effective compared to ape-like quadrupedalism when approximately 60% of foraging time is spent on the ground. (Foley & Elton 1998). Travel between trees and feeding on terrestrial plant resources would be a sufficient factor in driving the hominoids towards a bipedal adaptation. Furthermore, such a shift would be enhanced by increases in day range, as would be expected to occur in drier environments regardless of whether plants or animals were exploited." (Stanford, Craig B. & Henry T. Bunn p. 320).

CAPTURE

When exploring the diet of the Australapithicus, we need to consider our assumptions thus far: that given he had about the same size body and brain and digestive system of the Chimpanzee, his metabolic needs were about the same--that is, he needed foods about equally as refined as that of the Chimpanzee. However, most of the tree foods, fruits and tender leaves, were disappearing but other equally refined or even more refined foods were appearing--that is, tubers, grass corms and seeds, as well as perhaps berries and maybe even legumes, as well as many different animal foods. Fortunately we have other lines of research available to us to determine if those foods were actually consumed.

At the microscopic level, we can also analyze the type of carbon in their bones, either c3 or c4, which can determine the basic categories of plants and animals they consumed over their lifetime. We can also look at the other artifacts scattered amongst their bones, such as the bones of other animals, stone tools, and occasionally other, softer matter. Using various techniques we can also partially reconstruct their environment and landscape and, to some extent, determine what sorts of foods were available to them.

DIET

CARBON ANALYSIS

We also have another line of evidence about the diet of Australopithecus through something called "stable carbon isotope analysis" on the enamel of primate's tooth enamel--which can tell us so much, in simple terms, about whether these Hominids were eating foods from the trees or from other sources, such as grass and tubers. As we have noted, plants use photosynthesis to create glucose and fructose and use that same source of energy to in part help with the creation of their fatty and amino acids. In the process of creating photosynthesis, they borrow carbon from the atmosphere but they "fix" that carbon in different ways: some use the c3 pathway, such as trees, and some use the c4 pathway such as grass and tubers and other plants.

When animals eat these plants, these isotopes, with their 3 or 4 markers, are passed into the tissues, including their bones and enamel; this naturally happens with ourselves. When these bones are fresh, they can be analyzed reliably for these isotopes; however, when the bones are fossilized, as is the case with the hominids, the analysis does not work. But it does work for their tooth enamel. So in other words, we can analyze the tooth enamel of the Australopithecus and other primates--and determine the percentage of c3 and c4 plants they were eaten.

C3 FOODS

C3 foods come from trees--but any and all parts of the trees, including leaves, fruits, fruit seeds, nuts and piths or saps--as well as other parts of the tree which we can generally describe as mostly inedible, such as bark, trunks and roots. To complicate matters, C3 foods also include bushes and shrubs, which can provide primarily berries, which are quite similar to fruits in their nutrition, as well as the category of vegetables. Also, c3 foods also includes any animal that eats any of these plants--and then becomes food for another animal.

We then need to consider what of these animals are killed by the Australopithecus, our list comes to: other primates, termites (which eat wood) and other small animals like bugs and maybe lizards; but we must keep in mind that, with declining trees, most of these animal foods were becoming more scarce and perhaps harder to capture. When we factor in what foods on this list are actually eatable in meaningful amounts by Australopithecus, we can say C3 foods include the following: fruits, fruit seeds, tender leaves and nuts and possibly various saps and gums that trees sometimes produce, as well as other primates and other small animals that feed on the trees, with the exception of birds.

Incidentally, C3 foods also include grasses that grow in cooler temperatures, such as the ones that we eat, such as wheat, rice, barley, oats and many others. However, since these grasses do not grow in the same areas as the Australopithecus lives, we can rule them out as potential food.

C4 FOODS

C4 foods include all parts of tropical grasses and sedges including the roots, stems, blades and seeds; as we know grasses started to proliferate in Eastern Africa about seven or eight millions years ago with the beginning of the Rift and changes in the climate so by the time the Australopithecus came around, grasses would have covered most of the landscape. Since it's unlikely that Australopithecus could consume grass blades with any regularity, given the nature of their teeth, metabolism, and digestive system, realistic grass foods would include corms, stems and seeds, otherwise known as grains.

More on sedges, from article:

C4 foods also includes any animals that eat grass or tubers or, in turn, eat the animals that eat these foods, so the list is rather huge and includes most categories of animals alive on the Savannah today, such as all ungulates, ruminants, predators and many others. However, given that Australopithecus did not have the intelligence to use weapons or complicated strategy to kill these animals, and otherwise, was too slow to run them down, we can conclude that most of these animals were off the list, except as possible, opportunistic foods every now and then. However, other animals that were huntable could possibly be on this list, such many we have already placed upon our list, such as turtles, insects such as termites (which also eat grass) and other small animals.

Marine plants and the animals that eat them, including fish and shellfish, are also C4 foods. While fish would prove uncapturable, and therefore strictly opportunistic foods available with some luck, shellfish could have been regularly available, especially given that Australopithecus would have been one of the few animals that could crack them open. As we have noted before as well, Australopithecus would also have been one of the few animals capable of cracking open bones from many different animals, including prey animals like large ruminants, to attain the fatty brain and marrow within.

When all these factors are considered, realistic C3 foods for Australopithecus would have included the usual, primate foods: fruits, leaves, nuts and other primates and other small animals that rely upon the trees. C4 foods would include grass corms and seeds; and perhaps some amount of the same parts of sedges, as well as tubers; possible animal foods are marrow, brains, turtles, other small animals, as well as shellfish.

(source: Copeland, S.R. 2007).

SUMMARY

C3/C4 consumption Ardipithecus & Austral's through Homo:

"Previous research showed that 4.4 million years ago in Ethiopia, early human relative Ardipithecus ramidus ("Ardi") ate mostly C3 leaves and fruits. About 4.2 million to 4 million years ago on the Kenyan side of the Turkana Basin, one of Curling's new studies shows that human ancestor Australopithecus anamensis ate at least 90 percent leaves and fruits -- the same diet as modern chimps. By 3.4 million years ago in northeast Ethiopia's Awash Basin, according to

Wynn's study, *Australopithecus afarensis* was eating significant amounts of C4 grasses and sedges: 22 percent on average, but with a wide range among individuals of anywhere from 0 percent to 69 percent grasses and sedges. The species also ate some succulent plants. Wynn says that switch "documents a transformational stage in our ecological history." Many scientists previously believed *A. afarensis* had an ape-like C3 diet. It remains a mystery why *A. afarensis* expanded its menu to C4 grasses when it's likely ancestor, *A. anamensis*, did not, although both inhabited savanna habitats, Wynn writes.

Also 3.4 million years ago in Turkana, human relative *Kenyanthropus platyops* had switched to a highly varied diet of both C3 trees and shrubs and C4 grasses and sedges. The average was 40 percent grasses and sedges, but individuals varied widely, eating anywhere from 5 percent to 65 percent, Cerling says. About 2.7 million to 2.1 million years ago in southern Africa, hominids *Australopithecus africanus* and *Paranthropus robustus* ate tree and shrub foods, but also ate grasses and sedges and perhaps grazing animals. *A. africanus* averaged 50 percent C4 grass-sedge-based foods, but individuals ranged from none to 80 percent. *P. robustus* averaged 30 percent grasses-sedges, but ranged from 20 percent to 50 percent.

By 2 million to 1.7 million years ago in Turkana, early humans, *Homo*, ate a 35 percent grass-and-sedge diet -- some possibly from meat of grazing animals -- while another hominin, *Paranthropus boisei*, was eating 75 percent grass -- more than any hominin, according to a 2011 study by Cerling. *Paranthropus* likely was vegetarian. *Homo* had a mixed diet that likely included meat or insects that had eaten grasses. Wynn says a drier climate may have made *Homo* and *Paranthropus* more reliant on C4 grasses. By 1.4 million years ago in Turkana, *Homo* had increased the proportion of grass-based food to 55 percent.

Some 10,000 years ago in Turkana, *Homo sapiens*' teeth reveal a diet split 50-50 between C3 trees and shrubs and C4 plants and likely meat -- almost identical to the ratio in modern North Americans, Cerling says.

Baboons' high amount of c4 and c3 -- Curling's second new study shows that while human ancestors ate more grasses and other apes stuck with trees and shrubs, two extinct Kenyan baboons represent the only primate genus that ate primarily grasses and perhaps sedges throughout its history. *Theropithecus brumpti* ate a 65 percent tropical grass-and-sedge diet when the baboons lived between 4 million and 2.5 million years ago, contradicting previous claims that they ate forest foods. Later, *Theropithecus oswaldi* ate a 75 percent grass diet by 2 million years ago and a 100 percent grass diet by 1 million years ago. Both species went extinct, perhaps due to competition from hooved grazing animals. Modern *Theropithecus gelada* baboons live in Ethiopia's highlands, where they eat only C3 cool-season grasses. Cerling notes that primate tropical grass-eaters -- *Theropithecus* baboons and *Paranthropus* human relatives -- went extinct while human ancestors ate an increasingly grass-based diet. Why is it an open question." (University of Utah 2013).

Baboons, on the other hand, eat c4 foods in various proportions--lost of variations even extreme. Hominoids consumed more c4 foods. (Codron, D. et al. 2008).

“The broad view of these data is that early hominins did not have diets like those of extant African apes, but this conclusion belies the complexity of the varied results. For instance, the earliest taxon analyzed to date, *Ar. ramidus*, had in aggregate a C3 diet much like that of savanna chimpanzees (34). Other taxa, such as *Au. africanus*, *P. robustus*, and early *Homo*, were more middling, as they ate more than 50% C3 foods but also consumed substantial quantities of C4 foods (33, 35–38) that became increasingly available in the Plio-Pleistocene (39, 40). In marked contrast, *P. boisei* had a diet of about 75 to 80% C4 plants, unlike that of any other fossil hominin but similar to that of grass-eating warhogs, hippos, and zebras (18, 37, 41). Carbon isotopic variability between these taxa is also marked, with *Au. africanus* ranging from pure C3 to nearly pure C4 diets, whereas other taxa such as *P. boisei* have much reduced ranges.

All told, the early hominins analyzed to date fall roughly into three groups: (i) those with carbon isotope compositions indicating strong C3 diets similar to those of savanna chimpanzees, (ii) those with variably mixed C3/C4 diets, and (iii) those with carbon isotope compositions indicating diets of chiefly C4 vegetation, as is typically seen for grass-eating ungulates in tropical climes.” (Ungar & Sponheimer 2011).

Author's Research: “It appears that the higher percentage of C3 foods in the *Homo erectus* diet is the result of a greater abundance of C3 foods in their environment to choose from than C4 foods. C3 plants do include trees, but also include shrubs, bushes, and herbaceous plants, rushes, a few sedges, and grasses growing in cool, shaded areas. Overall, “the greatest number of potential wild plant food parts likely to have been eaten raw by early hominids (nuts, fruits, flowers, beans), the quality and quantity of which vary seasonally, are from C3 plants (deciduous trees, shrubs, aborescents, and perennial forbs - [i.e. herbaceous flowering plants]). Studies of sub Saharan plant toxicity, nutritional value, and availability also suggest the highest quality of plant foods available to early hominids may have been C3 nuts, mature fleshy fruits, flowers, dry fruits, and beans.” As you may recall, some of the underground storage organs are also from C3 plants.

“A small minority of Africa's wild plant foods are C4. These are primarily the seeds of some of the C4 grasses, the rootstocks and stem/leaf bases of some of the C4 sedges (especially papyrus), and the leaves of some of the C4 herbaceous dicots (forbes). These wild food plants are commonly found in disturbed ground and wetlands (particularly the grasses and sedges).”

And a quote that summarizes and furthers this explanation:

“The vast majority of Africa's wild food plants are C3. These plants provide the wild plant food diets characteristically consumed by the higher primates, including humans. There are 145 families (33 monocot, 112 dicot) and several hundred wild African species known to have been utilized by humans (Peters et al., 1992).

The wild C3 food plants of Africa provide food types both similar to and different from the C4 food plants. Similar food types include leaves, rootstocks, and a variety of seeds provided by C3 herbaceous and woody plants. In both growth form and habitat distribution, these plants are not as restricted as those of the C4 syndrome. Some are found in the same general habitats as members of the C4 group, e.g., seasonal and perennial shallow freshwater wetlands. Others are common where C4 plants are not, e.g., riverine forest and woodland.

The wild C3 food plants also provide food types not occurring in the potential C4 African plant food diet. Some of these may be of minor significance, e.g., nectar, gum, mushrooms. Others are clearly very important. Notably significant are the fleshy fruits and nutlike oil seeds that constitute important core staples in the potential wild plant food diet of sub-humid and semi-arid Africa. The fruits are provided by numerous trees and shrubs covering a variety of habitats (e.g., Peters et al., 1984; Peters and O'Brien, 1994). They are good sources of carbohydrates (sugars), minerals, and vitamins. The proteinaceous nutlike oil seeds are a special category of staples. In woodland savanna plant species, the nutlike seeds are part of an edible fruit, often a keystone fruit species for a variety of mammals (Peters, 1993). The nutlike seeds are rich in fat and protein, and an additional source of minerals and vitamins. For early hominids, they could have provided supplementary nutrients needed to put on fat reserves seasonally (Peters, 1987). In terms of landscape, C3 food plants are found almost everywhere. In the general habitats occupied by C4 food plants, C3 food plants also occur. It is difficult to envisage an environment with C4 food plants without important C3 food plants nearby. One exception might be a vast marsh, dominated by papyrus.

We conclude from this analysis that the hypothesis of a plant food diet for early hominids with C4 plants contributing the majority of food intake appears unlikely.”

Also, I found a few other sources that confirm that *Homo ergaster* had similar C4 % values as *Australopithecus africanus* and *Paranthropus robustus* (75% C3, 25% C4). As far as I know though, they are all referring to one study done by Julia Lee-Thorp.

"Paranthropus, Homo.all reflect carbon of mainly C3 origin but with some C4 input.Values for Homo & Paranthropus are almost identical, suggesting that both hominids had a similar mix of C3 and C4 based foods in their diets (~75% and ~25%, respectively) (Lee-Thorp et. al. 2000). The $\delta^{13}C$ pattern can be explained only by direct consumption of enough grass (as blades, rhizomes, or seeds) to form 25% of dietary carbon, consumption of animals that ate grass, or both. The results do not demonstrate, however, that Paranthropus and Homo had the same diet. For Paranthropus, occlusal enamel microwear studies do not support eating of grass blades that have scratchy phytoliths, but Homo enamel microwear has not yet been subjected to similar analysis. Furthermore, C4 grass seeds are seasonally restricted and uneconomical packages that are difficult to collect without specialized tools. One unexplored possibility is consumption of C4 sedges inhabiting damp areas or pan edges, some of which may have had edible roots.On present evidence, however, it seems reasonable to conclude that at least a good proportion of the 25% C4 carbon contribution is derived from animal foods. Animal foods

may also have been incorporated into the C3 component, but it is impossible to assess the proportions." (Lee-Thorp, Julia p. 132-133).

That being said, here is one source that does include a cautionary note at the end.

"The stable carbon isotope analyses reviewed here indicate that early South African hominid diets did have a significant C4 component. But it was not dominant. It is estimated to have averaged ca. 25% for all three hominid species sampled, *Australopithecus africanus*, *Paranthropus robustus*, and *Homo ergaster*. Some caution in interpreting the isotopic data is warranted. The samples are small and the minimum number of individuals represented has not been presented in the original reports. There are differences in variation across the species, even with these small samples, that may be significant. The samples span unknown temporal durations, with varying degrees of contemporaneity among the specimens and species within a particular deposit."

This 25% value for C4 plants may appear small at first, but actually may be considered relatively high in reference to the relatively low availability of C4 plants in the environment, compared to C3 plants. Since C4 foods are more sparsely distributed and overall less abundant, except in wetlands, scientists have posited that some of the C4 isotopic signal must be the result of the intake of animals that ingested C4 plants. This makes the 25% C4 signal appear more achievable.

"Analysis of Africa's edible wild plants indicates that the leaves of some forbes, the rootstocks and stem/leaf bases of some sedges, and the seeds of some grasses are possible candidates for a theoretical early hominid C4 plant food diet. However, these plant foods are not commonly encountered or abundant in dryland settings, and a variety of C3 plants offer alternative sources of nutrition. It is easier to imagine a hominid diet devoid of C4 plants than one dominated by C4 plants. The type of landscape where wild C4 plant foods would be relatively abundant is that of a mosaic of extensive seasonal and perennial shallow-freshwater wet-lands. Extensive marshes dominated by the giant sedge *Cyperus papyrus* are a special case.""The environmental reconstructions available for the early South African hominid sites do not indicate the presence of large wetlands, and therefore probably the absence of a strong potential for a C4 plant food diet."

Another quote that explains the majority of edible species for humans today in the African savanna are from C3 sources:

"In the 1970s, we began a systematic survey and synthesis of the literature on the dietary use and ecology of the edible wild plants exploited historically by the indigenous peoples of Africa. The purpose was to gain background information to aid ecological interpretations of human prehistory and evolution in Africa by describing one of the natural factors likely to have governed the distribution and dietary ecology of our ancestors: the spatial variation in the diversity and seasonal availability of plant foods. The results to date demonstrate that out of a native flora of about 40 000 (identified) taxa (cf. Gibbs Russell 1985), probably fewer than 1500 provide

edibles for humans (Peters, O'Brien, and Drummond 1992); and that, among other things: .c) the potential plant food mainstays are: fruits, nut-like oilseeds, and rootstocks, exploited seasonally (Peters 1987, 1988; Peters and O'Brien 1981, 1984). d) most of the "edible" plant species are woody plants (trees, shrubs, etc.), the remainder being primarily perennial forbs, with grasses and annual forbs contributing relatively few edible species (Peters, O'Brien, and Box 1984)." (O'Brien, E.M. & Peters, C.R. p. 267).

Thus, to summarize, the African landscape is dominated by edible C3 plants, making it likely and logical that the diets of early hominins would too.

CARBON AND AUSTRAL GRACILE

We are obviously most curious about what is revealed in these analyses for our dead ancestor, the Australopithecus--and what that revealed about his diet. Do the results ultimately confirm that they migrated in their diet from the usual tree foods of apes, like fruits and leaves, to the starches found on the plains, such as seeds, corms and tubers. Before answering that question, we need to be reminded that there are several species of Australopithecus, almost as many as ten altogether and most of them show variable results on their analysis and for some of them we do not even have data. But when all these species are considered, we can begin to see some noticeable trends that, as we shall, begin to harmonize nicely with our other lines of research.

First of all, the results show that, as you might expect, nearly all of the Australs showed differences in their markers from the Chimps, showing greater transitions towards C4 foods, such as tropical grasses and tubers and the animals that ate those plants. Of course, this meshes with other evidence: that the Australs were adapting to an environment where these foods were becoming more predominant, and the C3 foods were vanishing. As we will explore further, this conforms to other trends, some of which we have already observed--but will explore further later.

ARDIPITHECUS

Before we move into the Australs, however, let's backup for one moment and consider the carbon analysis of the predecessor to the Australopithecus--that is, the Ardipithecus, the one we discussed in passing. The research reveals, as we may have predicted, that they ate almost exclusively c3 foods like the chimps, which supports our best guess that these animals likely ate the usual fruits and leaves but just needed to move around better to gather enough of them to maintain their efficiency.

ANAMNESIS

Likewise, with the earliest of the Gracile Australopithecus that emerged about four million years ago, we see similar results on the carbon analysis: that is, they ate almost exclusively c3 foods,

even though they were clearly inhabiting open environments that likely contained lakes and streams. But this raises one interesting question; if they were indeed eating the usual fruits and leaves, why did they have such different teeth from their chimps who were eating the same foods.

There are, to my mind, two possible answers to this question: One is that they developed different hardware to adjust to fallback foods such as seeds or tubers which, though essential to their survival, were nonetheless eaten in small enough quantities so as not to affect their carbon markers all that much. Another possibility is that, while they were eating tree foods like the chimps, those foods may have differed in type and physicality. For example the fruits, in these harsher, drier environments, may have been considerably smaller so as not to need the incisors and also harder and more full of seeds; therefore requiring larger and harder molars.

AFARENSIS

With the other Graciles, starting with the Afarensis that lived from about three to four million years ago, we see a gradual transition towards more c4 foods. Analysis reveals that they were eating about twenty percent c4 foods but with considerable variation in this percentage from one individual to the next, ranging from about zero to sixty percent. More detailed microwear patterns on their teeth indicated they were eating smaller fruits along with smaller, harder fallback foods.

This species, that contains the specimen known as "Lucy" lived in eastern Africa where Ethiopia is now, in habitats that consisted of woodlands separated by grasslands and also contained many lakes. Since they were living in regions with wetlands in their area, some researchers have suggested that they may have been getting their C4 foods from the corms and roots or seeds of sedges, although we have to keep in mind that these foods are rather difficult to gather for animals more accustomed to crawling in trees. It is also equally, if not more, possible that they were getting these foods from grasses or tubers.

Or from animals. As we have noted, given the likely ability of Australopithecus to use simple, smashing tools, as well as the abundance of animal bones left from predation on the African Savannah, it's possible that they ate marrow and brains. And indeed we have evidence that this was indeed the case for Afarensis, at least for marrow. Researchers have found animal bones that were shattered with rocks; on those same bones were also cut marks, showing some signs of some kind of butchery. Since all this dated back to the time and place of Afarensis, it's reasonable to conclude that they were smashing bones, just like chimps, to access the marrow within and evidently, too, cutting away some chunks of meat. (Source: McPherron, S.P. et al. 2010 <http://adsabs.harvard.edu/abs/2010Natur.466..857M>).

It's difficult to know, though, if this type of feeding was merely opportunistic, as it usually is for other primates, or a regular part of their diet. As we mentioned, it was likely impossible for the Australapithic to hunt and kill many animals, so they would have to rely upon predation first by other animals; whether or not these opportunities were frequent or occasional is not known. In

any case these animal foods may have contributed significantly to the c4 markers in the Afarensis.

Notes: Hard seeds, however, are not thought to have comprised a major part of the diet of Australopithecus afarensis. Hard seeds would have left broader scratches and more pits than were observed with the microwear analysis of A. afarensis. Hard fruits would have also left broader scratches and more pits making them an unlikely major food for A. afarensis as well. Leaves can also be ruled out since they are known to leave finer scratches and fewer pits than was observed.

AFRICANUS

With Gracile Africanus, from around two to three million years ago, we see even more transition to C4 foods. They ate on average about fifty percent C4 foods but the individuals ranged from none to eighty percent. Microwear studies on the wear and tear on their teeth also indicates tougher foods. Because of this range and the fact that some of the Africanus did not eat any C4 foods, we should acknowledge that, while these foods were obviously important for them, they nonetheless were not essential nutritionally and perhaps not even preferred. We could surmise several possibilities here: that these were either fallback foods for many of them; and in some environments where fruits, leaves and nuts were more scarce, these foods became an even greater part of their diet. Africanus was the only Gracile to live in South Africa

Another Gracile, the Garhi, lived during this same time but in eastern Africa. But since we only have limited fossils from him, only about four skulls and some skeleton fragments, we do not have any carbon analysis on him. But we do have some evidence that he, like Afarensis, may have smashed bones for marrow and brains. Otherwise the Garhi is known for his relatively longer femur, which suggests even greater adaptation towards efficient bipedalism.

Notes: The diet of Australopithecus africanus, on the other hand, is believed to have been composed mainly of grass seeds, grass rhizomes, and bulbs. Microwear analysis, carbon isotope analysis, and the ratio of strontium to calcium were all taken into consideration in forming this postulation.

GRACILE SEDIBA

breaks the pattern, bigger jaws and all, but still lived on forest foods
2 million years ago, south africa, savannah but fed in the woodlands; adapted for climbing trees and upright walking...

As we moved closer in time to our own age, the other Australopithecus were transitioning to more C4 foods--but that is not the case with Sediba. While the others were getting more of their foods from the ground, he was still evidently staying in the trees, even though he was surrounded by vast grasslands; he ate more than ninety percent c3 foods, even though he lived

about two million years ago. In this particular case, they were enabled to use another line of research--that is, they isolated tiny plant particles, called phytoliths, from the Sediba's teeth which further confirmed the eating of plant foods from the trees. They also did analysis of microwear on two individuals but received mixed results: one of the specimens showed evidence of hard foods, the other less so. While may seem frustrating to our neat pattern, it mostly just suggests that the Sediba found some particular niche in South Africa that allowed him to maintain the same eating habits of his ancestors. Since the Sediba also has teeth similar to other Australopithecus, we once again have some suggestion that these larger, back teeth and smaller incisors were not just an adaptation to C4 foods, such as grains and tubers--but also an adaptation to the smaller, tougher and harder foods they were eating in the trees.

(Source: Wilford, J.N. 2012

http://www.nytimes.com/2012/06/28/science/australopithecus-sediba-preferred-forest-foods-fossil-teeth-suggest.html?_r=1&h) Referring to Journal Article: (Henry, A.G. et al. 2012).

AUSTALAPITHICUS ROBUSTUS

Australopithecus Robustus also had the larger dental hardware of the Bosie and lived in more recent times in another neck of the woods--that is, South Africa, only about two million years ago. For all these reasons it seems predictable that he probably ate greater amounts of C4 foods; but in fact that is not the case at all. He ate mostly c3 foods from the trees--and only ate about thirty percent c4 foods with the range between individuals between twenty and fifty percent--all of which throws some kinks in our thinking. If they were still eating foods from the trees, likely fruits and maybe leaves, why are their teeth larger than all the other Australopithecus that stayed reliant upon the trees. Of course, I can propose the usual answers to this quandary but we cannot draw any conclusions.

Notes: The carbon isotopes present in the enamel of Australopithecus robustus indicate that either grasses or grass-eating animals formed a significant part of their diet. The possible edible portions of grass that may have been ingested by this species and other species of Australopithecus include the grass root (or rhizome), the leaves (or blades) of grass, and the grass seeds. Of these, grass seeds seem to be the most likely candidate for A. robustus. The flat, low-crowned teeth of A. robustus would have been poorly suited for chewing the leaves of grass, and the molars do not appear pitted enough to suggest that they were consuming an abundance of grass roots. Furthermore, scientists can use the ratio of strontium to calcium to determine the relative amount of leaves versus roots, fruits, and seeds consumed. The ratio of Sr/Ca found in the teeth of A. robustus indicates that a significant consumption of grass rhizomes would be unlikely. Thus, as stated before, we are left with the possibility of either grass seeds or grass-eating animals forming a significant part of the A. robustus diet.

ROBUSTUS BOISEI

The Robustus Boisei also lived in eastern Africa perhaps even in the same lands as the Graciles around one to two million years ago, so later in time than many of the Graciles. Since we already know that they came later in time and had thicker teeth, we can possibly predict that

they may have eaten greater amounts of C4 foods and the analysis does offer confirmation. In fact Bousei ate more C4 foods than any other Hominid, a primate that either preceded him or followed him, with the one exception of the Baboons we mentioned earlier that lived millions of years ago. On average they consumed seventy-seven percent C4 foods, ranging across individuals from sixty-one percent to ninety-one percent; furthermore they maintained this same pattern across considerable ranges in habitat and time. We also have more complete analysis on the wear and tear of their teeth and from this analysis, scientist have concluded that they were likely constantly chewing hard, small objects. (source: Ungar, Grine, Teaford 2008).

Since the range here is tighter, with all individuals eating substantial amounts of C4 foods, even while inhabiting different terrains, it could possibly mean that these foods were not just important but essential for their diet. Or in other words, they may have been physiologically adapted to get more starch in their diet, as opposed to the sugars found in fruits, like fructose.

Curiously enough, this level of C4 is about the same for grazing animals that feed almost exclusively on the blades and seeds of grass, such warthogs, hippos, zebras, deer and antelopes, so it includes the ruminants. However, this does not mean that they were eating the same parts of these foods: as already discussed, it's most unlikely that Bousei possessed either the digestive hardware or metabolism to eat the blades of grass.

Incidentally, you may have heard Bousei referred to as "nutcracker man" in the past before he was tested for carbon markers; due to thickness of the enamel on his teeth and large molar teeth with twice the surface area of the molars of modern humans, researchers concluded that he likely ate nuts; and since he ate twenty percent c3 foods that is possible but now nobody refers to him that way anymore.

When we combine all this information together, that Bousei was eating predominantly C4 foods that were hard and brittle--and therefore required large amounts of protective enamel--we can more or less conclude, in my opinion, that they were eating grass seeds, otherwise known as grains. But it's also likely, too, that they were eating other parts of the plants as well and perhaps even considerable amounts of animal foods. Since Bousei has the most pronounced teeth of all the Australopithecus, and perhaps ate the most seeds, we can at least conjecture that the design of all of the teeth of Australopithecus was always leaning towards the purpose of grinding smaller, harder seeds into pulp, either as fallback or regular foods. But given too that so many Australopithecus continued to eat foods from the trees--but still had the larger back teeth--we could also argue that these teeth were adaptations, first and foremost, to different types of foods from the trees. (Source: Cerling, T.E. et al. 2011)

Notes: Thus, as to whether or not the species of Australopithecus consumed grass seeds or grass blades, it appears that they may have eaten varying amounts of grass seeds, although they likely did not specialize solely in their consumption. Grass leaves seem less likely since their teeth would have been maladapted for their consumption in large amounts. This is also supported by the microwear analysis that indicates that the ingestion of significant portions of grass blades was unlikely. Overall, the grass seeds and grass roots may be considered more

probable foods of *Australopithecus* than the grass blades. The high nutritional values of both grass seeds and roots would have made them both valuable foods.

The exception might lie in the diet of *Paranthropus boisei* who appears to be the most likely candidate for consuming grass blades in considerable amounts. *P. boisei* is generally recognized for its thick molar enamel and the high percentage of C4 (including grasses and sedges) foods that is greater than any other hominin sampled thus far. This early hominin has also been characterized by its powerful masticatory abilities which have been commonly associated with a diet composed of nuts, seeds, and hard fruit. However, recent research into the microwear of *P. boisei* has unveiled no supporting evidence for the consumption of hard foods by *P. boisei*, challenging a decades old traditional theory that hard nuts or fruits were behind such a massive masticatory complex.

This new finding combined with data from carbon isotope analysis suggests that it was grasses, sedges, or both that spurred the changes in *P. boisei*'s dental abilities. Through other lines of research, sedges have become a rather viable candidate due to their presence in the riverine woodlands commonly inhabited by savanna primates today and thus possibly inhabited by the savanna-dwelling *P. boisei* once upon a time. In addition, the tubers from sedges would be a high energy food packed with carbohydrates. Furthermore, *P. boisei*'s flat molars with their low, rounded cusps would be expected for a diet composed of plant pith (the tissue found in the center of stems) and tough rhizomes. Nevertheless, many pending questions remain when considering sedges as a major food for *P. boisei* including the relative digestibility and nutritional value of the tubers of sedges without cooking them. Their limited availability across landscapes would have significantly restricted the distribution of *P. boisei*. Moreover, not all sedges are considered to be C4 foods, causing us to question whether sedges would have formed a high enough C4 signal to be considered the "missing C4 food" that dominated the diet of *P. boisei*.

Next, we may ponder whether or not *P. boisei* depended upon grass as a major food source, possibly filling the role for the "missing C4 food" so vital to *P. boisei*'s existence. Unlike sedges, grass thrives in a wide variety of habitats and only uses the C4 photosynthetic pathway. Grasses are consumed by a diverse group of mammals including the ancient "cousin" to the baboons, the primate "*Theropithecus*." Interestingly, this grass eating *Theropithecus* primate has a similar microwear complexity profile as *P. boisei*, possibly indicating a diet of comparable mechanical properties. Despite this congruence, the teeth of these two species vary drastically in other ways. The most blaring and problematic difference is *P. boisei*'s lack of the typical shearing crests or ridges on its cheek teeth customary to ALL grazers, including the only predominantly grass eating high primate *Theropithecus*. *P. boisei*'s teeth are flat which are usually associated with the consumption of hard foods among the fruit eating primates. Furthermore, the directionality of the microwear on the teeth of *P. boisei* and *Theropithecus* differ so that if they both were consuming grass in considerable amounts, they must have been chewing them in different ways, a possibility that could be hard to prove. Nevertheless, there is still potential for grass blades to have been a significant part of the diet of *P. boisei*, especially due to their wide distribution and thus availability. Keep in mind that the research is still young.

Grass blades may be a more viable candidate as a major food source for *Paranthropus boisei* and other Australopithecines down the road as new research becomes available.

Summary of Science Daily Article from Jan 9, 2014, "Two Million Years Ago, Human Relative 'Nutcracker Man' Lived On Tiger Nuts"<http://www.sciencedaily.com/releases/2014/01/140109003949.htm>.

Ever since scientists discovered through stable isotope analysis that the East African early hominin *Paranthropus boisei* subsisted mainly upon C4 foods including grasses and sedges, there has been a widespread lingering question within the science community as to how our ancestors could have survived on such a fibrous, low-quality diet of grasses and sedges. This has led scientists to expand beyond the fibrous grass and sedge blades to consider all of the various parts of the grasses and sedges as potential foods of a higher quality for this early East African hominin.

Keeping with this line of thought, a recent study from Oxford University published in January 2014 suggests that *Paranthropus boisei*, commonly referred to as the "Nutcracker Man," may have relied upon tiger nuts (i.e. corms) as a staple food. Tiger nuts are the edible grass bulbs that are still eaten by humans in many parts of the world today. These tiger nuts are also commonly consumed by modern-day baboons in Kenya who are thought to seek out these nuts for their relatively high levels of minerals, vitamins and fatty acids. Assuming that *P. boisei*, a medium bodied and large brained primate living among the baboons, had similar nutritional needs, tiger nuts would have been a potential nutrient-rich food source that would have satisfied many of the early hominins' dietary requirements. The scientist estimates that tiger nuts would have been able to provide up to 80% of the required daily calorie intake with just 2.5-3 hours of foraging. The nuts would have also been a rich source of starch (carbohydrate). Although, this starch would have been relatively difficult to break down via amylase (the enzyme that breaks down starch), requiring a lot of chewing time, and causing notable tooth abrasion in the process. Of course, this would not have been a problem for *P. boisei* who acquired the "Nutcracker Man" title from the large and powerful jaw and big, flat molar teeth likely making *P. boisei* adept to chewing starch-filled abrasive nuts such as the tiger nuts. *P. boisei*'s diet was probably not all nuts. Besides tiger nuts, this study also suggests that *P. boisei* may have supplemented his diet with fruits and invertebrates such as worms as grasshoppers.

Thus, overall, it is safe to say that *P. boisei* was a dietary generalist like other primates, but with a special preference for corms. Such a proposed diet is supported by the fairly wooded, well-watered environments supposedly inhabited by *P. boisei* that would have supplied an abundance of tiger nuts (i.e. corms). Furthermore, a diet rich in corms is consistent with *P. boisei*'s unique dental morphology and microwear, would have provided sufficient nutrition without an excess of fiber, and also would have been harvestable within the time range *P. boisei* would have had to spend foraging.

P. boisei's reliance on corms may have eventually led to their extinction. With the aridification that occurred in E. Africa, *P. boisei* likely was confronted with a decline in corms, forcing *P.*

boisei into the exploitation of other food resources which Papio (baboons) and early Homo would have been competing for as well, possibly leading to an overall lack of food.

CONCLUSIONS ON CARBON

When we synthesize all this information, we can see various patterns emerge: that in the beginning of our evolution, we seemed to stay with tree foods, even though those foods were slowly disappearing and even though C4 foods, like tubers and seeds, are abounding all around. However, starting around four millions years ago, we see some of the Australapithicus convert to more and more C4 foods while some of them also continued to stay eating almost exclusively tree foods--as though maybe they began to separate into two, different species filling, different dietary niches. While nearly all of them ate less than fifty percent of their diet as C4, one of them, the Bosei, converted to nearly all C4 foods and also had some of the thickest and strongest teeth of all the Australapithicus. It's also important to note that, while all the other Australs maintained about the same brain size, the Bosei actually increased the size of his brain, by around 100 cc and while this may not sound like much, it does represent an expansion of twenty percent, suggesting a possible correlation between conversion to more C4 foods, in the form of starch, and intelligence--an issue we will explore later.

(Also possible correlation between intelligence and more ground dwelling, avoidance of predation, etc).

Why were not eating C4 foods: maybe not adapted, maybe were, avoid predation, tubers difficult to unearth, seeds difficult to gather.....

C4

But as time progressed, the environment continued to change, becoming even more open and drier. During this time, it appears that some of the Australs managed to stay in ecosystems that contained enough trees so they could continue to practice their ancestral ways. But some were located in environments where the trees could not continue to keep them, fed even with their superior locomotion--and as a result, they needed to adapt further by finding foods in other places, especially at times when the food in the trees became more scarce due to drought or other reasons. So they needed to start to eat more foods from the earth.

After we have completed our analysis, we can more or less conclude that the likeliest and perhaps even the only possible choices for C4 foods that could be eaten with any regularity fall into two categories--that is, tubers and the corms and seeds of grasses. And it's likely that Australapithicus may have already been eating these foods back four million years ago, as fallback foods: as we have noted, their teeth may have even been most adapted to eating these foods in particular. So they did not necessarily need to radically change their morphology to gather these foods; Australapithicus did not show any particular morphological changes, such as the claws and snouts we find on other animals that eat tubers; instead its possible that they were able to use digging stick to unearth them, given that we have some reason to believe that Chimpanzees can do the same. However, it's hard to imagine this process being particularly efficient or graceful, given that this level of tool-use would likely be at the limits of their

intelligence: even digging with shovels is not particularly easy, especially if the ground is impacted. However, it is all within the realm of possibility.

As for grass seeds--the mechanics of gathering grass seeds..... could gather but how and why.....Maybe way easier than gathering tubers but lots of bounty on that tuber.....efficiency of each food....

While scientists, thus far, have shown great preference in thinking that Australopithecus consumed tubers, over grains, the preference is perhaps prejudiced and not evidential. For many years now, anthropologists and the media in turn, especially the authors of popular books, have pushed the ideas that grains did not become part of the human diet until the Neolithic--though, as we shall see more conclusively, this is definitely not the case; at the same time, they pushed the idea that grains are not healthy. Anyway, it seems that anthropologists are now resistant to overturning this idea. But the argument for grains is strong: furthermore, as we have seen, the scientist who really study the morphology of the jaw and teeth of Australopithecus, did not conclude they were designed to eat tubers; though at the same time their teeth would work for those purposes; they concluded instead that the teeth were particularly designed for small, hard, brittle objects, which would include seeds; furthermore they concluded that this hardware of Australopithecus mostly closely resembled that of extant animals that eat seeds. (We know that Borei was not designed for fruit)

But there is another argument for seeds: next to animal foods, they may be the most nutritious food on the planet, far superior to both fruit and tubers.

CARBON AND EXTANT SPECIES

When we consider the extant primates today, we can see that the results are entirely predictable. For example Chimpanzees contain nearly all C3 markers in their enamel as you would expect, given that they eat exclusively both plant and animal foods derived from the trees in their jungles. And interestingly enough, Savannah Chimps have about the same amount of C3 markers, even though they have adapted to an environment that contains fewer trees, and even though they eat some C4 foods such as tubers but obviously only in small amounts. The results are also predictable for baboons:

they eat both tree foods and grass foods and accordingly, they show some mixture of C3 and C4 foods. (Source: Sponheimer et al. 2006) Incidentally, several species of Baboons now extinct, that lived from one to four millions years ago, ate anywhere from sixty-five to one hundred percent of its foods as C4, higher than nearly any other primate on record. But they went extinct, perhaps due to competition for the same food from other animals or from predation, since they had to gather these foods on the ground when they are most vulnerable. Many of the Baboons of today live in higher altitudes, and get much of their calories from grass but since these grasses are in cooler climates, they register as c3 like the grains we consume, such as wheat and oats and barley.

We Americans show in our enamel that we eat as we do—that is, about half of our calories come from cool weather grasses, like wheat and rice, as well as the animals that eat those grains in our feedlots; and the other half of our calories come from the tropical grasses like corn and the animals, such as the cow, that eat plentiful amount of that particular grain.

Source: University of Utah 2013,
<http://www.sciencedaily.com/releases/2013/06/130603163749.htm>
have added C3 and C4 signals to the teeth of human ancestors.
The Findings: A Dietary History of Human Ancestors and Relatives

DIET CONCLUSIONS

RECONSTRUCTION OF DIET BY ANALOGY WITH OTHER PRIMATES

In another article, the authors attempted to reconstruct the diets of australopithecus in another manner; they identified the chimps, baboons and humans that live today—or have lived recently—in environments in Africa thought to resemble the environment of the australopiths living millions of years ago. They then identified the foods that these three Great Apes consumed—and lumped them into categories. Furthermore, at some of Austral archaeological sites, they found some fossilized plants that are still used by extant apes as food, including humans. On top of that, they found that many of the foods eaten currently by extant apes, like chimps and baboons, are also eaten by humans—although humans generally exploit a larger and more diverse range of plants than any others. Then from there, they estimated what they thought the Australpiths might have eaten during their time. And based on their analysis, they came to the conclusion that, even in the drier, harsher environments, that the australs likely got the bulk of their calories from plant-foods, from fruits and leaves, then tubers and seeds as second. (Source: Peters, C.R. et al. 1981).

NOTES: Clarification: actually, suggests the fruits were likely the most desired food (which makes sense) and probably the focus of any conflicts around territory. Second important foods were leaves and shoots. Third was grains.

PLANT FOODS

In another, more recent article, the authors used an approach that was similar; they found environments in Tanzania that were similar to the environment inhabited by the Australpiths in the Olduvai Gorge. Both environments, modern and paleo, would have suffered through dry-spells and generally, especially as compared to rainforests, the amount of plant foods would have been minimal. However, this was mitigated because, within a geographic region that could have been travelled by food, the australopiths would have been able to access a variety of environments and ecologies, ranging from springs, marsh, woodlands and grasslands. These

different environments would have given them access to marsh plants, grass grains, roots, fruits from shrubs, palms, leaves, pods, flowers and gums. In other words, the australopiths were probably capable of accessing many different environments, and choosing amongst, not any particular category, but many, plant-foods.

analyses foods eaten in similar habitats as Australapithicus (east and south Africa) by Humans, Chimps and Baboons who are typically sharing habitats. Results about 500 edible plants for one or the other or combined. all show preference for fruit, humans and chimps most of all...next leaves and shoots, next seeds and next tubers are eaten by humans and baboons but not chimps. Most overlap in our diet with chimps, the least overlap with chimps and baboons, and next is human and baboon--some considerable overlap. We are a hybrid of chimps and baboons, in other words. Half of the plants were under competition from one or the other species--most of the competition for fruits, next leaves, and next seeds, and last tubers. Almost all of these plants are widely distributed across Africa and Asia. She notes that in one day the baboon's diet might include unripe tree-fruit, sweet berries, beans from leguminous trees, leaves, green grass seeds, assorted insects, and occasionally small vertebrate prey. On the other hand, in more severe semi arid habitats, this variety can be reduced to practically zero: the Masai-Amboseli baboons are forced to rely on perennial grass rhizomes for most of their diet during the dry season (Altmann and Altmann 1970). (Peters, C.R. et al.).

As for their particular diets, we do not know much but generally guess that they ate similarly to the chimps, with lots of fruit and some leaves and scattering of other foods, with some variation from one species to the next. Otherwise little is known about them, especially since they have been discovered somewhat recently.

“High-tech tests on tooth enamel by researchers indicate that prior to about 4 million years ago, Africa's hominids were eating essentially chimpanzee style, likely dining on fruits and some leaves, said CU-Boulder anthropology Professor Matt Sponheimer, lead study author. Despite the fact that grasses and sedges were readily available back then, the hominids seem to have ignored them for an extended period, he said...“We don't know exactly what happened,” said Sponheimer. “But we do know that after about 3.5 million years ago, some of these hominids started to eat things that they did not eat before, and it is quite possible that these changes in diet were an important step in becoming human.” Sponheimer specializes in stable isotope analysis, comparing particular forms of the same chemical element, like carbon, that are present in hominid fossil teeth. The stable carbon isotopes obtained from ancient hominids helps researchers determine what types of plants they were eating, he said.

Carbon signals from hominid teeth are derived from two distinct plant photosynthetic pathways, said Sponheimer: The C3 signals are from plants like trees and bushes, while the C4 signals are from plants like grasses and sedges. The researchers also looked at the microscopic wear of hominid teeth, which provides scientists with more information on the foods they were eating, he said.

While the hominids from the genus *Homo* that evolved from australopithecines like the 3 million-year-old fossil Lucy -- considered by many the matriarch of modern humans -- were broadening their food choices, a short, upright hominid known as *Paranthropus boisei* that lived side by side with them in eastern Africa was diverging toward a more specific, C4 diet. Scientists initially had dubbed *P. boisei* "Nutcracker Man" because of its large, flat teeth and powerful jaws, but recent analyses indicate it might have instead used its back teeth to grind grasses and sedges, Sponheimer said.

"We now have the first direct evidence that as the cheek teeth on hominids got bigger, their consumption of plants like grasses and sedges increased," he said. "We also see niche differentiation between *Homo* and *Paranthropus* -- it looks probable that *Paranthropus boisei* had a relatively restricted diet, while members of the genus *Homo* were eating a wider variety of things. "The genus *Paranthropus* went extinct about 1 million years ago, while the genus *Homo* that includes us obviously did not.'" (University of Colorado Boulder 2013).

CHANGE IN FOOD SUPPLY

One interesting question is: once the ecosystem changed on the eastern side of the mountain, what happened to the food supply? Before proceeding with exploring this question, we first need to consider how to define food for these early Hominids. As we have already learned, the foods need to be of the same or approximate quality as eaten by Chimpanzees and therefore relatively low in fiber and richer in sugars, fatty and amino acids from either plant or animal sources. At the same time, they have to be able to physically gather and in some cases kill this food. Given this, we can generally disqualify many plants from possibilities, like grass blades, tough leaves, stems, roots, as well as many animals, like birds, that would generally prove uncatchable. Though some have surmised that *Australopithecus* may have been able consume grass blades or other rough foods more suited for ruminants, it is, in fact, most unlikely that these foods would be consumed except in small quantities or during times of starvation.

We do not have much hard evidence, in the form of fossils, to determine what foods were available back then; furthermore, we cannot even reconstruct the ecosystems with much detail--but we can nonetheless make some excellent guesses about how the food supply changed. For starters the climate remained warm, since all of these regions are still within the tropics and even close to the equator, with the exception of South Africa; some of these ecosystems at certain times were probably considerably hotter than the jungle. Rain, however, would have decreased to one degree or another throughout all the various ecosystems or at least become more variable with perhaps even rainy and dry seasons as we now see in the Kalahari Desert. It's possible, too, that rain became increasingly rare as time progressed.

While trees would have persisted in many of these areas, they would be more scattered between large swaths of grasslands or deserts, full of either grass, shrubs or other plants and even just dirt. When considering both horizontal and vertical space, you would have way less vegetation overall. Furthermore the nature of the trees--and the fruits and leaves they bear--would also have changed: For example, fruits and leaves may have appeared in edible

forms only at certain times of the year, probably in relation to rainfall. Since there was less moisture, too, and shorter growing seasons, fruits may have been smaller and less succulent and leaves rougher and dryer. When all this information is considered together, it seems rather obvious that the primary food of most apes, fruit, were becoming way more unreliable, rare and harder to digest. Also one of their main sources of protein--tender leaves--may have become even more scarce and, as they became tougher, harder or even impossible to digest.

Chimps get much of their fatty acids from fruit seeds, palm nuts and other nuts, which are also all tree based, so it's possible that the Australopithecus saw considerable decline in these foods as well. Furthermore, palm nuts, Cocoa and Kola--all fatty plant foods eaten by Chimps--only currently prosper in west Africa, not east Africa and it's likely that was the case millions of years ago. However some nuts are currently indigenous to eastern Africa, such as Mongongo and Pistachio, and still eaten by some foraging humans inhabiting drier regions such as the Kalimari desert. It's possible that this newer, drier environment was more conducive to tree nuts--but not likely. Altogether, while the trees provided excellent sources of both sugars and fatty and amino acids for the chimps, all these foods were in decline for the Australopithecus, forcing them to adapt to other diets.

And fortunately this environment provided other sources of foods that did not come from the trees.

As we have seen, tubers, such as potatoes, are plants that learn to store vast quantities of glucose and water underground so the plant can survive periods of drought and other forms of hardship; and accordingly, it is most likely that they grew in the drier environments of east and south Africa back millions of years ago. (Source: As pointed out by Hatley and Kappelman (1980), reconstruction of the Omo Basin suggests that USOs would have been common in the Pliocene (Bonnefille, 1976 and Carr, 1976). A similar conclusion about the presence of USOs at Laetoli comes from palynological evidence (Harris, 1985 and Bonnefille et al., 1987; Andrews, 1989). (Laden & Wrangham 2005). They are found currently across the drier regions of Africa, such as the Kalamari, and relied upon by many of the indigenous people there today. Also we already know that Savannah Chimps are able to use digging sticks to unearth them, so it's safe to assume that Australopithecus could do the same, if so inclined. Furthermore, since so few animals can actually access tubers, the Australopithecus would have even less competition from other animals, making this an even better and more reliable source of food.

Current evidence indicates an increased diversity, size and edibility of USO's on savannas versus rainforest...

"Available data suggest that the diversity of all USOs, both edible and inedible by humans, is high in savanna compared to rainforest. In their study of a central African rainforest, [Hladik et al. \(1984\)](#) reported 29 species of plants with tubers, representing 12 families, including both edible (to humans) and inedible species. This is substantially less than the number of USOs recorded by [Lee \(1979\)](#) to be eaten by Kung San in the semi-desert of the Kalahari (69 species from 12

families). If inedible USOs were included, the number in the Kalahari would presumably be considerably higher.” (Laden & Wrangham 2005).

“Thus, despite a paucity of studies, current data suggest a consistent increase in the diversity, biomass density, and edibility of USOs in savanna compared to rainforest. This is striking because rainforest sites are floristically more diverse than savannas. The fact that taxonomic diversity does not account for the USO production in savannas supports the prediction that USOs are adapted to seasonal climatic conditions and can therefore be expected to be routinely abundant in African habitats outside, but not inside, rainforest.” (Laden & Wrangham 2005).

same quote as above in Luke’s text: “As pointed out by Hatley and Kappelman (1980), reconstruction of the Omo Basin suggests that USOs would have been common in the Pliocene (Bonnefille, 1976 and Carr, 1976). A similar conclusion about the presence of USOs at Laetoli comes from palynological evidence (Harris, 1985 and Bonnefille et al., 1987; Andrews, 1989).” (Laden & Wrangham 2005).

FALLBACK FOODS

The first of all established that only several species, bears, pigs and humans, possess the abilities to unearth tubers: pigs and bears have morphological tools, such as claws and snouts, and humans have their digging-stitch which, in addition to being used by chimps, are also used these days by hunter-gatherers in Africa for the same purpose. They then proceeded to present the research, showing that the environments in which the Ausrals lived and evolved, were in fact conducive for growing tubers—tubers that could have been eaten raw. Since archaeologists have yet to discover any evidence showing directly that Austral consumed tubers, they took another approach: through fossilized animal remains at Austral sites, they were able to prove that mole-rats, which rely upon tubers for their sustenance, were living along with the Australs. From this evidence, we can perhaps conclude that tubers were available and that the australopiths likely possessed the abilities to find them, collect them and, given the nature of their teeth, eat them. (Amylase.)

However, the author do not make the claim that tubers were necessarily the preferred food of the australs; rather, they claim that this food was the fallback food—the term used to describe foods for animals that are eaten when other more preferred, and more nutritious goods become scarce such as during the dry-season for example. As a possible analogy, for example, the Kung-San, who live in the arid and semi-arid desert of Kalahari, prefer fruits and seeds and other foods when available but, during the dry-season when these foods become scarce, they exploit tubers—eighty different kinds altogether—for their sustenance.

Contend that tubers were fallback foods—and fallback foods play a large role in how organisms evolve—birds and beaks etc...

Curiously enough, fallback foods can often determine, throughout the animal kingdom, more about the morphology and behavior of animals than preferred foods. The reason is that, during times of scarcity, the animals that do not have the necessary traits to exploit the fallback

foods—such as tool-use to unearth tubers—will likely starve and die, thus selecting for the austral with certain traits.

Evidence for tubers as fallback foods—used by modern hunter gatherers in this way...

“The postulated shift away from teeth suitable for shearing herbaceous leaves and piths makes sense because the more seasonal habitats increasingly occupied by early hominids would have had relatively low densities of these foods compared to the rainforest habitats occupied by hominid ancestors. For example, even in the relatively high-rainfall areas of Gabon, savannas have insufficient herbs to sustain apes, whereas the adjacent rainforests commonly produce large densities of edible leaves and piths ([White et al., 1995](#)). Occupation of savannas by early hominids therefore implies that when preferred foods were scarce, a new type of fallback food was required.” (Laden & Wrangham 2005).

“Human foragers' reliance on USOs is well documented for the savanna and semi-desert habitats of tropical Africa and in similar environments elsewhere through ethnography, ethnoarchaeology, and archaeology. In the Kalahari, roots indeed conform to the concept of fallback foods because, although they are not preferred compared to meat, fruits, honey, or fatty seeds, for example, they become the dominant dietary item during periods of food scarcity. For example, [Silberbauer \(1981: 202\)](#) reported that the G/wi used 13 plant species as staple foods. Sweet fruits were preferred, whereas USOs were mainly fallback foods eaten when preferred foods were not available. The worst time of year was early summer, when people complained of hunger and thirst, body weight was low, illness was more common, and there were even occasional episodes of starvation. At this time, the density of food that a household gathered (and, by inference, that it is likely capable of gathering) was measured as 0.15 kg/km² per household per day (i.e., per woman). All foods came from four species of tuber. This annual minimum compares to a maximum of 128 kg/km² per day when local fruit crops are abundant, i.e., almost 10,000 times higher.” (Laden & Wrangham 2005).

“A similar kind of reliance on USOs was observed for the !Kung at Nyae Nyae: The roots are of the utmost importance to the Kung diet in the Nyae Nyae area. Whereas many items of food, especially the fruits, are available only in the season of the rains and for a time after, the underground parts remain preserved in the ground throughout the year. In the territory of Band 1, they are the mainstay during the winter—the dry season (Marshall, 1976: 108).” (Laden & Wrangham 2005).

“Roots and bulbs are likewise explicitly claimed by informants to be available all year for Hadza in northern Tanzania and for Kung San in Botswana (Lee, 1979 and Vincent, 1985). However, they become important in the diet only on a seasonal basis. They are eaten by Hadza principally during the main rainy season and the late dry season and by !Kung San during the winter dry season, when the major summer foods are not available (Lee, 1979). In both cases, the ethnographers noted that the degree of difficulty in harvesting roots is a major factor affecting the degree to which they are preferred. Accordingly, the fact that USOs are eaten more when fruits are not available may have more to do with their being hard to extract from the ground than with their merit as a good-tasting or highly valued food item.” (Laden & Wrangham 2005).

“Plant underground storage organs were also important to Australian Aborigines. The magnitude of this importance is seen not only in foraging strategies, but also in some cosmogonies. For example, the origin story of the Kakadu people in Arnhemland refers to the ancestress “Imberombera,” who arrived from across the sea with her “womb filled with children and from her head...suspended woven dilly bags in which she carried yams, bulbs and tubers” (Flood, 1983: 30). There is even an art form in the Northern Territory based on the anthropomorphism of yams (Flood, 1983: 133). Aboriginal Australians in many areas are documented to have made important use of USOs (Gott, 1982). One of the few archaeological examples of a USO from a non-agricultural area is a lily tuber found in Rocky Cape Cave in Tasmania (Flood, 1983: 164).” (Laden & Wrangham 2005).

“The use of USOs in the African Later Stone Age (LSA) is inferred from the widespread occurrence of torus-shaped, bored stone artifacts, believed to be digging stick weights ([Phillipson, 1982](#)), as well as a number of actual digging sticks.” (Laden & Wrangham 2005). “Thus, USOs are known to be fallback foods for people in at least two African savannas, as well as in the Australian bush. For a primate that cannot readily eat leaves, USOs provide a systematic supply of food during periods when seeds and fruits are not available, as inevitably occurs.” (Laden & Wrangham 2005).

Consider that hominid fossils usually do not show evidence of tubers as well; however, strong correlation with mole rats that eat tubers—so easy to assume that they were available.

In sum, large, relatively flat, heavily enameled teeth and a large mouth are potentially explicable as adaptations to USO-eating. These occur in gracile australopiths and to an even greater degree in “robust” australopiths.

“Previously, it was widely believed that early human ancestors acquired tougher tooth enamel, large grinding teeth and powerful muscles so they could eat foods like hard nuts and seeds. This research finding suggests that the diet of early hominins diverged from that of the standard great ape at a much earlier stage. The authors argue that it is unlikely that the hominins would have eaten the leaves of the tropical grasses as they would have been too abrasive and tough to break down and digest. Instead, they suggest that these early hominins may have relied on the roots, corms and bulbs at the base of the plant.

Professor Lee-Thorp said: “Based on our carbon isotope data we can't exclude the possibility that the hominins' diets may have included animals that in turn ate the tropical grasses. But as neither humans nor other primates have diets rich in animal food, and of course the hominins are not equipped as carnivores are with sharp teeth, we can assume that they ate the tropical grasses and the sedges directly.” ”
(source:<http://www.sciencedaily.com/releases/2012/12/121214200916.htm>, University of Oxford 2012).

While most grasses just have roots, with little if any nutritional value, some do indeed have corms--larger roots which store nutrients, especially starch, for longer term use; and as we have seen, Baboons eat this food. However, corms, since they are underground, are not easy to

attain and otherwise are small--and since they require lots of effort and little reward, they may not have been all that viable.

However, many grasses create edible grains--that is, seeds that for the most part large enough to be effectively gathered and eaten. (Edible grasses of Africa) Furthermore many of the wild grasses in Africa today provide edible grains and are eaten by native people, both ones that are foragers and farmers; and it's my guess that these grains were available back millions of years ago or at least other grains that were edible. This category also includes all parts of plants called sedges, such as papyrus, water chestnut, sawgrass and nutgrass, which are similar to grass but more commonly grown in wetlands and areas that contain poor soil. (which ones grow in Africa).

Tubers are also C4 foods. And as especially as compared to the rainforest of the Chimpanzees, we have plenty of reason to believe that tubers were available and even abundant on the Savannah, especially given that these plants are designed to withstand long, dry periods as were probably common back then.

TOOLS

While sedges may have been consumed by early Hominids, there is reason to see these plants as problematic as a source of food: compared to grass, they were likely way less abundant, since much of African was dry and hot Savannah; furthermore, wetlands are difficult to navigate. Also, while these plants can have edible parts, such as the corm on water-chestnut, they do not seem to contain grains and otherwise appear to be tough, fibrous plants that probably did not offer much nutrition. Furthermore, we have at least one study that confirms that these foods were not all that abundant in Africa millions of years ago and the ones that were likely available used, paradoxically, the c3 pathway instead unlike nearly all other sedges. (SOURCE?) Even though all this argues as sedges being one of the chief, stable foods of Hominoids, it is known that some more contemporary foraging humans have used these plants as sources of food; and as such, it's possible that some or one of the Australopithecus did as well, for at least certain parts of the year.

Australopithecus likely did not eat the grass blades, but may have consumed the roots, tubers, corms, stems and seeds of wild grasses and sedges—

Another possibility—and the one that might initially seem more obvious—is that australopithecus ate grass—or at least some part of the plant. We have plenty of reason to assume that grass was, in fact, around and abundant during the times of the australopithecus; However, this assumption is problematic for several reasons because grass—or the blades of grass commonly eaten by ruminants—is not a select, nutrient dense food; it is bulky and dense in cellulose and frequently ensheathed in silica coats that can make the blades sharp enough to cut flesh; it is difficult to chew, harder to swallow, low in carbohydrates, but rich and abundant in fibre. As we know, ruminants specialize in grass and thus have specialized digestive systems for dealing with grass—mult-stage, fermenting chambers, for example. And we can easily

assume—but not conclude--that australopithecus's gut probably resembled a chimps and was, thus, not suited to eating grass—or at least using grass as one of the staples of the diet. Furthermore, as we know, primates are known for dealing with challenges around food-gathering by becoming smarter, adjusting their behavior and, ultimately, finding the richer and denser foods. Blades of grass, too, though somewhat rich in protein and other nutrients, nonetheless, do not contain that many carbs or fats—the foods that most primates seem to crave the most and need to satisfy the energy demands of their bodies and larger brains. Furthermore, Austral did not have the teeth for threshing or shearing blades of grass.

What about the primates that do, in fact, consume grass? (Not likely that primates can acquire enough energy from grass—in the same sense that cannot acquire from leaves—only leaves seeds as a possibility.)

Grasses and sedges also would have become way more abundant. We know that grasslands were already well scattered across parts of eastern and southern Africa well before the Australopithecus emerged. But we do not know much about what species of grass grew back then--or what parts of them were edible. It's unlikely that the Australopithecus ate the blades of grass, given their tough and fibrous consistency but other parts of grass contain way more sugars relative to fiber. As we have seen with the Baboon, many of them eat the roots, tubers, corms and stems of the grass which provide good amounts of glucose in the form of starch. Obviously, too, grass seeds, otherwise known as grains, were likely abundant; currently many wild, edible grasses grow in Africa, such as various forms of millet, teft and many others, which are currently collected and consumed by many of the indigenous populations there today so it's probably that many of these same species were growing back four or five million years ago, at least in various parts of east and south Africa. Given that baboons can collect and eat grains, it's likely that Australopithecus could as well and, as we shall, he did develop some teeth and jaws that would allow him to chew and swallow seeds. But whether or not he could digest them is another matter; as we have already seen, starch and fruit, though both consisting of sugars, are made of different sugars that are strung together in different ways. We know that Chimpanzees are excellent at digesting fruit, but not starch, so for Australopithecus to eat lots of starch, he would likely need to adapt to create different enzymes, namely amylase--which, as we shall see, is quite possible.

Shrubs and bushes on the savanna may have provided some foods such as berries and roots, but likely did not make a substantial contribution to the diet— Given that most of the land was replaced by grasslands and desert, it's unlikely that bushes and shrubs increased in quantity--but still, in the absence of trees, may have become a source of food--but mostly in the form of berries and maybe some roots. But given that both of these would have been difficult to collect, it's hard to imagine these plants becoming meaningful in their diet.

GRAINS

The case for Grains as a part of the Australopithecus' diet:

But what about the seeds of grass, otherwise known as grains. Despite suffering through some stigma lately due to the writing of some dietary gurus, grains are, in fact, one of the richest and well-rounded foods on the planet. For example, tubers, both domesticated and wild, though rich in starch, are deficient in both protein and fats—this due to the fact that these organs are little more than starch and water storage for plants during times of trouble. Also all tubers—at least the ones that I have studied—also are abundant in potassium, one of the macrominerals, but almost devoid of others such as sodium, calcium, magnesium and phosphorus; generally they are low, too, in manganese, zinc and iron—and not rich in vitamins either. Grass seeds, however, are designed to provide the energy and nutrients necessary to germinate a plant; as such, most grass seeds, both wild and domesticated, are both abundant in starch but also reasonably rich in fats and proteins as well. Nearly all these seeds are abundant in macro and micro minerals—in ratios somewhat conducive for human physiology. Certainly seeds have anti-nutrients, such as phytates which can block the absorption of certain nutrients but not in quantities any greater than other plants.

Another bonus is that grains, as compared to tubers and perhaps even fruit, may have been easier to attain. Tubers are not easy to access, usually requiring the use of a tool to work through dry, impacted earth; and once unearthed, tubers are usually covered in hard, outer shells. Many grains, such as wheat and barley, require some processes perhaps too complicated for the australopiths but many grasses, millet amongst them, give off their grains rather easily—one just needs to shake or pull or thrash the seeds during certain times of the year. Another positive of grains is that they can be stored, provided they are kept dry, for many years and still maintain all of their attributes and we can assume that if a squirrel can bury his nuts in preparation for the winter, then australopithecus likely could have collected seeds and buried them someplace cool and dry for use in the future.

For some reason, anthropologists have been reluctant to consider the possibility that the one of the staples of the austral's diet was not grass, or tubers, or termites but, rather, the same food that modern humans consume these days: grass seeds, otherwise known as grains. However, I have not been able to find any theories to support or undermine the possibility that edible grass-seeds were abundant during this time—and, in fact, consumed, perhaps even abundantly, amongst the australopithecus. However, wild, edible grains, such as wild versions of rice, millet, sorghum, are abundant in Africa now and in the recent past, as many as sixty different species known to be eaten throughout Africa, usually in areas either in or around the sahara—in dry, arid lands or savannah; and some grains also appear to thrive in wetter conditions. An edible grain, called *urochloa mosambicensis*, inhabits central and eastern Africa. Many of these grains, throughout the Stone Age, were eaten and many were recently eaten or still eaten by herders, nomads and hunter-gatherers. In fact, for many people, wild-grains was one of the staples of their diet. (National Research Council 1996).

But, as we all know, grains in their natural, untouched form are hard and dry—not easy to eat raw. Well, to test their palatability raw, I sampled some of the raw, dry grains in my cupboard: I could chew both wheat, spelt, oatmeal, and millet with my teeth, without any fear of breaking them, and swallow without any problems; however, I would not want to eat many grains in this

way. But when biting down on wild rice, I was afraid I might break some of my teeth. As we already know, the austral's teeth were large, flat and thick with enamel; clearly they are not designed for impaling or shearing, as you might expect from someone eating leaves and fruits. They are designed for grinding; in fact, many anthropologists have called them the "millstone molars," because they have the design of the devices used to grind grains for porridges and breads. Furthermore, any grains, including rice, can be rendered soft and more palatable merely by soaking them in water for several hours; most, in fact, will germinate and sprout, adding to their digestibility and nutrients. However, we might easily assume that the australopiths did not yet possess this level of sophistication; and if they did, they probably would not have the teeth that seemed designed for grinding away on hard, fibrous seeds.

Anyhow, if australs consumed sedges, leaves, hard fruits and even tubers, we might have to assume that, in terms of diet and evolution, they were not advancing towards ourselves, humans; these foods are superior and likely could not provide the fuel to allow that austral to evolve into Homo, or man. However, seeds, as compared to the fruits of the chimpanzees, are dense in carbohydrates, and much richer in fats and proteins—and as such, would have provided the fuel to allow the austral's to evolve.

Grains in Africa (the book) just nomads hg collected wild grains, fairly simple: seeds just fall, include teff, rice, millet, sorghum grasses been around for millions of years: dinosaurs ate it

ANIMAL FOODS

As for available animal foods, they would have both changed and increased overall. Since termites—one of the favorite foods of chimps—feeds on trees, they may have become more scattered across the terrain but other insects may have increased or decreased in number—but may have been abundant enough in any case. Certainly other primates would have decreased, given that trees were in decline. However, other types of animals would have increased dramatically. Since rainforests are too dense for most terrestrial animals, the savannah would therefore contain many more of them: ruminants, rodents, predators and many others but nearly all of these would have proven too difficult to catch with any regularity, although they may have been opportunistic foods.

In the past some researches posed the possibility that Australapithics or other Hominids may have become scavengers; they could have waited until predators ate their fill, and then come in for some of the scraps. While this is possible and perhaps happened occasionally, I see it as unlikely for several reasons: given the heat of the Savannah, any exposed meat would spoil quickly and to this particular Hominid—that is, me—nothing is more vile or alarming smelling than rotting meat; since Chimps do not show any predilection to scavenging, along with nearly all animals, except for the ones that have special adaptations like buzzards, I find it hard to believe that Australapithicus evolved taste for and defenses against rotting meat, especially given that we now do not have much taste for rotting meat, unless it is carefully cultured. Even if they were lucky and found meat that was still fresh, they would not have the smarts to preserve that meat through drying or other techniques, so at the most, they could only get one or two meals before the meat became terribly foul. At the same time, many vicious and predators, such as

hyenas, also feed on carrion killed by other animals, so it's possible that the Australs would have had too much dangerous competition for such foods.

But one food, from carrion, may have become prime for primates--that is, the fatty marrow and brains contained within the bones. As we have already seen, Chimpanzees show definite predilection to both brains and marrow--foods that are carefully preserved inside of bones and therefore likely to not spoil as quickly as exposed meat and fat. At the same time Chimpanzees, as well as Capuchins, can use rudimentary tools to crack open nuts; Chimpanzees, even work diligently, to open the skulls of the Colobus Monkey to get the brains within--and by analogy, it's possible and even probable that Australopithecus could crack the skulls and bones of even large ungulates and even dead predators to access the fats inside. While some animals like hyenas can crack bones, most cannot, including most predators, so there would be limited competition for these foods; so they could have contributed meaningfully to the diets of the Australopithecus and, at the same time, provided the best fuel around--balanced fatty acids--for creating ATP, as well as the essential polyunsaturated needed for building cell walls and nervous tissue.

And still other, animal foods may have been available to primates due to their ability to use crude tools, especially any animal encased inside shells, including turtles and most importantly--shellfish--a food that features prominently in the history of Homo Sapien. Given, too, that Australopithecus was inhabiting dry lands, they would need to make effort to attain water and therefore were probably intimate with the creeks and lakes--and the foods they offered. Certain animal foods may have contributed to the C4 signature, but are unlikely to have made a significant contribution...

Another possibility, too, is that australopithecus consume significant amounts of animals that, in turn, consume lots of grass. The environment, in which the australs lived, was abundant in all sorts of ruminants and ungulates. In the case of chimpanzees, we know that they are capable of catching and eating young antelopes that dwell in the forest; furthermore, we have already learned that chimps can collaborate with each other, for example, to block and possible escapes from other monkeys—and then catching and killing them. Given the size of the austral's brain, we can assume that he might have some similar skills but, nonetheless, australopithecus, though in part ground-dwelling, was not exactly fast and agile. But ruminants are: extremely swift and alert and the likelihood of australopithecus killing them regularly, especially given that they were in competition with other, more capable predators, such as sabre-tooth tigers, was low. So yes, they may have scavenged an antelope here and there—but not eaten this flesh enough to account for the analysis of their enamel.

Some termites eat part of their diet as grass; one termite for example gets 35% of its calories from grass while other termites eat grass much less. Also, as we know, chimps also eat termites. However, even if australopithecus ate exclusively this one termite that consumes large amounts of grass, it still would not account for C4 in the diet of australopithecus. Evidently some anthropologists believe that australopithecus got their C4 foods from animal sources (Peters & Vogel 2005). However some are not convinced; and I must say I am not either. QUOTE FROM ARTICLE MENTIONED ABOVE: "We conclude that although termites and sedges might

have contributed to the C4 signal in South African australopiths, other C4 foods were also important. Lastly, we suggest that the consumption of C4 foods is a fundamental hominin trait that, along with bipedalism, allowed australopiths to pioneer increasingly open and seasonal environments.”

Australians ate a more varied diet than Homo who ate more animals (University of the Witwatersrand 2012).

Incidence where baboons would abandon plants to feed on insect outbreaks, howler on caterpillars so this type of feeding is opportunistic generally, not intentional: and not reliable enough to be trusted, so have to stay with plants or risk starvation

SUMMARY

We can summarize this information by saying that the primary foods of chimps--tender leaves and fruits, provided by trees--were in decline with the advent of Australopithecus and probably continued to decline through much of our evolution. With this, they lost most of their sources for sugars, fatty acids and even amino acids. But at the same time other sources of sugars became available--that is, starches in the form of tubers, corms, and seeds. At the same time, the animal foods of chimps--termites and other primates--would have also gone into decline but this source, too, could have been replaced by other animal foods, including marrow, brains, shellfish, turtles, insects as well as many other possible opportunities. As we move into other sections, we will continue to explore the evidence as to whether or not these foods were indeed consumed and therefore an intimate part of our own evolutionary history--and therefore an intimate part of what makes us human.

At this point we have arduously moved through much of the research around the foodways and even culture of Australopithecus in both of his forms. And now below, for the sake of better clarity and greater entertainment, summarize that date into a narrative; when presenting the information in this way, we perhaps lost some accuracy and precision--but hopefully enhanced our understanding. When the climate and geography started to change millions of years ago, a primate, quite similar in size and encephalization to the Chimpanzee, started to lose his primary form of food and protection--that is, the trees. They became more scattered, in clumps, across larger swaths of land and, at the same time, grasslands started to emerge along with wetlands and even deserts

METABOLISM/DIGESTION

same metabolism, similar digestion and needs for nutrients

But our ancestor at first was not terribly interested in those other parts of the ecosystem--just the trees--so at first, he merely adapted like the Savannah Chimp, he just expanded his terrain to include more trees. Since he was travelling larger distances, he then kept his troop-mates closer to him at all times, to protect against predation and for other reasons. But as the trees

became more and more scattered, he could not cover enough terrain to maintain efficiency--that, he was starting to expend more calories trying to attain his food than he acquired from his food; he was walking the proverbial mile to eat one apple. As some of our ancestors started to starve, others began to adapt: while they were knuckle-walking across the earth, some of them could also stand upright for shorter periods--which would have provided an immediate advantage--that is, they could see predators off in the distance and therefore better avoid them which also probably made them more popular with the ladies for more breeding opportunities. While it's possible that one change in the genes caused the primates to then start walking upright, it seems more probable that shift happened over time, perhaps thousands of years: since the trait was helping in survival and reproduction, it developed gradually until all our ancestors had started to walk upright. At that point the whole troop was moving more efficiently over the land and dissipating heat better, so they became more efficient--that is, they cover more ground to gather more food, to avoid starvation.

So, even though their environment changed, they were still enabled to eat from the trees like their ancestors; however, it's possible that the nature of their tree food changed because their teeth are so different from the Chimpanzees. Their jaw and teeth are designed to eat smaller foods that require less tearing, shredding and shearing and more grinding; furthermore due to the thicker enamel, they are designed to eat foods that are harder. But what were those foods: nobody really knows for sure. But it's possible that due to the shorter, growing seasons, the fruits were smaller and harder overall, less succulent and as such could be fit whole into the mouth and grinded into pulp. It's also possible that they started to consume more nuts as well but nobody recently has been suggesting that their teeth were designed for this purpose--and evidence suggests otherwise. In this drier environment the leaves and shoots would become tougher and more fibrous but the mouth and digestive system of the Australapithicus was not suited to these foods, so the amounts of these foods were reduced.

Since lost source of protein, maybe more hunting or maybe more from other source: beans or nuts--who knows or other tree seeds

Conclusion about tree foods: continued to eat fruits, maybe nuts, less leaves, maybe more beans and nuts
and more animal foods

Bottom line: the preponderance of the evidence strongly suggests that, even back four millions years ago, we can already witness an adaptation to a more human diet.

PROCESSING/INGESTION

From analysing the structure and wear of their teeth and jaw, we can draw some conclusions about what foods they were likely chewing.

While they all (all Ardi & Austral) seem to have slightly different jaws and teeth, it is believed that they likely ate diets similar to the chimps--that is, plenty of fruits and leaves but with some

rougher and harder foods as well; one species in particular may have eaten a diet considerably rougher than the chimps that required chewing in the back of the mouth.

TEETH AND JAWS

To attempt to understand the diet of the Austral's better, scientists have studied the anatomy and wear and tear of their teeth and jaws quite extensively. As we have noted, one of the primary differences between Chimps and Australapithicus is the size and design of their teeth and jaws. Chimpanzee's teeth are perfectly designed for the foods they predominantly eat. For example they frequently eat foods that are larger than their mouths so, for that reason, they have larger incisors that are good at puncturing and tearing their foods into smaller, more swallowable pieces. Their back teeth, like their molars, are smaller and evidently designed to both grind and shred foods like leaves and fruits into bolus. As we have noted, Chimps spend about four hours per day chewing, suggesting the great importance of their teeth and jaws.

By comparison the Australapithicus had significantly different teeth--that is, their incisors are smaller, suggesting that they did not need to tear and shred their food into smaller pieces as much as the Chimpanzee. On the other hand, their back teeth, their molars in particular, are much larger; furthermore these back teeth tend to be flat and broad at the top, so it appears they were used more for grinding hard and brittle foods into smaller pieces, rather than shredding or shearing them. (Source) They all also have thick enamel, suggesting they needed to better protect their teeth from damage from harder foods. In short it is obvious that this was a meaningful adaptation over the Chimpanzees that suggests, if not proves, that their diet was different.

We can furthermore conclude, somewhat reliably I believe, that they were eating foods that generally were smaller, that needed less tearing and shredding--and that instead needed more grinding into smaller pieces all the way into bolus. Furthermore, it's conclusive that these foods were also harder and brittle.

But before we draw our conclusions, let's consider another line of research--that is the analysis of tiny, microscopic wear patterns on teeth, usually trying to determine if the teeth are scratched, pitted or smooth--which can suggest something about the physical qualities of their food. While this method cannot determine what an Australapithicus ate over their lifetime, it can nonetheless suggest what they ate at certain times in their life, like the months before their death. This method, too, can be limiting as well because we can not be clear what foods create what effects; furthermore, there are other complicating scenarios; for example, an Australapithicus might eat soft foods but eat those foods with sand or grit or pieces their bones, which would then impact the teeth, leading to incorrect assumptions. When you get into the details of this analysis, you can encounter confusing and inconclusive results; however, in the end, the results can be highly suggestive as we shall see.

When these two lines of research are combined together, we can start to draw some conclusions; however, to add extra veracity to our conclusions, I will instead use the words of

the leading researchers in the field, who have been doing this work for decades, Peter Ungar and Mark Teaford, who basically draw this conclusion about the teeth and jaws of Australopithecus. As part of their research, they also come to understand the teeth and jaws and microwear of other extant animals, including primates, so they can draw analogies. In the end they draw the conclusion that the Australopithecus were typically eating harder, smaller, more brittle foods. And when comparing what we know about Australopithecus to extant animals, they draw the conclusion that the Australs were most analogous to animals that eat seeds and small, soft fruit. Furthermore they conclude that they were not designed for eating many leaves or meats that would require considerable shredding for digestion. However, they do conclude at the same time that they could also eat other, softer foods. Since this point is somewhat controversial, I thought I would let the experts speak for themselves:

"The Australopithecus exhibited a complex of morphological features related to diet that are unique compared with living hominoids or Miocene apes. These early hominids all had small-to-moderate sized incisors; large, flat molars with little shear potential; a ratio of first to third molar area low compared with extant apes, but generally higher than those of Miocene apes; thick tooth enamel; and thick mandibular corpora. This suite of traits is distinctive of australopithecines, and suggests a dietary shift at or near the stem of hominid evolution. Their thick-enameled, flattened molars would have had great difficulty propagating cracks through tough foods, suggesting that the australopithecines were not well-suited for eating tough fruits, leaves or meat. The dental microwear data agree with this, as the australopithecine patterns documented to date are most similar to those of modern-day seed predators and soft fruit eaters. Further, given their comparatively small incisors, these hominids probably did not specialize on large, husked fruits or those requiring extensive incisal preparation. Instead, the australopithecines would have been easily able to break down hard, brittle foods. Their large flat molars would have served well for crushing, and their thick enamel would have withstood abrasion and fracture. Their mandibular corpora would probably have conferred an advantage for resisting failure given high occlusal loads. In essence, for much of their history, the australopithecines had an adaptive package that allowed them ready access to hard objects, plus soft foods that were not particularly tough. These hominids could have eaten both abrasive and non-abrasive foods. (Ungar & Sponheimer 2011)

Though this analysis does not address tubers directly, it most certainly does not exclude them. While tubers are frequently large and therefore need to be reduced into smaller sizes for fitting into the mouth, they nonetheless are typically softer foods; even I, with my limited incisors, can easily puncture a raw potatoes or turnip or carrot and break them into smaller pieces; while raw tubers are considerably tougher, they can nonetheless be consumed the same way, so larger incisors were likely not needed; in the worst case scenario, the tuber could also probably be smashed into smaller pieces as well with a rock. Once tubers are punctured and in the mouth, they could then easily be ground into pulp with their flat molars.

AUSTRALOPITHECUS ROBUSTUS

AKA: PARANTHROPUS

It is believed, but not known, that the Australopithecus (aka Paranthropus) evolved from the Graciles back around two to three millions years ago--and then lived at the same time as them for one or two million years before becoming extinct. As we have already noted: while both the Gracile and Robustus have thicker teeth and jaws than the chimps, the Robustus are even thicker still--and therefore show more of an adaptation to foods that were not part of the Chimpanzee diet. One species of Robustus, Bosei, inhabited eastern Africa around where Ethiopia is now and perhaps lived in the same ecosystem as the Graciles; but the other species, the Robustus, lived far away in south Africa,. Apart from the difference in their jaws and teeth, it does appear that the Gracile and Robustus were otherwise quite similar, even though most scientists are moving towards distinguishing them as separate species. While its possible that one of the Robustus are our direct ancestor, most tend to think that he is not due to reasons that we can explore later.

Even from the beginning, we know two facts about these Robust primates: they came later in the timeline and also possessed teeth even more different from the Chimpanzees, both of these suggesting further adaptations in their diet. And we will see if the testing upholds this conclusion.

DIGESTION

When investigating the foodways of the Australs, we should first consider their digestion: like nearly every primate, the Austals probably had the same configuration in their guts as ourselves--that is, an acid stomach, small intestine and colon. Additionally, since they both have a similar shape and sizes as the Chimpanzee, their digestive system was likely about the same size relative to their bodies. This likelihood is increased considering that some studies have suggested that Australs, considering the size of their pelvis and other surrounding bones, were likely potbellied to account for larger digestive systems relative to their bodies. In any case we can assume that their digestive system was considerably larger than our own and more in line with other Apes. As we have seen already, when apes are adapted to eat rougher, more fibrous foods, their small intestines tend to be smaller and their colons lager to ferment all the additional fiber. With the Australs, we do not have any anatomical evidence to support this claim one way or the other. So, in that sense, it's possible that their colons became smaller, the same or larger, or that some other adaptation in their digestive system took place. But when we consider other lines of information, as we will do next, we can see that maybe the best guess is that the relative dimensions of their digestive systems stayed approximately the same.

Since they needed about same kind of nutrients, it's likely, too, that the Australopithecus had about the same digestive system as the Chimpanzee, certainly at least the same one that nearly all other primates possess--that is, the acidic stomach, small intestine and colon which appears to be suitable only for middling to highly refined foods. Some anatomical studies done on the fossils of Australopithecus further confirm this likelihood. (NOTE: article confirming potbellied)

--the data on starch and its importance to this chapter--that is, chimps need to digest starch in sugars and other foods; but nonetheless we know that they can actually only digest one third of the amount of starch as ourselves. Over time, their ability to digest starch increased but we do not know when: my bet is that it started as far back as Australapithicus, possibly Ardipethicus and gradually increased over time.

—So while Australapithicus evidently did not need to undergo any morphological adaptations to consume these foods, which is supported by the fossil record, he would likely need to adapt his nutritional physiology, by becoming more adjusted to the consumption of starch and its particular sugars, glucose. So, overall, it probably happened this way: as the Australapithic moved from clumps of trees that were dwindling, they felt more and more hungry, so they started to stop more on the plains and eat the occasional mouthful of seeds or take the time to disinter that tuber. But they probably regarded these foods with caution, sort of the way we humans have historically regarded one of our relatively recent foods, milk, because of our inability to digest milk later in life. If they ate too much of these foods, they probably would not be able to digest them--which could have made them sick, especially given that so much starch would ultimately dump into their colon and maybe treat diarrhea, gas or other disturbances. But if any particular animal showed greater adaptation to these foods--that is, any better ability to digest them--he could consume more of them, without any negative effects, while creating superior energy--and thereby passing on his genes better into the future.

Furthermore this starch may have provided meaningful benefits, physiologically, to Australapithicus. As we have seen fructose is not really a nutrient--but rather a molecule that needs to be converted into glucose or some other energetic molecule before it can be properly utilized. At the same time, fructose is more physiologically damaging to tissues, especially given its greater tendency to wrongfully stick to other molecules and for many other reasons as well. At the same time foods like tubers and grains may have provided more glucose overall than fruit, even taking into account the conversion of fructose to glucose. So for many different reasons, the conversion to starch from fruit, may have provided some survivalistic advantages, in overall energy, and especially for the brain: greater fructose may have increased greater brain metabolism, even though the brain stayed the same size. Furthermore the only Australapithicus that primarily consumed starch--the Bosei--is the only that showed any increase in encephalization, as much as twenty percent.

“We can now be sure that Paranthropus boisei ate foods that no self-respecting chimpanzee would stomach in quantity,” said Sponheimer. (University of Colorado Boulder & University of Arkansas 2011).

METABOLISM

But still because all these creatures were all dead, there is so much that we cannot know about them, at least not for certain; however, for many reasons which have already been revealed and will be increasingly revealed, the Australapithicus was quite similar to the Chimpanzee so I think it's safe to say that they shared much of the same anatomy, as well as digestive and nutritional

physiology. We have many reasons to believe that they did--and little, if any, to believe that they did not, although I believe that variations are likely.

Also, since Australs were about the same size as the chimps, we can assume that they maintained about the same metabolism. As we have already discussed, smaller primates have higher metabolisms, and larger primates slower metabolisms. We have also theorized that metabolism is likely to increase somewhat if the primates are more encephalized due to the fact that the brain needs considerably more energy than other organs per mass. Chimps are middling in size for primates, but with lots of encephalization and, as such, to feed that metabolism, they eat rather refined foods as we have seen and, since the Australs basically mimicked them, it's likely that the Australs did as well; in fact, it's likely that to maintain both their size and intelligence, the Australs were under lots of pressure to maintain the more refined quality of their diet; it's doubtful, say, that converting to a diet of leaves or grass could support the demands of their metabolism. Or, in short, like the chimps, the Australs probably ate a diet that was more refined and greater in sugars and fatty and amino acids and more moderate in fiber; however, the particular foods they ate may have differed entirely.

Author's Note: Resting Metabolic Rate Homo vs. Australs- "Early hominin australopithecines had a cranial capacity slightly larger than extant apes (Robson and Wood 2008)...resting metabolic rate of female Homo ergaster was an estimated 1.53 times higher than that of Australopithecus afarensis and is 1.64 times higher for female H. sapiens (Aiello and Wells 2002). An even more striking estimate is that the daily energy expenditure in female H. erectus may have been more than 80 percent higher than female australopithecines (Stuedel-Numbers 2006)." (Dunbar, Gamble, & Gowlett Eds.)

Since Australapithic was about the same size as the Chimpanzee and close in evolution, its likely--perhaps even certain--that they both had about the same metabolism--and therefore needed about the same level of refinement in their diet; or more specifically they needed about same amounts of energy in the form of glucose and fatty acids, as well as amino acids and even fiber. In other words when the Australs, as we shall see, wandered from their jungles onto the Savannas of Africa, they were likely, at least initially, looking for approximately the same kinds of nutrients as the Chimpanzee to support the same basic metabolism and physiology.

GENOMICS

Additionally, in understanding our own genes, we can make some reasonable guesses about when certain changes in our physiology happened in the past--even when we were in the form of Australopithecus.

Genetic Adaptations to Starch observed among modern humans may have begun to evolve with earlier hominins, after the divergence from chimpanzees and the other great apes.

"To understand better the evolutionary context of human AMY1 copy number variation, we analyzed patterns of AMY1 copy number variation in chimpanzees (Pan troglodytes) and

bonobos (*Pan paniscus*). In contrast to the extensive copy number variation we observed in humans, each of 15 wild-born western chimpanzees (*P. t. verus*) showed evidence of only 2 diploid AMY1 copies (Fig. 3c and Supplementary Fig. 4 online), which is consistent with previous findings 18-21. Although we observed evidence of a gain in AMY1 copy number in bonobos relative to chimpanzees (Supplementary Fig. 4 online), our sequence-based analyses suggest that each of these AMY1 copies has a disrupted coding sequence and may be non-functional (Supplementary Fig. 5 online). Therefore, the average human has ~3 times more AMY1 copies than chimpanzees, and bonobos may not have salivary amylase at all. Outgroup comparisons with other great apes suggest that AMY1 copy number was most likely gained in the human lineage, rather than lost in chimpanzees 21,22. Given that AMY1 copy number is positively correlated with salivary amylase protein level in humans, it stands to reason that the human-specific increase in copy number may explain, at least in part, why salivary amylase protein levels are ~6-8 times higher in humans than in chimpanzees²³. These patterns are consistent with the general dietary characteristics of *Pan* and *Homo*; chimpanzees and bonobos are predominantly frugivorous and ingest little starch relative to most human populations²⁴. Considering other primates, whole New World monkeys do not produce salivary amylase and tend to consume little starch, cercopithecines (a subfamily of Old World monkeys including macaques and mangabeys) have relatively high salivary amylase expression, even compared to humans²³. Although the genetic mechanisms are unknown, this expression pattern may have evolved to facilitate the digestion of starchy foods (such as the seeds of unripe fruits) stowed in the cheek pouch, a trait that among primates is unique to cercopithecines²⁵. The initial human-specific increase in AMY1 copy number may have been coincident with a dietary shift early in hominin evolutionary history. For example, it is hypothesized that starch-rich plant underground storage organs (USOs) were a critical food resource for early hominins 26,27. Changes in USO consumption may even have facilitated the initial emergence and spread of *Homo erectus* out of Africa 5,28. Yet such arguments are difficult to test, mainly because direct evidence for the use of USOs is difficult to obtain, particularly for more remote time periods. USOs themselves are perishable, as are many of the tools used to collect and process them. Therefore, understanding the timing and nature of the initial human-lineage AMY1 duplications may provide insight into our ecological and evolutionary history.” (Perry, G.H. et al. 2007).

Key genetic mutations during later hominid evolution were critical to promoting the enhanced lipid metabolism necessary for subsisting on diets with greater levels of animal material. This ultimately enabled humans to properly regulate the uptake of cholesterol and lipids that is necessary with the consumption of higher fat diets. (from Author's Research on Apes)

In addition, recent work in human evolutionary genetics suggests that the selection for key “meat-adaptive” genes were critical for allowing our hominid ancestors to more effectively exploit diets with higher levels of animal fat. Finch and Stanford (2004) argued that the evolution of the unique E3 allele in *Homo* at the apolipoprotein E (apoE) locus was important for allowing our ancestors to exploit diets with greater animal material. ApoE plays a critical role in regulating the uptake of cholesterol and lipids throughout the body. The E3 allele is evident in humans, but not in chimpanzees and gorillas, and is associated with reduced metabolic and cardiovascular risks with the consumption of higher fat diets. (Leonard WR et. al.)

A gene duplication event took place 2-3 million years ago around the time that Homo was emerging from Australopithecus that is thought to have played an important role in the expansion and the increased complexity of the developing human brain. The duplicated gene known as SRGAP2 promotes the density of neurons by slowing brain development to allow for neurons to develop more and better connections that ultimately increase the brain's processing power.:

“Australopithecus species played a significant part in human evolution, the genus Homo being derived from Australopithecus at some time after three million years ago. Among other things, they were the first hominids to show the presence of a gene that causes increased length and ability of neurons in the brain, the duplicated SRGAP2 gene.” (Wikipedia, The Free Online Encyclopedia “Australopithecus.”)

“This gene is one of the 23 genes that are duplicated in humans but not in other primates.[7] This protein in humans has been duplicated three times in the human genome in the past 3.4 million years: one duplication 3.4 million years ago (mya) called SRGAP 2B, a second duplication 2.4 mya (called SRGAP2C), and one final duplication ~1 mya (SRGAP2D). The ancestral gene SRGAP2 is found in all mammals and the human copy has been renamed SRGAP2A. The 2.4 million year-old duplication (SRGAP2C) expresses a shortened version that 100% of humans possess.[8] This shortened version SRGAP2C inhibits the function of the ancestral copy SRGAP 2A and (1) allows faster migration of neurons by interfering with filopodia production and (2) slows the rate of synaptic maturation and increases the density of synapses in the cerebral cortex.[6]” (Wikipedia “SRGAP2”).

“Our analysis indicates that the duplications spread across 80 Mbp of chromosome 1 at a time corresponding to the transition from Australopithecus to Homo (Figure 5). This included an initial large interspersed duplication (258 kbp) from chromosome 1q32.1 to 1q21.1, creating SRGAP2B ~3.4 mya. The initial duplication was followed by larger (>500 kbp), secondary duplications of the 1q21.1 locus, creating SRGAP2C and SRGAP2D (~2.4 and 1 mya, respectively). Consistent with these timing estimates, archaic Homo species, including Neanderthal and Denisova, carry these SRGAP2 paralogs (Figure S5). It is intriguing that the general timing of the potentially functional copies, SRGAP2B and SRGAP2C, corresponds to the emergence of the genus Homo from Australopithecus (2–3 mya). This period of human evolution has been associated with the expansion of the neocortex, use of stone tools, as well as dramatic changes in behavior and culture (Jobling et al., 2004).” (Dennis, M.Y. et al. 2012).

ENCEPHALIZATION

Generally these creatures (ardi & austral) are all somewhat similar to each other and the Chimpanzee: they all have similar bodies and encephalization.

Author's Note: Australs actually had slightly (~20% or more) larger brain volumes and EQ volumes than living chimps, suggesting that brain expansion in the hominin lineage took place

before the emergence of Homo, contrary to conventional belief that brain expansion began with the appearance of Homo.

“The human brain is three times larger than that of our australopithecine ancestors, in terms of absolute size (Holloway et al. 2004) and in terms of brain size scaled to body size (EQ, Jerison 1973; McHenry 1994). The australopithecines (e.g., *Australopithecus afarensis*, *A. africanus*) had modestly larger brain volumes and EQ values than living chimpanzees (*Pan troglodytes*) and presumably larger volumes and EQ values than the ancestor common to australopithecines, chimpanzees, and humans (McHenry 1994; Tobias 1987).” (Bailey & Geary 2009).

“It now seems that by 2.5 million years ago, mean endocranial capacity in at least one early hominid species, *A. africanus*, had already increased some 23% over that in modern chimpanzees (*Pan troglodytes*; 366 cm³ vs. 451 cm³) suggesting that relative brain expansion in the hominid lineage started some half-million years before the earliest appearance of the genus Homo and nearly a million years or so before the appearance of *A. robustus* (both australopithecine species have now been shown as having a mean endocranial capacity of about 450 cm³). Evidence for brain expansion in a pre-Homo stage of hominid evolution is compatible with recent reports of enhanced tool-making skills and carnivory (acquisition of meat and marrow) nearly 2.5 million years ago (de Heinzelin et al., 1999; Roche et al., 1999).” (Conroy et al. 2000).

“Relative brain expansion in the hominid lineage started some half-million years before the earliest appearance of the genus Homo, possibly coincident with enhanced tool-making skills and carnivory.” (Conroy et al. 2000).

Author's Note: Analysis of the brain of *A. africanus* revealed some cortical reorganization that more closely resembled a human brain. Thus, in spite of having a significantly smaller brain volume relative to modern humans, this australopithecine, and presumably others, already had a brain that had undergone some degree of reorganization prior to the significant cortical enlargement that occurred with the emergence of Homo. This supports the notion that cortical reorganization preceded the expansion of the hominid brain. Many potential drivers of this reorganization of the *Australopithecus* brain have been proposed including adaptation to more open habitats with more widely dispersed food resources. This would necessitate longer-term, more sophisticated memory of spatial locations and their associated objects, resources, potential prey and predators. The primitive use of stone tools requiring enhanced visuospatial skills and the need for greater communication skills may have also led to the reorganization of the *Australopithecus* brain. If so, these changes may have laid the foundation for the more sophisticated tool making and the more advanced social skills typically associated with the emergence of Homo.

“Clearly, this Stw 505 specimen of *A. africanus* has an indisputable crescentic, concave-posterior, lunate sulcus as seen in Fig. 3B and it is in a posterior, non-Pan position, indicating that at least one member of the species had undergone some cortical reorganization toward a more human-like condition...The Stw 505 specimen indicates that at least this early hominid brain was indeed reorganized toward a more human-like pattern despite its small brain

volume, and prior to any significant cortical enlargement as seen in the genus Homo. In sum, this endocast strongly suggests that cortical reorganization preceded brain enlargement in hominid evolution as argued elsewhere [14], [15], [16] and [17]. We repeat that in brains with strongly developed lunate sulcus, the sulci are the anterior limit to PVC. We have not found evidence that this finding is violated in either humans or apes (please refer to the literature discussed in [26]).” (Holloway, Clarke, & Tobias 2004).

“It is tempting to speculate about what selection pressures may have played a role in the evolution of this derived neural condition. Relative to the earliest hominids [37], the associated faunal and geological evidence from the later Australopithecus-bearing sites suggest more open habitats and an expansion of niches with food resources separated by increased distances. Stone tools, while showing minimal standardization but primitive patterns exist as early as 2.6 Myr [5] and [12], a date not at odds with that of Member 4 of Sterkfontein [36]. Elsewhere [14], [15], [16], [17] and [23], RLH has speculated that reorganization of the Australopithecus brain indicates an expanded posterior parietal cerebral cortex, and was most likely associated with enhanced social behavior including communication: [1] this region involves multimodal processing involving visual, auditory, and sensorimotor integration; [2] visuospatial integration related to tool use and making, throwing objects with force and accuracy, as well as more sophisticated longer-term memory of spatial locations and qualities of self, others (i.e., facial recognition), prey and predators, including objects and resources (stone, digging sticks, trees, waterholes, etc.). All of these were possibly adding to a more advanced cognitive adaptation within a changing and expanding ecological zone, and formed the basis for additional cognitive changes, such as patterned tool-making, and possibly more advanced communicative skills that accompanied the evolution of the genus Homo.” (Holloway, Clarke, & Tobias 2004).

NOTE: Since they were about equally encephalized as the chimps, meaning they had about one third the encephalization of ourselves, we can assume that they probably possessed about the same amount of intelligence as the chimps but way less than our own, though the nature of that intelligence may have been different. Furthermore, some anatomists have noted that the shape of their cranium is different from chimps, which may mean that their brains were shaped and operated differently. (Falk , D. 2001. Skulls and ‘Minds’)

While nearly all of them ate less than fifty percent of their diet as C4, one of them, the Bosei, converted to nearly all C4 foods and also had some of the thickest and strongest teeth of all the Australapithicus. It's also important to note that, while all the other Australs maintained about the same brain size, the Bosei actually increased the size of his brain, by around 100 cc and while this may not sound like much, it does represent an expansion of twenty percent, suggesting a possible correlation between conversion to more C4 foods, in the form of starch, and intelligence--an issue we will explore later.(Also possible correlation between intelligence and more ground dwelling, avoidance of predation, etc).

TOOLS

Like the chimps the Australs were likely good at finding and remembering the whereabouts and behavior of their food supply; maintaining complex social relationships with perhaps as many as one hundred individuals. They probably could use crude tools too like rocks for smashing open nuts or twigs for fishing for termites and maybe even rudimentary spears for impaling small animals. However we do not see any evidence in the fossil record so far that the Australs were using stone tools that they themselves altered in some way, like spear points or cleavers.

Some evidence of stone tools dating to the middle Pliocene (~3.8—3.0 Ma), thus occurring before the appearance of Homo who has been traditionally associated with emergence of stone tool use. “The recent surge of stable isotopic data from hominins also makes it clear that the middle Pliocene marked significant hominin paleodietary change, when hominins first began to exploit substantial C4/CAM-based foods in more open environments (Lee-Thorp et al., 2012; Cerling et al., 2013; Sponheimer et al., 2013; Wynn et al., 2013; Alemseged, 2015; Levin et al., 2015). The timing of this C4 dietary expansion, combined with other middle Pliocene discoveries, including possible hominin tool use and manufacture (McPherron et al., 2010; Harmand et al., 2015) and potentially increased diversity of hominin taxonomic diversity (Wood and Boyle, 2016), have heightened interest in the ecological, dietary, and behavioral patterns of hominins in the middle Pliocene (~3.8e3.0 Ma).” (Wynn, J.G. et al. 2016).

“Human evolutionary scholars have long supposed that the earliest stone tools were made by the genus Homo and that this technological development was directly linked to climate change and the spread of savannah grasslands. New fieldwork in West Turkana, Kenya, has identified evidence of much earlier hominid technological behaviour. We report the discovery of Lomekwi 3, a 3.3-million-year-old archaeological site where in situ stone artefacts occur in spatiotemporal association with Pliocene hominin fossils in a wooded palaeoenvironment. The Lomekwi 3 knappers, with a developing understanding of stone’s fracture properties, combined core reduction with battering activities. Given the implications of the Lomekwi 3 assemblage for models aiming to converge environmental change, hominin evolution and technological origins, we propose for it the name ‘Lomekwian’, which predates the Oldowan by 700,000 years and marks a new beginning to the known archaeological record.” (Harmand, S. et al. 2015).

“Conventional wisdom in human evolutionary studies has assumed that the origins of hominin sharp-edged stone tool production were linked to the emergence of the genus Homo^{1, 2} in response to climate change and the spread of savannah grasslands^{3, 4}. In 1964, fossils looking more like later Homo than australopithecines were discovered at Olduvai Gorge (Tanzania) in association with the earliest known stone tool culture, the Oldowan, and so were assigned to the new species: Homo habilis or ‘handy man’¹. The premise was that our lineage alone took the cognitive leap of hitting stones together to strike off sharp flakes and that this was the foundation of our evolutionary success. Subsequent discoveries pushed back the date for the first Oldowan stone tools to 2.6 million years ago^{5, 6} (Ma) and the earliest fossils attributable to early Homo to only 2.4–2.3 Ma^{7, 8}, opening up the possibility of tool manufacture by hominins other than Homo⁹ before 2.6 Ma...Cut-marked bones from Dikika, Ethiopia²⁰, dated at 3.39 Ma, has added to speculation on pre-2.6-Ma hominid stone tool use. It has been argued that percussive activities other than knapping, such as the pounding and/or battering of

plant foods or bones, could have been critical components of an even earlier, as-yet-unrecognized, stage of hominin stone tool use 21, 22, 23, 24, 25. Any such artefacts may have gone unrecognized if they do not directly resemble known Oldowan lithics, occur at very low densities or were made of perishable materials¹⁰.” (Harmand, S. 2015).

“Based on the lithic material recovered in 2011 and 2012, the current total assemblage (n = 149 surface and in situ artefacts) incorporates 83 cores, 35 flakes (whole and broken), seven passive elements or potential anvils, seven percussors (whole, broken or potential), three worked cobbles, two split cobbles, and 12 artefacts grouped as indeterminate fragments or pieces lacking diagnostic attributes (Extended Data Table 1a)...The technological features of flakes and flake fragments are clear, unequivocal and seen repeatedly, demonstrating that they were intentionally knapped from the cores...LOM3 predates the oldest fossil specimens attributed to Homo in West Turkana at 2.34 ± 0.04 Ma⁷ by almost a million years; the only hominin species known to have been living in the West Turkana region at the time is *K. platyops*²⁷, while *Australopithecus afarensis* is found in the Lower Awash Valley at 3.39 Ma in association with cut-marked bones from Dikika²⁰...The LOM3 knappers’ understanding of stone fracture mechanics and grammars of action is clearly less developed than that reflected in early Oldowan assemblages and neither were they predominantly using free-hand technique. The LOM3 assemblage could represent a technological stage between a hypothetical pounding-oriented stone tool used by an earlier hominin and the flaking-oriented knapping behaviour of later Oldowan toolmakers.” (Harmand, S. 2015).

New (2015) research also indicates that the Australopiths’ could achieve the manual power grips and precision that has been associated with the use of tools.:

“The distinctly human ability for forceful precision and power “squeeze” gripping is linked to two key evolutionary transitions in hand use: a reduction in arboreal climbing and the manufacture and use of tools. However, it is unclear when these locomotor and manipulative transitions occurred. Here we show that *Australopithecus africanus* (~3 to 2 million years ago) and several Pleistocene hominins, traditionally considered not to have engaged in habitual tool manufacture, have a human-like trabecular bone pattern in the metacarpals consistent with forceful opposition of the thumb and fingers typically adopted during tool use. These results support archaeological evidence for stone tool use in australopiths and provide morphological evidence that Pliocene hominins achieved human-like hand postures much earlier and more frequently than previously considered.” (Skinner, M.M. et al. 2015).

“However, based on morphology and the absence of directly associated archaeological evidence, most australopiths are generally considered to lack human-like forceful precision and power (squeeze) grips and a commitment to tool-related manipulative behaviors [(2, 3, 5, 11, 15), but see (13, 17)]...Recent evidence of stone tool cut marks at 3.4 Ma associated with *A. afarensis*-bearing sediments suggests that stone tool use evolved much earlier than traditionally thought [(21), but see (24)] and in a hominin whose hand morphology displays only a few derived, human-like features, such as asymmetrical metacarpal heads and possibly a long thumb (4, 13). This evidence suggests that stone tool-use ability does not require the complete suite of derived later Homo-like hand morphology. However, it is uncertain whether early

hominin tool-use behaviors were opportunistic and infrequent (25) and whether a Homo-like external hand morphology evolved only in response to habitual tool use and tool production (5).” (Skinner, M.M. et al. 2015).

“Nonetheless, the distribution of the trabecular structure in *A. africanus* and Swartkrans specimen SK 84 is similar to the characteristic pattern of committed tool makers, Neandertals and *H. sapiens*, and distinctly unlike that of other apes. The palmar concentration of trabecular bone in the Mc1 base and the asymmetrical distribution of trabeculae in the third and fifth metacarpal heads in all hominins, as well as the absence of this pattern in *Pan* and other apes, suggests that the hominin trabecular pattern reflects the forceful opposition of the thumb and fingers during human-like precision and power (squeeze) grips (1–3, 38). Although hominins may have used forceful hand grips for any number of manipulative behaviors (16), tool-related behaviors probably generated some of the largest (non locomotor) forces on the hands and are thus considered to be a strong selective pressure on hominin hand morphology (2, 5, 6, 8, 17, 18, 25). Experimental evidence has demonstrated that forces are highest on the thumb during precision grips used during flake use rather than stone tool making (50), which is consistent with the earliest tool technologies (25) and, in particular, the archaeological evidence for use of stone flakes to remove meat from bone in early hominins (20, 21). These results show that *A. africanus* was capable of habitual and forceful human-like opposition of the thumb and fingers during precision and power (squeeze) grips that are used during tool-related behaviors, providing morphological evidence of committed tool use in a hominin hitherto considered not to be capable of these behaviors and evolving ~500,000 years earlier than the first evidence of stone tool production.” (Skinner, M.M. et al. 2015).

SOCIAL DYNAMICS

GROUP SIZE

Like the Savannah Chimpanzee, the Australopithecus probably stayed together as one troop, perhaps nearly all of the time to ward against predation, which kept them social.

“Hunter/gatherer group sizes tend to cluster tightly around the 15-50 range, and optimally sized groups can probably be assumed for all savannah primates such as baboons and early Australopithecines for defense against predators.” (Hayden).

“In 1993, Leslie Aiello and Robin Dunbar showed that there was a correlation between neocortex size and group size, at least among primates. Following their original article (Aiello and Dunbar 1993), further work by Dunbar revealed that the correlation worked for general brain size as well as for neocortex size...Using predicted figures, we have australopithecine group sizes averaging 65 or 70, *Homo habilis* about 75 or 80, *Homo erectus* variable, but typically at around 110, ‘Archaic’ *Homo sapiens* 120 or 130 and Neanderthals at 140 or slightly higher.” (Barnard pp. 53-54).

TERRITORY PROTECTION

There is some evidence that one of these creatures was more gentle than the chimps, with less competition and conflict between males within groups and other groups.

Overall the Australs probably have much greater territories in total and per animal than both jungle and Savannah chimps and probably had many more nesting areas within those territories, so they would not need to travel as much everyday. It's possible this meant that the Australs could not defend their territory as well as chimps because they are so much scattered, so they may have had more overlap as we see with other primates like the Spiders and Howlers and others, though if two troops encountered each other, my guess is that it was plenty nasty, as they were then competing for limited resources in more challenging environment.

PREDATION WARNING

Early hominids such as the Australs would have relied upon their intelligence, cooperation, and socialization to outsmart the many potential predators—"The predators living at the same time as *Australopithecus afarensis* were huge and there were 10 times as many as today. There were hyenas as big as bears, as well as saber-toothed cats and many other mega-sized carnivores, reptiles and raptors. *Australopithecus afarensis* didn't have tools, didn't have big teeth and was three feet tall. He was using his brain, his agility and his social skills to get away from these predators. "He wasn't hunting them," says Sussman. "He was avoiding them at all costs."

Approximately 6 percent to 10 percent of early humans were preyed upon according to evidence that includes teeth marks on bones, talon marks on skulls and holes in a fossil cranium into which sabertooth cat fangs fit, says Sussman. The predation rate on savannah antelope and certain ground-living monkeys today is around 6 percent to 10 percent as well. Sussman and Hart provide evidence that many of our modern human traits, including those of cooperation and socialization, developed as a result of being a prey species and the early human's ability to out-smart the predators. These traits did not result from trying to hunt for prey or kill our competitors, says Sussman.

"One of the main defenses against predators by animals without physical defenses is living in groups," says Sussman. "In fact, all diurnal primates (those active during the day) live in permanent social groups. Most ecologists agree that predation pressure is one of the major adaptive reasons for this group-living. In this way there are more eyes and ears to locate the predators and more individuals to mob them if attacked or to confuse them by scattering. There are a number of reasons that living in groups is beneficial for animals that otherwise would be very prone to being preyed upon." *Man the Hunted: Primates, Predators and Human Evolution* Robert Sussman (Schoenherr, Neil 2006).

As one group they could better warn of predators with their cries and, if they stayed together as one group, then the males collectively would be better at defending the females and children better from predators and rival groups.

DOMINANCE/HIERARCHY

From both of these lines of evolution, we can probably extrapolate that the Australapithic were probably way more male dominated in general. And if that was the case, they probably followed the trends found in other primates: there may have been substantial conflicts and competition between the males themselves but at the same time, since most of the males may have been brothers or cousins, this may have been less. It's also possible that one alpha-male may have had total dominance over the other males, like the Gorillas; but it could be that the alpha was more like the chimp with limited dominance.

On the other, darker side, it's possible that the females had little if any sway over the males and were much weaker in counterbalancing their power as compared to say the chimps or ourselves.

If we knew the relative size of their tests, we may be able to draw some strong conclusions about their sexual practices but, since we do not have that information, we can only make some educated guesses. As for breeding, it could be that like the Gorillas one alpha male tended to dominate all the females, with the other males seeking opportunities here and there or, like the Baboons, various males contained their harems within larger groups which they jealously guarded and protected from other males.

MATRILOCAL/PATRILOCAL

And at the same time, they (the Australs) may have been more patrilocal (than chimps); one study has confirmed that at least one species of them was more patrilocal, based on some complicated evidence, meaning that the females disperse at puberty, leaving behind a group of males more genetically bonded and also larger than the females.

While it's possible, too, that the various species of Australapithicus developed different societies, just like the various primates we have investigated, it seems most probable, however, that they were patrilocal, since the Chimpanzees are that way as well; we also have some evidence to support this claim, at least for one species of Australopithecus. Furthermore, patrilocal would have continued to deliver greater survivability: because the males would be more bonded, they could continue to hunt cooperatively

patrilocal: fight of predators better? but chimps don't" but do fight off rival troops.....

sexually dimorphic and perhaps patrilocal, too, just like the Chimpanzees. Since our common ancestor was likely patrilocal like the Chimpanzee, the Australapithicus probably just stayed with that society because it would then allow greater bonding and cooperation between the males

which, in this new environment, would allow the males to continue to work together cooperatively to hunt. This cooperation, too, could provide greater protection from predation as well as provide protection from predation in a pinch--that is, if the troop was actually attacked. While this behavior is not necessary would also pose distinct advantages in survival--that is, even more protection from predation, since this responsibility tends to fall to the males with primates; it would also provide greater cooperation for hunting, as well as for protecting territory.

"In most mammals, the females stay in the home community and the males disperse after adolescence to avoid inbreeding. But chimpanzees and many human hunter-gatherer groups are unusual in following the opposite pattern. The reason may have to do with the aggressive territoriality of both species: A group of males who have grown up with one another is more cohesive and better at defending a territory against competitors. This obliges the females to be the gender that disperses." "It's really nice to see there is biological continuity from chimpanzees to australopithecines," said Joan B. Silk, an expert on primate social behavior at the University of California, Los Angeles." (Wade, Nicholas).

SEXUAL DIMORPHISM & DIVISION OF LABOR

We have several areas of evidence and enquiry.

From fossilized bones and teeth, we can draw some conclusions about when in time they existed: we can also reconstruct much of their morphology and anatomy, including their size and weight.

However, the Australopithecus also differed from the chimps: they were way more sexually dimorphic like the Gorillas and Baboons. Extrapolating from what we know about Chimpanzees and other extant Apes, it's likely that the males bore greater responsibility for protecting the women and children both from predators and other rival troops of Austral--and maybe greater responsibility for hunting due to much greater physical size and strength while, at the same time, providing little if any assistance in the way of raising the children.

Later we will discuss why the conditions in the environment may have caused this adaptation towards matrilineal and sexual dimorphism.

(Note: exception to this rule: Afarensis (Lucy): evidence to suggest that were about as dimorphic as ourselves) Source: Larsen, C.S. 2003

This may in part explain why the Austral were more sexually dimorphic. Both the Gorilla and Baboon are ground-dwelling species and are therefore more prone to predation. For this reason, evolution will likely not select for smaller males; most predators it seems prefer to attack smaller and weaker animals and, as such, smaller males would likely be attacked and at the same time, larger males could fight predators off better and also protect the women and children. While this can easily describe why males maintained their size and strength, it does not explain why females would shrink relative to them and lose much of their power. However, I can also make some guesses here. As we have already noted, it's likely that food became more scarce in these environments and when this happens to animals, they tend to shrink in size to

compensate; since evolution could not afford to shrink the size of male Australs because the whole troop would then lose its protection, it may have then decided to shrink the females instead to compensate for this lack of nutrition; the troop therefore maintains its ability to protect itself almost as well while needing less food on the whole.

****Author's Note:** It is also advantageous for females to be smaller in size to compensate for the increased energetic costs of child rearing.

At the same time, the males may have used their superior size and strength, even from the beginning, to dominate limited supplies of food more, especially perhaps animal foods as we have already seen in chimps, therefore causing evolution to select for smaller females who could survive on smaller amounts of calories. It is important to note, too, that smaller animals have higher metabolisms so, while they need more food per mass than larger animals, they do not need more food in total. On another line of reasoning, it's possible that the higher metabolism of smaller females contributed some greater survivability to the troop overall.

While some researchers have proposed that *Australopithecus afarensis* had similar levels of skeletal size dimorphism as humans, the predominant consensus is that *Australopithecus afarensis* displayed strong sexual size dimorphism. Note that there is not, however, significant dimorphism in the size of *Australopithecus* female and male canines. Typically, reduced sexual dimorphism of canines would indicate reduced male to male competition for mates, but the extreme skeletal size sexual dimorphism indicates the opposite, and further suggests that Australs were polygynous (not pair bonded).—

“Most analysts have concluded that *A. afarensis* possesses a degree of postcranial skeletal size dimorphism matched or exceeded only by the most dimorphic of extant great apes (i.e., Pongo and Gorilla) (e.g., Johanson and White, 1979; McHenry, 1986, 1991; Kimbel and White, 1988b; Richmond and Jungers, 1995; Lockwood et al., 1996; Plavcan et al., 2005; Harmon, 2006; Gordon et al., 2008)...High levels of skeletal size dimorphism in *A. afarensis* contrast strikingly with the relatively small amount of canine sexual dimorphism...Reduced canine size dimorphism in *A. afarensis*, relative to the presumed ancestral condition exemplified by the extant and fossil great apes, implies that male–male competition was reduced, but the high degree of skeletal size dimorphism implies that it was not (Plavcan and van Schaik, 1997; Plavcan, 2001). There appears to be no appropriate extant analog among anthropoids for understanding the pattern of sexual dimorphism in canine size and postcranial skeletal size expressed by *A. afarensis*, which makes inferences about social behavior difficult from a comparative perspective (Plavcan, 2000).” (Kimbel & Delezene 2009).

“There is only so much we can make of the fossil record, though. Paleoanthropologist J. Michael Plavcan of the University of Arkansas urges caution in making the leap from fossilized bones to social behavior in hominins. Consider *Australopithecus afarensis*, the species to which “Lucy” belonged, which lived between 3.9 million and three million years ago. Like *Ardipithecus*, *A. afarensis* had small canines, but its skeleton displays a level of dimorphism between that of modern chimpanzees and gorillas. “You have [a level of] body-size dimorphism suggesting that [*A. afarensis*] males were competing for females and [a] loss of canine dimorphism that suggests they weren’t,” Plavcan says. “It’s a puzzle.”” (Edgar, B. 2014).

“The magnitude of sexual size dimorphism in the fossil record is difficult to assess. The best-represented early hominin is *Australopithecus afarensis*. Numerous analyses of the skull, teeth, and postcrania suggest that this taxon was characterized by strong sexual size dimorphism approaching or even exceeding that of gorillas (Gordon et al. 2008; Harmon 2006; Kimbel and Delezene 2009; Lockwood et al. 1996; Richmond and Jungers 1995; Scott and Stroik 2006). In contrast, Reno et al. (2003, 2010) present an analysis suggesting that sexual size dimorphism in *Au. afarensis* was humanlike, challenging the notion of strong size dimorphism. Additionally, Nelson et al. (2011) present an analysis of digit ratios in modern apes and humans, and several extinct hominids, implying that *Au. afarensis* may have been less dimorphic than commonly thought.” (Plavcan, J.M. 2012).

“Still, current consensus in the paleoanthropological literature is that *Australopithecus afarensis* showed very strong sexual size dimorphism...It seems most likely that early hominins were characterized by intense male mate competition.” (Plavcan, J.M. 2012).

“Extensive simulations using modern humans, chimpanzees, and gorillas confirm that this technique is accurate and that skeletal size dimorphism in *A. afarensis* was most similar to that of contemporary *Homo sapiens*. These data...greatly increase the probability that the reproductive strategy of *A. afarensis* was principally monogamy...

As a consequence of numerous nonsystematic appraisals, it is now widely believed that *A. afarensis* was substantially more dimorphic than modern humans (6). Some have gone beyond this orthodoxy to argue that sexually based variation exceeded that seen in any living hominoid (7). None of these analyses, however, has adequately compensated for the effects of temporal and geographic variation as opposed to normative population-level dimorphism. Because anatomical structure evolves through time, it is mandatory that sexual dimorphism within a species not be conflated with variation augmented by evolutionary change. Here we use the contemporaneous Afar Locality (A.L.) 333 hominid sample to show that dimorphism in *A. afarensis* is unlikely to have exceeded that of modern humans.” (Reno et al. 2003).

“As Hamada and Usono (33) have argued, “the social system and ecology of human ancestors, who evolved a characteristic growth pattern, must have been different from that of chimpanzees” (ref. 33, p. 283). First, their marked demographic success and capacity to invade new potentially dangerous habitats strongly suggest that they, like chimpanzees, dwelled in multimale groups (27, 28)...Instead, the moderate skeletal dimorphism of *A. afarensis* (greater than *Pan* and less than *Gorilla*) suggests a somewhat longer developmental period in males compared with females and is therefore inconsistent with a chimpanzee-like territorial strategy. At the same time, it is also markedly inconsistent with strategies like those of gorillas and orangutans, in which skeletal dimorphism is much more pronounced. Therefore, the co-occurrence of moderate skeletal dimorphism, such as that found in modern humans and *A. afarensis*, and a reduced male canine is fully consistent with a pair-bonded reproductive strategy in early hominids...” (Reno et al. 2003).

A reduction in canine dimorphism is characteristic of hominins. *Ardipithecus* & *Australopithecus* have insignificant canine tooth size dimorphism...

“A reduction in canine tooth size dimorphism is recognized as one of the defining characteristics of the hominin clade (Brace 1972; Greenfield 1992; White et al. 2009; Wolpoff 1976). Canine tooth size dimorphism is minimal in *Australopithecus afarensis*, the earliest taxon for which sample sizes are adequate to assess the trait (Kimbel and Delezene 2009). There is no evidence of substantial canine dimorphism in earlier hominins (Plavcan and van Schaik 1997a), including *Sahelanthropus*, *Ardipithecus* (White et al. 2009), and *Australopithecus anamensis* (Plavcan et al. 2009; Ward et al. 2010), or later hominins.” (Plavcan, J.M. 2012).

“At the moment, current evidence suggest two major shifts in dimorphism in the line leading to humans: the development of strong size dimorphism in early *Australopithecus* through a reduction in female size (Gordon 2006; White et al. 2009), and the loss of strong dimorphism through a disproportionate increase in female size in *Homo*.

The development of size dimorphism in early *Australopithecus* presents an intriguing signal. On the one hand, a reduction in female size implies a shift in selective pressures targeting females alone, which would imply selection associated with early reproduction, unreliable resources, or fecundity (Gordon 2006). On the other hand, no primate shows such strong size dimorphism without selection favoring larger males. The implication would be that selection for smaller females might also have led to a shift in the ecologically optimal body size, with males under selective pressure to maintain larger body size, presumably in association with agonistic male mating competition.” (Plavcan, J.M. 2012).

Besides *Australopithecus afarensis*, other *Ardipithecus/Australopithecus* (*afarensis*, *anamensis*, *robustus*, and *boisei*) generally display strong size dimorphism, with the exception of *Ardipithecus ramidus* who does not show any significant size dimorphism. Adult specimens of *A. sediba* are lacking leaving the degree of dimorphism in this particular species unknown.: “Evidence of dimorphism in other australopithecines is more ambivalent. Strong size dimorphism nearing that of gorillas has been inferred for *Australopithecus africanus* on the basis of craniodental remains (Lockwood 1999). In contrast, postcranial evidence suggests more chimplike or humanlike levels of size dimorphism (Harmon 2009). *Au. anamensis* has been suggested to show strong size dimorphism (Ward et al. 2001), though far fewer remains are available for this taxon than for others. Berger et al. (2010) suggest monomorphism in *Au. sediba*, but this assessment is based on a single juvenile male and adult female, rendering any conclusion about dimorphism in this taxon dubious without more adult specimens. *Au. robustus* and *boisei* have both been inferred as showing strong size dimorphism, again on the basis of variation in craniodental remains (Lockwood et al. 2007; Wood and Constantino 2007)...One last intriguing taxon is *Ardipithecus ramidus*. The large amount of skeletal and dental material recently announced apparently shows no evidence of substantial size dimorphism (White et al. 2009). Though no independent studies have been published to confirm this suggestion, it is intriguing, as discussed below.” (Plavcan, J.M. 2012).

MATING & CHILD REARING

The mating practices (monogamy, polygyny) of the Australis is a major point of debate. This is largely rooted in the debates on the degree of sexual dimorphism present among most Australis. Though, in line with the general consensus that the Australis did indeed have strong sexual dimorphism in body size, they would be predicted to have been polygynous. Still, another method for determining mating practices that is not based upon sexual dimorphism turned up conflicting results. Using a novel approach, scientists looked at the ratios of the second and fourth fingers that have been found to correlate with sexual competition and social systems. With this method, *Ardipithecus ramidus* was predicted to have been polygynous and *A. afarensis* monogamous. This is in direct opposition to what was concluded from looking at sexual dimorphism of the two species. *Ardipithecus ramidus* which has been found to have a low canine and body dimorphism would be predicted to be pair bonded (monogamous), and *A. afarensis*' high degree of sexual dimorphism would normally be indicative of a polygynous mating system.

“Social behaviour of fossil hominid species is notoriously difficult to predict owing to difficulties in estimating body size dimorphism from fragmentary remains and, in hominins, low canine size dimorphism. Recent studies have shown that the second-to-fourth digit ratio (2D : 4D), a putative biomarker for prenatal androgen effects (PAEs), covaries with intra-sexual competition and social systems across haplorrhines; non-pair-bonded polygynous taxa have significantly lower 2D : 4D ratios (high PAE) than pair-bonded monogamous species. Here, we use proximal phalanx ratios of extant and fossil specimens to reconstruct the social systems of extinct hominids. *Pierolapithecus catalaunicus*, *Hispanopithecus laietanus* and *Ardipithecus ramidus* have ratios consistent with polygynous extant species, whereas the ratio of *Australopithecus afarensis* is consistent with monogamous extant species.” (Nelson, Rolian, Cashmore, Shultz 2010).

“Sexual dimorphism in canine and skeletal features is the main method used to predict social behaviour in extinct primates [1,2]. In species where males compete strongly for females, reproductive skew manifests as sexual dimorphism in canine and body size; where intra-sexual competition is reduced, such as with social monogamy, dimorphism in these characters is reduced...Although this model provides a rule of thumb for most extant primates [3], it is more problematic to apply to extinct primates, including hominins...The controversy resulting from inferences based on dimorphism in postcranial remains is exemplified by predictions of social systems for *Australopithecus afarensis*, which range from monogamous [4,8] to highly promiscuous [2,6]. The debate has been reviewed in detail in a series of publications [4,6,9–11] and hinges on a number of methodological issues that could significantly impact the estimated levels of dimorphism (reviewed in [6]). The story is not much clearer for other early hominins. Most recently, evidence has been put forward for low canine and body dimorphism in *Ardipithecus ramidus*, leading to the proposal that human-like pair-bonded (PB) characteristics evolved early and, therefore, could be a cardinal trait of the hominin lineage [12]. However, based on facial dimorphism and maturation rates, a gorilla-like harem social system has been

proposed for the later *Paranthropus robustus* [2], which appears to have differed from that of *Australopithecus africanus* [2].” (Nelson, Rolian, Cashmore, Shultz 2010).

“The relationship between social system and digit ratio across extant haplorhines suggests that 2D : 4D reflects links between prenatal androgen effects (PAEs) and sexually selected social behaviours [26,27]. We have used this hypothesis to predict social systems of extinct hominids from digit ratios calculated from fossil remains...The predicted social system of *Ardipithecus* was non-pair-bonded (NPB) polygyny and differed from that of *Australopithecus*, predicted to be pair-bonded (PB) monogamy (table 3 and figure 2)...Our inferred social system for *Au. afarensis* tentatively supports the claim by Lovejoy [8] and Reno et al. [4] that this species may have been monogamous (contra [6,9,11])...*Ardipithecus ramidus* fossil hand bones were found associated in situ, and our analysis of the phalanges conflicts with Lovejoy's recent claim, based on canine and body dimorphism, that *Ar. ramidus* was PB [12].” (Nelson, Rolian, Cashmore, Shultz 2010).

According to some scientists, the pair-bonding now characteristic of humans may have been a more recent phenomena in human evolution:

“Pair-bonding, in a broad sense, is universal among humans [40], but it is not known when the transition from a promiscuous mating system to a stable bonded one occurred. The persistence of marked levels of skeletal dimorphism in *Homo* until the Middle Pleistocene (e.g. [14]), combined with genetic evidence indicating that male population size (ancestral to people today) was low compared with females' until the spread of agriculture [46], implies that human-like pair-bonding was not common until late in human evolution. The fact that human 2PP : 4PP ratios fall between those of PB and NPB apes (figure 2) also suggests that human pair-bonding differs from that of other socially monogamous primates (in this case gibbons). Unlike PB monogamous gibbons, humans live within a multi-male–multi-female social system [40]; the potential therefore remains for variation in levels of male–male competition. Maintaining this potential may be adaptive during range expansion across ecologically diverse environments.” (Nelson, Rolian, Cashmore, Shultz 2010).

“IT IS ENTIRELY POSSIBLE that our most distant ancestors were monogamous. Fossil evidence, says anthropologist C. Owen Lovejoy of Kent State University, suggests that monogamy predates even *Ardipithecus ramidus*, the species best known from a 4.4-million-year-old partial female skeleton, nicknamed "Ardi," discovered in the Middle Awash region of Ethiopia...According to this hypothesis, an ancestral polygamous mating system was replaced by pair bonding when lower-ranked hominin males diverted energy from fighting one another toward finding food to bring females as an incentive to mate. Females preferred reliable providers to aggressive competitors and bonded with the better foragers. Eventually females lost the skin swelling or other signs of sexual receptivity that would have attracted different males while their partners were off gathering food...For evidence, Lovejoy points to *Ar. ramidus*'s teeth. Compared with living and fossil apes, *Ar. ramidus* shows a stark reduction in the differences between male and female canine- tooth size. Evolution has honed the dagger like canines of many male primates into formidable weapons used to fight for access to mates...A rough correlation also exists between mating behavior in primates and sexual dimorphism -- that is, differences in body mass and size between males and females of the

same species. The more dimorphic a primate species is, the more likely it is that males fight over females. At one extreme, polygamous gorilla males grow to be more than twice as massive as females. At the opposite extreme, both male and female gibbons, which are mainly monogamous, are nearly equal in mass. Humans lie closer to gibbons on the dimorphism spectrum: human males can be up to 20 percent more massive than females.”(Edgar, B. 2014).

“The body-size sexual dimorphism of *Australopithecus afarensis* was previously thought to have been large (McHenry, 1994), indicating that this was a polygynous species. However, more recent studies suggest that the sexual dimorphism of *A. afarensis* was similar to that of modern humans (Reno et al., 2003, 2005, 2010), although this is still a matter of debate (Plavcan et al., 2005). Recent research of *Ardipithecus ramidus* also shows nearly monomorphic body size that was less dimorphic than that of *Australopithecus* (White et al., 2009a). Moreover, male canines were small in both *A. ramidus* (Suwa et al., 2009a) and *Sahelanthropus tchadensis* (Brunet et al., 2002). Thus, male–male competition may already have been weak in early hominids. The group size of A.L.333, an *A. afarensis* group known as the “First Family,” may have included at least 17 hominids: nine adults, three adolescents, and five juveniles (Johanson, 2004). Thus, early hominids may have had multiple- male–multiple-female groups in which male–male competition was weak. In short, we can speculate that early hominids already had a mating system similar to that of modern humans.” (Nakahashi & Horiuchi 2012).

“In contrast to the species above, *A. ramidus* (4.4 Ma) has been researched in detail. This hominid had a nearly monomorphic body size and small male canines (White et al., 2009a; Suwa et al., 2009a), implying a mating system similar to that of modern humans. However, *A. ramidus* lived in woodland and forest patches, not open savanna (Louchart et al., 2009; White et al., 2009b; WoldeGabriel et al., 2009), similar to the habitat in which modern chimpanzees live. The body size of *A. ramidus* was also similar to that of chimpanzees (Lovejoy et al., 2009). Although *A. ramidus* molar enamel is intermediate in thickness between that of chimpanzees and *Homo*, implying diet that differed from that of chimpanzees (Suwa et al., 2009a), their habitat can be assumed to be similar to that of modern chimpanzees. Thus, *A. ramidus* and chimpanzees may have had different mating systems in a similar habitat.” (Nakahashi & Horiuchi 2012).

Due to Australopithecine females’ smaller body size, their energetic requirements are significantly lower than *Homo* females which are estimated to have been over 50% heavier than the average Australopithecine female. This would have provided the Australopithecine an energetic advantage in terms of meeting the high energetic costs of pregnancy and lactation.: “...*Homo erectus* females, estimated to have been over 50% heavier than the average australopithecine females...comparing the estimated caloric requirements of a large-bodied *Homo erectus* female to those of smaller-bodied australopithecine females. An average *Homo erectus* female with a mass of 52.3 kg would have a DEED of approximately 1,815 kcal, which is 47% higher than the average DEE for the australopithecines and paranthropines... This implies that *Homo erectus* females would have required, on average, considerably more calories per day to survive and reproduce. *Homo erectus* females must have been eating more

food, or eating food of higher quality, than their robust australopithecine counterparts.” (Aiello & Key 2002).

POPULATION CONTROL

Was done according to food availability: “High infant mortality rates among chimpanzees are attributed to the unique inability of infants to cling adequately to their mothers and the high frequency with which they are dropped (Goodall 1968: 252). Among the major causal factors listed were the frequent ‘charging displays’ by males, which might well be related to fluctuations in resource densities and is definitely linked to a dominance structure. The inability of infants to cling effectively would probably be highly analogous to the early hominid situation. Whatever the details, social dominance very plausibly plays a key role in controlling population levels. In most cases, it seems that males are the direct causative factor inducing mortality...Again, the inability of chimpanzee infants to effectively cling to their mothers would probably be directly analogous to the situation among late Pliocene or Early Pleistocene Australopithecines, and the development of this type of population control system in pre-tool using hominids would seem at least plausible.” (Hayden).

LIFE HISTORY

“Similar to chimpanzees, *Au. afarensis* children grew rapidly after birth and reached adulthood earlier than modern humans. This meant *Au. afarensis* had a shorter period of growing up than modern humans have today, leaving them less time for parental guidance and socialization during childhood.” (Smithsonian Institution).

“It is now fairly certain that the outline of human life history took shape within the evolution of *Homo* and not before. Indeed, australopithecines probably lived at a pace nearly twice as fast as modern humans—fast enough to be reflected even in gross developmental sequences such as tooth emergence.” (Smith & Tompkins 1995).

“Currently, there is little evidence—and little reason to suspect—that *A. afarensis* departed from a Pan-like pace of life-history (e.g., Dean et al., 2001; Dean, 2006).” (Kimbel & Delezene 2009).

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