

Evolution of Dentition - A Literature Review

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Abstract

Teeth play an important role in mastication and speech. In fossils, teeth found within the rima oris were usually embedded in the jaws, although mineralised structures with similar histological patterns as teeth were found in fossils even before jaws appeared. Conodonts were the complex structures having enamel and dentine which were described in the earliest jawless vertebrates. These fossil findings led researchers to believe that teeth and jaws evolved as well as developed independently. Since the evolution of Homo sapiens from the our chimpanzee various factors such as the mastication pattern, food ingested and the processing of this foodstuff by fire and other tools affected the entire course of evolution. Further, development of mastication is interlinked to supplementary bodily characteristics like size of the brain and bipedalism, which also contributed to crucial happenings like development of linguistics and speech. So, a brief comprehension of these interactions is necessary to support the current evidence-based scenarios. Therefore, the aim of this review is to understand the various evolutionary aspects of dentition and basic genetic interactions which control tooth initiation, morphogenesis and patterning.

Keywords: Dentition; Genetics; Hominid; Homo Sapiens; Orofacial; Maxilla; Mandible

Introduction

Our mastication is made up of the upper and the lower jaw, teeth, temporomandibular joint, and the muscles of mastication and has a huge role in ingestion of food and speech. Similar to all other bodily characteristics in humans, the process of mastication has also unfolded over a span of decades. The human lineage is being separated from the other hominoids around 5 to 8 million years ago has been estimated in literature studies [1]. According to the latest classification, the earlier definitions we used to describe the human clade are not relevant. Thus, the clade cannot be used now to describe the term 'hominids' for the family. "Hominidae" is used for our common ancestor and its descendants. The term hominin is now considered as the vernacular term used for any member of human clade including the members of tribe Hominini. It further includes Hominina and Australopithecina as sub tribes and the therefore, it is that the term "hominid evolution" should now be referred as "hominin evolution" [2].

Theories on evolution of dentition

The 'outside in' theory

The classical theory states that teeth are derived from the dermal denticles (skin odontodes) that got internalized and occupied the oral cavity when the odontode-forming cells invaded the mouth during the genesis of jaws. Concepts on homology of odontodes are

built on prehistoric findings, the structural similarities of teeth and odontodes, exhibiting similar pathways of development. The major elemental structure is dentin in teeth and odontodes with cellular or acellular bone like tissue. Generally, the dentin maybe covered by a hypermineralized layer predominantly made up of enameloid or enamel in few cases. And these structures have an internal pulp chamber with connective tissue, odontoblastic cells, blood and nerve [3].

The 'inside out' theory

This theory affirms that teeth evolved before the jaws did, as they were adapted from the pharyngeal denticles. These facts, along with other factual by M.M. Smith; M. Coates as, are based on both a new understanding of the fossil records and other embryological studies of remaining species. First, Conodonts were thought to be the first vertebrate group to exhibit mineralisation of the skeletal components, and conodont elements were assumed as the first expression of oropharyngeal denticles by Smith and co-workers. Further, the typical spiral arrangement, termed as tooth whorls, in some thelodonts, agnathans (= jawless vertebrates) found in 425 million year (Ma) old Silurian deposits was marked as critical proof that teeth were present in the pharynx before jaws were established [3].

A modified 'outside in' hypothesis

This is an different theory that compiles the prehistoric and embryological findings, and is in accordance with the above mentioned discoveries. However, the Eucodonts are presently perceived as vertebrates, but there seems to be no agreement about the organizational association of the denticles with other odontodes. It was hypothesized that teeth which were originally ectodermal in origin, are derived from odontodes, according to the 'outside in' theory. These ectodermal odontodes were developed inside the oropharyngeal cavity as a result of exodus of ectoderm inwards -via the mouth and the gill slits. We agree with the 'inside out' theory as we believe that teeth likely arose before the jaws but the way jaws originated is itself gravely argued and talked out among researchers [3].

Theories of cuspal evolution

There are different theories that are proposed for the origin of cusps and various teeth patterns. One of it is the concrescence theory, which states that the mammalian teeth evolved as a result of the fusion of separate reptilian teeth. But this is not accepted as there is no evidence of different transitional forms of these teeth. Other accepted theory is the differentiation theory, which states that even the most complex mammalian molar tooth structures may have been derived from conical tooth forms as in the case of reptiles [4].

The Modified differentiation theory includes the Cope-Osborn theory and the tritubercular theory. It embarks to assemble the structures of cusps, describes their origin, detailing their progressive history. It is has been successfully accepted with the biological terms rather than with evolution. An American paleontologist Edward Drinker Cope first put forth the tritubercular theory in 1875. This was further modified in 1888 by Henry Fairfield Osborn and is now known as Cope -Osborn theory. This explanation justifies the different sizes and shapes of teeth [4].

The evolution of the classical haplodont conical teeth seen in reptiles was from the molars which consisted of in-line cusps in series as seen in the higher evolutionary animals. In the Greek terminology, Protocone (proto meaning first in time) in maxillary jaw is referred as the oldest cusp which represents the original conical tooth in reptiles. Paracone (para means at the side of, in greek) and it refers to the mesial of the protocone, whereas the metacone (in Greek, meta meaning in the midst of or after) refers to a cusp that is distal to the protocone. This is similar in the mandible. It has a similar naming, only difference is the addition of the suffix -id which means connected with. The designation for cusps in the mandible are termed as protoconid, paraconid, and metaconid respectively [4].

Differentiating cuspal anatomy: In mammals, the molar and premolar crown are structured into vivid patterns with conical protrusions termed as cusps and those separating them are termed valleys. Crenulations are the cusps that contain both enamel and dentine, which represent minor projections on crown, and are a result of different enamel thickness. The incomplete ridges that are seen passing

around peculiar base of the crown are often termed as Cingula. Additional cusps which have arisen by budding and outgrowth from the crown have been considered as evolutionary according to the widely accepted “differentiation theory”, whereas the complex teeth are evolved by majorly clustering of separate conical teeth is stated by the “conrescence theory”. Therian mammals are said to have evolved from a unique ancestor having tribosphenic cheek teeth which are characterised by main three cusps forming a triangle [5].

Distinct features

From an evolutionary-developmental perspective there are these following important features that make teeth a different kind of model system [6]:

1. Cusp patterns, tooth shapes and their arrangement in a dental pattern are unique to each species and as indicative of a species as its DNA.
2. Because tooth pattern is intimately connected to feeding, survival changes in tooth design in evolution provide a major foundation for remodelling related to exploitation of new feeding opportunities.
3. Tooth formation and genesis is a rather simple process that involves just two cell types embryonically.
4. Further, *in vitro* cultivation of embryonic tooth primordia can be easily done to completely recapitulate normal development.

This enables many different types of experimental manipulation to be carried out, including recombination’s between different species [6].

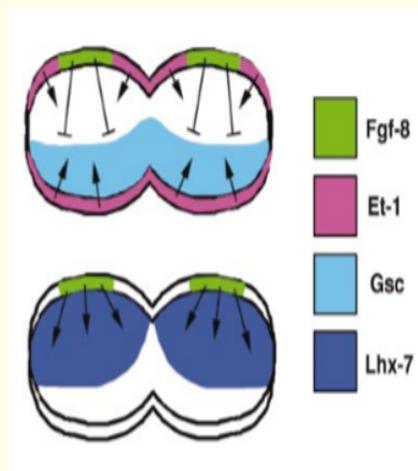


Figure 1: Diagrammatic representation of the signalling interactions [6].

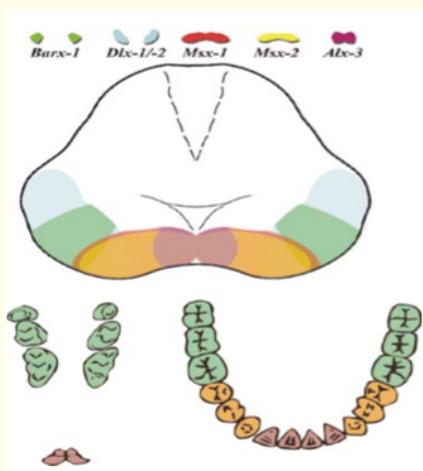


Figure 2: Diagrammatic representation of Odontogenic Homeobox - Code model of dental patterning [6].

Orofacial features of the extinct hominin taxa

The teeth and jaws of humans are comparatively smaller than the ape families of yester years. Investigations on fossils There is an evidence noted during the investigation of fossils which suggest that the ancestors of *Homo sapiens* had a decreased size and structure of the masticatory system in the hominins. It is stated by the researchers that this shrinkage in size and structure was attributed to the differences in the dietary patterns [7,8].

It has been found out that certain morphological differences which distinguish the modern humans from living apes include the majority of oro-facial features like the dentition, trunk, teeth, skull and brain. For example, canine teeth in the apes show sexual dimorphism in contrast to the humans and they usually do not show attrition to the level of the occlusal surfaces of the posterior teeth. It was been evidenced in the literature studies that the human jaws are comparatively smaller, project less and are more gracile as compared to those of equivalent sized living beings. These characteristics, distinguishing the humans from great ape families, could be found between modern humans and early hominins, along with the resemblance between the taxa [9-11].

Also, Lucas., *et al.* have studied the changes in diet of the extinct species and categorized them into 4 groups [12,13]:

1. Earliest hominins (7 - 4 Ma) These include *Ardipithecus kadabba*, *Ardipithecus ramidus*, *Sahelanthropus tchadensis* and *Orrorin tugenensis*.
2. Archaic Hominins (4 - 2.5 Ma) - This group includes *Australopithecus afarensis*, *Australopithecus africanus*, *Australopithecus anamensis*, *Australopithecus garhi*, *Australopithecus bahrelgazali*, *Kenyanthropus platyops* etc.
3. Archaic megadont hominins (2.5 - 1 Ma) - This group has *Paranthropus robustus*, *Paranthropus aethiopicus*, *Paranthropus boisei*.
4. Pre- modern Homo (2 Ma- 18 ka)- This group includes *Homo rudolfensis*, *H. ergaster*, *H. erectus*, *H. floresiensis*, *Homo habilis*, *H. heidelbergensis*, *H. neanderthalsensis*, *H. sapiens* *H. antecessor* [13].

Lucas., *et al.* have also accepted that the dental characteristics of the Last Common Ancestor of chimpanzees and hominins were markedly the same. When first erupted the incisors were huge as well as procumbent. The canines showed sexual dimorphism, with males having more prominent canines than the females. Premolars with comparatively smaller crowns and the second molar being the largest of the molar teeth as in the case of the great ape family. Moreover, as in monkeys, the upper canine's posterior slope were honed and sharp as compared to the anterior extension of lower premolar in *Ardipithecus*. Incisors were most likely procumbent at the time of eruption in both the earliest as well as archaic hominins. Moreover, the incisor teeth were comparatively smaller, and somewhat vertical in both genus *Homo* and archaic megadont hominins. The enlargement of the premolars and molars attributed to the reduction in size of the incisors [13].

Canine teeth are assumed to be smaller in the hominins and this reduction in size did continued during the early period. Wood and Stack reported that the greatest size reduction of the canines and the premolars is present in Megadont archaic hominins in these taxa [12] Hominin males usually exhibit smaller canines, it is also proven that, the higher the joint, the smaller the canines are in males and the temporomandibular joint is high in the hominoids [13,14].

In the modern humans, the first molar teeth were considered the enormous among the molars, then the second molars followed and the third molars were similar in size to the second molar. Lucas., *et al.* stated that cheek muscles and the tongue have a major role in chewing the food particles. Second premolars majorly have a role in tooth row when the ratio of first molar and third molar is high and this is related to the canine morphology. This might be due to the premolars extending anteriorly reducing the size of the mouth aperture [15-17].

Homo sapiens

The characteristics of the “modern human” have been analysed and authors claim that the taxon *H. sapiens* should include more than just the modern humans, for instance *H. erectus* should also be a part of *H. sapiens* too. Even though small bodied modern humans have smaller crania, the size differences amongst the human crania is not significantly different amongst individuals. Human posterior teeth have smaller crowns relative to body mass with a propensity for reduction in the number of cusps and roots [18].

Characteristic maxillofacial anatomical features of *Homo sapiens*

The *Homo sapiens* are differentiated from our ancestors by the presence of a chin that protrudes and this is regarded as one of the major evolutionary features. A protrusion of the chin was absent in archaic humans and the Neanderthals. There are different studies performed primarily to know the function and steps of chin formation [15]. Some authors [19,20] suggests that the chin provided some amount of resistance to the flexural forces on the mandible while others including Liberman concluded that the chin had no basically no functional importance. An important role is played by the Masticatory system related biomechanical forces, mainly in the formation of human chin. However, some school of thoughts have opposing views.

Some authors [19,20] have also proposed that the reduction of the dental arch might have left the chin as a protrusion in the mandible. Ichim., *et al.* have stated that the emergence of the chin is due to constant cyclic contractions of the tongue and the perioral muscles which are the results of development of speech in the modern day humans. They have proposed that the origin of the chin could coincide with appearance of speech 50,000 years ago. Biomechanical studies showed that both chinned and non-chinned mandible models resisted the same to flexural and other forms of forces. The occlusal plane in humans is not horizontal. When there is an inclination of the teeth, where the anterior cheek teeth exhibit a plane sloping upward palatally and the more posterior teeth have a plane sloping upward buccally together forming a deviant plane of occlusion. This pattern is considered typical of the orofacial region of *Homo*. Smith proposed that, the foreshortening of the of the arch may result in molars lying posteriorly to the root of the zygoma and medially to the masseter- pterygoid complex, such factors contributed to the development of the helicoidal plane [21]. Further, axial inclination of the molar roots was possible due to the reduction of the dental arches and their retraction under the cranium. It has been claimed that this axial inclination of the teeth has been also paralleled by changes in cuspal heights in order to keep the mastication and its development functional. The posterior teeth are inclined in the sagittal plane and lower third molars have undergone a forward tilt to certain degree due to displacement of the temporomandibular joint in relation to the occlusal plane. This led to development of the curve of spee. It is proposed that only because of this curve molars function in a smooth grinding movement on the working side. In *Homo sapiens* the joint has moved forward, but it has maintained the same elevation distribution in the case of the Neanderthals [22]. The condyles of the mandible on the other hand occupy a confined place with respect to the occlusal plane. All the variable positions also put a substantial effect on the jaw movements and jaw closure, thus affecting the ways in which food is processed during every chewing cycle [23].

Genetic interactions, tooth patterning and morphogenesis

A transition from agnathon to gnathostome

The orofacial development in a species that has teeth, cartilage and bone involves the same genes as development of a species with cartilage and bone but no teeth. Data, principally from gene knockouts in mice, suggests that even though there are genetics responsible for tooth and jaw development, tooth morphogenesis shares many key genes with skeletal morphogenesis [24,25].

Specification of dental and skeletal cells

During development of the mammalian mandible, different hard tissues, teeth (dentine and cementum), bone and cartilage develop from neural crest-derived ectomesenchyme cells. The mechanisms that determine which cells differentiate into these different tissues

are beginning to be elucidated [26]. It is now clear that the ectomesenchyme cells of the developing mandible, (and presumably other orofacial primordia), are capable of differentiating into any of these different hard tissue producing cell types, odontoblasts (dentine), osteoblasts (bone), and chondrocytes (cartilage) and the signals that direct differentiation come from the overlying epithelium. Cranial neural crest cells that populate each facial primordium do not appear to be prepatterned into specific odontogenic, osteogenic or chondrogenic populations but rather are directed down the appropriate differentiation pathway under the influence of ectodermal signals. Evidence for how the early specification of odontogenic from skeletogenic cells occurs in the developing mandible comes from expression of the Limdomain homeobox genes *Lhx6* and *Lhx7* and *Gsc*. Expression of *Lhx6* and *Lhx7* is restricted to the ectomesenchyme closest to the oral epithelium (oral) that forms teeth whereas *Gsc* is expressed more posteriorly (aboral) in ectomesenchyme cells that do not form teeth but which do form skeletal cells [26-28]. This early oral aboral division of the mandibular primordium is regulated by FGF8 from the oral epithelium. FGF8 is required for expression of *Lhx6* and *Lhx7* and *Lhx6* and *Lhx7* repress *Gsc* expression [27,28].

Control of dental patterning

Tooth shape is indelibly linked to position in the jaws. Tooth shapes have evolved for particular functions. Incisors and canines are grasping} cutting teeth, premolars and molars are both grinding and cutting teeth. In heterodont dentitions there is little point in having grasping} cutting teeth at the rear of the mouth and grinding teeth at the front [29].

The Odontogenic Homeobox model of tooth patterning states that in mice, genes such as *Barx1*, *Dlx1* and *Dlx2* have certain roles in directing mesenchyme cells to follow a multicuspoid pathway during tooth morphogenesis [30].

Genes such as *Msx1* and members of the *Alx* family have roles in directing cells to follow a monocuspid (incisor) pathway. An additional key feature of this model is that it is not only the expression of these genes in particular mesenchymal cells that is important but also the absence of expression of other genes. Thus, maxillary molar morphogenesis not only requires the presence of *Barx1*, *Dlx1* and *Dlx2* but also the absence of *Msx1* and *Alx* genes [28,29].

Mandible and maxilla

In many respects, tooth patterning is very similar to patterning of the axial skeleton. Vertebral bodies are mineralised 'organs' with a basic structure that is modified according to rostral-caudal position. The morphogenesis of each individual vertebrae is fixed in any given species such that the relative order in the spine can easily be reconstructed from fossil remains. Similarly, arrangements of different shapes and sizes of teeth on the two jaws are fixed and dental patterns can be reconstructed even when teeth are isolated from the jaws. This is markedly apparent for teeth that are in occlusion. Mammalian molar teeth are such that they only function by making contacts with the opposite jaw. Thus, in the same way that each vertebra precisely 'fits' with immediate neighbours, each tooth aligns precisely with its counterpart on the opposing jaw. In the absence of any conflicting constraints, the most logical developmental mechanism for ensuring tooth development on opposing jaws is coordinated, would be to use the same basic genetic mechanism that is subtly modified to produce slight differences in shape between opposing teeth. It is now clear that this is not the mechanism and morphogenesis of teeth on the different facial primordia is in fact regulated by different genetic pathways [30]. The most striking demonstration of this involves the activin signalling pathway. Activin is a member of the TGF β superfamily of signalling proteins that binds to membrane receptors and activates gene transcription via the Smad-mediated pathway. Mouse mutants in the activin βA gene have a tooth phenotype where all incisors and mandibular molars are arrested at the developmental early bud period but maxillary molars develop normally. Significantly, loss of expression of downstream genes, such as *follistatin*, is evident in all tooth germs, including developing maxillary molars, in activin βA mutant embryos. Thus, activin signalling pathway, although important for incisor as well as mandibular molar tooth morphogenesis, is not necessary in the development of upper molar teeth. Thus, molar specification on the mouse maxillary primordia involves a different genetic pathway to specification of molars on the mandible [31].

Conclusion

This review gives a brief insight of the elucidative data on evolution of dentition in humans and updates their analysis according to recent studies. The continual growth of teeth is common in animals, and other polyphyodonts as well as humans. It has been found that the extent of enamel coverage on the teeth is also varied in specific species. Although there are vast differences, almost all teeth, including those of humans, have a common origin and develop under similar molecular instruction and patterning pathways. There are tooth deformities that can severely affect human health in more ways than one can count. Hence, evolutionary and developmental biologists have suggested that investigation and comparison of the tissue origin, patterning and growth of different teeth parts in order to restore healthy or repair the damaged tissue, as it constitutes an essential component for studying the evolution of human dentition. Detailed knowledge of the evolution helps in understanding dental morphogenesis and its implications in recent times. Thus, the evolution of human dentition and mastication is significantly related to various factors like changes in food patterns, the use of tools and invention of fire, and has a more crucial role in the evolution of mankind as teeth form a linchpin between the past and the present. It is the role of a dental professional to know this history as well as comparative dental anatomy in order to better understanding of the dentition.

Conflicts of Interest

None.

Bibliography

1. Emes Y, *et al.* "On the evolution of human jaws and teeth: A review". *Bulletin of the International Association for Paleodontology* 5.1 (2002): 37-47.
2. Ruvolo M. "Genetic diversity in hominoid primates". *Annual Review of Anthropology* 26 (1997): 515-540.
3. Huysseune A., *et al.* "Evolutionary and developmental origins of the vertebrate dentition". *Journal of Anatomy* 214 (2009): 465-476.
4. Osborn H. "The Evolution of Mammalian Molars to and from the Tritubercular Type". *The American Naturalist* 30.22 (1998): 1067-1079.
5. Koppe T., *et al.* "Comparative Dental Morphology". *Frontiers of Oral Biology* 13 (2009): 1-2.
6. Mccollum M and Sharpe P. "Evolution and development of teeth". *Journal of Anatomy* 199 (2001): 153-159.
7. Wood B and Richmond BG. "Human Evolution: taxonomy and paleobiology". *Journal of Anatomy* 196 (2001): 19-60.
8. Aiello L and Dean C. "An introduction to Human Evolutionary anatomy". London Academic Press (1990).
9. Leonard WR and Robertson ML. "Nutritional requirements and Human Evolution: a bioenergetics model". *American Journal of Human Biology* 4 (1992): 179-195.
10. Milton K. "Primate diets and gut morphology: implications for hominid evolution". In Harris M, Ross EB (eds): *Food and Evolution: Toward a Theory of Food Habits*, Philadelphia, Temple University Press (1987): 93-115.
11. Kelley J. "Sexual dimorphism in canine shape among extant great apes". *American Journal of Physical Anthropology* 96 (1995): 365-389.
12. Le Gros Clark WE. "New paleontological evidence bearing on the evolution of the Hominoidea". *Journal of the Geological Society* 105 (1950): 225-264.

13. Lucas PW, *et al.* "Inferences regarding the diet of extinct hominins: structural and functional trends in dental and mandibular morphology within the hominin clade". *Journal of Anatomy* 212 (2008): 486-500.
14. Lucas PW, *et al.* "Sexual dimorphism of teeth in anthropoid primates". *Journal of Human Evolution* 1 (1986): 23-39.
15. Wood BA and Stack CG. "Does allometry explain the differences between 'gracile' and 'robust' australopithecines?" *American Journal of Physical Anthropology* 52 (1980): 55-62.
16. Haile-Selassie Y. "Late Miocene hominids from the Middle Awash, Ethiopia". *Nature* 412 (2001): 178-181.
17. Asfaw B., *et al.* "Australopithecus garhi: a new species of early hominid from Ethiopia". *Science* 284 (1999): 629-635.
18. McHenry HM. "Introduction to the fossil record of human ancestry". In: Hartwig WC (ed) *The Primate Fossil Record* (2002): 401-406.
19. Brace CL., *et al.* "Gradual change in human tooth size in the late Pleistocene and post-Pleistocene". *Evolution* 41 (1987): 705-720.
20. Wood BA and Abbott SA. "Analysis of the dental morphology of Plio-Pleistocene hominids. I. Mandibular molars: crown area measurements and morphological traits". *Journal of Anatomy* 136 (1983): 197-219.
21. Mayr E. "Taxonomic categories in fossil hominids". *Cold Spring Harbor Symposia on Quantitative Biology* 15 (1995): 109-118.
22. Howells WW. "Cranial Variation in Man: A Study by Multivariate Analysis of Pattern of Differences Among Recent Human Populations". Cambridge, MA: Harvard (1973).
23. Mellars P. "The Neandertal Legacy: An Archaeological Perspective of Western Europe". Princeton, NJ: Princeton University Press (1996).
24. Acampora D., *et al.* "Craniofacial, vestibular and bone defects in mice lacking the Distal-less-related gene *Dlx5*". *Development* 126 (1999): 3795-3809.
25. Attisano L and Wrana JL. "Mads and Smads in TGF β signalling". *Current Opinions in Cell Biology* 10 (1998): 188-194.
26. Grigoriou M., *et al.* "Expression and regulation of *Lhx6* and *Lhx7*, a novel subfamily of LIM homeodomain encoding genes, suggests a role in mammalian head development". *Development* 125 (1998): 2063-2074.
27. Zhao Y., *et al.* "Isolated cleft palate in mice with a targeted mutation of the LIM homeobox gene *Lhx8*". *Proceedings of the National Academy of Sciences of the USA* 96 (1998): 15002-15006.
28. Tucker AS and Sharpe PT. "Molecular genetics of tooth morphogenesis and patterning: the right shape in the right place". *Journal of Dental Research* 78 (1998): 826-834.
29. Mckenzie AL., *et al.* "Expression patterns of the homeobox gene *Hox-8* in the mouse embryo suggest a role in specifying tooth initiation and shape". *Development* 115 (1992): 403-420.
30. Thomas BL and Sharpe PT. "Patterning of the murine dentition by homeobox genes". *European Journal of Oral Sciences* 106.1 (1998): 48-54.
31. Yamada G., *et al.* "Targeted mutation of the gene results in craniofacial defects and neonatal death". *Development* 121 (1997): 2917-2922.

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