On The Evolution of Human Jaws and Teeth: A Review

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Abstract

The jaws and teeth of Homo sapiens have evolved, from the last common ancestor of chimpanzee and men to their current form. Many factors such as the foods eaten and the processing of foods by fire and tools have effected this evolution course. The evolution of the masticatory complex is related to other anatomical features such as brain size and bipedal posture, and leads to important proceedings like the formation of speech and language. In this review, the evolution of human jaws and teeth and its impact on the general course of human evolution is discussed.

Keywords: Evolution; Human Masticatory Complex; Jaws

Introduction

Human masticatory, system, which consists of maxilla, mandible, teeth, temporomandibular joint, and the masticatory muscles, is functionally involved in not only feeding, but also speech. Just like all other anatomical features of our species, the masticatory system has also evolved during the history of men.

It has been estimated that the human lineage separated from the rest of the hominoids between 5 and 8 million years ago (Ma) (1). The new classification states that the vernacular terms we have been using to describe the human clade are no longer applicable. Thus the clade can no longer be described as containing 'hominids' for the family Hominidae has become more inclusive, and now refers to the common ancestor of the living African apes and all of its descendants. The appropriate vernacular term for a member of the human clade is now hominin for this is the way to refer to members of the tribe Hominini, and its 2 component subtribes, the Australopithecina and the Hominina. So it is recommended that the phrase hominid evolution to be used as hominin evolution (2).

With the help of absolute dating methods, it is now suggested that about 2.5 Ma, distinctly different hominin taxa have existed in the same geological period, and same region. It is now believed that there was more than one evolutionarty lineage within the human clade, and human evolution is more like a bush than a straight line, as Wood et al have suggested (2).

A list of the extinct hominin taxa are given in Table 1.

The aim of this article is to review the evolution of the oral system of the hominin clade, and its impact on human evolution. For this purpose, studies and articles on the evolution of human jaws and teeth, fossil studies on the cranial findings of extinct hominins, mechanical studies on the jaws and teeth of hominin taxa were included in the review. Also studies and articles on food preparation techniques which affect the evolution of human jaws and teeth were selected from the databases.

Reference lists of the retrieved articles were also searched to identify any other articles relevant to the research topic. These findings also provided additional information for the review. While selecting the information on the maxillofacial of the taxa retrieved from fossil studies, post cranial findings were excluded.

Table 1 List of the extinct hominin taxa

Possible and probable primitive hominins
Adipithecus. Ramidus
(5.7–4.5 Ma)
Archaic hominins
-*Australopithecus anamensis* (4.2–3.9 Ma)
-*Australopithecus afarensis* (4.0–3.0 Ma)
-*Australopithecus bahrelghazali* (3.5–3.0 Ma)
-*Australopithecus africanus* (3.0–2.4 Ma)
Megadont archaic hominins
- *Australopithecus garhi* (2.5 Ma)
- *Paranthropus aethiopicus* (2.5–2.3)
- *Paranthropus boisei* (2.3–1.3 Ma)
- *Paranthropus robustus* (2.0–1.5 Ma)
Transitional hominins
-*Homo habilis* (2.4–1.6 Ma)
-*Homo rudolfensis* (2.4–1.6 Ma)
Pre-modern Homo
-*Homo ergaster* (1.9–1.5 Ma)
- *Homo erectus* (1.8–0.2 Ma)
- *Homo antecessor*(0.7–0.5 Ma)
-*Homo heidelbergensis* (0.6–0.1 Ma)
-*Homo neanderthalensis* (0.2–0.03)
Anatomically modern humans
-*Homo sapiens* (0.19 Ma- present)

Dental and orofacial features of the extinct hominin taxa

The teeth and jaws of humans are smaller that todays great apes (3). Investigations on fossils have also shown the evidence of a decrease in the size of the masticatory system in the hominins which are accepted to be the ancestors of Homo Sapiens. Researchers have stated that this decrease was mostly due to the changes in the dietary habits of the species (4-6).

There are morphological differences that separate the modern humans from living apes, these include the characteristic of the dentition, skull, brain, trunk and the teeth. For example, canine teeth of the apes are sexually dimorphic when compared to the humans ad they usually are not worn down to the level of the occlusal surfaces of the posterior teeth (7). Human jaws are also smaller, more gracile, and project less than those of equivalent sized living apes (8). These features, that distinguish the modern humans from living apes, could also be found between modern humans and early hominins, together with similarities between the taxa (2).

Recently, Lucas et al. (9) have studied the dietary adaptations of extinct hominins and classified them into 4 groups stating that it was difficult specify the dietary changes of the hominin clade at the species level.

1. Earliest hominins (7 - 4 Ma) This group included *Sahelanthropus tchadensis, Orrorin tugenensis, Ardipitechus kadabba,* and *Ardipitechus ramidus.*
2. Archaic Hominins (4 - 2.5 Ma) *Australopithecus afarensis, Australopithecus africanus, Australopithecus anamensis, Australopithecus garhi, Australopithecus bahrelgazali, Kenyanthropus platyops*
3. Archaic megadont hominins (2.5 - 1 Ma) *Paranthropus robustus, Paranthropus aethiopicus, Paranthropus boisei*
4. Pre- modern Homo (2 Ma- 18 ka) *Homo rudolfensis, Homo habilis,, H. ergaster, H. erectus, H. floresiensis, H. antecessor, H. heidelbergensis, H. neanderthaslensis, H. sapiens.*

Lucas et al (10) have also agreed that the dental properties of the Last Common Ancestor of chimpanzees/ bonobos and hominins were similar to today's chimpanzee. They had large incisors and were procumbent when first erupted. The canines were sexually dimorphic, males had more projected canines than the females. Premolars had relatively small crowns and the second molar was the largest of the molar teeth just like in all of the great apes (10). Also similar to most monkeys and great apes, the upper canines posterior edge was sharpened against the anterior extension of the anterior lower premolar in Ardipithecus (11).

Incisors were probably procumbent at the time of eruption in the earliest and archaic hominins (12). However, the incisor teeth were relatively small and more vertical in the archaic megadont hominins and the genus Homo (13). This reduction in the incisal size was combined with the enlargement of the premolars and molars (14).

Canine teeth are believed to be small in the earliest hominins (9) and this reduction in size continues during the early period (11). Megadont archaic hominins present the greatest size reduction of the canines and the premolars are abnormally large in these taxa as reported by Wood and Stack (15). Hominin males generally have small canines, it is stated that, the higher the jaw joint, the smaller the canines are in males (10) and generally, temporomandibular joint is high in the hominoids. Lucas et al (9) also suggest that this reduction might also be due to the size of the post canine teeth.

In the modern humans, the first molar teeth are the largest among the molars and the overall tooth size is reduced (16) In the earliest hominins and archaic hominins, second molars were generally the largest of the molar teeth and the third molars were closer in size to the second molar (17) Lucas et al (9) state that food particles are not certain to be broken totally by the teeth, for the tooth surfaces form only a small amount of the oral surface and this is why the cheek muscles and the tongue have a great importance in chewing and keeping the food particles between the teeth. It is generally believed that the early hominins and archaic megadonts were small object feeders. Second premolars contribute more to the tooth row when the first molar/ third molar ratio is high and this is correlated to the canine tooth size. This might be due to the larger premolars extending the cheeks anteriorly reducing the size of the mouth slith (10).

Homo sapiens

The features of the “modern human” have been a subject of discussion. Some authors claim that the the taxon H. sapiens should include more than only the humans of today. It has been previously suggested that H. erectus should also be included to H. sapiens. (18). Even though small bodied modern humans have smaller crania, the size differences of human crania differ very little between the individuals (19). Human posterior teeth have small crowns relative to body mass and they have a tendency to reduce the number of cusps and roots. In Europe, Modern humans are believed to appear at the same time with the “upper Pleistocene revolution” which shows advances in behaviour (20) like speech and ability to manufacture fine stone and bone tool such as needles and fish hook. In Africa modern anatomy and modern behaviour did not appear at the same time, and in Africa, these changes occurred earlier than in Europe.

Distinctive maxillofacial anatomical features of Homo sapiens

The protruding chin is one of the evolutionary features which separate Homo sapiens from our ancestors. A protruding chin was absent in archaic humans and Neanderthals (3, 21). Many studies have been performed on the function and biomechanical basis on the formation of the chin. While Some authors have claimed that the chin provided resistance to bending forces on the mandible (22) some others including Liberman (23) stated that the chin had no functional importance. Masticatory system related biomechanical forces were believed to play a role on the formation of the human chin

(21). However, opposing views claim that the development of the human chin emerged at a time of constant or decreased dental use and at a time of mandibular shortening (24) Some authors have claimed that the reduction of the dental arch left the chin as a protrusion in the mandible. Ichim et al. (25) have claimed that the formation of the chin might have been due to the repetitive contractions of the tongue and the perioral musculature which are the results of the originating of speech in the modern humans. They have stated that the originating of the chin coincides with the apeearance of speech 50.000 years ago. It has also been shown in biomechanical studies that chinned and non chinned mandible models resisted the same to bending masticatory forces (23, 25).

The occlusal plane in humans is often not horizontal. A helicoidal occlusal plane is an inclination of the teeth where the anterior cheek teeth show a plane sloping upward palatally while the more posterior teeth have a plane sloping upward buccally forming a twisted occlusal plane (26) Even though the helicoidal occlusal pattern has been regarded as a feature typical for the orofacial region of Homo (27) it is also seen in the plio- Pleistocene hominids and in non human primates, especially the chimpanzees (28). Smith (29) has stated that, the foreshortening of the of the dental arcade in hominids resulted in molars coming to lie mostly posterior to the root of the zygomatic arch and medially to the massater- pterygoid complex, and both factors appeared to be important for the development of the helicoidal occlusal plane. Also the reduction of the dental arches and their retraction under the cranium required axial inclination of the molar roots. It has been proposed that this axial inclination of the teeth in the course of evolution has been paralleled by differential changes in cusp heights in order to keep the masticatory complex functional (30). The posterior teeth of the humans are also inclined in the sagittal plane. Human lower third molars have undergone a forward tilt during the course of evolution as a result of the displacement of the temporomandibular joint in relation to the oclusal plane. This developed the curve of spee which is more pronounced in humans when compared to the other hominids. This also rendered the third molars functional despite their disadvantageous position (31). It has been stated that, because of this curve, molars on the working side function in a smooth griding movement because of this curve. A complex relationship between the curve of spee and the helicoidal occlusal plane the molars function in series rather than simultaneously and the third molars keep their functional importance (31). even though the helicoidal occlusal plane has been accepted as a by product of evolutionary changes in the mascicatory system, Macho and Berner (30) have concluded that helicoidal occlusal plane could possibly be considered as a functional adaptation in itself.

When the evolution of the mandibular condyle is evaluated, it was shown that the early hominins inherited a low and anteriorly placed joint from some ramamorph ancestor with a similarly placed joint point. In the ausralopitecine line, the joint remained forward but was raised. In the H.erectus group it was raised less and displaced backward. Neanderthals had a high ramus width, but they had widely different values of ramus height (28)

In Homo sapiens the joint has moved forward, but it has maintained the same distribution of elevations as that for the Neanderthals. The mandibular condyles of hominoids occupy a restricted position in relation to the occlusal plane. Different positions (high, low, forward and backward) have a considerable effect on the movements of the lower molars when the jaws are closed and thereby affect the way in which food is processed during mastication. During human evolution there have been fairly well defined changes in the position of the temporomandibular joint which were probably related, to changes in food processing and diet (32).

Diet and dental evolution

Teaford and Ungar (33) have shown that 4.4 to 2.3 million years ago, there have been changes in the dietary capacities of the early hominins (australopithecines) which have provided them the chance to survive in different habitats making them able to eat a larger variety of food.

Analyses of the tooth shape, tooth size, enamel shape and dental micro wear together with dental biomechanics, suggest that there have been a shift in the dietary capacities of the australopithecines which has helped them survive in climatic variability. Studies on the teeth of A anamensis to A. Afarensis and to A. Africanus suggest that hard and abrasive foods had gained importance through the Pliocene period (33).

Jolly (34) have stated that the australopithecines had smaller incisors compared to the molars and speculated that this ratio might have been due to terrestrial seed eating .

Australopithecines also had large and flat molars (35). Studies on the teeth of australopithecines have shown that they had larger molar teeth area than today's orangutan. Also these species had a large variety of tooth sizes and variation in tooth size shows adaptation to various types of foods depending on their shapes, sizes and abrasiveness (33) .

It has been stated that, the large blunt teeth of australopithecines lacked the long shearing crests, and some authors believe that this indicates that these early species were mostly capable of eating buds, flowers and shoots (33). Lucas and Peters (36) have claimed that the australopithecines were dentally adapted to consuming meat.

It is mostly believed that these Miocene period apes fed on folivory, soft fruits and hard objects. Australopithecines, who had large and flat molar teeth were suitable for hard and brittle foods like some fruits nuts flowers and buds. Studies also show that the australopithecines have acquired the ability to eat hard objects through time. Teaford and Ungar (33) claim that there is a possibility of the australopithecines using tools for meat, that overcomes their anatomical disadvantages for meat consumption. They also say that the studies on teeth abrasion assume that all the meat have the same toughness but there might be variations in the toughness between animal tissues that make the consumption of meat easier. It is hypothesized that, with the use of tools for cutting and grinding, the need for carnivore adaptative characteristics such as strong jaw bones, large canines and stronger masticatory muscles started to decrease.

The transition from foraging to food providing economies involved profound changes in immobility, social organization and technology. (36, 37) . Studies in the Levant show that with the invention of pottery (the pottery Neolithic period, 7.600-7.000 uncalibrated radiocarbon years before present) ended the trsansformation from hunter- gatherer society to fully agricultural economy, and ended hunting (38). Reduction in the jaws and teeth of human populations have been previously reported in early Holocene populations from various regions (39, 40) This reduction was linked to transition from hunter gatherer community to a fully Neolithic (agriculturist) community by some authors (41, 42). When compared to the whole human evolution, these changes in the human masticatory complex have occurred in a very short period (43).. Several evolutionary models have been proposed in order to explain the mentioned reduction in the mentioned regions: The probable mutation effect: This model suggests that, in the absence or natural selection, mutations will be the main force acting towards a reduction of structural size and complixity of teeth and other organs. A simplified or incomplete dental structure will develop as a result of the disruption of complex genetic mechanisms controlling the dental development (44). It has been hypothesized that the invention of pottery and changes in food production following the use of pottery, relaxed the selective forces on the masticatory system and the onset of probable mutation effect resulted in a consequent reduction in tooth size (45).

According to this theory, all dental dimensions are reduced indicating a general decrease in size over time, variation in all dimensions either increases or constant over time (46).

Increasing population density effect: This model suggests that the transition to a sedentary lifestyle resulted in changes in population and reduction in dental crown size had been derived from these population changes. A new set of adaptive pressures were formed by these new post Pleistocene environmental conditions. A selection for reduction in nutritional and methabolic requirements led to a corresponding reduction in body size was triggered by these new adaptive forces. And this reduction in body size resulted in a decrease in tooth size (47).

According to the Increasing population density effect model, an overall reduction in the main mandibular and dental dimensions and a corresponding reduction in their metric variation is observed.

Selective compromise effect: This model suggests that larger morphologically complex crowned teeth provide more surface area for caries, which in turn can significantly effect the individuals health. However, abrasive foods require a large crown area. Populations in transition to agriculture a selective compromise must occur between a selection for smaller teeth with less complex crown morphology, and thin enamel and selection for larger teeth with thicker enamel to compensate occlusal wear. A central aspect of this model is the assumption that selection for smaller dentition is triggered by dental crowding and high prevalence of cariogenic disease in the near eastern and Nubian early halocene archeological populations (38, 48)

According to this theory, overall reduction in the main mandibular dimensions and a corresponding reduction in dental dimensions are seen. These changes include a total change in overall crown area or a uniform trend of change in crown dimensions that may affect certain tooth groups such as posterior teeth to reduce the prevalence of caries (16)

According to The probable mutation effect model, mutation is the predominant mechanism that induces the morphometric change. The other two models emphasize the role of selective forces on the evolution of the human masticatory system. Recently, the findings of Pinhasi et al (39) seem to support some aspects of the Selective compromise effect model, while not showing correspondence with the Increasing population density effect. They also exclude the probable mutation effect model because of the uniform changes they observe which best fits a model of directional selection rather than one that proposes the accumulation of random mutations.

Cooking is another factor on lessening the need for carnivore adaptations (49), and the first evidence of cooking dates back to 200.000- 300.000 years ago (50)

It has been reported by various authors that a decrease in the dental dimensions started to appear with the use of controlled fire for cooking (49, 51), It is also stated that the control of fire and the use of language are strongly related, for the teaching the next generation how to use fire needs the use of language (52).

It is known that australopithecines had the use of flake tools (53). Experiments have shown that the cut marks on the long bones from the Pliocene- Pleistocene period were not made by carnivore teeth but by tools (54).

Speech and The Upper Airway

Evolution of human masticatory system is not only related to diet and food processing techniques, but also brain size, bipedalism and speech (language).

Appearance of spoken complex language is believed to be the result of the critical change in the human evolution that occurred 40.000 years ago, named “the great leap forward” which resulted in the formation development of human civilization. It has been claimed that the formation of the anatomic basis for the complex speech was the cause of this leap (55). The anatomical changes necessary for the formation of language also have some drawbacks. The evolutionary changes for speech result in pharyngeal collapse, which are believed to be the cause of obstructive sleep apnea. Davidson (56) has proposed that the supralaryngeal vocal chord tract (SVT) has been medified to form a 1:1 ratio between the horizontal and vertical segments. The horizontal dimension of the SVT has decreased by the shortening of the midface and lengthening of the vertical SVT by the descent of the larynx, for this purpose. These changes in the SVT were accompanied by a narrowed, elongated distensible pharynx and posterior displacement of the tongue from the oral cavity into the pharynx. Craniobase angulation was also a cause for the enhancement of speech (56, 57). Davidson (56) also has shown that the evolutionary changes in the upper respiratory tract including shortening of the mandible which are necessary for the development speech have resulted in the development of obstructive sleep apnea in humans.

Speech and language need a flexible oral system (58), This flexibility is maintained by providing processed and softened food, which does not require a strong musculoskeletal build and sharp teeth. It has also been stated by Milton (6) that, language enabled humans to coordinate their actions for providing food and increase the foraging ability of our species. Hiimae (58) also has stated that human oropharyngeal system differed from other mammals for having communication as a dominant function.

He has stated that speech is formed by the coordination in the functions of oropharynx, tongue, teeth and lips.

The importance of speech on human maxillomandibular and oropharyngeal evolution was also stated by Lieberman (59) who has reported that the supralaryngeal airway of humans was different from other mammals, with food following the same path with the air, which increased the risk of airway obstruction while eating by the falling of food into the larynx. He also has stated that the chewing activity of humans was less efficient when compared to the other mammals and archaic hominids because of the reduced size of the palate and the mandible. According to Lieberman (59), this reduction in the size of maxilla and mandible also lead to the crowding of the teeth and tooth impactions, which could have fatal results in the absence of modern medicine. But these drawbacks are balanced by the increased phonetic ability of human oral system.

Cziko (60) has stated that the evolution of the maxillo mandibular system was closely related to the development of brain, by stressing that language provides communication and coordination between the individuals and also plays an important role in “thinking” for humans think in their native language.

It has been hypothesized previously that, a larger cranial vault for a larger brain is maintained by the decrease in the size of the mouth. It has also been stated that bipedal posture required a smaller mouth for the arrangement of the center of gravity of human cranium (3).

Even though most primates, together with some hominins like the australopithecines, have powerful masticatory muscles, members of Homo tend to have smaller masticatory muscles (3) It has been stated that, the masticatory apparatus of the hominin clade shifted towards gracilization accompanied by accelerated encephalization in early Homo (61) Stedman et al. (62) have claimed that, a gene encoding the predominant myosin heavy chain (MYH) expressed in the masticatory muscles was inactivated by a mutation at the time of divergence between humans and chimpanzee. They have dated this mutation back to 2. 4 Ma predating the appearance of modern human body size and emigration of Homo from Africa (63). The loss of this protein isoform resulted in size reductions in the muscle fibers and entire masticatory muscles. (62).It is believed that the cranial capacity increases as a result of this weakening of the muscles, relaxing the pressure on the sutures leading to larger encephalization (63).

Conclusion

The evolution of human masticatory complex is strongly related to diet, the use of tools and fire, and finally speech, and has a more important part in the evolution of mankind than the dentists know.

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