The Reconstruction of Diet in the Past

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The retrospective reconstruction of our ancestors' diet is far more difficult than it is for recent populations, offers numerous options and usually depends on a successful transdisciplinary cooperation at the interface between prehistory (archaeology), anthropology (bioarchaeology), chemistry, biochemistry, geology, and evolutionary medicine.

Keywords: environment ; behavior ; cultural evolution

1. Introduction

1.1. From the Origin of Life to the Evolution of Homo Sapiens

> "Nothing in biology makes sense except in the light of evolution."
>
> Theodosius Dobzhansky 1973

Life on Earth began with the formation of the first molecules and dates back to approximately four billion years ago. As yet, it is unclear how the primordial cell (Last Universal Common Ancestor), or LUCA, came into being. Presumably, purely chemical processes were responsible for the beginning of biological evolution [1]. The diversity of life as it presents itself today shows how successful this process has been so far. It was another milestone in the history of evolution when, about 400 million years ago (mya), vertebrates left their aquatic habitats and began to adapt to terrestrial life. The preconditions for this process included the oxygenation of the atmosphere, the ability to breathe atmospheric oxygen, alternative modes of reproduction and locomotion, access to new food sources, etc. With regard to the masticatory system, functional and constructional morphological changes had already begun in the ocean (the formation of teeth and of a secondary temporomandibular joint and increased diversification of teeth for the exploitation of specific food niches). Within the mammals, whose origins date back to 250 mya, the first primates emerged in an ecological niche 65 mya. Eight mya, the human evolutionary lineage separated from that of today's apes. Hominins evolved from the human lineage approximately three mya with the single genus *Homo*, all species of which, except for *Homo sapiens*, are now extinct. The fossil representatives of *Homo sapiens* are now dated to 300,000 years ago [2][3].

1.2. Evolutionary Frameworks for Understanding Human Nature

In order to understand the biological nature of humans and their special features, one must deal with their development and look way back into the history of evolution [4]. A differentiated study of the phylogeny of our biological species allows people to better understand and assess the typical characteristics of the genus *Homo* including its habitual upright gait, the freeing of its hands, its large brain as well as its language, thinking and numerous cultural achievements. As far as humans are concerned, it is only through direct comparison with our closest relatives within a long line of ancestors that it is possible to gain a substantial insight into the evolution of *Homo sapiens* in the context of primate evolution. This limitation also explains why there is no fundamental human–animal dichotomy. Science and scientists are not immune to hubris and egocentrism. The image of the worldviews and lives of our fossil ancestors is often shaped by our modern cultural perspective. Taking into account its biological origins, the genus *Homo* seems unique only in the sense that it implemented a revolutionary change out of the "continuum" of evolution by deliberately manipulating its ecological environment [5]. This supposedly unique step appears to have held more disadvantages than advantages for the future of the biosphere on planet Earth.

Physics can be considered the natural science, as it examines the fundamental principles that determine the processes of life in nature. Chemistry, by contrast, deals with the properties of chemical elements and compounds and with their reactions. Both disciplines together form the framework within which the biological makeup of all organisms, including humans, functions. Biochemistry represents a borderline discipline between biology/medicine and chemistry and, among other things, aims to explore metabolic processes and genetic reproduction. At the species level, two mechanisms in particular are essential: ensuring reproduction for subsequent generations (reproduction) and the physiological functional maintenance of the body in its interactions with the environment (nutrition). The chemistry of life is organised in metabolic pathways [6]. After water, carbon compounds (proteins, DNA, carbohydrates, fats, etc.) form the second most important component of a cell. The diversity of organic molecules is based on the variation of the carbon skeleton (C). Hydrogen (H), oxygen (O), nitrogen (N), sulphur (S) and phosphorus (P) frequently occur as functional groups combined with carbon; together they represent the “elements of life”.

These elements created the living conditions for the first microorganisms on Earth approximately 3.5 billion years ago. But it was not until 350 mya that a particular level of oxygen in the atmosphere had been reached and a stratospheric layer of ozone had developed which enabled higher organisms to evolve under the protection of this UV filter. The atmosphere of the Earth’s recent history was characterised by a high proportion of nitrogen and oxygen and has hardly changed since its formation. The climate was less stable, and extreme climatic crises caused by meteoritic impacts, volcanic eruptions, intense solar activity, continental drift, etc. repeatedly disturbed the balance to such an extent that several mass extinctions occurred. One such global catastrophe, which occurred 65 mya, finally paved the way for the emergence of primates, including humans, and the flora and fauna that exists today [7].

While autotrophic, photosynthetically active organisms (chemolithoautotrophic microorganisms, phototrophic microorganisms, and plants) as primary producers use sunlight as an energy source to obtain carbon from inorganic substrates such as carbon dioxide (CO_2), heterotrophic organisms (fungi, bacteria, animals, humans) as consumers obtain the carbon required to build their own bodily substances from already synthesised organic COH compounds. Because the chemical elements that are necessary for the formation of organic matter only exist in limited quantities, life on Earth directly depends on the recycling of essential elements. These elements circulate inside organisms, ecosystems, and the biosphere through a constant cycle of build-up and breakdown processes. The driving force behind the cycle of materials is a synergy of biological, geological, and chemical processes involving the ecosystems’ biotic and abiotic components [8].

1.3. Nature’s Cycle of Materials and the Role of Nutrition in Sustaining Life

Living organisms are instrumental in maintaining the vital “recycling” process in biogeochemical cycles through food intake and metabolism. Through nutrient uptake, respiration, and the excretion of waste products, living organisms constantly exchange chemical components with their environment. Primary production (plant biomass) is defined as the total amount of chemical energy that is produced within ecosystems through photosynthetic activity. In terrestrial ecosystems, limiting factors include the temperature, the level of humidity and the nutrients available. Secondary production is defined as the rate at which primary consumers within an ecosystem (herbivores) convert the chemical energy of their food into their own new biomass. The importance of the trophic structure for people's understanding of the dynamic processes that occur within ecosystems is emphasised by the relationship between herbivores and plants. Nutrients are moved between organic and inorganic reservoirs by means of biological and geological processes. The rate of nutrient cycling is mainly determined by the rate of decay. Nutrient cycles are strongly influenced by the vegetation. From an early phase of the Pleistocene, humans had a profound impact on the natural nutrient cycle and permanently changed the existing flora and fauna [9][10][11].

The term nutrition combines all processes that ensure the supply of substances that contain energy to a living organism. Accordingly, nutrition is a prerequisite for sustaining the life-force of every living being. Food consists of energy-rich organic compounds in solid or liquid form, which are required for the formation of cells, tissue, bones, and teeth and for maintaining the organism’s energy metabolism. Both animal- and plant-based foods contain nutrients (carbohydrates, proteins, fats) and supplements (vitamins, minerals, trace elements, fibre). Lipophilic and hydrophilic vitamins flank the metabolic functions by regulating the utilisation of nutrients. Because most of these vitamins are not synthesised by the human body, they must be ingested through food. The same applies to minerals (major minerals and trace elements), which regulate the cellular and bodily functions; they cannot be produced by the organism itself and must be supplied through nutrition. These natural inorganic nutrients occur in various chemical compounds, but the body can only ingest them from very specific ones. Major minerals (calcium [Ca], potassium [K], magnesium [Mg], sodium [Na], chlorine [Cl]) occur in the body in high concentrations, while essential trace elements (iron [Fe], chromium [Cr], cobalt [Co], fluorine [F], zinc [Zn], copper [Cu], iodine [I], manganese [Mn], selenium [Se], silicon [Si], molybdenum [Mo], vanadium [V]) occur in low concentrations. Deficiencies or overdosages of minerals result in impaired bodily functions [12].

From an evolutionary perspective, *Homo sapiens* is a relatively recent product of history. Its success since its emergence is illustrated, for instance, by the fact that it has managed to adapt to his environment all over the world [13]. It was supported in this endeavour by cultural evolution [14]. In addition to food and drink, the core factors that have ensured the species' survival over the course of its history were cultural achievements such as clothing, housing, the use of energy, etc. These achievements could not have been made without cultural, social standards. And without social integration, human beings themselves would neither have been conceivable nor would they have been capable of surviving. With regard to nutrition, it could not speak of a single, "natural" way of consuming food. It was, in fact, the very indeterminacy of the human diet, i.e., a cultural factor, that worked to the species' advantage and was ultimately what allowed *H. sapiens* to adapt to any eco-system on Earth [15]. While the Inuit subsisted mainly on animal proteins, people in the Andes lived primarily on a plant-based diet [16]. For the majority of recent hunter-gatherers, however, well over half of their diet came from animals. Sufficient consumption of plants is advantageous for the human organism because, unlike carnivores, it cannot synthesise vitamin C on its own. However, the ascorbic acid content of fresh meat and offal is often sufficient to prevent scurvy.

2. Methods and Techniques for the Reconstruction of Diet in the Past

The retrospective reconstruction of our ancestors' diet is far more difficult than it is for recent populations, offers numerous options and usually depends on a successful transdisciplinary cooperation at the interface between prehistory (archaeology), anthropology (bioarchaeology), chemistry, biochemistry, geology, and evolutionary medicine. In terms of the biohistorical source material, the starting point for the reconstruction of diet in the context of archaeological research are plant, animal, and human remains from archaeological excavations. Archaeobotany and archaeozoology study the environmental, economic, and nutritional history, the human impact on the environment and, since the beginning of domestication, the economic importance of domestic animals and cultivated plants, and also reconstruct the range of plant- and animal-based food consumed. Taking into account the chronology and the archaeological data available, diachronic conclusions can be drawn with regard to the subsistence (procurement) and consumption behaviours and insight can also be gained into social history. Reconstructions of the environment, the technical achievements, and the traces in the landscape (e.g., clearings, terracing, irrigation, stables) provide indirect evidence of the nutritional situation in different periods.

Archaeobotany is the study of plant remains, primarily from anthropogenic deposits from the past (e.g., settlements, latrines). Together with archaeozoology, it is an important cornerstone in the research and reconstruction of the economic, natural and settlement history of past epochs. The source materials studied by archaeobotanists primarily include plant macroremains such as seeds, fruits, wood, leaves, stems and other parts of plants such as tubers, roots, and bulbs [17]. The most important finds categories are seeds and fruits, which can be identified to species level. In addition, plant microremains such as pollen and spores, phytoliths and starch grains are examined. In terms of the emergence of agriculture, the Neolithic period is a main chronological focus [18].

Animal bones are the primary source material studied by archaeozoologists. The bones mainly derive from the slaughter waste of domestic and/or wild animals consumed by humans [19]. Occasionally, additional information can be obtained from animal substances (e.g., fats, proteins) found in containers. Taken together, these sources provide quantitative and qualitative evidence of dietary trends and the availability of hunted or farmed animals. In this way, and in combination with archaeobotany and archaeozoology, it is possible to reconstruct the environment, economy, general supply, and social differences with regard to human diet in different eras [20][21].

Direct statements concerning human nutrition in the past are the domain of anthropology and can essentially be inferred from the preserved hard tissue remains of our ancestors such as bones and teeth. While the phylogeny of humankind (palaeoanthropology) as a discipline deal with various species and focuses on the trans-specific course of human evolution, prehistoric anthropology (bioarchaeology) investigates the intraspecific variability of the species *H. sapiens*, represented by more recent populations (from approx. 40,000 years ago in Europe). The focus of prehistoric anthropology, therefore, is not on the evolutionary process (macroevolution), but rather on recent human history, which is characterised by a gradual emergence of (supra)regional groups (archaeological cultures). The population concept of biology (microevolution) enters the discussion with the attempt to obtain evidence of the lifestyles and living conditions of past populations from their biological makeup. With that, it is no longer the individual fossil-no matter how spectacular-that is the focus of attention, but the population as a whole, which is analysed by raising questions about the general living conditions and life processes [22][23].

The human skeleton and teeth provide numerous clues about the type of food consumed and about nutritional deficiencies and malnutrition [24]. The study of prehistoric and historical diets is fundamental for the understanding of human behavioural patterns and subsistence strategies. Like animals, humans invest a considerable amount of time in procuring and stockpiling food. Then as now, the focus was on developing new strategies and techniques to achieve maximum yield with minimum effort (cost-benefit effect). Until the 1980s, fundamental information on the subsistence behaviour of past populations was derived from archaeological settlement features, technological complexes, household effects, archaeozoological and archaeobotanical evidence as well as osteological parameters (stress markers, body height, tooth wear and others). Since then, the analysis of stable isotopes found in biohistorical materials from humans and animals has opened up a new biogeochemical approach to the study of our ancestors' diet [25]. The experimental dietary reconstruction using the stable isotopes of carbon (C) and nitrogen (N) is based on the assumption that the isotopic composition of human hard tissues can be seen as direct and constant evidence of the food consumed and that there is a measurable and systematic difference between the signals of the consumers and their food due to accumulation (fractionation), which can be detected by mass spectrometry [26]. To validate the isotopically determined δ13C and δ15N isotope values, the animal bones examined for comparison should always be taken from the same archaeological context.

Analyses of stable CN isotope ratios have a broad application potential within archaeology. Depending on the initial conditions and study design, they generate relevant information at an individual and collective level that provides an insight into the subsistence conditions and dietary habits of our ancestors. While the results do not allow people to reproduce detailed daily menus from the past, they do distinguish between food categories such as meat and other animal proteins versus plant-based foods, terrestrial versus aquatic sources of protein, C3 plants versus C4 plants, all of which made up our ancestors' diet during their lifetime. No other method of analysis in anthropology can provide as much dietary information for all age groups, from the weaning of infants and the dietary changes at toddler age, to older children and adolescents to adults. In terms of the consumption of animal products, women often yield moderately lower δ15N values compared to men. Besides behavioural characteristics, numerous other factors play a role in the assessment of the nutritional balance of individuals. Apart from an individual's social position within the community, which may be reflected in their diet, geographical and diachronic differences across groups, and even economic conditions can be identified. As well as attempting to reconstruct past menus which, however, does not allow people to distinguish between "good" and "bad" foods, the goal is to reconstruct nutritional differences within and between populations. On this basis, it is possible to make statements regarding the general state of health, the pathophysiology, nutritional stress, physical growth, and the development of diseases [27].

Dental calculus, like bones and teeth, remains preserved for millennia [28] and contains viruses and biomolecules from all areas of life [29] with the oral cavity serving as a long-term reservoir for bacteria that are responsible for local and systemic diseases [30]. Interestingly from a diagnostic point of view, systemic diseases such as diabetes are always preceded by local oral pathologies. Genetic studies on dental calculus from prehistoric and historical skeletal finds allow people to characterise specific DNA sequences [31]. This, in turn, has enabled people to identify food sources, pathogenically altered oral microbiomes, opportunistic pathogens, human-associated antibiotic resistance genes and human and bacterial proteins. Thanks to the results obtained, periodontal pathogens such as *Tannerella forsythia* have been detected genetically, which has confirmed the suspected links between host immunity factors, "red complex" pathogens and periodontal disease [29]. Usually abundant in historical burials, dental calculus thus allows people to carry out parallel examinations of pathogen and host activities on the one hand and nutritional aspects on the other. Both the identification of plant remains in dental calculus and the palaeogenetic analysis of the oral microbiome [32][33] are innovative methods for anthropologists to study the procurement of food, nutrition, the pathogenic potential, and the behavioural patterns, and have also provided evidence of medically relevant uses of certain plants [29][33]. In this respect, studies of closest relatives are particularly interesting and informative [34].

References

1. Weiss, M.C.; Sousa, F.L.; Mrnjavac, N.; Neukirchen, S.; Roettger, M.; Nelson-Sathi, S.; Martin, W.F. The Physiology and Habitat of the Last Universal Common Ancestor. Nat. Microbiol. 2016, 1, 16116.
2. Hublin, J.-J.; Ben-Ncer, A.; Bailey, S.E.; Freidline, S.E.; Neubauer, S.; Skinner, M.M.; Bergmann, I.; Le Cabec, A.; Benazzi, S.; Harvati, K. New Fossils from Jebel Irhoud, Morocco and the Pan-African Origin of Homo sapiens. Nature 2017, 546, 289–292.
3. Richter, D.; Grün, R.; Joannes-Boyau, R.; Steele, T.E.; Amani, F.; Rué, M.; Fernandes, P.; Raynal, J.-P.; Geraads, D.; Ben-Ncer, A.; et al. The Age of the Hominin Fossils from Jebel Irhoud, Morocco, and the Origins of the Middle Stone Age. Nature 2017, 546, 293–296.
4. Muehlenbein, M.P. Basics in Human Evolution; Elsevier: Amsterdam, The Netherlands, 2015.
5. Vogel, C. Die Hominisation, ein singulärer Sprung aus dem Kontinuum der Evolution? Nova Acta Leopold. NF 1989, 62, 141–154.

6. Urry, L.A.; Meyers, N.; Cain, M.L.; Wasserman, S.A.; Minorsky, P.V.; Orr, R. Campbell Biology, 12th ed.; Pearson: London, UK, 2021.
7. Blonder, B.; Royer, D.L.; Johnson, K.R.; Miller, I.; Enquist, B.J. Plant Ecological Strategies Shift across the Cretaceous–Paleogene Boundary. PLoS Biol. 2014, 12, e1001949.
8. Shock, E.L.; Boyd, E.S. Principles of Geobiochemistry. Elements 2015, 11, 395–401.
9. Gamble, C. Settling the Earth: The Archaeology of Deep Human History; Cambridge University Press: Cambridge, UK, 2013.
10. Boivin, N.L.; Zeder, M.A.; Fuller, D.Q.; Crowther, A.; Larson, G.; Erlandson, J.M.; Denham, T.; Petraglia, M.D. Ecological Consequences of Human Niche Construction: Examining Long-Term Anthropogenic Shaping of Global Species Dstributions. Proc. Nat. Acad. Sci. USA 2016, 113, 6388–6396.
11. Barnosky, A.D.; Koch, P.L.; Feranec, R.S.; Wing, S.L.; Shabel, A.B. Assessing the Causes of Late Pleistocene Extinctions on the Continents. Science 2004, 306, 70–75.
12. Smolin, L.A.; Grosvenor, M.B. Nutrition: Science and Applications, 4th ed.; John Wiley & Sons: Hoboken, NJ, USA, 2019.
13. Sayers, K.; Lovejoy, C.O. Blood, Bulbs, and Bunodonts: On Evolutionary Ecology and the Diets of Ardipithecus, Australopithecus, and Early Homo. Q. Rev. Biol. 2014, 89, 319–357.
14. Tomasello, M.; Kruger, A.C.; Ratner, H.H. Cultural Learning. Behav. Brain Sci. 1993, 16, 495–511.
15. Cordain, L.; Miller, J.B.; Eaton, S.B.; Mann, N.; Holt, S.H.; Speth, J.D. Plant-Animal Subsistence Ratios and Macronutrient Energy Estimations in Worldwide Hunter-Gatherer Diets. Am. J. Clin. Nutr. 2000, 71, 682–692.
16. Mann, N. Meat in the Human Diet: An Anthropological Perspective. Nutr. Diet. 2007, 64, S102–S107.
17. Thompson, P.; Harris, S. Seeds, Sex and Civilization: How the Hidden Life of Plants Has Shaped Our World; Thames & Hudson: London, UK, 2010.
18. Bogaard, A. Neolithic Farming in Central Europe: An Archaeobotanical Study of Crop Husbandry Practices; Routledge: London, UK, 2004.
19. O'Connor, T. The Archaeology of Animal Bones; The History Press: Cheltenham, UK, 2013.
20. Reitz, E.J.; Wing, E.S. Zooarchaeology, 2nd ed.; Cambridge Manuels in Archaeology; Cambridge University Press: Cambridge, UK, 2008.
21. Lee-Thorp, J.; Katzenberg, M. (Eds.) The Oxford Handbook of the Archaeology of Diet; Oxford University Press: Oxford, UK, 2015; ISBN 978-0-19-175688-7.
22. Buikstra, J.; Beck, L. Bioarchaeology. The Contextual Analysis of Human Remains; Elsevier: Burlington, MA, USA, 2006.
23. Larsen, C.S. A Companion to Biological Anthropology; Wiley-Blackwell: Hoboken, NJ, USA, 2010.
24. Haidle, M.N. Mangel-Krisen-Hungersnöte? Ernährungszustände in Süddeutschland und der Nordschweiz. Vom Neolithikum bis ins 19. Jahrhundert. Archäol. Inf. 1997, 20, 185–188.
25. Lee-Thorp, J.A. On Isotopes and Old Bones. Archaeometry 2008, 50, 925–950.
26. Ambrose, S.H.; Katzenberg, M.A. Biogeochemical Approaches to Paleodietary Analysis; Kluwer Academic: New York, NY, USA, 2000.
27. Alt, K.W. Kulinarischer Streifzug durch 8000 Jahre Ernährung in Sachsen-Anhalt—Das Potenzial der stabilen Kohlenstoff- und Stickstoffisotopenanalysen. Blickpkt. Archäol. 2016, 4, 178–187.
28. Pacey, L. Calculus Is a Long-Term Reservoir of Disease. Br. Dent. J. 2014, 216, 438.
29. Warinner, C.; Rodrigues, J.F.M.; Vyas, R.; Trachsel, C.; Shved, N.; Grossmann, J.; Radini, A.; Hancock, Y.; Tito, R.Y.; Fiddyment, S.; et al. Pathogens and Host Immunity in the Ancient Human Oral Cavity. Nat. Genet. 2014, 46, 336–344.
30. Hujoel, P. Dietary Carbohydrates and Dental-Systemic Diseases. J. Dent. Res. 2009, 88, 490–502.
31. Warinner, C. Dental Calculus and the Evolution of the Human Oral Microbiome. J. Calif. Dent. Assoc. 2016, 44, 411–420.
32. Adler, C.J.; Dobney, K.; Weyrich, L.S.; Kaidonis, J.; Walker, A.W.; Haak, W.; Bradshaw, C.J.; Townsend, G.; Sołtysiak, A.; Alt, K.W.; et al. Sequencing Ancient Calcified Dental Plaque Shows Changes in Oral Microbiota with Dietary Shifts of the Neolithic and Industrial Revolutions. Nat. Genet. 2013, 45, 450–455.

33. Weyrich, L.S.; Duchene, S.; Soubrier, J.; Arriola, L.; Llamas, B.; Breen, J.; Morris, A.G.; Alt, K.W.; Caramelli, D.; Dresely, V.; et al. Neanderthal Behaviour, Diet, and Disease Inferred from Ancient DNA in Dental Calculus. Nature 2017, 544, 357–361.
34. Power, R.C.; Salazar-García, D.C.; Wittig, R.M.; Freiberg, M.; Henry, A.G. Dental Calculus Evidence of Taï Forest Chimpanzee Plant Consumption and Life History Transitions. Sci. Rep. 2015, 5, srep15161.
