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Correlative growth of upper and lower tooth germs in the human foetus

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Growth of corresponding upper and lower teeth was compared, using tooth germs dissected from human foetuses. Length, height and calcified height were measured on the deciduous teeth and first permanent molars. During rapid growth, corresponding upper and lower measurements are highly correlated, with a mean r of 0.976. All the measurements are correlated with crown-rump length of the foetus (mean r, 0.940); when this effect was removed by partial correlation the upper-lower correlations remained highly significant (mean r, 0.814). Later in development growth is inhibited by the spread of calcification and the correlation is reduced. This is especially so on the first deciduous molars, where the buccal cusps unite first on m^1 and the mesial cusps on m_1. Later growth in length of m_1 is correlated with that of the upper canine. The times of starting growth and calcification, calculated from the regression equations against crown-rump length, are also highly correlated ($r = 0.96$). A common morphogenetic basis for the opposing dentitions is indicated, predetermining their eventual occlusal relationship.

1. Introduction

In a study of correlation in the mammalian dentition, Björn Kurtén (1953) showed that the 'rule of neighbourhood' (Lewentz & Whiteley 1902) applied, not only to teeth in the same jaw but to their opponents. Opposing teeth, with different patterns, were frequently more highly correlated in size than neighbouring teeth with similar patterns in the same jaw. Subsequent studies of dental correlations have confirmed this result: Gabriel (1955) for man, Van Valen (1962) for the rodent *Peromyscus*, Suarez & Bernor (1972) for the gorilla, Lavelle (1978) for man and the chimpanzee, and Gingerich & Winkler (1979) for the fox. In a factor analysis of the human dentition Lombardi (1978) found that each factor applied to corresponding regions of the upper and lower dentitions together; thus factor I affected mainly the upper and lower molars and factor II the upper and lower incisors. A common genetic influence on opposing teeth seems to be implied.

This relationship between opposing teeth extends to their developmental stages. In the bat *Hipposideros* coordinated growth of upper and lower molars results in their post-eruptive occlusal fit (Marshall & Butler 1966). In *Alouatta* and *Macaca* growth in height of the upper and lower canines is highly correlated, except that in the male *Macaca* the upper canine continues growing for a longer time than the lower (Zingeser 1968). Correlated growth of corresponding upper and lower deciduous teeth occurs in man (Kraus & Jordan 1965, Butler 1971b).

The purpose of the present paper is to examine foetal growth of the human dentition in more detail, with special reference to upper-lower correlations.

2. Material and methods

I have used the B. S. Kraus collection of tooth germs, dissected from foetuses (Kraus 1959, 1963, Kraus & Jordan 1965). During a visit to Pittsburgh in 1966 I made camera lucida drawings of numerous specimens from the collection, on the basis of which several papers on dental growth have been published (Butler 1967a, 1967b, 1967c, 1968, 1971a). These drawings are used again here to investigate a further aspect of growth. The tooth germs had been dissected out and stained with alizarin red S, by the method described by Kraus & Jordan (1965). The superficial layers of the enamel organ had been removed, so what was left was a papilla with the superincumbent inner dental epithelium. The foetuses had been preserved in 10% neutral formalin, and the tooth germs were kept in 50% glycerin. Camera lucida drawings were made of each tooth germ, in crown, buccal and mesial views, and measurements were made on the drawings. Repetition of the drawings of a number of specimens showed that the measurement error did not exceed ±4%. Variability of the material, as indicated by deviation from regression, was much greater than this, reaching as much as ±15% in overall diameters and ±20% in cuspal heights. Part of this variability was probably due to shrinkage, but obviously shrunken specimens were excluded. The collection came from a wide area of the United States, and was racially and sexually heterogeneous, but white males predominated. Foetuses with signs of pathological condition were excluded.

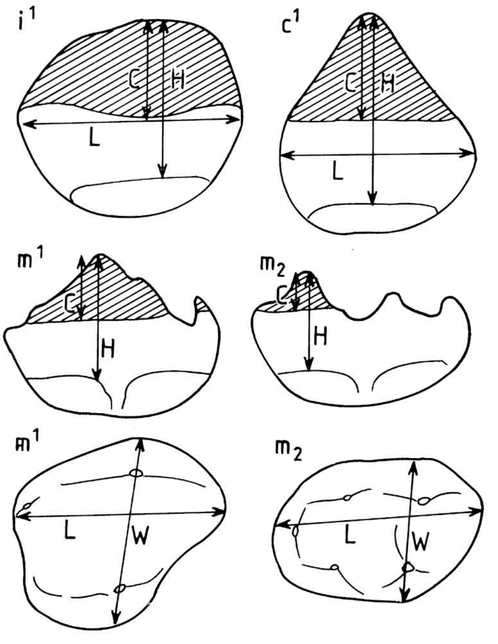

Fig. 1. To illustrate system of measurements. H, height; C, calcified height; L, mesiodistal length; W, buccolingual width.

The youngest specimens are from foetuses with crown-rump length (CR) of 79–95 mm and an estimated age of 12 weeks. They show early stages in the development of the primary cusp (paracone or protoconid), which forms a blunt cone, later to become more acute as its ameloblasts and odontoblasts differentiate (Turner 1963). On the incisors the primary cusp becomes extended by mesial and distal ridges to form the incisal edge. Growth continues in the zone around the primary cusp (zona cingularis), adding to the height of the tooth, and also to its width and length. Secondary molar cusps (protocone and metacone on upper teeth, metaconid and the talonid cusps on lower teeth) arise from the zona cingularis (Butler 1956). Calcification appears at the tip of the primary cusp and spreads downwards, subsequently appearing on the secondary cusps. Meanwhile growth continues in the uncalcified basal zone, so that the gain in height keeps pace with the downward spread of calcification (Butler 1968). When calcification reaches the level of the valleys between the cusps, growth

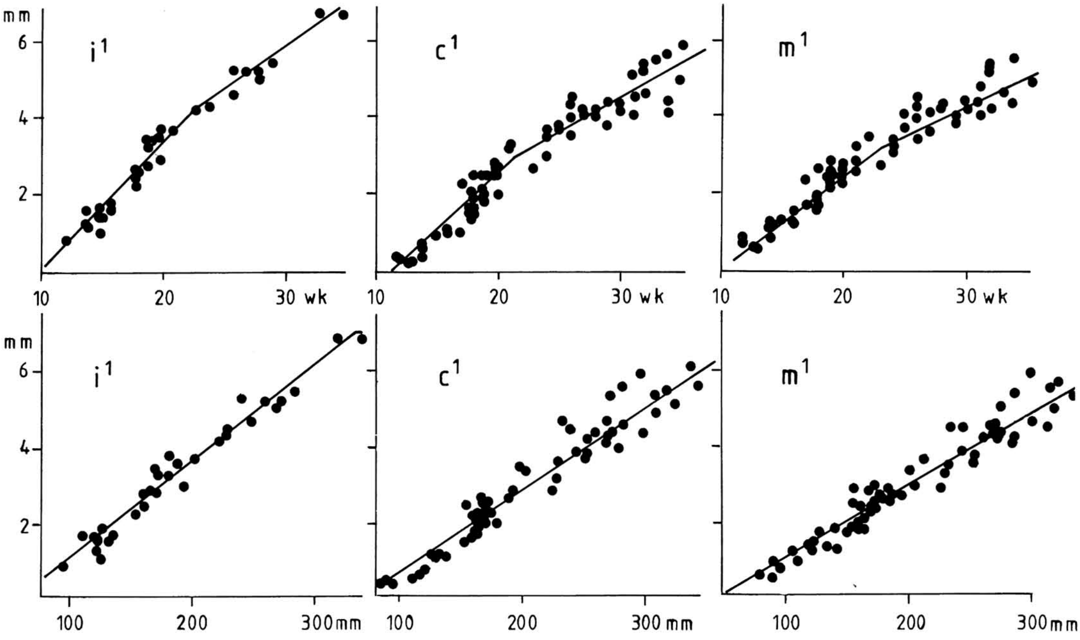

Fig. 2. Height of i^1, c^1, and m^1 plotted (above) against age in weeks, and (below) against crown-rump length in mm. Growth of teeth slows after 22 weeks, but relative to growth of CR it remains constant.

in length or width is reduced, as the cusps can no longer move apart, and growth is confined to the margins of the crown.

Height and mesiodistal length were measured on each tooth, and also buccolingual width on the molars. Height was measured from the tip of the primary cusp to the base of the enamel organ. As it increases throughout development, height was used as a measure of the growth of the tooth as a whole. However, it is subject to two periods of acceleration, at first due to remodelling of the cusp, and later due to apposition of enamel at its tip. Increase of height therefore probably over-estimates the true growth. Width was measured across the mesial cusps, and therefore not necessarily perpendicularly to length; as the molars increase in width more rapidly distally than mesially, the angle between length and width tends to become larger with growth. Calcified height was measured on the primary cusp in buccal view (Fig. 1).

Correlations and regressions were computed as follows: (a) measurements on lower teeth against equivalent measurements on corresponding upper teeth; (b) width and length against height in each tooth; (c) all measurements against crown-rump length of the foetus (CR). When plotted against foetal age, growth of the teeth is seen to decelerate, and the regression is curvilinear. However, when plotted against CR the relationship approximates to a straight line (Fig. 2). This implies that tooth growth keeps in constant proportion to growth of the foetus. CR was therefore used in preference to age as a measure of foetal development. It was found that all tooth measurements were significantly correlated with CR, and partial correlations, with CR fixed, were calculated to eliminate this effect of general growth.

Upper teeth will be referred to as i^1, i^2, c^1, m^1, m^2, M^1; lower teeth as i_1, i_2, etc. i1, i2, etc. refer to upper and lower teeth together.

3. Results

3.1. Height

Lower/upper relations (Table 1)

Correlations between opposing teeth are in the range 0.96 to 0.98. Partial correlations after removal of the effect of CR are lower (0.61–0.81), but still highly significant ($P < 0.001$). i_1, c_1, and m_2 grow somewhat more slowly than the corresponding upper teeth ($P < 0.05$), but the slope of the regression lines for the other opponents does not differ significantly from 1.0. The regression lines pass near the origin ($P < 0.05$), except in the case of m2, where the intercept on the y axis is significantly positive, i.e. m_2 begins to grow before m^2.

Relations with CR (Table 2)

The heights of all the teeth are highly correlated with crown-rump length (r, 0.90 to 0.98). Growth relative to that of the foetus declines from the incisors to the permanent molars; per 100 mm increase in CR, increase of tooth height ranges from 2.54 mm in i^1 to 1.75 mm in M^1. Growth rates of corresponding upper and lower teeth are not significantly different, except that i_1 grows more slowly than i^1 ($P < 0.02$).

Estimated initiation of growth (Table 2)

From the regression equations may be calculated the CR at which tooth height = 0, i.e. the CR at which the tooth begins to grow. No significant difference between upper and lower teeth was found. In both jaws m1 is the first, followed by i1. Growth in height may be considered to begin with the development of the bell stage from the cap stage, and the results agree reasonably well with the observations of Radlanski (1989). However, he found that the canines reached the bell stage relatively earlier, with m1 instead of with m2. Garn & Burdi (1971), who studied 15–36 mm embryos, with teeth in the

Table 1. Relation (regression, lower H / upper H) between heights (H) of upper and lower teeth.

Tooth	N	Slope ± SE	Intercept (Upper = 0)	r	Partial CR
i 1	26	0.826 ± 0.030	–0.078 ± 0.191	0.984	0.814
i 2	22	0.991 ± 0.048	–0.031 ± 0.150	0.977	0.698
c	23	0.863 ± 0.050	+0.191 ± 0.154	0.965	0.799
m 1	54	0.946 ± 0.035	+0.126 ± 0.119	0.966	0.613
m 2	46	0.928 ± 0.031	+0.219 ± 0.086[a]	0.976	0.773
M1	26	1.025 ± 0.061	–0.038 ± 0.150	0.958	0.763

[a] significant at $P < 0.02$

Table 2. Relation (regression, H/CR) between tooth height (H) and crown-rump length (CR).

Tooth	N	Slope ± SE	Initiation, H=0; CR, mean and 95% range, mm	Earliest bell-stage (Radlanski)	r
i^1	31	0.0254 ± 0.0016	45.0 – 59.3 – 70.9	64	0.964
i_1	28	0.0219 ± 0.0014	46.3 – 64.2 – 78.1	60	0.953
i^2	23	0.0226 ± 0.0015	53.6 – 72.3 – 86.3	>64	0.955
i_2	22	0.0231 ± 0.0013	57.1 – 73.4 – 86.2	64	0.968
c^1	48	0.0206 ± 0.0014	48.3 – 69.2 – 84.6	53	0.906
c_1	28	0.0203 ± 0.0011	52.8 – 71.4 – 86.0	53	0.960
m^1	56	0.0193 ± 0.0008	38.8 – 51.9 – 63.0	53	0.955
m_1	55	0.0176 ± 0.0009	46.0 – 59.2 – 70.8	56	0.953
m^2	47	0.0185 ± 0.0009	64.6 – 77.1 – 87.4	>64	0.953
m_2	47	0.0176 ± 0.0010	53.9 – 70.4 – 83.7	64	0.941
M^1	30	0.0175 ± 0.0014	112.5 – 134.8 – 150.9		0.925
M_1	29	0.0176 ± 0.0017	109.2 – 138.5 – 158.3		0.897

cap stage or earlier, found variation in the sequence of development of the deciduous teeth, including opposing teeth.

3.2. Calcified height

Lower/upper relations (Table 3)

Correlations between upper and lower deciduous teeth are 0.97–0.99; partial correlations with CR fixed range from 0.76 to 0.92 ($P < 0.001$). Only 11 pairs of M1 were available; these gave a correlation of 0.93, and a partial correlation of 0.54 ($P < 0.1$). All the regression lines pass close to the origin ($P < 0.05$), and their slopes are less than 1.0; thus the calcified heights of opposing teeth keep in proportion, that of the upper tooth being the greater.

Initiation of calcification

Passage of the regression lines close to the origin implies that upper and lower teeth begin to calcify at nearly the same time. However, differences between opposing teeth at early stages of calcification were commonly observed. In 61 cases in which the calcified height of the less calcified tooth was 1 mm or less, the upper tooth was the more advanced in 39 (64%), the lower tooth in 18 (29%). Kraus (1959) gives the order in which teeth begin to calcify as i1, m1, i2, c, m2, M1. My observations agree with this, except that the canine and m2 may be interchangeable: at early stages of calcification m^2 was in advance of c^1 in 6/16 cases, and m_2 was in advance of c_1 in 5/13 cases. Nomata (1964) reported earlier calcification of the canine, between i1 and m1.

Table 3. Relation (regression, lower C/ upper C) between calcified heights of upper and lower teeth.

Tooth	*N*	Slope ±*SE*	Intercept (upper = 0)	*r*	Partial CR	Calculated CR at initiation Upper	Lower
i 1	28	0.831 ± 0.024	–0.076 ± 0.075	0.989	0.837	126.7	128.2
i 2	21	0.876 ± 0.036	+0.118 ± 0.095	0.984	0.851	134.5	133.8
c	22	0.847 ± 0.036	–0.020 ± 0.079	0.982	0.916	143.4	151.0
m 1	42	0.934 ± 0.027	–0.108 ± 0.068	0.982	0.854	116.1	119.6
m 2	40	0.876 ± 0.032	–0.011 ± 0.065	0.975	0.763	146.5	148.7
M 1	11	0.779 ± 0.105	+0.187 ± 0.124	0.928	0.541[a]	267.3	263.8

Table 4. Relation (regression, L/H) of mesiodistal length to height. The late phase is that of slow growth, except in the case of the canines, where it covers the period from 20–34 weeks.

Tooth	*N*	Early phase Slope ± *SE*	*r*	*N*	Late phase Slope ± *SE*	*r*
i^1	20	1.43 ± 0.06	0.983	15	0.64 ± 0.07	0.899
i_1	18	1.08 ± 0.07	0.967	14	0.40 ± 0.05	0.908
i^2	14	1.26 ± 0.11	0.946	15	0.59 ± 0.09	0.920
i_2	12	1,08 ± 0.08	0.972	16	0.38 ± 0.07	0.836
c^1	33	0.84 ± 0.04[a]	0.968	32	0.94 ± 0.07	0.929
c1	14	0.80 ± 0.07	0.962	13	1.03 ± 0.10	0.950
m^1	36	1.67 ± 0.08	0.963	40	0.54 ± 0.07	0.782
m_1	38	1.58 ± 0.05[b]	0.979	28	0.48 ± 0.12	0.623
m^2	38	1.77 ± 0.07	0.977	12	0.74 ± 0.32	0.588
m_2	40	2.13 ± 0.10	0.958	21	0.53 ± 0.18	0.553
M^1	37	1.69 ± 0.07	0.974			
M_1	34	1.81 ± 0.09	0.966			

Intercept significantly different from 0: [a] $P < 0.001$; [b] $P < 0.01$.

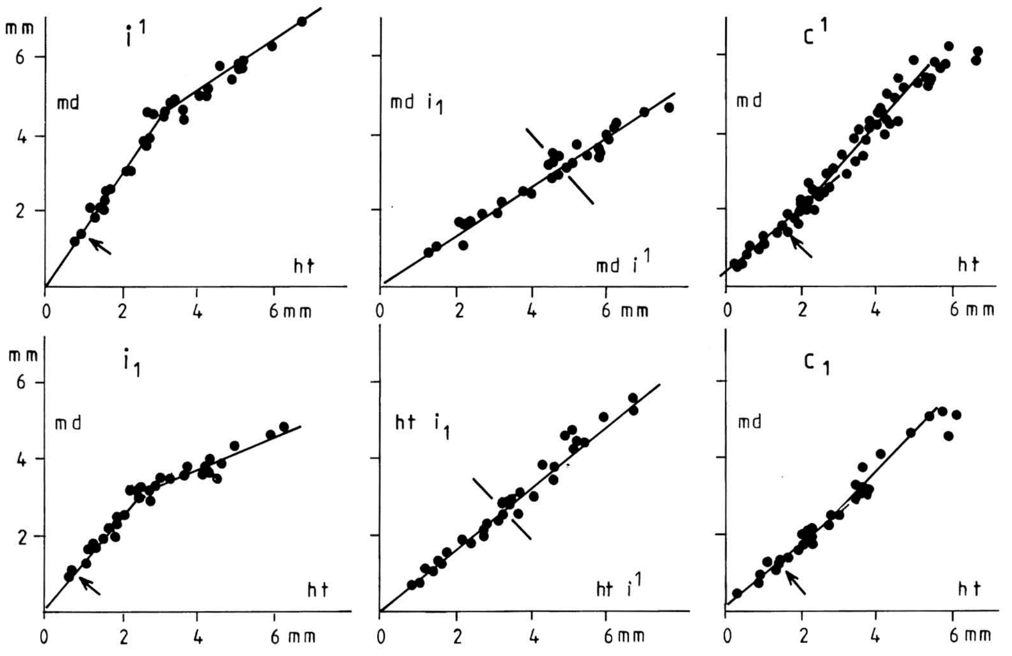

Fig. 3. Mesiodistal growth of incisors and canine. Left, mesiodistal plotted against height, i^1 and i_1. Note change from rapid to slow growth. The arrows indicate appearance of calcification. Centre, above, mesiodistal i_1 against mesiodistal i^1. Transverse line shows position of change of growth rate. Absence of break shows that the change occurs simultaneously in upper and lower teeth. Centre, below, height i_1 against height i^1, showing proportionality. Right, mesiodistal plotted against height, c^1 and c_1. Mesiodistal growth accelerates in both teeth. Arrows indicate appearance of calcification.

3.3. Length (mesiodistal) (Figs. 3 and 4).

Relation of length to height (Table 4)

In the incisors an early phase of rapid growth in length is followed by a phase of slow growth. The change takes place in all incisors at a CR of about 185 mm (20 weeks). It may be ascribed to the spread of calcification to involve the whole of the incisal edge; the subsequent slower growth is probably due to enamel apposition. During the early phase the upper incisors grow faster in length than in height; in the lower incisors height and length increase at about the same rate.

The canines grow in length continuously until the 34th week of pregnancy. There is a slight increase in growth rate after 20 weeks: before this, height grows faster than length; after 20 weeks, length and height grow at the same rate.

In the deciduous molars growth in length is greatly reduced when the buccal cusps are united by calcification. The metacone joins the paracone on m1 at about CR 200 mm, and the hypoconid joins the protoconid at about CR 240 mm; thus mesiodistal growth is reduced earlier on m^1 than on m_1. On m^2 and m_2 the buccal cusps unite at more nearly the same time (CR 240–260 mm). On M1 the cusps do not join till after birth. Prior to cuspal union, the molars grow much faster in length than in height (ratio, 1.6 to 2.1); afterwards more slowly (0.4–0.7).

At the 95% level of probability, the regression lines pass through the origin, except in the cases of c^1 and m_1. In these the intercept is positive ($P < 0.01$), implying that growth in length begins earlier than growth in height.

Lower/upper relations (Table 5)

During rapid growth, the lengths of corresponding lower and upper teeth are correlated at r 0.96–0.98. After removal of the CR effect the correlations

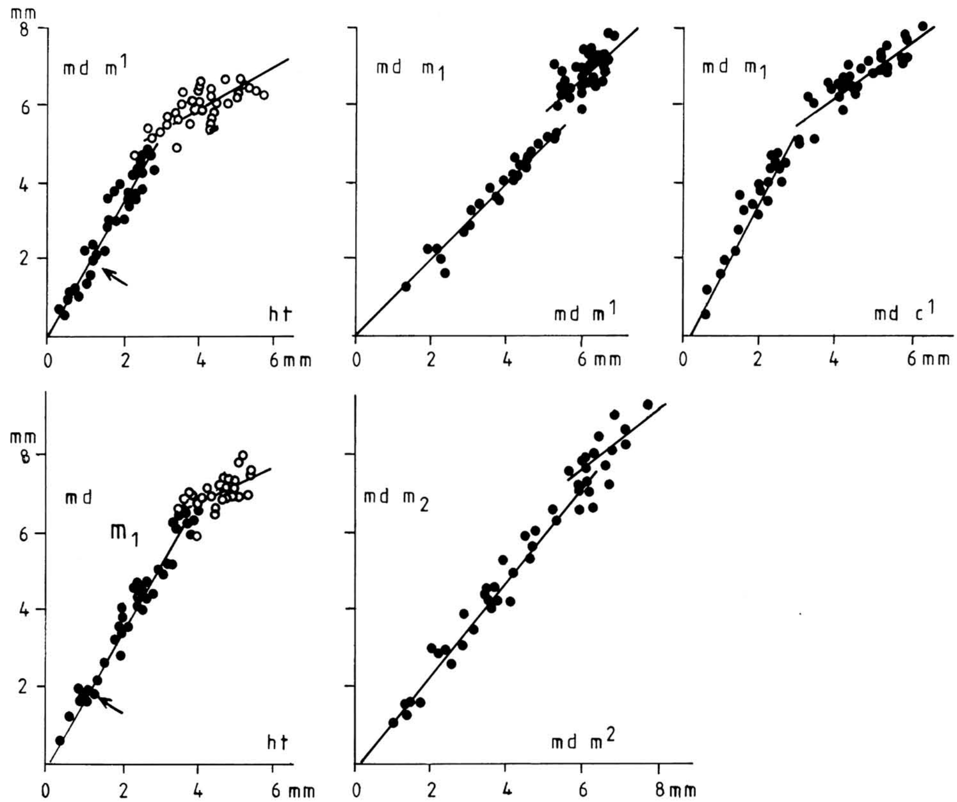

Fig. 4. Left, mesiodistal plotted against height, m^1 and m_1. Growth slows with union of the buccal cusps (open circles). Arrows indicate appearance of calcification. Centre, above, discontinuity in relation of mesiodistal of m_1 to m^1, due to growth slowing earlier in m^1 than in m_1. Centre, below, there is less discrepancy between m_2 and m^2. Right, slow mesiodistal growth of m_1 is correlated with the upper canine.

remain significant (0.70–0.92). In the slow phase correlation is reduced, and much of it reflects variation in body size (partial, 0.35–0.69). The greatest reduction is in m1, where rapid growth terminates earlier in m^1 than in m_1. In the late phase m_1 is more closely correlated with c^1 than with m^1 (0.87; partial 0.69). This is interesting in view of the occlusal ('honing') relation between the anterior premolar and the upper canine in the permanent dentition of catarrhine primates.

Regression lines representing early growth pass through the origin (at the 95% level of significance), except in the case of M1, where the lower tooth begins to grow in length earlier.

3.4. Width (buccolingual) (Fig. 5)

Growth in width was investigated only in the molars (Table 6). As in growth in length, there is an early phase of rapid growth followed by slower growth. During the early phase teeth grow faster in width than in height, and upper teeth grow faster than lower teeth. The regression lines of width/height pass close to the origin, except for M_1, in which width appears to start growing before height. Regression of lower/upper width indicates that growth of m^2 begins before that of m_2. Correlations between upper and lower teeth are high (0.97–0.99; partial, 0.82–0.88).

The mesial cusps (protoconid, metaconid) of m_1 join earlier (CR 235– 266 mm) than the mesial cusps (protocone, paracone) of m^1 (CR 268–285 mm); those of m^2 and m_2 join at about the same time (CR 268–285 mm). There is less discrepancy between m^1 and m_1 in the time of slowing of growth in width than is the case with growth in length, and correlation in the late phase is less reduced in width than in length. Moreover, both in m1 and in m2, this correlation is less affected by body size, the partial coefficients remaining highly significant (m1, 0.70; m2, 0.76). This may mean that growth at the buccal and lingual margins of the teeth persists longer than growth at the mesial and distal margins.

4. Discussion

The growth of corresponding upper and lower teeth is highly correlated. This is true for growth in height, in calcified height, and, prior to the retardation associated with the spread of calcification, in width and length. Except for calcified height in M 1, where the sample was small, correlation coefficients ranged from 0.96 to 0.99, with a mean of 0.976. High correlations would be expected between structures that are growing at the same time, and all the measurements were correlated with body size, as measured by crown-rump length; *r* ranged from 0.89 to 0.97, with a mean of 0.940. Partial correlation between upper and lower teeth, removing the effect of body size, averaged 0.814; except for calcified height in M1, they were significant in all cases at the 0.001 level. They compare with those found by Kurtén (1953) for the lengths of upper and lower molars in the hippopotamus (0.72–0.87), widths of teeth in the orang (0.72–0.85) and lengths of molars of the tapir (0.80–0.94); Lavelle (1978) found upper/lower correlations of 0.62–0.74 in the human permanent dentition. The correlative variation of opposing teeth in the functional dentition extends back to their development.

This development is a regular process, such that the relationships of length, width and height

Table 5. Relation (regression, lower L/upper L) of mesiodistal lengths of upper and lower teeth. Late phase as in Table 4.

Tooth	Early phase				Late phase			
	N	Slope ± *SE*	*r*	Partial	*N*	Slope ± *SE*	*r*	Partial
i1	17	0.66 ± 0.04	0.975	0.868	17	0.49 ± 0.09	0.821	0.568
i2	12	0.85 ± 0.08	0.960	0.779	14	0.63 ± 0.08	0.912	0.686
c	15	0.74 ± 0.08	0.970	0.822	18	0.85 ± 0.06	0.966	0.889
m1	27	1.01 ± 0.04	0.984	0.924	34	0.54 ± 0.16	0.511	0.354[b]
m2	32	1.22 ± 0.04	0.985	0.870	15	0.82 ± 0.21	0.728	0.427[b]
M1	28	1.11 ± 0.07[a]	0.957	0.702				

[a] Intercept significantly different from 0, $P < 0.05$; [b] not significant.

Table 6. Relation between buccolingual width and height (regression, W/H), and between upper and lower teeth (regression, lower W /upper W).

	Early phase				Late phase			
	N	Slope ± *SE*	*r*	Partial CR	*N*	Slope ± *SE*	*r*	Partial CR
W / H								
m^1	45	1.66 ± 0.05	0.981		17	0.69 ± 0.13	0.808	
m_1	39	1.21 ± 0.04	0.983		30	0.67 ± 0.10	0.774	
m^2	40	1.99 ± 0.10	0.953		17	1.23 ± 0.12	0.936	
m_2	40	1.57 ± 0.08	0.955		23	0.61 ± 0.18	0.616	
M^1	36	1.90 ± 0.08	0.969					
M_1	37	1.47 ± 0.07	0.966					
Lower W / upper W								
m1	32	0.72 ± 0.03	0.975	0.871	26	0.70 ± 0.09	0.832	0.702
m2	42	0.87 ± 0.02	0.986	0.878	17	0.61 ± 0.11	0.878	0.759
M1	27	0.84 ± 0.04	0.973	0.819				

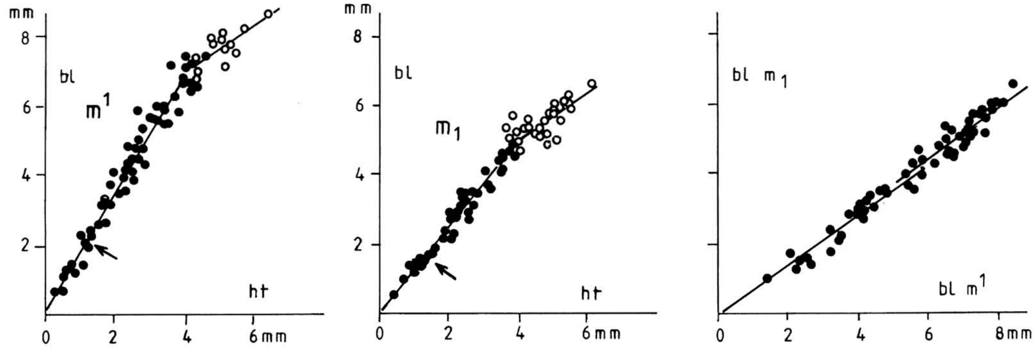

Fig. 5. Left, buccolingual width plotted against height, m^1 and m_1. Symbols as in Fig. 4. Right, buccolingual m_1 plotted against buccolingual m^1. Union of cusps has less effect than in the case of mesiodistal length.

in each tooth, and the relationships of these to crown-rump length, can be represented by straight-line regressions. From the regression equations can be estimated the crown-rump lengths at which processes of growth or calcification of the teeth begin (Table 7). Correlation between opposing teeth in this respect is again close (0.96 for 21 comparisons). The similarity of timing is also shown by the finding that, of the 21 regression lines (lower tooth/upper tooth), 18 pass through the origin with a probability of 95%. The proportions between opposing teeth therefore remain nearly constant during their growth.

The relationships are disturbed when growth in length and width becomes limited by the spread of calcification. The time at which this happens depends upon the shape of the tooth surface: in incisors when calcification involves the whole of the incisal edge, in molars when cusps are united by calcified bridges. In the incisors mesiodistal growth is reduced nearly coincidentally in upper and lower teeth. The greatest divergence is between the first deciduous molars, the buccal cusps uniting first in m^1 and the mesial cusps uniting first in m_1. The relative proportions of m^1 to m_1 therefore change during late stages of development, the length of m_1 then being more closely correlated with that of the upper canine.

Coordinated growth of opposing teeth may be regarded as a preparation for their ultimate occlusion. Drawings of developing teeth in occlusal view can be superimposed so as to fit at all stages of development; paracones and metacones alternate with protoconids and hypoconids, and protocones and hypocones alternate with metaconids and entoconids (Fig. 6). Similarly in a bat (*Hipposideros*) Marshall & Butler (1966) fitted together wax models of developing upper and lower molars. The occlusal relationships between upper and lower dentitions are potentially present at an early stage of development, when not only

Table 7. Estimated crown-rump length (mm) at initiation of growth.

	Upper				Lower			
	height	calc^n	length	width	height	calc^n	length	width
i1		127	66		64	128	58	
c	69	143	69		71	151	68	
m1	56	116	54	53	59	120	67	56
m2	77	146	77	68	73	149	88	80
M1	135	267	141	124	139	264	126	116

$r_{upper.lower} = 0.962$

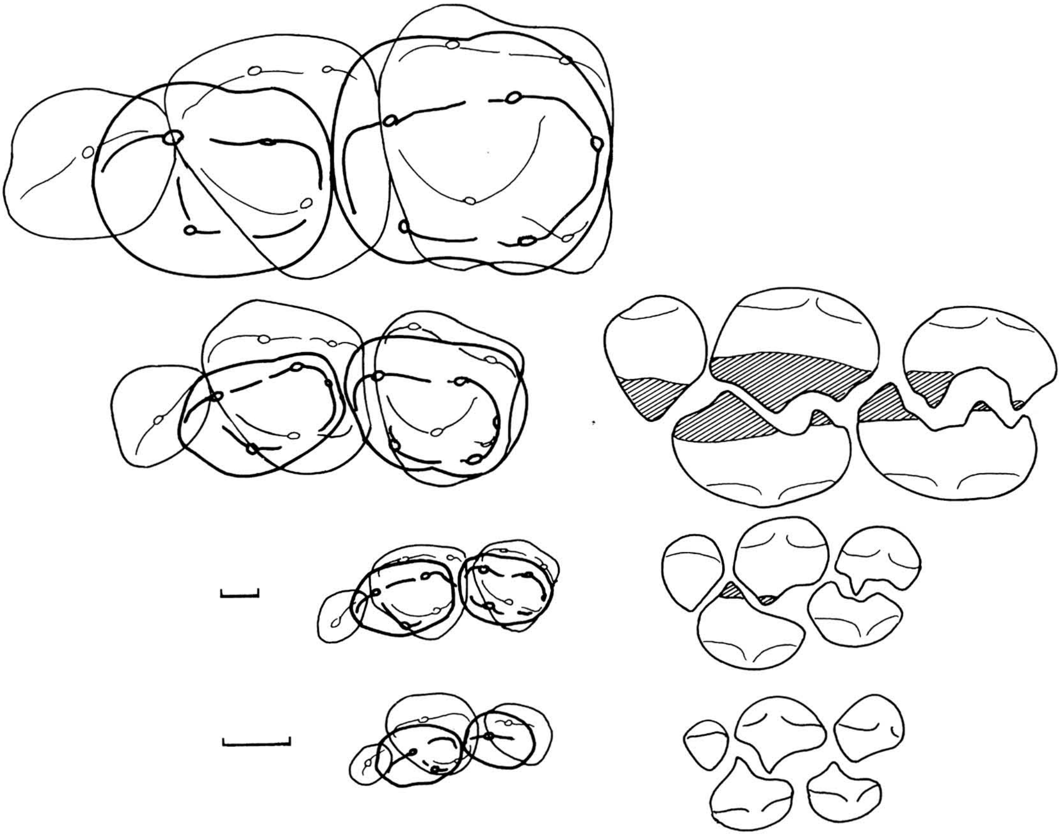

Fig. 6. Superimposed camera lucida drawings of c^1 to m_2, in occlusal and buccal views, to show constancy of the relations between upper and lower cusps. Ages 14, 16, 24 and 36 weeks. The bars represent 1 mm (earliest stage at higher magnification).

the patterns of the teeth are determined, but also their growth rates. The program established in the embryo is worked out during foetal life.

The morphogenetic processes that underlie the differentiation of the dental series have been a subject of speculation (Osborn 1978, Butler 1978). Whether one thinks of field effects, or of clones of migrating mesenchyme cells, it is evident that position in the jaw is an important determining factor of tooth form. Butler (1952), in a study of the spread of the molar pattern, in the course of evolution, along the series of deciduous molars in perissodactyls, noted the coordination of upper and lower teeth, and postulated that the morphogenetic field involved both jaws. That view is supported by the correlated development of teeth in corresponding positions in the two jaws. Despite the functionally necessary differences between opposing dentitions, the parallelism between them indicates a common underlying morphogenetic mechanism.

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