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Evolution of the human face: an overview *

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Abstract

The phylogenetic changes that have occurred through the process of evolution of human face from the time of earliest ancestors is a matter of great interest for the anthropologists. Various researchers all over the world have extensively studied paleontological remains of previous generations. Face and dentition, in particular, can be indicative of a population's dietary and social habits as well as climatic conditions. Researchers have aimed to determine the development of the skull, parts of the face, facial features, expressions and their transition from nonhuman primates to modern homo sapiens. The present review attempts to provide an insight pertaining to transitional changes that have happened with respect to various features of human face over time since the time of early ancestors and the observed difference of these features from modern-day human.

Keywords: dentition; evolution; facial morphology; Homo sapiens

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Introduction

The term 'metamorphosis', meaning 'transformation', is derived from the Greek words 'meta' – after and 'morphe' – form. With its inception dating back as far as 25 million years ago, the transformation process of primitive ancestral apes into modern Homo sapiens sapiens is one of the most perplexing topics for paleontologists and anthropologists. The incredible story of the human evolution dates back as far as 2.5 million years ago where our ape-like ancestors were born and eventually transformed into the modern-day Homo sapiens sapiens (1). Over the years, various remarkable discoveries have shed light on this hierarchal transformation. The famous fossils of 'Lucy', the first Australopithecus, dug up in Ethiopia in 1974, were the first human species who walked upright (2). Around 2.4 million years ago, Homo habilis- aka 'the handy man' appeared who had even sharper features and the ability to create tools and hunt for their survival (3). Shortly afterwards, fossils of homo erectus were unearthed in Indonesia 1891 (4). Continuing along the timeline, the Neanderthals existed about 20,000 years ago which had the most characteristically similar skeletal and soft tissue features to the modern man. Along with this, capacity for art, language, complex hunting methods were developed during this era. The homo sapiens came into existence 20,000 years ago and have continued to evolve through time into modern-day humans (5).

The human face is a distinctive yet universal entity, modern yet ancient and mechanical yet expressive. A lot of phenotypic diversity is seen in human skulls and face over the course of evolution. Modern humans have a smaller, retracted face, beneath a large cranium as opposed to the early Hominins who had coarse facial features and a smaller brain. In facial and dental morphology, primates such as chimpanzees, baboons and gorillas differ from the early hominids like Australopithecus in fundamental ways (6). In the African great apes, postnatal growth results in prognathic deep, long and strongly inclined snout with a prominent pre-maxilla (7). As opposed to these features, the early Hominins project a vertical profile similar to the modern humans (8). The present review attempts to highlight the earliest evidence of Homo Sapiens' face and consider the impact of genetic, environmental and social factors; population history and migration in shaping the morphology of face over time.

Materials and Methods

Specimens of primates and human skulls were obtained from the museum of institutional department. Only satisfactorily intact specimens were selected for subsequent analysis and were photographed in suitable settings of light and distance. Additionally, a review of literature was performed with respect to craniofacial and skull characteristics of various species across the

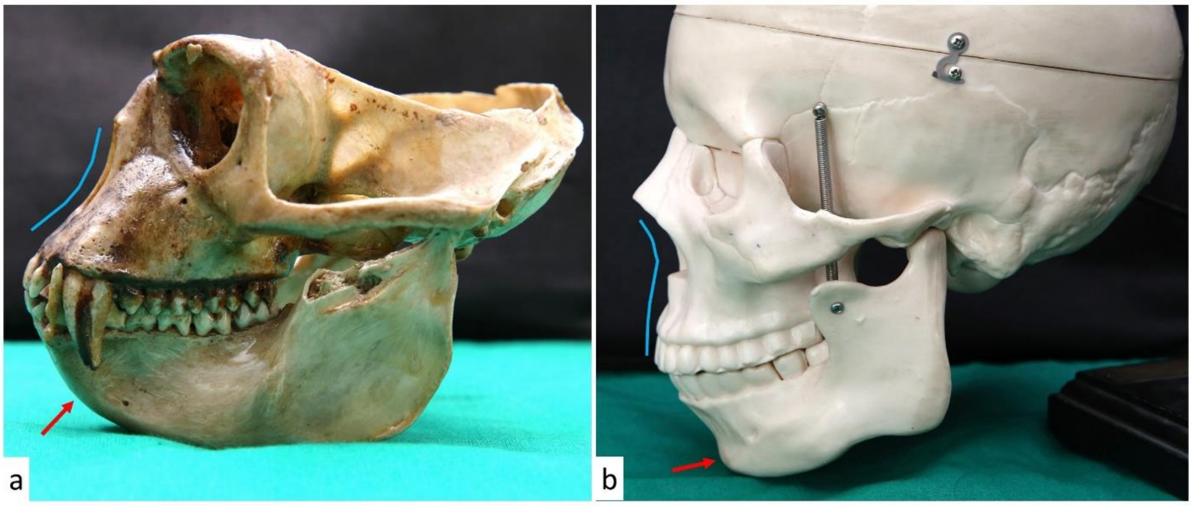

Figure 1. Flattening of face (blue outline) owing to remodelling of maxillary and mandibular bones from a) Earlier primates to b) Human skull; Arrow denotes difference in chin prominence between ancestral and human skulls. [Source: Museum specimens, Government Dental College and Hospital, Mumbai].

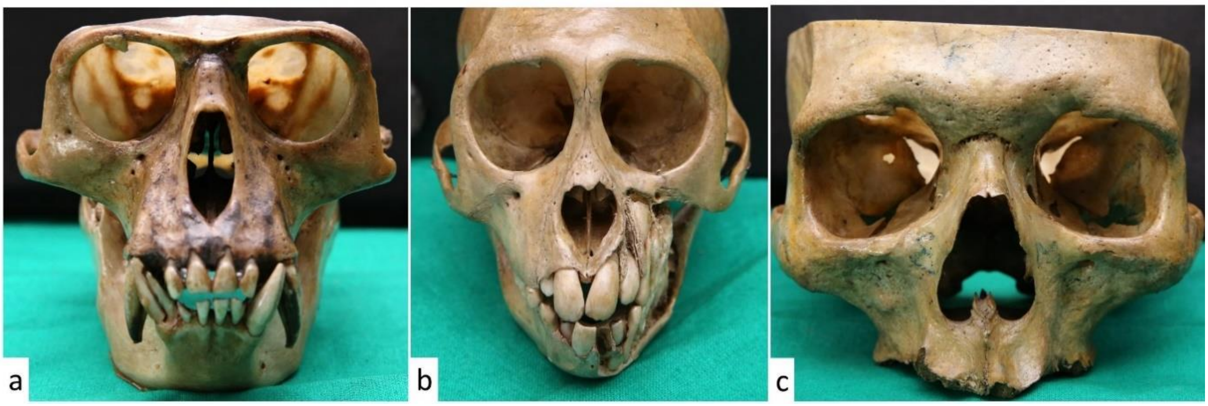

Figure 2. Variation in brow ridge form (rounded to flattened prominent) amongst a) Earlier primates, b) Monkeys and c) Human. [Source: Museum specimens, Government Dental College and Hospital, Mumbai].

evolutionary process of modern-day Homo sapiens sapiens. The findings were identified, compiled in datasheets and compared for subsequent analysis. Variations and comparison in the growth and development of early hominins and modern sapiens can be better understood by categorizing and studying the different skeletal and soft tissue aspects of the face and thus, have been described as the following sub-headings.

Maxilla and Mandible

From the evolutionary perspective, the most significant remodeling in craniofacial structures has been noted in the jawbones, namely- maxilla and mandible. There has been considerable shortening of the face due to greater flexion and increased length of the cranial base over the evolutionary course (9). This may be attributed to refined diet and social features of modern-day lifestyle (10). During the growth and development of craniofacial skeleton, bone growth centers and sites are present to optimize the organism's physiological requirement and carry out remodeling of the bones. In modern humans, there is a predominance of widely distributed resorptive fields over the maxilla, infraorbital, anterior zygoma, mental region and coronoid process which contributes to the evolved facial retraction. In prognathic facies of the apes and early Australopithecus, bone deposition patterns are seen along these respective bones (6).

Overall, there was a progressive flattening of the face from primates up to the modern-day human being attributable modification in dietary habits with the advent of cooking and processing of foods which subsequently led to lesser forces on the jaws (Figure 1). On the contrary, a prominent chin was absent in our early ancestors. Various theories have been put forth to determine this evolution such as mastication related biomechanical forces, reduction of the dental arch, a sexual trait, contractions of tongue and development of speech (11).

Nose

The shape of the nose sends the strongest differentiation signals which suggest that the soft tissues play a greater role in the development of the face and ultimately, the body. Earlier skull and soft tissues variations based on genetic markers have been used to determine the path of evolution (12). It has also been suggested that the shape of nose may be influenced by climatic adaptation and the geographical area (13). Populations in colder climate such as an extreme European face presents with a narrower, longer face with a more pointed nose. On the other hand, the extreme Chinese face is wider, flatter with prominent cheek bones. A narrow, prominent nasal ridge characterizes the Europeans whereas a broad nasal base, recessive nose dorsum is attributed to East Asians (12,14).

Brow ridge

The brow ridge size is directly co-related with the intensity of mechanical stresses because of mastication. As a result, the brow size has decreased considerably from earlier ancestors such as Homo erectus to Modern Homo Sapiens accompanying the transition from coarse, raw food to refined, cooked meals (Figure 2). For the soft tissue part, brows are significant for expressing greetings, surprise, smile, sadness as well as grief. To make the eyebrows more prominent, there has been a relative hairlessness of the human face as compared to primates. Noticeable brows help in signaling these expressions to other humans and enhance our communication (15).

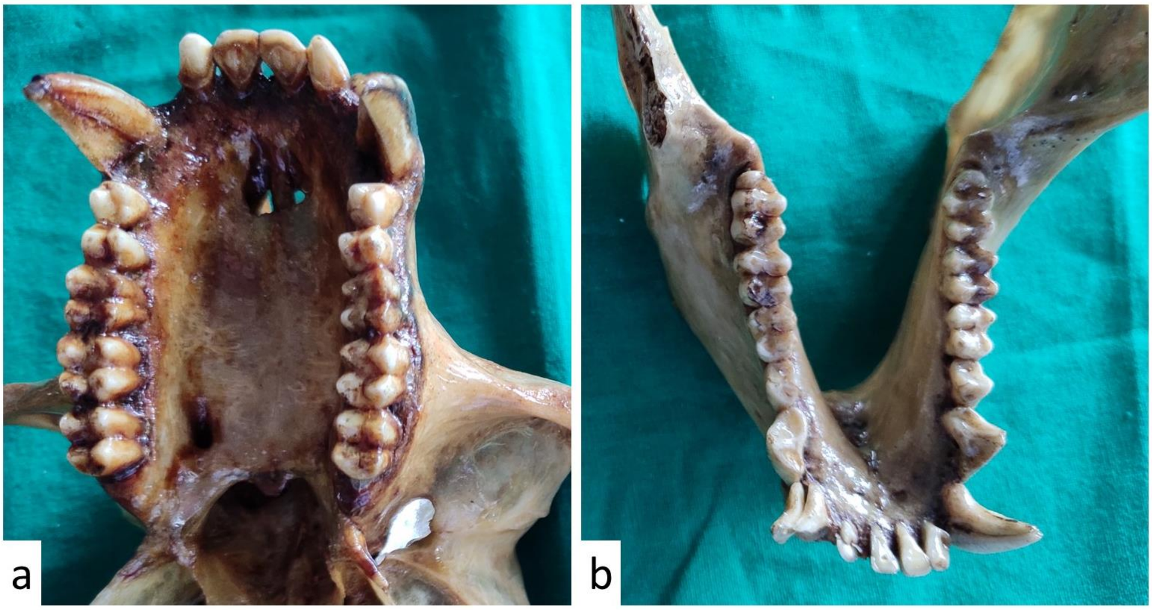

Figure 3: a) Maxillary jaw and b) Mandibular jaw of primates. Note the prominent, sharp cust tips and sharp line angles. [Source: Museum specimens, Government Dental College and Hospital, Mumbai].

Facial muscles and expressions

Anthropologists have devised the homology of facial expressions and its phylogenetic perspectives. An inherent greater intellect bred more expressive and efficient communication amongst humans and the consequent socializing nature inculcated in greater development of muscles of facial expression (16). Remarkable similarities have been noted in the facial expressions of nonhuman primates and modern humans. Particular expressions such as the fear grimace, silent bared teeth and relaxed open mouth have been carried forward to fear, smile and laughter respectively (17). This transition could be the result of the same muscles stretched over a modified and retracted jaws and nose.

A common neurological basis is hypothesized to control the facial expressions both of these species. Bilateral cortical projections to the facial nuclei control frontalis and orbicularis oculi muscles, and contralateral projections to the opposite facial nucleus, control the muscles around the mouth (18). Human anger and embarrassment have also been proposed as a homologue of primate displays. Characteristics such as withdrawal, minimizing appearance, smile with downward glance are also derived from the primates. These ape-like ancestors used their hands to hide their expressions in times of need (19). However, we modern sapiens have complex facial muscles that incorporate various expressions to conceal our emotions. The use of depressor anguli oris to pull the lips downward and the 'twisting' of the smile to avoid appearing too pleased are documented as ways to minimize our expressions (20).

Diet has played a crucial role in reduced size of the muscles of mastication as well. For example, the temporalis muscle was much larger in the apes due to consumption of primitive diet comprising of more fibrous plant material which has reduced in modern-day hominids as a consequence of cooking and refinement of diet (21).

Dental characteristics

Recently, scientists have unfolded various complex phylogenetic aspects through analyzing dentition of early ancestral remains. Dental records are essentially important markers of health, diet and social behavior to anthropologists (22). Thicker enamel to withstand the dietary shift to hard seeds and roots has been demonstrated in carbon signatures of ancient teeth (23). In 2015, researchers discovered 47 teeth in a cave in Southern China belonging to Homo Sapiens as far back as 80-120 thousand years ago. The migration patterns of people were also examined based on the teeth remains by correlating the geographical influences on the shape and structure of the teeth (24). Krueger examined the wear of Neanderthal teeth as they used their mouths as a supplementary tool (25). People living in cold and open conditions used their teeth

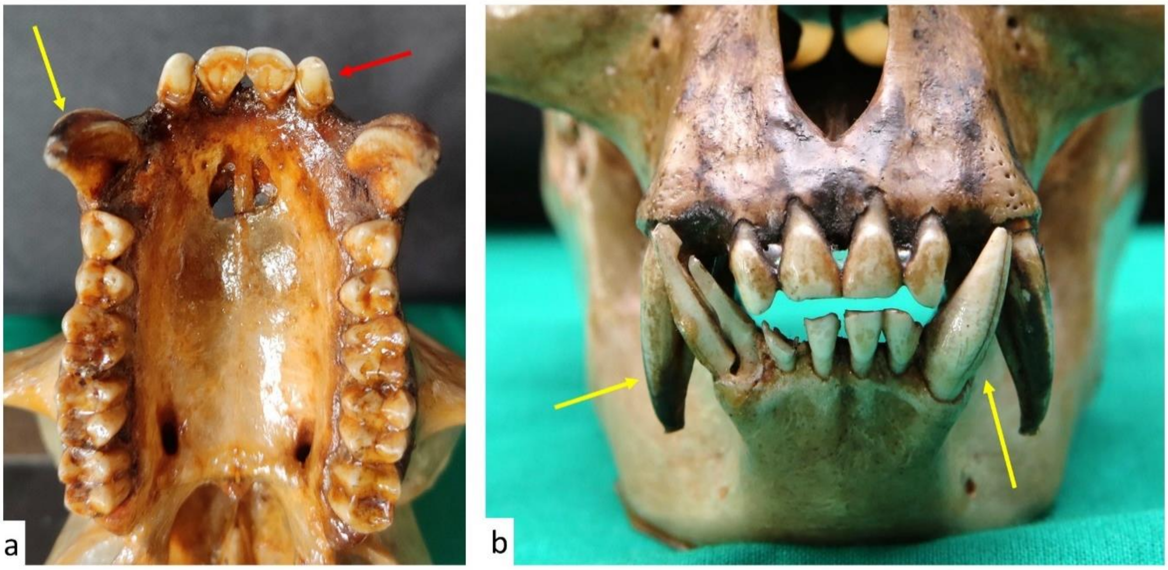

Figure 4. Occlusal view of primate dentition exhibitng sharp incisors (red arrow) and Prominent canines (yellow arrows) in Male Primates. [Source: Museum specimens, Government Dental College and Hospital, Mumbai].

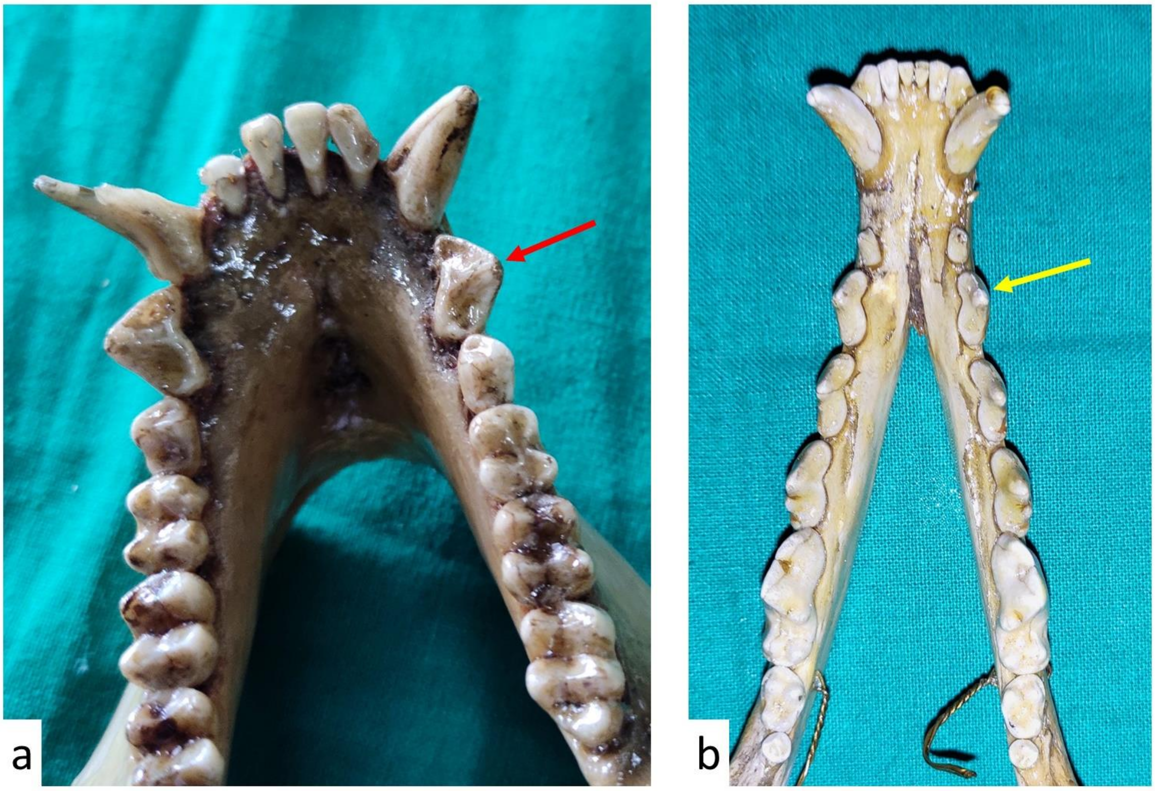

Figure 5. Specimens of Mandibular dentition of a) early primate and b) dog exhibiting similarity in morphologic form of first premolar. [Source: Museum specimens, Government Dental College and Hospital, Mumbai].

on clamping and grasping resulting in more attrition, as opposed to those in warm environments. The evolution of the tooth is immensely significant in determining various aspects of the development and recognition of species. In the archaic hominins, smaller and protruding incisors and larger premolars and molars were observed (26). Earlier hominins

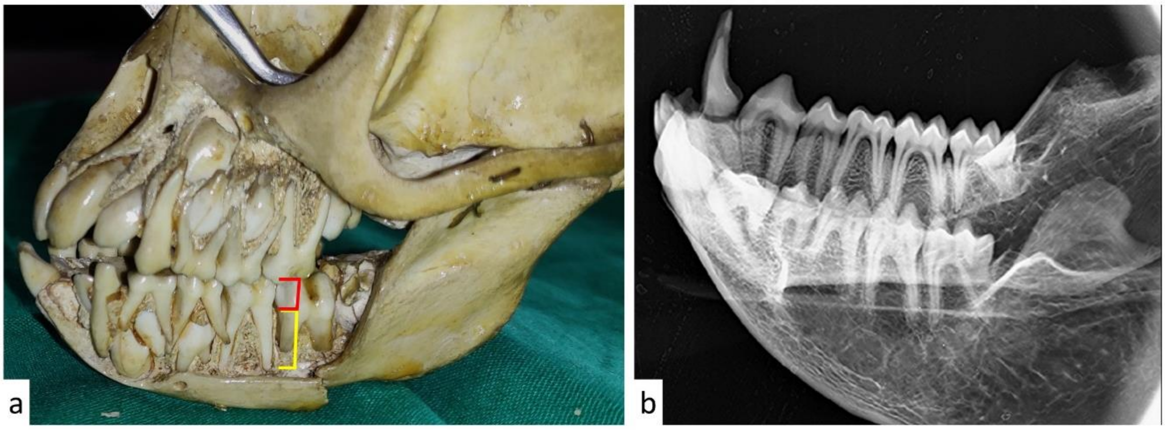

Figure 6. Smaller dimension of crowns (red) as compared to roots (yellow) in a) Skull specimen of monkey with mixed dentition and b) Radiograph of Primate jaw. [Source: Museum specimens, Government Dental College and Hospital, Mumbai].

such as Paranthropus boisei, also known as 'The Nutcracker' that lived 2.3 million years ago, had the largest molars and the thickest enamel of any hominin (27). The teeth of earlier primates had much prominent cusps with sharper line angles and incisal edges (Figure 3). Earlier male primates also exhibited larger and prominent canines (Figure 4) which are representative of their aggressive social behavior and coarse diet (28). Additionally, the prominent canines and first premolars closely resembled to those of earlier mammals such as Canidae (dogs) indicative of a phylogenetic linkage (Figure 5). Furthermore, the embedded area of root within the supporting bone was much greater as exhibited with a lesser crown-to-root ratio (Figure 6) in concordance with the masticatory requirement in earlier primates (29). As the evolutionary trend continued, the size of the teeth and jaws gradually decreased to the present accompanied by development of modern Dryopithecus pattern with well-rounded cusps (30). An overall summarative comparison of various facial parameters through the phylogenetic course of human beings has been summarized in Table 1.

Conclusion

There has been a massive transformation in the growth and development of the skeletal and soft tissue elements of the face. Genetics have played a major role in the evolution of human face. Along with it, climatic adaptations, dietary modifications, behavior and advancements in hunting patterns also greatly influenced the progression of human face. A resultant short-faced human with a larger braincase, smaller and retracted jaws, smaller brow ridge, evolved facial expressions, decreased tooth size are the numerous aspects that have been transformed. These ground breaking revelations help us understand better the scientific basis of our existence. Hence, additional research and studies in paleodontology will be of paramount importance to further explore the evolutionary pattern of homo sapiens

Table 1. Overall summative comparison of various facial parameters through the phylogenetic course of human beings.

Species	Dryopithecus [31]	Ramapithecus [32]	Australopithecus [33]	Homo Habilis [34,35]	Homo Erectus [36]	Neanderthal man [37,38]	Cro-Magnon man [39]	Homo Sapiens [36,38]
Time Range [40]	23-25 million years ago	12-14 million years ago	3.3-2.1 million years ago	2.4-1.4 million years ago	1.89 million-110000 years ago	400000-40,000 years ago	20,000 years ago	Since 20,000 years
Brain capacity	500cc	500cc	500cc	700cc	1000cc	1200cc	1370cc	1470cc
Maxilla and Mandible	Large, prognathic	Large, prognathic	Large, relatively less prognathic	Large, less prognathic	Large, less prognathic	Large, less prognathic	Large, less prognathic	Small, flattened
Nose	Large	Large	Large, flat	Large, flat	Prominent	Large, prominent	Prominent, narrow	Prominent, narrow
Chin	Absent	Absent	Less prominent	Less prominent	Less prominent	Less prominent	Prominent	More prominent
Forehead	Small forehead	Rounded forehead	Low forehead	Low forehead	Low, flat forehead	Receding forehead	Near vertical forehead	Flat, vertical forehead
Teeth	Prominent canines	Large canines and heavy molars	Smaller canines and large molars	Large incisors, narrow molars	Large incisors. narrow molars	Large taurodontic teeth	Large, differentiated	Small, differentiated
Speech [41]	Absent	Absent	Absent	Rudimentary speech	Primitive speech	Primitive speech	Capable of speech	Modern speech
Diet	Fruits	Seeds and savannah grasses	Grass seeds, roots and nuts	Woody plants, animal tissues	Meat-rich foods and dietary fibres	Meat-rich diet	Cooked meat and plants	Soft cooked refined food

References

1. Ambrose SH. Paleolithic technology and human evolution. Science. 2001 Mar 2;291(5509):1748-53.
2. Gibbons A. In search of the first hominids. Science. 2002 Feb 15;295(5558):1214-9.
3. Mithen S. Creations of Pre-Modern Human Minds: Stone Tool Manufacture and Use by Homo habilis, heidelbergensis, and neanderthalensis. Creations of the mind. theories of artifacts and their representation. 2007 Jun 14:289-311.
4. Holloway RL. The Indonesian Homo erectus brain endocasts revisited. Am. J. Phys. Anthropol. 1981 Aug;55(4):503-21.
5. Stringer C. The origin and evolution of Homo sapiens. Philosophical Transactions of the Royal Society B: Biological Sciences. 2016 Jul 5;371(1698):20150237.
6. McCollum MA. Nasomaxillary remodeling and facial form in robust Australopithecus: a reassessment. J Hum Evol. 2008 Jan 1;54(1):2-14.
7. Moyà-Solà S, Köhler M, Alba DM, Casanovas-Vilar I, Galindo J. Pierolapithecus catalaunicus, a new Middle Miocene great ape from Spain. Science. 2004;306(5700):1339-44.
8. Emes Y, Aybar B, Yalcin S. On the evolution of human jaws and teeth: a review Bull Int Assoc Paleodont 2011;5(1):37-47.

9. Kimbel WH, Suwa G, Asfaw B, Rak Y, White TD. Ardipithecus ramidus and the evolution of the human cranial base. PNAS 2014;111(3):948-53.
10. Gibbons A. Evolutionary biology. An evolutionary theory of dentistry. Science. 2012 May 25;336(6084):973-5.
11. Lacruz RS, Stringer CB, Kimbel WH, Wood B, Harvati K, O'Higgins P, Bromage TG, Arsuaga JL. The evolutionary history of the human face. Nat Ecol Evol 2019;3(5):726-36.
12. Guo J, Tan J, Yang Y, Zhou H, Hu S, Hashan A, Bahaxar N et al. Variation and signatures of selection on the human face. J Hum Evol 2014;75:143-52.
13. Guglielmino-Matessi CR, Gluckman P, Cavalli-Sforza LL. Climate and the evolution of skull metrics in man. Am J Phys Anthropol 1979 May;50(4):549-64.
14. Kau CH, Richmond S, Zhurov A, Ovsenik M, Tawfik W, Borbely P, English JD. Use of 3-dimensional surface acquisition to study facial morphology in 5 populations. Am J Orthod Dentofacial Orthop 2010 Apr 1;137(4):S56-e1.
15. Schmidt KL, Cohn JF. Human facial expressions as adaptations: Evolutionary questions in facial expression research. Am J Phys Anthropol 2001;116(S33):3-24.
16. Dobson SD. Allometry of facial mobility in anthropoid primates: implications for the evolution of facial expression. Am J Phys Anthropol. 2009 Jan;138(1):70-81.
17. Preuschoft S. Primate faces and facial expressions. Soc Res. 2000 Apr 1:245-71.
18. Morecraft RJ, Louie JL, Herrick JL, Stilwell-Morecraft KS. Cortical innervation of the facial nucleus in the non-human primate: a new interpretation of the effects of stroke and related subtotal brain trauma on the muscles of facial expression. Brain. 2001 Jan 1;124(1):176-208.
19. Tomasello M. If they're so good at grammar, then why don't they talk? Hints from apes' and humans' use of gestures. Lang Learn Dev. 2007 Mar 29;3(2):133-56.
20. Schmidt KL, Cohn JF. Human facial expressions as adaptations: Evolutionary questions in facial expression research. Am J Phys Anthropol 2001;116(S33):3-24.
21. Demes B, Creel N. Bite force, diet, and cranial morphology of fossil hominids. J Hum Evol. 1988 Nov 1;17(7):657-70.
22. Lukacs JR. Dental trauma and antemortem tooth loss in prehistoric Canary Islanders: prevalence and contributing factors. Int J Osteoarchaeol 2007 Mar;17(2):157-73.
23. Van Der Merwe NJ, Thackeray JF, Lee-Thorp JA, Luyt J. The carbon isotope ecology and diet of Australopithecus africanus at Sterkfontein, South Africa J Hum Evol. 2003 May 1;44(5):581-97.
24. Turner CG 2nd. Teeth and prehistory in Asia. Sci Am. 1989 Feb;260(2):88-91, 94-6.
25. Moncel MH, Fernandes P, Willmes M, James H, Grün R. Rocks, teeth, and tools: New insights into early Neanderthal mobility strategies in South-Eastern France from lithic reconstructions and strontium isotope analysis. PLoS One. 2019 Apr 3;14(4):e0214925.
26. Xing S, Tafforeau P, O'Hara M, Modesto-Mata M, Martín-Francés L, Martinón-Torres M, Zhang L, Schepartz LA, de Castro JM, Guatelli-Steinberg D. First systematic assessment of dental growth and development in an archaic hominin (genus, Homo) from East Asia. Sci adv. 2019 Jan 1;5(1):eaau0930.
27. Lee-Thorp J. The demise of "Nutcracker Man". PNAS. 2011 Jun 7;108(23):9319-20.
28. Plavcan JM. Sexual size dimorphism, canine dimorphism, and male-male competition in primates. Hum Nat. 2012 Mar 1;23(1):45-67.
29. Dean MC, Vesey P. Preliminary observations on increasing root length during the eruptive phase of tooth development in modern humans and great apes. J Hum Evol 2008 Feb 1;54(2):258-71.
30. Begun DR. Relations among the great apes and humans: new interpretations based on the fossil great ape Dryopithecus. Am J Phys Anthropol. 1994;37(S19):11-63.
31. Begun DR. Relations among the great apes and humans: new interpretations based on the fossil great ape Dryopithecus Am J Phys Anthropol 1994;37(S19):11-63.
32. Rukang W, Qinghua X, Qingwu L. Morphological features of Ramapithecus and Sivapithecus and their phylogenetic relationships—Morphology and comparison of the crania. Acta Archaeol Sin 1983;2(1):1-0.
33. Available at https://humanorigins.si.edu/evidence/human-fossils/species/australopithecus-afarensis [Last accessed on 19 March, 2021]
34. Available at https://www.pathwayz.org/Tree/Plain/HOMO+HABILIS [Last accessed on 19 March, 2021]
35. Available at https://australian.museum/learn/science/human-evolution/homo-habilis/ [Last accessed on 19 March, 2021]
36. Available at homo erectus sapiens https://pediaa.com/wp-content/uploads/2018/08/Difference-Between-Homo-Erectus-and-Homo-Sapiens-Comparison-Summary-1.jpg [Last accessed on 20 March, 2021]

37. Bailey SE. A closer look at Neanderthal postcanine dental morphology: the mandibular dentition. The Anatomical Record. 2002 Jun 15;269(3):148-56.
38. Available at https://pediaa.com/wp-content/uploads/2017/12/Difference-Between-Neanderthals-and-Homo-Sapiens-Comparison-Summary.png [Last accessed on 21 March, 2021]
39. Available at https://humanorigins.si.edu/evidence/human-fossils/fossils/cro-magnon-1 [Last accessed on 24 March, 2021]
40. Available at https://humanorigins.si.edu/sites/default/files/styles/full_width/public/Time%20-%20Evolutionary%20Change%20-%20Adaptive%20Benefits_L_0.jpg?itok=CNqjvBKG [Last accessed: 24 March, 2021]
41. Available at https://australian.museum/learn/science/human-evolution/how-do-we-know-if-they-could-speak/ [Last accessed on 24 March, 2021]