

Tooth Enamel Tells a Complex Story

The thickness of the enamel layer on teeth once assumed an especially pertinent diagnostic significance in paleoanthropology: thick enamel permitted entry to the human family (the hominids), thin enamel betokened an ape. This simple equation has crumbled in recent years, and a current publication by Lawrence Martin, of University College, London, reveals something of the true complexity of enamel morphology (1).

Tooth enamel in modern humans is thick, which contrasts with the thin coating on chimpanzee and gorilla teeth. The anthropocentric interpretation was that thick enamel represented the specialized, or derived, condition, whereas thin enamel was primitive. The discovery of thick enamel in the australopithecines, fossil hominids that lived in south and east Africa between 4 and 1 million years ago, fitted this preconception. And thick enamel was one of the supposed human attributes of *Ramapithecus*, an ape-like creature that lived in Africa and Asia between 15 and 8 million years ago (2). *Ramapithecus* is no longer considered by most to be a hominid. Just recently enamel thickness was adduced in support of a proposed ancestral relationship between humans and orangutans (3), which, unlike their African cousins, have a relatively thick tooth cap.

Martin's work shows, however, that thickness is only one property of enamel that must be examined in taxonomic comparisons: details of enamel formation are also diagnostic. But, most important, thick enamel

turns out to be a primitive, not derived, character for the great ape and human group and therefore cannot be used to define hominids, according to Martin's interpretation.

Enamel is deposited in two basic patterns in the teeth of hominoids, the group to which apes and humans belong. The first is a fast mode, which produces a characteristic appearance known as pattern 3 and is primitive for hominoids. The second is a slow mode, whose product is pattern 1 and is derived within the hominoid group.

In gibbons, for instance, a relatively short-lived burst of pattern 3, fast enamel deposition leaves a thin tooth cap. A longer period of maturation in humans builds up thick enamel by the same, pattern 3, growth. Now, chimpanzees and gorillas, like gibbons, have thin enamel, but deposition proceeds in two stages. The bulk (60 percent) of the initial phase is fast growth, but there is an abrupt switch to slow deposition for the remainder. Martin terms this pattern thin, slowed growth, which is developmentally and phylogenetically distinct from the thin, fast pattern in gibbons.

Orangutans, which have intermediate thick enamel, also go through a two-stage deposition, but again it is not

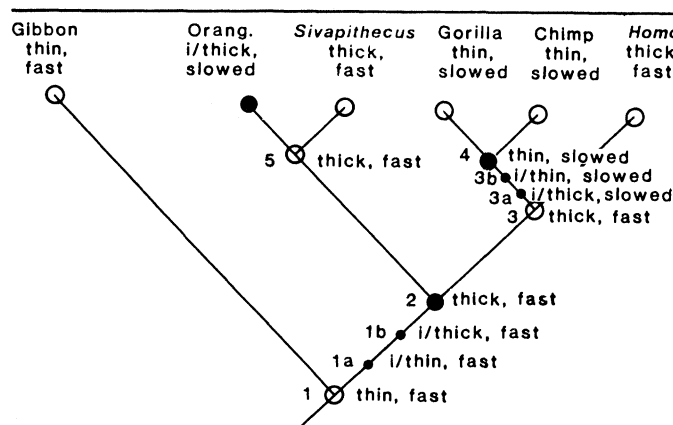
homologous with that in the African apes. After the initial fast phase (80 percent of the total), deposition slows to 2.5 μm per day for about 200 μm , and then slows again to the African apes' lower rate for the final 50 μm .

A phylogenetic picture begins to emerge, into which the data for the fossil ape *Sivapithecus* fit very neatly. This creature, which existed in Eurasia and Africa 15 to 8 million years ago and represents the group to which *Ramapithecus* belongs, turns out to have thick, fast-forming enamel, like humans. On the basis of facial morphology, this fossil is considered to be related to the orangutan. Overall, then, the hominoids' primitive dental structure is with thin, fast-forming enamel, which is represented today by gibbons. An increase in deposition time produced a derived state of thick, fast-forming enamel, as displayed by the extinct *Sivapithecus*, possibly via intermediate stages. The orangutan evolved a secondary slowing.

The scheme, as interpreted by Martin, now shows that

the common ancestor of the African great apes and humans had thick, fast-forming enamel. He considers that the African apes shared a common ancestor, in which the characteristic slowing process developed: both then derived from this ancestor, which had thin, slow-forming enamel. Once again, there may have been transitional forms with intermediate thick and intermediate thin, slow-forming enamel. If true, the identification of putative African great ape ancestors in the fossil record will be facilitated.

Martin's version of the hominoid family tree runs counter to a newly emerging notion, based, among other things, on DNA-DNA hybridization studies (4): to wit, that gorillas diverged first, leaving humans and chimpanzees briefly to share a common ancestor. This interpretation would require that chimpanzees and gorillas developed their identical slow enamel deposition process independently. Martin considers this to be possible but unlikely. In a recent study of 125 morphological characters in humans and the African apes he concluded that chimpanzees and gorillas form an ancestral group, with humans having split off separately (5), which is in accord with the enamel data.—ROGER LEWIN



Enamel growth among the hominoids

Diagram shows one interpretation of relationships within the hominoids based on enamel formation patterns.

References

1. L. Martin, *Nature (London)* **314**, 260 (1985).
2. R. F. Kay and E. L. Simons, in *New Interpretations of Ape and Human Ancestry*, R. L. Ciochon and R. S. Corruccini, Eds. (Plenum, New York, 1983), p. 783.
3. J. H. Schwartz, *Nature (London)* **308**, 501 (1984).
4. P. Andrews, *ibid.* **314**, 498 (1985).
5. L. Martin, in *Major Topics in Primate and Human Evolution*, B. A. Wood, L. Martin, P. Andrews, Eds. (Cambridge University Press, New York, 1985).