Received: 22 July 2020 | Revised: 7 December 2020 | Accepted: 19 January 2021
DOI: 10.1002/ajpa.24247

YEARBOOK OF PHYSICAL ANTHROPOLOGY ARTICLE

Yearbook of PHYSICAL ANTHROPOLOGY
WILEY

The evolution of the human trophic level during the Pleistocene

Miki Ben-Dor[1] | **Raphael Sirtoli**[2] | **Ran Barkai**[1]

[1]Department of Archaeology, Tel Aviv University, Tel Aviv, Israel
[2]Health Sciences, University of Minho, Braga, Portugal

Correspondence
Miki Ben-Dor, Department of Archaeology, Tel Aviv University, P.O.B 39040 Tel Aviv, Israel.
Email: bendor.michael@gmail.com

Abstract

The human trophic level (HTL) during the Pleistocene and its degree of variability serve, explicitly or tacitly, as the basis of many explanations for human evolution, behavior, and culture. Previous attempts to reconstruct the HTL have relied heavily on an analogy with recent hunter-gatherer groups' diets. In addition to technological differences, recent findings of substantial ecological differences between the Pleistocene and the Anthropocene cast doubt regarding that analogy's validity. Surprisingly little systematic evolution-guided evidence served to reconstruct HTL. Here, we reconstruct the HTL during the Pleistocene by reviewing evidence for the impact of the HTL on the biological, ecological, and behavioral systems derived from various existing studies. We adapt a paleobiological and paleoecological approach, including evidence from human physiology and genetics, archaeology, paleontology, and zoology, and identified 25 sources of evidence in total. The evidence shows that the trophic level of the *Homo* lineage that most probably led to modern humans evolved from a low base to a high, carnivorous position during the Pleistocene, beginning with *Homo habilis* and peaking in *Homo erectus*. A reversal of that trend appears in the Upper Paleolithic, strengthening in the Mesolithic/Epipaleolithic and Neolithic, and culminating with the advent of agriculture. We conclude that it is possible to reach a credible reconstruction of the HTL without relying on a simple analogy with recent hunter-gatherers' diets. The memory of an adaptation to a trophic level that is embedded in modern humans' biology in the form of genetics, metabolism, and morphology is a fruitful line of investigation of past HTLs, whose potential we have only started to explore.

KEYWORDS
carnivore, diet, ethnography, paleobiology, paleolithic

1 | INTRODUCTION

“The first task of the prehistorian must be to decide which trophic level the population he is studying occupied” (Wilkinson, 2014, p. 544).

Despite Wilkinson's advice, few researchers referred to past human food consumption in terms of a “trophic level.” This tendency may stem from the perception of humans as the ultimate omnivore, generalist, flexible creatures, capable of adapting their trophic level at short notice to meet variable local ecological conditions. Some even consider acquiring these capabilities as the core of human evolution, including increased brain size (Potts, 1998; R. W. Wrangham et al., 1999).

By seeking a “trophic level,” we examine the possibility that unlike 20th-century hunter-gatherers (HG), Paleolithic humans may not have been as flexible in the selection of plant or animal-sourced foods during the Pleistocene as one would infer from an examination of the ethnographic record.

Perception of humans' dietary flexibility regarding plant and animal-sourced foods during the Pleistocene (2,580,000–11,700 years ago) receives much support from analogy with 20th century HG's varied diets. The difference in preservation potential between plants and animals in archaeological assemblages has led to the wide use of ethnography in the reconstruction of Paleolithic diets (Cordain et al., 2000; Crittenden & Schnorr, 2017; Eaton & Konner, 1985; Konner & Eaton, 2010; Kuipers et al., 2012; Kuipers et al., 2010; Lee, 1968; F. W. Marlowe, 2005; Stahl et al., 1984; Ströhle & Hahn, 2011). All of the reconstructions present a picture of HG as flexible in their trophic level, depending largely on local ecologies. However, the varied diets of 20th century HG may result from post-Paleolithic technological and physiological adaptations to Anthropocene ecological conditions that are non-analogous to the conditions that humans experienced during most of the Pleistocene. In fact, with a markedly lower abundance of megafauna and with technological features like the use of dogs, bows and arrows, iron, and contact with neighboring herders and farmers, one would expect 20th century HG to be more analogous in terms of dietary patterns to their probable ancestors of the terminal and post-Paleolithic humans rather than to Lower, Middle and even Early Upper Paleolithic humans (Ben-Dor & Barkai, 2020a; Faith et al., 2019).

The human trophic level (HTL) and its degree of variability during the Pleistocene are the basis, explicitly or tacitly, of many explanations regarding human evolution, behavior, and culture (Aiello & Wheeler, 1995; Bramble & Lieberman, 2004; Domínguez-Rodrigo & Pickering, 2017; Hawkes & Coxworth, 2013; Kaplan et al., 2007; Munro et al., 2004; Potts, 1998; M. C. Stiner, 2002; Ungar et al., 2006; R. W. Wrangham et al., 1999). For example, competing explanations for humans' extended longevity, the "grandmother hypothesis" (Hawkes & Coxworth, 2013), and "embodied capital hypothesis" (Kaplan et al., 2009), are based on different assumptions of the relative dietary importance of gathered plants versus hunted animal food during human evolution. Potts (1998) assigns the human ability to vary trophic levels in response to climate as critical to human evolution. HTL estimates also support hypotheses about health-promoting, evolutionarily compliant, contemporary diets (Eaton & Konner, 1985).

A related question is whether humans evolved toward specialization (stenotopy) or generalization (eurytopy) (Wood & Strait, 2004). Some have hypothesized that human survival and wide dispersal result from evolved dietary flexibility, that is, generalization (Potts, 1998; Ungar et al., 2006), while others (Arcadi, 2006; Vrba, 1980) attribute wide dispersal to carnivory.

Humans have inarguably always been omnivores, feeding on more than one trophic level. However, omnivory in mammals is disassociated with dietary variability in terms of animal–plant food selection ratios. Omnivores exist on a wide range of trophic levels and have variable degrees of specialization (Johnston et al., 2011; Lefcheck et al., 2013; Pineda-Munoz & Alroy, 2014). Analysis of a large ($N = 139$) dataset of mammals' trophic levels (Pineda-Munoz & Alroy, 2014) shows that some 80% of the mammals in the dataset are omnivores, but most of the omnivores (75%) consume more than 70% of their food from either plants or animals, leaving only 20% of the mammals in the dataset to be omnivores-generalists. Interestingly, while all the 16 primates in the dataset are omnivores, 15 of the 16 are specialists. Bioenergetic and physiological constraints may limit the flexibility of omnivores. For example, both chimpanzees and wolves are technically omnivores yet are ill-adapted to high flexibility in their food sources. We intend to examine some of these constraints in humans to assert their impact on the human's trophic level, specialization, and dietary flexibility during the Pleistocene.

Little systematic evolution-guided reconstruction of HTL has been published to date. Henneberg et al. (1998) cited the similarity of the human gut to that of carnivores, the preferential absorption of haem rather than iron of plant origins, and the exclusive use of humans as a carnivore host by the *Taenia saginata*, a member of the *Taeniidea* family of carnivores' parasites, as supporting *Homo sapiens*' adaptation to meat-eating. Mann (2000) Pointed to gut structure and acidity, insulin resistance, and high diet quality as evidence of physiological adaptation to consuming lean meat during the Paleolithic. Hancock et al. (2010) explored the association of humans' specific genes with diet, subsistence, and ecoregions, seeking adaptations in recent populations. A notable evolution-based analysis of the degree of carnivory in early humans was performed by Foley (2001, p. 327). He composed a list of behavioral and physiological changes that would have been expected to occur in humans had they adopted carnivory. Foley was mainly interested in the initial shift to carnivory and found that *Homo ergaster/erectus* comply with many of the predicted changes, concluding that "…the lines of evidence and reasoning put forward here strongly suggest that meat-eating has played a significant role in the evolution of *Homo*, not just *Homo sapiens*."

Through natural selection, physiological adaptation to a specific, broader, or narrower food niche is the primary cause of observed biological diversity (Darwin, 1859). Attempting to mitigate the dominance of the analogy with 20th century HG ("the tyranny of ethnography" in the words of Lieberman et al., 2007) in reconstructing Paleolithic diets, we searched the literature on human metabolism and genetics, body morphology, dental morphology and pathology, and life history for signs of adaptations to HTLs, or evolution toward dietary generalization or specialization. We also reviewed relevant archaeological, paleontological, and zoological literature to identify changing patterns in fauna, flora, lithic industries, stable isotopes, and other geoarchaeological data, as well as human behavioral adaptations to carnivory or omnivory, that reflected past HTLs.

We concentrate on the lineage leading to *H. sapiens* because a large part of our evidence comes from the biology of *H. sapiens*. There is little information about species like *rudolfensis*, *ergaster*, *heidlebergensis*, and possibly *antecessor*, which may have belonged to the *H. sapiens* lineage. We thus focused our attention on *H. erectus* (sensu *lato*) and *H. sapiens*, as many relevant sources refer mostly to these species. Because we relied on *H. sapiens*' biology, we do not deal and do not make any claims regarding the trophic level of other *Homo* species that do not seem to have belonged to the lineage leading to *H. sapiens* like *floresiensis*, *naledi*, *neanderthalensis*, Denisovan, and *luzonensis*.

Evolution-based information provides a longer-term view of HTL than that based on 20th century HG, or the ever-localized and partial data from archaeological sites. This view should, in turn, be more relevant to explain profound evolutionary physiological and behavioral phenomena in human prehistory.

Below we discuss in some detail each piece of evidence. A summary for quick reference can be found in Table 2 at the beginning of the discussion section.

2 | PHYSIOLOGICAL EVIDENCE

2.1 | Bioenergetics

Compared with other primates, humans have a higher energy requirement for a given fat-free mass (Pontzer et al., 2016), and thus faced intense selective pressure to efficiently acquire adequate and consistent energy, especially to reliably energize the brain (Navarrete et al., 2011). Additionally, due to tool acquisition, prolonged child care, and education, humans need more time free from food acquisition than other animals (Foley & Elton, 1998).

Animal-sourced calories are generally acquired more efficiently; carnivores, therefore, spend less time feeding than similar-sized herbivores (Shipman & Walker, 1989). For example, baboons (*Papio cynocephalus*) devote almost all their daylight hours to feeding (Milton, 1987, p. 103) while adult Ache and Hadza men spend only a third of the day in food acquisition, preparation, and feeding (Hawkes et al., 1997; Hill et al., 1985).

Acquiring and consuming medium size animals, at a return rate in the range of tens of thousands of calories per hour, is an order of magnitude more time-efficient than plant-gathering (Kelly, 2013, table 3-3, 3-4). In other words, the price differences in “the supermarket of nature” were likely opposite to the price differences in the supermarkets of today. In nature, for humans, plant-sourced calories cost 10 times the price of meat if it is available. Given limited time and energetic budgets, such a difference in energetic returns leaves little room for flexibility (also referred to as plasticity) in the selection of the two dietary components. Nonetheless, a background consumption of plants and smaller prey is expected when women gather and do not participate in hunts (see Plants section for discussion). Also, differences in the relative availability of plants and animals affect the actual consumption.

In particular, large animals are the highest-ranking food according to ethnographic data (Broughton et al., 2011). According to classic optimal foraging theory, an animal would specialize in the highest-ranking type if the encounter rate is high enough (Futuyma & Moreno, 1988). Applied to humans, it means that they should have specialized in large prey if the encounter rates were high enough. Moreover, seasonal fluctuations in many plant species' availability may hinder their reliability as food for a significant portion of the year. In contrast, animals are always available, although with fluctuating fat content.

Carnivory could have, therefore, been a more time-efficient and reliable caloric source. The relative abundance of large prey, and thus encounter rate, relative to smaller prey and plants, was probably higher during most of the Pleistocene, at least before the Late Quaternary extinction of megafauna (see the Ethnography, Paleontology and Zooarchaeology sections and Ben-Dor and Barkai (2020a) for references).

2.2 | Diet quality

In relation to body size, brain size is strongly associated with dietary energetic density in primates and humans (Aiello & Wheeler, 1995; DeCasien et al., 2017; Leonard et al., 2007). Human brains are over three times larger than other primates' brains, and as such, human dietary energetic density should be very high. The most energy-dense macronutrient is fat (9.4 kcals/g), compared with protein (4.7 kcals/g) and carbohydrates (3.7 kcals/g) (Hall et al., 2015). Moreover, plant proteins and carbohydrates typically contain anti-nutrients, which function in plant growth and defense (Herms and Mattson, 1992; Stahl et al., 1984). These anti-nutrients, such as lectins or phytate, appear in complex cellular plant matrix and fibers and limit full energetic utilization and nutrient absorption by humans (Hervik & Svihus, 2019; Schnorr et al., 2015). The most generous estimates from in vitro, human, and animal data suggest that well below 10% of total daily caloric needs can be met from fiber fermentation, and most likely below 4% (Hervik & Svihus, 2019; Høverstad, 1986; Topping & Clifton, 2001). Hence, the protein and fat mixture in animals would probably have provided higher energetic density, and therefore dietary quality.

Brain size declined during the terminal Pleistocene and subsequent Holocene (Hawks, 2011; Henneberg, 1988), indicating a possible decline in diet quality (increase in the plant component) at the end of the Pleistocene.

2.3 | Higher fat reserves

Humans have much higher fat reserves than chimpanzees, our closest relatives (Zihlman & Bolter, 2015). Carrying additional fat has energy costs and reduces human speed in chasing prey or escaping predators (Pond, 1978). Most carnivores and herbivores do not have a high body fat percentage as, unlike humans, they rely on speed for predation or evasion (Owen-Smith, 2002, p. 143). Present-day HG (the Hadza) were found to have sufficient fat reserves for men and women to fast for three and six weeks, respectively (Pontzer et al., 2015).

Humans seem very well adapted to lengthy fasting when fat provides their major portion of calories (Cahill Jr & Owen, 1968). Rapid entry to ketosis (when the liver synthesizes ketones from fat) allows ketone bodies to replace glucose as an energy source in most organs, including the brain. During fasting, ketosis allows muscle-sparing by substantially decreasing the need for gluconeogenesis (the synthesis of glucose from protein), and humans enter ketosis relatively quickly.

Dogs share similar digestive physiology and animal-rich dietary patterns with humans but do not enter ketosis quickly (Crandall, 1941). Indeed, dogs typically require a diet supplemented by medium-chain triglyceride to increase blood ketones to derive therapeutic benefit, but even then, they do not achieve deep physiological ketosis like humans (Packer et al., 2016). Cahill Jr (2006, p. 11) summarizes the evolutionary implications of humans' outstanding adaptation to ketosis: "brain use of βOHB [a ketone body], by displacing glucose as its major fuel, has allowed man to survive lengthy periods of starvation. But more importantly, it has permitted the brain to become the most significant component in human evolution." Rapid entry into ketosis has been found in the brown capuchin monkey (Friedemann, 1926), suggesting that this adaptation to fasting may have already existed in early *Homo*.

Researchers who argue against a massive reliance on acquiring large animals during the Pleistocene mention their relative scarcity (Hawkes, 2016). However, besides the fact that they were more prevalent during the Pleistocene (Hempson et al., 2015), the ability to store large fat reserves and to more easily endure fasting may represent an adaptation, enabling humans to endure extended periods between acquiring the less frequently encountered large animals.

2.4 | Genetic and metabolic adaptation to high-fat diet

Swain-Lenz et al. (2019) performed comparative analyses of the adipose chromatin landscape in humans, chimpanzees, and rhesus macaques, concluding that their findings reflect differences in the adapted diets of humans and chimpanzees. They (p. 2004) write: "Taken together, these results suggest that humans shut down regions of the genome to accommodate a high-fat diet while chimpanzees open regions of the genome to accommodate a high sugar diet."

Speth (1989) hypothesized that humans eating an animal-based diet would display an obligatory requirement for significant fat amounts because they are limited in the amount of protein they can metabolize to energy. Dietary fat is also a macronutrient with priority storage within subcutaneous fat stores; this agrees with assumptions of adaptation to higher fat consumption.

The ability to finely tune fat-burning is a prominent feature of human metabolism (Akkaoui et al., 2009; Mattson et al., 2018). The lipase enzyme plays a dominant role in fat storage and metabolism. Comparing the pace of genetic changes between humans and other primates, Vining and Nunn (2016) found that lipase production underwent substantial evolution in humans.

Weyer and Pääbo (2016) found some indication of differences in both the regulation and activity of pancreatic lipase in modern humans compared with Neandertals and Denisovans. Given that Neandertals probably consumed a diet higher in meat and fat than anatomically modern humans, the latter was possibly adapting to lower fat consumption. However, these changes are also found in present-day humans, but there is no indication of how early they occurred in *H. sapiens* evolution. They could have resulted from a shift to a diet higher in plants in the period leading up to the adoption of agriculture, in which a marked increase in genetic changes is evident (Hawks et al., 2007). Additionally, storing larger fat reserves is a derived trait in humans, regardless of nutritional source (Pontzer, 2015). Thus, changes in fat metabolization capacity may, in part, be associated with metabolizing stored fat.

In humans, eating predominantly animal foods, especially fatty animal foods, promote nutritional ketosis. This pattern provides generous amounts of bioavailable essential micronutrients with crucial roles in encephalization, such as zinc, heme iron, vitamin B12, and long-chain omega-3 and 6 fatty acids (DHA and arachidonic acid, respectively) (Cunnane & Crawford, 2003). Infants' brains meet all of their cholesterol needs in situ, with 30% to 70% of the required carbons being supplied by ketone bodies (Cunnane et al., 1999). Recently, nutritional ketosis has gained popularity as a possible therapeutic tool in many pathologies, such as diabetes, Alzheimer's disease, and cancer (Ludwig, 2019).

2.5 | Omega 3 oils metabolism

Another aspect of fat metabolism is the hypothesis that the early human brain's enlargement was made possible through acquiring aquatic foods. Presumably, these foods were the only source of high amounts of docosahexaenoic acid (a long-chain omega-3 fatty acid; DHA) found in the expanding human brain (Crawford, 2010; Cunnane & Crawford, 2014; Kyriacou et al., 2016). In contrast, Cordain et al. (2002) argue that terrestrial animal organs contained sufficient DHA amounts for brain growth. Furthermore, Speth (2010, p. 135) proposed that humans biosynthesized sufficient DHA de novo from precursors. This last argument is compatible with the present existence of several billion people, including some HG, who have never eaten aquatic-sourced food, yet they and their offspring can grow and support much larger brains than early humans. A large part of this population does not consume high proportions of animal-derived food and practices multigenerational vegetarianism without cognitive decline (Crozier et al., 2019). An increased need for DHA to sustain larger brains cannot even support claims for a terrestrial animal-based diet in early humans. Stable isotope analysis shows that at least some Neandertals did not consume much, if any, aquatic dietary resources (M. Richards & Trinkaus, 2009), though their brains were at least as large as that of modern humans.

Mathias et al. (2012) identified a genetic change that occurred in African humans about 85 thousand years ago (Kya) in the fatty acid desaturase (FADS) family of genes, showing a marginal increase in efficiency of converting plant-derived omega-3 fatty acids into DHA. This change may signify an increase in dietary plant components at that time in Africa. In Europe, however, a similar change took place only with the arrival of the Neolithic (Ye et al., 2017), suggesting that a plant-based diet was uncommon beforehand. Furthermore, tracer studies show modern adult humans can only convert <5% of the inactive plant-derived omega-3 polyunsaturated fatty acid alpha-linolenic acid (18:3Ω3, ALA) into the animal-derived active version docosahexaenoic acid (20:6Ω3, DHA) (Plourde & Cunnane, 2007).

Ye et al. (2017) found that positive genetic selection on FADS in Europe took the opposite direction in HG groups in the period leading up to the Neolithic, possibly signifying increased reliance on aquatic foods. The pre-Neolithic surge in aquatic foods exploitation is also supported by stable isotope analysis (see the section Isotopes and trace elements).

2.6 | Late genetic adaptation to the consumption of underground storage organs

A recent adaptation to a high-starch diet may be postulated from a study by Hancock et al. (2010, table 4), which showed that populations presently dependent on roots and tubers (underground storage organs [USOs]) are enriched in single nucleotide polymorphisms (SNPs) associated with starch and sucrose metabolism and folate synthesis, presumably compensating for their poor folic acid content. Another SNP in these populations may be involved in detoxifying plant glycosides, such as those in USOs (Graaf et al., 2001). Some researchers consider USOs ideal candidates for significant plant consumption by early humans (Dominy, 2012; B. L. Hardy, 2010; K. Hardy et al., 2016; Henry et al., 2014; R.W. Wrangham et al., 1999). If genetic adaptations to USOs consumption were rather recent, it suggests that USOs did not previously comprise a large dietary component.

2.7 | Stomach acidity

Beasley et al. (2015) emphasize the role of stomach acidity in protection against pathogens. They found that carnivore stomachs (average pH, 2.2), are more acidic than in omnivores (average pH, 2.9), but less acidic than obligate scavengers (average pH, 1.3). Human studies on gastric pH have consistently found a fasted pH value <2 (Dressman et al., 1990; Russell et al., 1993). According to Beasley et al. (2015), human stomachs have a high acidity level (pH, 1.5), lying between obligate and facultative scavengers. Producing acidity, and retaining stomach walls to contain it, is energetically expensive. Therefore it would presumably only evolve if pathogen levels in human diets were sufficiently high. The authors surmise that humans were more of a scavenger than previously thought. However, we should consider that the carnivorous activity of humans involved transporting meat to a central location (Isaac, 1978) and consuming it over several days or even weeks. Large animals, such as elephants and bison, presumably the preferred prey, and even smaller animals such as zebra, provide enough calories to sustain a 25-member HG group from days to weeks (Ben-Dor et al., 2011; Ben-Dor & Barkai, 2020b; Guil-Guerrero et al., 2018). Moreover, drying, fermentation, and deliberate putrefaction of meat and fat are commonly practiced among populations that rely on hunting for a large portion of their diet (Speth, 2017), and the pathogen load may consequently increase to a level encountered by scavengers.

2.8 | Insulin resistance

Another hypothesis claiming a human genetic predisposition to a carnivorous, low-carbohydrate diet is the “Carnivore Connection.” It postulates that humans, like carnivores, have a low physiological (non-pathological) insulin sensitivity. It allows prioritizing of glucose toward tissues like the central nervous system, erythrocytes, and testes that entirely or significantly depend on glucose, rather than muscles which can rely on fatty acids and ketosis instead (Brand-Miller et al., 2011); this sensitivity is similarly lower in carnivores (Schermerhorn, 2013). Brand-Miller et al. (2011) speculate that physiological insulin resistance allows humans on a low-carbohydrate diet to conserve blood glucose for the energy-hungry brain. The genetic manifestation of insulin resistance is complex and difficult to pinpoint to a limited number of genes (Moltke et al., 2014). However, Ségurel et al. (2013) found a significantly higher insulin resistance (low sensitivity) in a Central Asian population (Kirghiz) of historical herders, compared with a population of past farmers (Tajiks), despite both groups consuming similar diets. Their findings indicate a genetic predisposition to high physiological insulin resistance levels among groups consuming mainly animal-sourced foods. Additionally, a significant difference in the prevalence of this resistance exists between groups with long-term exposure to agriculture and those that do not, such as Australian aborigines, who have higher resistance. If higher physiological insulin resistance is indeed ancestral, its past endurance suggests that high carbohydrate (starch, sugar) consumption was not prevalent.

2.9 | Gut morphology

Most natural plant food items contain significant amounts of fiber (R. W. Wrangham et al., 1998), and most plant-eaters extract much of their energy from fiber fermentation by gut bacteria (McNeil, 1984), which occurs in the colon in primates. For example, a gorilla extracts some 60% of its energy from fiber (Popovich et al., 1997). The fruits that chimps consume are also very fibrous (R. W. Wrangham et al., 1998). The human colon is 77% smaller, and the small intestine is 64% longer than in chimpanzees, relative to chimpanzee body size (Aiello & Wheeler, 1995; Calculated from Milton, 1987, table 3.2). Because of the smaller colon, humans can only meet less than 10% of total caloric needs by fermenting fiber, with the most rigorous measures suggesting less than 4% (Hervik & Svihus, 2019; Høverstad, 1986; Topping & Clifton, 2001). A 77% reduction in human colon size points to a marked decline in the ability to extract the full energetic potential from many plant foods. The elongated small intestine is where sugars, proteins, and fats are absorbed. Sugars are absorbed faster in the small intestine than proteins and fats (Caspary, 1992; Johansson, 1974). Thus, increased protein and fat consumption should have placed a higher selective pressure on increasing small intestine length. A long small intestine relative to other gut parts is also a dominant morphological pattern in carnivore guts (Shipman & Walker, 1989, and references therein).

This altered gut composition meets the specialization criteria proposed by Wood and Strait (2004) for adaptations that enable animals but hinder plant acquisition for food.

A marked reduction in chewing apparatus and a genetic change that reduced the jaw muscle bite force had already appeared 2–1.5 million years ago (Mya) (Lucas et al., 2006). A smaller mandibular-dental complex points to a smaller gut (Lucas et al., 2009); therefore, the carnivorous gut structure may have already been present in *H. erectus*.

2.10 | Reduced mastication and the cooking hypothesis

Together with the whole masticatory system, teeth should closely reflect the physical, dietary form because masticatory action is repeated thousands of times each day and is thus under continuous pressure to adjust to efficient dietary processing (Lucas et al., 2009).

One of *Homo*'s main derived features is the reduced relative size of the masticatory apparatus components (Aiello & Wheeler, 1995). This reduction is associated with a substantially decreased chewing duration (approximately 5% of daily human activity, compared with 48% in chimpanzees), starting with *H. erectus* 1.9 Mya (Organ et al., 2011).

The masticatory system size in *H. erectus*, together with reduced feeding duration, is attributed to the increased dietary meat proportion and availability of stone tools (Aiello & Wheeler, 1995; Zink & Lieberman, 2016), high portion of dietary fat (Ben-Dor et al., 2011), or the introduction of cooking early in *Homo* evolution (R. Wrangham, 2017). We consider cooking plants as a possible but less likely explanation for the reduction in mastication since most researchers date the habitual and controlled use of fire to over a million years after the appearance of *H. erectus* (Barkai et al., 2017; Gowlett, 2016; Roebroeks & Villa, 2011; Shahack-Gross et al., 2014; Shimelmitz et al., 2014); but see R. Wrangham (2017). It seems that habitual use of fire appeared with the appearance of post-*H. erectus* species and so can signal increased plant consumption in these species. It should also be noted that although fire was undoubtedly used for cooking plants and meat, a fire has many non-cooking uses for humans (Mallol et al., 2007), including protection from predation, a significant danger in savanna landscapes (Shultz et al., 2012). Also, fire maintenance has bioenergetic costs (Henry, 2017), and in some environments, sufficient wood may not be available to maintain fire (Dibble et al., 2018). While the contribution of cooking to the consumption of plants is not contested, cooking also contributes to the consumption of meat. There is no archaeological indication of a net quantitative contribution of cooking to the HTL. We, however, assume that cooking signals a somewhat higher consumption of plants.

2.11 | Postcranial morphology

Several derived postcranial morphologic phenotypes of humans are interpreted as adaptations to carnivory. Ecologically, the body size is related to trophic strategies. Researchers have attributed the increase in body size in *Homo* to carnivory (Churchill et al., 2012; Foley, 2001; T. Holliday, 2012). A recent body size analysis shows that *H. erectus* evolved larger body size than earlier hominins (S. C. Antón et al., 2014; Grabowski et al., 2015). Simultaneously, larger body size reduces the competitivity in arboreal locomotion and hence in fruit gathering. It is interesting to note that in Africa, humans' body size reached a peak in the Middle Pleistocene, and *H. sapiens* may have been smaller than his predecessors (Churchill et al., 2012). Since carnivore size is correlated with prey size (Gittleman & Harvey, 1982), this development ties well with an apparent decline in prey size at the Middle Stone Age (MSA) in East Africa (Potts et al., 2018). A similar decrease in body size was identified in the Late Upper Paleolithic and Mesolithic (Formicola & Giannecchini, 1999; Frayer, 1981), also with a concomitant decline in prey size following the Late Quaternary Megafauna Extinction (Barnosky et al., 2004).

A series of adaptations to endurance running was already present in *H. erectus*, presumably to enable "persistence hunting" (Bramble & Lieberman, 2004; Hora et al., 2020; Pontzer, 2017). A recent genetic experiment concerning exon deletion activity in the *CMP-Neu5Ac* hydroxylase (*CMAH*) gene in mice led Okerblom et al. (2018) to propose that humans, in whom the deletion was already fixed at 2 Mya, had already acquired higher endurance capabilities at that time. Whether this endurance was used for hunting, scavenging, or another unknown activity early in human evolution is debated (Lieberman et al., 2007; Pickering & Bunn, 2007; Steudel-Numbers & Wall-Scheffler, 2009). Comparing the Early Stone Age sites of Kanjera South and FLK-Zinj, Oliver et al. (2019) suggested that different ecological conditions required different hunting strategies, either cursorial (suitable for persistence hunting), or ambush, which is more appropriate for a woodland-intensive landscape. Some endurance running adaptations may also suggest adaptation to increased mobility in hot weather conditions, as expected from carnivores, given their relatively large home ranges (Gittleman & Harvey, 1982).

Another feature associated with hunting in the early stages of human evolution is an adaptation of the shoulder to a spear-throwing action, already present in *H. erectus* (Churchill & Rhodes, 2009; J. Kuhn, 2015; Roach et al., 2013; Roach & Richmond, 2015). Young et al. (2015) and Feuerriegel et al. (2017) argue that this adaptation came at the expense of a reduced ability to use arboreal niches, meeting the criteria proposed by Wood and Strait (2004) to support compelling morphological evidence of evolution toward carnivorous stenotopy.

2.12 | Adipocyte morphology

Ruminants and carnivores, which absorb very little glucose directly from the gut, have four times as many adipocytes per adipose unit weight than non-ruminants, including primates, which rely on a larger proportion of carbohydrates in their diet (Pond & Mattacks, 1985). The authors hypothesize that this is related to the relative role of insulin in regulating blood glucose levels. Interestingly, omnivorous species of the order Carnivora (bears, badgers, foxes, voles) display more carnivorous patterns than their diet entails. Thus humans might also be expected to display organization closer to their omnivorous phylogenic ancestry. However, humans fall squarely within the carnivore adipocyte morphology pattern of smaller, more numerous cells. Pond and Mattacks (1985, p. 191) summarize their findings as follows: "These figures suggest that the energy metabolism of humans is adapted to a diet in which lipids and proteins rather than carbohydrates, make a major contribution to the energy supply."

2.13 | Age at weaning

Humans have a substantially different life history than other primates (Robson & Wood, 2008), a highly indicative speciation measure. One life history variable in which humans differ significantly from all primates is weaning age. In primates such as orangutans, gorillas, and chimpanzees, weaning age ranges between 4.5 and 7.7 years, but is much lower in humans in HG societies, at 2.5–2.8 years, despite the long infant dependency period (Kennedy, 2005; Robson & Wood, 2008, table 2). Psouni, Janke, and Garwicz (2012, p. 1) found that an early weaning age is strongly associated with carnivory level, stating that their findings "highlight the emergence of carnivory as a process fundamentally determining human evolution." It is interesting, however, that a comparison of early *Homo*, *Australopithecus africanus*, and *Paranthropus robustus* from South Africa reveals a substantially higher weaning age (4 years) in South African early *Homo* (Tacail et al., 2019), so it is unclear when the weaning age shortened.

2.14 | Longevity

Longevity is another life history variable in which humans differ markedly from great apes. While the modal age at death in chimpanzees is 15 years, in 20th century HG, it occurs in the sixth and seventh decades (Gurven & Kaplan, 2007, table 4). There is no argument that longevity extension began with early *Homo*, although disagreement exists regarding the pace of change. Caspari and Lee (2004) argue for an accelerated extension of longevity in *H. sapiens*, while others, such as Hawkes and Coxworth (2013), argue for an earlier extension. Two hypotheses attempt to explain life extension in humans; the disparity lies in different perceptions regarding HTL during evolution. Hawkes and Coxworth (2013) support the "grandmother hypothesis," by which grandmothers' longevity (post-menopausal females) enables sufficient plant food to be collected for infants, whose slower development in comparison with other primates necessitates extended care. The authors (see also Hawkes et al., 2018) base this argument on Hadza dietary patterns, in which gathering by females contributes a large portion of food calories, to demonstrate the marked effect of infant care by grandmothers in releasing their daughters' time for gathering food. As discussed in the Plants section, females may have contributed to hunting as well as gathering. Kaplan et al. (2000) (see also Kaplan et al., 2007) rely on a diet dominated by animal sources, such as in other 20th century HG groups, for example, the Ache. They propose that hunting experience, which fully develops at around 40 years, is crucial to group survival by enabling acquisition of the surplus calories needed to feed less productive, younger group members. The importance of hunting experience presumably caused longevity extension in humans. The problem in comparing the Hadza, with their different ecology, with iron-based material culture as a model for evolutionary dietary patterns is discussed in the Ethnography section. However, it is interesting that even in the Hadza, peak food-acquisition productivity is reached after age 40 in both sexes (F. Marlowe, 2010, fig. 5.11).

In summary, extended human longevity suggests that a need for efficient calorie acquisition to maintain both self and an extended sibling dependency period was a dominant driving force in human evolution. The two hypotheses are not necessarily mutually exclusive.

2.15 | Vitamins

Hockett and Haws (2003) developed a hypothesis that one of the basic tenets of the ancestral human diet was its diversity. They based this on research findings that present-day diets emphasizing diversity increase overall health patterns by lowering infant mortality rates and increasing average life expectancy. Presumably, the wide range of vitamins and minerals associated with diverse diets is advantageous. The relevancy of the initial findings, cited by Hockett and Haws (2003) to the Paleolithic, is questionable, as they relate to modern societies consuming an agricultural, mostly domesticated plant-based diet with declining nutritional value (Davis, 2009). Diversification may, in this case, confer benefit due to the mineral and vitamin accumulation derived from consuming multiple plant types, each of which individually has a narrower range of beneficial contents. Diversity can also refer to portion increases and animal variety in the diet. Kenyan schoolchildren on a high-plant diet receiving meat supplementation showed improved growth, cognitive, and behavioral outcomes (Neumann et al., 2007).

Hockett and Haws (2003, table 1) list the key vitamin content in 100 g of plants compared with 100 g of various animal foods (vitamins C, E, D [cholecalciferol], A [retinol & β-carotene], B1 [thiamin], B2 [riboflavin], B3 [niacin], B6 [pyridoxine or pyridoxal], B9 [folate or folic acid], B12 [cobalamin], and iron [heme & non-heme iron]). Comparison of vitamin density (per 100 calories) between terrestrial mammals and plants shows that, in eight of the ten vitamins, terrestrial mammal food is denser, and in most cases several times denser, than plants. If we consider factors like bioavailability and active nutrients, then animal foods appear even more nutritious (Frossard et al., 2000). This result is unsurprising given that humans are also terrestrial mammals, containing the same chemicals as other terrestrial mammals and requiring mostly the same vitamins.

Plant food is denser in vitamin E and C. It is well known, however, that scurvy did not affect Polar societies despite lower levels of dietary plant components (Draper, 1977; Fediuk, 2000; Thomas, 1927). Western individuals who lived among Polar populations for several years also showed no signs of vitamin shortage (Stefansson, 1960, p. 171). Controlled further monitoring in the United States of two of these individuals, who consumed meat exclusively for a year, revealed no adverse clinical symptoms (McClellan & Du Bois, 1930). According to the glucose–ascorbate antagonism (GAA) hypothesis (Hamel et al., 1986), the structural similarity between glucose and vitamin C means the two molecules compete to enter cells via the same transport system (Wilson, 2005). Thus, higher requirements for vitamin C in western populations may result from higher consumption of carbohydrates and consequently higher blood glucose levels. Two clinical studies comparing diabetic and non-diabetic patients showed, as predicted by the GAA hypothesis, that diabetic patients with higher blood glucose levels have decreased plasma ascorbic acid levels (Cunningham et al., 1991; Fadupin et al., 2007).

Dietary vitamin C requirements can be lowered in multiple ways in the context of very-low-carbohydrate diets high in animal sources, which can affect metabolism such that the oxaloacetate to acetyl-CoA ratio drops below one, stimulating ketogenesis and, in turn, increasing mitochondrial glutathione levels (Jarrett et al., 2008). More glutathione means more enzyme glutathione reductase to recycle dehydroascorbic acid (oxidized vitamin C) into ascorbic acid (reduced vitamin C). Ketogenic diets can also increase uric acid, the major antioxidant in human serum, putatively sparing vitamin C in its antioxidant capacity (Nazarewicz et al., 2007; Sevanian et al., 1985), and conserving it for other tasks. For instance, animal foods also provide generous amounts of carnitine, meaning that less vitamin C is needed to synthesize carnitine (a process to which vitamin C is crucial) (Longo et al., 2016).

Therefore, the evidence does not support the hypothesis of Hockett and Haws (2005). There is little argument that Paleolithic diets were higher in plants than recent Polar diets and thus did include some plant-derived vitamin C. Nevertheless, animal-sourced foods provide essential micronutrients in their active forms that plants do not, such as vitamin A (retinol), vitamin K (K2 menaquinones), vitamin B9 (folate), vitamin B12 (cobalamin), vitamin B6 (pyridoxine), vitamin D (cholecalciferol), iron (heme iron), and omega-3 (EPA and DHA). Animal foods are not only qualitatively but also quantitatively superior to plant foods, as determined by measures of nutrient density.

2.16 | *AMY1* gene

Although starch consumption is evident throughout the Pleistocene (K. Hardy, 2018), its relative importance is difficult to elucidate from the archaeological record. Salivary amylase is an enzyme degrading starch into glucose in preparation for cell energy metabolism, and Vining and Nunn (2016) discerned a significant evolution in amylase-producing genes in *Homo* species but could not determine the temporal dynamics. Initially, a higher number of copies, from 2 to 15, of the salivary amylase-producing gene *AMY1* in modern populations consuming high-starch diets was found (G. Perry et al., 2007). The few Neandertal and Denisovan genetic samples have only two *AMY1* copies (G. H. Perry et al., 2015), similar to chimpanzees, which consume little starch. G. H. Perry et al. (2015) conclude that the common ancestor of Neandertals and *H. sapiens*, some 500–600 Kya, also had only two copies, a conclusion supported by Inchley et al. (2016), who surmised that the appearance of multi-copy *AMY1* genes in *H. sapiens* probably occurred quite early after the split from the common ancestor.

Several studies have hypothesized that people with a low number of *AMY1* copies eating a high-starch diet would suffer from increased rates of obesity and diabetes but failed to find supporting evidence (Atkinson et al., 2018; Des Gachons & Breslin, 2016; Falchi et al., 2014; Fernández & Wiley, 2017; Mejía-Benítez et al., 2015; Yong et al., 2016). Usher et al. (2015) explain that when lower-precision molecular methods are avoided, not even a nominal association between obesity and the copy number of any amylase gene can be observed ($p = 0.7$). In summary, more research is needed to verify the functional role of salivary amylase in starch metabolism and the timing of the appearance of multiple copies of *AMY1*.

3 | ARCHAEOLOGICAL EVIDENCE

3.1 | Plants

Archaeobotanical remains, lithic use-wear, residue analyses on lithic/flint tools, and teeth plaque are often used to elucidate human consumption of specific plant food items at the site level (K. Hardy et al., 2016; Henry et al., 2011; Lemorini et al., 2006; Venditti et al., 2019; Melamed et al., 2016). The acquisition of plants requires little use of stone tools and thus is prone to leave fewer artifacts at archaeological sites (F. Marlowe, 2010). Wooden digging sticks are used in ethnographic contexts to extract tubers and are sometimes found in archaeological contexts (Aranguren et al., 2018; Vincent, 1985), but they also preserve poorly. Despite the poor discovery potential, a review of relevant studies of plant consumption in the Lower and Middle Paleolithic (K. Hardy, 2018, table 1) paints a picture of widespread consumption of a wide range of plants. Unfortunately, similarly to the vast number of studies of bones with cut marks in countless sites, these studies cannot provide quantitative information for evaluating even a localized HTL, let alone a global one.

According to ethnographic data (Kelly, 2013, table 3-3, 3-4), the energetic return on plant gathering is in the order of several hundred to several thousand calories per hour, while the return on medium-size animals is in the tens of thousands of calories; presumably gathering should be minimal. However, humans are unique in their division of labor in that the ethnographic record shows that females and males may target different foods that they eventually share.

Ethnography is a convincing source of evidence for females as plant gatherers. The lower risk of the gathering is compatible with females' role in child care and thus lends credence to this interpretation of the nature of the division of labor in humans. Further, it is proposed, based on ethnographic data, that female's longevity evolved to enable the contribution of gathered plants subsistence by grandmothers beyond their own needs (Hawkes & Coxworth, 2013). However, several scholars have theorized that such division of labor would have been less pronounced or even altogether absent among Paleolithic HG (Haas et al., 2020 and references therein). As discussed in the Ethnography section, the different ecological conditions in the Pleistocene may have also affected the extent to which females gathered plants compared to the Paleolithic period. There is evidence for female hunting in ethnographic and Paleolithic contexts (D. W. Bird et al., 2013; R. B. Bird & Power, 2015; Haas et al., 2020; Khorasani & Lee, 2020; Noss & Hewlett, 2001; Waguespack, 2005). Especially relevant to the Paleolithic is the potential participation of females in large game hunting (Brink, 2008; Haas et al., 2020) in driving large animals to a trap where their movement can be curtailed (Churchill, 1993) or in driving them to expecting male hunters (Waguespack, 2005); methods that provide the opportunity for communal hunting (Lee, 1979, p. 234). Also, females tend to perform more non-subsistence activities in highly carnivorous human groups (Waguespack, 2005). Since the extinction of large animals in the Upper Paleolithic (UP) and the Anthropocene, alternative forms of division of labor may have become less relevant. It may be that we see here what we see in other aspects of ethnographic subsistence analogy, an increase in plant food extraction by females as a result of an adaptation to the decline in prey size and a resultant increase in plant food relative abundance (Ben-Dor & Barkai, 2020a; Waguespack, 2005).

Ancient dental plaque has recently gained attention as a source of dietary information, as it enables the identification of plant particles accumulated in plaque (K. Hardy et al., 2012, 2016, 2017; Henry et al., 2011, 2014; Henry & Piperno, 2008). All studies, including the earliest-studied population of Sima del Elefante (1.2 Mya) (K. Hardy et al., 2017) and the Qesem Cave, Israel (400 Kya) (K. Hardy et al., 2016), identified plant remains in tooth plaque and even evidence for cooked starch (but see García-Granero, 2020).

Out of 31 dental calculus analysis cases listed in K. Hardy et al. (2018, table 1), only four cases did not show starch residues. The assemblage of cases suggests that consumption of plants was common, although one has to take into account that the consumption of starch encourages dental plaque formation (Brown, 1975; Scannapieco et al., 1993) and that we do not know the percentage of teeth that were not sampled because they had no calculus. But even if we had these data, the identification of plants in dental calculus cannot tell us what the relative plant consumption of the individual was. However, we can summarize that the archaeological and ethnographic record shows that plant foods were a frequent component of the Paleolithic diet.

3.2 | Stone tools

Although the study of stone-tools is a cornerstone of prehistoric research, its potential to inform a quantitative value, such as HTL, is frustratingly limited. There is plenty of evidence of stone-tool associations with meat and fat processing (Barkai et al., 2010; Lemorini et al., 2006; Lemorini et al., 2015; Nowell et al., 2016; Solodenko et al., 2015; M. C. Stiner, 2002; Toth & Schick, 2019; Venditti et al., 2019). Recently, however, stone-tool use for plant processing in the early Paleolithic has been detected (Arroyo & de la Torre, 2016; Lemorini et al., 2014). S. L. Kuhn and Stiner (2001) review the increased frequency of stone tools attributable to plant processing toward the end of the Pleistocene, Epipaleolithic, and Pre-Pottery Neolithic Near Eastern sites. Lithic tools such as sickle blades, pounding, and grinding stones specific to plant processing appear late in the Pleistocene, both in Southern Asia (Bar-Yosef, 1989, 2002, 2014) and Europe (S. L. Kuhn & Stiner, 2001; Stepanova, 2019). Sickle blades and grain-grinding stone tools appear in the Levant in the early Epipaleolithic at Ohalo some 23 Kya, and at earlier UP sites, but become widespread only during the Natufian, 15.0–11.6 Kya (Groman-Yaroslavski et al., 2016). Their frequency increases further toward the Neolithic (Bar-Yosef, 1989; Wright, 1994). The relative intensity of grinding tool use is also found in 20th century HG plant-dependent groups (S. L. Kuhn & Stiner, 2001). The dearth or complete absence of similar findings during earlier periods, such as the Middle Paleolithic (MP), can be interpreted as indicating lower plant consumption than the UP and later UP. A similar trend is found in Europe, where grinding stones first appear sporadically in the Early UP/Aurignacian, but it is from the advent of later cultures, such as the Gravettian and Magdalenian, that these tools become more frequent (Aranguren et al., 2007; S. L. Kuhn & Stiner, 2001; Revedin et al., 2010; M. C. Stiner, 2002). In a multidimensional analysis of the Eurasian archaeological record, M. C. Stiner (2002) found a significant HTL decline by the Late UP.

Grinding tools appear in Africa in the MSA, much earlier than elsewhere. However, they are mostly associated with pigment grinding (McBrearty & Brooks, 2000). Increases in plant-processing tools are less conspicuous in Africa than Europe and the Levant (Barton et al., 2016; Bar-Yosef, 2002; Clark, 1997) and include, in addition to MSA grinding stones, perforated stones that may have served as digging stick weights (Villa et al., 2012). Clark (1997) and Villa et al. (2012) indicate that hunting and cutting tools dominated the tool innovation list of the Later Stone Age (LSA) of Africa.

In summary, there is little lithic evidence of increased plant consumption in Africa, at least during the early LSA. In China, increased evidence for plant consumption seems to follow the same timeframe as the European–Levantine UP (Guan et al., 2014; Liu & Chen, 2012, pp. 46–57). In summary, the lithic analysis provides evidence for a gradual but significant increase in plant consumption during the UP, especially at its end (Power & Williams, 2018), in Europe and Asia, and thus a decline in HTL in the late UP and consequently, a higher HTL beforehand.

3.3 | Zooarchaeology

The vast zooarchaeological and the more limited archaeobotanical record may not, because of uneven preservation, directly point to an absolute HTL, but, as in lithics, lasting trends in the record may help identify HTL shifts.

Early human archaeological sites show a gradual increase in bones and stone tools, especially bones bearing tool-inflicted cut marks (Domínguez-Rodrigo & Pickering, 2017).

During the 1980s, support grew for scavenging as the primary mode by which early humans obtained animal food, to the extent that Blumenschine (1986) claimed a consensus had emerged, quoting Binford (1983); however, whether *H. erectus* was a hunter or scavenger was never settled. More recently, with the advent of taphonomic methods aimed at identifying early access to animals, a group working in Olduvai Gorge HWK EE, Bed II, identified substantial exploitation of a wide range of animals immediately before the Acheulian, possibly by *H. habilis* (Ferraro et al., 2013; Pante et al., 2018). Another group, operating in Olduvai Gorge, FLK Zinj, and Upper Bed II, identified signs of hunting by early *Homo* (Bunn & Gurtov, 2014; Bunn & Pickering, 2010). Early access to large animal flesh is also evident from the Okote Member of Koobi Fora, Kenya, in the Acheulian circa 1.5 Mya. The apparent transition from pre-Acheulian scavenging and possibly hunting of small to medium size animals to the addition of active predation and scavenging of large animals in the Acheulian points to an increased HTL.

Although evidence for the acquisition of small animals and aquatic resources does exist (Blasco & Fernández Peris, 2012; Braun et al., 2010), early access to large animals is evident globally from the Acheulian throughout the Paleolithic (Aranguren et al., 2018; Ben-Dor et al., 2011; Bunn & Ezzo, 1993; Carotenuto et al., 2016; Dominguez-Rodrigo et al., 2014; Domínguez-Rodrigo & Pickering, 2017; Gabunia et al., 2000; Klein, 1988; Speth, 2010). Ben-Dor and Barkai (2020a, 2020b) proposed that humans preferred to acquire large herbivores because of their high relative biomass abundance, net energetic return, relative acquisition simplicity, and higher fat content in the context of physiological limits on protein consumption.

M. C. Stiner (2002) suggested that carnivory was key in surviving the intensely cold Eurasian winter. M. Stiner (2012) employed competition theory analysis to argue that *Homo* entered the carnivore guild from peripheral sporadic to full-time carnivory by concentrating on prime adults and exploiting bone marrow. Competition between humans and carnivores is evident throughout the Pleistocene (Rosell et al., 2012; M. Stiner, 2012), implying a carnivorous HTL.

A higher HTL is implied by targeted hunting and exploitation of large carnivores. Evidence exists for the hunting of large carnivores by humans in the Middle Pleistocene and the MP (Blasco et al., 2010, and references therein), as well as for the European UP for skin and meat (Camarós et al., 2016; Tagliacozzo et al., 2013; Wojtal et al., 2020). Routine consumption of bear meat is known ethnographically, and bear fat was revered by American Indians (Ben-Dor, 2015). Carnivore hunting could also point to intraguild predation to reduce competition (Fedriani et al., 2000) and thus supports humans' membership in the large carnivores guild.

3.4 | Targeting fat animals

As shown in the section Fat metabolism, there is evidence of genetic adaptation to high-fat consumption in humans during the Pleistocene. Similar signs of relatively high-fat consumption are found in the zooarchaeological record.

Cursorial predators typically target young and old prey, while ambush predators are not specific (M. C. Stiner, 2002). Humans seem to have preferentially targeted large animals and prime adult prey (Bunn & Gurtov, 2014; Muttoni et al., 2018; Speth, 2010; M. C. Stiner, 2002), which both have relatively higher fat reserves than younger, older, and smaller animals (Ben-Dor et al., 2011; Owen-Smith, 2002; Pitts & Bullard, 1967). Both behaviors can be interpreted as targeting fatter animals, and targeting prime adults may be energetically more expensive than hunting randomly-encountered prey as they entail forgoing encountered hunting opportunities. Ethnographic evidence of prey abandonment once it was deemed fatless (Coote & Shelton, 1992; Tindale, 1972) and evidence for targeting fat-bearing animals (Brink, 2008, p. 42; Rockwell, 1993) support this interpretation (see extended discussion in Speth, 2010, chapter 4). Humans are limited in how much protein they can convert to energy (35%–50% of normal caloric requirements) (Ben-Dor et al., 2016; Bilsborough & Mann, 2006; Rudman et al., 1973; Speth, 1989). Hence, fat-targeting may suggest a high carnivory level if we consider fat-seeking behavior as an alternative to carbohydrate and fat-bearing plants when facing limited capabilities to metabolize protein to energy.

The targeting of fat, at substantial energetic costs, could point to chronic maximal protein consumption, coupled with a lack of energetically profitable plant resources, and hence a highly carnivorous HTL. In addition to preferring larger animals and prime adult prey, transporting relatively fatty and marrow-rich parts to a central location (Bunn & Ezzo, 1993; Byers, 2002; Morin & Ready, 2013; Speth, 2012) and exploiting bone fat at a great energetic expense (Boschian et al., 2019; Brink, 2008, 188; Manne et al., 2006; Outram, 2004) support a limited availability of energetically-profitable plant carbohydrate sources. These four behavioral patterns suggest a high proportion of animal-sourced food in the Paleolithic diet.

3.5 | Isotopes and trace elements

Stable Nitrogen δ^{15}N isotope measurement in human fossil collagen residues is the most extensively used method for estimating HTL (see Makarewicz and Sealy (2015) for a recent review). As dietary protein ascends the trophic food chain, isotope δ^{15}N becomes "enriched" in body proteins. Nitrogen isotope ratios (δ^{15}N values) of human bone collagen are between 3 to 5‰ higher than ratios in the dietary source (M. Richards & Trinkaus, 2009). Herbivores' δ^{15}N values are enriched by 3‰ from their forage; deducting 3 to 5‰ from the δ^{15}N values of humans can indicate the dietary herbivore/plant composition of the human diet, assuming a linear ratio between the two components.

This “trophic level effect” is widely used in archaeology and ecology to determine participants' trophic levels in food webs.

However, several theoretical concerns (reviewed in Hedges & Reynard, 2007, and Makarewicz & Sealy, 2015) may create bias in the results. According to Hedges and Reynard (2007), studies show that δ^{15}N values of plants vary, as do the δ^{15}N values of different animal species and the same species at different times and geographical locations. The background level of δ^{15}N values in herbivores and plants is often assumed rather than tested. Therefore, the potential background δ^{15}N value variations are not considered in many analyses. The degree of δ^{15}N accumulation varies between individuals, a significant factor due to the small number of human samples in Paleolithic archaeological contexts. Also, the assumption of a linear relation in the contribution of mixed animal–plant diets to δ^{15}N values has not been tested. Recently, the roasting of beef has been shown to increase δ^{15}N values by 2‰ (Royer et al., 2017, table 1).

Despite the described limitations, in practice, δ^{15}N values in hairs and fingernails of non-industrial populations with diversified diets show remarkable agreement with the known diets. For example, Papua horticulturalists with a tuber-based economy show an average δ^{15}N value of 8.4‰, 95% confidence interval (CI) [8.2, 8.5], while the meat-consuming Inuit show an average value of 16.0‰, 95% CI [15.7, 16.4]. Ethiopian pastoralist and peasant farmers registered δ^{15}N values of 13.8‰, 95% CI [12.6, 14.8] and 8.0‰, 95% CI [7.4, 8.5] respectively (Buchardt et al., 2007; Cooper et al., 2019; Umezaki et al., 2016; data obtained from M. Bird et al., 2020). The samples in the cited studies (N = 20–231) are larger than typical samples in prehistoric archaeological studies, meaning that the likelihood of an unrepresentative or biased result in archaeological studies is higher than in the present samples.

With these possible sources of bias in mind, we reviewed the results of δ^{15}N studies on *H. sapiens* from the Paleolithic. The collagen preservation limit means that these studies provide HTL information only from about 45–50 Kya and only from colder areas where relatively long-term protein preservation occurred. As we approach later periods, such as the Late UP, samples become available from warmer regions, including the Mediterranean.

A compilation of 242 individuals from 49 sites (Table 1) shows that European HG groups primarily pursued a carnivorous diet throughout the UP, including the Mesolithic.

The Mesolithic isotope record is substantial (Fontanals-Coll et al., 2014), and only partly represented in Table 1. While carnivorous diets may be expected in northern colder regions, samples from more southerly parts of Europe, such as Sicily (Mannino et al., 2012), also show carnivory throughout the Mesolithic. The comparative environmental sampling was small in some studies; hence a bias, such as the periodically high δ^{15}N levels for the early Aurignacian identified by Bocherens et al. (2014), may skew many results toward a highly carnivorous diet. Reviewing the Mesolithic isotope record throughout Europe, Fontanals-Coll et al. (2014) identified a north–south gradient in carnivorous and plant-based diets. In the Neolithic, while some sites show continuous carnivorous protein sources (Budd et al., 2013; Hoekman-Sites & Giblin, 2012), others show an increase in dietary plant incorporation (Mörseburg et al., 2015; Szczepanek et al., 2018). Attempting to explain the contrast between archaeological findings and isotope studies in identifying relative carnivorous diets in the

TABLE 1 Stable isotope studies

Period (Kya)	Region	# individuals	# Sites	Diet	Reference
38–33	Ukraine	3	1	Mixed	Drucker et al. (2017)
32	Ukraine	1	1	Carnivore	Prat et al. (2011)
31–29	Moravia	2	1	Carnivore	Bocherens et al. (2015)
31–29	Belgium	2	1	Carnivore	Wissing et al. (2019)
35–23	Europe	10	9	Carnivore	Richards & Trinkaus (2009)
UP	Med. Eur.	15	5	Carnivore	Mannino et al. (2012)
Late UP	Spain	1	1	Mixed	García-González et al. (2015)
Late UP	Europe	31[a]	11[a]	Carnivore	Richards et al. (2015)
Late UP	Germany	1	1	Carnivore	Drucker et al. (2016)
Mesolithic	Spain	15	3	Carnivore	Salazar-García et al. (2014)
Mesolithic	Sweden	31	2	Carnivore	Eriksson et al. (2018)
Mesolithic	Germany	3	1	Carnivore	Bollongino et al. (2013)
Mesolithic	Italy	5	2	Carnivore/plant	Mannino et al. (2011)
Mesolithic	Belgium	23	2	Carnivore	Bocherens et al. (2007)
Mesolithic	Med. Eur.	27[a]	10[a]	Carnivore	Mannino et al. (2012)
Mesolithic	France	2	2	Carnivore	Naito et al. (2013)
Mesolithic	Doggerland	56	—	Carnivore	van der Plicht et al. (2016)

Abbreviations: Kya, thousands of years ago; Med. Eur., Mediterranean Europe; UP, Upper Paleolithic.

[a] 16 individuals and 5 sites overlap between Mannino et al. (2012) and Richards et al. (2015).

Mesolithic, Salazar-García et al. (2014) note that isotope analysis may not detect significant plant consumption because of relatively low protein content in plants. However, an alternative explanation could be that carnivory is expected to be associated with high animal fat consumption (see the Targeting fat animals section) that would not have registered any nitrogen stable isotope accumulation.

Toward the later UP, an interesting phenomenon was the increase in isotopic evidence for the consumption of aquatic resources (Eriksson et al., 2018; Fischer et al., 2007; Lightfoot et al., 2011; Naito et al., 2013; M. P. Richards et al., 2015; van der Plicht et al., 2016). Although aquatic resource exploitation was identified 1.95 Mya in East Turkana, Kenya (Braun et al., 2010) and other sites during the Pleistocene, its increase, in comparison with the earlier UP, may be indicative of the need to offset declines in the availability of terrestrial animals in Europe because of the Late Quaternary Megafauna Extinction (LQE) and the higher ranking of aquatic resources compared to plants in certain regions. In summary, with the stated caveats, stable isotope analysis points to a carnivorous diet in Europe during the UP with a reduction in trophic levels in the Mesolithic.

The trace elements strontium and barium, relative to calcium, have also been used, alongside isotopes, to gauge the relative importance of plant versus animal foods in the early human diet. Trace elements have an advantage over isotopes because they are measurable in longer-lasting bone and tooth tissue; however, concern regarding diagenesis has halted their use (Ungar & Sponheimer, 2013). Balter et al. (2012) reported that they overcame this limitation by using laser ablation of tooth enamel. They tested permanent molars from *A. africanus*, *P. robustus*, and early *Homo* from Sterkfontein, Swartkrans, and Kromadraai in South Africa. They (p. 559) found that: "Compared to fauna…early Homo and *P. robustus* are indistinguishable from carnivores and browsers respectively." The method they used has not yet been widely adopted, but their finding nonetheless supports a trend toward an elevated trophic level in early humans.

3.6 | Dental pathology

Caries is readily observable in fossilized human remains. Its presence in wild chimpanzees (up to 30.6% in older animals) supports its production by natural carbohydrate sources (Lanfranco & Eggers, 2012). Single human cases of caries appear as early as 1.8 Mya (Lordkipanidze et al., 2013). Dental caries is present but still rare among early modern humans in Europe and the Near East during the UP (Lanfranco & Eggers, 2012). A high caries prevalence, a sign of intensive carbohydrate consumption, first appears in Morocco 13.7–15.0 Kya (Humphrey et al., 2014), together with evidence for starchy food exploitation. Phylogenetic analysis of the dental caries-associated pathogen *Streptococcus mutans* indicates that it underwent a rapid population expansion within the last 10,000 years, strongly implicating the adoption and intensification of agriculture (Cornejo et al., 2013). Caries prevalence in humans increased markedly after the transition to agriculture (Adler et al., 2013; Eshed et al., 2006).

Caries is extremely rare among Neandertals, which relied heavily on animal-sourced food; Lanfranco and Eggers (2012) found only six cases among approximately 1250 known Neandertal teeth. The low caries prevalence during most of the Pleistocene thus supports low carbohydrate consumption and hence, a high HTL during the Pleistocene.

3.7 | Dental wear

Both short-term microscopic and long-term macroscopic tooth wear have been used to infer HTL in the Paleolithic human diet. Microwear studies were used to infer australopith and early human diets (Pontzer et al., 2011; Ungar et al., 2012); however, non-specificity of the results for plant and animal-sourced food preclude their usage for inferring HTL.

Several studies have compared ancient tooth microwear with tooth microwear in 20th century HG groups to determine diet (El Zaatari et al., 2016; Fiorenza et al., 2011; Zaatari & Hublin, 2014). Unfortunately, the reference groups' diets remain uncertain. Fiorenza et al. (2011) rely on the Khoe-San and Australian aborigines as groups indicative of a "mixed diet," citing Janette C Brand-Miller and Holt (1998) as evidence. However, Brand-Miller and Holt define aborigines' diet as being "animal-dominated." Similarly, another research group (El Zaatari et al., 2011; Estalrrich et al., 2017; Zaatari & Hublin, 2014) used the San (without reference to a specific San group) as a comparison group supposedly representing a plant-dominated diet. They refer to reports on the Kalahari-based San diet but use reference teeth from the "montane forest" South African San site of Oakhurst Shelter. The reference article they cite (Sealy, 2006) points to a diet abundant in shellfish rather than plants. The δ^{15}N value for the population (13‰) is indicative of a high trophic level, and most faunal remains at the site were shellfish. There is no mention in the article of a plant-dominated diet. Another group that they (El Zaatari et al., 2011) use for comparison, supposedly representing a "mixed diet," is the Chumash of California. However, the article they cite (Erlandson et al., 2009) discusses the subtleties of an aquatic-based diet on the Santa Cruz island without mentioning plant-sourced food.

The problem with using the ethnographic record for comparison in this type of analysis is emphasized by Pérez-Pérez et al. (2003), who concluded that Australian aborigines and San show a less abrasive microwear pattern than UP humans, indicative of higher meat content in 20th century HG diets. Questioning the usefulness of comparison with HG, they state that buccal microwear patterns in the model HG groups did not accord with their stated diet.

van Casteren et al. (2020) cast doubt on the ability of microwear analysis to identify grass and sedge seed consumption as, according to their study, they barely influence microwear textures. Reviewing tooth wear and archaeobotanical assemblages from Western Eurasia, Power and Williams (2018) conclude that there is evidence for increased plant consumption intensity during the UP.

3.8 | Behavioral adaptations

The behavioral ecology of humans also reflects their trophic level. Several researchers (cited in Arcadi, 2006) studied behavioral similarities between humans and carnivores, comparing them with similarities between humans and primates. Schaller and Lowther (1969) compared the behavior of 20th century HG with social carnivores in Africa, concluding that the selective forces shaping human society differed from those of primates and were more similar to carnivores, especially those concerning co-operative hunting, food transport, and sharing, sharing dependent care, and labor divisions. P. R. Thompson (1975) also proposed that humans were much closer to carnivores than primates in social organization and behavior. Of seven human behaviors, he identified six that resemble carnivores: food sharing, food storage, cannibalism, surplus killing, interspecies intolerance, and alloparenting. Only one behavior, group defense, resembled primates.

Shipman and Walker (1989) employed a method combining physiological and behavioral evidence to predict patterns evolved by humans in adapting to becoming significantly predatory and tested these predictions against the record. They predicted that humans would become much faster in locomotion, more social, develop dental or technological ways of slicing meat, develop longer small intestines and smaller colons, gain free time, have low population densities and shorter gestation, and so become more altricial. They found that all five testable predictions were indeed present in the record to a certain degree and that three were likely already present in *H. erectus*.

Investigating the evolution of cooperation among carnivores, J. E. Smith et al. (2012) identified similar physiological and behavioral correlates to collaboration among prehistoric humans. Focusing on spotted hyenas, which live in relatively complex societies, they found important correlates that were similar between humans and hyenas: reduced dimorphism, increased reproductive investment, fission-fusion dynamics, endurance hunting of big game in open habitats, and large brains.

Arcadi (2006) proposed that humans became similar to other specific carnivores—wolves. Firstly, they were adapted for endurance locomotion; secondly, they acquired a diverse range of prey sizes; and thirdly, they were socially flexible. Variability in prey size selection is extreme in wolves, ranging between 1 and 1000 kg; human prey size range is also extreme, at 0.1 to 6000 kg. Similar to humans, wolves are morphologically poorly adapted to catch large prey alone.

Carnivore species tend to be more geographically dispersed because consuming animal tissue requires less adaptation to specific species (Foley, 2001). In contrast, plant-eating species are more localized because plants boast many physical and chemical defenses that require specific adaptations (Vrba, 1980). Most indicatively, according to Arcadi (2006), humans and wolves are the most and second-most widely spread species, respectively. The conclusion provided by the analogy between humans and wolves is that it is likely that carnivory, and specifically the ability to hunt a wide range of animals, were key facilitators of human dispersal. This conclusion contrasts with other hypotheses attributing the successful human introduction into diverse environments to a general omnivorous dietary flexibility (Teaford et al., 2002; Ungar et al., 2006, for early humans). In summary, human behavioral adaptions support early adaptation to carnivory.

4 | PALEONTOLOGICAL EVIDENCE

Paleontology, with its broad ecological view, can help in locating humans on the specialization spectrum through studying the impact of HTL on human prey and the interspecific competition with other animals for the same food niche.

After 65 million years of continuous increase, the mean body weight (MBW) of terrestrial mammals plummeted during the Pleistocene, from 500 kg at its beginning to some tens of kilograms at its end, a level that last prevailed 60 Mya (F. A. Smith et al., 2018). While the LQE that started some 50 Kya is well documented and discussed (Koch & Barnosky, 2006), there is mounting evidence that the decline in terrestrial mammal body weight began in Africa much earlier. Faith et al. (2018) identified a longer-term megaherbivore richness decline beginning ~4.6 Mya and attributed it to C4 grassland expansion, not human intervention; their data extend to 1 Mya. Malhi et al. (2016) identified a pronounced reduction in proboscidean diversity in Africa around 1 Mya, attributing it to the evolution of *H. erectus* into a carnivore. F. A. Smith et al. (2018) found that, by 126 Kya, the mammal MBW in Africa had declined to 50% of the expected value for such a vast continent, which they attribute to pre-*H. sapiens* human activity. In a recent article, Faith et al. (2020) argue against the claim by F. A. Smith et al. (2018) that pre-*H. sapiens* humans caused megaherbivores' decline. They propose that humans began to affect megaherbivores abundance starting with *H. sapiens*. In Africa, megaherbivore MBW continued to decline between 500 and 400 Kya, as evident in Lainyamok, Kenya (Faith et al., 2012), and before 320 Kya in Olorgesailie (Potts et al., 2018). Despite declining African megaherbivore richness, megaherbivores comprised a very substantial portion of herbivore biomass throughout the continent. Reconstructing African herbivore biomass 1 Kya, Hempson, Archibald, and Bond (2015, p. 1057) note that "Elephants dominate African herbivore biomass, often having biomasses equivalent to those of all other species combined." For a predator capable of acquiring large herbivores (Agam & Barkai, 2018), megaherbivores provided an attractive niche.

The extent of anthropogenic contributions to the LQE is still debated (Monjeau et al., 2015), where the climate is cited as an alternative cause (Meltzer, 2020; Grayson & Meltzer, 2015; Meltzer, 2015; Wroe et al., 2013). However, the minimal evidence for a pre-Pleistocene size-biased large mammal extinction, its close association with human migrations to new continents and islands, and the extinction's extent led many researchers to support anthropogenic association (Braje and Erlandson, 2013; Cooke et al., 2017; Johnson et al., 2016; Saltré et al., 2016; Sandom et al., 2014; F. A. Smith et al., 2019; Tomiya, 2013). An anthropogenic cause for the extinction is also supported by its bias toward larger species in a wide range of orders and relatively small influence on specific orders (F. A. Smith & Lyons, 2011). An anthropogenic contribution to megafauna extinction points to a highly carnivorous trophic position.

Lewis and Werdelin (2007) and Werdelin and Lewis (2013) argue that beginning 1.5 Mya, humans joined the hypercarnivore guild, evidenced by the extinction of sabretooth predators, along with some hyenas. No unusual patterns were seen in the under-21 kg hypocarnivore group (but see Faith et al., 2018, 2020). Interestingly, *Megantereon* sabretooth went extinct in Europe around 1 Mya, soon after the arrival of *Homo antecessor* (M. Antón, 2013). A similar situation of decreased carnivore richness, despite increased large herbivore numbers, was interpreted by Palombo and Mussi (2006) as ideal conditions for introducing humans into Italy and other parts of the Southwestern Mediterranean 0.65 Mya, a hypothesis that places humans in the large-prey carnivore guild.

Akin to conditions that accompanied human emergence in Africa, Palombo (2014) sees the dispersal of humans to Southern Europe 1.5 Mya as resulting from an opening of the environment, leading to change and expansion of the prey spectrum. In a similar vein, Muttoni et al. (2010) developed the "migration with the herd" hypothesis for human colonization of Italy, France, and possibly Spain around 0.9 Mya, when migrating large herbivores, particularly elephants, entered Europe through the Danube-Po Gateway (Muttoni et al., 2014; Muttoni et al., 2015). They identified that the landscape became savannah-like in the Danube and Po valleys, leading to large herbivores and human migrations; humans were already consuming these or similar herbivores, such as the African straight-tusked elephant and Asian steppe mammoth. In summary, the paleontological record supports an interpretation of humans as members of the large predator guild.

5 | ZOOLOGICAL ANALOGY

Present-day predator guild characteristics may provide analogies that help determine Paleolithic HTL. J. A. Holliday and Steppan (2004) define hypercarnivores as carnivores that derive at least 70% of their food from animals. Human acquisition of large animals may indicate hypercarnivory, i.e., high trophic level and specialization. Firstly, predation on large prey is exclusively associated with hypercarnivory (van Valkenburgh et al., 2004; van Valkenburgh et al., 2016; Wroe et al., 2005). Secondly, at a weight of around 66 kg (McHenry, 2009, table 1), larger than a wolf (Okarma, 1989), *H. erectus* was a large predator. All large social carnivores are hypercarnivores, specializing in large prey, although they acquire smaller prey (Nudds, 1978; van Valkenburgh & Wayne, 2010). There is a direct relationship between the hunting group's cumulative biomass and the biomass of the prey. Therefore, social animals hunt larger prey than solitary animals of the same size (Earle, 1987).

Moreover, the relatively large group effort needed to acquire megaherbivores required specialization and sociality (van Valkenburgh et al., 2016; van Valkenburgh & Wayne, 2010). Also, as in humans (Kaplan et al., 2007), recent studies of wolves, lions, and cheetahs have shown that the skills required for killing large prey take years to acquire (van Valkenburgh & Wayne, 2010). In summary, the analogy with the predatory behavior of present-day social large carnivores supports a high level of carnivory in *Homo* during the Pleistocene, beginning with *H. erectus*, and also points to specialization in large prey. Still, humans are unique in their use of technology and possibly other aspects of behavior like subsistence division of labor, and therefore a further study is warranted to elucidate the extent to which the analogy holds. On a side note, carnivores' group size is a function of prey size and abundance (Nudds, 1978), and analysis of zooarchaeological assemblages may inform Pleistocene trends in human group size.

6 | ETHNOGRAPHY

Researchers who introduced and developed the use of ethnographic analogies in archaeology were aware of the need to consider ecological and technological differences between the 20th century and Paleolithic HG (Ascher, 1961; Binford, 2001). The dramatic decline in prey size throughout the Pleistocene has been described in the Paleontology section herein. Its relevance to the validity of analogies with 20th century HG is summarized by Faith, Rowan, and Du (2019, p. 21478), stating that the ecological differences between the Paleolithic and the recent periods are so vast that "modern communities may not be suitable analogs for the ancient ecosystems of hominin evolution.". The megafauna declines also caused a substantial increase in vegetation density and change of vegetation type (Doughty, 2017; Estes et al., 2011; Ripple et al., 2014) such that "…the Late Quaternary Extinctions represent a regime shift for surviving plant and animal species." (Gill, 2014, p. 1163). In other words, because of the change in the relative biomass between plants and animals and the change in their respective composition, the ethnographic record represents decisions under different risk–reward conditions and energetic returns than those that prevailed during most of the Paleolithic.

Ben-Dor and Barkai (2020a) argued that large and very large prey had a significant role in the ecology and the economy of humans' food sources during the Paleolithic. They proposed that the gradual increase in plants consumption during the UP (see the Stone Tools section) and the change in technology to include items like bows and dogs, which aid in smaller fleeing prey hunting, represent adaptations to the decline in prey size during the concurrent Late Quaternary Megafauna Extinction. Thus, facing an ecology that is the result of even greater megafaunal decline and using technologies like bows and dogs that become common in the Late UP, the high plant consumption of many 20th century HG groups may be used as an analogy for their late UP counterparts rather than for earlier Paleolithic humans in general.

In terms of social and behavioral patterns, such as allocare, sharing, personal autonomy, the transmission of knowledge, and more, the ethnographic analogy is suitable for providing insights into Paleolithic human societies. Thus, we acknowledge its significance in reconstructing Paleolithic cultural evolution and lifeways. However, in trophic levels, we strongly argue that it is too ecologically and technologically distanced from cultures predating the UP. In summary, 20th century HG, as expected, continue the subsistence and technological trends that began in the UP and therefore may represent a better analogy for this period rather than much earlier ones.

Interestingly, another pattern that appears to be similar between the UP and 20th century HG is the extreme material cultural variability and fragmentation compared to earlier material cultures persistence in the Paleolithic (Bar-Yosef, 2002). Most of the Paleolithic is characterized by fairly homogeneous cultural complexes that spanned widely in time and space. The Lower Paleolithic Oldowan lasted for almost a million years and could be found in Africa, Europe, South Asia, and the Middle East. The Acheulian lasted over one million years and was even more widespread than the Oldowan. The Middle Paleolithic/Middle Stone Age/Mousterian lasted some 150/200 thousand years and could be found in the same regions as the Acheulian (notwithstanding within-the-box variations in time and space for the Acheulian and the Mousterian). The transition to the UP period, 40 Kya, has been preceded in Europe and elsewhere by a set of short-term, more localized "transition cultures." Since then, there was a trend of increase in regionality and decrease in longevity characterized material cultures worldwide until agriculture.

The cultural variability of 20th century HG is the subject of many studies (Ames, 2004). Ethnographic studies found that material cultural diversity often reflects diversity in subsistence (Binford, 2001). We can then deduce that the diversifying material culture in the UP might reflect an accelerating increase in the variability of subsistence patterns. Plant species tend to be localized (Vrba, 1980) and demand specific preparation techniques (see Diet quality and Stone tools sections herein), and hunting smaller prey requires more complex tools (Churchill, 1993). Thus, the variability of the ethnographic record in material culture and trophic levels can imply, by analogy, that it is a better candidate for subsistence analogy with the Upper Paleolithic than the Early and Middle Paleolithic.

7 | DISCUSSION

7.1 | Summary of the evidence

The actual HTL during the Pleistocene is unobservable; therefore, we looked for evidence of the impact of the HTL on the studied humans' biological, behavioral, and ecological systems. Observing only its reflection and not the HTL itself, we are left employing varying degrees of interpretation in forming an opinion about what HTL caused a specific impact and whether it denotes a step toward specialization or generalization. We reviewed 25 different evidence sources, 15 of which are biological and the remainder archaeological, paleontological, zoological, and ethnographic. With a list of 25 evidence items, by necessity, the descriptions of the findings and the justification of the various interpretations cannot be thorough, leaving much room for further review and debate. One of the main aims of this article was to present the power of paleobiology in particular and to cast a wide net of scientific fields in general in investigating HTL. The evidence here is by no means comprehensive. There is additional genetic and physiological evidence for biological adaptations to a higher and lower trophic level in the past and additional evidence for Paleolithic HTLs in other fields of science, which we chose not to include, and others that we probably missed. Thus, although we do not shy away from presenting a clear hypothesis based on the evidence, the article should be looked at as a first iteration in what hopefully will be a continuous scientific endeavor.

The presented evidence can be organized into three epistemological groups with potentially increasing levels of validity regarding a specific trophic level (see text or Table 2 for a description of the evidence):

7.2 | Type 1. Change in trophic level

• Higher fat reserves	• Adaptations to a high-fat diet	• Late adaptation to USO
• FADS—omega 3 metabolism	• Amy1 multicopy	• Longevity—Fathers
• Longevity—Mothers	• Dental pathology	• Cooking
• Zooarchaeology	• Stone tools	• Ethnography

This group includes evidence for physiological or behavioral adaptations to acquire and consume higher or lower amounts of either animal or plant-sourced food. There is no argument that the evolution of the genus *Homo* was associated with increasing HTLs in *H. habilis* and further in *H. erectus*; therefore, it is not surprising that most of this type of evidence in the Lower Paleolithic includes evidence for adaptation to carnivory. Detailing these pieces of evidence may thus appear to be superfluous; however, identifying a trend in the number and timing of the acquisition of the adaptation may supply important indications for the occurrence of a change in trophic level. Accumulation of type 1 evidence in the Late UP supports a significant change to lower HTL at that period. Also, evidence in one period and not in the other can be interpreted as evidence for a different HTL in the last. For example, if we accept that the appearance of the AMY 1 gene multicopy sometime in *H. sapiens* evolution suggests a higher consumption of starch, we have to accept that there was no pressure to adapt in prior species to high consumption of starch. The same logic applies to the appearance of grains handling stone tools and dental pathology that appear only toward the Paleolithic end.

7.3 | Type 2. Specialization—Reduced flexibility

• Bioenergetics	• Diet quality	• Gut morphology
• Mastication	• Postcranial morphology	• Targeting fat

TABLE 2 Paleolithic human trophic level: Summary of results (summary of the evidence)

Item	Description
Biology	
Bioenergetics	Humans had high energetic requirements for a given body mass and had a shorter time during the day to acquire and consume food. Hunting provides tenfold higher energetic return per hour compared to plants, leaving little room for flexibility (plasticity) between the two dietary components. Animals tend to specialize in the highest return items in their niche. (Specialization)
Diet quality	In primates, a larger brain is associated with high energy density food. With the largest brain among primates, humans are likely to have targeted the highest density food, animal fats, and proteins. Brain size declined during the terminal Pleistocene, and subsequent Holocene. Diet quality declined at the same time with the increased consumption of plants. (Specialization)
Higher fat reserves	With much higher body fat reserves than primates, humans are uniquely adapted to lengthy fasting. This adaptation may have helped with overcoming the erratic encountering of large prey. (Change in trophic level) (Change in trophic level)
Genetic and metabolic adaptation to a high-fat diet	Humans adapted to higher fat diets, presumably from animals. Study (Swain-Lenz et al., 2019): "*suggests that humans shut down regions of the genome to accommodate a high-fat diet while chimpanzees open regions of the genome to accommodate a high sugar diet*" (Change in trophic level)
FADS-Omega3 oils metabolism	Genetic changes in the FADS gene in African humans 85 Kya allowed for a slight increase in the conversion of the plant DHA precursor to DHA signaling adaptation to a higher plant diet (Change in trophic level)
Late adaptations to tubers' consumption	Tubers were assumed to be a mainstay of Paleolithic diets that cooking could prepare for consumption. Recent groups that consume high quantities of tubers have specific genetic adaptations to deal with toxins and antinutrients in tubers. Other humans are not well adapted to consume large quantities of tubers. (Change in trophic level)
Stomach acidity	Higher stomach acidity is found in carnivores to fight meat-borne pathogens. Humans' stomach acidity is even higher than in carnivores, equaling that of scavengers. Adaptation may have evolved to allow large animals' consumption in a central place over days and weeks with pathogen build-up. (Categorization to a trophic group)
Insulin resistance	Humans, like carnivores, have a low physiological (non-pathological) insulin sensitivity.
Gut morphology	Humans' gut morphology and relative size are radically different from chimpanzees' gut. Longer small intestines and shorter large intestines are typical of carnivores' gut morphology and limit humans' ability to extract energy from plants' fiber. (Specialization)
Mastication	Reduction of the masticatory system size already in *Homo erectus*, compared to early hominins, who relied on terrestrial vegetation as a food source. The reduced size is compatible with meat and fat consumption. (Aiello & Wheeler, 1995; Zink & Lieberman, 2016) (Change in trophic level)
Cooking	Cooking was hypothesized to have enabled plants' high consumption despite the need for a high-quality diet, starting with *H. erectus*. Other researchers argue that habitual use of fire is evident only around 0.4 Mya. Also, a fire has other uses and is costly to maintain. (Change in trophic level)
Postcranial morphology	A set of adaptations for endurance running is found already in *H. erectus*, useful in hunting. Shoulders adapted to spear-throwing in *H. erectus*. But limited tree climbing capability. (Specialization)
Adipocyte morphology	Similar to the morphology in carnivores. "*These figures suggest that the energy metabolism of humans is adapted to a diet in which lipids and proteins rather than carbohydrates, make a major contribution to the energy supply*." (Pond & Mattacks, 1985). (Categorization to a trophic group)
Age at weaning	Carnivores wean at a younger age, as do humans. Early weaning "*highlight the emergence of carnivory as a process fundamentally determining human evolution*" (Psouni et al., 2012). (Categorization to a trophic group)
Longevity	Kaplan et al. (2007) hypothesized that a large part of the group depended on experienced hunters due to long childhood. Extended longevity in humans evolved to allow utilization of hunting proficiency, which peaks by age 40. The grandmother hypothesis claim women's longevity allowed additional gathering. (Change in trophic level)
Vitamins	Hypothesis for required nutritional diversity to supply vitamins is contested. It appears that all vitamins, including vitamin C are supplied in adequate quantities on a carnivorous diet. (Neutral)
Multicopy AMY1 genes	Multi-copies of the AMY1 gene have been hypothesized as adaptive to high starch diets. However, both findings of its possible lack of functionality and the unclear timing of its appearance limits the use of the evidence to support a change in trophic level. (Change in trophic level)
Archaeology	
Plants	Plants were consumed throughout the Paleolithic, but their relative dietary contribution is difficult to assess. Recent advances in plant residues identification in dental pluck provide non-quantitative evidence of widespread plants' consumption. Division of labor may point to a background level of plant supply, but the evidence is based largely on ethnography, which may not be analogous to the Pleistocene. (Inconclusive)

TABLE 2 (Continued)

Item	Description
Stone tools	Stone tools specific to plant food utilization appear only some 40 Kya, and their prevalence increases just before the appearance of agriculture, signaling increased plant consumption toward the end of the Paleolithic. (Change in trophic level)
Zooarchaeology	First access to large prey, denoting hunting, appears already in *H. erectus* archaeological sites 1.5 Mya. Humans also hunted large carnivores. (Change in trophic level)
Targeting fat	Humans concentrated on hunting fatty animals at substantial energetic costs. They preferentially brought fatty parts to base camps, hunted fattier prime adults, and exploited bone fat. That behavior may indicate that plants could not have been easily obtained to complete constrained protein consumption. (Specialization)
Stable Isotopes	Nitrogen ^{15}N isotope measurement of human fossil collagen residues is the most extensively used method for determining trophic level in the last 50 thousand years. All studies show that humans were highly carnivorous until very late, before the appearance of agriculture. The method has some shortcomings but was able to identify variation in trophic level among present-day traditional groups. (Categorization to a trophic group)
Dental pathology	Dental caries, evidence of substantial consumption of carbohydrates, appeared only some 15 Kya in groups with evidence of high plant food consumption. (Change in trophic level)
Dental wear	Different wear on fossilized teeth as a result of different diets has the potential to reconstruct diets. However, the claim for the reconstruction of variable diets in Paleolithic humans could not be verified as the comparison the groups' diets were unclear. (Inconclusive)
Behavioral adaptations	A comparison of humans' behavior patterns with chimpanzees and social carnivores found that humans have carnivore-like behavior patterns. Food sharing, alloparenting, labor division, and social flexibility are among the shared carnivorous behaviors. (Categorization to a trophic group)
Others	
Paleontological evidence	Evidence for hunting by *H. erectus* 1.5 Mya was associated with the extinction of several large carnivores, but not smaller carnivores. This suggests that *H. erectus* became a member of the large carnivores' guild. Extinction of large carnivores in Europe also coincided with the arrival of humans (Categorization to a trophic group) Extinctions of large herbivores were associated with humans' presence in Africa and arrival to continents and islands, such as Australia and America, suggesting preferential hunting of large prey.
Zoological analogy	Humans were predators of large prey. In carnivores, predation on large prey is exclusively associated with hypercarnivory, i.e., consuming over 70% of the diet from animals. (Categorization to a trophic group)
Ethnography	Variability in trophic level in the ethnographic context is frequently mentioned as proof of HTL variability during the Paleolithic. However, ecological and technological considerations limit the analogy to the terminal Paleolithic. (Change in trophic level)

Since we cannot observe our subjects, evidence for specialization is defined here as evidence that is similar to Type 1 but that, at the same time, potentially reducing the phenotypic plasticity of humans by hindering the acquisition or assimilation of the other food group (plant or animal).

Specialization and generalization must be defined with reference to particular axes such as temperature, habitat, and feeding (Futuyma & Moreno, 1988). Pineda-Munoz and Alroy (2014) defined feeding specialization as selecting 50% or more of the food from a certain food group (fruits, seeds, green plants, insects, or vertebrates). By this definition, humans could be called specialists if they selected to consume 50% or more of their diet from vertebrates or another group of plants or invertebrates.

Another axis on which specialization can be defined is prey size. Large carnivores specialize in large prey. Evidence for humans' specialization in large herbivores can contribute to the continuing debate regarding humans' role in megafauna extinction (Faith et al., 2020; Faurby et al., 2020; Sandom et al., 2014; F. A. Smith et al., 2018; Werdelin & Lewis, 2013) and the implications of megafauna extinction on humans. Potts et al. (2018) identified an association between prey size decline during the Middle Pleistocene and the appearance of the MSA, and Ben-Dor et al. (2011) further proposed that the extinction of elephants in the Southern Levant led to the appearance of the Acheulo-Yabrudian cultural complex 420 Kya. Ben-Dor and Barkai (2020a) have argued that humans preferred to acquire large prey and that large prey is underrepresented in zooarchaeological assemblages (Ben-Dor & Barkai, 2020b). Listed in Table 3 is evidence, among the ones collected here, that can be interpreted as supporting humans' specialization in acquiring large prey.

Dietary plasticity is a function of phenotypic plasticity (Fox et al., 2019) and technological and ecological factors. In many cases, evolution is a process of solving problems with trade-offs (Garland, 2014). Identifying features that were traded-off in specific adaptations could inform us of changing dietary phenotypic plasticity levels. Relative energetic returns on primary (plant) and secondary (animal) producers are key to assessing plasticity's ecological potential. In humans, technology can expend plasticity by enabling and increasing the energetic return on the acquisition of certain food items. Bows for the hunting of smaller, faster prey and grinding stones are two examples of such technologies.

TABLE 3 Specialization in the acquisition of large prey

Bioenergetic	Large prey provides higher energetic returns than smaller prey. The need to substitute large prey for smaller prey is energetically costly.
Higher fat reserves	Large prey is less abundant than smaller prey. Fat reserves may have evolved to allow extended fasting of several weeks, thereby bridging an erratic encountering rate with large prey. Humans have adapted to easily synthesize ketones to replace glucose as an energy source for the brain.
Stomach acidity	Stronger acidity than carnivores' can be interpreted as an adaptation to a large prey's protracted consumption over days and weeks, whereby humans are acting as scavengers of their prey.
Targeting fat	The recognition of targeting fat as a driver of human behavior supports the importance of large, higher fat bearing animals to humans' survival.
Stable isotopes	Higher levels of nitrogen isotope 15 than carnivores were interpreted by researchers as testifying to the higher consumption of large prey than other carnivores.
Paleontology	A decline in the guild of large prey carnivores 1.5 Mya is interpreted as resulting from humans' entrance to the guild. Also, the extinction of large prey throughout the Pleistocene is interpreted by some researchers as anthropogenic, testifying to humans' preference for large prey.
Zoological analogy	Large social carnivores hunt large prey.
Ethnography	Interpreting ethnographic and Upper Paleolithic technologies as an adaptation to the acquisition of smaller prey means that humans were less adapted to the acquisition of smaller prey in earlier periods.

We mainly listed specialization adaptations that affected phenotypic plasticity, but there are technological and ecological pieces of evidence that potentially changed dietary plasticity like the invention of bows that increased the level of plasticity regarding prey size and the appearance and disappearance of savannas with the accompanied change in primary to secondary production ratios that swayed plasticity toward primary or secondary producers.

7.4 | Type 3. Categorization to a trophic group

• Stomach acidity	• Adipocyte morphology	• Age at weaning
• Stable isotopes	• Behavioral adaptations	• Paleontologic evidence
• Zoological analogy	• Insulin resistance	

All the eight pieces of evidence of membership in a trophic group concluded that humans were carnivores. Assigning humans to a specific dietary trophic group has the highest potential validity, as it answers the research question with minimal interpretation.

In some cases, interpretation is required to assign a phenomenon to HTL. Belonging to the carnivores' trophic groups still does not tell us if humans were 90% or 50% carnivores. It does tell us, however, that humans were carnivorous enough and carnivorous long enough to justify physiological and behavioral adaptations unique to carnivores. Following the zoological analogy with large social carnivores that acquire large prey, we hypothesized that humans were hypercarnivores, defined as consuming more than 70% of the diet from animal sources.

8 | SUMMARY

Figures 1 and 2 summarize our interpretation for the evidence of evolution of the HTL throughout the Paleolithic.

In Figure 1, the evidence appears according to the *Homo* species and the inferred HTL with reference to their evidence type.

Figure 2 demonstrates the evolution of the HTL during the Pleistocene as we interpret it, based on the totality of the evidence. Each line in the figure represents one mammalian species of the 137 species in the Pineda-Munoz and Alroy (2014) dataset, and they appear from left to right in descending relative plant consumption.

The primates in Pineda-Munoz and Alroy (2014) dataset are specialized plant-eaters. There is little argument that meat was not the main food of early hominins (Ungar & Sponheimer, 2011), but it appears that at least 3.2 Mya, australopiths may have increased the portion of meat in their diet (McPherron et al., 2010). The appearance of the genus *Homo* was associated with a gradual increase of the animal component in the diet. Early *Homo* has initially expanded the diet from major reliance on plant foods to scavenging of bone marrow and brains and meat (S. C. Antón et al., 2014; Pante et al., 2018; Sayers & Lovejoy, 2014; J. Thompson et al., 2019; Ungar, 2012). Consistent signs of increased concentration on animal-sourced foods appear in *H. erectus* (Foley, 2001, and see Zooarchaeology section in this article).

Most of the evidence that has been collected and analyzed in this article (Figure 1) points to a carnivore trophic level for humans during most of the Paleolithic, starting with *H. erectus*. In seven pieces of evidence (adipocyte morphology, stomach acidity, age at weaning, stable isotopes, paleontology, behavioral adaptations, Insulin resistance), the authors themselves allocate humans to the carnivore guild. A further six pieces of evidence point to humans' specialization in animals' exploitation, while an additional six pieces of evidence simply point to increased consumption of animals. However, eight pieces of evidence cannot safely be assigned to *H. erectus* as they are found in present humans, and it is not known if they also occurred in *H. erectus*. Safe evidence for some decline in trophic level start to appear toward the Middle Paleolithic (cooking) in the MP (AMY 1 multicopy), and a slight increase in plant-sourced food consumption in Africa some 85 Kya is suggested by a change in the *FADS* gene family, which enable the synthesis of omega 3 fats from vegetal sources (see Fat metabolism

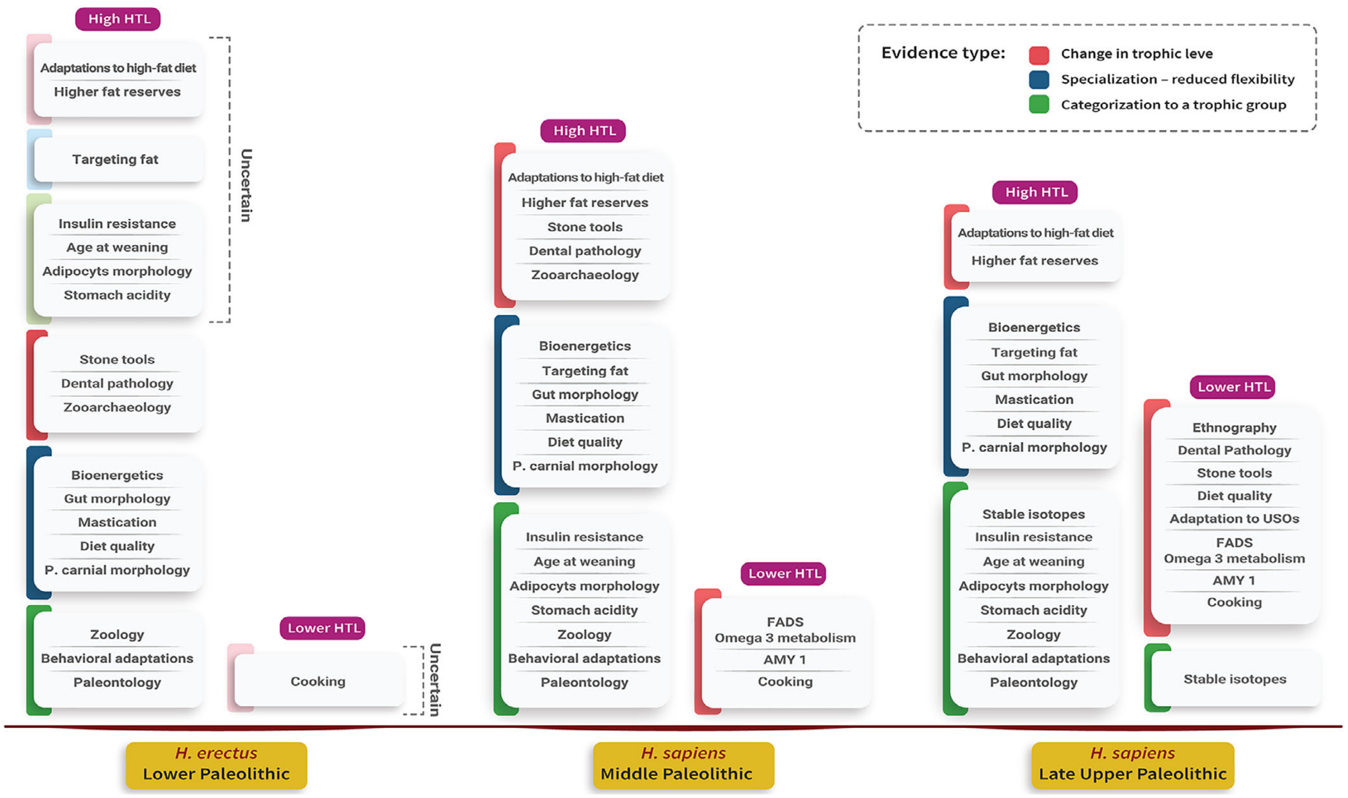

FIGURE 1 A list of evidence by human trophic level, human species, period, and type of evidence (see text for the typology of evidence). Uncertain association of an item with *Homo erectus* appears in muted color

section herein). Evidence for a significant decline in trophic level appears mainly at the end of the Paleolithic with plants-dedicated stone tools, dental pathology, and analogies of 20th century HG technology and ecological conditions.

Thus, we can present a hypothesis for the evolution of the HTL during the Paleolithic whereby consumption of animal-sourced food increased with early *Homo* and peaked in *H. erectus*. *H. erectus* was morphologically and behaviorally adapted to carnivory, was a social hunter of megafauna, possibly specializing in large prey, which, by zoological analogy, would have been a hypercarnivore with some 70% of the diet derived from animals. A certain decline in HTL may have occurred in *H. sapiens* in Africa, especially toward the end of the MP; however, it was not significant enough or long enough to change substantial carnivorous biological features that prevail until today. A significant decline in HTL occurred late in the Paleolithic, when technological changes allowed a significantly higher consumption of plants, possibly compensating for a marked decline in prey size and abundance and the consequent decline in fat availability to complete the non-protein portion of the diet.

Taking a broader perspective, we note that, among mammals, there are fewer speciations within omnivory, but more speciations from omnivory to carnivory and from carnivory to omnivory (Price et al., 2012). Taken together with the general mammalian tendency toward specialization (Pineda-Munoz & Alroy, 2014), we suggest that the described “zig-zag” travel of *Homo* along the trophic spectrum from a lower trophic level to carnivory specialization and then back to the lower trophic level omnivory, was a natural mammalian evolutionary pathway.

The evidence of an adaptation to a highly carnivorous trophic level for *H. erectus* and *H. sapiens*, and possibly a further specialization in the acquisition of large prey, present an alternative hypothesis to the one marking human adaptive transitions toward general resource variability (Potts et al., 2020). The selection for specialization in large prey instead of dietary variability, if accepted, can provide causality to the association made by Potts et al. (2018) between a decline in prey size in East Africa and the appearance of the MSA. Prey size decline drove cultural and physiological adaptation to acquire a larger portion of smaller prey in the hunting mix without sacrificing too much energy. A similar phenomenon of declining prey size followed by the cultural change was also identified in the Southern Levant continuously throughout the Paleolithic (Ben-Dor et al., 2011; Speth & Clark, 2006; M. C. Stiner et al., 2000) and in North America (Waters et al., 2020). A carnivorous trophic level can also support explanations of reliance on prey acquisition rather than adaptation to dietary variability as the enabling factor in *H. erectus* expansion to Eurasia 1.8 Mya and to humans' global dispersals in general.

We found the ethnographic record to be a useful analogy not to a trophic level during all of the Pleistocene but rather to the terminal Pleistocene when cultural fragmentation and increased plant food consumption is evident. On a general note, the substantial ecological and technological, as well as the social changes that 20th-century HG

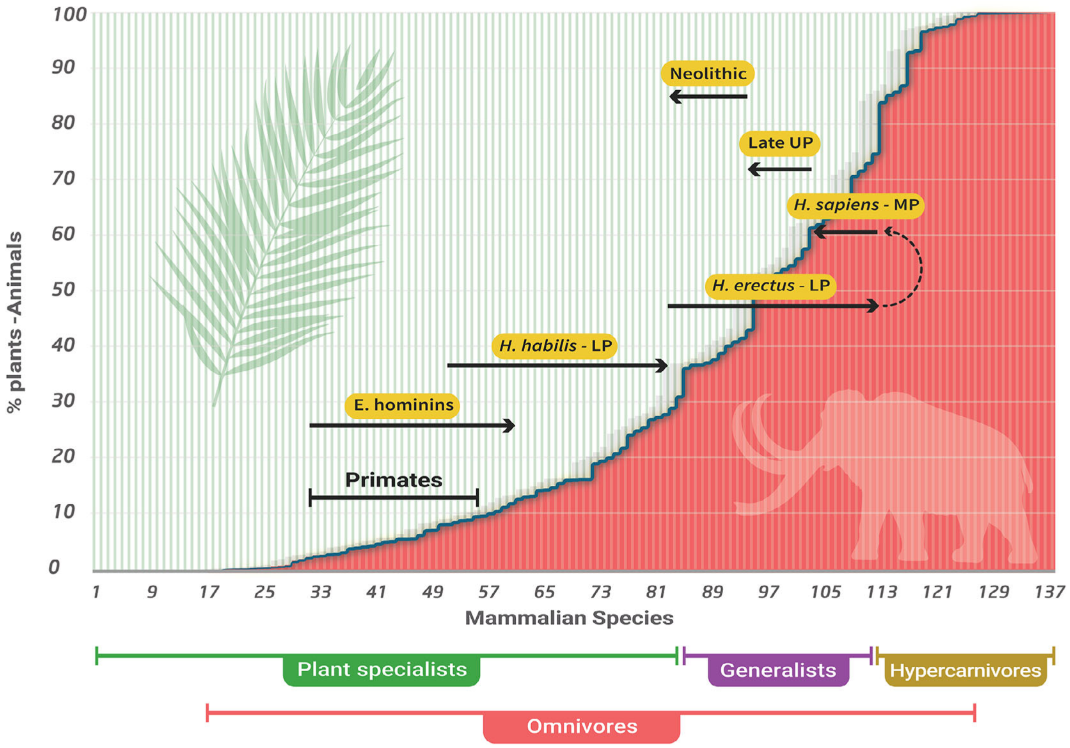

FIGURE 2 Proposed evolution of the human trophic level during the Pleistocene. E. hominins, Early hominins, (Australopithecus, Paranthropus); LP, Lower Paleolithic; MP, Middle Paleolithic; UP, Upper Paleolithic. Background and position of primates—Adapted from (Pineda-Munoz & Alroy, 2014). Each line corresponds to the plants and animals' food-source ratio of one mammalian species. Plant specialists and Hypercarnivores—Mammals that obtain over 70% of their food from plants and animals, respectively. Omnivores—Any mammal that obtains food from both plants and animals

went through, should caution us from the simplistic employment of analogies with the Pleistocene. As we noted, the best candidates for valid analogies are those that remain common in many groups of 20th-century HG, regardless of variability in their ecological, technological, and social circumstances. Sharing or, indeed, preference for fatter and larger prey are good examples of such candidates (Jerozolimski & Peres, 2003; Jochim, 1981; Kaplan et al.,).

Regarding future research, specialization in carnivory and large prey calls for additional research of changes in the abundance of prey in general, and large prey in particular as a potential ecological driver of evolutionary and cultural changes during the Paleolithic. Further, the relative dearth of plant remains, and the inability to quantify plants and animals' consumption from the archaeological record is frustrating. However, quantitative measures may be applied to a set of archaeological assemblages to elucidate patterns of consumption. For example, quantification of dental plaque findings and their content, relative to previous periods, may point to trends in plant consumption. Similarly, although the absolute portion of animals' contribution to the diet cannot be learned from zooarchaeological assemblages, temporal trends in prey size can be quantified.

A deeper study of phenotypic plasticity and technological and ecological influence on dietary plasticity can help understand humans' degree of dependence on one trophic group or another and the need for evolutionary and cultural change to meet changing ecological conditions. For example, the genetic change in the ability of *H. sapiens* to convert plant source omega-3 oils to DHA 85 Kya in Africa seems like an increase in dietary phenotypic plasticity, and it may be worthwhile to look for technological and ecological signs of increased dietary plasticity at the same time and place.

There is no need to expand on the contribution of multidisciplinarity to the understanding of almost any subject. Future investigations, similar to this article, could benefit from the contribution of a wider group of experts than we have assembled. We are looking forward to specific criticism of our findings and interpretations and to additional evidence of the type that was presented in this article so that, as Wilkinson (2014) stated, we make progress in the first task of the prehistorian—study which trophic level humans occupied during the course of their evolution.

ACKNOWLEDGMENTS

Raphael Sirtoli is the co-founder of a food tracking app called Nutrita as well as a freelance writer for ThePaleoDiet.com. We would like to express our sincere appreciation for the outstanding work of the editors and reviewers of the manuscript. While the responsibility for the final outcome remains ours, the contribution of their challenges to the final content and to the organization and presentation of the material was significant.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Miki Ben-Dor https://orcid.org/0000-0001-9512-1160

REFERENCES

Adler, C. J., Dobney, K., Weyrich, L. S., Kaidonis, J., Walker, A. W., Haak, W., Bradshaw, C. J. A., Townsend, G., Sołtysiak, A., Alt, K. W., Parkhill, J., & Cooper, A. (2013). Sequencing ancient calcified dental plaque shows changes in oral microbiota with dietary shifts of the Neolithic and Industrial revolutions. *Nature Genetics*, *45*(4), 450–455.

Agam, A., & Barkai, R. (2018). Elephant and mammoth hunting during the Paleolithic: A review of the relevant archaeological, ethnographic and ethno-historical records. *Quaternary*, *1*(1), 3.

Aiello, L. C., & Wheeler, P. (1995). The expensive-tissue hypothesis: The brain and the digestive system in human and primate evolution. *Current Anthropology*, *36*(2), 199–221.

Akkaoui, M., Cohen, I., Esnous, C., Lenoir, V., Sournac, M., Girard, J., & Prip-Buus, C. (2009). Modulation of the hepatic malonyl-CoA–carnitine palmitoyltransferase 1A partnership creates a metabolic switch allowing oxidation of de novo fatty acids1. *Biochemical Journal*, *420*(3), 429–438.

Ames, K. M. (2004). Supposing hunter-gatherer variability. *American Antiquity*, *69*(2), 364–374.

Antón, M. (2013). *Sabertooth*. Indiana University Press.

Antón, S. C., Potts, R., & Aiello, L. C. (2014). Evolution of early Homo: An integrated biological perspective. *Science*, *345*(6192), 1236828.

Aranguren, B., Becattini, R., Lippi, M. M., & Revedin, A. (2007). Grinding flour in upper Palaeolithic Europe (25000 years bp). *Antiquity*, *81*(314), 845–855.

Aranguren, B., Revedin, A., Amico, N., Cavulli, F., Giachi, G., Grimaldi, S., Macchioni, N., & Santaniello, F. (2018). Wooden tools and fire technology in the early Neanderthal site of Poggetti Vecchi (Italy). *Proceedings of the National Academy of Sciences*, *115*(9), 2054–2059.

Arcadi, A. C. (2006). Species resilience in Pleistocene hominids that traveled far and ate widely: An analogy to the wolf-like canids. *Journal of Human Evolution*, *51*(4), 383–394.

Arroyo, A., & de la Torre, I. (2016). Assessing the function of pounding tools in the early Stone age: A microscopic approach to the analysis of percussive artefacts from beds I and II, Olduvai Gorge (Tanzania). *Journal of Archaeological Science*, *74*, 23–34.

Ascher, R. (1961). Analogy in archaeological interpretation. *Southwestern Journal of Anthropology*, *17*(4), 317–325.

Atkinson, F. S., Hancock, D., Petocz, P., & Brand-Miller, J. C. (2018). The physiologic and phenotypic significance of variation in human amylase gene copy number. *The American Journal of Clinical Nutrition*, *108*, 1–12.

Balter, V., Braga, J., Télouk, P., & Thackeray, J. F. (2012). Evidence for dietary change but not landscape use in south African early hominins. *Nature*, *489*(7417), 558–560.

Barkai, R., Lemorini, C., & Gopher, A. (2010). Palaeolithic cutlery 400 000–200 000years ago: Tiny meat-cutting tools from Qesem cave, Israel. *Antiquity*, *84*(325). Online.

Barkai, R., Rosell, J., Blasco, R., & Gopher, A. (2017). Fire for a reason: Barbecue at middle Pleistocene Qesem cave, Israel. *Current Anthropology*, *58*(S16), S314–S328.

Barnosky, A. D., Koch, P. L., Feranec, R. S., Wing, S. L., & Shabel, A. B. (2004). Assessing the causes of late Pleistocene extinctions on the continents. *Science*, *306*(5693), 70–75.

Barton, R., Bouzouggar, A., Collcutt, S., Marco, Y. C., Clark-Balzan, L., Debenham, N., & Morales, J. (2016). Reconsidering the MSA to LSA transition at Taforalt cave (Morocco) in the light of new multi-proxy dating evidence. *Quaternary International*, *413(A)*, 36–49.

Bar-Yosef, O. (1989). The PPNA in the Levant–an overview. *Paléorient*, *15*, 57–63.

Bar-Yosef, O. (2002). The upper paleolithic revolution. *Annual Review of Anthropology*, *31*, 363–393.

Bar-Yosef, O. (2014). Upper Paleolithic hunter-gatherers in Western Asia. In V. Cummings, P. Jordan, & M. Zvelebil (Eds.), *The Oxford handbook of the archaeology and anthropology of hunter-gatherers* (pp. 252–278). Oxford University Press.

Beasley, D. E., Koltz, A. M., Lambert, J. E., Fierer, N., & Dunn, R. R. (2015). The evolution of stomach acidity and its relevance to the human microbiome. *PLoS One*, *10*(7), e0134116.

Ben-Dor, M. (2015). Use of animal fat as a symbol of health in traditional societies suggests humans may be well adapted to its consumption. *Journal of Evolution and Health*, *1*(1), 10.0.

Ben-Dor, M., & Barkai, R. (2020a). The importance of large prey animals during the Pleistocene and the implications of their extinction on the use of dietary ethnographic analogies *The. Journal of Anthropological Archaeology*, *59*, 101192.

Ben-Dor, M., & Barkai, R. (2020b). Supersize does matter: The importance of large prey in Paleolithic subsistence and a method for measurement of its significance in zooarchaeological assemblages. In G. Konidaris, R. Barkai, V. Tourloukis, & K. Harvati (Eds.), *Human-elephant interactions: From past to present*. Tübingen University Press.

Ben-Dor, M., Gopher, A., & Barkai, R. (2016). Neandertals' large lower thorax may represent adaptation to high protein diet. *American Journal of Physical Anthropology*, *160*(3), 367–378. https://doi.org/10.1002/ajpa.22981

Ben-Dor, M., Gopher, A., Hershkovitz, I., & Barkai, R. (2011). Man the fat hunter: The demise of Homo erectus and the emergence of a new hominin lineage in the Middle Pleistocene (ca. 400 kyr) Levant. *PLoS One*, *6*(12), e28689. https://doi.org/10.1371/journal.pone.0028689

Bilsborough, S., & Mann, N. (2006). A review of issues of dietary protein intake in humans. *International Journal of Sport Nutrition and Exercise Metabolism*, *16*(2), 129–152.

Binford, L. R. (1983). *In pursuit of the past: Decoding the Archaeological record*. Thames and Hudson.

Binford, L. R. (2001). *Constructing frames of reference: An analytical method for archaeological theory building using ethnographic and environmental data sets*. Univ of California Press.

Bird, D. W., Codding, B. F., Bird, R. B., Zeanah, D. W., & Taylor, C. J. (2013). Megafauna in a continent of small game: Archaeological implications of Martu Camel hunting in Australia's Western Desert. *Quaternary International*, *297*, 155–166.

Bird, M., Crabtree, S., Haig, J., Ulm, S., and Wurster, C. (2020). A global carbon and nitrogen isotope perspective on modern and ancient human diet. *Preprint - Research Square*. 10.21203/rs.3.rs-61331/v1

Bird, R. B., & Power, E. A. (2015). Prosocial signaling and cooperation among Martu hunters. *Evolution and Human Behavior*, *36*, 389–397.

Blasco, R., & Fernández Peris, J. (2012). A uniquely broad spectrum diet during the Middle Pleistocene at Bolomor Cave (Valencia, Spain). *Quaternary International*, *252*, 16–31.

Blasco, R., Rosell, J., Arsuaga, J. L., de Castro, J. M. B., & Carbonell, E. (2010). The hunted hunter: The capture of a lion (*Panthera leo* fossilis) at the Gran Dolina site, Sierra de Atapuerca, Spain. *Journal of Archaeological Science*, *37*(8), 2051–2060.

Blumenschine, R. J. (1986). Carcass consumption sequences and the archaeological distinction of scavenging and hunting. *Journal of Human Evolution*, *15*(8), 639–659.

Bocherens, H., Drucker, D. G., Germonpré, M., Lázničková-Galetová, M., Naito, Y. I., Wissing, C., Brůžek, J., & Oliva, M. (2015). Reconstruction of the Gravettian food-web at Předmostí I using multi-isotopic tracking (13 C, 15 N, 34 S) of bone collagen. *Quaternary International*, *359*, 211–228.

Bocherens, H., Drucker, D. G., & Madelaine, S. (2014). Evidence for a 15 N positive excursion in terrestrial foodwebs at the Middle to Upper Palaeolithic transition in south-western France: Implications for early modern human palaeodiet and palaeoenvironment. *Journal of Human Evolution*, *69*, 31–43.

Bocherens, H., Polet, C., & Toussaint, M. (2007). Palaeodiet of Mesolithic and Neolithic populations of Meuse Basin (Belgium): Evidence from stable isotopes. *Journal of Archaeological Science*, *34*(1), 10–27.

Boschian, G., Caramella, D., Saccà, D., & Barkai, R. (2019). Are there marrow cavities in Pleistocene elephant limb bones, and was marrow available to early humans? New CT scan results from the site of Castel di Guido (Italy). *Quaternary Science Reviews*, *215*, 86–97.

Bollongino, R., Nehlich, O., Richards, M. P., Orschiedt, J., Thomas, M. G., Sell, C., Fajkosova, Z., Powell, A., & Burger, J. (2013). 2000 Years of parallel societies in stone age central europe. *Science*, *342*(6157), 479–481. https://doi.org/10.1126/science.1245049.

Braje, T. J., & Erlandson, J. M. (2013). Human acceleration of animal and plant extinctions: A Late Pleistocene, Holocene, and Anthropocene continuum. *Anthropocene*, *4*, 14–23.

Bramble, D. M., & Lieberman, D. E. (2004). Endurance running and the evolution of Homo. *Nature*, *432*(7015), 345–352.

Brand-Miller, J. C., Griffin, H. J., & Colagiuri, S. (2011). The carnivore connection hypothesis: Revisited. *Journal of Obesity*, *2012*, 1–9. https://www.hindawi.com/journals/jobe/2012/258624/.

Brand-Miller, J. C., & Holt, S. H. (1998). Australian Aboriginal plant foods: A consideration of their nutritional composition and health implications. *Nutrition Research Reviews*, *11*(01), 5–23.

Braun, D. R., Harris, J. W., Levin, N. E., McCoy, J. T., Herries, A. I., Bamford, M. K., Bishop, L. C., Richmond, B. G., & Kibunjia, M. (2010). Early hominin diet included diverse terrestrial and aquatic animals 1.95 Ma in East Turkana, Kenya. *Proceedings of the National Academy of Sciences*, *107*(22), 10002–10007.

Brink, J. (2008). *Imagining head-smashed-in Aboriginal buffalo hunting on the northern plains*. Athabasca University Press.

Broughton, J. M., Cannon, M. D., Bayham, F. E., & Byers, D. A. (2011). Prey body size and ranking in zooarchaeology: Theory, empirical evidence, and applications from the northern Great Basin. *American Antiquity*, *76* (3), 403–428.

Brown, A. T. (1975). The role of dietary carbohydrates in plaque formation and oral disease. *Nutrition Reviews*, *33*(12), 353–361.

Buchardt, B., Bunch, V., & Helin, P. (2007). Fingernails and diet: Stable isotope signatures of a marine hunting community from modern Uummannaq, North Greenland. *Chemical Geology*, *244*(1–2), 316–329.

Budd, C., Lillie, M., Alpaslan-Roodenberg, S., Karul, N., & Pinhasi, R. (2013). Stable isotope analysis of Neolithic and Chalcolithic populations from Aktopraklık, northern Anatolia. *Journal of Archaeological Science*, *40*(2), 860–867.

Bunn, H. T., & Ezzo, J. A. (1993). Hunting and scavenging by Plio-Pleistocene hominids: Nutritional constraints, archaeological patterns, and behavioural implications. *Journal of Archaeological Science*, *20*(4), 365–398.

Bunn, H. T., & Gurtov, A. N. (2014). Prey mortality profiles indicate that Early Pleistocene Homo at Olduvai was an ambush predator. *Quaternary International*, *322*, 44–53.

Bunn, H. T., & Pickering, T. R. (2010). Bovid mortality profiles in paleoecological context falsify hypotheses of endurance running–hunting and passive scavenging by early Pleistocene hominins. *Quaternary Research*, *74*(3), 395–404.

Byers, D. A. (2002). Paleoindian fat-seeking behavior: Evidence from the Hell Gap Site, Localtiy II Agate Basin Faunal Assemblage. *Plains Anthropologist*, *47*(183), 359–377.

Cahill, G. F., Jr. (2006). Fuel metabolism in starvation. *Annual Review of Nutrition*, *26*, 1–22.

Cahill, G. F., Jr., & Owen, O. E. (1968). Starvation and survival. *Transactions of the American Clinical and Climatological Association*, *79*, 13.

Camarós, E., Münzel, S. C., Cueto, M., Rivals, F., & Conard, N. J. (2016). The evolution of Paleolithic hominin–carnivore interaction written in teeth: Stories from the Swabian Jura (Germany). *Journal of Archaeological Science: Reports*, *6*, 798–809.

Carotenuto, F., Tsikaridze, N., Rook, L., Lordkipanidze, D., Longo, L., Condemi, S., & Raia, P. (2016). Venturing out safely: The biogeography of Homo erectus dispersal out of Africa. *Journal of Human Evolution*, *95*, 1–12.

Caspari, R., & Lee, S.-H. (2004). Older age becomes common late in human evolution. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(30), 10895–10900.

Caspary, W. F. (1992). Physiology and pathophysiology of intestinal absorption. *The American Journal of Clinical Nutrition*, *55*(1), 299S–308S.

Churchill, S. E. (1993). Weapon technology, prey size selection, and hunting methods in modern hunter-gatherers: Implications for hunting in the Palaeolithic and Mesolithic. *Archeological Papers of the American Anthropological Association*, *4*(1), 11–24.

Churchill, S. E., Berger, L. R., Hartstone-Rose, A., & Zondo, B. H. (2012). Body size in African Middle Pleistocene Homo. In *Body size in African Middle Pleistocene Homo. African genesis: Perspectives on hominin evolution* (pp. 319–346). Cambridge University Press.

Churchill, S. E., & Rhodes, J. A. (2009). The evolution of the human capacity for "killing at a distance": The human fossil evidence for the evolution of projectile weaponry. In J. J. Hublin & M. P. Richards (Eds.), *The evolution of hominin diets* (pp. 201–210). Springer.

Clark, A. M. (1997). The MSA/LSA transition in southern Africa: New technological evidence from Rose Cottage Cave. *The South African Archaeological Bulletin*, *52*, 113–121.

Cooke, S. B., Dávalos, L. M., Mychajliw, A. M., Turvey, S. T., & Upham, N. S. (2017). Anthropogenic extinction dominates Holocene declines of West Indian mammals. *Annual Review of Ecology, Evolution, and Systematics*, *48*(1), 307–327.

Cooper, C. G., Lupo, K. D., Zena, A. G., Schmitt, D. N., & Richards, M. P. (2019). Stable isotope ratio analysis (C, N, S) of hair from modern humans in Ethiopia shows clear differences related to subsistence regimes. *Archaeological and Anthropological Sciences*, *11*(7), 3213–3223.

Coote, J., & Shelton, A. (1992). *Anthropology, art, and aesthetics*. Clarendon Press.

Cordain, L., Miller, J. B., Eaton, S. B., Mann, N., Holt, S. H. A., & Speth, J. D. (2000). Plant-animal subsistence ratios and macronutrient energy estimations in worldwide hunter-gatherer diets 1, 2. *The American Journal of Clinical Nutrition*, *71*(3), 682–692.

Cordain, L., Watkins, B. A., Florant, G., Kelher, M., Rogers, L., & Li, Y. (2002). Fatty acid analysis of wild ruminant tissues: Evolutionary implications for reducing diet-related chronic disease. *European Journal of Clinical Nutrition*, *56*(3), 181–191.

Cornejo, O. E., Lefébure, T., Bitar, P. D. P., Lang, P., Richards, V. P., Eilertson, K., Do, T., Beighton, D., Zeng, L., Ahn, S.-J., Burne, R. A., Siepel, A., Bustamante, C. D., & Stanhope, M. J. (2013). Evolutionary and population genomics of the cavity causing bacteria *Streptococcus mutans*. *Molecular Biology and Evolution*, *30*(4), 881–893.

Crandall, L. A. (1941). A comparison of ketosis in man and dog. *Journal of Biological Chemistry*, *138*, 123–128.

Crawford, M. A. (2010). Long-chain polyunsaturated fatty acids in human brain evolution. In S. C. Cunnane & K. M. Stewart (Eds.), *Human brain evolution* (pp. 13–31). John Wiley & Sons.

Crittenden, A. N., & Schnorr, S. L. (2017). Current views on hunter-gatherer nutrition and the evolution of the human diet. *American Journal of Physical Anthropology*, *162*(S63), 84–109.

Crozier, S. R., Godfrey, K. M., Calder, P. C., Robinson, S. M., Inskip, H. M., Baird, J., Gale, C. R., Cooper, C., Sibbons, C. M., Fisk, H. L., & Burdge, G. C. (2019). Vegetarian diet during pregnancy is not associated with poorer cognitive performance in children at age 6–7 years. *Nutrients*, *11*(12), 3029.

Cunnane, S. C., & Crawford, M. A. (2003). Survival of the fattest: Fat babies were the key to evolution of the large human brain. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *136*(1), 17–26.

Cunnane, S. C., & Crawford, M. A. (2014). Energetic and nutritional constraints on infant brain development: Implications for brain expansion during human evolution. *Journal of Human Evolution*, *77*, 88–98.

Cunnane, S. C., Menard, C. R., Likhodii, S. S., Brenna, J. T., & Crawford, M. A. (1999). Carbon recycling into de novo lipogenesis is a major pathway in neonatal metabolism of linoleate and alpha-linolenate. *Prostaglandins, Leukotrienes, and Essential Fatty Acids*, *60* (5–6), 387–392. https://doi.org/10.1016/s0952-3278(99)80018-0

Cunningham, J. J., Ellis, S. L., McVeigh, K. L., Levine, R. E., & Calles-Escandon, J. (1991). Reduced mononuclear leukocyte ascorbic acid content in adults with insulin-dependent diabetes mellitus consuming adequate dietary vitamin C. *Metabolism*, *40*(2), 146–149.

Darwin, C. (1859). *On the origin of species*. John Murray.

Davis, D. R. (2009). Declining fruit and vegetable nutrient composition: What is the evidence? *Horticultural Science*, *44*(1), 15–19.

DeCasien, A. R., Williams, S. A., & Higham, J. P. (2017). Primate brain size is predicted by diet but not sociality. *Nature Ecology & Evolution*, *1*(5), 0112.

Des Gachons, C. P., & Breslin, P. A. (2016). Salivary amylase: Digestion and metabolic syndrome. *Current Diabetes Reports*, *16*(10), 102.

Dibble, H. L., Sandgathe, D., Goldberg, P., McPherron, S., & Aldeias, V. (2018). Were western european neandertals able to make fire? *Journal of Paleolithic Archaeology*, *1*(1), 54–79. https://doi.org/10.1007/s41982-017-0002-6.

Dominguez-Rodrigo, M., Diez-Martin, F., Yravedra, J., Barba, R., Mabulla, A., Baquedano, E., Uribelarrea, D., Sánchez, P., & Eren, M. I. (2014). Study of the SHK Main Site faunal assemblage, Olduvai Gorge, Tanzania: Implications for Bed II taphonomy, paleoecology, and hominin utilization of megafauna. *Quaternary International*, *322*, 153–166. https://doi.org/10.1016/j.quaint.2013.09.025

Domínguez-Rodrigo, M., & Pickering, T. R. (2017). The meat of the matter: An evolutionary perspective on human carnivory. *Azania: Archaeological Research in Africa*, *52*(1), 4–32.

Dominy, N. J. (2012). Hominins living on the sedge. *Proceedings of the National Academy of Sciences*, *109*(50), 20171–20172.

Doughty, C. E. (2017). Herbivores increase the global availability of nutrients over millions of years. *Nature Ecology & Evolution*, *1*(12), 1820–1827.

Draper, H. H. (1977). Aboriginal eskimo diet in modern perspective. *American Anthropologist*, *79*, 309–316. https://doi.org/10.1525/aa.1977.79.2.02a00070

Dressman, J. B., Berardi, R. R., Dermentzoglou, L. C., Russell, T. L., Schmaltz, S. P., Barnett, J. L., & Jarvenpaa, K. M. (1990). Upper gastrointestinal (GI) pH in young, healthy men and women. *Pharmaceutical Research*, *7*(7), 756–761. https://doi.org/10.1023/a:1015827908309

Drucker, D. G., Naito, Y. I., Péan, S., Prat, S., Crépin, L., Chikaraishi, Y., Ohkouchi, N., Puaud, S., Lázničková-Galetová, M., Patou-Mathis, M., Yanevich, A., & Bocherens, H. (2017). Isotopic analyses suggest mammoth and plant in the diet of the oldest anatomically modern humans from far southeast Europe. *Scientific Reports*, *7*(1), 6833.

Drucker, D. G., Rosendahl, W., van Neer, W., Weber, M.-J., Görner, I., & Bocherens, H. (2016). Environment and subsistence in north-western Europe during the Younger Dryas: An isotopic study of the human of Rhünda (Germany). *Journal of Archaeological Science: Reports*, *6*, 690–699.

Earle, M. (1987). A flexible body mass in social carnivores. *The American Naturalist*, *129*(5), 755–760.

Eaton, S. B., & Konner, M. (1985). Paleolithic nutrition - A consideration of its nature and current implications. *New England Journal of Medicine*, *312*(5), 283–289. https://doi.org/10.1056/nejm198501313120505

El Zaatari, S., Grine, F. E., Ungar, P. S., & Hublin, J.-J. (2011). Ecogeographic variation in Neandertal dietary habits: Evidence from occlusal molar microwear texture analysis. *Journal of Human Evolution*, *61*, 411–424. https://doi.org/10.1016/j.jhevol.2011.05.004

El Zaatari, S., Grine, F. E., Ungar, P. S., & Hublin, J.-J. (2016). Neandertal versus modern human dietary responses to climatic fluctuations. *PLoS One*, *11*(4), e0153277.

Eriksson, G., Frei, K. M., Howcroft, R., Gummesson, S., Molin, F., Lidén, K., Frei, R., & Hallgren, F. (2018). Diet and mobility among Mesolithic hunter-gatherers in Motala (Sweden)-the isotope perspective. *Journal of Archaeological Science: Reports*, *17*, 904–918.

Erlandson, J. M., Rick, T. C., & Braje, T. J. (2009). Fishing up the food web?: 12,000 years of maritime subsistence and adaptive adjustments on California's channel islands1. *Pacific Science*, *63*(4), 711–724.

Eshed, V., Gopher, A., & Hershkovitz, I. (2006). Tooth wear and dental pathology at the advent of agriculture: New evidence from the Levant. *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists*, *130*(2), 145–159.

Estalrrich, A., El Zaatari, S., & Rosas, A. (2017). Dietary reconstruction of the El Sidrón Neandertal familial group (Spain) in the context of other Neandertal and modern hunter-gatherer groups. A molar microwear texture analysis. *Journal of Human Evolution*, *104*, 13–22.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., … Wardle, D. A. (2011). Trophic downgrading of planet earth. *Science*, *333*(6040), 301–306.

Fadupin, G., Akpoghor, A., & Okunade, K. (2007). A comparative study of serum ascorbic acid level in people with and without type 2 diabetes in Ibadan, Nigeria. *African Journal of Medicine and Medical Sciences*, *36* (4), 335–339.

Faith, J. T., Potts, R., Plummer, T. W., Bishop, L. C., Marean, C. W., & Tryon, C. A. (2012). New perspectives on middle Pleistocene change in the large mammal faunas of East Africa: Damaliscus hypsodon sp. nov.(Mammalia, Artiodactyla) from Lainyamok, Kenya. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *361*, 84–93.

Faith, J. T., Rowan, J., & Du, A. (2019). Early hominins evolved within non-analog ecosystems. *Proceedings of the National Academy of Sciences*, *116*, 21478–21483.

Faith, J. T., Rowan, J., Du, A., & Barr, W. A. (2020). The uncertain case for human-driven extinctions prior to *Homo sapiens*. *Quaternary Research*, *96*, 88–104.

Faith, J. T., Rowan, J., Du, A., & Koch, P. L. (2018). Plio-Pleistocene decline of African megaherbivores: No evidence for ancient hominin impacts. *Science*, *362*(6417), 938–941.

Falchi, M., Moustafa, J. S. E.-S., Takousis, P., Pesce, F., Bonnefond, A., Andersson-Assarsson, J. C., Sudmant, P. H., Dorajoo, R., Al-Shafai, M. N., Bottolo, L., Ozdemir, E., So, H.-C., Davies, R. W., Patrice, A., Dent, R., Mangino, M., Hysi, P. G., Dechaume, A., Huyvaert, M., … Froguel, P. (2014). Low copy number of the salivary amylase gene predisposes to obesity. *Nature Genetics*, *46*(5), 492–497.

Faurby, S., Silvestro, D., Werdelin, L., & Antonelli, A. (2020). Brain expansion in early hominins predicts carnivore extinctions in East Africa. *Ecology Letters*, *23*, 537–544.

Fediuk, K. (2000). *Vitamin C in the Inuit diet: Past and present*. McGill University.

Fedriani, J. M., Fuller, T. K., Sauvajot, R. M., & York, E. C. (2000). Competition and intraguild predation among three sympatric carnivores. *Oecologia*, *125*(2), 258–270.

Fernández, C. I., & Wiley, A. S. (2017). Rethinking the starch digestion hypothesis for AMY1 copy number variation in humans. *American Journal of Physical Anthropology*, *163*(4), 645–657.

Ferraro, J. V., Plummer, T. W., Pobiner, B. L., Oliver, J. S., Bishop, L. C., Braun, D. R., Ditchfield, P. W., Seaman, J. W., III, Binetti, K. M., Seaman, J. W., Jr., Hertel, F., & Potts, R. (2013). Earliest archaeological evidence of persistent hominin carnivory. *PLoS One*, *8*(4), e62174.

Feuerriegel, E. M., Green, D. J., Walker, C. S., Schmid, P., Hawks, J., Berger, L. R., & Churchill, S. E. (2017). The upper limb of Homo naledi. *Journal of Human Evolution*, *104*, 155–173.

Fiorenza, L., Benazzi, S., Tausch, J., Kullmer, O., Bromage, T. G., & Schrenk, F. (2011). Molar macrowear reveals Neanderthal eco-geographic dietary variation. *PLoS One*, *6*(3), e14769.

Fischer, A., Olsen, J., Richards, M., Heinemeier, J., Sveinbjörnsdóttir, Á. E., & Bennike, P. (2007). Coast–inland mobility and diet in the Danish Mesolithic and Neolithic: Evidence from stable isotope values of humans and dogs. *Journal of Archaeological Science*, *34*(12), 2125–2150.

Foley, R. A. (2001). The evolutionary consequences of increased carnivory in hominids. In C. B. Stanford & H. T. Bunn (Eds.), *Meat-eating and human evolution* (pp. 305–331). Oxford University Press.

Foley, R., & Elton, S. (1998). Time and energy: the ecological context for the evolution of bipedalism. *Primate Locomotion*, (pp. 419–433).

Fontanals-Coll, M., Subirà, M. E., Marín-Moratalla, N., Ruiz, J., & Gibaja, J. F. (2014). From Sado Valley to Europe: Mesolithic dietary practices through different geographic distributions. *Journal of Archaeological Science*, *50*, 539–550.

Formicola, V., & Giannecchini, M. (1999). Evolutionary trends of stature in Upper Paleolithic and Mesolithic Europe. *Journal of Human Evolution*, *36*(3), 319–333.

Fox, R. J., Donelson, J. M., Schunter, C., Ravasi, T., & Gaitán-Espitia, J. D. (2019). Beyond buying time: the role of plasticity in phenotypic adaptation to rapid environmental change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *374*(1768), 20180174. https://doi.org/10.1098/rstb.2018.0174.

Frayer, D. W. (1981). Body size, weapon use, and natural selection in the European Upper Paleolithic and Mesolithic. *American Anthropologist*, *83*(1), 57–73.

Friedemann, T. E. (1926). The starvation ketosis of a monkey. *Proceedings of the Society for Experimental Biology and Medicine*, *24*(3), 223–226.

Frossard, E., Bucher, M., Mächler, F., Mozafar, A., & Hurrell, R. (2000). Potential for increasing the content and bioavailability of Fe, Zn and Ca in plants for human nutrition. *Journal of the Science of Food and Agriculture*, *80*(7), 861–879.

Futuyma, D. J., & Moreno, G. (1988). The evolution of ecological specialization. *Annual review of ecology and systematics*, *19*(1), 207–233. https://doi.org/10.1146/annurev.es.19.110188.001231.

Gabunia, L., Vekua, A., & Lordkipanidze, D. (2000). The environmental contexts of early human occupation of Georgia (Transcaucasia). *Journal of Human Evolution*, *38*(6), 785–802.

García-González, R., Carretero, J. M., Richards, M. P., Rodríguez, L., & Quam, R. (2015). Dietary inferences through dental microwear and isotope analyses of the Lower Magdalenian individual from El Mirón Cave (Cantabria, Spain). *Journal of Archaeological Science*, *60*, 28–38.

García-Granero, J. J. (2020). Starch taphonomy, equifinality and the importance of context: Some notes on the identification of food processing through starch grain analysis. *Journal of Archaeological Science*, *124*, 105267. https://doi.org/10.1016/j.jas.2020.105267.

Garland, T. (2014). Trade-offs. *Current Biology*, *24*(2), R60–R61. https://doi.org/10.1016/j.cub.2013.11.036.

Gill, J. L. (2014). Ecological impacts of the late Quaternary megaherbivore extinctions. *New Phytologist*, *201*(4), 1163–1169.

Gittleman, J. L., & Harvey, P. H. (1982). Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Sociobiology*, *10*(1), 57–63.

Gowlett, J. (2016). The discovery of fire by humans: A long and convoluted process. *Philosophical Transaction of the Royal Society of London B: Biological Sciences*, *371*(1696), 20150164.

Graaf, M. D., Veer, I. V., Meulen-Muileman, I. V. D., Gerritsen, W., Pinedo, H., & Haisma, H. (2001). Cloning and characterization of human liver cytosolic b-glycosidase. *Biochemical Journal*, *356*(3), 907–910.

Grabowski, M., Hatala, K. G., Jungers, W. L., & Richmond, B. G. (2015). Body mass estimates of hominin fossils and the evolution of human body size. *Journal of Human Evolution*, *85*, 75–93.

Grayson, D. K., & Meltzer, D. J. (2015). Revisiting Paleoindian exploitation of extinct North American mammals. *Journal of Archaeological Science*, *56*, 177–193.

Groman-Yaroslavski, I., Weiss, E., & Nadel, D. (2016). Composite sickles and cereal harvesting methods at 23,000-years-old Ohalo II, Israel. *PLoS One*, *11*(11), e0167151.

Guan, Y., Pearsall, D. M., Gao, X., Chen, F., Pei, S., & Zhou, Z. (2014). Plant use activities during the upper Paleolithic in east Eurasia: Evidence from the Shuidonggou site, Northwest China. *Quaternary International*, *347*, 74–83.

Guil-Guerrero, J. L., Tikhonov, A., Ramos-Bueno, R. P., Grigoriev, S., Protopopov, A., Savvinov, G., & González-Fernández, M. J. (2018). Mammoth resources for hominins: From omega-3 fatty acids to cultural objects. *Journal of Quaternary Science*, *33*(4), 455–463.

Gurven, M., & Kaplan, H. (2007). Longevity among hunter-gatherers: A cross-cultural examination. *Population and Development Review*, *33*(2), 321–365.

Haas, R., Watson, J., Buonasera, T., Southon, J., Chen, J. C., Noe, S., Smith, K., Llave, C. V., Eerkens, J., & Parker, G. (2020). Female hunters of the early Americas. *Science Advances*, *6*(45), eabd0310.

Hall, K. D., Bemis, T., Brychta, R., Chen, K. Y., Courville, A., Crayner, E. J., Goodwin, S., Guo, J., Howard, L., Knuth, N. D., Miller, B. V., III, Prado, C. M., Siervo, M., Skarulis, M. C., Walter, M., Walter, P. J., & Yannai, L. (2015). Calorie for calorie, dietary fat restriction results in more body fat loss than carbohydrate restriction in people with obesity. *Cell Metabolism*, *22*(3), 427–436.

Hamel, E. E., Santisteban, G. A., Ely, J. T., & Read, D. H. (1986). Hyperglycemia and reproductive defects in non-diabetic gravidas: A mouse model test of a new theory. *Life Sciences*, *39*(16), 1425–1428.

Hancock, A. M., Witonsky, D. B., Ehler, E., Alkorta-Aranburu, G., Beall, C., Gebremedhin, A., Sukernik, R., Utermann, G., Pritchard, J., Coop, G., & Di Rienzo, A. (2010). Human adaptations to diet, subsistence, and ecoregion are due to subtle shifts in allele frequency. *Proceedings of the National Academy of Sciences*, *107*(Suppl. 2), 8924–8930.

Hardy, B. L. (2010). Climatic variability and plant food distribution in Pleistocene Europe: Implications for Neanderthal diet and subsistence. *Quaternary Science Reviews*, *29*, 662–679. https://doi.org/10.1016/j.quascirev.2009.11.016

Hardy, K. (2018). Plant use in the Lower and Middle Palaeolithic: Food, medicine and raw materials. *Quaternary Science Reviews*, *191*, 393–405.

Hardy, K., Buckley, S., Collins, M. J., Estalrrich, A., Brothwell, D., Copeland, L., García-Tabernero, A., García-Vargas, S., de la Rasilla, M., Lalueza-Fox, C., Huguet, R., Bastir, M., Santamaría, D., Madella, M., Wilson, J., Cortés, Á. F., & Rosas, A. (2012). Neanderthal medics? Evidence for food, cooking, and medicinal plants entrapped in dental calculus. *Die Naturwissenschaften*, *99*, 617–626. https://doi.org/10.1007/s00114-012-0942-0

Hardy, K., Buckley, S., & Copeland, L. (2018). Pleistocene dental calculus: Recovering information on Paleolithic food items, medicines, paleoenvironment and microbes. *Evolutionary Anthropology: Issues, News, and Reviews*, *27*(5), 234–246.

Hardy, K., Radini, A., Buckley, S., Blasco, R., Copeland, L., Burjachs, F., Girbal, J., Yll, R., Carbonell, E., & de Castro, J. M. B. (2017). Diet and environment 1.2 million years ago revealed through analysis of dental calculus from Europe's oldest hominin at Sima del Elefante, Spain. *The Science of Nature*, *104*(1–2), 2.

Hardy, K., Radini, A., Buckley, S., Sarig, R., Copeland, L., Gopher, A., & Barkai, R. (2016). Dental calculus reveals potential respiratory irritants and ingestion of essential plant-based nutrients at Lower Palaeolithic Qesem Cave Israel. *Quaternary International*, *398*, 129–135.

Hawkes, K. (2016). Ethnoarchaeology and Plio-Pleistocene sites: Some lessons from the Hadza. *Journal of Anthropological Archaeology*, *44*, 158–165.

Hawkes, K., & Coxworth, J. E. (2013). Grandmothers and the evolution of human longevity: A review of findings and future directions. *Evolutionary Anthropology: Issues, News, and Reviews*, *22*(6), 294–302.

Hawkes, K., O'Connell, J., & Blurton Jones, N. (2018). Hunter-gatherer studies and human evolution: A very selective review. *American Journal of Physical Anthropology*, *165*(4), 777–800.

Hawks, J. (2011). Selection for smaller brains in Holocene human evolution. *arXiv preprint arXiv:1102.5604*.

Hawks, J., Wang, E. T., Cochran, G. M., Harpending, H. C., & Moyzis, R. K. (2007). Recent acceleration of human adaptive evolution. *Proceedings of the National Academy of Sciences*, *104*(52), 20753–20758.

Hawkes, K., O'Connell, J. F., & Blurton Jones, N. G. (1997). Hadza women's time allocation, offspring provisioning, and the evolution of long postmenopausal life spans. *Current Anthropology*, *38*(4), 551–577. https://doi.org/10.1086/204646.

Hedges, R. E., & Reynard, L. M. (2007). Nitrogen isotopes and the trophic level of humans in archaeology. *Journal of Archaeological Science*, *34*(8), 1240–1251.

Hempson, G. P., Archibald, S., & Bond, W. J. (2015). A continent-wide assessment of the form and intensity of large mammal herbivory in Africa. *Science*, *350*(6264), 1056–1061.

Henneberg, M. (1988). Decrease of human skull size in the Holocene. *Human Biology*, *60*(3), 395–405.

Henneberg, M., Sarafis, V., & Mathers, K. (1998). Human adaptations to meat eating. *Human Evolution*, *13*(3–4), 229–234.

Henry, A. G., Brooks, A. S., & Piperno, D. R. (2011). Microfossils in calculus demonstrate consumption of plants and cooked foods in Neanderthal diets (Shanidar III, Iraq; Spy I and II, Belgium). *Proceedings of the National Academy of Sciences*, *108*(2), 486–491.

Henry, A. G., Brooks, A. S., & Piperno, D. R. (2014). Plant foods and the dietary ecology of Neanderthals and early modern humans. *Journal of Human Evolution*, *69*, 44–54. https://doi.org/10.1016/j.jhevol.2013.12.014

Henry, A. G. (2017). Neanderthal cooking and the costs of fire. *Current Anthropology*, *58*(S16), S329–S336. https://doi.org/10.1086/692095.

Henry, A. G., & Piperno, D. R. (2008). Using plant microfossils from dental calculus to recover human diet: A case study from Tell al-Raqā'i, Syria. *Journal of Archaeological Science*, *35*(7), 1943–1950.

Herms, D. A., & Mattson, W. J. (1992). The dilemma of plants: To grow or defend. *The Quarterly Review of Biology*, *67*(3), 283–335.

Hervik, A. K., & Svihus, B. (2019). The role of Fiber in energy balance. *Journal of Nutrition and Metabolism*, *2019*, 1–11.

Hill, K., Kaplan, H., Hawkes, K., & Hurtado, A. M. (1985). Men's time allocation to subsistence work among the Ache of Eastern Paraguay. *Human Ecology*, *13*(1), 29–47. https://doi.org/10.1007/bf01531087.

Hockett, B., & Haws, J. (2003). Nutritional ecology and diachronic trends in Paleolithic diet and health. *Evolutionary Anthropology: Issues, News, and Reviews*, *12*(5), 211–216.

Hockett, B., & Haws, J. a. (2005). Nutritional ecology and the human demography of Neandertal extinction. *Quaternary International*, *137*, 21–34. https://doi.org/10.1016/j.quaint.2004.11.017

Hoekman-Sites, H. A., & Giblin, J. I. (2012). Prehistoric animal use on the Great Hungarian Plain: A synthesis of isotope and residue analyses from the Neolithic and Copper Age. *Journal of Anthropological Archaeology*, *31*(4), 515–527.

Holliday, J. A., & Steppan, S. J. (2004). Evolution of hypercarnivory: The effect of specialization on morphological and taxonomic diversity. *Paleobiology*, *30*(1), 108–128.

Holliday, T. (2012). Body size, body shape, and the circumscription of the genus Homo. *Current Anthropology*, *53*(Suppl. 6), S330–S345.

Hora, M., Pontzer, H., Wall-Scheffler, C. M., & Sládek, V. (2020). Dehydration and persistence hunting in Homo erectus. *Journal of Human Evolution*, *138*, 102682.

Høverstad, T. (1986). Studies of short-chain fatty acid absorption in man. *Scandinavian Journal of Gastroenterology*, *21*(3), 257–260.

Humphrey, L. T., De Groote, I., Morales, J., Barton, N., Collcutt, S., Ramsey, C. B., & Bouzouggar, A. (2014). Earliest evidence for caries and exploitation of starchy plant foods in Pleistocene hunter-gatherers from Morocco. *Proceedings of the National Academy of Sciences*, *111*(3), 954–959.

Inchley, C. E., Larbey, C. D., Shwan, N. A., Pagani, L., Saag, L., Antão, T., Jacobs, G., Hudjashov, G., Metspalu, E., Mitt, M., Eichstaedt, C. A., Malyarchuk, B., Derenko, M., Wee, J., Abdullah, S., Ricaut, F.-X., Mormina, M., Mägi, R., Villems, R., … Kivisild, T. (2016). Selective sweep on human amylase genes postdates the split with Neanderthals. *Scientific Reports*, *6*(37198), On line

Isaac, G. L. (1978). The Harvey Lecture series, 1977-1978. Food sharing and human evolution: Archaeological evidence from the Plio-Pleistocene of east Africa. *Journal of Anthropological Research*, *34*(3), 311–325.

Jarrett, S. G., Milder, J. B., Liang, L. P., & Patel, M. (2008). The ketogenic diet increases mitochondrial glutathione levels. *Journal of Neurochemistry*, *106*(3), 1044–1051.

Jerozolimski, A., & Peres, C. A. (2003). Bringing home the biggest bacon: A cross-site analysis of the structure of hunter-kill profiles in Neotropical forests. *Biological Conservation*, *111*(3), 415–425.

Jochim, M. A. (1981). *Strategies for survival: Cultural behavior in an ecological context*. Academic Press.

Johansson, C. (1974). Studies of gastrointestinal interactions. VII. Characteristics of the absorption pattern of sugar, fat and protein from composite meals in man. A quantitative study. *Scandinavian Journal of Gastroenterology*, *10*(1), 33–42.

Johnston, K., Robson, B. J., & Fairweather, P. G. (2011). Trophic positions of omnivores are not always flexible: Evidence from four species of freshwater crayfish. *Austral Ecology*, *36*(3), 269–279.

Kaplan, H., Gangestad, S., Gurven, M., Lancaster, J., Mueller, T., & Robson, A. (2007). The evolution of diet, brain and life history among primates and humans. In W. Roebroeks (Ed.), *Guts and brains: An integrative approach to the hominin record* (pp. 47–48). Leiden University Press.

Kaplan, H., Gurven, M., & Winking, J. (2009). An evolutionary theory of human life span: Embodied capital and the human adaptive complex. In V. L. Bengston, D. Gans, N. M. Pulney, & M. Silverstein (Eds.), *Handbook of theories of aging* (pp. 36–90). Springer.

Kaplan, H., Hill, K., Lancaster, J., & Hurtado, A. M. (2000). A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology Issues News and Reviews*, *9*(4), 156–185.

Kelly, R. L. (2013). *The lifeways of hunter-gatherers: The foraging spectrum*. Cambridge University Press.

Kennedy, G. E. (2005). From the ape's dilemma to the weanling's dilemma: Early weaning and its evolutionary context. *Journal of Human Evolution*, *48*(2), 123–145.

Khorasani, D. G., & Lee, S.-H. (2020). Women in human evolution Redux. In C. Willermet & L. Sang-Hee (Eds.), *Evaluating evidence in biological anthropology: The strange and the familiar*. Cambridge Un iversity Press.

Klein, R. G. (1988). The archaeological significance of animal bones from Acheulean sites in southern Africa. *African Archaeological Review*, *6*(1), 3–25.

Koch, P. L., & Barnosky, A. D. (2006). Late quaternary extinctions: State of the debate. *Annual Review of Ecology, Evolution, and Systematics*, *37*, 215–252. https://doi.org/10.1146/annurev.ecolsys.34.011802.132415

Konner, M., & Eaton, S. B. (2010). Paleolithic nutrition twenty-five years later. *Nutrition in Clinical Practice*, *25*(6), 594–602.

Kuhn, J. (2015). Throwing, the shoulder, and human evolution. *American Journal of Orthopedics (Belle Mead, NJ)*, *45*(3), 110–114.

Kuhn, S. L., & Stiner, M. C. (2001). The antiquity of hunter-gatherers. In C. Panter-Brick, R. Layton, & P. Rowley-Conwy (Eds.), *Hunter–gatherers: Interdisciplinary perspectives* (pp. 99–142). Cambridge University Press.

Kuipers, R. S., Joordens, J. C., & Muskiet, F. A. (2012). A multidisciplinary reconstruction of Palaeolithic nutrition that holds promise for the prevention and treatment of diseases of civilisation. *Nutrition Research Reviews*, *25*(01), 96–129.

Kuipers, R. S., Luxwolda, M. F., Janneke Dijck-Brouwer, D. A., Eaton, S. B., Crawford, M. A., Cordain, L., & Muskiet, F. A. J. (2010). Estimated macronutrient and fatty acid intakes from an east African Paleolithic diet. *The British Journal of Nutrition*, *104*(11), 1666–1687. https://doi.org/10.1017/S0007114510002679

Kyriacou, K., Blackhurst, D., Parkington, J., & Marais, A. (2016). Marine and terrestrial foods as a source of brain-selective nutrients for early modern humans in the southwestern Cape, South Africa. *Journal of Human Evolution*, *97*, 86–96.

Lanfranco, L. P., & Eggers, S. (2012). Caries through time: An anthropological overview. In *Contemporary approach to dental caries*. InTech.

Lee, R. B. (1968). What hunters do for a living, or, how to make out on scarce resources. In R. B. Lee & I. DeVore (Eds.), *Man the hunter* (pp. 30–47). Aldine Publishing Company.

Lee, R. B. (1979). *The Kung San: Men, women, and work in a foraging society* (p. 526). Cambridge University Press.

Lefcheck, J. S., Whalen, M. A., Davenport, T. M., Stone, J. P., & Duffy, J. E. (2013). Physiological effects of diet mixing on consumer fitness: A meta-analysis. *Ecology*, *94*(3), 565–572.

Lemorini, C., Plummer, T. W., Braun, D. R., Crittenden, A. N., Ditchfield, P. W., Bishop, L. C., Hertel, F., Oliver, J. S., Marlowe, F. W., Schoeninger, M. J., & Potts, R. (2014). Old stones' song: Use-wear experiments and analysis of the Oldowan quartz and quartzite assemblage from Kanjera South (Kenya). *Journal of Human Evolution*, *72*, 10–25.

Lemorini, C., Stiner, M. C., Gopher, A., Shimelmitz, R., & Barkai, R. (2006). Use-wear analysis of an Amudian laminar assemblage from the Acheuleo-Yabrudian of Qesem Cave, Israel. *Journal of Archaeological Science*, *33*(7), 921–934.

Lemorini, C., Venditti, F., Assaf, E., Parush, Y., Barkai, R., & Gopher, A. (2015). The function of recycled lithic items at late Lower Paleolithic Qesem Cave, Israel: An overview of the use-wear data. *Quaternary International*, *361*, 103–112.

Leonard, W. R., Snodgrass, J. J., & Robertson, M. L. (2007). Effects of brain evolution on human nutrition and metabolism. *Annual Review of Nutrition*, *27*, 311–327. https://doi.org/10.1146/annurev.nutr.27.061406.093659

Lewis, M. E., & Werdelin, L. (2007). Patterns of change in the Plio-Pleistocene carnivorans of eastern Africa. In *Hominin environments in the East African Pliocene: An assessment of the faunal evidence* (pp. 77–105). Springer.

Lieberman, D. E., Bramble, D. M., Raichlen, D. A., & Shea, J. J. (2007). The evolution of endurance running and the tyranny of ethnography: A reply to Pickering and Bunn (2007).

Lightfoot, E., Boneva, B., Miracle, P., Šlaus, M., & O'connell, T. (2011). Exploring the Mesolithic and Neolithic transition in Croatia through isotopic investigations. *Antiquity*, *85*(327), 73–86.

Liu, L., & Chen, X. (2012). *The archaeology of China: From the late Paleolithic to the early Bronze Age*. Cambridge University Press.

Longo, N., Frigeni, M., & Pasquali, M. (2016). Carnitine transport and fatty acid oxidation. *Biochimica et Biophysica Acta (BBA)-Molecular Cell Research*, *1863*(10), 2422–2435.

Lordkipanidze, D., de León, M. S. P., Margvelashvili, A., Rak, Y., Rightmire, G. P., Vekua, A., & Zollikofer, C. P. (2013). A complete skull from Dmanisi, Georgia, and the evolutionary biology of early Homo. *Science*, *342*(6156), 326–331.

Lucas, P. W., Ang, K. Y., Sui, Z., Agrawal, K. R., Prinz, J. F., & Dominy, N. J. (2006). A brief review of the recent evolution of the human mouth in physiological and nutritional contexts. *Physiology & Behavior*, *89*(1), 36–38.

Lucas, P. W., Sui, Z., Ang, K. Y., Tan, H. T. W., King, S. H., Sadler, B., & Peri, N. (2009). Meals versus snacks and the human dentition and diet during the Paleolithic. In *The evolution of Hominin diets* (pp. 31–41). Springer.

Ludwig, D. S. (2020). The kKetogenic diet: evidence for optimism but high-quality research needed. *The Journal of Nutrition*, *150*(6), 1354–1359. https://doi.org/10.1093/jn/nxz308.

Makarewicz, C. A., & Sealy, J. (2015). Dietary reconstruction, mobility, and the analysis of ancient skeletal tissues: Expanding the prospects of stable isotope research in archaeology. *Journal of Archaeological Science*, *56*, 146–158.

Malhi, Y., Doughty, C. E., Galetti, M., Smith, F. A., Svenning, J.-C., & Terborgh, J. W. (2016). Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *Proceedings of the National Academy of Sciences*, *113*(4), 838–846.

Mann, N. (2000). Dietary lean red meat and human evolution. *European Journal of Nutrition*, *39*(2), 71–79.

Manne, T. H., Stiner, M. C., & Bicho, N. F. (2006). *Evidence for bone grease rendering during the Upper Paleolithic at Vale Boi (Algarve, Portugal)*. Paper presented at the Promontoria Monografica.

Mannino, M. A., Catalano, G., Talamo, S., Mannino, G., Di Salvo, R., Schimmenti, V., Lalueza-Fox, C., Messina, A., Petruso, D., Caramelli, D., Richards, M. P., & Sineo, L. (2012). Origin and diet of the prehistoric hunter-gatherers on the Mediterranean island of Favignana (Ègadi Islands, Sicily). *PLoS One*, *7*(11), e49802.

Mannino, M. A., Thomas, K., Leng, M., Di Salvo, R., & Richards, M. P. (2011). Stuck to the shore? Investigating prehistoric hunter-gatherer subsistence, mobility and territoriality in a Mediterranean coastal landscape through isotope analyses on marine mollusc shell carbonates and human bone collagen. *Quaternary International*, *244*(1), 88–104.

Marlowe, F. (2010). *The Hadza: Hunter-gatherers of Tanzania*. University of California Press.

Marlowe, F. W. (2005). Hunter-gatherers and human evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, *14*(2), 54–67.

Mallol, C., Marlowe, F. W., Wood, B. M., & Porter, C. C. (2007). Earth, wind, and fire: ethnoarchaeological signals of Hadza fires. *Journal of Archaeological Science*, *34*(12), 2035–2052. https://doi.org/10.1016/j.jas.2007.02.002.

Mathias, R. A., Fu, W., Akey, J. M., Ainsworth, H. C., Torgerson, D. G., Ruczinski, I., Sergeant, S., Barnes, K. C., & Chilton, F. H. (2012). Adaptive evolution of the FADS gene cluster within Africa. *PLoS One*, *7*(9), e44926.

Mattson, M. P., Moehl, K., Ghena, N., Schmaedick, M., & Cheng, A. (2018). Intermittent metabolic switching, neuroplasticity and brain health. *Nature Reviews Neuroscience*, *19*(2), 63–80.

McBrearty, S., & Brooks, A. S. (2000). The revolution that wasn't: A new interpretation of the origin of modern human behavior. *Journal of Human Evolution*, *39*(5), 453–563.

McClellan, W. S., & Du Bois, E. F. (1930). Clinical calorimetry XLV. Prolonged meat diets with a study of kidney function and ketosis. *Journal of Biological Chemistry*, *87*(3), 651–668.

McHenry, H. (2009). *Human evolution*. Harvard University Press.

McNeil, N. (1984). The contribution of the large intestine to energy supplies in man. *The American Journal of Clinical Nutrition*, *39*(2), 338–342.

McPherron, S. P., Alemseged, Z., Marean, C. W., Wynn, J. G., Reed, D., Geraads, D., Bobe, R., & Béarat, H. A. (2010). Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature*, *466*(7308), 857–860.

Mejía-Benítez, M. A., Bonnefond, A., Yengo, L., Huyvaert, M., Dechaume, A., Peralta-Romero, J., Klünder-Klünder, M., Mena, J. G., El-Sayed Moustafa, J. S., Falchi, M., Cruz, M., & Froguel, P. (2015). Beneficial effect of a high number of copies of salivary amylase AMY1 gene on obesity risk in Mexican children. *Diabetologia*, *58*(2), 290–294.

Meltzer, D. J. (2015). Pleistocene overkill and north American mammalian extinctions. *Annual Review of Anthropology*, *44*, 33–53.

Meltzer DJ. (2020). Overkill, glacial history, and the extinction of North America's Ice Age megafauna. Proceedings of the National Academy of Sciences:202015032.

Melamed, Y., Kislev, M. E., Geffen, E., Lev-Yadun, S., & Goren-Inbar, N. (2016). The plant component of an Acheulian diet at Gesher Benot Yaʿaqov, Israel. *Proceedings of the National Academy of Sciences*, *113*, (51), 14674–14679. https://doi.org/10.1073/pnas.1607872113.

Milton, K. (1987). Primate diets and gut morphology: Implications for hominid evolution. In M. Harris & E. Ross (Eds.), *Food and evolution: Toward a theory of human food habits* (pp. 93–115). Temple University Press.

Moltke, I., Grarup, N., Jørgensen, M. E., Bjerregaard, P., Treebak, J. T., Fumagalli, M., Korneliussen, T. S., Andersen, M. A., Nielsen, T. S., Krarup, N. T., Gjesing, A. P., Zierath, J. R., Linneberg, A., Wu, X., Sun, G., Jin, X., Al-Aama, J., Wang, J., Borch-Johnsen, K., … Hansen, T. (2014). A common Greenlandic TBC1D4 variant confers muscle insulin resistance and type 2 diabetes. *Nature*, *512*(7513), 190–193.

Monjeau, J., Araujo, B., Abramson, G., Kuperman, M., Laguna, M., & Lanata, J. (2015). The controversy space on Quaternary megafaunal extinctions. *Quaternary International*, *30*(1), e11.

Morin, E., & Ready, E. (2013). Foraging goals and transport decisions in western Europe during the Paleolithic and early Holocene. In *Zooarchaeology and modern human origins* (pp. 227–269). Springer.

Mörseburg, A., Alt, K. W., & Knipper, C. (2015). Same old in Middle Neolithic diets? A stable isotope study of bone collagen from the burial community of Jechtingen, southwest Germany. *Journal of Anthropological Archaeology*, *39*, 210–221.

Munro, N. D. (2004). Zooarchaeological measures of hunting pressure and occupation intensity in the natufian. *Current Anthropology*, *45*(S4), S5–S34. https://doi.org/10.1086/422084.

Muttoni, G., Kent, D. V., Scardia, G., & Monesi, E. (2014). Migration of hominins with megaherbivores into Europe via the Danube-Po Gateway in the late Matuyama climate revolution. *Rivista Italiana di Paleontologia e Stratigrafia (Research In Paleontology and Stratigraphy)*, *120*(3), 351–365.

Muttoni, G., Scardia, G., Dimitrijević, V., Kent, D. V., Monesi, E., Mrdjić, N., & Korać, M. (2015). Age of Mammuthus trogontherii from Kostolac, Serbia, and the entry of megaherbivores into Europe during the Late Matuyama climate revolution. *Quaternary Research*, *84*(3), 439–447.

Muttoni, G., Scardia, G., & Kent, D. V. (2010). Human migration into Europe during the late Early Pleistocene climate transition. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, *296*(1), 79–93.

Muttoni, G., Scardia, G., & Kent, D. V. (2018). Early hominins in Europe: The Galerian migration hypothesis. *Quaternary Science Reviews*, *180*, 1–29.

Naito, Y. I., Chikaraishi, Y., Ohkouchi, N., Drucker, D. G., & Bocherens, H. (2013). Nitrogen isotopic composition of collagen amino acids as an indicator of aquatic resource consumption: Insights from Mesolithic and Epipalaeolithic archaeological sites in France. *World Archaeology*, *45*(3), 338–359.

Navarrete, A., Schaik, C. P. V., & Isler, K. (2011). Energetics and the evolution of human brain size. *Nature*, *480*, 91–93. https://doi.org/10.1038/nature10629

Nazarewicz, R. R., Ziolkowski, W., Vaccaro, P. S., & Ghafourifar, P. (2007). Effect of short-term ketogenic diet on redox status of human blood. *Rejuvenation Research*, *10*(4), 435–440.

Neumann, C. G., Murphy, S. P., Gewa, C., Grillenberger, M., & Bwibo, N. O. (2007). Meat supplementation improves growth, cognitive, and behavioral outcomes in Kenyan children. *The Journal of Nutrition*, *137*(4), 1119–1123.

Noss, A. J., & Hewlett, B. S. (2001). The contexts of female hunting in Central Africa. *American Anthropologist*, *103*(4), 1024–1040.

Nowell, A., Walker, C., Cordova, C., Ames, C., Pokines, J., Stueber, D., De Witt, R., & Al-Souliman, A. (2016). Middle Pleistocene subsistence in the Azraq Oasis, Jordan: Protein residue and other proxies. *Journal of Archaeological Science*, *73*, 36–44.

Nudds, T. D. (1978). Convergence of group size strategies by mammalian social carnivores. *The American Naturalist*, *112*(987), 957–960.

Okarma, H. (1989). Distribution and numbers of wolves in Poland. *Acta Theriologica*, *34*(35), 497–503.

Okerblom, J., Fletes, W., Patel, H. H., Schenk, S., Varki, A., & Breen, E. C. (2018). Human-like Cmah inactivation in mice increases running endurance and decreases muscle fatigability: Implications for human evolution. *Proceedings of the Royal Society B: Biological Sciences*, *285* (1886), 20181656.

Oliver, J. S., Plummer, T. W., Hertel, F., & Bishop, L. C. (2019). Bovid mortality patterns from Kanjera South, Homa Peninsula, Kenya and FLK-Zinj, Olduvai Gorge, Tanzania: Evidence for habitat mediated variability in Oldowan hominin hunting and scavenging behavior. *Journal of Human Evolution*, *131*, 61–75.

Organ, C., Nunn, C. L., Machanda, Z., & Wrangham, R. W. (2011). Phylogenetic rate shifts in feeding time during the evolution of Homo. *Proceedings of the National Academy of Sciences*, *108*(35), 14555–14559.

Outram, A. K. (2004). Identifying dietary stress in marginal environments: Bone fats, optimal foraging theory and the seasonal round. In M. Miondini, S. Munoz, & S. Wickler (Eds.), *Colonisation*, *migration and marginal areas: A zooarchaeological approach* (pp. 74–85). Oxford Books.

Owen-Smith, R. N. (2002). *Adaptive herbivore ecology: From resources to populations in variable environments*. Cambridge University Press.

Packer, R. M., Law, T. H., Davies, E., Zanghi, B., Pan, Y., & Volk, H. A. (2016). Effects of a ketogenic diet on ADHD-like behavior in dogs with idiopathic epilepsy. *Epilepsy & Behavior*, *55*, 62–68.

Palombo, M. R. (2014). Deconstructing mammal dispersals and faunal dynamics in SW Europe during the Quaternary. *Quaternary Science Reviews*, *96*, 50–71.

Palombo, M. R., & Mussi, M. (2006). Large mammal guilds at the time of the first human colonization of Europe: The case of the Italian Pleistocene record. *Quaternary International*, *149*(1), 94–103.

Pante, M. C., Njau, J. K., Hensley-Marschand, B., Keevil, T. L., Martín-Ramos, C., Peters, R. F., & de la Torre, I. (2018). The carnivorous feeding behavior of early Homo at HWK EE, Bed II, Olduvai Gorge, Tanzania. *Journal of Human Evolution*, *120*, 215–235.

Pérez-Pérez, A., Espurz, V., de Castro, J. M. A. B., de Lumley, M. A., & Turbón, D. (2003). Non-occlusal dental microwear variability in a sample of Middle and Late Pleistocene human populations from Europe and the Near East. *Journal of Human Evolution*, *44*(4), 497–513.

Perry, G., Dominy, N., Claw, K., & Lee, A. (2007). Diet and the evolution of human amylase gene copy number variation. *Nature*, *39*(10), 1256.

Perry, G. H., Kistler, L., Kelaita, M. A., & Sams, A. J. (2015). Insights into hominin phenotypic and dietary evolution from ancient DNA sequence data. *Journal of Human Evolution*, *79*, 55–63.

Pickering, T. R., & Bunn, H. T. (2007). The endurance running hypothesis and hunting and scavenging in savanna-woodlands. *Journal of Human Evolution*, *53*(4), 434–438.

Pineda-Munoz, S., & Alroy, J. (2014). Dietary characterization of terrestrial mammals. *Proceedings of the Royal Society B: Biological Sciences*, *281* (1789), 20141173.

Pitts, G. C., & Bullard, T. R. (1967). Some interspecific aspects of body composition in mammals. In *Body composition in animals and man* (pp. 45–70). National Academy of Sciences.

Plourde, M., & Cunnane, S. C. (2007). Extremely limited synthesis of long chain polyunsaturates in adults: Implications for their dietary essentiality and use as supplements. *Applied Physiology*, *Nutrition*, *and Metabolism*, *32*(4), 619–634. https://doi.org/10.1139/H07-034

Pond, C. M. (1978). Morphological aspects and the ecological and mechanical consequences of fat deposition in wild vertebrates. *Annual Review of Ecology and Systematics*, *9*(1), 519–570.

Pond, C. M., & Mattacks, C. A. (1985). Body mass and natural diet as determinants of the number and volume of adipocytes in eutherian mammals. *Journal of Morphology*, *185*(2), 183–193.

Pontzer, H. (2015). Constrained total energy expenditure and the evolutionary biology of energy balance. *Exercise and Sport Sciences Reviews*, *43*(3), 110–116.

Pontzer, H. (2017). Economy and endurance in human evolution. *Current Biology*, *27*(12), R613–R621.

Pontzer, H., Brown, M. H., Raichlen, D. A., Dunsworth, H., Hare, B., Walker, K., Luke, A., Dugas, L. R., Durazo-Arvizu, R., Schoeller, D., Plange-Rhule, J., Bovet, P., Forrester, T. E., Lambert, E. V., Thompson, M. E., Shumaker, R. W., & Ross, S. R. (2016). Metabolic acceleration and the evolution of human brain size and life history. *Nature*, *533*(7603), 390–392.

Pontzer, H., Raichlen, D. A., Wood, B. M., Emery Thompson, M., Racette, S. B., Mabulla, A. Z., & Marlowe, F. W. (2015). Energy expenditure and activity among Hadza hunter-gatherers. *American Journal of Human Biology*, *27*(5), 628–637.

Pontzer, H., Scott, J. R., Lordkipanidze, D., & Ungar, P. S. (2011). Dental microwear texture analysis and diet in the Dmanisi hominins. *Journal of Human Evolution*, *61*(6), 683–687.

Popovich, D. G., Jenkins, D. J., Kendall, C. W., Dierenfeld, E. S., Carroll, R. W., Tariq, N., & Vidgen, E. (1997). The western lowland gorilla diet has implications for the health of humans and other hominoids. *The Journal of Nutrition*, *127*(10), 2000–2005.

Potts, R. (1998). Variability selection in hominid evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, *7*(3), 81–96.

Potts, R., Behrensmeyer, A. K., Faith, J. T., Tryon, C. A., Brooks, A. S., Yellen, J. E., Deino, A. L., Kinyanjui, R., Clark, J. B., Haradon, C. M., Levin, N. E., Meijer, H. J. M., Veatch, E. G., Owen, R. B., & Renaut, R. W. (2018). Environmental dynamics during the onset of the Middle Stone Age in eastern Africa. *Science*, *360*(6384), 86–90.

Potts, R., Dommain, R., Moerman, J. W., Behrensmeyer, A. K., Deino, A. L., Riedl, S., Beverly, E. J., Brown, E. T., Deocampo, D., & Kinyanjui, R. (2020). Increased ecological resource variability during a critical transition in hominin evolution. *Science Advances*, *6*(43), eabc8975.

Power, R. C., & Williams, F. L. E. (2018). Evidence of increasing intensity of food processing during the upper paleolithic of western eurasia. *Journal of Paleolithic Archaeology*, *1*(4), 281–301. https://doi.org/10.1007/s41982-018-0014-x.

Prat, S., Péan, S. C., Crépin, L., Drucker, D. G., Puaud, S. J., Valladas, H., Lázničková-Galetová, M., van der Plicht, J., & Yanevich, A. (2011). The oldest anatomically modern humans from far southeast Europe: Direct dating, culture and behavior. *PLoS One*, *6*(6), e20834.

Price, S. A., Hopkins, S. S., Smith, K. K., & Roth, V. L. (2012). Tempo of trophic evolution and its impact on mammalian diversification. *Proceedings of the National Academy of Sciences*, *109*(18), 7008–7012.

Psouni, E., Janke, A., & Garwicz, M. (2012). Impact of carnivory on human development and evolution revealed by a new unifying model of weaning in mammals. *PLoS One*, *7*(4), e32452.

Revedin, A., Aranguren, B., Becattini, R., Longo, L., Marconi, E., Lippi, M. M., Skakun, N., Sinitsyn, A., Spiridonova, E., & Svoboda, J. (2010). Thirty thousand-year-old evidence of plant food processing. *Proceedings of the National Academy of Sciences*, *107*(44), 18815–18819.

Richards, M., & Trinkaus, E. (2009). Isotopic evidence for the diets of European Neanderthals and early modern humans. *Proceedings of the National Academy of Science*, *106*(38), 16034–16039.

Richards, M. P., Karavanić, I., Pettitt, P., & Miracle, P. (2015). Isotope and faunal evidence for high levels of freshwater fish consumption by Late Glacial humans at the Late Upper Palaeolithic site of Šandalja II, Istria, Croatia. *Journal of Archaeological Science*, *61*, 204–212.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., & Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, *343*(6167), 1241484.

Roach, N. T., & Richmond, B. G. (2015). Clavicle length, throwing performance and the reconstruction of the Homo erectus shoulder. *Journal of Human Evolution*, *80*, 107–113.

Roach, N. T., Venkadesan, M., Rainbow, M. J., & Lieberman, D. E. (2013). Elastic energy storage in the shoulder and the evolution of high-speed throwing in Homo. *Nature*, *498*(7455), 483–486.

Robson, S. L., & Wood, B. (2008). Hominin life history: Reconstruction and evolution. *Journal of Anatomy*, *212*(4), 394–425.

Rockwell, D. (1993). *Giving voice to bear: Native American Indian myths, rituals and images of the bear*. Roberts Reinhardt Publishing.

Roebroeks, W., & Villa, P. (2011). On the earliest evidence for habitual use of fire in Europe. *Proceedings of the National Academy of Sciences*, *108*(13), 5209–5214.

Rosell, J., Baquedano, E., Blasco, R., & Camarós, E. (2012). New insights on Hominid-Carnivore interactions during the Pleistocene. *Journal of Taphonomy*, *10*(3), 125–128.

Royer, A., Daux, V., Fourel, F., & Lecuyer, C. (2017). Carbon, nitrogen and oxygen isotope fractionation during food cooking: Implications for the interpretation of the fossil human record. *American Journal of Physical Anthropology*, *163*(4), 759–771.

Rudman, D., Difulco, T. J., Galambos, J. T., Smith, R. B., Salam, A. A., & Warren, W. D. (1973). Maximal rates of excretion and synthesis of urea in normal and cirrhotic subjects. *Journal of Clinical Investigation*, *52*, 2241–2249. https://doi.org/10.1172/jci107410

Russell, T. L., Berardi, R. R., Barnett, J. L., Dermentzoglou, L. C., Jarvenpaa, K. M., Schmaltz, S. P., & Dressman, J. B. (1993). Upper gastrointestinal pH in seventy-nine healthy, elderly, North American men and women. *Pharmaceutical Research*, *10*(2), 187–196. https://doi.org/10.1023/a:1018970323716

Salazar-García, D. C., Aura, J. E., Olària, C. R., Talamo, S., Morales, J. V., & Richards, M. P. (2014). Isotope evidence for the use of marine resources in the Eastern Iberian Mesolithic. *Journal of Archaeological Science*, *42*, 231–240.

Saltré, F., Rodríguez-Rey, M., Brook, B. W., Johnson, C. N., Turney, C. S. M., Alroy, J., Cooper, A., Beeton, N., Bird, M. I., Fordham, D. A., Gillespie, R., Herrando-Pérez, S., Jacobs, Z., Miller, G. H., Nogués-Bravo, D., Prideaux, G. J., Roberts, R. G., & Bradshaw, C. J. A. (2016). Climate change not to blame for late Quaternary megafauna extinctions in Australia. *Nature Communications*, *7*(1). https://doi.org/10.1038/ncomms10511.

Sandom, C., Faurby, S., Sandel, B., & Svenning, J.-C. (2014). Global late Quaternary megafauna extinctions linked to humans, not climate change. *Proceedings of the Royal Society B*, *281*, 20133254.

Sayers, K., & Lovejoy, C. O. (2014). Blood, bulbs, and bunodonts: On evolutionary ecology and the diets of Ardipithecus, Australopithecus, and early Homo. *The Quarterly Review of Biology*, *89*(4), 319–357.

Scannapieco, F. A., Torres, G., & Levine, M. J. (1993). Salivary α-amylase: Role in dental plaque and caries formation. *Critical Reviews in Oral Biology and Medicine*, *4*(3), 301–307.

Schaller, G. B., & Lowther, G. R. (1969). The relevance of carnivore behavior to the study of early hominids. *Southwestern Journal of Anthropology*, *25*, 307–341.

Schermerhorn, T. (2013). Normal glucose metabolism in carnivores overlaps with diabetes pathology in non-carnivores. *Frontiers in Endocrinology*, *4*, 188.

Schnorr, S. L., Crittenden, A. N., Venema, K., Marlowe, F. W., & Henry, A. G. (2015). Assessing digestibility of Hadza tubers using a dynamic in-vitro model. *American Journal of Physical Anthropology*, *158*(3), 371–385.

Sealy, J. (2006). Diet, mobility, and settlement pattern among Holocene hunter-gatherers in southernmost Africa. *Current Anthropology*, *47*(4), 569–595.

Ségurel, L., Austerlitz, F., Toupance, B., Gautier, M., Kelley, J. L., Pasquet, P., Lonjou, C., Georges, M., Voisin, S., Cruaud, C., Couloux, A., Hegay, T., Aldashev, A., Vitalis, R., & Heyer, E. (2013). Positive selection of protective variants for type 2 diabetes from the Neolithic onward: A case study in Central Asia. *European Journal of Human Genetics*, *21*(10), 1146–1151.

Sevanian, A., Davies, K. J., & Hochstein, P. (1985). Conservation of vitamin C by uric acid in blood. *Journal of Free Radicals in Biology & Medicine*, *1* (2), 117–124.

Shultz, S., Nelson, E., & Dunbar, R. I. M. (2012). Hominin cognitive evolution: identifying patterns and processes in the fossil and archaeological record. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1599), 2130–2140. https://doi.org/10.1098/rstb.2012.0115.

Shahack-Gross, R., Berna, F., Karkanas, P., Lemorini, C., Gopher, A., & Barkai, R. (2014). Evidence for the repeated use of a central hearth at Middle Pleistocene (300 ky ago) Qesem Cave, Israel. *Journal of Archaeological Science*, *44*, 12–21.

Shimelmitz, R., Kuhn, S. L., Jelinek, A. J., Ronen, A., Clark, A. E., & Weinstein-Evron, M. (2014). 'Fire at will': The emergence of habitual fire use 350,000 years ago. *Journal of Human Evolution*, *77*, 196–203.

Shipman, P., & Walker, A. (1989). The costs of becoming a predator. *Journal of Human Evolution*, *18*(4), 373–392.

Smith, F. A., & Lyons, S. K. (2011). How big should a mammal be? A macroecological look at mammalian body size over space and time. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *366*(1576), 2364–2378.

Smith, F. A., Smith, R. E. E., Lyons, S. K., & Payne, J. L. (2018). Body size downgrading of mammals over the late Quaternary. *Science*, *360* (6386), 310–313.

Smith, F. A., Smith, R. E. E., Lyons, S. K., Payne, J. L., & Villaseñor, A. (2019). The accelerating influence of humans on mammalian macroecological patterns over the late Quaternary. *Quaternary Science Reviews*, *211*, 1–16.

Smith, J. E., Swanson, E. M., Reed, D., & Holekamp, K. E. (2012). Evolution of cooperation among mammalian carnivores and its relevance to hominin evolution. *Current Anthropology*, *53*(S6), S436–S452.

Solodenko, N., Zupancich, A., Cesaro, S. N., Marder, O., Lemorini, C., & Barkai, R. (2015). Fat residue and use-wear found on Acheulian biface and scraper associated with butchered elephant remains at the site of Revadim, Israel. *PLoS One*, *10*(3), e0118572.

Speth, J. D. (1989). Early hominid hunting and scavenging - The role of meat as an energy-source. *Journal of Human Evolution*, *18*, 329–343. https://doi.org/10.1016/0047-2484(89)90035-3

Speth, J. D. (2010). Big-game hunting: Protein, fat, or politics? In *The paleoanthropology and archaeology of big-game hunting* (pp. 149–161). Springer.

Speth, J. D. (2012). *Paleoanthropology and archaeology of big-game hunting*. Springer-Verlag.

Speth, J. D. (2017). Putrid meat and fish in the Eurasian Middle and Upper Paleolithic: Are we missing a key part of neanderthal and modern human diet? *PaleoAnthropology*, *2017*, 44–72.

Speth, J. D., & Clark, J. L. (2006). Hunting and overhunting in the Levantine Late Middle Palaeolithic. *Before Farming*, *2006*, 1–42.

Stahl, A. B., Dunbar, R., Homewood, K., Ikawa-Smith, F., Kortlandt, A., McGrew, W., Milton, K., Paterson, J. D., Poirier, F. E., Sugardjito, J., Tanner, N. M., & Wrangham, R. W. (1984). Hominid dietary selection before fire [and comments and reply]. *Current Anthropology*, *25*(2), 151–168.

Stefansson, V. (1960). *The fat of the land*. The Macmillam Company.

Stepanova, K. (2020). Upper Palaeolithic grinding stones from Eastern European sites: An overview. *Quaternary International*, *541*, 162–181. https://doi.org/10.1016/j.quaint.2019.11.035.

Steudel-Numbers, K. L., & Wall-Scheffler, C. M. (2009). Optimal running speed and the evolution of hominin hunting strategies. *Journal of Human Evolution*, *56*(4), 355–360.

Stiner, M. (2012). Competition theory and the case for Pleistocene Hominin-Carnivore Co-evolution. *Journal of Taphonomy*, *10*(3), 129–145.

Stiner, M. C. (2002). Carnivory, coevolution, and the geographic spread of the genus Homo. *Journal of Archaeological Research*, *10*(1), 1–63.

Stiner, M. C., Munro, N. D., Surovell, T. A., Bar-Oz, G., Dayan, T., Bicho, N. F., Bietti, A., Brugal, J.-P., Carbonell, E., & Flannery, K. V. (2000). The tortoise and the hare: Small-game use, the broad-spectrum revolution, and Paleolithic demography. *Current Anthropology*, *41*(1), 39–79.

Ströhle, A., & Hahn, A. (2011). Diets of modern hunter-gatherers vary substantially in their carbohydrate content depending on ecoenvironments: Results from an ethnographic analysis. *Nutrition Research*, *31*(6), 429–435.

Swain-Lenz, D., Berrio, A., Safi, A., Crawford, G. E., & Wray, G. A. (2019). Comparative analyses of chromatin landscape in white adipose tissue suggest humans may have less beigeing potential than other primates. *Genome Biology and Evolution*, *11*(7), 1997–2008.

Szczepanek, A., Belka, Z., Jarosz, P., Pospieszny, Ł., Dopieralska, J., Frei, K. M., Rauba-Bukowska, A., Werens, K., Górski, J., Hozer, M., Mazurek, M., & Włodarczak, P. (2018). Understanding Final Neolithic communities in south-eastern Poland: New insights on diet and mobility from isotopic data. *PLoS One*, *13*(12), e0207748.

Tacail, T., Martin, J. E., Arnaud-Godet, F., Thackeray, J. F., Cerling, T. E., Braga, J., & Balter, V. (2019). Calcium isotopic patterns in enamel reflect different nursing behaviors among South African early hominins. *Science Advances*, *5*(8), eaax3250.

Tagliacozzo, A., Romandini, M., Fiore, I., Gala, M., & Peresani, M. (2013). Animal exploitation strategies during the Uluzzian at Grotta di Fumane (Verona, Italy). In *Zooarchaeology and modern human origins* (pp. 129–150). Springer.

Teaford, M. F., Ungar, P. S., & Grine, F. E. (2002). Paleontological evidence for the diets of African Plio-Pleistocene hominins with special reference to early Homo. *Human Diet: Its Origin and Evolution*, 143–166. Greenwood Publishing Group.

Thomas, W. A. (1927). Health of a carnivorous race: A study of the Eskimo. *Journal of the American Medical Association*, *88*(20), 1559–1560.

Thompson, J., Carvalho, S., Marean, C., & Alemseged, Z. (2019). Origins of the human predatory pattern: The transition to large-animal exploitation by early hominins. *Current Anthropology*, *60*(1), 1–23.

Thompson, P. R. (1975). A cross-species analysis of carnivore, primate, and hominid behaviour. *Journal of Human Evolution*, *4*(2), 113–124.

Tindale, N. B. (1972). The Pitjandjara. In M. G. Bicchieri (Ed.), *Hunters and gatherers today* (pp. 217–268). Holt, Rinehart and Winston.

Tomiya, S. (2013). Body size and extinction risk in terrestrial mammals above the species level. *The American Naturalist*, *182*(6), E196–E214.

Topping, D. L., & Clifton, P. M. (2001). Short-chain fatty acids and human colonic function: Roles of resistant starch and nonstarch polysaccharides. *Physiological Reviews*, *81*(3), 1031–1064.

Toth, N., & Schick, K. (2019). Why did the Acheulean happen? Experimental studies into the manufacture and function of Acheulean artifacts. *L'Anthropologie*, *123*(4–5), 724–768.

Umezaki, M., Naito, Y. I., Tsutaya, T., Baba, J., Tadokoro, K., Odani, S., Morita, A., Natsuhara, K., Phuanukoonnon, S., Vengiau, G., Siba, P. M., & Yoneda, M. (2016). Association between sex inequality in animal protein intake and economic development in the Papua New Guinea highlands: The carbon and nitrogen isotopic composition of scalp hair and fingernail. *American Journal of Physical Anthropology*, *159*(1), 164–173. https://doi.org/10.1002/ajpa.22844.

Ungar, P. S. (2012). Dental evidence for the reconstruction of diet in African early Homo. *Current Anthropology*, *53*(S6), S318–S329.

Ungar, P. S., Grine, F. E., & Teaford, M. F. (2006). Diet in early Homo: A review of the evidence and a new model of adaptive versatility. *Annual Review of Anthropology*, *35*, 209–228.

Ungar, P. S., Krueger, K. L., Blumenschine, R. J., Njau, J., & Scott, R. S. (2012). Dental microwear texture analysis of hominins recovered by the Olduvai Landscape Paleoanthropology Project, 1995–2007. *Journal of Human Evolution*, *63*(2), 429–437.

Ungar, P. S., & Sponheimer, M. (2013). Hominin diets. In B. David (Ed.) *A companion to paleoanthropology* (pp. 165–182). John Wiley & Sons.

Ungar, P. S., Sponheimer, M. (2011). The Diets of Early Hominins. *Science*, *334*(6053), 190–193. https://doi.org/10.1126/science.1207701.

Usher, C. L., Handsaker, R. E., Esko, T., Tuke, M. A., Weedon, M. N., Hastie, A. R., Cao, H., Moon, J. E., Kashin, S., Fuchsberger, C., Metspalu, A., Pato, C. N., Pato, M. T., McCarthy, M. I., Boehnke, M., Altshuler, D. M., Frayling, T. M., Hirschhorn, J. N., & McCarroll, S. A. (2015). Structural forms of the human amylase locus and their relationships to SNPs, haplotypes and obesity. *Nature Genetics*, *47*(8), 921–925.

van Casteren, A., Strait, D. S., Swain, M. V., Michael, S., Thai, L. A., Philip, S. M., Saji, S., Al-Fadhalah, K., Almusallam, A. S., Shekeban, A., McGraw, W. S., Kane, E. E., Wright, B. W., & Lucas, P. W. (2020). Hard plant tissues do not contribute meaningfully to dental microwear: Evolutionary implications. *Scientific Reports*, *10*(1), 1–9.

van der Plicht, J., Amkreutz, L., Niekus, M. T., Peeters, J., & Smit, B. (2016). Surf'n Turf in Doggerland: Dating, stable isotopes and diet of Mesolithic human remains from the southern North Sea. *Journal of Archaeological Science: Reports*, *10*, 110–118.

van Valkenburgh, B., Hayward, M. W., Ripple, W. J., Meloro, C., & Roth, V. L. (2016). The impact of large terrestrial carnivores on Pleistocene ecosystems. *Proceedings of the National Academy of Sciences*, *113* (4), 862–867.

van Valkenburgh, B., Wang, X., & Damuth, J. (2004). Cope's rule, hypercarnivory, and extinction in North American canids. *Science*, *306* (5693), 101–104.

van Valkenburgh, B., & Wayne, R. K. (2010). Carnivores. *Current Biology*, *20*(21), R915–R919.

Venditti, F., Cristiani, E., Nunziante-Cesaro, S., Agam, A., Lemorini, C., & Barkai, R. (2019). Animal residues found on tiny Lower Paleolithic tools reveal their use in butchery. *Scientific Reports*, *9*(1), 1–14.

Villa, P., Soriano, S., Tsanova, T., Degano, I., Higham, T. F., d'Errico, F., Backwell, L., Lucejko, J. J., Colombini, M. P., & Beaumont, P. B. (2012). Border Cave and the beginning of the Later Stone Age in South Africa. *Proceedings of the National Academy of Sciences*, *109*(33), 13208–13213.

Vining, A. Q., & Nunn, C. L. (2016). Evolutionary change in physiological phenotypes along the human lineage. *Evolution, Medicine, and Public Health*, *2016*(1), 312–324.

Vincent, A. S. (1985). Plant foods in savanna environments: A preliminary report of tubers eaten by the Hadza of northern Tanzania. *World Archaeology*, *17*(2), 131–148. https://doi.org/10.1080/00438243.1985.9979958.

Vrba, E. S. (1980). Evolution, species and fossils-how does life evolve. *South African Journal of Science*, *76*(2), 61–84.

Waguespack, N. M. (2005). The organization of male and female labor in foraging societies: Implications for early Paleoindian archaeology. *American Anthropologist*, *107*(4), 666–676.

Waters, M. R., Stafford, T. W., & Carlson, D. L. (2020). The age of Clovis—13,050 to 12,750 cal yr BP. *Science Advances*, *6*(43), eaaz0455.

Werdelin, L., & Lewis, M. E. (2013). Temporal change in functional richness and evenness in the eastern African Plio-Pleistocene carnivoran guild. *PLoS One*, *8*(3), e57944.

Weyer, S., & Pääbo, S. (2016). Functional analyses of transcription factor binding sites that differ between present-day and archaic humans. *Molecular Biology and Evolution*, *33*(2), 316–322.

Wilkinson, P. (2014). Ecosystem models and demographic hypotheses: Predation and prehistory in North America. In D. Clark (Ed.), *Models in archaeology* (pp. 543–576). Routledge.

Wilson, J. X. (2005). Regulation of vitamin C transport. *Annual Review of Nutrition*, *25*, 105–125.

Wissing, C., Rougier, H., Baumann, C., Comeyne, A., Crevecoeur, I., Drucker, D. G., Gaudzinski-Windheuser, S., Germonpré, M., Gómez-Olivencia, A., Krause, J., Matthies, T., Naito, Y. I., Posth, C., Semal, P., Street, M., & Bocherens, H. (2019). Stable isotopes reveal patterns of diet and mobility in the last Neandertals and first modern humans in europe. *Scientific Reports*, *9*(1), 4433.

Wojtal, P., Svoboda, J., Roblíčková, M., & Wilczyński, J. (2020). Carnivores in the everyday life of Gravettian hunters-gatherers in Central Europe. *Journal of Anthropological Archaeology*, *59*, 101171.

Wood, B., & Strait, D. (2004). Patterns of resource use in early Homo and Paranthropus. *Journal of Human Evolution*, *46*(2), 119–162.

Wrangham, R. (2017). Control of fire in the Paleolithic evaluating the cooking hypothesis. *Current Anthropology*, *58*(Suppl. 16), S303–S313. https://doi.org/10.1086/692113

Wrangham, R. W., Conklin-Brittain, N. L., & Hunt, K. D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *International Journal of Primatology*, *19*(6), 949–970.

Wrangham, R. W., Jones, J. H., Laden, G., Pilbeam, D., & Conklin-Brittain, N. L. (1999). The raw and the stolen. *Current Anthropology*, *40*, 567–594.

Wright, K. I. (1994). Ground-stone tools and hunter-gatherer subsistence in southwest Asia: Implications for the transition to farming. *American Antiquity*, *59*, 238–263.

Wroe, S., McHenry, C., & Thomason, J. (2005). Bite club: Comparative bite force in big biting mammals and the prediction of predatory behaviour in fossil taxa. *Proceedings of the Royal Society B: Biological Sciences*, *272* (1563), 619–625.

Wroe, S., Field, J. H., Archer, M., Grayson, D. K., Price, G. J., Louys, J., Faith, J. T., Webb, G. E., Davidson, I., Mooney, S. D. (2013). Climate change frames debate over the extinction of megafauna in Sahul (Pleistocene Australia-New Guinea). *Proceedings of the National Academy of Sciences*, *110* (22), 8777–8781. https://doi.org/10.1073/pnas.1302698110.

Ye, K., Gao, F., Wang, D., Bar-Yosef, O., & Keinan, A. (2017). Adaptation of the FADS gene family in Europe: Variation across time, geography and subsistence. *bioRxiv*, 111229.

Yong, R. Y., Mustaffa, S. A. B., Wasan, P. S., Sheng, L., Marshall, C. R., Scherer, S. W., Teo, Y. Y., & Yap, E. P. (2016). Complex copy number variation of AMY1 does not associate with obesity in two East Asian cohorts. *Human Mutation*, *37*(7), 669–678.

Young, N. M., Capellini, T. D., Roach, N. T., & Alemseged, Z. (2015). Fossil hominin shoulders support an African ape-like last common ancestor of humans and chimpanzees. *Proceedings of the National Academy of Sciences*, *112*(38), 11829–11834.

Zaatari, S., & Hublin, J. J. (2014). Diet of Upper Paleolithic modern humans: Evidence from microwear texture analysis. *American Journal of Physical Anthropology*, *153*(4), 570–581.

Zihlman, A. L., & Bolter, D. R. (2015). Body composition inPan paniscuscompared withHomo sapienshas implications for changes during human evolution. *Proceedings of the National Academy of Sciences*, *112* (24), 7466–7471. https://doi.org/10.1073/pnas.1505071112.

Zink, K. D., & Lieberman, D. E. (2016). Impact of meat and Lower Palaeolithic food processing techniques on chewing in humans. *Nature*, *531*(7595), 500–503.

How to cite this article: Ben-Dor M, Sirtoli R, Barkai R. The evolution of the human trophic level during the Pleistocene. *Yearbook Phys Anthropol*. 2021;175(Suppl. 72):27–56. https://doi.org/10.1002/ajpa.24247