Primate Dental Development: Ontogenetic Processes of Pattern Formation

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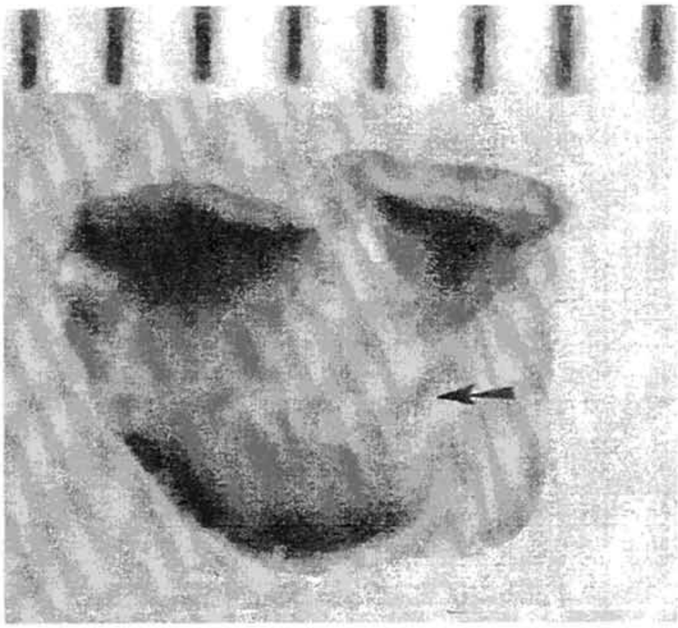
The development of tooth germs is a dynamic process. It involves proliferation of the cells of the dental papilla and the enamel organ, differentiation of the pre-odontoblasts and pre-ameloblasts into definitive odontoblasts and ameloblasts, and dentin and enamel apposition. The final size and shape of the tooth's crown results from the growth and differentiation of the inner enamel epithelium.

Variations in the pattern, timing, rate, and duration of theses events can cause considerable variation in the external morphology of the completed crown (Keene, 1982, 1991). Because morphological evolution can be thought of as "phyletic alteration of the developmental mechanisms of pattern formation" (Hanken, 1989:339), understanding how mechanisms of pattern formation produce the completed morphology is important for better understanding of evolutionary processes and may ultimately be of value in assessing phylogenetic relationships. Documenting the development of tooth germs in various primate taxa can aid in understanding how these events interact to produce the completed crown and can provide a foundation for understanding underlying evolutionary changes that have occurred in primate dentitions.

Direct examination of tooth germs dissected from members of three primate genera (*Pan, Macaca*, and *Alouatta*) was undertaken. Specimens used in this study were from the collections of D. R. Swindler and the late B. S. Kraus. The sample consisted of 171 individuals: *Macaca* (137 individuals), *Alouatta* (19 individuals) and *Pan* (15 individuals). The tooth germs were soaked in alizarin red S stain in order to distinguish the calcified areas of the crown from the uncalcified areas (the calcified areas absorb the stain and are red, while the uncalcified areas remain clear). The specimens were video taped in buccal, lingual, and occlusal views using a video camera fitted with a lens and billows to magnify specimens. Measurements were made using the Peak 2-D Motion Analysis software. The video images were digitized and measurements were made and scaled on the computer monitor. Detailed analyses of both quantitative and qualitative aspects (relative rates of growth and differential patterns of growth) of tooth germ development in *Pan, Macaca*,



Lingual

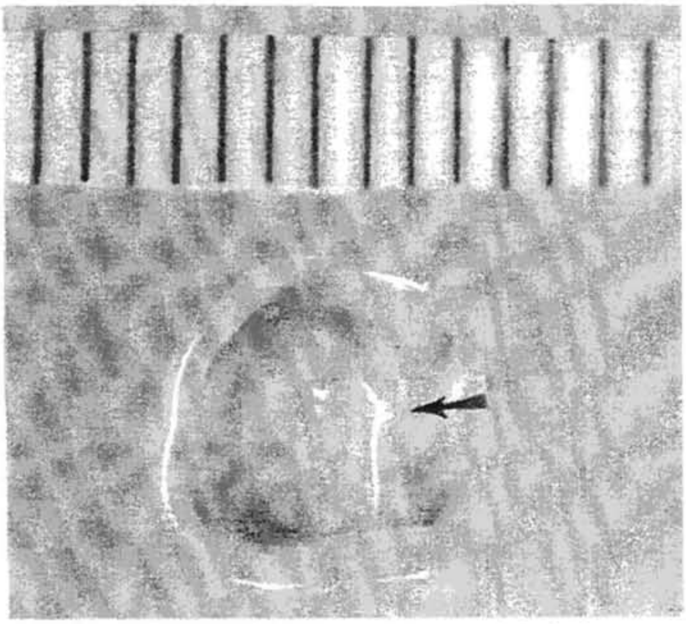


Fig. 1. Development of the *crista obliqua* on dm^3 of *Alouatta caraya* (top) and dm^2 of *Pan troglodytes*. Orientation: left is mesial; right is distal for both figures. Top is buccal for top figure; bottom is buccal for bottom figure.

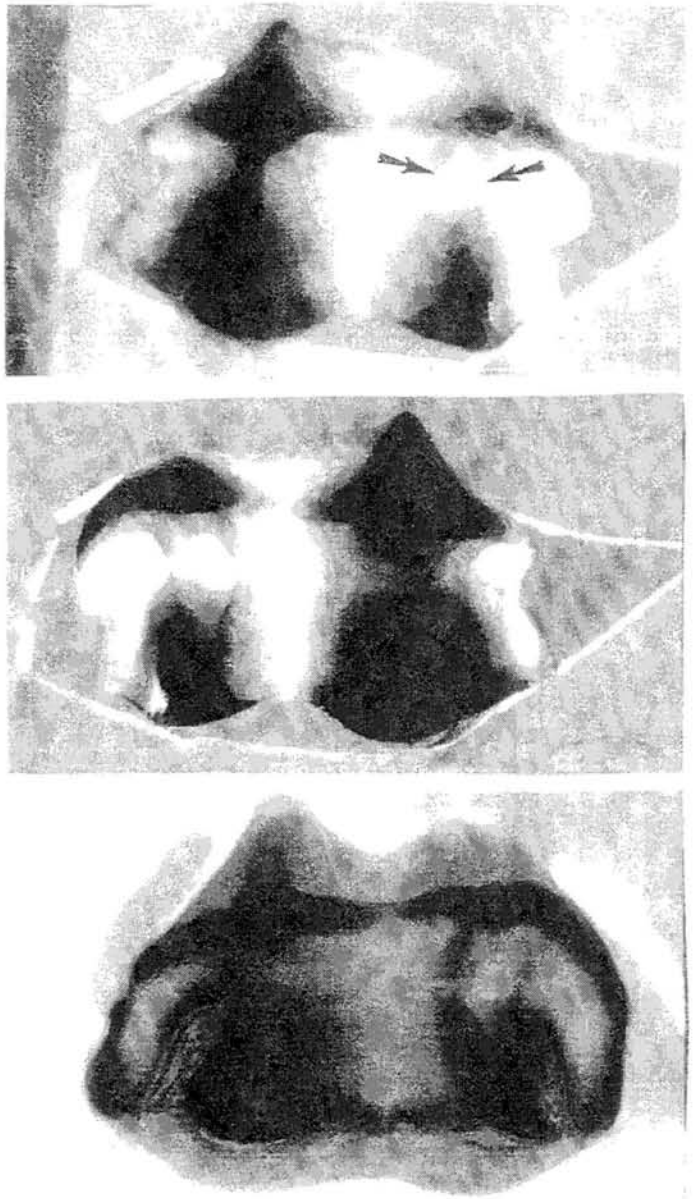


Fig. 2. Development of dm^2 of *Macaca mulatta*. Note lack of *crista obliqua* and development of two distal folds on the surface of the inner enamel epithelium. Orientation: mesial is on the left and distal on the right for the top and bottom specimens. Distal is on the left and mesial on the right for the middle specimen.

and *Alouatta* were made. These were compared with the findings of Butler (1967*a,b,c*, 1968, 1971, 1992) and Kraus and Jordan (1965) for the molars of *Homo sapiens*.

The basic pattern of growth of the IEE (inner enamel epithelium) is influenced by the rates of proliferative growth. Cessation of mitotic activity in some cells and continued division of others is thought to produce the folds on the surface of the IEE.

The pattern of calcification is influenced by the pattern of these folds. Calcification is initiated in the tips of the cusps and the calcifying front advances along the ridges and crests before reaching the valleys and basins. The size of the completed crown is determined by the rate and duration of proliferative mitotic growth of the papilla and the inner enamel epithelium and, to a lesser extent, the rate and duration of appositional growth (*i.e.*, enamel secretion).

The shape of the completed crown results from differential growth within the various dimensions of the developing tooth germ. In comparing odontogenesis in members of the four primate genera, variation in all of these aspects of development are evident.

Topographical differences exist on the surface of the IEE. For example, a *crista obliqua* develops on the surface of the maxillary molars of *Pan, Homo*, and *Alouatta*, but not on the surface of the maxillary molars of *Macaca* (compare Figs. 1 and 2). Differences in both the timing and pattern of initiation of calcification are also evident. The order of initiation of calcification at the tips of the cusps is similar in all four genera, but variations in timing exist.

Calcification is underway in the tips of all of the major cusps of *Pan, Homo*, and *Macaca* prior to the coalescence of the calcifying fronts between the cusps. In *Alouatta*, some coalescence occurs prior to the initiation of calcification in the hypocone of the maxillary molars and the entoconid of the mandibular molars. Figs. 3 through 6 contain diagrammatic comparisons of the patterns of calcification.

Differences in the relative rates of growth within the molars of *Pan, Homo, Macaca*, and *Alouatta* are very complex. One notable difference is the greater rate of growth in the mesiodistal diameter (as measured by buccal length) relative to buccolingual diameter (as measured by mesial width) in the maxillary molars of *Macaca*. This results in molars that are longer and narrower than *Pan, Homo*, and, *Alouatta* molars. The rates of growth in the maximum mesiodistal and buccolingual diameters are essentially equal in the maxillary molars of *Pan, Homo*, and *Alouatta*. This results in molars that are about as long as they are wide. More subtle differences in the relative rates of growth can also result in differences in morphology. For example, dm_2 and M_1 of *Homo* grow faster in length than the talonid grows in width, whereas growth in these dimensions do not differ significantly in dm_2 and M_1 of *Pan*. Comparisons of the changes in shape in these teeth reveal that the talonids of the dm_2 and M_1 of *Homo* become mesiodistally elongated as the molars develop. The talonids of the dm_2 and M_1 of *Pan* do not elongate mesiodistally to the same extent. As a result, the talonids of these molars are shorter and wider relative to the length of the tooth in *Pan* (Figs. 7, 8).

The pattern of initiation of calcification and the relative rates of growth can interact to influence the completed morphology considerably. For example, in dm^3 and M^1 of *Alouatta* the rate of growth in length (as measured by buccal length) does not differ significantly from that in distal width. This is also true for the dm^2 and M^1 of *Pan* and *Homo* but, because the hypocone develops and calcifies later in the development of these teeth in *Alouatta*, there is a greater increase in the size of the distal moiety of the tooth relative to the mesial moiety in *Alouatta*. The dm^2 and M^1 of *Pan* and *Homo* retain a much more rectangular shape.

Kraus (1964:206) has emphasized that "the aspect of the dentition that is critical in evolutionary interpretation is its *morphogenesis* rather than its final morphology." In fact, Kraus and Jordan (1965) hypothesized that the relative lengths of common ontogenetic patterns would be greater for the molars of more closely related taxa.

In comparing the development of the molars of *Alouatta, Macaca, Pan*, and *Homo* it is clear that the phylogenetic relationships cannot be inferred simply from comparisons of the length of common ontogeny. This is because dental development entails a complex interaction of factors to produce the completed crown and changes can (and apparently do) occur in any of these. Although the unfolding of the dental ontogenies does not provide a neat picture of phylogenetic relationships, dental morphogenesis can potentially provide information that is useful when making phylogenetic inferences.

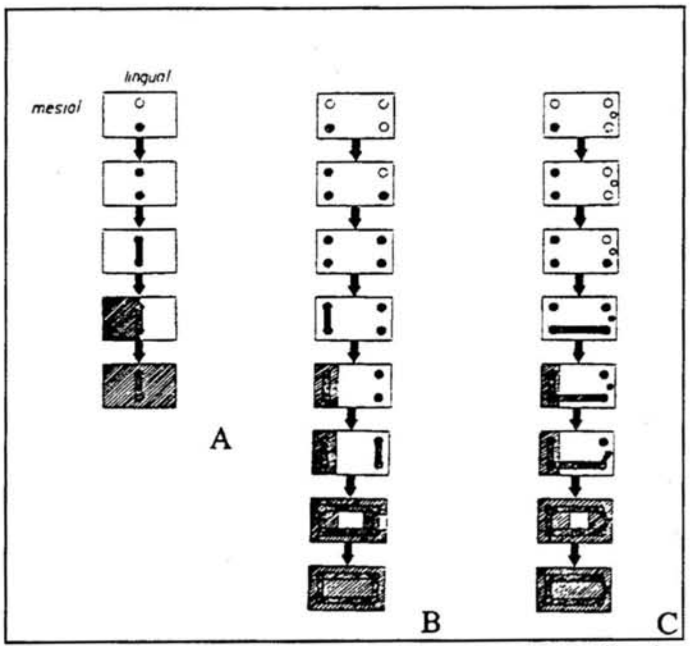


Fig. 3 .Diagrammatic representation of the patterns of calcification in: A dm_2 of *Alouatta*, B dm_1 of *Macaca*, and C dm_1 of *Pan* and *Homo*.

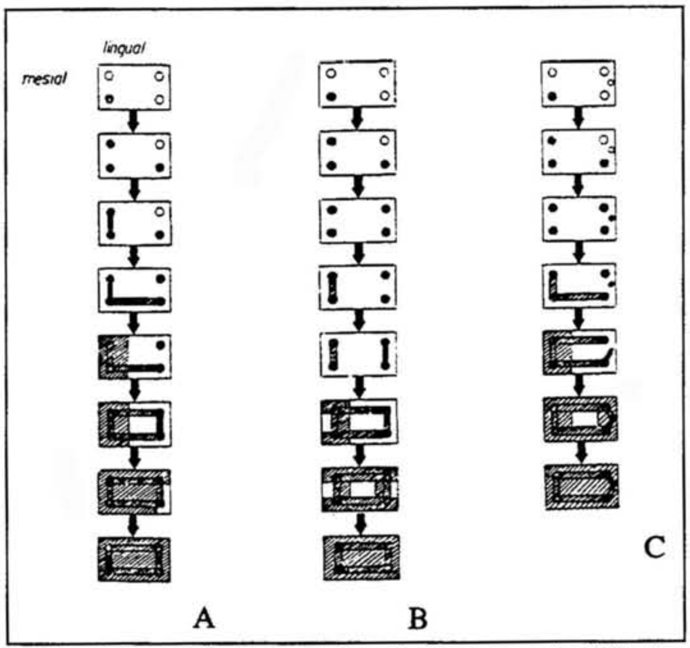


Fig. 4. Diagrammatic representation of the patterns of calcification in: A dm_3 of *Alouatta*, B dm_2 of *Macaca*, and C dm_2 of *Pan* and *Homo*.

Understanding the developmental mechanisms that determine the size and shape of the completed crown can assist in assessing whether characters are more likely to be similar due to common descent or to

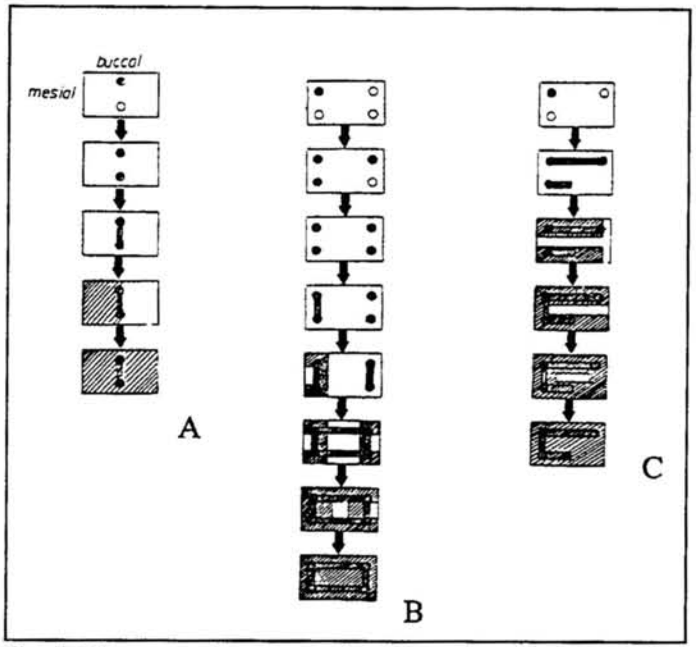


Fig. 5. Diagrammatic representation of the patterns of calcification in: A dm^2 of *Alouatta*, B dm^1 of *Macaca*, and C dm^1 of *Pan* and *Homo*

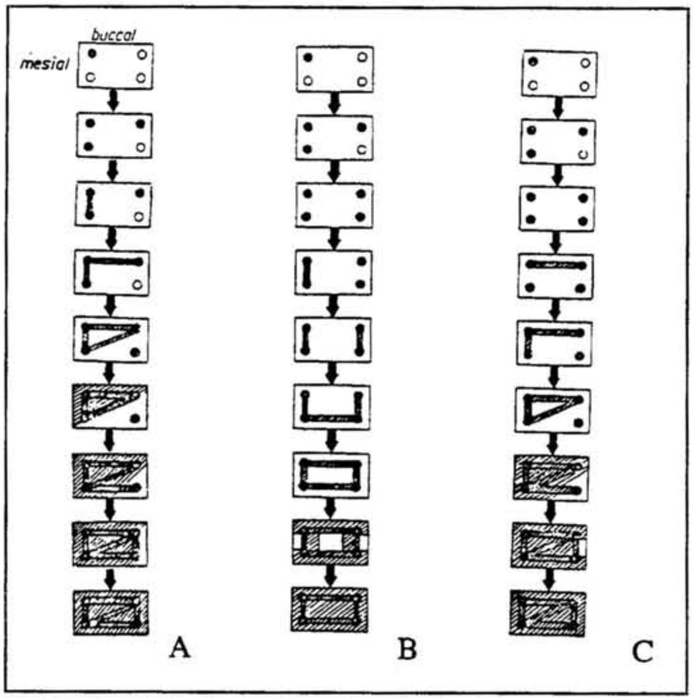


Fig. 6. Diagrammatic representation of the patterns of calcification in: A dm^3 of *Alouatta*, B dm^2 of *Macaca*, and C dm^2 of *Pan* and *Homo*.

homoplasy. This is because understanding how a given morphology is formed during ontogeny, and how variable the developmental processes are, can help in assessing how mutable the morphology may be (i.e., whether the character could easily change in different lines of descent).

Moreover, if the ancestral condition is reasonably well established (either from the fossil record or out-group analysis), an understanding of how differences in shape and size are achieved developmentally can aid in determining the polarity of change. Thus, although dental morphogenesis alone may not be sufficient to infer phylogenetic relationships, it can provide insights that, when coupled with paleontological data and data from out-group analyses, can be used to make such inferences.

References Cited

Butler PM (1967a) The prenatal development of the human first upper permanent molar. Arch. Oral Biol. *12*:551-563.

Butler PM (1967b) Relative growth within the human first upper permanent molar during the prenatal period. Arch. Oral Biol. *12*:983-992.

Butler PM (1967c) Comparison of the development of the second deciduous molar and first permanent molar in man. Arch. Oral Biol. *12*:1245-1260.

Butler PM (1968) Growth of the human second lower deciduous molar. Arch. Oral Biol. *13*:671-682.

Butler PM (1971) Growth of human tooth germs. In AA Dahlberg (ed.): Dental Morphology and Evolution. Chicago: University of Chicago Press, pp. 3-13.

Butler PM (1992) Correlative growth of upper and lower tooth germs in the human foetus. Ann. Zool. Fennici *28*:261-271.

Hanken J (1989) Development and evolution in amphibians. Am. Sci. *77*:336-343.

Keene HJ (1982) The morphogenetic triangle: A new conceptual tool for application to problems in dental morphogenesis. Am. J. Phys. Anthropol. *59*:281-287.

Keene HJ (1991) On heterochrony in heterodonty: A review of some problems in tooth morphogenesis and evolution. Yearbook Phys. Anthropol. *34*:251-282.

Kraus BS (1964) The Basis of Human Evolution. New York: Harper and Row.

Kraus BS, and Jordan RE (1965) The Human Dentition Before Birth. Philadelphia: Lea and Febinger.

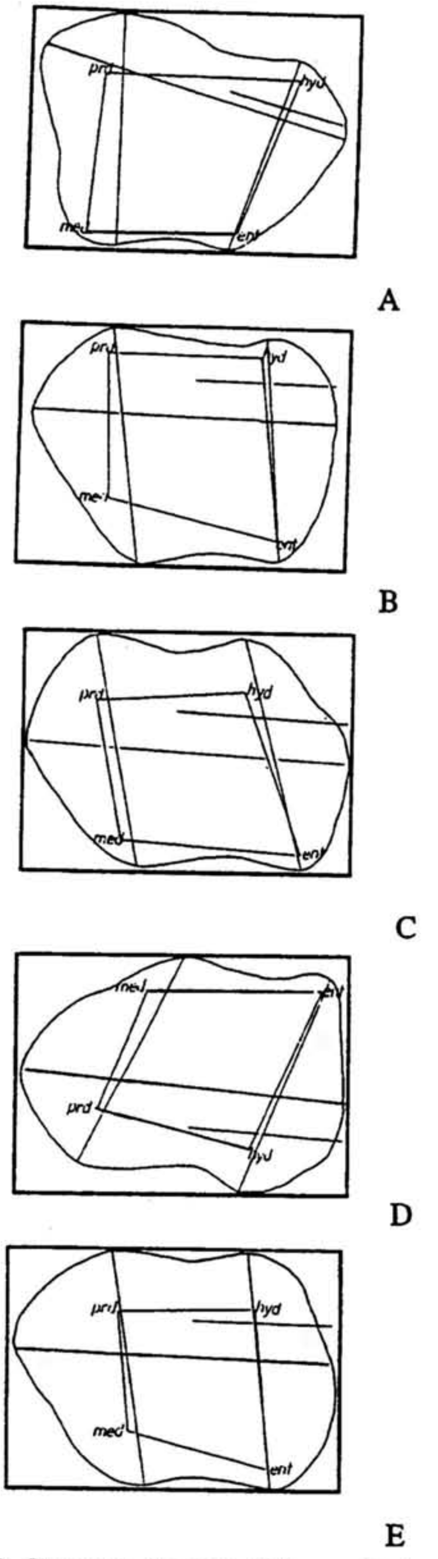


Fig. 8. Changes in the shape of the mandibular second molars of *Pan troglodytes*. A 3 cusps calcifying; B 4 cusps calcifying; C mesial and buccal cusps coalesced; D mesial, buccal, and lingual cusps coalesced; E entire occlusal surface calcifying.

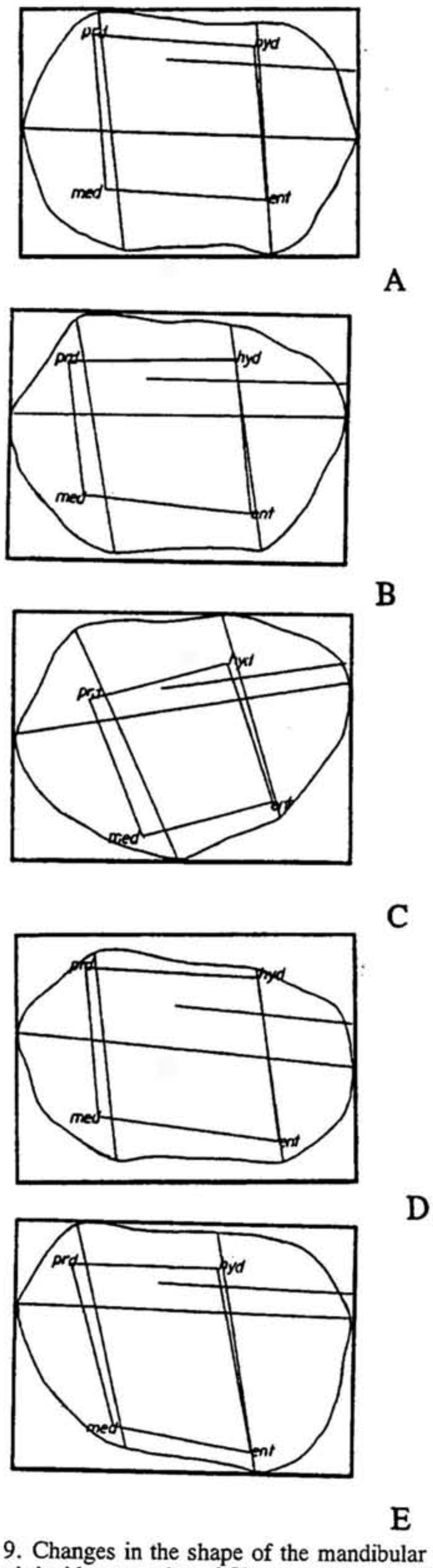


Fig. 9. Changes in the shape of the mandibular second deciduous molar of *Homo sapiens*. A 18 weeks gestation; B 25 weeks gestation; C 28 weeks gestation; D 32 weeks gestation; E 36 weeks gestation.