Review Article

THE EVOLUTION OF STRUCTURAL AND FUNCTIONAL TRENDS IN DENTAL AND FACIAL MORPHOLOGY WITHIN THE HOMININ CLADE

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Abstract

Here we attempt to reconstruct the evolutionary history of hominin life from the fossil evidence which uses the current morphological evidence to evaluate the facial morphology of the human ancestor including chimpanzee/bonobo (panin) and human (hominin) lineages. Some of the problems involved in reconstructing ancestral morphologies so close to the formation of a lineage are discussed. It is not possible to determine with any confidence whether the facial morphology of any of the current candidate Last Common Ancestor taxa (*Ardipithecus kadabba*, *Ardipithecus ramidus*, *Orrorin tugenensis* and *Sahelanthropus tchadensis*) is representative of the LCA, or a stem hominin, or a stem panin or, in some cases, a hominid predating the emergence of the hominin lineage.

Key Words: - *Australopithecus*, Hominin fossil, Megadonts

Introduction

Dental anthropology utilizes information obtained from the teeth of either skeletal remains of prehistoric or modern human populations in order to reach for conclusions regarding various anthropological problems. The physical form and positioning of the dentition are used to address several kinds of questions. First, teeth exhibit variables with a strong hereditary component that are useful in assessing population relationships and evolutionary dynamics.

Given their role in chewing food, dental pathologies and patterns of tooth wear can indicate kinds of food eaten and other aspects of dietary behaviour, including food preparation techniques. Teeth can also exhibit incidental or intentional modifications, which reflect patterns of cultural behaviour. Finally, as the process of tooth formation is highly canalized (i.e., buffered from environmental perturbations), developmental defects provide a general measure of environmental stress on a population. Researchers in several disciplines, including physical anthropology, archaeology, palaeontology, dentistry, genetics, embryology, and forensic science, conduct research that falls directly or indirectly within the province of dental anthropology[1].

The dentition in development and maturity

The development of each tooth begins with the action of genes at specific sites in the adjacent tissues of the epithelium and the mesenchyme in the oral cavity. At the molecular level there are over 300 genes.[2] There are interactions between genes in which the functional genes are switched on by the action of signature sequences that have been activated by the release of regulatory proteins from regulatory 'master' genes.

Self-adaptation

Three characteristics of complex self-adaptive systems are diversity, critical phases and robustness. Self-adaptation is seen in the diversity of the dentitions which are present in different species.

This diversity arises not so much from different number or type of genes, which are similar in the different species, but rather from the genetic switches that are used to turn genes on and off. Substantial differences between four human ethnic groups in mesiodistal tooth dimension and in the relative sizes in different tooth types has been shown[3]. There are a series of critical phases during dental development which determine whether a mature tooth will be formed, and, if it is formed, whether it will have a developmental defect or not. Although it incorporates many detailed interactions with critical phases, another aspect of dental development is the robustness of the process and the relative efficiency of the outcome system even with variations and mild or moderate anomalies. Within species dental variations also allow adaptation to different environmental challenges. Dental development has multiple critical phases, interference with which lead to a range of dental anomalies. Even so, the process and outcome have a degree of robustness[4].

The evidence available about the natural history of an extinct primate taxon is indirect and is therefore much more 'broad brush' Information about morphology has to come from whatever survives of individual members of the taxon, and what the fossil record of each taxon consists of is determined by a complex mix of predator behaviour, tissue durability and the many other factors that result in differential preservation of the skeleton[5].

The combination of the morphological evidence and the new insights prompted by developments in cognate research areas have enabled us to suggest new avenues of research that could shed light on how these morphological data can be used to generate testable hypotheses about the dietary adaptations of extinct hominins.

Hominin fossil record

In most aspects, it is probably wisest to assume that the dentition of chimpanzees/bonobos and hominins resembled that of the modern common chimpanzee. (Figure 1) The incisors were likely to have been large and, when first erupted, procumbent (i.e. with the occlusal margins of the

sloping crowns projecting forwards). The canines were sexually dimorphic, with much more projection beyond other teeth in males than females as is true of all great apes[6]. The premolar crowns were relatively small, with the largest of the molars being the second (M2), as is also true of the other great apes.
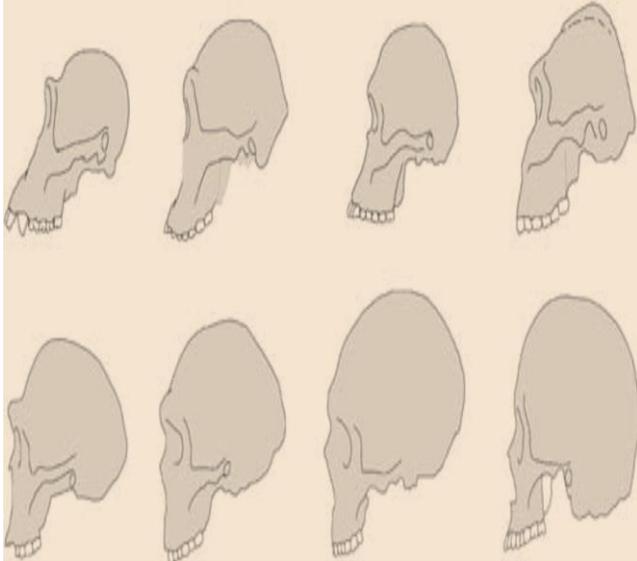

Figure 1: The facial skeleton of the chimpanzee-human last common ancestor

Evolutionary changes in various tooth forms.

The incisors were probably also procumbent on eruption in both the earliest and archaic hominins [7]. However, archaic megadont hominins, along with members of the genus *Homo*, had more vertically implanted and relatively smaller incisors [8]. Incisal reduction in the archaic megadonts was coupled with enlargement of the premolars and molars.

In the earliest hominins, the canine teeth are said to have been relatively small, and further size reduction continued within this time period.[9] The greatest relative canine reduction is seen in the megadont archaic hominins, but there is some evidence that the premolars and molars are abnormally large in these taxa, especially when compared with the relatively modest size of the canine.

The second molars were generally the largest of the molar teeth in the earliest and in the archaic hominins, but there was a distinct tendency for M3 to be as large, if not the largest, of the molars particularly with respect to the mandibular dentition of the archaic megadonts[10] . In modern *Homo*, the first molar is usually the largest of the molars, following extensive reduction in overall tooth size. Hominins all tend to have low blunt cusped molars and premolars – the so-called bunodont type of dentition. It is generally agreed that the earliest hominins to have had thick enamel were the archaic hominins. Even in modern humans, the enamel of the postcanine teeth is much thicker than in the equivalent teeth of the extant apes[11]. (Table 1)

Tooth shape

Dentitions designed to break down hard foods look very different from those that are designed to break down tough foods[12]. Tough foods are very difficult to fragment (i.e. to fracture into separable pieces) without very sharp features on tooth crowns. Due to their usually low modulus, the areas of teeth in contact with such food particles are extensive, and as the load is increased, the food particle spreads across the tooth. Sharp features are needed continually to re-initiate (re-sharpen) crack tips that otherwise tend to blunt, stop moving and frustrate fragmentation. Such crack tips may or may not jump slightly ahead of the sharp tooth feature that produces them – this depends on the microstructure of the food but their progress will always arrest quickly without the proximity of these sharp features. Such teeth are usually not pointed because cracks will not spread laterally. So, in order to subdivide such food particles, teeth need to have bladed features – sharp points that are extensive in one plane. In contrast, hard foods fragment very easily because *R (symbolising toughness) is* low. Contact areas stay small as the load is increased because of the high *E (symbolising ratio of elastic modulus)* of such foods. Sharp features on teeth would be quickly lost because of the locally high energy densities that lead to fracture. Further, cracks spread laterally very easily. So, the design for teeth optimized to break down hard foods involves low, blunt points (i.e.what we refer to as 'cusps').

Predicted dietary adaptations of fossil hominins

In terms of a general adaptive pattern, we believe that most hominins were adapted to cope with hard foods even if such items were only ingested for a small part of the year. Some of the ingested objects were likely to have been very small in order to explain the extensive surface wear of the tooth surface: these particles could easily have been grit or phytoliths rather than foods[13]. The low, blunt cusps of the postcanine teeth of hominins attest to this dietary specialization, as does the thickness of the enamel and the tendency for rod decussation only to be present in inner enamel. (Table 2)

Canine reduction is a chief feature which has been reported in *Ouranopithecus* from the late Miocene of Greece and controversially proposedas a synapomorphy linking that taxon with the modern human lineage[15]. In this case canine reduction was assessed by relating cervical crown dimensions of the canine to overall size of the molar dentition. However[16], showed the canines are relatively small not because they are absolutely smaller than in later taxa, but because the molars are absolutely larger. Canine crown height in *Ouranopithecus* far exceeds that expected for *Australopithecus afarensis* of a similar body size, but it is within the range of extant apes, excluding *Pan paniscus.[17]*

Table 1: General trends in hominin dental and gnathic morphology

Morphological trait	*Pan troglodytes*	LCA	Stem hominin	Earliest hominins	Archaic hominins	Archaic megadonts	Pre-modern *Homo*	*Homo sapiens*
DENTITION								
Incisor size	Large	large	Large	Medium	medium	small	Medium	Medium
Incisor orientation	procumbent	procumbent	procumbent	procumbent	procumbent	vertical	vertical	vertical
Incisor to postcanine ratio	High	high	medium	Medium	medium	low	medium	medium
Canine size	Large	large	medium	Medium	medium	small	small	Small
Canine sexual dimorphism	High	high	moderate	moderate	reduced	low	low	Low
Relative premolar size	Small	small	Small	small	medium	large	medium	Medium
Molar size	Small	small	medium	medium	large	Very large	small	Small
Molar size gradient	M2 largest	M2 largest	M2 largest	M2 largest	M2 largest	M3 largest	variable	M1 largest
Enamel thickness	Thin	thick	Thick	thin	thick	Hyper-thick	thick	Thick
MANDIBLE								
Mandibular corpus height (h) at M1	Tall	tall	Moderately tall	?	Mederately tall	Very tall	Short	Short
Mandibular corpus breadth (b) at M1	Slightly broad	Slightly broad	Slightly broad	Slightly broad	broad	Very broad	broad	narrow
Mandibular robusticity at M1 (b/hX100)	Gracile	gracile	*slightly robust*	?	Moderately robust	Very robust	robust	gracile

Table2 Summary of facial measurements of *P. Troglodytes* and hominins[14]

		Palatal length (mm)	Palatal breadth at M 2 (mm)	Facial height (nasion-prosthion) (mm)	Bizygomatic breadth (mm)	Biorbital breadth (mm)
Pan troglodytes						
Male††	Mean	71	61	93	112	89
	n	10	10	10	10	10
	Range	64-84	56-72	82-106	100-127	82-101
Female††	Mean	65	58	88	109	91
	n	10	10	10	10	10
	Range	58-70	56-60	81-99	103-116	86-96
Australopithecus afarensis ††	Mean	66	60	75	n/a	91
	n	7	7	2	2	3
	Range	57-76	56-82	74(100)	136,142	83-95
Australopithecus africanus ††	Mean	67	68	78	115	82

	n	4	4	4	2	2
	Range	64-68	64-74	71-90	110,120	79,85
Australopithecus robustus ††	Mean	66	70	76	113	92
	n	3	3	1	2	2
	Range	61-69	68-72	-	128-138	84-100
Homo erectus		n/a	66	83	138	104
Homo sapiens ††	Mean	52	66	69	113	95
	n	10	10	50	10	10
	Range	46-58	63-71	60-80	107-120	85-101

††Data from Kimbel *et al.* (2004).
n/a, not available.

Maxillary and mandibular dental arcade morphology

The shape of the maxillary dental arcade of the megadont archaic hominins (*Australopithecus aethiopicus*, *Australopithecus boisei*, *Australopithecus robustus* and *Australopithecus garhi*) is very distinct from that of the above mentioned archaic hominins. The general trend among these taxa is a varying degree of enlargement of the postcanine dentition, thickened molar enamel, and molarization of the premolars[17,18,19] and *Au. robustus*, the postcanine enlargement is in conjunction with a considerable reduction in the anterior dentition. The overall shape of the archaic megadont hominin dental arcades, with the exception of *Au. aethiopicus*, is therefore somewhat trapezoid rather than the elongated parabolic shape of the archaic hominins with smaller postcanine dentitions. the premaxilla and hard palate can develop and function with some degree of independence; however, insertion of the vomer onto the premaxilla acts as a constraint and so gives rise to a flat and smooth nasal floor[20].

In experiments on modern human subjects[21], found that the mastication of hard foods (foods of low *R/E*) was associated with larger lateral excursions of the mandible than was the case with softer foods. Such hard foods are exactly those that would be predicted above to lead to thicker enamel in order to resist deep (radial) EDJ-type cracks. To the extent that jaw structures might be linked to such dietary patterns, then it is possible that a hard diet requiring wider excursions might lead to the development of a relatively broader mandibular corpus.

Conclusions

The reconstruction of facial morphology and the determination of its taxonomic and phylogenetic significance is fraught with difficulty when the fossil evidence is close to the formation of a lineage. This is because of the likelihood of both homoplasy and a paucity of defining derived features. It is therefore difficult to list the facial morphology that would be hypothesized to distinguish the last known ancestor of chimp/bonobos and modern humans from stem members of either the hominin or panin lineages.

Even if the fossil record were better for this period, the problems of homoplasy mean that it might be unrealistic to think that facial morphology will neatly resolve the systematic ambiguities presented by these putative early hominids.

References

1. G. Richard Scott. Dental Anthropology. University of Alaska, Fairbanks.
2. Thesleff I. The genetic basis of tooth development and dental defects. American Journal of Medical Genetics Part A. 2006;140:2530-2535.
3. Brook A.H., Griffin R.C., Smith R., Townsend G.C., Kaur G., Davis G.R., and Fearne G. Tooth size patterns in patients with hypodontia and supernumerary teeth. Archives of Oral Biology 2009;54:S63-S70.
4. Grant Townsend, Eisaku Kanazawa, Hiroshi Takayama. New Directions in Dental Anthropology: paradigms, methodologies and outcomes.
5. Sherwood CC, Subiaul F, Zawidzki TW. A natural history of the human mind: tracing evolutionary changes in brain and cognition. J Anat. 2008;212:426–454.
6. Lucas PW, Corlett RT, Luke DA. New approach to postcanine tooth size applied to Plio-pleistocene hominids. 1986 In Primate Evolution (eds Else JG, Lee PC), pp. 191–201. Cambridge: Cambridge University Press.
7. Asfaw B, White T, Lovejoy O, Latimer B, Simpson S, Suwa G. Australopithecus garhi: a new species of early hominid from Ethiopia. Science. 1999;284:629–635
8. McHenry HM. Introduction to the fossil record of human ancestry. In The Primate Fossil Record (ed. Hartwig WC), 2002 pp. 401–406. Cambridge: Cambridge University Press.
9. Haile-Selassie Y, Suwa G, White TD. Late Miocene teeth from Middle Awash, Ethiopia, and early hominid dental evolution. Science 2004;303:1503–1505.

10. Wood BA, Abbott SA, Analysis of the dental morphology of Plio-Pleistocene hominids. I. Mandibular molars: crown area measurements and morphological traits. J Anat 1983;136:197–219.
11. Kono RT. Molar enamel thickness and distribution patterns in extant great apes and humans: new insights based on a 3- dimensional whole crown perspective. Anthrop Sci 2004;112:121–146.
12. Lucas PW. Dental Functional Morphology. Cambridge:Cambridge University Press; 2004.
13. Baker G, Jones LHP, Wardrop ID. Cause of wear in sheeps'teeth. Nature 19591;84:1583–1584.
14. Kimbel WH, Johanson DC, Rak Y. Systematic assessment of a maxilla of Homo from Hadar, Ethiopia. Am J Phys Anthropol. 1997;103:235–262.
15. De Bonis L, Koufos GD. The face and the mandible of Ouranoithecus macedoniensis: description of new specimens and comparisons. J Hum Evol 1993;24, 469–91.
16. Kelley J. Phylogeny and sexually dimorphic characters: Canine reduction in Ouranopithecus. In Hominoid Evolution and Climatic Change in Europe: Phylogeny of the Neogene Hominoid Primates of Eurasia (eds de Bonis L, Koufos GD, Andrews P), 2001; pp. 269–283. Cambridge: Cambridge University Press.
17. Robinson JT. The dentition of the Australopithecinae.Transvaal Mus Mem 1956;9:1–179.
18. Tobias PV, Gorge O. The Cranium andMaxillary Dentition of Australopithecus (Zinjanthropus) boisei. 1967; Volume 2: Cambridge: Cambridge University Press.
19. Grine FE. Evolutionary History of the 'Robust' Australopithecines. New York: 1988; Aldine de Gruyter.
20. Samuel N. Cobb. The facial skeleton of the chimpanzee-human last common ancestor. J. Anat 2008;212:469–485.
21. Agrawal KR, Lucas PW. Mechanics of the first bite. Proc R Soc Lond 2003;270:1277–1282.

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