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ASSESSING THE ROLE OF MEAT CONSUMPTION IN HUMAN EVOLUTIONARY CHANGES. A REVIEW

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Abstract
The historical study of changes in food patterns is an integral part of the study of biological and social adaptations during the formation and further development of Homo sapiens species. For quite a long time, diets have been considered the driving force of human evolution. Changes in the type of food consumed and the way it was obtained have been associated with encephalization and the emergence of bipedalism, as well as ecological, social and cultural evolution of hominins[1]. Archaeological and paleontological evidence indicates that at least about 3 million years ago, hominins increased their meat consumption and developed the necessary fabricated stone tools, while their brains and bodies evolved for a novel foraging niche and expanded hunting grounds. Animal-source foods have always been an integral part of the human diet. However, the way they are obtained and processed changed dramatically during human evolution. Meat became a common food source when systematic hunting began using technologies and tools focused on killing animals and meat cutting, which reduced the time and effort spent on chewing food, and later, on its cooking. At some point after this, humans began to hunt together, which made it possible to obtain meat from big game, and as a result, develop the social and altruistic skills to distribute the prey between sexes and ages. The eating habits of our ancestors have been studied using a variety of methods, including anthropometry, the use of archaeological data, and isotope analysis of bones and teeth to determine trophic status. The adaptive biological significance of meat-eating, which played an important role in human evolution, was analyzed, including the "expensive tissue hypothesis" draw attention to the evolutionary forces responsible for the increase in hominin brain size. Furthermore, data on changes in human anatomy, digestion and metabolism are systematized, indicating an evolutionary dependence on and compatibility with significant meat consumption. At the same time, a number of changes in the human body are associated with the skill of using fire in cooking. Heat processing of food stimulated our ancestors to overcome the food specialization intrinsic to animals. The question of what is the right diet for the human species and what are the potential consequences of limiting meat consumption is briefly addressed.

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Introduction

Food affects a variety of aspects in human biology, including the characteristics of behavior. The nutritional factor has always been decisive in the struggle for existence and passing on genes to future generations [1]. Traditions of obtaining food are a fundamental characteristic of the economic and cultural structure of society. "Food is the element of material culture in which traditional features are preserved more than other ones... and at the same time, it more easily and quickly borrows, varies and changes itself" [2]. Nutrition is something special in the life of *Homo sapiens* compared to what it is in other species. The image of the actual human specificity of nutrition phenomenon is formulated in a phrase belonging to Claude Lévi-Strauss: "Humanity starts from cooking" [3].

The nutritional needs of modern people and their diets arose as a result of a multimillion-year evolutionary process in which almost all genetic changes reflected the life circumstances of our ancestors [4].

Human nutrition played a key role in the process of hominization (the process of evolutionary transformation of the human ancestor from anthropoid ape into modern humans) [5]. In the 5-to-7-million-year period since the evolutionary emergence of hominins (bipedal primates within the taxonomic tribe *hominini*), 20 species may have existed [6]. Studies of hunter-gatherers have shown that there was no only universal diet consumed by all extinct

[1] The original meaning of "hominid" term referred only to humans (Homo) and their closest extinct relatives. However, by the 1990s, humans, primates, and their ancestors were considered "hominids." The former restrictive meaning is now largely assigned to "hominin" term, which includes all members of the human clade after the split from chimpanzees. The main difference between hominid and hominin: hominid is the family level that includes humans, whereas hominin is the tribe level that includes humans. (https://translated.turbopages.org/proxy_u/en-ru.ru.e1cacc63–649e6558–1ff4b86b-74722d776562/https/en.wikipedia.org/wiki/Hominidae).

hominin species. Most likely, diet varied depending on geographic location, climate, and specific ecological niche [6]. However, researchers should strive to uncover the dietary flexibility rather than any 'ideal food' that drove hominin adaptation [5].

Archaeological and paleontological evidence indicates that at least about 3 million years ago, hominins increased their meat consumption and developed the necessary fabricated stone tools, while their brains and bodies evolved for a novel foraging niche and expanded hunting grounds. Tools helped in hunting and cutting meat and reduced the time and effort spent on chewing food, and later, on its cooking [7,8].

Meat is one of the most valuable protein sources; also, it contains fats, vitamin B complex, especially vitamin B12 [9] playing an important role in maintaining the nervous system and genetic material of the body through the synthesis of methyl donors, which are necessary for the development and maintenance of methylation patterns in the body, vitamins A and D, large amounts of iron, zinc and other minerals [10]. It contains heme iron, an exclusive animal nutrient that is more easily absorbed than non-heme iron [11]. Although meat consumption is currently associated with a number of diseases, including cardiovascular disease, cancer and diabetes, meat plays an important role not only in maintaining proper growth, development and health, but also in human evolution [9].

Aspects of human anatomy, digestion, and metabolism differ from other primates, indicating an evolutionary dependence on and compatibility with significant meat consumption [12]. Meat consumption has a long history in human evolution, potentially going back to the earliest known anthropomorphic ancestor, who lived 5 to 7 million years ago [13,14]. Primitive stone tools discovered in eastern Africa age-dated back to about 2.5 million years indicate that early humans likely had the ability to cut and process animal meat. For example, cuts made by stone tools on the bones of carnivores found in Kenya and Ethiopia indicate meat consumption [14,15,16]. There is no archaeological evidence of meat consumption before 2.5 million years ago, but the commonality of hunting and meat-eating in our closest common ancestor and chimpanzee suggests that meat-eating has an ancient history, which originated before the anthropomorphic primate evolved, i. e. about 6 to 8 million years ago [17].

Materials and methods

A methodology used the article is an interdisciplinary approach, which combined in the context of the study such areas of anthropology as archaeology, biological and sociocultural anthropology, as well as a number of medical aspects of meat consumption impact on human health.

The advanced search methodology used to conduct the study consisted of two stages. At the first stage, a literature search was conducted to collect representative studies to achieve the purpose of this article; the second stage involved a selection process performed by reviewing the title and abstract of each publication.

To present a global vision of how the scientific community considers methodological problems in assessing the role of meat consumption in human evolutionary changes, a review and analysis of publications on key words and phrases was conducted: eating behavior and hominin adaptations, dietary reconstruction, meat eating and human evolution, encephalization in meat eating, strategies for obtaining food by hominids.

The search was focused on scientific articles and/or book chapters published in English and Russian from 1983 to 2023 in Scopus, PubMed, Google Scholar, Science Direct, eLibrary, and Russian Science Citation Index (RSCI) database.

Inclusion criteria were as follows:

1. Scientific research in the following areas:
   - Human eating behavior and problems of anthropogenesis;
   - Food strategies in prehistoric hunter-fisher-gatherer societies;
   - Anthropological and archaeological evidence of the transition to meat consumption;
   - Climate changes and changes in the diet of hominins;
   - Social role of fire and food innovations of Homo;
   - Nutritional requirements for encephalization.
2. Methods used to prove meat consumption.

Exclusion criteria were as follows:

Scientific articles presenting reviews of human attitudes towards meat-eating based on cravings (positive attitude) and aversion (negative attitude) in a given socio-economic context.

The role of feeding strategies in the evolution of human ancestor

The study of nutrition in past societies is an integral part of the study on biological and social adaptations during the formation and further development of *Homo sapiens*. When describing a species, it is the tradition of biology to give characteristics of the feeding base, food adaptation, and behavioral patterns associated with obtaining, preparing and consuming food. Studies of the behavior of various representatives of the Primates order have shown that, within the entire taxon, the choice of one or another feeding strategy certainly affects the social behavior of individuals within the community. This indicates the extreme importance of variability in nutrition types at various stages of anthropogenesis [18].

As studies of the nutrition in modern representatives of the Primates order have shown, the choice of one or another feeding strategy is associated with the environment and the behavior of animals. Consequently, reconstruction of nutrition types in human ancestors may be used as one of the keys to understanding the anthropogenesis [18]. Diet is related to the behavior, cognitive abilities, life and growth history of each hominin. The adoption of hunting strategies is hypothesized to have led to improved health in early hominids, which explains the increase in adult height about 2.0 to 1.7 million years ago.

The origin of humans from anthropoid apes is confirmed by the similarity of their anatomy, physiology, ethology, immunology and genetic organization, as well as by the bone remains of intermediate fossil animals (Pithecanthropus) and, in general, is also practically assured in natural science. Obtaining food in anthropoid apes is associated with special forms of "food extraction." The cognitive abilities of anthropoid apes have improved greatly due to these skills. All primates are predominantly herbivorous species, and obtaining meat by hunting provides a small proportion of diet [3].

The corpses of dead and killed animals may be considered an affordable and valuable source of animal protein. An interesting method for determining the source type of animal-source foods was used by R. Brantingham. He compared the taphonomic parameters of prey remains typical of Plio-Pleistocene necrophages (some species of hyenas), predators (wolf) and early australopithecines (Koobi Fora). It was revealed that the set of bones in the layers associated with the activity of early australopithecines is more reminiscent of the remains of wolves' meals than of hyenas' meals. Based on this, the author concludes that Plio-Pleistocene australopithecines were hunters, not scavengers [19]. As evidenced by observations of the hunting behavior of modern primates, hunting contributes to the development of more complex relationships within the hunting group, and also stimulates the use of various types of tools.

Anthropologists discovered the remains of ancient humans age-dated back to about one million years in the regions of Central and Southern Africa, Mediterranean, Java Island. The first archaeological evidence was found in 1892 on the island of Java and was named Pithecanthropus (from Greek "pithekos" — ape, "anthropos" — human), i. e. ape-man. And in 1962, Bernard Campbell introduced the concept of *Homo erectus*, i. e. erect man, synanthrope. Therefore, most anthropologists classified Pithecanthropus and Sinanthropus, who lived 2.5 million to 400 thousand years ago, as the species of ancient humans [18].

During the Middle Paleolithic age, about 250 thousand years ago (with a total duration of about 200 thousand years), a glacier advanced. At this time, intensive adaptation of the human body to harsh environmental conditions occurs. More high-calorie foods (fats, proteins) were required than in previous, warm climatic conditions, the main suppliers of which were meat and animal-source foods. Under the influence of climate, nutrition and social system (the primitive communal system was replaced by the clan system), the human himself changes. In particular, the consumption of meat, which is rich in easily digestible proteins, in addition to saving time for the development of a primitive crafts, contributed to significant changes in the structure of the human higher nervous system. According to many researchers of evolutionary processes, this was a significant step in the formation of *Homo sapiens* as a species. The gradually dying out Pithecanthropus was replaced by the Neanderthal man during the Upper Paleolithic age (lasting about 30 to 36 thousand years). About 150 to 30 thousand years ago, Neanderthal man became the most common type of hominid [18].

Neanderthals inhabited mainly the periglacial zone of Europe. Especially many remains were found by archaeologists in the territories southward of 50° north latitude (France, Belgium, Germany, Italy, Spain, Yugoslavia, Czech Republic, Slovakia, etc.) [18]. Neanderthals knew well how to handle fire, and they also learned to use animal skin as clothing. Unlike *Homo erectus*, Neanderthals hunted constantly, and not from time to time.

The food patterns of Neanderthals are more consistent with the harsh conditions of the Ice Age. Simulating of the energy expenditure of Neanderthals, based on body proportions and reconstructed body mass, showed that these expenditures were very high. Heavy physical activity combined with the moderate body size of Neanderthals required the absorption of large amounts of energy-dense food, therefore, their diet had to include a large number of high-energy and highly nutritious foods [18]. During the late Pleistocene (100,000 years ago), meat consumption by Neanderthals was so regular that animal-source foods were the dominant component in the diet [20].

Neoanthrope ("new human", i. e. the first *Homo sapiens*, Cro-Magnon man) is a generalized name for modern humans who replaced all their predecessors during the period of 40 to 10 thousand years ago. Cro-Magnon men habitat was the territory of modern Africa, Europe, southern part of North America, northern part of South America, European part of Russia. All activities of the Cro-Magnon men were improved compared to their ancestors [18].

Homo sapiens (from Latin "intellectual human") is the only one currently living species of the genus Homo (humans) from the family of hominids in the order of primates. In addition to a number of anatomical features, it differs from modern anthropoids in a significant development of material and non-material culture (including the manufacture and use of tools), the ability for articulate speech and abstract thinking [21].

Since the first Homo, humans have always remained omnivores. The proportion of animal proteins and food of plant origin varied in evolution and history. However, the ability for maximum omnivory more than once was a property that provided humans with the prospect of survival in a variety of conditions, and specialization to any single food source became only a temporary "salvation", which closed the prospect of developing for such a specialized group. This pattern of specialization/omnivory alternating still emerged in later stages of human evolution and history [3].

Findings from paleontological and archaeological research have supported the theory that the inclusion of more animal proteins began with the earliest Homo.

It is assumed that *Homo habilis*, whose appearance is age-dated back to approximately 2.4 million years, obtained meat primarily by scavenging (and a smaller portion by hunting), while for *Homo erectus*, hunting was the predominant method of obtaining animal proteins, and this appears to be an important adaptive shift in human evolution [22].

The adaptive biological significance of meat-eating was summarized by Milton [23], who concluded that "the inclusion of animal-source foods in the diet played an absolutely important role in human evolution", otherwise the arid and seasonal environment that was probably the cradle of hominids would not have provided sufficient amount of protein.

Changes in the diet of early men: biological and cultural evolution

Diet is fundamental to an organism's ecology, and it is not surprising that changes in diet have been perceived as key milestones in human evolution [24].

The first revolution in eating habits occurred with the "discovery" of fire by the modern human ancestor, *Homo erectus*. Cooking and using fire were originally very rare and may have originated with *Homo erectus* in Africa about 1.8 million years ago [25]. Fire must have allowed them and subsequent modern humans (such as *Homo sapiens*) to make better use of food. Cooking improves digestion and can eliminate possible toxins contained in food. Thus, this likely included several foods in the early man's diet. Scientists hypothesize that, in addition to the nutritional aspect, fire facilitated the social gathering for meals. Primitive human beings also used fire apparently to surround their prey during the chase and to scare off predators [26].

The "discovery" of fire by *Homo erectus*, the direct ancestor of *Homo sapiens*, is not accepted by other researchers. Some researchers argue that *Homo erectus* was able to control and maintain fire, but did not generate it [26].

The second revolution occurred approximately 11,000 years ago with the advent of agriculture in Southwest Asia. This not only marked the introduction of grains into the human diet (e. g. oats, barley, rye, wheat, etc.), but also established human populations in certain places. While humans were still hunter-gatherers, populations remained in the same place until migration in search of food became necessary. With the development of agriculture, men no longer needed to be nomads because food could be grown near their habitats. Raising animals has also facilitated human efforts to survive in fixed locations [26].

Omnivory allowed the human species to establish itself throughout the world. If humans were exclusively vegetarians, they would not settle in areas with few plants, such as Alaska. If they were purely carnivores, they would have faced considerable difficulties, mainly because successful hunting was not guaranteed. When some authors argue that the diet of hunter-gatherers during the Paleolithic period was more suitable, one question arises. If people today have no proper food, while diets were better before agriculture, then why are people living longer today? [26]

The use of animal-source foods in the human diet has a long history of at least 5 million years. Meat consumption in human evolution may be divided into four periods: 1) occasional hunting and possibly gathering; 2) the beginning of regular hunting presumably about 2 million years ago; 3) the transition from hunting and gathering to domestic food sources, both animal and plant based, began 10,000 years ago; and 4) sustainable meat consumption, especially after World War II [14].

Hunter-gatherer food obtaining strategies. The role of hunting in meat eating

Analysis of both ethnographic and quantitative dietary data showed that, even at lower latitudes where plant food sources are available year-round, animal-source foods were the preferred source of energy for most hunter-gatherers around the world [27].

Although meat consumption has a long history, it was probably not a common food source until systematic hunting using meat-focused technology began presumably about two million years ago. Hunting large prey by groups of cooperative adults provided humans with regular and predictable access to protein and micronutrients [14].

Traditionally, special attention is paid to the consumption of meat by the first humans, because hunting is followed by the subsequent division of prey. This procedure involves some altruistic behavior towards members of the community who did not participate in the hunt, which is extremely important for human behavior. On the other hand, gathered foods are also distributed among members of society [18]. Hunting strategies are thought to have led to the division of labor and the development of more complex social systems [28].

H. erectus used stone tools [29]. The creation of tools of the Olduvai culture allowed for successful hunting and easier processing of carcasses, as well as increased access to meat, marrow, and bones of the animals [30]. Hunting requires cooperative interaction, which led to pantomime and vocalization, which was a turning point in the development of language [31].

Archaeological evidence indicates that after cutting, prey was transported to the place of distribution, cutting and common eating of food. In the opinion of a number of researchers, such a place is the prototype of home as the center of the economic and social life of society. According to Foley [32], the wider use of meat as the main source of proteins allowed early humans to solve the problem of surviving the unfavorable dry hungry season, which is why it was a decisive adaptation for humans.

Cooperation in hunting and distributing meat was one of the first steps in sociogenesis. Even today, hunting may be a way to escape social tensions in the presence of close friends, while common meat and food consumption remains a bonding mechanism. Additionally, the origins of the art are linked to hunting rituals, and animals that were hunted as prey, such as bison, became the first known subjects of animalistic art during the Upper Paleolithic age. Later, the rituals of hunting and animal sacrifice became an integral part of various religions and were firmly attached to the cultural framework of myths and folk tales [31].

Humans obtaining food are similar to other animals in their natural environments in that they attempt to maximize the ratio of energy intake to energy expenditure when hunting, fishing, or gathering food [33].

An assessment of the energy values while consuming various plant-source and animal-source foods that are components of hunter-gatherer diets shows that animal-source foods provide the greatest energy and that consumption of larger animals tends to provide greater energy than smaller animals. For example, the potential food mass would be the same for one deer weighing 44.8 kg and 1600 mice weighing 28 g each. However, people obtaining food have to use significantly more energy to catch 1600 mice than to catch one deer [33]. Likewise, varying amounts of fat in the edible carcass also determine the ratio of energy from protein and fat [27]. Hunter-gatherers tended to avoid very small or low-fat animals due to their excessive protein content [33]. Historical and ethnographic evidence shows the adverse health effects that occurred when men were forced to consume fat-poor lean wild meat [34]. Excessive consumption of lean protein without sufficient fat or carbohydrates causes a condition that early American researchers called "rabbit fasting", which leads to nausea, diarrhea and ultimately death [34]. For humans obtaining food, preventing the physiological consequences of excess protein in the diet has been an important factor in forming their feeding strategies [34,35]. Thus, lean meat could not be consumed in unlimited quantities, but had to be accompanied by sufficient fat or carbohydrates from plant food sources.

Using archaeological data and isotope analysis to study changes in diet (evidence of meat consumption)

The first cases of meat consumption by early hominins were noted in Africa about 3.4 million years ago in Dikika, Ethiopia [25].

To obtain sufficient data on diet and meat consumption during human evolution, scientists use indirect and direct approaches. The indirect approach is based on evidence of fossil morphology as well as on plant and animal remains found during archeological excavations. The direct approach involves isotope analysis of bones and teeth. The stable isotopes contained in foods are incorporated into the growing teeth and bones of food consumers. These tissues then acquire an isotopic composition that matches that of the original food, which may reveal a lot about the paleo diet [24].

Archaeological evidence

Significant evidence of the consumption of meat and bone marrow are traces of meat cutting found on the bones. About 2 million years ago, an increase in the number of sites with animal remains with cut marks and stone tools was noted in East Africa [25]. The earliest, well-documented evidence of persistent carnivorous feeding behavior for early humans and animal consumption (carnivory) from fossil fauna obtained *in situ* comes from a large concentration of stone tools and numerous bone elements processed by hominins and age-dated back to about 2.0 million years, which are located at the Oldowan site in Kanjera, Kenya [36]. In addition to terrestrial animals, evidence from one site at Koobi Fora suggests that approximately 1.95 million years ago, hominins began to include aquatic animals in their diets, such as turtles, crocodiles and fish [37].

Tool sets may also have been necessary for hominins to cut carcasses, with cutting edges for processing soft tissue, as well as percussion tools for extracting bone marrow. With the onset of the Acheulean period and the emergence of *Homo erectus* populations *sensu lato* in Africa, between 1.9 and 1.7 million years ago, a change in diet was observed with more evidence of carnivorous and predatory behavior [25].

Meat consumption occurred quite early in human evolution, but habitual meat consumption, complex forms of cooperative hunting, entire meat cutting sequences, and the transport of bones and carcasses, which require advanced cognitive skills such as planning and decision-making, appear to have evolved later, not earlier than 1 million years ago, throughout the African continent and the Levant in combination with environmental changes of the early Middle Pleistocene [25]. Later, in Western Europe, a large number of remains of herbivores were discovered at Middle Paleolithic sites (about 400 to 40 thousand years ago) [25]. Results from isotope ratio studies [38,39] and dental wear data [40] show a significant intake of animal proteins in the diet of Neanderthal men. Neanderthals could rely for up to 80% on animal protein and 20% on plant proteins, making them the most emblematic carnivorous and competitive big-game hunters among extinct hominins [25].

Isotope analysis

This approach is based on the analysis and comparison of the presence and ratios for stable isotopes of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$). The relative values for stable isotopes of carbon and nitrogen may be useful for understanding the ratio of animals and plants in the diet.

The use of carbon isotope analysis in paleodietary studies is based on the simple concept that you are what you eat. Isotopic traces of past meals are frozen in tooth enamel, and are recoverable after millions of years, because enamel is essentially prefossilized and therefore, resistant to postmortem isotopic alteration [41].

Isotope studies of Neanderthal and Paleolithic human bones indicate that the dominance of animal-source foods in the human diet has a long history. These studies provide objective data showing that the diets of hominids living in Europe during the Paleolithic were indistinguishable from top trophic level carnivores such as arctic foxes and wolves [33].

It is believed that early in the evolution of our genus, hominids may have experienced a number of genetic adaptations to animal-source diets similar to those of obligate carnivores such as cats. The carnivore diet reduces evolutionary selection pressure to maintain certain anatomical and physiological characteristics necessary to process and digest large quantities of plant foods. Inclusion of ever increasing quantities of animal-source foods into a diet of hominids led to a decrease in the gut size, as in the case of felines, with a concomitant increase in the brain size and metabolic activity [33].

Until recently, most of our understanding of past diet was based on the remains of plants and animals found at archaeological sites. These data sources provide a complete list of what humans ate, but not their relative proportions. The complete list presents a picture of diet, while proportions reflect nutrition, which is actually what we want to know. New insights into nutrition are provided by the chemical evidence of diet found in the bones and teeth of earlier humans [42]. The intensity of accumulation for stable isotopes of nitrogen ^{15}N and carbon ^{13}C is subject to environmental laws that have now been fairly well studied [43]. The accumulation of these isotopes in the main structural protein of bone tissue, i. e. collagen, follows these general laws. This fact allows for paleoecological reconstructions of the average diets of individuals. Some of the best information comes from stable isotope analysis of carbon [$^{13}C/^{12}C$ ratio ($d^{13}C$)] and nitrogen [$^{15}N/^{14}N$ ratio ($d^{15}N$)] extracted from human bones. Analysis of carbon isotope ratios shows the use of C3 plants versus C4 plants in the diet, since the isotope ratios of these plants are different (and therefore, the tissues of the men consuming these plants are different). C3 plants grow primarily in temperate climates, while C4 plants are tropical ones, such as corn in the Americas, millet in Europe and Asia, and sorghum in Africa.

Stable nitrogen isotope ratios are also used to determine the relative contribution of plant and animal protein sources or the position of the organism in the food chain (trophic level) [20].

There are a number of regions where we currently know a lot about dietary changes. For example, on the southeastern Atlantic coast of the United States (Georgia and Florida), a simultaneous decrease in seafood consumption and an increase in corn consumption have been documented [42]. Overall meat consumption has also likely declined. Although seafood sources have decreased in the Atlantic coastal areas with the development of agriculture, they still play an important role in the nutrition of the population. In Neolithic Greece and some other coastal areas where agriculture became important, seafood sources appear to have been greatly reduced (or even eliminated), at least as identified by stable isotope analysis. In general, the emerging picture indicates that over the last 10,000 years of human evolution, there has been a reduction in animal-source foods in the diet [14].

What did meat consumption give? Changes in the body of ancient humans associated with meat consumption

Diet and nutrition type significantly affect the formation of the digestive system and other systems of the human body and are one of the most important components of the external environment during the evolutionary development of human. A leap in development, i. e. increasing brain complexity and volume, is directly related to changes in food patterns. And those fossil primates who did not switch to a mixed diet are not associated with the origin of the genus Homo [44].

Archanthropes were the first humans to reliably hunt large animals. A sharp increase in brain volume, body length, body weight, life expectancy, a decrease in sexual dimorphism (anatomical differences between males and females of the same biological species, not counting the genitals) indicate significant changes in food patterns due to an increase in the proportion of meat [18,45].

Hunting and meat eating resulted in increased body size. *Homo erectus/ergaster* males had an average body mass of 66 kg compared to *Homo habilis*, which weighed 37 kg, while body mass of females increased by 53%, from 32 kg for *Homo habilis* to 56 kg for *Homo erectus/ergaster*. The height increased from 131 cm to 180 cm (by 33%) for males and from 100 cm to 160 cm (by 37%) for females.

Bipedalism, which distinguished ancient humans from other apes, appeared in the oldest known species of Australopithecus, who lived in Africa about four million years ago. According to some investigations, 'postural' bipedalism was found in *Australopithecus afarensis*, and locomotor bipedalism did not appear until the emergence of *Homo ergaster* between 1.9 and 1.5 million years ago. Some authors consider that bipedalism in *Homo ergaster* was associated with climate changes in Africa where more open habitat formed and food resources became patchily distributed forcing humans to move in order to find food. Moreover, bipedalism may be considered one of the first strategies in the evolution of human nutrition [22].

As meat became more common in the diet, changes occurred in the digestive tract. Despite the fact that during the evolution of australopithecines, the total area of chewing teeth increased from 460 mm^2 in *Australopithecus afarensis* to 756 mm^2 in *Australopithecus boisei*, in early species from the genus Homo, there was a decrease in the posterior dentition. The surface area of postcanine teeth decreased from 478 mm^2 in *Homo habilis* to 377 mm^2 in early *Homo erectus* [30].

While changes in molar size reduction and anterior teeth strengthening may have been caused by changes in diet associated with tearing and chewing meat, changes in intestinal morphology reflected the impact of a transition to a high-quality diet. Typically, large primates have a dilated colon, which is necessary to extract additional energy in the form of volatile fatty acids obtained during fermentation of plant fibers. On the other hand, humans have a thinner colon and an enlarged small intestine. These differences in intestinal morphology are the result of adaptation to the easily digestible animal proteins in the human diet.

The genus Homo had significantly smaller molars, chewing muscles, weaker maximum bite force, and relatively smaller intestines than earlier hominids. It is believed that this paradoxical combination of increased energy requirements along with decreased masticatory and digestive abilities became possible by the addition of meat to the diet, mechanical processing of food using stone tools, or cooking. Researchers found that if meat comprised one-third of the diet, the number of chewing cycles per year would have declined by nearly 2 million (a 13% reduction) and total masticatory force required would have declined by 15%. Furthermore, by simply slicing meat and pounding USOs, hominins would have improved their ability to chew meat into smaller particles by 41%, reduced the number of chews per year by another 5%, and decreased masticatory force requirements by an additional 12% [47].

Meat and body height

It is possible that the adoption of hunting strategies led to improved health in early hominids about 2.0 to 1.7 million years ago, which explains the increase in adult height [14]. McHenry and Coffing documented a dramatic increase in body weight by 44% in males (from 37 kg in *Homo habilis* to 66 kg in *Homo erectus/ergaster*) and by 53% in females (from 32 kg in *Homo habilis* to 56 kg in *Homo erectus/ergaster*) [45,46]. This represents an increase in height by 33% for males (from 131 cm to 180 cm) and by 37% for females (from 100 cm to 160 cm) [46].

Numerous studies show that in different eras of *Homo sapiens* existence, periods of increase and decrease in body size periodically replaced each other. The height of the first representatives of the Cro-Magnon men was no less than that of modern Europeans, while by the Middle Ages, the body length of the population in this part of the world had noticeably decreased. The cyclical nature of acceleration and retardation processes (acceleration and deceleration of growth) is typical for various regions of the planet.

At the level of entire nations, differences in height are determined not by ethnicity or race, but by living conditions [48]. The height of certain population representatives may be considered a historical indicator, showing both the quantity and quality of foods consumed in youth, and the living conditions that existed at a given time [49].

Study of archaeological specimens shows variations in the height of modern humans. These variations are associated with an access to high-quality food, which includes meat. In a number of countries around the world, the transition to agriculture has led to a decline in height, reflecting a focusing on the use of domesticated plants, probably less meat consumed, and certainly a reduction in diet in general [14].

A significant amount of anthropometric historical data on height variation is derived from analysis of military and other records. Costa and Steckel [50] analyzed data on the height of recruits in North America from the eighteenth to the twentieth centuries and found a maximum increase of about an inch in height from 1710 to 1830, followed by a decline of two inches during the remainder of the nineteenth century. Since about 1890 and up to the present day, there has been a steady increase in height. Studies conducted in the 20th century also found an association between meat consumption and increased height, for example in Belgium [51].

In other human populations, access to meat appears to improve health as measured by height. The Equestrian Plains tribes of North America, for example, are among the tallest of any native American population. Their access to buffalo and other animals was greatly facilitated by the use of horses for hunting and the subsequent distribution of food [14].

According to measurements taken in 1974, the average height of Russian male city dwellers born between 1916 and 1957 showed an increase from 167.03 cm (born in 1916) to 172.42 cm (born in 1957) respectively [52]. Systematization of research results shows how periods of malnutrition, social cataclysms and wars affected the height of males.

The above results are consistent with research conducted by scientists from the Department of Anthropology of Moscow State University named after M. V. Lomonosov [53], who showed that despite the significant variability in secular changes in body size at different regions of Russia, a common pattern was identified for all populations, which consisted of an increase in definitive body length over the studied period of time. The analysis includes materials on body length for the adult population of 50 territorial subjects of the Russian Federation (34 regions, 9 republics, 6 territories, 1 autonomous district), surveyed from the end of the 19th to the beginning of the 21st century. The average values of secular increases in definitive body length in the Russian population over the entire survey period were about 8 cm in men and over 4.5 cm in women, which is comparable to global values [53].

From the mid-1950s to 1978, meat consumption *per capita* increased from 60.8 kg/y to 98.0 kg/y, representing a 50% increase. At the same time, grain consumption declined and fruit consumption increased. Heights showed dramatic increases. After World War II, this trend was repeated globally in developed and developing countries [14].

Encephalization role in evolution

In hominins, the increase in brain size has occurred primarily over the last 2 to 3 million years. In fact, since the time of *Australopithecus afarensis* about 4 million years ago, brain size has tripled [54,55]. The driving force behind the dramatic increase in brain size is unknown, although many reasonable hypotheses have been put forward based on socio-ecological factors.

Irrespective of the driving force for encephalization, two critical requirements had to be met: the brain's chemical requirement for long chain (LC) polyunsaturated fatty acids (PUFA), particularly arachidonic acid (AA, 20:4, n-6) and docosahexaenoic acid (DHA, 22:6, n-3) and the increased metabolic requirements of a larger brain. The fatty acids mentioned are the major structurally significant and biochemically active components of the brain gray matter in all mammalian species. The availability of these particular fatty acids may have provided a selective pressure acting to increase brain size, by simply supplying adequate dietary substrate to allow formation of brain tissue [55].

It should be noted that in the gray matter of the human brain, the ratio of major lipids is approximately the following: 25% is DHA, 25% is stearic acid, 14% is AA and 12% is oleic acid. In the photoreceptors of the retina, DHA content exceeds 59% of the total fatty acids, since high photosensitivity must be combined with high membrane fluidity [56].

Along with the body size, brain size also increased from 400 cm^3 in the earliest australopithecines to 1300–1400 cm^3 in modern humans, although similar changes in brain size were not found during regular periods of evolution. The greatest level of encephalization was found in *Homo erectus*, which had a larger brain relative to body mass than any other primate during evolution. The brain size of *H. erectus* reached 800–900 cm^3, which is approximately 200 to 300 cm^3 larger than the brain size of *Homo habilis* [30].

Larger brains were required for complex feeding behavior and tool use [31]. It is hypothesized that the practice of cooking using fire was critical for the development and maintenance of the enlarged hominin brains that began to evolve around 1.9 million years ago [57].

The human brain is a metabolically high-demand organ. On the basis of *in vivo* determinations, the mass-specific metabolic rate of the brain is approximately 11.2 W/kg (watts per kilogram). This is over 22 times the mass-specific metabolic rate of skeletal muscle (0.4 W/kg) [58].

Due to the process of "encephalization" in humans, the brain size is larger than it would be expected for their body size. To support an extremely large brain, energetic compensation was required during hominin evolution. When examining individual organs, excess brain mass (and its energy requirements) is closely balanced by a decrease in size (and correspondingly reduced energy requirements) of the gastrointestinal tract. This is not surprising given that the intestine is the only organ whose size may vary sufficiently to counterbalance the metabolic costs of a larger brain. This process required a transition from a diet high in low digestibility plants (requiring large fermentation compartments such as rumen or cecum, or large colon), to a higher quality diet where foods are higher in calories and require less digestive processing [12].

In 1995, Aiello L. C. and Wheeler P. developed the "expensive-tissue hypothesis" to explain how our huge brains evolved without causing a huge increase in our metabolic rate. They suggested that the energy demands of the large brain could be counterbalanced by a decrease in the size of the liver and gastrointestinal tract; these organs, like brain, have metabolically "expensive" tissues [54].

By considerably lowering the energetic cost for basal metabolism, a reduced intestinal mass may permit disposal of sufficient energy to cover the extra-expenditure required by a larger brain. Aiello and Wheeler based their argument on the relationship between body mass and Basal Metabolic Rate (BMR): the Kleiber line characterizing relationship between BMR and body size is identical for all mammals, including humans [12]. Because intestine and brain tissue are equally costly to maintain, Aiello and Wheeler proposed that intestine decrease led to the emergence of large brains in hominids. They argue that without the significant number of calories provided by eating meat, the human brain simply would not have been able to develop to its current size [54].

The role of fire. Eating raw or cooked meat: what are the energy effects?

The beginning of the active evolutionary development of mankind is associated with the use of fire, which occurred approximately 700 thousand years ago. In addition to the numerous functions of fire, one of the most important is the ability to process food, which led to the development of culture and, one can safely say, contributed to the "humanization" of a creature that at the dawn of history was only a project of what we now call man. Not raw, but cooked food became the most important milestone, a revolutionary anthropological turn that oriented human to the difficult process of evolutionary development and expansion of cultural forms. The process of food heat treatment stimulated a new quality of life for early humans, who began to evolve and formed their human identity overcoming the food specialization characteristic of animals [59].

In 1999, a process of hominization was hypothesized, which became possible by the early use of fire for cooking. It was assumed that the early archanthropes, who appeared about 1.9 million years ago, already knew how to cook food over fire, which made it possible to sharply reduce the metabolic cost of digestion [60]. The hypothesis was based on indirect data. For example, on the fact that in early archanthropes, not only the brain increased, but also the overall body size did. In addition, their teeth became smaller. This mean that they had to work less with their jaws. By comparison, chimpanzees spend an average of 5 hours a day for chewing, while modern hunter-gatherers who cook over fire spend only one hour for chewing.

Human is the only species in the world that cook over controlled fire, and there is archaeological evidence that at least some hominins were cooking over fire as early as 1.5 million years ago [61]. Interestingly, there are other scientists who suggest that hominin cooking behavior must have originated around 2 million years ago. This logic is based on the basic nutritional benefits of cooking. Specifically, the cooking process breaks down nutrients and softens food, making it easier to digest, thereby providing more energy. Cooking also allows to eat a wider variety of foods and acts as a short-term food preservative. Additionally, approximately at the same time, hominin teeth began to decrease in size [62], possibly because larger teeth were no longer needed for chewing softened food.

Controlling fire and using it for cooking marks an important shift in nutrition. Despite the apparent importance of meat consumption in human evolution, some studies [63] have shown that raw food diets provide insufficient energy to maintain body weight, suggesting that food processing and cooking are very important. Indeed, when carbohydrates or proteins are cooked, they become more tender, better digestible, easier to chew (chewing time is reduced), metabolic cost is reduced, and energy extraction per mass unit increases [25]. Cooking also kills foodborne pathogens. However, the content of iron and some vitamins, such as vitamins B12 and C (which primates cannot synthesize), decreases at high temperatures and long cooking times. Cooking may be quite an expensive process in terms of the energy required to gather fuel, time required to start and maintain a fire, and requires some cognitive skills, e. g. for gathering fuel (selecting wood, bones, stones, etc.) and fireplace organization [64].

According to some authors [25], the increased energy requirements of a larger brain are compensated by a decrease in mass-specific metabolic rates in other tissues, such as gastrointestinal tract. Their studies in humans and nonhuman primates suggest coevolution between brain and intestine size, which is dependent on energy intake and may be determined by the dietary quality. They believe that hominins, especially after 2 million years ago (such as early *Homo erectus sensu lato*), had small intestines and would have required the use of fire and cooking to efficiently process lowly digestible foods such as meat. However, some authors believe that this compromise scenario appears to be insufficient, and they emphasize that brain size does not correlate with other energetically expensive organs or with the mass of the digestive tract, and that encephalization and fat accumulation in primates is a strategy to control calorie deficit [25].

Thus, cooking played a special role in the development of human diet. Primitive food cooking, as it was among early humans, went through a long and difficult path of development before it turned into the refined culinary art, which included the achievements of modern science [44].

Potential consequences of limiting meat consumption. What is the proper diet for the human species?

This question has been of concern to scientists for a long time, and current discussions and controversies are not resolved yet. In addition to scientific aspects, many other factors influence our eating habits, such as religion, tradition and socio-political situation, etc. [6,23,26,29,33,44,55].

It is not easy to answer this question. Each advocate of the eating habits hypothesis has his own arguments, often based on scientific evidence, but not always. Some scientific "evidence" changes very quickly. To better understand the question above, it is necessary to understand how the eating habits and behavior of our species evolved. It is also necessary to compare human eating behavior today and at the time when our species appeared [26].

From an anatomical point of view, several studies have shown that modern humans are unchanged from their Paleolithic ancestors. This leads to the conclusion that our diet must correspond to the standards of that period, because our species established itself on Earth exactly during that time [33].

In Western diets, increased consumption of meat (especially red and processed meat) is positively correlated with mortality from cardiovascular disease. However, a number of researchers provide additional evidence confirming the dominant role of animal-source foods in the diets of hunter-gatherers, and show how these dietary patterns do not necessarily contribute to the development of atherosclerosis and cardiovascular disease [33].

An analysis of the Ethnographic Atlas data by Cordain et al. (2002) showed that most foods in the diets of most hunter-gatherers were obtained from animal food sources [33]. The majority (73%) of the world's hunter-gatherers obtained >50% of their diet from consuming animal-source foods, and only 14% of hunter-gatherers obtained >50% of their diet from plants, respectively. For the 229 hunter-gatherer communities studied, the average dependence on animal-source foods was 66–75%. On the contrary, the average dependence on gathered plant-based foods was 26–35%. Re-analysis of data from Lee's original subsample (n¼58) of the Ethnographic Atlas showed the results almost identical to the above studies [27]. Dependence on animal-source foods obtained by hunting and fishing was 66–75% (median value), while the median value of gathered plants was 26–35%.

Scientists estimate that the food of ancient humans contained much less saturated fatty acids than the food of current people. Moreover, ancient foods contained almost equal amounts of n-6 and n-3 acids (about 1.5:1 ratio) and fewer trans fatty acids than modern foods. During our evolution, the total fat content of food was slightly more than 20%. In the middle of the 19th century, the situation began to change in the direction of increasing this indicator, and currently the fat content reaches almost 40% [65].

Humans also exhibit a range of specific adaptations indicative of extensive reliance on animal-source foods in the diet. Similar to obligate carnivores, humans have an inefficient ability to elongate 18carbon fatty acids from plant into the 20- and 22carbon polyunsaturated fatty acids (PUFA) essential for cell membrane and brain tissue function, hence requiring direct consumption from animal tissue. Likewise, humans have inherited a decreased ability to synthesize the amino sulfonic acid, taurine, which is involved in numerous essential physiological functions.

Studies on vegans reveal a plasma level of taurine 78% lower than in omnivores [55].

In addition, animal-source foods (especially red meat) are a well-known source of heme iron, which is absorbed more efficiently than non-heme iron found in plants [55].

There are potential nutritional benefits and risks associated with limiting meat consumption that vary depending on context, population, life cycle phase, and substitute foods. In many low- and middle-income countries, especially in sub-Saharan Africa and South Asia, meat consumption is very low and rates of malnutrition are high [66]. These populations could benefit from increasing, rather than decreasing, meat consumption. Livestock and animal-source foods are vital to sustainable development as they play a critical role in improving nutrition, reducing poverty, increasing gender equality, improving living conditions, increasing food security and improving health [67]. At certain stages of life, nutrient-dense and bioavailable foods are needed to meet all requirements: women of reproductive age, pregnant and lactating women, infants and young children, and the elderly. Diet changes in high-income countries, which tend to involve a decrease in red meat consumption, have been accompanied by a simultaneous increase in iron deficiency. For women of reproductive age, meeting iron requirements in any diet may be challenging, but limiting consumption of ruminant meat, one of the richest sources of bioavailable iron, makes it difficult to address this problem in the absence of iron-fortified foods or supplements [12].

Recently, research has shown that particular problems arise with brain functionality when a person's diet lacks animal foods, and this primarily manifests itself in children and the elderly [55].

An assessment of the Western diet shows that it distorts the finely tuned metabolism that has evolved over the long period of human evolution, leading to increased oxidative stress, immunopathological processes, chronic inflammation and hyperinsulinemia. These mechanisms create a single pathophysiological platform for the development of many chronic non-infectious diseases. Epigenetic modifications play an important role in the transmission of civilization diseases to subsequent generations. Returning to eating pattern close to the ancestral diet may be beneficial, but is associated with significant challenges. In general, the influence of nutrition on health reflects the well-known postulate that everything is good in moderation [68].

Conclusion

It is increasingly recognized that some of the fundamental changes in diet and habits that have occurred since the Neolithic Revolution, and especially since the Industrial Revolution and in the modern times, have occurred too recently on an evolutionary time scale for the human genome to fully adapt to them.

Meat is undoubtedly an important factor in human evolution. Changing dietary strategies was one of the triggers for brain evolution. In this sense, improving the quality of a meat-dominated diet allowed overcoming the limitations on brain growth.

Currently, various trends influence the choice to eat or not eat meat. The nutritional composition of meat makes an important contribution to the human diet, influencing proper growth, physical and cognitive development. However, awareness of animal welfare, environmental pollution and some of the disorders and diseases associated with meat production and consumption have created a meat-free trend. On the other hand, millions of people, mostly children, in a number of developing countries are starving due to a lack of animal protein.

A summary of the results of a number of studies shows that there is no historical or scientifically proven argument for eliminating lean meat from the human diet. There are a significant number of reasons to suggest that it should be the basis of a well-balanced diet.

The spread of a Western-style diet, which differs from the evolutionary dietary pattern, is significantly correlated with an increase in the incidence of chronic noninfectious diseases. The Western-style diet resulted from new foods and food processing procedures that emerged during the Neolithic and Industrial periods. At the same time, the key characteristics of the diet have changed: glycemic load, composition of fatty acids and macronutrients, concentration of micronutrients and amino acids, acid/base and sodium/potassium balance and fiber content. It is assumed that pathological processes are caused by disorders in the metabolic processes of the human body, which has been adapting to Paleolithic food for thousands of years. This is caused by too rapid environmental changes during the era of industrialization.

Systematizing all the facts allows to state that the choice of whether to eat meat remains with each person, since we are what we eat. Just like thousands of years ago, today humanity is still yet to solve the problems of healthy and safe nutrition.

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