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A histological reconstruction of dental development in the common chimpanzee, *Pan troglodytes*

Much is known about the dental development of *Pan* compared with that for other extant great apes. The majority of information available has concentrated either on the emergence times of teeth or on the sequence of mineralization stages of the teeth as revealed from radiographs. However, the problems of defining stages of tooth formation sufficiently accurately on radiographs are only now becoming recognized. All of the data available to date suggest the presence of a more variable picture for the timing of mineralization stages in chimpanzees than for the timing of tooth emergence. In particular, arguments persist in the literature over the time of initial mineralization and the time it takes to form each anterior tooth crown in chimpanzees. Therefore we attempt to provide a more precise chronological time scale for dental development in our closest living relative. Furthermore, we examine the sequence of molar cusp formation relative to enamel formation times related specifically to those cusps and to try to tie these data in with information from functional studies of molar crowns. Histological sections of 14 maxillary and 28 mandibular teeth from four chimpanzee (*Pan troglodytes*) individuals and three molar teeth from three chimpanzees of unknown origin were prepared in accordance with a well-established protocol. By combining data on short-period and long-period incremental lines (including daily secretion rates, periodicity, prism lengths and enamel thickness) in both enamel and dentine, we reconstruct times for the onset and duration of crown formation as well as construct a schedule for the pattern and timing of dental development in this one hominoid species. Interestingly, our histologically-derived data confirms that the data from radiographic studies underestimate crown formation times by the following amounts for each tooth type: I_1 2.5 years, I_2 3.1 years, C 1.6 years, P_3 1.9 years, P_4 0.1 years, M_1 0.8 years, M_2 1.1 years and M_3 0.3 years. When combined with data on gingival emergence, it seems that chimpanzee teeth have a greatly reduced time for root growth before emergence occurs and that the major differences between *Homo sapiens* and *Pan* lie in the first part of the root formation rather than in the total period of crown formation. Maxillary and mandibular molar functional cusps take longer to complete enamel formation to the cervix than any other cusp in that same tooth, which makes sense as these cusps are thick enamelled. These results suggest that new links can be made between developmental aspects, occlusal morphology and tooth function.

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Introduction

The primary goal of this study is to document and provide a chronological time scale for the dental development of our closest

living relative, the chimpanzee, through well-established histological techniques. The type of analysis carried out here marks an important transition in studies geared at inferring paleobiological aspects of mammals by relating aspects of dental development to other life history variables (e.g., Schultz, 1935; Smith, 1994; Smith *et al.*, 1994; Conroy & Kuykendall, 1995; Smith & Tompkins, 1995). Until recently, the traditional method for gauging the relative developmental status of great apes has been either through direct dissections of specimens or plain-film radiography. Both techniques can be highly accurate and precise though the former suffers from the inability to investigate large samples while the latter may sometimes suffer from inaccuracies related to the geometry of X-ray beams and the morphology of the teeth themselves (see Beynon *et al.*, this volume). The goal of this study is to supplement pre-existing data on several aspects of dental development in *P. troglodytes* and at the same time, to tease out information on the underlying growth mechanism(s) responsible for final tooth form.

Background

Some of the earliest studies to document details of dental development in chimpanzees are those of Keith (1895, 1899), Zuckerman (1928), Krogman (1930), Schultz (1935) and Bennejeant (1940). Zuckerman (1928) in particular trawled the literature for data concerning the ages of eruption of teeth in chimpanzees that had been captured for European zoos. In addition, Zuckerman took radiographs of chimpanzees in the London Zoo and made original observations about the sequence and stages of mineralization of their teeth. Zuckerman (1928) concluded, after a considerable effort, that “all the available data indicate that the duration of the chimpanzee stages of tooth-development are the same

as in [humans]”. Therefore, Zuckerman argued, the “Taungs ape must have been in its sixth or seventh year” and not in its fourth year as had been suggested previously.

These days, more is known about chimpanzee dental development than for any other greater or lesser ape. In one sense, however, this is simply a reflection of how little we know about dental development in the gorilla, the orang-utan and especially the gibbon (see Smith *et al.*, 1994; Dirks, this volume). In a broad comparative context, Swindler (1985) has drawn attention to the more or less common sequence of tooth mineralization in the deciduous and permanent dentitions of monkeys, apes and humans, to the similar sequence of tooth emergence (excepting the sequential plasticity of the canine and premolar teeth with respect to the second molar tooth; Schultz, 1935; Clements & Zuckerman, 1953; Smith, 1994; Harvati, 1998) and to the common sequence of cusp initiation (but not coalescence, where humans differ) in the permanent molar teeth of hominoids. All this probably relates to a common functional molar morphology. Swindler (1985) has also drawn attention to the similarities in circumnatal dental development among hominoids (Tarrant & Swindler, 1972; Moxham & Berkovitz, 1974; Oka & Kraus, 1969; Kraus & Jordan, 1965; Siebert & Swindler, 1991).

Subsequent studies on chimpanzees have concentrated either on the emergence times of teeth, on the sequence of mineralization stages of the teeth as revealed from radiographs or from dissections or, less successfully, on both at the same time. The studies of Nissen & Riesen (1945, 1964) are classic longitudinal studies on the emergence times of the deciduous and permanent teeth of chimpanzees. Newer studies, often on larger numbers of animals, have documented astonishingly similar median emergence ages to these first studies (Kraemer

et al., 1982; Conroy & Mahoney, 1991; Kuykendall *et al.*, 1992). Importantly, Conroy & Mahoney (1991) have demonstrated a significant time lag for the first permanent molar-central incisor emergence time in chimpanzees. The figures for the time lag between males and females, respectively, are 2.44 (S.E.=0.322) and 2.00 (S.E.=0.152) years in the upper right quadrant, 2.43 (S.E.=0.32) and 2.00 (S.E.=0.219) years in the upper left quadrant, 2.7 (S.E.=0.25) and 2.15 (S.E.=0.101) years in the lower left quadrant and 2.27 (S.E.=0.25) and 2.12 (S.E.=0.119) years in the lower right quadrant thus confirming a time lag in the emergence of these two teeth in chimpanzees of about twice that of modern humans. These findings underscore an inconsistency between those results and results for attainment of mineralization stages in two longitudinal studies (see also later). The difference in the time of crown completion between the first permanent molar and the permanent central incisor is reported to be little more than a year (Kuykendall, 1996) or even just under a year (Anemone *et al.*, 1991). This is especially puzzling since permanent incisors emerge through the gingiva at the level of the cervical margin of the remaining deciduous teeth (i.e., well below the occlusal plane) whereas molar teeth emerge through the gingiva almost at the level of the occlusal plane. These combined results for emergence times and mineralization times imply that permanent incisors take twice the time to erupt half the distance that permanent first molars do after crown completion.

Kuykendall *et al.* (1992) have in addition provided excellent data on the variability of emergence times in chimpanzees and furthermore, demonstrate significant differences in the emergence times between some male and female teeth (but notably not of the permanent canines which differ so greatly in size; this result may have resulted

from the small sample size for this tooth type). In addition, Smith (1994) has provided an excellent analysis of the sequence polymorphisms of tooth emergence in chimpanzees in the context of a comparison with humans, macaques and *Australopithecus*.

Early studies on the sequence and timing of stages of mineralization of chimpanzee teeth came some time after good data were available for several New and Old World monkey species (see Swindler, 1985 and Swindler & Beynon, 1993 for good reviews and discussion on this). Dean's & Wood's (1981) first attempt to establish a chart or atlas of mineralization stages of great ape teeth purposely minimized within-group variation and sought to portray a model or generalized pattern of dental development in great apes by excluding teeth whose developmental stages were intermediate between the nine defined stages (see Anemone *et al.*, 1996). Inevitably, a combined cross-sectional sample of wild shot chimpanzees, gorillas and orang-utans of unknown age was less than satisfactory for documenting small details but the data were aimed at improving the current method used to age great ape crania in comparative cross-sectional growth studies of hominoids. Nonetheless, that study pointed to important absolute differences between crown and root formation times and suggested relative differences between the times taken to form anterior tooth crowns between humans and great apes. Anemone *et al.* (1991), Simpson *et al.* (1992), Kuykendall (1996) and Anemone *et al.* (1996) have all subsequently refined or proposed revisions to the findings of Dean & Wood (1981) using longitudinal or mixed-longitudinal samples of known-age chimpanzees. Kuykendall (1996) has documented differences between sexes in some tooth mineralization stages but, oddly in the light of the differences documented by Kuykendall *et al.* (1992), only those relating to the canine are statistically significant. For the permanent canine, statistical tests show

stage six (defined as the stage where the "root length is equal to or greater than the crown height") to differ significantly between sexes: the mean age attainment of this stage differed by 1.4 years between males and females. (Thus, male canine crown formation time was prolonged with respect to females.) Other stages of canine development also showed smaller, less significant, differences between the sexes. [Kuykendall's \(1996\)](#) study is the first to clearly document biologically meaningful sex differences between developing mineralization stages of male and female chimpanzee teeth in a large sample ($n=118$) of chimpanzees of known age. However, [Kuykendall \(1996\)](#) also concludes that, in absolute terms, human and chimpanzee canines take an equivalent time to form but that relatively less of that time is devoted to root formation in the chimpanzee.

[Winkler \(1995\)](#) has drawn attention to the fact that radiographs may fail to reveal the early stages of tooth formation in great apes and that these stages are better demonstrated by direct dissection of the specimens. Additionally, [Beynon *et al.* \(1991\)](#) have pointed out that dissections of great ape tooth germs reveal some stages of formation in some tooth types that follow a different sequence to those known for modern humans. For example, the root bi- or trifurcation of great ape upper premolar teeth began to form before the end of enamel formation ([Beynon *et al.*, 1991](#)). All this, together with the problems of defining stages of tooth formation sufficiently accurately on radiographs (see [Liversidge, 1995](#) for a review) has now generated a more variable picture for the timing of mineralization stages in chimpanzees than for the timing of tooth emergence. This is surprising since there is fundamental recognition that data for tooth mineralization stages are better than tooth emergence data for estimating both skeletal maturity and chronological age ([Gleiser & Hunt, 1955](#)).

Histological studies of developing dentitions are much more limited with respect to the numbers of individuals they can include and the degree of variation they can portray than are large, longitudinal, radiographic studies ([Beynon *et al.*, 1991](#)). On the other hand, they are able to resolve some issues such as defining the end of enamel formation and the initiation of mineralization¹ with greater precision. Several issues arise from the aforementioned studies that warrant further attention. Additionally, there are new links to be made between studies of tooth development with those that have concentrated on crown shape, enamel thickness and tooth function.

Specific aims

The aims of this study are several. First, confusion exists about both the times of initial mineralization and time it takes to form each anterior tooth crown in chimpanzees. While studies of tooth emergence ([Conroy & Mahoney, 1991](#)) and tooth formation ([Dean & Wood, 1981](#); [Beynon *et al.*, 1991](#)) demonstrate a long time lag between first permanent molars and permanent central incisors in chimpanzees, others do not (e.g., [Anemone *et al.*, 1991](#); [Kuykendall, 1996](#)). Thus, one aim of this study is to document the times of enamel formation in chimpanzee anterior teeth using data derived from a histological analysis. A second aim is to document the time of initial mineralization of all permanent teeth in chimpanzees more precisely. A third aim is to relate the known sequence of molar cusp formation and cusp coalescence in chimpanzees to enamel formation times related specifically to those cusps and to try to correlate these data with information from

¹In past studies, authors described the various stages of tooth growth in several different ways. In this study, the term "onset of mineralization" is equivalent to "initiation of crown formation" whereas the term "crown formation" refers to "enamel cap completion".

Table 1 Specimen number and description, maturational status and sex, tooth type and the number of ground sections (in brackets) prepared from each tooth of *Pan troglodytes*

	Specimen no.	Maturational status and sex	Tooth type and no. of ground sections
Animal 1	43/87	Adult, female	I ₁ [1], I ₂ [1], C[1], P ₃ [1], P ₄ [1], M ₁ [2], M ₂ [1], M ₃ [2]
Animal 2	88/89	Juvenile, sex unknown	I ₁ [2], I ₂ [2], C[1], P ₃ [2], P ₄ [1], M ₁ [1], M ₂ [1], M ₃ [1]; I ¹ [1], I ² [1], C[1], P ³ [1], P ⁴ [1], M ¹ [1], M ² [1], M ³ [3]
Animal 3	28/90	Juvenile, sex unknown	I ₁ [2], I ₂ [2], C[1], P ₃ [1], P ₄ [1], M ₁ [1], M ₂ [2]
Animal 4	89/89	Infant, sex unknown	I ₁ [1], I ₂ [1], C[1], P ₃ [1], P ₄ [1]; I ¹ [1], I ² [1], C[1], P ³ [1], P ⁴ [1], M ¹ [1]
Specimen 5	—	Adult	M ₂ [2]
Specimen 6	—	Adult	M ₃ [1]
Specimen 7	—	Adult	M ³ [1]

functional studies of molar crowns. One final overall aim is to try to document aspects of dental development in chimpanzees with sufficient confidence and in new and novel ways so that we can eventually make reliable comparisons between chimpanzees and other great apes. At present, it is not possible to say with any confidence how gorillas, chimpanzees or orang-utans differ in any aspect of their dental development, yet it is expected that these taxa should differ from one another even if only in some small ways.

Materials and methods

The teeth used in this study included 14 maxillary and 28 mandibular teeth from four chimpanzee (*P. troglodytes*) individuals and three molar teeth from three chimpanzees of unknown origin. The specimen number and description, maturational status and sex, tooth type and number of ground sections are provided in Table 1. Descriptive statistics (mesio-distal length, bucco-lingual/palatal width, crown height and root length) for teeth belonging to animals 2, 3 and 4 are provided in Table 2.

Specimen descriptions

The following is a brief overview of the developmental status of each of the four chimpanzee specimens as well as an account

of the number and type of teeth included in the analysis. The sex of each animal is unknown except for animal no. 1. In addition to the four complete chimpanzee specimens, three isolated molars are also included in the analysis.

Animal 1 (HT 43/87). This specimen is a left hemi-mandible from an adult female chimpanzee from the comparative anatomy collections in the Anatomy Department at University College London, but of unknown origin. The erupted teeth are I₁, I₂, C, P₃, P₄, M₁, M₂ and M₃. The animal is judged to be adult, since the M₃ root is complete, and I₁, I₂, C, M₁ and M₂ show marked attrition on the incisal and occlusal surfaces.

Animal 2 (HT 88/89). This specimen is a right mandible and maxilla of a juvenile chimpanzee also derived from the preserved collections at UCL. In the mandible, di₁ is lost; di₂, dc, dm₁, dm₂ and M₁ are present and I₁ is just emerging from the jaw. Radiographs showed unerupted I₂, C, P₃, P₄, M₂ and M₃ at different stages of development and all exhibited incomplete root formation, though the roots of M₁ were almost complete. The M₃ crown was incomplete and lingually tilted.

In the maxilla, dc, dm¹, dm² and M¹ are present with I¹ just emerging and exposing 2–3 mm of its crown. Radiographs showed

Table 2 Descriptive statistics of tooth size, crown height and root length for the sample of *P. troglodytes* animals used in this study

	Specimen	I1	I2	C	P3	P4	M1	M2	M3
<i>Mandibular:</i>									
Mesiodistal	28-90	8.7	9.5	11.0*	8.2	8.0	13.0	12.0	—
	88-89	9.9	8.7	8.2	7.7	9.7	12.6	12.7	—
	89-89	—	7.2*	—	6.0*	6.0*	11.0*	—	—
Buccolingual	28-90M	9.0	9.5	9.5*	11.8	10.8	10.6	11.0	—
	28-90D	—	—	—	—	11.0	11.3	—	—
	88-90M	7.6	9.6	7.2	9.4	10.5	10.0	9.5	—
	88-90D	—	—	—	—	10.8	11.0	—	—
	89-89M	7.5*	8.8*	—	9.8*	8.8*	9.5*	—	—
	89-89M	—	—	—	—	9.0*	—	—	—
Crown height	28-90B	13.4	13.5	17.0*	9.5	8.0	7.1	—	—
	28-90L	13.4	13.5	—	—	7.0	6.8	7.0	—
	88-89B	12.7	13.0	11.7*	11.3*	8.7*	7.0, 8.4	6.8, 7.0*	—
	88-89L	13.1	14.2	11.8*	—	6.2*	6.2	6.4, 6.1*	—
	89-89B	10.8*	10.5*	9.0*	7.5*	5.0, 6.0*	6.0*	—	—
	89-89L	11.8*	11.3*	—	4.5*	3.5*	6.0*	—	—
Root length	28-90M	7.9	6.0	—	4.0	5.0	13.0	—	—
	28-90D	6.0	5.5	—	—	6.5	14.0	6.0	—
	88-89M	1.8	0.1	—	—	—	9.9, 9.6	—	—
	88-89D	1.4	0.1	—	—	—	10.5, 8.9	—	—
	89-89M	—	—	—	—	>1.0	—	—	—
	89-89D	—	—	—	—	>0.5	—	—	—
<i>Maxillary:</i>									
Mesiodistal	88-89	12.7	10.0	8.5*	8.3	7.5	11.0	10.4	11.5
	89-89	—	7.3*	—	6.6*	7.0*	9.8*	—	—
Buccopalatal	88-89M	10.2	9.0	11.0*	12.0	11.0	12.2	12.2	10.0
	88-89D	—	—	—	11.4	10.5	8.8	—	—
	89-89M	9.0*	6.7*	—	9.5*	8.8*	10.0*	—	—
	89-89D	—	—	—	—	—	—	—	—
Crown height	88-89B	15.0	13.0	19.0*	8.5	7.0	7.5	6.2	5.5
	88-89L	14.0	12.0	16.0*	5.0	6.0	6.0	6.0	4.4
	89-89B	13.2*	9.8*	10.6*	7.3*	6.0*	5.5	—	—
Root length	89-89L	13.2*	9.6*	—	5.5*	5.5*	6.5	—	—
	88-89M	10.0	4.0	—	3.5	5.5	10.0	5.5	—
	88-89P	10.5	5.0	—	5.0	5.0	13.0	5.0	—
	89-89M	—	—	—	1.0	—	4.5, 3.8	—	—
	89-89P	—	—	—	—	—	4.5	—	—

*=incomplete crowns; section: M=mesial; D=distal; B=buccal; L=lingual; P=palatal. All measurements in mm.

unerupted I², C, P³, P⁴, M² and M³ with incomplete roots at different stages of development. M¹ roots were almost complete. M³ crown mineralization had started but was not complete.

Animal 3 (HT 28/90). This specimen is a hemi-mandible of a juvenile chimpanzee of unknown age obtained from the Osman Hill collection at the Royal College of Surgeons,

London. Radiographs showed unerupted I₁, I₂, C, P₃, P₄, M₁ and M₂ with complete crown development of all teeth except C and M₂.

Animal 4 (HT 89/89). This specimen is a dry, defleshed, left hemi-mandible and maxilla of an infant chimpanzee. In the mandible di₂, dc, dm₁, and dm₂ are present and di₁ is lost. None of the permanent teeth have

erupted. Radiographs show incomplete crowns of I_1 , I_2 , C, P_3 , P_4 and I^1 , I^2 , C, P^3 and P^4 . M^1 is crown complete and the roots remain incomplete. M_1 is missing while M_2 and M^2 are present within the developmental crypts.

Specimens 5, 6 and 7 (HT 59/89, 11/88 and 10/88 respectively). These specimens are wet, isolated teeth of adult chimpanzees of unknown age from the comparative anatomy collection at UCL. The teeth are an M_2 , M_3 and M^3 , respectively, all of which show completed crowns and roots. Specimens 6 and 7 exhibit attrition on all cusps.

Specimen preparation

The entire sample of mandibulae and maxillae were radiographed and subsequently, all teeth were dissected from the jaws, photographed and measured using vernier calipers. All teeth were then embedded in polyester resin and 150–180 μm thick longitudinal sections were taken from the midline axial plane in anterior teeth and from the bucco-lingual plane of both mesial and distal cusps of posterior teeth using a Microslice 2 annular saw. All of the sections were lapped down from both sides (using a Logitech PM2A precision lapping machine) to a final thickness of 100 μm , so that the plane of section passed through the dentine horns, and then mounted to microscope slides. Sections were placed in an ultrasonic bath to remove surface debris, dehydrated through a graded series of alcohol baths and mounted in DPX mounting medium. The sections were then studied using polarized, incident and transmitted light microscopy (Zeiss Universal photomicroscope).

Measurements

Two methods are used here to estimate crown formation times: (1) estimates based on cumulative prism length divided by measured daily increments (referred to as "Method A"), and (2) striae counts linked

with estimates of buried increments in cuspal enamel (referred to as "Method B").

Prism lengths (Method A). Cumulative prism lengths used in Method A are based on the measurement of prism lengths in cuspal, lateral and cervical enamel as shown in Figure 1. Successive segments, or regions, of the crown are formed by tracking prisms from their origin at the enamel-dentine junction (EDJ) to a long-period line (stria of Retzius) and then determining the formation time of that region by dividing the length of the prism by the daily secretion rate (formerly referred to as the cross striation repeat interval). The total crown formation time is equivalent to the sum of formation times for all regions of the crown (see Figure 1). It should be borne in mind that several inaccuracies can result by estimating crown formation times with this method. Firstly, because prisms decussate and therefore do not follow a straight course from the EDJ outwards, it is necessary to use a corrected value for prism length (see Risnes, 1986); however, this value is based on modern humans, not great apes. At present, it is unknown whether prisms decussate to the same degree in other primate teeth as they do in modern humans. Secondly, the thickness of enamel varies with the plane of section such that prism length increases as section obliquity increases. Therefore, accurate measurements of prism lengths could only be obtained when the plane of section passed through the tip of the dentine horns. In an attempt to minimize errors in estimated crown formation times, we also employ another method using striae counts, the number of which do not alter markedly with changes in the plane of section.

Striae counts linked with buried increments (Method B). The total number of striae reaching the surface in imbricational enamel are counted in each section and a mean

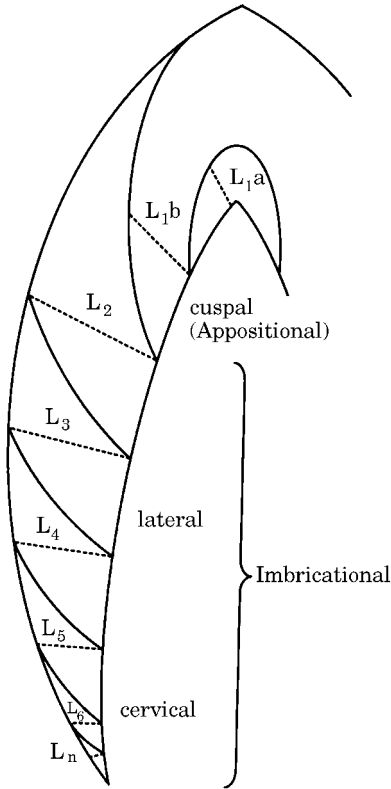


Figure 1. Schematic drawing of a cuspal cross section to demonstrate one method (Method A) for estimating total crown formation times in chimpanzee teeth. The bold lines within the enamel cap represent longer-period accentuated lines (striae of Retzius) which appear throughout the formation of a tooth and represent the developing enamel front at a particular point in time. Method A relies on counts of cumulative prism lengths in cuspal, lateral and cervical enamel which are depicted in the diagram as dotted lines extending from the EDJ to the outer enamel surface. The amount of time taken to form the cuspal (or appositional) portion of the tooth is determined by measuring the length of a prism from the dentine horn to an accentuated line and then following that accentuated line back towards the EDJ just lateral to the dentine horn, thereby creating the region L₁a. Where the accentuated line associated with region L₁a contacts with EDJ, another prism is chosen and measured from the EDJ to the accentuated line associated with the transition from cuspal to imbricational enamel thereby creating the region L₁b. The amount of time taken to form each region (e.g., L₁a or L₁b) is determined by dividing the length of the prism corresponding to each region by the daily rate of enamel matrix secretion. Total cuspal formation times can be generated by adding up the time taken to form regions L₁a and L₁b. Imbricational enamel formation times are measured in the same manner so that total crown formation times (CF) can be derived from the following generalized formula: CF = ((L₁a + L₁b) + L₂ + L₃ + L₄ + L₅ + L₆ + . . . + L_n), where (L₁a + L₁b) represents cuspal formation time and (L₂ + L₃ + L₄ + L₅ + L₆ + . . . + L_n) represents imbricational formation time.

value is obtained for each tooth. The daily rate of enamel formation is measured by recording the spacing of enamel cross striations in the cuspal, lateral and cervical portions in the inner, middle and outer regions of the enamel cap. Outer and inner measurements are not made within a minimum distance of 100 μm from the EDJ and enamel surface, respectively, due to convergence of striae. Measuring cuspal cross striations in this way provides an accurate estimate of the daily rate of enamel secretion in each region of the cusp. In addition to these cross striation measurements, counts of the number of cross striations between adjacent striae (the periodicity) are made in each tooth of each individual.

Cuspal enamel thickness, or cusp height, is measured from × 25 drawings along the direction of the enamel prisms from the EDJ

at the dentine horn towards the outer enamel surface.

The cuspal (i.e., appositional)¹ and imbricational enamel formation times are calculated using the following equations:

Cuspal enamel formation time in years (after Risnes, 1986) =

$$\frac{\text{cuspal enamel thickness} \times 1.15}{\text{mean daily rate of secretion}} \times \frac{1}{365} \quad (1)$$

Imbricational enamel formation time in years =

$$\frac{\text{number of striae}}{365} \times \text{periodicity} \quad (2)$$

¹The term "cuspal" is used here rather than "appositional" as all enamel is secreted in an appositional fashion. Cuspal enamel therefore refers only to the region of enamel associated with buried increments, or regular striae of Retzius, over the cusp tips of teeth.

The sum of cuspal and imbricational enamel formation times, using stria counts and cuspal enamel thicknesses, equals the total crown formation time.

Both Methods A and B were carried out in this study and the results are compared with one another. However, only data from Method B (which is least influenced by section obliquity and correction factors for prism lengths) was chosen to reconstruct the timing and sequence of crown formation.

Dental chronology

Tooth sections were examined microscopically seeking accentuated striae in the enamel. Accentuated striae corresponding to hypoplastic episodes are present in both the mandibular and maxillary teeth of all animals. These striae were used to register teeth of differing developmental stages at the same time period (see [Beynon *et al.*, 1991](#)). A neonatal line is present in each of the first molars and was used to calculate the amount of crown formed prenatally from prism lengths and daily secretion rates. The timing of accentuated striae in the first molar crowns were calibrated in years from the neonatal line. This information was used to construct a bar chart of the sequence of tooth development for maxillary and mandibular teeth in *P. troglodytes*.

Results

Crown measurements, including mesiodistal length, buccolingual breadth, crown height and root length for teeth belonging to animals 2, 3 and 4 are reported in [Table 2](#). The spacing of enamel cross striations (i.e., the daily rate of enamel secretion) for each region of each tooth type at the outer, middle and inner portions of the enamel cap are listed in [Table 3](#). [Table 4](#) provides data on imbricational striae counts per millimetre of tooth crown height from the cervix to the cusp tip, the total number of imbricational striae, the amount of time (in years) taken to

form both imbricational and cuspal enamel, and the total crown formation time (time to form cuspal enamel+time to form imbricational enamel) in years for maxillary and mandibular teeth. As stated previously, two methods (Methods A and B) were used to determine cuspal and imbricational enamel formation times. Estimates of crown formation times from each method are provided in [Table 5](#) along with the percentage difference between methods.

A constant finding was that, on average, daily secretion rates show a gradual increase from inner through middle to outer areas in all three (occlusal, lateral and cervical) levels of enamel ([Table 3](#)). In two mandibular molars (M_1 mb, M_1 ml and M_3 mb) and in one maxillary incisor (I^2), the daily secretion rates in outer enamel were slightly lower (5%) than those in middle enamel in the lateral region of the enamel cap ([Table 3](#)). [Beynon *et al.* \(1991\)](#) reported a gradual increase in daily secretion rates from the inner to the outer portions in cuspal, lateral and cervical enamel in *Homo*, *Gorilla*, *Pongo* and *Pan*, except in lateral enamel in a smaller sample of *Pan*. This showed either similar values in middle and outer enamel in molars or a 7% reduction in outer enamel, but only in premolars.

There is also a consistent reduction in daily secretion rates from occlusal, or cuspal, through lateral to cervical with the lowest values being present in cervical enamel ([Table 3](#)). This is consistent with the observations in *Homo*, *Gorilla*, *Pongo* and *Pan* recorded by [Beynon *et al.* \(1991\)](#). The difference between outer cervical and outer lateral cross striation values in this study are smaller (premolars 0.87 μ m, molars 0.93 μ m) than that in modern humans (premolars 1.90 μ m, molars 2.20 μ m). The slowing of secretion in the cervical region appears to be a characteristic of enamel formation in great apes.

Determining the periodicity, or the number of short-period incremental lines

Table 3 Data on the spacing between successive enamel cross striations (i.e., the daily secretion rate) in the outer, middle and inner portions of the occlusal, lateral and cervical regions of the enamel cap

	Occlusal			Lateral			Cervical		
	Outer	Mid	Inner	Outer	Mid	Inner	Outer	Inner	
	I_1	4.75 ± 0.56	4.40 ± 0.34	3.63 ± 0.43	4.51 ± 0.41	4.19 ± 0.41	3.22 ± 0.27	3.70 ± 0.25	2.80 ± 0.50
I_2	5.05 ± 0.28	4.65 ± 0.50	3.90 ± 0.55	4.75 ± 0.12	4.08 ± 0.35	3.28 ± 0.75	3.63 ± 0.41	3.06 ± 0.60	
C	4.68 ± 0.20	4.24 ± 0.38	3.51 ± 0.42	4.30 ± 0.30	3.75 ± 0.30	3.22 ± 0.17	3.65 ± 0.23	2.89 ± 0.65	
P_3	4.89 ± 0.37	4.34 ± 0.38	3.56 ± 0.58	4.54 ± 0.55	4.24 ± 0.27	3.19 ± 0.66	3.64 ± 0.47	3.13 ± 0.36	
P_4	4.86 ± 0.57	4.48 ± 0.43	3.75 ± 0.15	4.24 ± 0.27	4.23 ± 0.44	3.55 ± 0.39	3.68 ± 0.32	3.04 ± 0.17	
P_4	5.08 ± 0.28	4.62 ± 0.28	3.93 ± 0.52	4.32 ± 0.35	4.08 ± 0.52	3.27 ± 0.33	3.84 ± 0.32	3.10 ± 0.09	
M_1	4.88 ± 0.51	4.71 ± 0.49	4.06 ± 0.19	4.17 ± 0.78	4.40 ± 0.70	3.87 ± 0.18	3.79 ± 0.56	3.33 ± 0.32	
M_1	4.66 ± 0.81	4.61 ± 0.66	3.67 ± 0.23	4.39 ± 0.74	4.10 ± 0.56	3.80 ± 0.40	3.79 ± 0.18	3.23 ± 0.21	
M_1	4.76 ± 0.04	4.37 ± 0.18	3.93 ± 0.34	4.41 ± 0.60	4.21 ± 0.40	3.65 ± 0.11	3.55 ± 0.34	3.02 ± 0.20	
M_1	4.58 ± 0.03	4.14 ± 0.44	4.05 ± 0.35	4.35 ± 0.92	3.84 ± 0.62	3.44 ± 0.09	3.78	3.00	
M_2	4.66 ± 0.19	4.42 ± 0.22	3.82 ± 0.38	4.32 ± 0.26	3.84 ± 0.21	3.23 ± 0.26	3.44 ± 0.34	2.91 ± 0.08	
M_2	4.85 ± 0.44	4.39 ± 0.16	3.68 ± 0.17	4.16 ± 0.20	3.65 ± 0.28	3.19 ± 0.04	3.28 ± 0.50	2.67 ± 0.21	
M_2	4.35 ± 0.32	3.91 ± 0.33	3.35 ± 0.19	4.12 ± 0.11	3.68 ± 0.25	3.10 ± 0.40	3.43 ± 0.24	2.81 ± 0.20	
M_2	4.47 ± 0.22	3.99 ± 0.28	3.42 ± 0.15	4.16 ± 0.09	3.80 ± 0.19	3.06 ± 0.34	3.48 ± 0.41	2.98 ± 0.36	
M_3	4.16 ± 0.74	3.77 ± 0.37	3.00 ± 0.27	3.47 ± 0.26	3.63 ± 0.34	2.83 ± 0.15	2.88 ± 0.67	2.43 ± 0.40	
M_3	4.03 ± 0.59	3.61 ± 0.54	3.06 ± 0.38	3.75 ± 0.31	3.69 ± 0.29	3.10 ± 0.18	3.33 ± 0.31	2.89 ± 0.10	
M_3	4.27 ± 0.48	3.68 ± 0.47	3.17 ± 0.15	3.88 ± 0.55	3.37 ± 0.25	3.09 ± 0.30	3.39 ± 0.32	2.65 ± 0.23	
M_3	4.27 ± 0.45	3.75 ± 0.44	3.13 ± 0.38	4.01 ± 0.52	3.32 ± 0.21	2.94 ± 0.21	3.33 ± 0.42	2.61 ± 0.18	
I^2	4.89 ± 0.26	4.49 ± 0.26	3.50 ± 0.57	4.56 ± 0.36	4.09 ± 0.17	3.55 ± 0.63	3.50 ± 0.43	2.97 ± 0.23	
C	4.87 ± 0.37	4.54 ± 0.19	4.13 ± 0.18	4.84 ± 0.33	4.89 ± 0.54	3.15 ± 0.64	3.85 ± 1.06	3.29 ± 0.54	
P^3	4.93 ± 0.11	4.81 ± 0.28	3.45 ± 0.35	4.42 ± 0.12	3.87 ± 0.09	3.27 ± 0.04	3.50 ± 0.42	3.10 ± 0.42	
P^3	5.03 ± 0.35	4.67 ± 0.47	3.73 ± 0.63	4.34 ± 0.47	3.92 ± 0.69	3.60 ± 0.71	3.52 ± 0.40	2.83 ± 0.81	
P^4	4.39 ± 1.15	4.07 ± 1.17	3.70 ± 1.00	4.23 ± 0.62	4.02 ± 0.83	3.20 ± 0.75	3.25 ± 0.03	2.59 ± 0.48	
P^4	4.40 ± 0.28	3.90 ± 0.14	3.55 ± 0.08	4.30 ± 0.14	3.96 ± 0.49	3.26 ± 1.20	3.12 ± 0.02	2.83 ± 0.11	
M^1	4.38 ± 0.74	4.19 ± 0.40	3.29 ± 0.25	4.60 ± 0.56	4.05 ± 0.50	3.30 ± 0.57	3.24 ± 0.06	3.06 ± 0.11	
M^1	4.76 ± 0.06	4.06 ± 0.46	3.53 ± 0.04	4.76 ± 0.23	4.39 ± 0.55	3.54 ± 0.52	3.32 ± 0.26	2.86 ± 0.35	
M^1	4.79 ± 0.95	4.36 ± 0.06	3.45 ± 0.35	4.63 ± 0.81	3.88 ± 0.00	3.28 ± 0.17	3.25 ± 0.07	2.86 ± 0.23	
M^1	4.76 ± 0.35	4.29 ± 0.01	3.16 ± 0.63	4.75 ± 0.35	4.00 ± 0.00	3.39 ± 0.02	3.29 ± 0.44	2.87 ± 0.18	
M^2	4.80	4.10	3.70	4.50	4.10	3.25 ± 0.35	3.17 ± 0.62	2.86 ± 0.21	
M^2	4.80	3.70	3.60	4.00	3.50	3.40	3.40	3.20	
M^3	4.20	3.60	3.00	3.60	3.00	2.90	3.85	2.70	
M^3	4.40	3.20	2.80	3.33	2.80	2.80	3.60	2.60	

Means ± 1 S.D. are shown for each tooth type pooled across all chimpanzee individuals included in the analysis. Measurements are taken from a minimum of two ground sections and a maximum of six ground sections.

(i.e., cross striations) between adjacent long-period lines (i.e. striae of Retzius) for each specimen is essential for estimating the time taken to form imbricational enamel (see Equation (2) above). Animals 1 and 4 (HT 43/87 and HT 89/89, respectively) both have a periodicity of 7 while animals 2 and 3 (HT 88/89 and HT 28/90, respectively) have a periodicity of 8.

Table 5 is a comparison of crown formation times as estimated using both methods and the percentage difference between the means of each. Data are presented as means and standard deviations based on values for all histological sections of each tooth type as listed in Table 4 columns "E", "F" and "G", and thus do not represent values based on any particular chimp individual included in the analysis. Neither method consistently produces higher estimates for either imbricational or cuspal enamel formation times, though interestingly, total crown formation times derived from Method B are greater for four out of the seven maxillary teeth (I^1 and M^{1-3}) while Method A always produces greater total crown formation times in the mandibular dentition. While the comparison between different measurement techniques may prove interesting to those who wish to reconstruct dental development in future comparative studies, it is imperative to bear in mind that results generated from Method A are highly influenced by obliquity of section. Similarly, determining rates of tooth formation via Method A requires the introduction of a correction factor into the equation to account for prism decussation from the EDJ towards the future outer enamel surface. This correction factor (1.15, see Equation (1)) is based on the degree of prism decussation in modern humans. As no research has been done into the degree of decussation in great apes, it is not possible to assess how closely decussation in human teeth compares with that in ape teeth. Therefore, crown formation times based on Method B only are used here to evaluate the

dental chronology in chimpanzees and for comparisons with previously published results (Table 6).

Teeth of differing developmental stages within each individual chimpanzee specimen were registered and cross-matched with one another using accentuated striae associated with stress, hypoplasia or metabolic disturbances (see for example Dean, 1987, 1989; Macho *et al.*, 1996; Hillson & Bond, 1997). As an illustration, animal no. 3 (HT 28/90) exhibited a marked developmental defect resulting in pitting of the incisor enamel (Figure 2(a)). This event is calculated to have occurred at 0.95 years and continued through to 1.65 years (Table 7). Another strong accentuated line evident in the imbricational enamel of all teeth of this specimen (with the exception of the M_1) was calculated to have occurred at 3.97 yrs (Figure 2(b)). The I_2 , C , P_3 and M_2 crowns were incomplete and death occurred at 5.61 years (Table 7).

Results on the timings of crown initiation and completion are used to construct bar charts for each individual chimpanzee in the analysis (Figure 3(a-d)).

Discussion

Three previous radiographic studies have estimated crown formation times of chimpanzees. However, the first was a cross-sectional radiographic analysis of a museum sample of immature *Pan*, *Pongo* and *Gorilla* jaws, and may not be appropriate as a standard for *Pan* only (Dean & Wood, 1981). The other studies on tooth growth and crown formation times in *Pan* (Anemone *et al.*, 1991, 1996; Kuykendall, 1996) used longitudinal radiographic methods and present data comparable with those presented here. Crown formation times, however, were consistently lower than those in the present study (Figure 3). These careful radiographic studies appear to underestimate crown formation times of *Pan* when

Table 4 Cuspal, imbricational and total crown formation times (in years) for the teeth of *Pan troglodytes*

Specimen no.	Tooth	Imbricational striae counts per millimetre of tooth crown height*	TIS	TIF	TAF	TCF
Maxillary						
88/89	RI1	3 12 11 16 20 25 19 19 17 17 16 13 10 12 10 8 8	236	5.17	0.48	5.65
89/89	LI1	INC 8 21 23 23 21 19 16 18 12 10 9 5 5	200+	4.38+	0.46	4.84+
88/89	RI2	7 11 1 18 20 18 18 20 19 16 7 9 6	180	3.94	0.55	4.49
89/89	LI2	INC 14 23 23 24 22 17 14 11 8 1	157+	3.44+	0.44	3.88+
88/89	RC	INC 15 13 16 17 17 18 20 24 21 16 16 16 17 16 16 14 12 5	305+	6.68	0.46	7.14
89/89	LC	INC 12 26 23 21 21 17 13 13 11 6	163+	3.57+	0.55	4.12+
88/89	RP3 b	7 19 25 32 27 22 17 18 7	174	3.81	0.50	4.31
89/89	LP3 b	INC 12 19 20 16 1 9 5	92+	2.02+	0.64	2.66+
88/89	RP3 pal	15 24 24 21 21 7	112	2.45	0.50	2.95
89/89	LP3 pal	INC 14 27 20 11 4 2	78+	1.71+	0.53	2.24+
88/89	RP4 b	18 19 28 24 23 19 11	142	3.11	0.50	3.61
89/89	LP4 b	INC 19 32 22 18 13 9 7	120+	2.63+	0.64	3.27+
88/89	RP4 pal	18 21 29 22 16 14 6	126	2.76	0.61	3.37
89/89	LP4 pal	INC 6 24 19 14 10 4	77+	1.69+	0.55	2.24+
88/89	RM1 mb	11 18 18 16 10 11 9	93+	2.04	0.57	2.61
89/89	LM1 mb	15 19 13 14 9 9 8	87	1.91	0.48	2.39
88/89	RM1 mpal	15 16 18 16 12 9 7	93	2.04	0.48	2.52
89/89	LM1 mpal	6 10 15 16 18 15 13 15	108	2.37	0.53	2.90
88/89	RM1 db	10 15 12 14 11 9 8	79	1.73	0.55	2.28
89/89	LM1 db	14 17 15 13 10 10 2	81	1.77	0.50	2.27
88/89	RM1 dpal	16 16 12 11 8 3	66	1.45	0.61	2.06
89/89	LM1 dpal	26 29 26 24 8 5 8 4	90	1.97	0.50	2.47
88/89	RM2 mb	14 23 22 23 20 13 2	117	2.56	0.64	3.20
88/89	RM2 mpal	18 24 18 27 19 16 8 3	135	2.96	0.59	3.55
10/88	RM3 db	14 24 22 24 20 11 9 3	127	2.78	0.61	3.39
10/88	RM3 dpal	17 24 28 23 12 9 2	115	2.52	0.61	3.13
Mandibular						
43/87	LI1	11 11 14 19 20 18 19 19 15 11 11 5 A	173+	3.79+	0.57	4.36+
28/90	RI1	# 16 21 25 26 21 20 18 15 12 12 11 6	203+	4.45+	0.55	5.00+
28/90	RI1	# 18 21 24 25 21 20 21 16 12 10 10	198+	4.34+	0.61	4.95+
88/89	RI1	8 17 18 20 21 18 17 18 14 10 13 12 8 10	204	4.47	0.42	4.89
88/89	RI1	8 18 18 18 21 19 17 19 17 10 7 9 6 1	188	4.12	0.42	4.54
89/89	LI1	INC 12 17 24 22 22 19 15 15 12 9 9	176+	3.86+	0.53	4.39+
43/87	LI2	14 17 19 24 27 28 19 16 14 11 9 A	180+	3.94+	0.53	4.47+
28/90	RI2	11 15 19 20 22 23 22 21 20 21 16 12 10	232	5.08	0.57	5.65
28/90	RI2	12 18 21 19 21 22 22 20 20 20 18 8 8	229	5.02	0.50	5.52
88/89	RI2	11 15 17 19 20 21 19 20 15 11 13 11 11 10	213	4.67	0.44	5.11
88/89	RI2	7 16 18 21 21 20 19 17 19 17 14 14 13 13	229	5.02	0.53	5.55
89/89	LI2	INC 10 25 24 24 20 18 15 14 11 10 6 5	182+	3.99+	0.48	3.98+
43/87	LC	6 9 16 25 23 24 23 23 19 19 18 23 20 22 18 11	299	6.55	0.48	6.23
88/89	RC	INC 12 16 16 16 17 15 18 17 19 19 19 17 17 16 16 12 10 6	278+	6.09+	0.52	5.87+
89/89	LC	INC 9 29 24 24 21 15 12 13 10 8 7	172+	3.77+	0.50	3.81+
28/90	RC	INC 16 20 22 23 23 29 22 24 20 16 5	220+	4.82+	0.60	4.83+
43/87	LP3	10 11 12 34 29 26 26 15 19 18 15	2.15	4.71	0.69	4.82
88/89	RP3	8 15 21 28 22 21 16 15 15 13 6	180	3.94	0.55	4.49
88/89	RP3	6 5 17 25 23 22 20 17 17 14 10 9	185	4.05	0.68	4.73
89/89	LP3	INC 14 21 25 21 17 16 10	124+	2.72+	0.46	3.18+
28/90	RP3	11 31 25 25 23 23 18 17 11 6	190	4.16	0.77	4.93
43/87	LP4 buc	13 16 17 27 26 17 15 11 7	149	3.26	0.79	4.05

Table 4 Continued

Specimen no.	Tooth	Imbricational striae counts per millimetre of tooth crown height ¹	TIS	TIF	TAF	TCF
88/89	RP4 buc	15 18 27 22 16 15 12 8 4	146	3.20	0.59	3.79
89/89	LP4 buc	INC 15 28 22 18 12 9 2	106+	2.32+	0.48	2.80+
28/90	RP4 buc	16 19 19 26 23 19 17 9 6 2	156	3.42	0.70	4.12
43/87	LP4 ling	18 25 18 19 16 6	102	2.23	0.53	2.76
88/89	RP4 ling	18 21 23 19 13 4	98	2.12	0.66	2.78
89/89	LP4 ling	INC 11 22 17 14 9 5	78	1.71	0.44	2.15
28/90	RP4 ling	18 18 18 19 10	83	1.82	0.66	2.48
43/87	LM1 mb	12 18 20 16 13 10 A	89	1.95	0.59	2.54
88/89	RM1 mb	11 20 20 19 16 10 10 12 A	118	2.59	0.44	3.03
28/90	RM1 mb	13 20 20 15 12 10 9 7	106	2.32	0.48	2.80
43/87	LM1 ml	18 16 11 8 9 8	73	1.53	0.55	2.08
88/89	RM1 ml	9 18 16 14 9 10 4	80	1.75	0.44	2.19
43/87	LM1 db	14 25 20 18 5	82	1.80	0.81	2.61
88/89	RM1 db	10 23 18 16 13 8 5 7 4	104	2.28	0.55	2.83
28/90	RM1 db	18 23 20 16 12 8 7 8 4	116	2.54	0.57	3.11
43/87	LM1 dl	189 19 13 6	57	1.25	0.83	2.08
88/89	RM1 dl		70	1.53	0.57	2.10
28/90	RM1 dl	11 17 16 9 6	59	1.29	0.77	2.06
43/87	LM2 mb	18 17 21 33 15 A	104	2.28	0.79	3.07
88/89	RM2 mb	14 19 16 22 27 17 10	125	2.74	0.79	3.53
28/90	RM2 mb	OBL 17 25 25 20 18 16 10 1	132	2.89	0.72	3.61
28/90	RM2 mb	OBL 10 23 22 22 17 13 8	115	2.52	0.61	3.13
59/89	M2 mb	14 17 20 28 24 19 14	136	2.98	0.81	3.79
59/89	M2 mb	18 21 18 26 22 18 10	133	2.92	0.88	3.80
43/87	LM2 ml	20 22 24 16 13 10	105	2.30	0.79	3.09
88/89	RM2 ml	7 22 21 17 13 11 11	102	2.23	0.55	2.78
28/90	RM2 ml	OBL 15 19 20 13 14 11 2	94	2.06	0.77	2.83
59/89	M2 ml	12 19 21 23 18 14	107	2.35	0.77	3.12
59/89	M2 ml	15 19 20 20 16 3	93	2.04	0.92	2.96
88/89	LM2 db	25 23 21 21 17 8	115	2.52	0.88	3.40
28/90	RM2 db	INC 42 27 22 20 15 13 9 3	151	3.31	0.94	4.25
28/90	RM2 db	INC 38 29 20 10 15 13 4	138	3.02	0.94	3.96
59/89	M2 db	24 24 27 19 17 11 2	124	2.72	1.12	3.84
59/89	M2 db	13 20 27 23 18 10	113	2.48	1.10	3.58
88/89	LM2 dl	20 22 21 17 16 3	99	2.17	0.85	3.02
28/90	RM2 dl	15 22 21 18 14 10 5	105	2.30	0.72	3.02
28/90	RM2 dl	22 26 22 18 13 9	110	2.41	0.92	3.33
59/89	M2 dl	14 18 16 20 15	83	1.82	0.94	2.76
59/89	M2 dl	16 20 19 15 13 10 2	95	2.08	0.77	2.85
43/87	LM3 mb	12 34 24 23 20 17 5	135	2.96	1.05	4.01
88/89	LM3 mb	# 19 25 23 26 15 12 7	127	2.78	0.83	3.61
11/88	M3 mb	20 36 39 41 17 13 2	168	3.68	1.01	4.69
43/87	LM3 ml	36 28 18 12 10	104	2.28	0.68	2.96
88/89	LM3 ml	#	97	2.13	0.72	2.85
11/88	M3 ml	15 19 35 16 11 9	105	2.30	0.83	3.13
88/89	LM3 db	22 25 21 20 17 11 6	122	2.67	0.88	3.55
11/88	M3 db	22 22 33 32 12 3	124	2.72	1.05	3.77
43/87	LM3 dl	23 26 25 18 13 11	116	2.54	0.59	3.13
88/89	LM3 dl	20 23 19 19 14 9	104	2.28	0.72	3.00
11/88	M3 dl	17 33 15 12 5	82	1.80	0.83	2.63

Abbreviations (Maxillary section): TIS=total number of imbricational striae; TIF=time of formation of imbricational enamel; TAF=time of formation of appositional (i.e., cuspal) enamel; TCF=total crown formation time; INC=incomplete crown; b=buccal; mb=mesiobuccal; d=distal; pal=palatal.

Abbreviations (Mandibular section): OBL=oblique section; #=fractured at enamel surface; A=attrition; ling=lingual.

¹Measured from the cervical margin towards the cusp tip.

Table 5 Cuspal, imbricational and total crown formation times (in years; mean \pm S.D.) as estimated by Methods A and B

	Method A			Method B			% Difference*
	Cuspal enamel	Imbr. enamel	Total	Cuspal enamel	Imbr. enamel	Total	
I ₁	0.61 \pm 0.06	4.45 \pm 0.42	5.06 \pm 0.37	0.51 \pm 0.09	4.14 \pm 0.31	4.66 \pm 0.23	8.58
I ₂	0.48 \pm 0.11	5.34 \pm 0.09	5.82 \pm 0.19	0.52 \pm 0.04	4.78 \pm 0.38	5.33 \pm 0.37	9.19
C	0.62	7.84	8.46	0.55	0.55	7.10	19.2
P ₃	0.75 \pm 0.17	5.31 \pm 0.59	6.06 \pm 0.72	0.73 \pm 0.10	4.29 \pm 0.37	5.01 \pm 0.45	20.9
P ₄	0.57 \pm 0.04	3.60 \pm 0.53	4.16 \pm 0.57	0.70 \pm 0.10	3.20 \pm 0.08	3.90 \pm 0.14	6.67
M ₁	0.73 \pm 0.08	2.20 \pm 0.09	2.95 \pm 0.12	0.65 \pm 0.14	2.20 \pm 0.38	2.85 \pm 0.26	3.51
M ₂	0.80 \pm 0.06	3.13 \pm 0.23	3.93 \pm 0.25	0.92 \pm 0.16	2.80 \pm 0.35	3.69 \pm 0.28	6.50
M ₃	1.18 \pm 0.40	3.00 \pm 0.05	4.15 \pm 0.44	0.90 \pm 0.13	3.14 \pm 0.48	4.04 \pm 0.45	2.72
I ¹	0.55	4.75	5.30	0.47	5.17	5.64	-6.03
I ²	0.51	4.20	4.71	0.55	3.95	4.50	4.67
C				6.68	0.46	7.14	—
P ³	0.48	4.30	4.78	0.49	3.81	4.30	11.2
P ⁴	0.50	3.20	3.70	0.50	3.11	3.61	2.49
M ¹	0.65 \pm 0.02	1.97 \pm 0.66	2.62 \pm 0.62	0.53 \pm 0.08	2.20 \pm 0.23	2.73 \pm 0.31	-4.03
M ²	0.63	2.70	3.33	0.60	2.96	3.56	-6.46
M ³	0.61	2.57	3.18	0.70	2.78	3.48	-8.62

Means and standard deviations are based on values from all of the sections and not only from the four individuals.
*The mean percentage difference is defined as follows: [(Method A - Method B)/(Method B)] \times 100.

compared with the present histological study. The underestimations are considerable for most tooth types: I₁ 2.5 years, I₂ 3.1 years, C 1.6 years, P₃ 1.9 years, P₄ 0.1 years, M₁ 0.8 years, M₂ 1.1 years, and M₃ 0.3 years. In the present study, initial crown mineralization of both I₁ and I₂ was estimated between birth and six months, I₂ taking a longer time to complete its crown than I₁. In the radiographic study, initial mineralization of both incisors was estimated between six and nine months and took 2.4 years to complete their crowns. When compared with the present study, the radiographic studies show a delay in initial mineralization and an early completion of crowns of all teeth. This finding is consistent with the observations made by *Beynon et al.* (1991) on *Gorilla* and *Pongo*.

Crown heights are much greater in incisors (11 to 15 mm) and canines (>17 mm) than in premolars (5.0 to 9.5 mm) and molars (5.5 to 8.4 mm) (see Table 2). The greater difference in the crown formation

times between the radiographic and present study in anterior teeth probably relates directly to their longer crowns. Thinning of cervical enamel of anterior teeth, when compared with the molar teeth with their short crowns and relatively bulbous cervical enamel undoubtedly results in a different radiographic appearance of the cervical enamel. The thin cervical enamel is likely to be "burned out" or missed in radiographic images therefore reducing radiographically determined crown formation times (*Beynon et al.*, 1998).

Aside from this potential problem associated with tooth geometry, assessments of the stage of crown completion via standard radiographic techniques, or histological methods, can vary depending on which region of the tooth is subjected to observation. When enamel formation ends at the same point in time along the buccal and lingual cervices, estimates of crown formation times should be equal regardless of which cusp is examined. However, if there is

Table 6 Ages at crown initiation and crown completion (CC) in years for all teeth from each of the four *P. troglodytes* individuals used in this study

Specimen	Crown initiation	Striae before "A"	Accentuated striae	Total no. of striae	Crown formation	Age at CC/death
43/87:						
I ₁	0.15	146	2.95	232	4.45	4.60
I ₂	0.20	143	2.95	261	5.00	5.20
C	0.40	133	2.95	284	5.45+	5.85+
P ₃	1.10	91	2.95	240	4.60	5.70
P ₄	1.40	81	2.95	216	4.15	5.55
M ₁	-0.05	—	2.95	125	2.45	2.40
M ₂	1.80	60	2.95	190	2.65	5.45
M ₃	3.60	—	—	177	3.40	7.00
88/89:						
I ₁	0.46	73	2.05	244	5.35	5.81
I ₂	0.66	64	2.05	235	5.15	5.81
C	0.57	68	2.05	290	6.36 inc	6.93
P ₃	1.40	30	2.05	185	4.05	5.45
P ₄	1.75	14	2.05	178	3.90	5.65
M ₁	-0.15	94	2.05	139	3.20	3.05
M ₂	1.67	18	2.05	130	2.85	4.52
M ₃	3.62	—	—	151	3.31 inc	6.93
I ¹	0.26	82	2.05	183	4.00	4.26
I ²	1.25	37	2.05	203	4.45	5.70
C	0.42	75	2.05	297	6.51 inc	6.93
P ³	1.21	39	2.05	201	4.40	5.61
P ⁴	1.67	18	2.05	162	3.55	5.22
M ¹	-0.15	94	2.05	105	2.45	2.30
M ²	1.40	30	2.05	146	3.20	4.60
M ³	3.84	—	—	141	3.09 inc	—
28/90:						
I ₁	0.30	—	—	226	4.95	5.25
I ₂	0.70	—	—	224	4.91 inc	5.61 inc
C	0.45	—	—	236	5.16 inc	5.61 inc
P ₃	1.20	—	—	202	4.41 inc	5.61 inc
P ₄	1.95	—	—	164	3.60	5.55
M ₁	-0.15	—	—	121	2.80	2.65
M ₂	1.95	—	—	167	3.66 inc	5.61 inc
89/89:						
I ₁	0.15	16	0.45	213	4.09 inc	4.24
I ₂	0.19	14	0.45	211	4.05 inc	4.24
C	0.38	4	0.45	201	3.86 inc	4.24
P ₃	1.11	—	—	163	3.13 inc	4.24
P ₄	1.40	—	—	148	2.84 inc	4.24
I ¹	0.21	13	0.45	209	4.01 inc	4.24
I ²	0.86	—	—	175	3.34 inc	4.24
C	0.38	4	0.45	201	3.86 inc	4.24
P ³	1.27	—	—	155	2.97 inc	4.24
P ⁴	1.19	—	—	117	2.25 inc	4.24
M ¹	-0.15	24	0.45	112	2.30	4.24

All measurements based on Method B.

"inc" indicates that tooth formation is incomplete; "+" indicates attrition so that estimates of crown formation/age at death are slightly greater than the values reported here.

a disparity between the initial times of cusp mineralization and/or a cervical margin which continues to form for longer on the buccal or lingual aspect, then estimates of

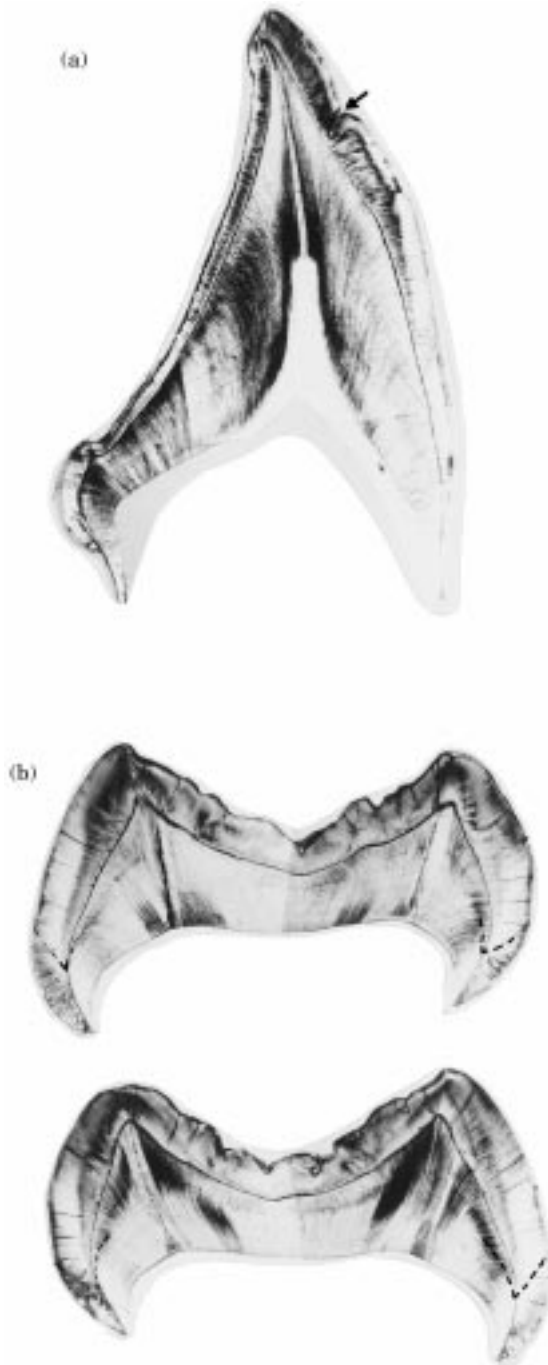


Figure 2. (a) Histological sections of a chimpanzee I_1 (HT 28/90) illustrating the developmental defect resulting in pitting of the incisor enamel (arrow) and is calculated to have occurred at 0.95 years and continued through to 1.65 years of age. (b) Mesial (top) and distal (bottom) sections of the lower right M_2 from HT 28/90 showing another strong accentuated line evident in the dentine and imbricational enamel and is illustrated by the dotted lines.

Table 7 Crown formation data for Animal no. 3 (specimen 28/90) including data on the ages (in years) associated with the occurrences of a hypoplastic episode (measured from line A to line B) and the metabolic disturbance (labeled as "C")

Specimen	Crown initiation	Striae initiated during hypo.	hypoplastic episode	Striae (C . . . cc)	Age at stress (C)	Total striae	Crown formation	Age at CC/death
28/90:								
I ₁	0.30	30 . . . 32	0.95-1.65	106 . . . 58	3.97	226	4.95	5.25
I ₂	0.70	11 . . . 32	0.95-1.65	106 . . . 75	3.97	224	4.91 inc	5.61 inc
C	0.45	23 . . . 32	0.95-1.65	106 . . . 75	3.97	236	5.16 inc	5.61 inc
P ₃	1.20	. . . 21	0.95-1.65	106 . . . 75	3.97	202	4.41 inc	5.61 inc
P ₄	1.95	—	0.95-1.65	92 . . . 72	3.97	164	3.60	5.55
M ₁	-0.15	43 . . . 32	0.95-1.65	46	3.97	121	2.80	2.65
M ₂	1.95	—	0.95-1.65	92 . . . 75	3.97	167	3.66 inc	5.61 inc

Abbreviations: same as for Table 6.

total enamel formation time will differ when made on different aspects of the same tooth. This is especially problematic in analyses of molariform teeth as it seems to often be assumed that crown completion occurs simultaneously across the entire tooth crown. All of this is made worse in radiographic studies where only the mesial or distal cervical margins can be imaged in molar teeth; both of these tooth regions complete enamel formation earlier than either the buccal or lingual aspects. No data are yet available on the disparity in the total times of cusp formation within modern humans, although this is the focus of work in progress (Reid, Schwartz & Dean, in prep.). Data of this type was also lacking for great apes though we present here some observations on differences in cusp formation times within both maxillary and mandibular molars of *Pan*. These data support the reasons outlined above for major discrepancies in estimates of molar crown formation times made using different techniques.

Principle, or functional cusps (mesio- and disto-palatal on maxillary molars and mesio- and disto-buccal on mandibular molars)¹

¹Maxillary molars: mesio-palatal=protocone; mesio-buccal=paracone; disto-palatal=hypocone; and disto-buccal=metacone. Mandibular molars: mesio-lingual=metaconid; mesio-buccal=protoconid; disto-lingual=entoconid; and disto-buccal=hypoconid.

are generally larger, rounder and endowed with thicker enamel compared to non-functional cusps (e.g., Molnar & Gantt, 1977; Molnar & Ward, 1977; Kraus *et al.*, 1969; Re *et al.*, 1983; Khera *et al.*, 1990). Overall, the characteristically different morphology of functional and non-functional cusps affects the potential for abrasion and fracture under masticatory loads. Developmental differences such as the sequence of cusp initiation and completion are likely to relate to these morphological differences in some way. Data on cusp formation times in the molars of chimpanzees seem to correspond well with expectations based on differences in morphology and function of cusps within teeth and among molars. For maxillary first molars, protocones take longer to complete enamel formation to the cervix than any other cusp in that same tooth (Table 8; Figure 4). The same holds true for functional cusps on mandibular molars: protoconids/hypoconids take longer to form, on average, than corresponding metaconids/entoconids (Table 8). As functional cusps tend to possess thicker enamel than non-functional cusps, these results are not surprising: larger cusps endowed with more enamel *should* take longer to form than smaller cusps with relatively less enamel if the average daily rate of enamel formation

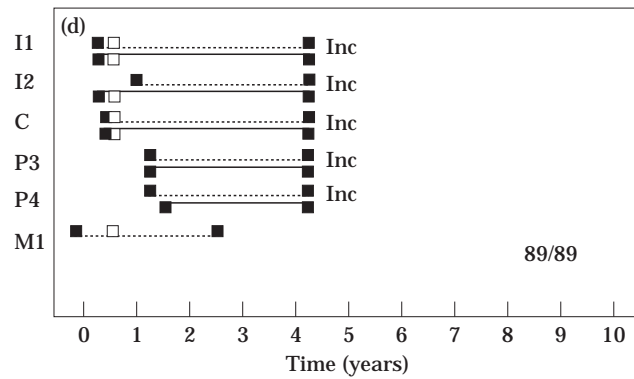
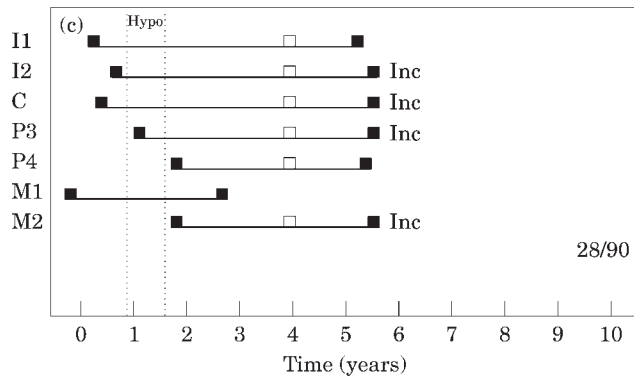
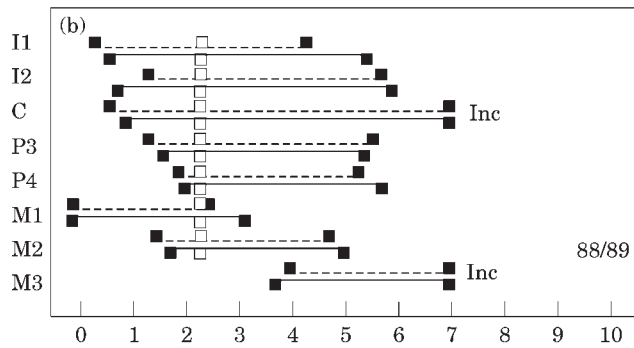
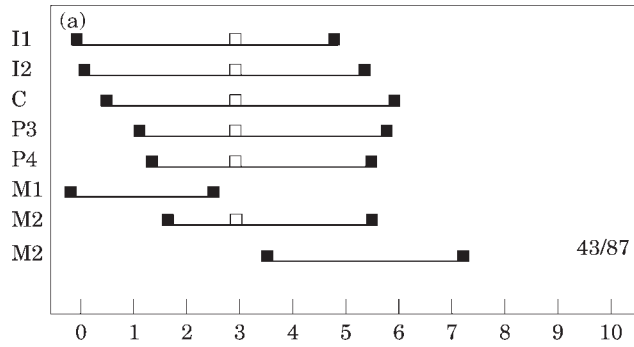


Table 8 Formation times (mean \pm S.D.) for individual cusps of *Pan* mandibular and maxillary molars

	Cusp	n	CF* time \pm S.D.
Maxillary molars:			
M ¹	Paracone	2	2:35
M ¹	Protocone	2	2:53
M ¹	Metacone	2	2:14
M ¹	Hypocone	2	2:12
M ²	Paracone	1	3:20
M ²	Protocone	1	3:55
M ³	Metacone	1	2:98
M ³	Hypocone	1	2:75
Mandibular molars:			
M ₁	Protoconid	3	2.69 \pm 0.41
M ₁	Metaconid	2	2.01 \pm 0.26
M ₁	Hypoconid	3	2.74 \pm 0.42
M ₁	Entoconid	3	1.99 \pm 0.15
M ₂	Protoconid	6	3.27 \pm 0.33
M ₂	Metaconid	5	2.72 \pm 0.09
M ₂	Hypoconid	5	3.61 \pm 0.46
M ₂	Entoconid	5	2.85 \pm 0.39
M ₃	Protoconid	3	3.74 \pm 0.32
M ₃	Metaconid	3	2.73 \pm 0.13
M ₃	Hypoconid	2	3.38 \pm 0.25
M ₃	Entoconid	3	2.68 \pm 0.35

*CF=cusp formation.

and the number of imbricational striae is identical in all of them. These results are tantalizing in that they suggest a direct link between microstructural features of enamel and occlusal morphology and tooth function. It may be that the sequence of cusp initiation and the speed at which a certain thickness of enamel is formed in each cusp dictate the sequence of cusp coalescence, the fissure pattern and the ultimate cusp area in all molar teeth (Wood & Abbott, 1983; Wood *et al.*, 1983; Wood & Engleman, 1988). Future studies on comparative tooth histology will determine whether this holds true for chimpanzees and other hominoids.

Estimates of the times and rates of root formation are not possible in the sample of chimpanzee teeth studied here. Data are available on root lengths (see Table 2) and these provide a useful, albeit preliminary, estimate of how much tooth root is formed between the time of crown completion and the age at gingival emergence. Rates of root formation differ depending on which part of the root is examined in apes (Dean & Wood, 1981). Root length cannot then be used as a direct measure of rate of growth. A comparison between the ages at the end of crown formation (from our histological analysis) and at gingival emergence (from Kuykendall *et al.*, 1992) does provide a broad measure of the time the first part of the root took to form (see Figure 5). For most *Pan* teeth, about a year elapses between crown completion and gingival emergence. Previous radiographic studies (Anemone *et al.*, 1991, 1996; Kuykendall *et al.*, 1992; Kuykendall & Conroy, 1996) document as much as three years for this period of root formation. It is the earlier completion of crown formation reported in these radiographic studies that underlies the longer estimates for the period of root formation in the time up to gingival emergence. The implication from this study is that chimpanzee teeth have a greatly reduced time for root growth before emergence occurs. This is in direct agreement with the findings of Dean & Wood (1981) based on observations of the incremental lines in the roots of great ape teeth. Future investigations of tooth root growth will focus specifically on how rates of formation regulate the time at which teeth are able to emerge into the mouth. It is clear that the major differences that exist between modern

Figure 3. Bar charts of dental development for each *Pan troglodytes* specimen included in this study. Closed squares indicate the onset of mineralization and crown completion, respectively, for each tooth. Solid horizontal lines represent mandibular teeth and dashed horizontal lines represent maxillary teeth. Open squares represent the appearance of accentuated striae (see Table 6) and the dotted lines for specimen 28/90 (animal no. 3) represent the duration of a hypoplastic episode occurring from 0.95 to 1.65 years of age (see Table 7).

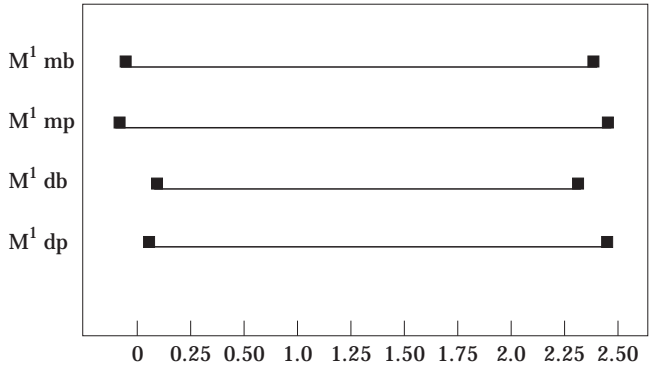


Figure 4. Bar chart of individual cusp initiation and formation times. mb=mesiobuccal; mp=mesiopalatal; db=distobuccal; dp=distopalatal.

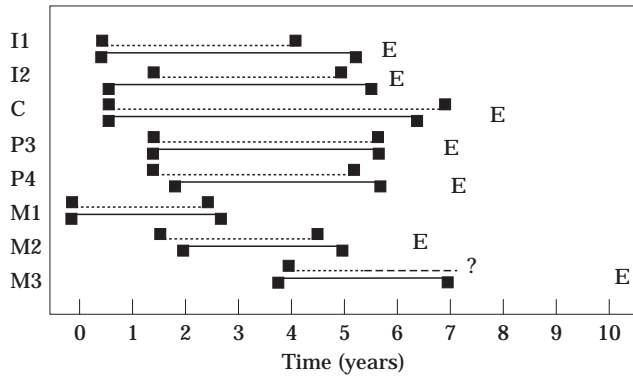


Figure 5. Bar chart of dental development in *Pan troglodytes* with emergence times for the maxillary and mandibular teeth. Times for onset of mineralization and crown completion are based on mean values for all of the specimens included in this study. Dashed lines represent maxillary teeth and solid lines represent mandibular teeth. Median gingival emergence ages are compiled from: Krogman, 1930; Schultz, 1940; Clements & Zuckerman, 1953; Nissen & Risen, 1945, 1964; Anemone *et al.*, 1991; Kraemer *et al.*, 1982; Conroy & Mahoney, 1991; Kuykendall *et al.*, 1992. The dashed line and question mark for M³ indicates that no histological data are available for the time at crown completion for this tooth. E=emergence through the gingiva.

humans and *Pan* lie in the first part of the root formation rather than in the total period of crown formation.

Previous studies of tooth crown development in primates have commented on the degree of sequential overlap in the formation of molar crowns. Dean & Wood (1981) did not record overlap between either M₁ and M₂ or M₂ and M₃ in a mixed sample of great apes. Subsequently, Swindler (1985) published data for *Macaca nemestrina* where there was also no overlap between successive molars. This has now been confirmed for

certain other catarrhine species including *Papio cynocephalus* (Swindler & Meekins, 1991) and *P. hamadryas anubis* (Reid & Dirks, 1997). Studies on *Theropithecus* (Swindler & Beynon, 1993) and *Pan* (Anemone *et al.*, 1991, 1996; Kuykendall *et al.*, 1992; Kuykendall & Conroy, 1996), however, have all noted considerable sequential molar overlap between M₁/M₂ and M₂/M₃ formation and this is confirmed in the present study for *Pan*. Some data for *Pongo* (Winkler, 1995) and *H. sapiens* (Fanning & Moorrees, 1969; Reid *et al.*, this

volume) do tend to suggest more variation in the degree of sequential molar overlap than is often appreciated. Future research may tie each of these observations in with the degree of facial prognathism, with molar tooth size, and with the space available within the jaws at molar crown initiation. Overlaps in molar crown formation also have the potential to increase the time between crown completion and gingival emergence by initiating enamel formation earlier. As such, it may be involved in determining how fast the first part of root formation is required to grow in order to achieve gingival emergence "on time" in the context of the general dental development schedule.

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