The human diet today is very different than the diets of other primates, implying major changes following the split of the human and chimpanzee/bonobo lineages about 6 million years ago. For example, at various timepoints our ancestors began consistently eating meat, cooking food with fire, and consuming products from domesticated plants and animals. Such dietary shifts are important to study because they were likely associated with important cultural and biological changes like tool use and increased brain size. However, the timing of some of these dietary shifts is extremely difficult to study with only archeological and fossil data, leading to uncertainty. In this article, we discuss how studies of human tapeworm parasites can help. Tapeworms could only have been acquired once meat was being consistently consumed and then may have later adapted to heat stress from human cooking.
HUMAN DIETARY SHIFTS: BIOLOGICAL AND CULTURAL EVOLUTION

What can studying the diets of our ancient ancestors tell us about human evolution and who we are today? Today, most humans are omnivores, meaning we eat many different types of food, including fruits, grains, nuts, vegetables, tubers (for example, potatoes), meats, and other animal products. The foods we enjoy and can digest today reflect ∼6 million years of hominin biological and cultural evolution. Some past cultural developments, such as tools for hunting, collecting, or processing foods, allowed our ancestors to begin eating new types of foods. At some point our ancestors learned to cook with fire, which softened food for easier chewing and digestion. Past dietary shifts may even have led to the growth and maintenance of our greatly enlarged (and energetically expensive) brains—the human brain requires the consistent consumption of highly nutritious foods. Also, modern human teeth and jaw muscles are smaller than those of our ancestors, possibly because it became much easier to chew food after cooking began.

USING THE ARCHAEOLOGICAL RECORD TO STUDY DIETARY SHIFTS

Some of our past dietary shifts are better understood than others. For example, from 6 million to 12,000 years ago, all humans and our hominin ancestors were hunter-gatherers, not farmers. We know that the agricultural revolution began ∼12,000 years ago. Agriculture is the domestication of plants and animals, or the purposeful breeding of these species by humans for the selection of desirable traits, such as larger fruit size in plants and friendly behavior in animals. The dietary shift from hunting and gathering to farming led to major changes in human lifestyles and cultures, including the development of towns and cities and greater numbers of people. These changes are well-documented in the archaeological record.

Evidence of dietary shifts prior to the agricultural revolution is more difficult to find in the archaeological record (Figure 1A). There were fewer individuals alive, and those people were not living in permanent towns or cities. These early shifts also occurred perhaps millions of years ago, so the evidence has had more time to degrade. Still, we have made some exciting progress in the reconstruction of this ancient history.

MEAT

We did not always consume meat to the extent that we do today. Very few non-human primates have any meat at all in their diets. Our closest
(A) Dietary transitions over the course of hominin evolution. The timing of clear vs. uncertain archaeological and fossil record evidence is shown for the development of stone tools, consistent meat-eating behavior, cooking with fire, and agriculture. For example, while there is clear evidence that hominins could control fire for cooking dated to around 800,000 years ago, some scientists hypothesize that this behavior had started much earlier, and at least by the time at which hominin brain sizes started increasing rapidly. (B) Average hominin brain size based on fossil skull measurements. Substantial increases in brain size began at around two million years ago (Image Credit: Shutterstock).

Primates, like modern humans, can eat meat, but not nearly as much as many modern humans. Meat may have been an especially attractive source of food for hominins because it provides a dense source of protein, iron, and other nutrients critical for growth, development, and body maintenance. As our ancestors ate more meat, the effects of this dietary transition may have been substantial. Some researchers hypothesize that eating more meat may have contributed to the enlarged human brain, enhanced cooperation and communication, and advances in stone tool technologies [1].

The domestication of livestock helped provide humans with a steady supply of meat and other animal products like milk, wool, and skins. However, our ancestors were already consuming meat long before the agricultural revolution [1]. Microscopic evidence of ancient cutmarks, possibly made by stone tools, on the fossilized bones of large wild mammals in Africa dating to ~3.4 and 2.5 million years ago suggests that early hominins butchered animals and ate meat [1]. More butchered animal remains were recovered from fossil deposits dating to about 2.0 million and 780,000 years ago. Because the fossil record is imperfect, we still cannot be certain about the origins of meat-eating behavior.

**COOKING**

Humans are the only species in the world that cooks food with controlled fire. Most researchers believe that at least some hominins were cooking with fire by about 790,000 years ago [1], but the archaeological record of this behavior may extend to as early as...
1.5 million years ago [2]. Interestingly, there are other scientists who infer that hominin cooking behavior must have originated by about 2 million years ago. This logic is based on the major nutritional benefits of cooking food. In particular, the process of cooking breaks down and softens food, making it easier for our bodies to digest, thereby providing more energy. Cooking also allows us to eat a wider variety of foods and acts as a brief food preservative. The hypothesis is that this cultural practice would have been critical to fuel development and maintenance of enlarged hominin brains, which began to evolve about 1.9 million years ago [3] (Figure 1B). Also, at around the same time, hominin tooth sizes began to decrease [4], perhaps because larger teeth became unnecessary for chewing softened foods.

Scientific knowledge develops through a repeated process of developing and testing hypotheses with different methods. As this process unfolds, it is not uncommon for researchers to disagree—this is especially true when trying to reconstruct patterns of behavior from the distant past. However, disagreement can be healthy if it leads to new ideas to explore and test. How could scientists settle the dispute about when hominin cooking behavior began?

**TAPEWORMS**

Amazingly, your body contains so much more than human cells. For example, trillions of bacteria live within and on your body, and many of them perform important digestive, immune, or other functions. Humans are also host to many parasitic organisms. Human parasites have adapted to the environments in our bodies and to our cultural practices. Thus, we can study the evolutionary histories of human parasites to help us learn about human biological and cultural evolution [5]. Such studies add to what we learn from studying living humans and the fossil and archaeological records.

Human tapeworms may be especially informative for studying our past dietary shifts to consistent meat eating and cooking food with fire. Tapeworms have a complex lifecycle involving two host species (Figure 2B). Adult tapeworms live in the intestines of carnivores or meat-eating omnivores. Worm segments containing thousands of eggs are released into the ground with the carnivores’ feces. Then, an herbivore, such as a cow, ingests those tapeworm eggs while feeding on grass or plants. The eggs migrate through the herbivore’s body and become cysts in muscle and other tissues. The tapeworm lifecycle is completed when a different individual from the same carnivore species eats those infected tissues; the cysts then develop into new adult tapeworms upon reaching the carnivore’s intestines.

Humans are parasitized by three different species of tapeworms: *Taenia solium*, *Taenia saginata*, and *Taenia asiatica*. How and when did our ancestors first acquire tapeworms? Based on their physical
The ancient acquisition of our tapeworms and the lifecycle of present-day human tapeworms. (A) It is hypothesized that our hominin ancestors acquired tapeworms by eating herbivore meat infected with the cysts of hyena and lion tapeworms. This occurred long before the agricultural revolution. (B) Life cycle of present-day human Taenia tapeworms. Today, the muscle tissues of domesticated cattle and pigs can become infected with tapeworm cysts. If we consume under-cooked, infected meat, we can develop a tapeworm infection, leading to continuation of the tapeworm lifecycle (Illustrations by Katharine Thompson).

similarities with lion and hyena tapeworms [6], we may have first acquired these parasites long ago, after consuming antelope meat that was infected with lion and hyena tapeworm cysts (Figure 2A). The transfer of our tapeworms to pigs and cattle as the herbivore hosts would have occurred much more recently, sometime after the domestication of these species. If this hypothesis is correct, then learning when humans initially acquired tapeworms would help us to understand the origins of our consistent meat-eating behavior. Scientists could study this by comparing the genomes of the humans and non-human tapeworms to count the number of genetic differences, which accumulate more or less steadily over time.

Once our ancestors acquired tapeworms, these parasites likely started adapting to the overall human environment. Human food-cooking behavior would have been a big environmental challenge for our tapeworms. While thoroughly cooking meat completely kills tapeworm cysts, if parts of the meat are not fully cooked, some tapeworm cysts can survive. This provides an opportunity for individual tapeworms that are more resistant to higher temperatures. Specifically, if genetic mutations helped some human tapeworm individuals survive heat stress better than others then, over time, our tapeworm species could have evolved to become more heat resistant. A recent study has in fact shown that certain genes that help species deal with heat are more prevalent in the *T. solium* genome than in the genomes of three other non-human tapeworm species [7].

**CONCLUSION**

The dietary transitions to meat eating and food cooking were critical events in human evolutionary history that led to significant changes in our biology and culture. Evidence of these behaviors in the fossil and archaeological records is scarce. However, our understanding of these dietary transitions can be aided by studying the co-evolutionary history of humans and tapeworms. Importantly, *Taenia* tapeworms are only three of the more than 400 different parasite species that infect
humans [5]. Just as our tapeworms hold clues about past dietary shifts, any of our other parasites could likewise be studied to help us learn about different aspects of human evolutionary history.

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YOUNG REVIEWERS

CATHERINE, AGE: 15
I love music and singing. I play the violin and guitar and I also enjoy writing! I am part of a highland dance troupe and volunteer with children at local kids clubs and guides. I enjoy attending youth events at my church and doing fitness. I hoped that by reviewing these articles I could learn about new and interesting stuff!

JOSHUA, AGE: 15
I have been very interested in science from a young age and am fascinated by the wonders of the world. I like to know as much as I can about everything and to be honest I am a bit of a nerd! I am interested in biology and chemistry and play rugby for my school.

MEGAN, AGE: 15
Hi, I am Megan, my hobbies include musical theater, baking, and surfing (only during summer though!). I got involved with Frontiers for Young Minds as I really want to learn more about science and the world around me. I thought reading these articles would be a good start!

SILAS, AGE: 10
My name is Silas. My favorite color is blue. My favorite food is carbonara. I like to draw, build with LEGOs, and do stop-motion. I have a lengthy neck, a long nose, average eyes, dirty glasses, and a lot of baby teeth. My favorite day of the week is Thursday. About a month and a half ago, I crashed my bike and because of that, there was a crack in my skull, but it is gone now. I hope that we can end this pandemic so we can visit our friends and family.

AUTHORS

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I am a Ph.D. student in Biology at Pennsylvania State University. I previously graduated from Hunter College City University of New York (CUNY) with both bachelor’s (2016) and master’s (2019) degrees in Anthropology. Through my studies and research experiences I became interested in human evolution, parasite biology, and genomics—and I have found ways to do research on multiple or even all three of these topics simultaneously! At CUNY, my research focused on understanding human evolution through computational/bioinformatic methods. Now at Penn State, I am studying how the evolutionary biology of human tapeworm parasites can inform our understandings of human adaptation, behavior, and culture.

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I am a professor at the Instituto de Ciencias Neurológicas and the Universidad Peruana Cayetano Heredia in Lima, Peru. I previously graduated in Medicine from the Universidad Peruana Cayetano Heredia and obtained my Ph.D. in International Health (Disease Prevention and Control) from the Johns Hopkins University School of Public Health. I work in Peru as part of a large group devoted to the study of the
pork tapeworm *Taenia solium*, looking for better diagnostics, better treatments, and hopefully a way to control this infection in the rural areas where it is transmitted from humans to pigs and *vice versa*. In most of the world, larvae of *T. solium* in the human brain are the cause of approximately one third of epilepsy cases; thus it is important to improve the management of *T. solium* infections and try to eliminate its transmission.

**GEORGE H. PERRY**

I am an associate professor of Anthropology and Biology and chair of the Bioinformatics and Genomics graduate program at Pennsylvania State University. I previously obtained my Ph.D. in Anthropology from Arizona State University. I lead a research group that is interested in human evolution, the impacts of human behavior on non-human species, and human evolutionary medicine—or how our evolutionary history impacts our health today. Some of our research has included the study of ancient DNA! We have a special ultra-clean lab in which we carefully extract the very tiny amounts of DNA that can sometimes be preserved in bones and teeth for many thousands of years. Our research involves partnerships with scientists and study participants all over the world, especially in Madagascar, Uganda, and Peru. We have also hosted visiting students from Madagascar and Peru in our lab at Penn State. *ghp3@psu.edu*