Analysis of individual, intraspecific and interspecific variability in quantitative parameters of caprine tooth enamel structure

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Qualitative and quantitative features of mammalian tooth enamel structure are increasingly being used in taxonomic and phylogenetic analyses, although the variability shown by these traits has not received adequate consideration. This study evaluates the variability displayed by nine quantitative parameters in deep, intermediate, and superficial molar enamel in the closely related bovids *Ovis aries* and *Capra hircus*. These parameters are assessed in terms of the absolute and/or relative variability evinced at a given depth within a single individual, among conspecific individuals, and between species samples. The degrees of relative variability expressed at a given depth are comparable among conspecific individuals and between taxonomic samples. Nevertheless, in many instances, there are significant differences in absolute variability amongst individuals. Also, in four parameters for which individual specimen averages could be calculated, the equality of these means among conspecifics can be rejected. Variability is not equivalent at different enamel depths. The null hypothesis of equality of individual, conspecific variances can be rejected most commonly for parameters measured in deep and superficial enamel, and coefficients of variation also tend to be higher for deep and superficial enamel than for enamel of intermediate depth. The greater variability displayed by deep and especially superficial enamel may be related to the initial onset and the terminal phase of ameloblastic secretory activity. Taxonomic and phylogenetic analyses that utilize quantitative data on enamel structure are valid only if comparisons have been made at equivalent enamel depths. □ *Anthropology; mammalian tooth enamel; phylogenetic analysis; taxonomic analysis*

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Attendant on the documentation of differences between various mammalian taxa in details of tooth enamel structure (e.g., 1–12), certain of these structural features have been increasingly utilized in taxonomic and phylogenetic analyses (e.g., 13–19). For the most part, these analyses have utilized qualitative, and sometimes rather subjective, observations of features such as prism packing patterns (usually classified in accordance with the three patterns defined by Boyde (5)) and prism decussation (often categorized as being 'weak', 'strong', etc.). Moreover, the taxonomic arguments that have utilized aspects of enamel ultrastructure commonly have been based on exceedingly small samples (oftentimes a single tooth of any given taxon). Whereas such sample restrictions might, of necessity, be unavoidable in analyses of rare paleontologic materials, they serve to negate the aspect of structural variability both within and between individuals comprising specific groups and between species. The fact that the question of variability has been largely ignored in many studies has likely contributed to the disputations that have arisen concerning the characteristics of the enamel of certain species (cf. Gantt et al. (13), Vrba & Grine (15), Shellis & Poole (10), and Boyde & Martin (11)).

In several studies of enamel ultrastructure, however, quantitative parameters have been defined and documented (e.g., 20–24). With the methods established by Fosse (22, 23), quantitative features have also been used in a few comparative analyses of fossil taxa (25–29). Even in these instances, however, the question of variability has not been assessed adequately.

The present study was undertaken to evaluate the extent of variability expressed in certain metric parameters of enamel ultrastructure at specified enamel depths. Variability is assessed here (i) in terms of the degree evinced over a given area at one of three enamel depths in a single individual, (ii) in terms of the amount expressed by different individuals of the same species at these enamel depths, and (iii) with regard to differences between closely related species.

Depending on the alignment and packing of the ameloblasts, one of three basic developmental prism patterns may result (1), and since these different patterns may be manifest at different depths or in different regions of a single tooth (12, 15, 27), or in teeth of closely related taxa (29), we present here a method by which the mensurable parameters defined by Fosse (22, 23) for one of these basic patterns (pattern 3) may be compared with those obtained for the others (patterns 1 and 2).

Materials and methods

The present sample comprised the mandibular first permanent molars of 10 specimens each of the domestic sheep *(Ovis aries)* and goat *(Capra hircus)*. Only one tooth, usually from the left side, of each individual was examined. The comparatively flat enamel wall on the distobuccal face of the M_1 hypoconid, which is nearly identical in absolute thickness in *O. aries* ($\bar{x}$ = 0.55 mm; SD = 0.07; SE = 0.02) and *C. hircus* ($\bar{x}$ = 0.53 mm; SD = 0.09; SE = 0.04), formed the basis of this study.

Specimen preparation

Each molar was sectioned with a Buehler Isomet low-speed saw with a 0.3-mm diamond wafering blade approximately 1.0 cm occlusal to the cervical margin in the middle of the distobuccal surface of the hypoconid. The tooth was positioned such that the blade was perpendicular to the buccal face of the crown; thus, the plane of section approximated the transverse horizontal plane (Fig. 1a). Each tooth was then placed with its relatively flat distobuccal surface on a standard microscope objective slide, with the sectioned margin aligned

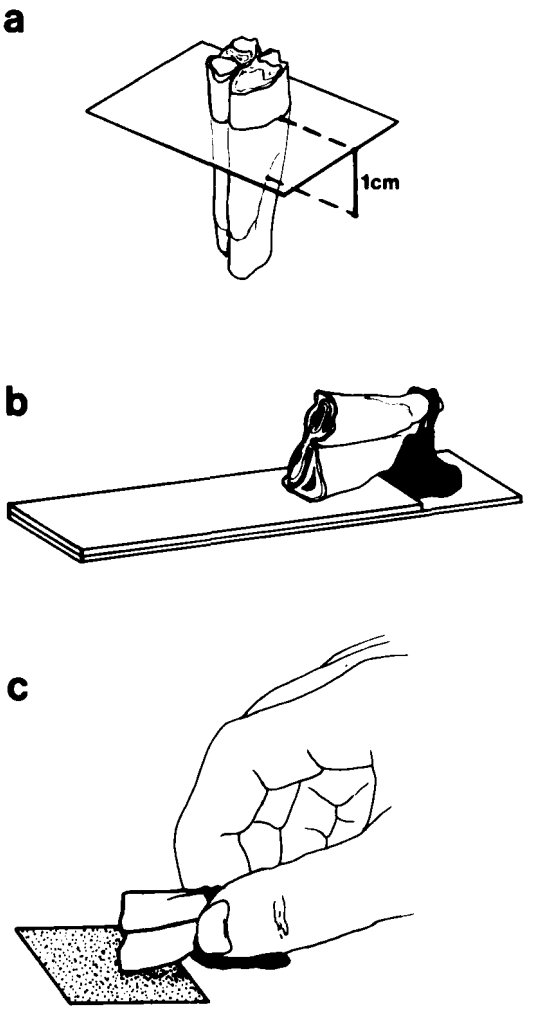


Fig. 1. Depiction of the principal steps in the preparation of a caprine molar for SEM examination. 1a. Level and orientation of plane of section. 1b. Position of specimen on mounting platform with resin. 1c. Production of ground facet.

along a line ruled 12 mm from and parallel to the end of the slide. This slide had previously been affixed to a second one, such that a step was formed between them; on the lower step, melted Kerr resin was applied just before positioning of the tooth, so that it was held firmly in position (Fig. 1b). A thin film of lubricant was applied to the step so that the set resin and bonded tooth could be removed easily from the platform. The distobuccal edge of the molar was then ground initially on 320° emery paper by moving the tooth buccolingually, with the resin step as a stabilizing platform near the edge of the paper (Fig. 1c). Grinding was continued until a crescent-shaped facet had been formed on the distobuccal face of the hypoconid, at which point polishing was completed, using 600° paper until a narrow crescent of dentin was exposed at the sectioned margin. Toward the end of the grinding and polishing regimen, the appearance of the dentin exposure was ascertained by means of Harris hematoxylin stain (without acetic acid) under a binocular light microscope. In accordance with this technique, the polished facet was inclined at approximately 11° to the outer distobuccal surface of the hypoconid.

After production of the polished facet, the Kerr resin was removed from the tooth, and the facet was rinsed with water and allowed to dry. Following the study by Grine (30), each facet was etched for 10 sec with 5% HCl without agitation, washed for 18 h in two baths of distilled water, and allowed to air-dry. Each tooth was mounted on an aluminum stub with colloidal graphite, the polished and etched facet being aligned horizontally, and was coated with carbon by vacuum evaporation. The specimens were then examined in an AMR 1400 scanning electron microscope (SEM) at an accelerating voltage of 20 kV.

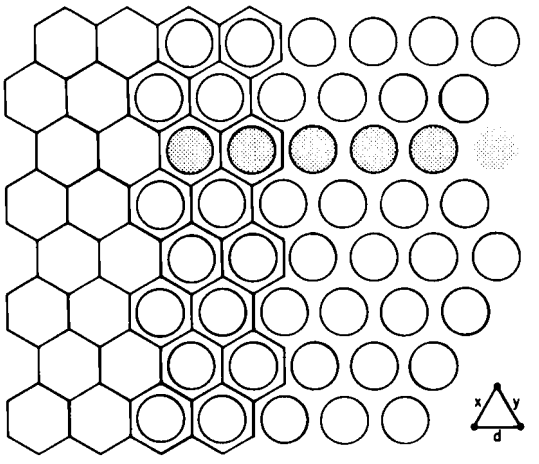
For each specimen the microscope stage was adjusted such that movement of the prepared facet along the x- and y-axes produced no change in focal working distance. Three fields, corresponding to deep, intermediate, and superficial enamel levels, were micrographed along a vertical, apicocervical axis that passed through the middle of the facet. The deep enamel region was defined as a point immediately adjacent to the dentin–enamel border, the superficial enamel level was examined at a point at the cervical margin of the facet, and the intermediate depth was defined as a point exactly midway between the other two. At each of these three points, the enamel field was micrographed at ×2000 and ×3500, using Polaroid Type 55 P/N film.

Variables measured

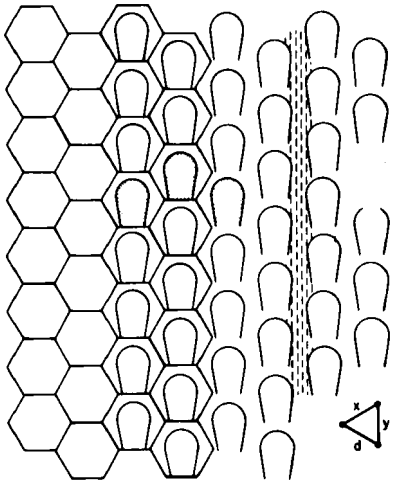
The distances between the centers of adjacent prisms were measured from the ×2000 micrographs, whereas the cross-sectional areas of the prism cores were obtained from those at ×3500.

In the first instance, the micrograph was placed under a transparent acetate sheet, on which the centers of adjacent prisms in the middle of the field were marked with ink. The prisms in the middle were used, so as to avoid the potential problem of geometric distortion around the field periphery. The centers were marked so that 10 contiguous triangles were delineated by them, and the three sides of each triangle (designated d, y, and x) were measured with a Mauser dial caliper with tapered ends. The average values obtained for the d, y, and x dimensions were used in the calculation of the computed central distance (CD), the vertical compression/distention value (K), the average ameloblastic cross-sectional secretory area (ASA), and the estimated prism density per mm^2 (EPD) for that specific region. The methods by which the individual d, y, and x dimensions were determined and the methods by which the CD, K, ASA, and EPD values were calculated for prism packing configurations corresponding to developmental patterns 1, 2, and 3 (Fig. 2) are detailed below.

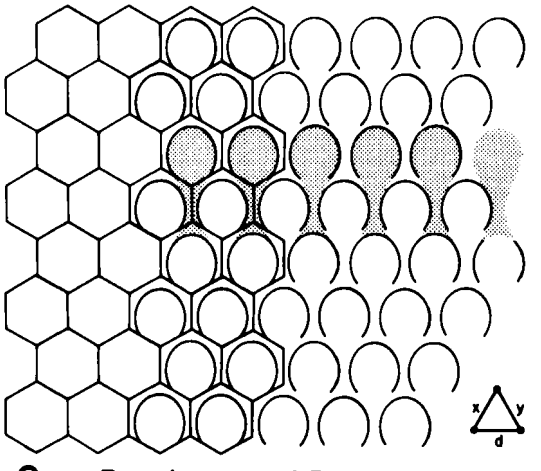
The cross-sectional areas of prism heads were measured for 10 prisms in the middle of each ×3500 micrograph, using a Science Accessories Graf-Pen sonic digitizer. With regard to pattern 1 prisms, the head is defined as the region surrounded by a boundary discontinuity (Fig. 2A). For pattern 2 prisms, the area of the prism head was defined as the region bordered by its own



A Developmental Pattern 1



B Developmental Pattern 2



C Developmental Pattern 3

boundary discontinuity and the top of the boundary of the cervically adjacent prism (Fig. 2B). With regard to fields showing pattern 3 packing, the area of the prism core was defined as the region circumscribed by its own boundary and a straight line drawn tangentially between the apical convexities of the two boundaries immediately cervical and adjacent to it (Fig. 2C). The 10 individual determinations were used to calculate the average cross-sectional prism head area (PA) for each field, and this value was compared with the average ameloblastic cross-sectional secretory area (ASA) for the same region (PA/ASA × 100), to obtain an estimate of the proportionate amount of prismatic matrix (PM) comprising that region.

Effect of facet inclination

Since the angle at which the prisms are cut by the polished facet will possibly influence many, if not all, of the parameters examined in this study, it is necessary to consider the relationship between the inclination of the polished surface and the underlying structure of caprine molar enamel.

Horizontal and longitudinal sections through the hypoconid of *C. hircus* and *O. aries* M_1s showed no discernible differences in the three-dimensional structure of the enamel in these taxa. In neither species do the prisms display significant varicosities along their lengths, and in both taxa the incremental, developmental surfaces (that is, the brown striae) are very nearly parallel to the completed, outer enamel face. The horizontal sections showed that the prisms follow a relatively straight path through the inner 50% to 60% and also through the outermost 10% to 20% of the enamel thickness, whereas they pursue a slightly wavy course through the intervening 20% to 40% of enamel. These gentle undulations are such that they would have no appreciable effect

Fig. 2. Schematic representation of prism packing patterns 1 (A), 2 (B), and 3 (C), showing the relationship among the secretory areas of ameloblasts (hexagons), prism boundary discontinuities (horse-shoe shaped lines), and prisms (stippled areas) and the measured distances (d, y, and x). (Adapted from Boyde (6).)

on the parameters considered in this study. The longitudinal sections showed that in both taxa, the prisms comprising the inner 40% to 50% of the enamel run outward and slightly occlusalward at angles of between about 60° and 70° to the dentin–enamel junction, whereas those that constitute the outer 50% to 60% of the enamel thickness follow a more horizontal course, being inclined at between 70° and 80° to both the dentin–enamel border and the outer enamel edge. The polished facet, which was produced at approximately 11° to the outer enamel face of the hypoconid, would intersect the deeper prisms at between some 70° and 80° to their long axes, whereas the prisms at the intermediate and superficial enamel depths would be cut by the facet at between about 80° and 90° to their long axes.

The differences in the angles at which the deeper and more superficial prisms approach the outer surface, which result in corresponding differences in the angles at which the prisms are cut by the polished facet, tend to be on the order of some 10°, with the prisms at the intermediate and superficial levels being sectioned somewhat more perpendicularly than those at the deep level. Thus, the measurements obtained for the superficial and intermediate levels are likely to be more similar to each other than to those recorded for the deep prisms. Nevertheless, the slope of the polished facet closely approximates the incremental line direction, and previous studies by Fosse (23) on the effect of facet inclination on the measurement of these parameters in human teeth would seem to suggest that the difference in the section angle between the deep and the intermediate/superficial prism levels is not of a magnitude that prohibits meaningful comparisons of the results obtained at these different enamel depths.

Definition and determination of quantitative parameters

As noted above, three basic developmental packing patterns of prisms (patterns 1, 2, and 3 of Boyde (5)) may be defined by the extent and alignment of the prism boundaries. Pattern 1 prisms are completely encircled by boundaries that serve to delineate separate interprismatic domains (Fig. 2A). With regard to the pattern 2 configuration, the boundary of one prism is open directly above the boundary of the cervically adjacent prism, such that the cores are aligned in longitudinal (apicocervical) columns ('vertical rows') (Fig. 2B). Pattern 2 prism columns are commonly separated by longitudinal sheets of interprismatic matrix, and the crystallites of the prism core may meld with those comprising the intercolumnar sheets. In the pattern 3 configuration the boundary of one prism opens between the boundaries of the two prisms cervical to it (Fig. 2C); adjacent prisms are thus aligned in rows rather than columns.

Depending on the arrangement of prisms in vertical columns (pattern 2) or horizontal rows (patterns 1 and 3), the sides of a triangle connecting three contiguous prisms will be orientated differently (Fig. 2). Fosse (22, 23) described a method for determining the computed central distance (CD), the average cross-sectional ameloblastic secretory area (ASA) (previously designated d h by Fosse (Ref. 22, p. 326)), and an estimate of the prism density per mm^2 (EPD), and also a model by which the degree of apicocervical compression or distention (K) of prisms in a pattern 3 packing arrangement could be described. Since the directions of the three measurements (designated d, y, and x) used to calculate these values are not the same for pattern 2 and pattern 3 configurations, it was necessary to develop a model that would permit description of the K values for pattern 2 prisms, and comparison of these values between enamel fields showing pattern 2 and pattern 3 prisms (Figs. 2B, C). The K value for pattern 1 prisms that exhibit the idealized packing arrangement illustrated in Fig. 2A will be directly comparable with that for pattern 3 prisms.

Pattern 3 model

If the idealized pattern 3 packing arrangement is visualized as being comprised of congruent, contiguous circles in horizontal alignment and hexagonal distribution, the

distances between the centers of the circles (d, y, and x) will be equal to the diameters of the circles (Fig. 3). The central distances between three mutually contiguous, congruent circles constitute an equilateral triangle (Fig. 3, angles A, B, and C), where two such triangles with one common side constitute a parallelogram (Fig. 3, angles A, B, C', C).

Given the above conditions, the number of circles and the number of such parallelograms per unit area will be equal, and the number of circles per mm^2 can be calculated as:

$$nc = \frac{10^6}{1/2\, Z^2(\sqrt{3})} \quad (1)$$

where nc is the number of circles, Z is a given distance between the centers of any two adjacent prisms, and the unit of measurement is the micrometer. The denominator, therefore, is the area of the parallelogram.

In the idealized pattern illustrated in Fig. 3, the central distance is equivalent to the diameter of the circle. The diameters of the circles may be reduced, but the central distances will remain constant; Eq. 1 will similarly obtain because it expresses only the number of centers per mm^2. Converting this to prism structure, the reduction in circle diameters would correspond to a reduction in the size of the boundary around the prism core and therefore to an increase in interprismatic matrix.

If the three sides (designated d, y, and x) of all contiguous, congruent triangles in a hexagonal distribution of prism centers are unequal, the model would continue to define the number of centers in asymmetric distribution, in accordance with the following equation:

$$nc = \frac{10^6}{1/2\sqrt{4d^2y^2 - (d^2 + y^2 - x^2)^2}} \quad (2)$$

where d, y, and x are defined as in Fig. 3. The denominator is the area of a parallelogram consisting of two congruent triangles with unequal sides and one common side. Using Eq. 2 to calculate the numerical density of cross-sectioned prisms, nc is representative of EPD, which designates the estimated density of prisms per mm^2. Similarly, the mean area of the parallelograms calculated in this manner represents the average cross-sectional secretory area of ameloblasts (ASA).

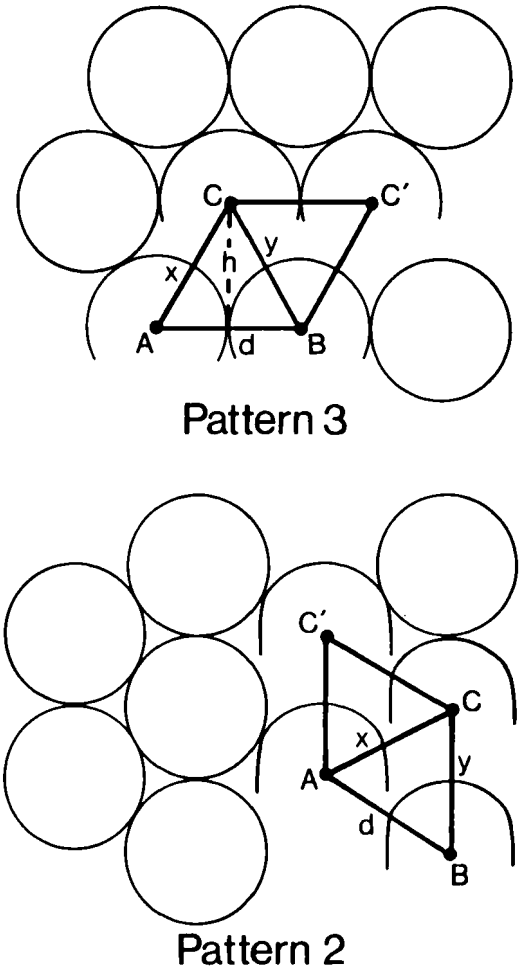


Fig. 3. Pattern 3 and pattern 2 prism packing represented by models of congruent, contiguous circles in symmetrical hexagonal distribution. The letters A, B, and C designate the angles of a unit triangle, the sides of which constitute the distances between the centers of three mutually contiguous circles or prisms. A, B, C', and C designate the angles of a parallelogram formed by two triangles with one side in common. See text for explanation. (Adapted from Fosse (Ref. 22, Fig. 1).)

It should be noted that the parallelogram expressed in the denominator of Eq. 2 is not real, since it is extrapolated from one triangle whose sides are the means of all measured d's, y's, and x's. In reality, there are no

parallelograms, but irregular tetragons that consist of pairs of incongruent triangles with one common side (22). The calculated parallelogram of Eq. 2 is a close approximation to ASA, or the 'theoretical mean area of the prism and half the thickness of the surrounding interprismatic substance' (Ref. 22, p. 321).

As represented in Fig. 3, the height between the levels of the prism center in one row and a line (d) between centers in the adjacent row may be designated h_d (Fig. 3), where

$$h_d = \frac{1/2\sqrt{4d^2y^2 - (d^2 + y^2 - x^2)^2}}{d}. \quad (3)$$

The numerator represents the area of the parallelogram, and the denominator represents the base of the same parallelogram (that is, the distance between two centers in one horizontal row).

If y and x are both smaller or larger than d, there is a compression or distention, respectively, of the prism pattern in an apicocervical direction (that is, normal to the base d). This compression/distention value (K) may be expressed as:

$$K\,(\text{pattern 3}) = \frac{1/2d\sqrt{3}}{h_d} \quad (4)$$

The numerator is the height on the base d in an equilateral triangle, and the denominator is the height on d in the measured triangle as calculated by Eq. 3. Thus, when $K > 1$, the triangle is apicocervically compressed; when $K < 1$, the triangle is apicocervically distended; and when $K = 1$, the triangle is equilateral.

When the distances between the centers of three contiguous circles, or prisms, are equivalent (an equilateral triangle), the dimension of any one side may be taken to represent the mean central distance. In those instances in which the sides of the triangle (d, y, and x) are not equivalent (the usual condition), the central distance of an equilateral triangle with the same area may be expressed as:

$$CD = \sqrt{\frac{2dh_d}{\sqrt{3}}} \quad (5)$$

where CD represents the computed central distance.

From the formulae detailed above, it is therefore possible to calculate the average cross-sectional secretory area of the ameloblasts (ASA) as represented by the areas of the parallelograms, the ratio of the degree of apicocervical compression or distention of the packing pattern (K), the estimated density of prisms per mm^2 (EPD), and the computed distance (CD) between prism cores for a given field, using the mean values for the individual d, y, and x diameters recorded for that field.

Pattern 2 model

If the idealized pattern 2 packing arrangement is visualized as consisting of congruent, contiguous circles in vertical alignment and hexagonal distribution (Figs. 2 and 3), the distances between the centers of the circles (d, y, and x) will be equal to their diameters. In Fig. 3 the central distances between three mutually contiguous circles constitute an equilateral triangle (angles A, B, and C), in which two such triangles with a common side constitute a parallelogram (angles A, B, C', C). Since the circles that define the pattern 2 packing arrangement are aligned vertically, it is not possible to calculate the degree of apicocervical distortion of the packing arrangement by using the formulae developed for the pattern 3 configuration, in which the circles are aligned horizontally.

This difficulty may be circumvented, however, by using the vertical side (y) as the base of the triangle in a pattern 2 arrangement (Fig. 3). The degree of transverse, or horizontal, distortion of the pattern on side y may be calculated by a modification of Eq. 3 in the form:

$$h_y = \frac{1/2\sqrt{4y^2x^2 - (y^2 + x^2 - d^2)^2}}{y} \quad (6)$$

where h_y represents the transverse distance from side y to angle A (Fig. 3). The degree of horizontal distortion described by the foregoing equation, while not equivalent to the degree of apicocervical distortion described by Eq. 4, may be converted to a

value that is comparable to that of K for pattern 3 packing arrangements.

Given that the triangles with angles A, B, and C and sides d, y, and x, which describe hexagonal distributions of pattern 2 and pattern 3 prisms, are of equivalent area (Fig. 3), it is possible to construct hexagons that are also equivalent in area (Fig. 4). If the centers of two such hexagons are coincident, and if their degrees of vertical distention are equal, geometrical considerations dictate that any diagonal line that runs from the center to a corner of one hexagon (say, for pattern 2) will cross the side of the other (in this case, for pattern 3) at midlength. Thus, the ratio between the center-to-side distance and a center-to-corner distance equals $1/2\sqrt{3}$, regardless of the degree of hexagonal compression or distention. The amount of apicocervical distortion of height h on base d in a pattern 3 triangle (Fig. 4, T_3) will then be equivalent to the inverse of the amount of transverse distortion of distance h_y on base y in a pattern 2 triangle (Fig. 4, T_2). Accordingly, the degree of apicocervical compression or distention of pattern 2 packing arrangements may be calculated as:

$$K\,(\text{pattern 2}) = \frac{h_y}{1/2\,y\sqrt{3}} \qquad (7)$$

where the value of K is directly comparable to that derived for a pattern 3 arrangement (Eq. 4).

Parenthetically, it is not necessary to modify either Eq. 2 or Eq. 5, utilized for pattern 3 prism packing arrangements, with regard to Pattern 2 configurations. The sequence of the variables (d, y, and x) in Eq. 2 is inconsequential to the value under the root sign, and the product dh_d in Eq. 5 is equivalent to yh_y.

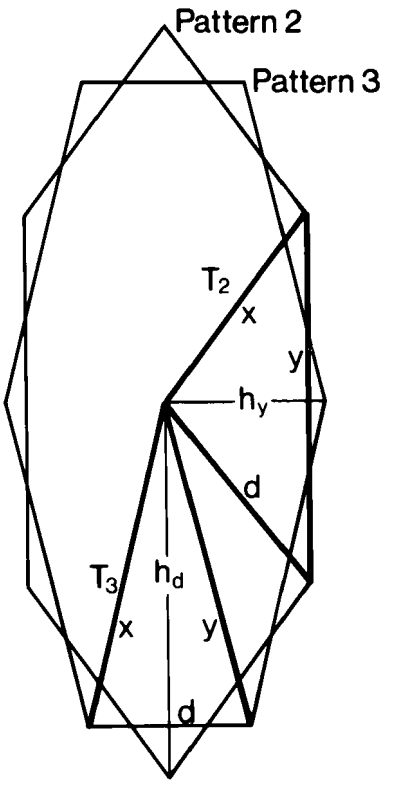


Fig. 4. Relationship between hexagons of equivalent area and lateral compression which describe pattern 2 and pattern 3 prism packing configurations. The center and corners of each hexagon correspond to the positions of the centers of seven adjacent prisms. Sides d, y, and x of triangles T_2 and T_3 represent distances between prism centers in pattern 2 and pattern 3 arrangements, respectively. The apicocervical compression/distention (K) value of T_3 is the inverse of the transverse compression of h_y on side y in T_2. See text for explanation.

Statistical analysis of variability

Variability in quantitative parameters of tooth enamel structure may be assessed within an area shown by a single individual at any one of various enamel depths (intraindividual variability), between and among individuals comprising a species sample (intraspecific variability), or between species samples (interspecific variability). Several methods may be used to assess absolute and relative variability.

A simple measure of relative variability is provided by the coefficient of variation (CV), which is calculated in accordance with the formula:

$$CV = (SD/\bar{x}) \cdot 100 \qquad (8)$$

where $\bar{x}$ is the sample mean, and SD is the standard deviation. In the present study CVs have been computed for the d, y, and x dimensions and for the PA measurements of each individual at the three enamel depths.

The CVs have also been obtained for all parameters in the assessment of relative intraspecific and interspecific variability.

In the assessment of the homogeneity (or equality) of absolute intraspecific variability (that is, among versus within individuals comprising each taxonomic sample), Levene's robust test was applied to untransformed data (31–34). This test statistic was selected as appropriate after individual histograms showed occasional departures from normality with regard to both raw and log-transformed values. Levene's statistic is obtained from a one-way ANOVA among groups 'where each observation has been replaced by its absolute deviation from its group mean' (Ref. 32, p. 364). A tail probability of $p < 0.05$ is used as the cutoff point for a significant departure from the null hypothesis of homoscedasticity. The Levene test was used here also in the assessment of the equality of absolute interspecific variability, where the species sample statistics for a given parameter were derived from the individual values or averages.

To test the null hypothesis of equality of individual parameter means within a species sample, two independent one-way analysis of variance (ANOVA) statistics were calculated: the Welch statistic and the standard ANOVA F ratio. Unlike the standard one-way ANOVA, the Welch statistic does not assume equality of variances in each group (34, 35). The equality of parameter means between species was tested in similar fashion.

Results

The pattern 2 developmental packing configuration predominates throughout the thickness of the enamel in both *C. hircus* and *O. aries*, although regions of pattern 3 prisms within fields composed principally of pattern 2 prisms were observed in the superficial enamel of one specimen of *Ovis* and two of *Capra*. The qualitative structural morphologies evinced by deep, intermediate, and superficial enamels of these two taxa are indistinguishable. Whereas a degree of individual difference was encountered, the deep enamel in both tends to show comparatively robust intercolumnar sheets (Fig. 5A). The interprismatic sheets tend to be thinner, if present at all, and the prisms tend to be aligned in regularly spaced, straight columns in the intermediate enamel (Fig. 5B). At the superficial level, the prism packing tends to be somewhat more irregular; the straight columnar pattern is commonly disturbed, and the crystallites comprising the interprismatic sheets or matrix are often continuous with those of the prism heads (Fig. 5C). As noted above, in three instances within the superficial fields examined (that is, micrographed) the pattern 2 alignment gave way to patches of pattern 3 configuration. The quantitative data presented here for the deep and intermediate enamel levels pertain to the pattern 2 configuration, and those recorded for the superficial enamel pertain also to this pattern, except where otherwise noted.

Individual d, y, and x dimensions

The degrees of variability expressed by each of the 20 caprine specimens in the d diameters for the deep, intermediate, and superficial enamel levels are recorded in Tables 1–3. In both species samples the individual CVs tend to be somewhat lower for the intermediate enamel than for the deep and superficial levels. The range between the lowest and highest CV values is smallest for the intermediate enamel in the *Capra* sample (4.85–14.25), whereas in the *Ovis* sample the smallest range occurs within the superficial values (6.80–13.72).

The degrees of y dimension variability evinced at the deep, intermediate, and superficial enamel levels are recorded in Tables 4–6. The individual CVs tend to be somewhat lower for the intermediate than for the deep or superficial fields in the *Ovis* sample, whereas the deep enamel values tend to be lower in the *Capra* sample. The observed range between the highest and lowest CV values is smallest for the intermediate enamel depth in both the *Ovis* (6.16–15.28) and *Capra* (6.81–13.14) samples.

The degrees of variability expressed by the individual x dimensions for the three enamel

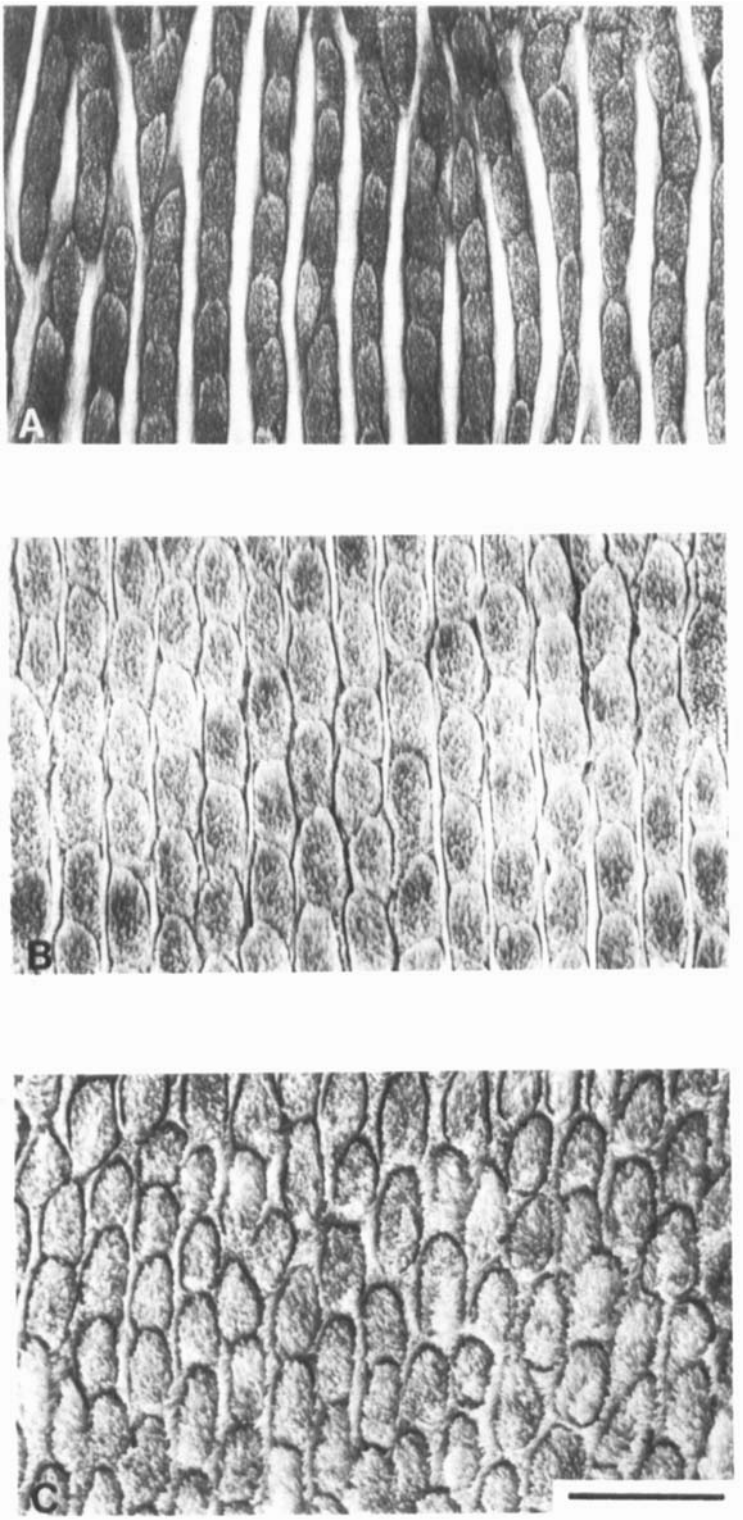


Fig. 5. Typical structure of deep (A), intermediate (B), and superficial (C) caprine molar enamel. Scale bar = 10 μm. Cervical at bottom.

Table 1. Individual variability in d values recorded for deep enamel (values in μm)

Specimen	*n*	$\bar{x}$	SD	SE	CV%
Ovis aries					
1	10	3.72	0.39	0.12	10.48
2	10	3.67	0.59	0.19	16.08
3	10	3.70	0.62	0.20	16.76
4	10	3.79	0.38	0.12	10.03
5	10	4.39	0.52	0.16	11.85
6	10	3.57	0.58	0.18	16.25
7	10	3.38	0.37	0.12	10.95
8	10	4.08	0.67	0.21	16.42
9	10	3.96	0.30	0.10	7.58
10	10	4.12	0.65	0.21	15.78
Capra hircus					
1	10	4.25	0.62	0.19	14.59
2	10	4.29	0.55	0.17	12.82
3	10	4.95	0.62	0.20	12.53
4	10	4.09	0.87	0.28	21.27
5	10	4.08	0.62	0.20	15.20
6	10	3.78	0.25	0.08	6.61
7	10	4.21	0.40	0.13	9.50
8	10	3.53	0.23	0.07	6.52
9	10	4.68	0.46	0.15	9.83
10	10	4.35	0.40	0.13	9.20

Table 2. Individual variability in d values recorded for intermediate enamel (values in μm)

Specimen	*n*	$\bar{x}$	SD	SE	CV%
Ovis aries					
1	10	4.41	0.49	0.15	11.11
2	10	3.94	0.51	0.16	12.94
3	10	3.60	0.36	0.11	10.00
4	10	4.03	0.48	0.15	11.91
5	10	3.96	0.72	0.23	18.18
6	10	3.79	0.16	0.05	4.22
7	10	3.26	0.24	0.08	7.36
8	10	4.06	0.66	0.21	16.26
9	10	4.31	0.40	0.13	9.28
10	10	3.82	0.26	0.08	6.81
Capra hircus					
1	10	4.66	0.48	0.15	10.30
2	10	4.42	0.63	0.20	14.25
3	10	4.98	0.64	0.20	12.85
4	10	4.84	0.31	0.10	6.41
5	10	4.59	0.32	0.10	6.97
6	10	3.92	0.19	0.06	4.85
7	10	3.94	0.41	0.13	10.41
8	10	3.90	0.35	0.11	8.97
9	10	4.30	0.40	0.13	9.30
10	10	4.39	0.32	0.10	7.29

Table 3. Individual variability in d values recorded for superficial enamel (values in μm)

Specimen	*n*	$\bar{x}$	SD	SE	CV%
Ovis aries					
1	10	5.49	0.43	0.13	7.83
2	10	3.89	0.48	0.15	12.34
3	10	3.95	0.52	0.17	13.16
4	10	4.66	0.39	0.12	8.37
5	10	4.41	0.30	0.10	6.80
6	10	3.67	0.49	0.15	13.35
7	10	4.12	0.38	0.12	9.22
8	10	4.24	0.43	0.13	10.14
9	10	4.10	0.56	0.18	13.66
10	10	4.30	0.59	0.19	13.72
	10	3.45	0.37	0.12	10.73*
Capra hircus					
1	10	4.18	0.39	0.12	9.33
2	10	5.17	0.77	0.24	14.89
3	10	5.24	0.58	0.18	11.07
4	10	5.10	0.65	0.21	12.75
5	10	4.48	0.75	0.24	16.74
6	10	4.38	0.27	0.09	6.16
7	10	4.63	0.61	0.19	13.18
8	10	3.51	0.44	0.14	12.54
9	10	3.46	0.35	0.11	10.12
	10	3.24	0.18	0.06	5.56*
10	10	4.21	0.37	0.12	8.79
	10	4.49	0.44	0.14	9.80*

* Data for pattern 3; all other data for pattern 2.

Table 4. Individual variability in y values recorded for deep enamel (values in μm)

Specimen	*n*	$\bar{x}$	SD	SE	CV%
Ovis aries					
1	10	4.81	0.52	0.16	10.81
2	10	4.53	0.36	0.11	7.95
3	10	4.54	0.84	0.27	18.50
4	10	4.28	0.44	0.14	10.28
5	10	4.87	0.76	0.24	15.61
6	10	4.48	0.72	0.23	16.07
7	10	4.27	0.53	0.17	12.41
8	10	5.55	1.22	0.39	21.98
9	10	4.51	0.23	0.07	5.10
10	10	4.95	0.89	0.28	17.98
Capra hircus					
1	10	4.83	0.42	0.13	8.70
2	10	5.51	0.55	0.17	9.98
3	10	5.64	0.44	0.14	7.80
4	10	5.03	0.28	0.09	5.57
5	10	4.84	0.59	0.19	12.19
6	10	5.17	0.18	0.06	3.48
7	10	5.17	0.33	0.10	6.38
8	10	4.25	0.23	0.07	5.41
9	10	5.79	0.60	0.19	10.36
10	10	4.69	0.35	0.11	7.46

Table 5. Individual variability in y values recorded for intermediate enamel (values in μm)

Specimen	*n*	$\bar{x}$	SD	SE	CV%
Ovis aries					
1	10	5.78	0.51	0.16	8.82
2	10	5.04	0.44	0.14	8.73
3	10	4.61	0.33	0.11	7.16
4	10	4.99	0.51	0.16	10.22
5	10	5.30	0.81	0.26	15.28
6	10	4.38	0.27	0.08	6.16
7	10	4.82	0.31	0.10	6.43
8	10	5.36	0.48	0.15	8.96
9	10	5.96	0.38	0.12	6.38
10	10	5.16	0.32	0.10	6.20
Capra hircus					
1	10	6.16	0.50	0.16	8.12
2	10	5.48	0.72	0.23	13.14
3	10	6.49	0.78	0.25	12.02
4	10	6.61	0.45	0.14	6.81
5	10	5.68	0.61	0.19	10.74
6	10	5.44	0.42	0.13	7.72
7	10	5.59	0.49	0.15	8.77
8	10	5.21	0.64	0.20	12.28
9	10	5.38	0.38	0.12	7.06
10	10	5.58	0.38	0.12	6.81

Table 6. Individual variability in y values recorded for superficial enamel (values in μm)

Specimen	*n*	$\bar{x}$	SD	SE	CV%
Ovis aries					
1	10	5.99	0.55	0.17	9.18
2	10	5.33	0.52	0.16	9.76
3	10	6.14	1.28	0.41	20.85
4	10	6.33	0.62	0.20	9.80
5	10	5.58	0.51	0.16	9.14
6	10	6.13	0.68	0.22	11.09
7	10	5.70	0.67	0.21	11.75
8	10	5.99	0.80	0.25	13.36
9	10	4.70	0.47	0.15	10.00
10	10	5.81	0.39	0.12	6.71
	10	4.95	0.53	0.17	10.71*
Capra hircus					
1	10	6.48	0.37	0.12	5.71
2	10	7.14	0.91	0.29	12.75
3	10	7.48	0.46	0.14	6.15
4	10	6.78	0.51	0.16	7.52
5	10	6.17	0.62	0.19	10.05
6	10	5.85	0.58	0.18	9.92
7	10	5.88	1.22	0.38	20.75
8	10	4.79	0.50	0.16	10.43
9	10	4.64	0.44	0.14	9.48
	10	4.83	0.38	0.12	7.87*
10	10	4.75	0.42	0.13	8.84
	10	4.59	0.56	0.18	12.20*

* Data for pattern 3; all other data for Pattern 2.

depths are recorded in Tables 7–9. As was noted above for the d dimension, in both species samples the CVs for the x diameter tend to be somewhat lower for the intermediate than for the deep and superficial enamel levels. In the *Ovis* sample the range between the lowest and highest CV values is smallest for the intermediate enamel (6.18–15.48), whereas in the *Capra* sample the smallest range pertains to the deep enamel (5.82–13.46).

Thus, in both species samples the individual variability expressed in the d and x diameters tends to be somewhat lower for the intermediate enamel than for the deep or superficial enamel. The CVs for the y diameter tend also to be lower for the intermediate enamel in the *Ovis* sample, but in the *Capra* sample these values tend to be lower for the deep enamel. In both samples the observed ranges between the lowest and highest CVs for the y diameter are smallest for the intermediate enamel. At the same time, however, the smallest observed ranges between CV values for the d diameter occur in the intermediate enamel in the *Capra* sample but in the superficial enamel in the *Ovis* sample. With regard to the x diameter, the smallest observed range is found in the intermediate enamel in the *Ovis* sample but in the deep enamel of the *Capra* sample.

Levene's robust test for equality of individual variances within a species sample (Table 10) suggests that the null hypothesis of equality of individual *variances* should not be rejected for all parameters (that is, those with $p > 0.05$). This observation pertains most notably to the d dimensions of deep, intermediate, and superficial enamel in the *Ovis* sample, the y diameter for deep enamel in the *Ovis* sample, the y diameter for intermediate enamel in the *Capra* sample, and to the x dimensions in *Capra* deep and intermediate enamel (Table 10). In most cases, however, there is significant heteroscedasticity.

The null hypothesis of equality of parameter means among individuals within each species sample can be rejected in each instance on the basis of both the Welch statistic and the standard ANOVA (Table 11). Thus, different conspecific individuals within

Table 7. Individual variability in x values recorded for deep enamel (values in μm)

Specimen	*n*	$\bar{x}$	SD	SE	CV%
Ovis aries					
1	10	4.05	0.67	0.21	16.54
2	10	3.86	0.57	0.18	14.77
3	10	3.77	0.67	0.21	17.77
4	10	3.38	0.34	0.11	10.06
5	10	3.79	0.35	0.11	9.24
6	10	3.31	0.37	0.12	11.18
7	10	3.57	0.28	0.09	7.85
8	10	5.40	1.63	0.52	30.19
9	10	4.23	0.27	0.08	6.38
10	10	3.96	0.53	0.17	13.38
Capra hircus					
1	10	4.16	0.56	0.18	13.46
2	10	4.25	0.46	0.15	10.82
3	10	4.97	0.59	0.19	11.87
4	10	4.46	0.53	0.17	11.88
5	10	3.58	0.39	0.12	10.89
6	10	3.61	0.21	0.07	5.82
7	10	3.77	0.37	0.12	9.81
8	10	4.00	0.29	0.09	7.25
9	10	4.47	0.45	0.14	10.07
10	10	4.11	0.27	0.08	6.57

Table 8. Individual variability in x values recorded for intermediate enamel (value in μm)

Specimen	*n*	$\bar{x}$	SD	SE	CV%
Ovis aries					
1	10	4.11	0.49	0.16	11.92
2	10	3.85	0.34	0.11	8.83
3	10	3.58	0.24	0.07	6.70
4	10	3.70	0.55	0.18	14.87
5	10	3.94	0.61	0.19	15.48
6	10	3.72	0.23	0.07	6.18
7	10	4.03	0.26	0.08	6.45
8	10	4.17	0.52	0.16	12.47
9	10	3.83	0.28	0.09	7.31
10	10	3.65	0.28	0.09	7.67
Capra hircus					
1	10	4.14	0.36	0.11	8.70
2	10	4.01	0.60	0.19	14.96
3	10	5.12	0.59	0.19	11.52
4	10	4.49	0.22	0.07	4.90
5	10	4.21	0.27	0.08	6.41
6	10	4.16	0.52	0.16	12.50
7	10	4.46	0.54	0.17	12.11
8	10	4.01	0.39	0.12	9.73
9	10	4.06	0.31	0.10	7.64
10	10	4.23	0.38	0.12	8.98

Table 9. Individual variability in x values for superficial enamel (values in μm)

Specimen	*n*	$\bar{x}$	SD	SE	CV%
Ovis aries					
1	10	4.60	0.25	0.08	5.44
2	10	4.01	0.78	0.25	19.45
3	10	4.27	0.59	0.19	13.82
4	10	3.83	0.32	0.10	8.36
5	10	4.44	0.38	0.12	8.56
6	10	4.57	0.67	0.21	14.66
7	10	4.20	0.52	0.16	12.38
8	10	4.30	0.41	0.13	9.54
9	10	3.57	0.48	0.15	13.45
10	10	4.04	0.44	0.14	10.89
	10	5.28	0.65	0.21	12.31*
Capra hircus					
1	10	4.39	0.40	0.12	9.11
2	10	5.10	0.57	0.18	11.18
3	10	5.23	0.60	0.19	11.47
4	10	4.54	0.38	0.12	8.37
5	10	4.22	0.82	0.26	19.43
6	10	4.43	0.36	0.11	8.13
7	10	4.26	0.47	0.15	11.03
8	10	3.92	0.63	0.20	16.07
9	10	4.17	0.56	0.18	13.43
	10	4.63	0.42	0.13	9.07*
10	10	4.74	0.44	0.14	9.28
	10	4.60	0.41	0.13	8.91*

* Data for pattern 3; all other data for pattern 2.

Table 10. Analysis of equality of variance of d, y, and x diameters among versus within individuals

	Levene test statistics	
Variable/depth	F	*p*
Ovis aries		
d Deep	1.77	=0.084
Intermediate	1.85	=0.069
Superficial	0.54	=0.843
y Deep	1.79	=0.080
Intermediate	2.47	=0.014
Superficial	2.76	=0.007
x Deep	8.19	<0.001
Intermediate	3.14	=0.002
Superficial	2.80	=0.006
Capra hircus		
d Deep	2.61	=0.010
Intermediate	2.61	=0.010
Superficial	2.60	=0.010
y Deep	3.81	<0.001
Intermediate	1.51	=0.157
Superficial	4.24	<0.001
x Deep	1.55	=0.142
Intermediate	1.75	=0.089
Superficial	2.07	=0.041

Table 11. One-way analysis of variance (among versus within individuals) of d, y, and x diameters recorded for deep, intermediate, and superficial enamel

	Welch statistic		Standard ANOVA	
Variable/depth	W	*p*	F	*p*
Ovis aries				
d Deep	3.48	=0.003	3.26	=0.002
Intermediate	8.75	<0.001	5.12	<0.001
Superficial	11.51	<0.001	11.96	<0.001
y Deep	1.94	=0.077	2.95	=0.004
Intermediate	16.09	<0.001	11.20	<0.001
Superficial	6.84	<0.001	4.78	<0.001
x Deep	7.50	<0.001	7.46	<0.001
Intermediate	3.00	=0.009	2.46	=0.015
Superficial	6.37	<0.001	4.13	<0.001
Capra hircus				
d Deep	10.52	<0.001	5.71	<0.001
Intermediate	11.19	<0.001	8.14	<0.001
Superficial	14.15	<0.001	13.40	<0.001
y Deep	17.09	<0.001	12.35	<0.001
Intermediate	7.69	<0.001	7.70	<0.001
Superficial	38.85	<0.001	24.23	<0.001
x Deep	9.81	<0.001	10.11	<0.001
Intermediate	4.44	<0.001	5.91	<0.001
Superficial	4.40	<0.001	5.85	<0.001

each of the samples of *Ovis* and *Capra* have significant average differences in the d, y, and x diameters.

The intraspecific sample variability in CV values for the three diameters at different enamel depths is summarized in Table 12. The means are of reasonable magnitude for all parameters in both samples. Within the *Ovis* sample the means for all three dimensions are highest for the deep enamel and lowest for intermediate enamel. Within the *Capra* sample this pattern is displayed by the means for the d diameter, but y diameter variability tends to be lowest for deep enamel and highest for superficial enamel, and x diameter variability tends to be lowest for intermediate and highest for superficial enamel.

The sample means for the d, y, and x dimensions, calculated from the individual averages (Tables 1–9), are recorded in Table 13. The CVs obtained for the d and y means in the *Ovis* sample are lower for the deep than for the intermediate and superficial enamel levels, whereas the CV of the x diameter at the intermediate depth is lower than those at the deep and superficial levels. Within the *Capra* sample, however, the CVs of all three dimensions are lower for the intermediate than for either the deep or superficial enamel levels. The coefficients of variation pertaining to these sample means are generally comparable to the CV value averages obtained for the same dimensions (Table 12), although a few rather noticeable discrepancies do occur (e.g., between the CV for the d diameter mean of deep *Ovis* enamel (7.81) and the corresponding CV value mean (13.22)). This would seem to suggest that whereas statistical computations based on the compilation of dimensional averages for individual specimens (Table 13) mask the inherent intraindividual variability in quantitative parameters of enamel structure, the degree of interindividual variability thus expressed bears a relationship to the amount of within-individual variation evinced by a given dimension.

There is a general similarity in CV value means (Table 12) and in the CVs pertaining to the dimensional averages (Table 13) obtained for the *Ovis* and *Capra* samples. The results of the Levene tests (Table 14) indicate that the null hypothesis of equality

Table 12. Intraspecific sample variability in CV value means of d, y, and x diameters recorded for deep, intermediate, and superficial enamel (all values are for pattern 2 prism packing)

Variable/depth	*n*	$\bar{x}$	SD
Ovis aries			
d Deep	10	13.22	3.39
Intermediate	10	10.81	4.27
Superficial	10	10.86	2.68
y Deep	10	13.67	5.25
Intermediate	10	8.43	2.80
Superficial	10	11.16	3.83
x Deep	10	13.74	6.87
Intermediate	10	9.79	3.58
Superficial	10	11.66	3.98
Capra hircus			
d Deep	10	11.81	4.49
Intermediate	10	9.16	2.92
Superficial	10	11.56	3.11
y Deep	10	7.73	2.64
Intermediate	10	9.35	2.46
Superficial	10	10.16	4.27
x Deep	10	9.84	2.52
Intermediate	10	9.75	3.06
Superficial	10	11.75	3.64

of species sample variances should not be rejected for all parameters. Indeed, the only instance in which the degree of absolute variability differed significantly between the

Table 13. Intraspecific sample variability in d, y, and x diameter means calculated from individual averages for deep, intermediate, and superficial enamel (all values for pattern 2 prism packing) (values in μm)

Variable/depth	*n*	$\bar{x}$	SD	SE	CV%
Ovis aries					
d Deep	10	3.84	0.30	0.09	7.81
Intermediate	10	3.92	0.33	0.10	8.42
Superficial	10	4.28	0.51	0.16	11.92
y Deep	10	4.68	0.38	0.16	8.12
Intermediate	10	5.14	0.49	0.15	9.53
Superficial	10	5.77	0.48	0.15	8.32
x Deep	10	3.93	0.59	0.19	15.01
Intermediate	10	3.86	0.20	0.06	5.18
Superficial	10	4.18	0.33	0.10	7.90
Capra hircus					
d Deep	10	4.22	0.40	0.13	9.48
Intermediate	10	4.39	0.39	0.12	8.88
Superficial	10	4.44	0.63	0.20	14.19
y Deep	10	5.09	0.47	0.15	9.23
Intermediate	10	5.76	0.48	0.15	8.33
Superficial	10	6.00	1.01	0.32	16.83
x Deep	10	4.14	0.43	0.14	10.39
Intermediate	10	4.29	0.34	0.11	7.93
Superficial	10	4.50	0.42	0.13	9.33

Table 14. Analysis of interspecific equality of variance of d, y, and x diameters between samples of *Ovis aries* and *Capra hircus*

	Levene test statistics	
Variable/depth	F	*p*
d Deep	0.20	=0.658
Intermediate	0.46	=0.506
Superficial	0.77	=0.393
y Deep	0.38	=0.543
Intermediate	0.03	=0.854
Superficial	5.51	=0.031
x Deep	0.13	=0.719
Intermediate	1.02	=0.326
Superficial	0.47	=0.503

Ovis and *Capra* samples pertains to the y diameter at the superficial enamel level. One-way analysis of variance tests indicate that the equality of species means should be rejected ($p < 0.05$) for the d and y diameters of deep and intermediate enamel and for the x diameter at the intermediate enamel level (Table 15).

Average computed central distance

The d, y, and x dimensional means recorded for each individual for deep, intermediate, and superficial enamel were used to calculate the corresponding computed central distance (CD) value. The CD means obtained for the *Ovis* and *Capra* samples are recorded in Table 16. In both samples the degrees of interindividual variability are lower for the intermediate than for the deep and superficial enamel levels. In the *Ovis* sample, however, the deep enamel CV is the highest, whereas in the *Capra* sample this distinction holds for the superficial enamel. In each instance the coefficient of variation pertaining to a given CD value mean is lower than the average CVs for the three variables used in the calculation of the CD.

The CD values presented in Table 16 are those for pattern 2 prism packing. As noted above and in Tables 3, 6, and 9, however, in three instances pattern 2 and pattern 3 packing were presented in the same superficial enamel field. In the single *Ovis* specimen the pattern 2 CD value was recorded

Table 15. One-way analysis of variance (between species) of d, y, and x diameters recorded for deep, intermediate, and superficial enamel

	Welch statistic		Standard ANOVA	
Variable/depth	W	*p*	F	*p*
d Deep	5.80	=0.028	5.80	=0.027
Intermediate	8.78	=0.008	8.78	=0.008
Superficial	0.35	=0.561	0.35	=0.560
y Deep	4.66	=0.046	4.66	=0.045
Intermediate	8.19	=0.010	8.19	=0.010
Superficial	0.41	=0.533	0.41	=0.530
x Deep	0.79	=0.388	0.79	=0.386
Intermediate	12.13	=0.003	12.13	=0.003
Superficial	3.63	=0.074	3.63	=0.073

Table 16. Computed central distance (CD) value means recorded for deep, intermediate and superficial enamel (pattern 2 prism packing) (values in μm)

Sample/depth	*n*	$\bar{x}$	SD	SE	CV%
Ovis aries					
Deep	10	4.08	0.37	0.12	9.07
Intermediate	10	4.15	0.24	0.08	5.78
Superficial	10	4.51	0.33	0.10	7.32
Capra hircus					
Deep	10	4.40	0.39	0.12	8.86
Intermediate	10	4.64	0.34	0.11	7.33
Superficial	10	4.75	0.56	0.18	11.79

as 4.48 μm and the pattern 3 CD value as 4.37 μm. In the two *Capra* specimens the CD values for the pattern 2 areas were 4.00 μm and 4.55 μm, whereas those for the corresponding pattern 3 regions were 4.07 μm and 4.57 μm, respectively. Clearly, in these three cases the CD values obtained for pattern 2 or pattern 3 prism packing configurations are but exiguously different.

Prism pattern compression or distention

The compression/distention (K) values obtained for the deep, intermediate, and superficial enamel levels are recorded in Table 17. In both species samples the degree of apicocervical distention tends to increase from deep to superficial levels, and, in both, the K value variability is greatest for the superficial enamel. On the other hand, whereas the degree of variability shown by the K value is lowest for the deep enamel in the *Ovis* sample, the variability within the *Capra* sample is notably the lowest with regard to the enamel in intermediate depth.

The K values presented in Table 17 pertain to pattern 2 prism packing configurations. In the single *Ovis* and two *Capra* specimens for which both superficial pattern 3 and pattern 2 prisms were observed, the pattern 2 K values were 0.59, 0.75, and 0.92. The corresponding pattern 3 K values were 0.62, 0.63, and 0.97. These two sets of values are very similar, and this suggests that the fundamental degree of apicocervical distention (or compression) within an individual is not noticeably affected by the prism packing pattern.

Estimated prism density

The estimated prism densities (EPD) per mm^2 calculated for the deep, intermediate, and superficial enamel levels in the *Capra* and *Ovis* samples are recorded in Table 18.

Table 17. Prism compression/distention (K) value means recorded for deep, intermediate, and superficial enamel (pattern 2 prism packing)

Sample/depth	*n*	$\bar{x}$	SD	SE	CV%
Ovis aries					
Deep	10	0.76	0.05	0.02	6.58
Intermediate	10	0.66	0.07	0.02	10.61
Superficial	10	0.62	0.10	0.03	16.13
Capra hircus					
Deep	10	0.75	0.09	0.03	12.00
Intermediate	10	0.65	0.04	0.01	6.15
Superficial	10	0.65	0.12	0.04	18.46

Table 18. Estimated prism density (EPD) value means recorded for deep, intermediate and superficial enamel (pattern 2 prism packing) (values signify number per μm^2)

Sample/depth	n	$\bar{x}$	SD	SE	CV%
Ovis aries					
Deep	10	70,916	11,787	3,727	16.6
Intermediate	10	67,784	7,858	2,485	11.6
Superficial	10	57,587	7,663	2,423	13.3
Capra hircus					
Deep	10	60,940	10,231	3,235	16.8
Intermediate	10	54,401	7,346	2,323	13.5
Superficial	10	53,112	12,564	3,973	23.7

Table 19. Cross-sectional ameloblast secretory area (ASA) means recorded for deep, intermediate, and superficial enamel (pattern 2 prism packing) (values in μm^2)

Sample/depth	n	$\bar{x}$	SD	SE	CV%
Ovis aries					
Deep	10	14.50	2.71	0.86	18.69
Intermediate	10	14.94	1.77	0.56	11.85
Superficial	10	17.67	2.63	0.83	14.88
Capra hircus					
Deep	10	16.87	3.05	0.96	18.08
Intermediate	10	18.72	2.85	0.90	15.22
Superficial	10	19.79	4.63	1.46	23.40

Since these estimates are directly affected by the CD value means (Table 16), it is not surprising that they tend to decrease from deep to superficial enamel just as the CD values increase outwards from the dentin enamel interface. Nor is it surprising that the coefficients of variation for the density averages display the same pattern as the CVs of the CD means. In the three instances in which superficial prism packing patterns 2 and 3 were observed, the EPD values recorded for the pattern 2 regions were 57,591, 72,011, and 55,883. The corresponding pattern 3 values of 60,549, 69,634, and 55,387 are, as might be expected, rather similar.

Cross-sectional ameloblastic secretory area

In concert with the average increase in the central distance values from deep to superficial enamel, the cross-sectional ameloblastic secretory area (ASA) means get progressively larger from the dentin–enamel junction to the outer surface of the enamel (Table 19). The CVs obtained for the ASA means for deep, intermediate, and superficial enamel in both samples are similar to the corresponding CVs for the EPD value averages (see Tables 18 and 19). These coefficients of variation are, in turn, approximately twice as large as those obtained for the respective central distance (CD) means (Table 16). The coefficients of variation recorded for the secretory area means, however, bear a very close relationship to the CVs obtained for the corresponding individual d, y, and x diameter means (see Tables 12 and 19). The three specimens that evinced superficial regions of pattern 2 and pattern 3 prism packing had cross-sectional ameloblast secretory areas of 17.36 μm^2, 13.89 μm^2 and 17.89 μm^2 for the pattern 2 fields. The pattern 3 values for these specimens are very similar at 16.52 μm^2, 14.36 μm^2, and 18.06 μm^2, respectively.

Cross-sectional prism head area

The average areas of 10 prism cores, as measured by digitized planimetry, for each specimen at the deep, intermediate, and superficial levels are recorded in Tables 20–22. Only single values are presented for the superficial enamel of the three specimens in which both pattern 2 and pattern 3 prisms were observed, because in each instance the ×3500 micrographs contained fewer than 10 prisms conforming to either packing pattern, so that the 10 cores that were measured comprised mixtures of pattern 2 and pattern 3 prisms. Since no discernible differences between the area values recorded for these two prism patterns were found in any of the three fields in question, the values for both were used to calculate the average.

In both species samples the individual CVs tended to be somewhat lower for the intermediate enamel than for either the deep or the superficial levels. Moreover, in both, the ranges between the lowest and highest CVs were smallest with regard to the enamel of intermediate depth (*Ovis*, 6.53–14.60; *Capra*, 7.66–16.15). Furthermore, in both, the ranges between the lowest and highest

Table 20. Individual variability in prism area (PA) values for deep enamel (values in μm^2)

Specimens	*n*	$\bar{x}$	SD	SE	CV%
Ovis aries					
1	10	6.58	0.58	0.18	8.82
2	10	7.27	0.83	0.26	11.42
3	10	6.72	1.03	0.33	15.33
4	10	5.65	0.73	0.23	12.91
5	10	7.58	0.99	0.31	13.06
6	10	6.60	0.65	0.21	9.85
7	10	7.69	0.64	0.20	8.32
8	10	6.43	0.92	0.29	14.30
9	10	6.31	0.63	0.20	9.99
10	10	8.09	1.47	0.46	18.18
Capra hircus					
1	10	10.33	1.62	0.51	15.69
2	10	8.79	1.66	0.52	18.89
3	10	7.49	0.71	0.23	9.48
4	10	6.72	0.72	0.23	10.71
5	10	6.95	1.00	0.32	14.39
6	10	7.90	0.76	0.24	9.62
7	10	6.77	0.63	0.20	9.31
8	10	6.91	0.74	0.23	10.70
9	10	7.18	0.85	0.27	11.84
10	10	9.29	0.94	0.30	10.12

CVs were notably the highest with regard to the superficial enamel (Table 22). Within the *Capra* sample, the two highest coefficients of variation recorded for the PA of the superficial enamel were those for the two specimens in which both pattern 2 and pattern 3 prisms were measured (Table 22, specimens 9 and 10). Within the *Ovis* sample, however, the CV obtained for the specimen with both prism patterns (Table 22, specimen 10) was clearly not the highest. This would seem to suggest that intraindividual variability in prism head area is not necessarily greater when pattern 2 and 3 prisms are sampled than when only one of these patterns is measured.

Levene's robust test for equality of individual variances within a species sample again suggests that the null hypothesis of equality of individual variances cannot be rejected in all instances (Table 23). This observation, however, pertains only to the PA values recorded for the intermediate enamel levels in both taxonomic samples. In the deep and superficial enamel in both species samples there is significant heteroscedasticity.

Table 21. Individual variability in prism area (PA) values for intermediate enamel (values in μm^2)

Specimens	*n*	$\bar{x}$	SD	SE	CV%
Ovis aries					
1	10	14.08	1.03	0.33	7.32
2	10	12.46	1.53	0.49	12.28
3	10	10.91	1.17	0.37	10.73
4	10	11.38	1.45	0.46	12.75
5	10	11.37	1.66	0.52	14.60
6	10	12.21	1.15	0.36	9.42
7	10	12.40	0.95	0.30	7.66
8	10	10.73	0.70	0.22	6.53
9	10	10.43	1.17	0.37	11.22
10	10	11.01	1.09	0.34	9.90
Capra hircus					
1	10	11.95	1.29	0.41	10.80
2	10	15.93	1.66	0.53	10.42
3	10	11.28	1.09	0.34	9.67
4	10	12.69	1.94	0.61	15.29
5	10	9.53	0.73	0.23	7.66
6	10	14.07	1.14	0.36	8.10
7	10	13.97	2.27	0.72	16.15
8	10	15.90	1.80	0.57	11.32
9	10	9.33	0.81	0.26	8.68
10	10	16.32	1.74	0.55	10.66

Table 22. Individual variability in prism area (PA) values for superficial enamel (values in μm^2)

Specimens	*n*	$\bar{x}$	SD	SE	CV%
Ovis aries					
1	10	17.90	2.07	0.66	11.56
2	10	16.04	1.81	0.57	11.28
3	10	13.11	2.12	0.67	16.18
4	10	13.86	1.76	0.56	12.70
5	10	14.95	1.23	0.39	8.23
6	10	13.31	0.74	0.23	5.56
7	10	15.06	3.35	1.06	22.25
8	10	11.21	1.55	0.49	13.82
9	10	13.24	1.13	0.36	8.54
10	10	15.39	1.54	0.49	10.01
Capra hircus					
1	10	11.81	1.11	0.35	9.40
2	10	20.70	1.81	0.57	8.75
3	10	15.35	1.45	0.46	9.44
4	10	14.18	1.17	0.37	8.25
5	10	10.50	0.94	0.30	8.96
6	10	16.53	1.39	0.44	8.41
7	10	14.16	1.75	0.55	12.36
8	10	12.44	1.21	0.38	9.73
9	10	14.20	2.21	0.70	15.57
10	10	16.08	3.42	1.08	21.27

Table 23. Analysis of equality of variance in prism area (PA) measurements among versus within individuals

Sample/depth	Levene test statistic F	*p*
Ovis aries		
Deep	1.96	=0.053
Intermediate	1.02	=0.432
Superficial	2.73	=0.007
Capra hircus		
Deep	3.06	=0.003
Intermediate	1.74	=0.092
Superficial	2.87	=0.005

The null hypothesis of equality of PA means among individuals within each species sample can be rejected on the basis of both the Welch statistic and the standard ANOVA (Table 24). These test statistics imply that different conspecific individuals within the separate *Ovis* and *Capra* samples have significant average differences in the PA values.

The averages of the individual coefficients of variation recorded for the prism core areas of the deep, intermediate, and superficial enamel levels in both samples are presented in Table 25. The CV means, like the observed ranges (Tables 20–22), were lowest for the intermediate enamel in both the *Ovis* and *Capra* samples. Moreover, in both, the CV averages obtained for the deep enamel were the highest.

The sample means of the prism area values, calculated from the individual averages (Tables 20–22), are recorded in Table 26. Within the *Ovis* sample the CV obtained for the intermediate enamel was somewhat lower than those for the deep and superficial levels, whereas in the *Capra* sample the deep enamel CV was the lowest of the three, and the coefficients pertaining to the intermediate and superficial levels were very nearly the same. In all three instances the

Table 25. Intraspecific sample variability in CV value means of prism area (PA) measurements recorded for deep, intermediate, and superficial enamel

Sample/depth	*n*	$\bar{x}$	SD
Ovis aries			
Deep	10	12.22	3.14
Intermediate	10	10.24	2.59
Superficial	10	12.01	4.70
Capra hircus			
Deep	10	12.08	3.21
Intermediate	10	10.89	2.85
Superficial	10	11.21	4.19

Table 26. Intraspecific sample variability in prism area (PA) measurements recorded for deep, intermediate, and superficial enamel (values in μm^2)

Sample/depth	*n*	$\bar{x}$	SD	SE	CV%
Ovis aries					
Deep	10	6.89	0.74	0.24	10.74
Intermediate	10	11.70	1.10	0.35	9.40
Superficial	10	14.41	1.87	0.59	12.98
Capra hircus					
Deep	10	7.83	1.24	0.39	15.84
Intermediate	10	13.10	2.58	0.81	19.70
Superficial	10	14.60	2.86	0.90	19.59

Table 24. One-way analysis of variance (among versus within individuals) of prism area (PA) measurements recorded for deep, intermediate, and superficial enamel

Sample/depth	Welch statistic W	*p*	Standard ANOVA F	*p*
Ovis aries				
Deep	6.85	<0.001	7.07	<0.001
Intermediate	9.97	<0.001	8.08	<0.001
Superficial	10.68	<0.001	10.08	<0.001
Capra hircus				
Deep	10.70	<0.001	14.57	<0.001
Intermediate	40.58	<0.001	28.43	<0.001
Superficial	35.48	<0.001	25.60	<0.001

Table 27. Analysis of interspecific equality of variance of prism area (PA) measurements between samples of *Ovis aries* and *Capra hircus*

	Levene test statistic	
Depth	F	*p*
Deep	2.58	=0.125
Intermediate	8.49	=0.009
Superficial	0.78	=0.390

CVs obtained for the *Capra* sample were higher than those for the *Ovis* sample.

Despite the foregoing observation about relative intraspecific variability being somewhat greater in *Capra* than in *Ovis*, the results of Levene's robust test for equality of absolute individual variances suggest that the null hypothesis of equality of species samples variances should not be rejected for deep and superficial enamel depths (Table 27). That is, only in the instance of intermediate enamel did the degree of absolute variability in prism head area differ significantly ($p < 0.01$) between the *Ovis* and *Capra* samples. However, one-way analysis of variance tests indicated that the null hypothesis of equality of species means should probably be rejected only for deep enamel (with $p < 0.05$) (Table 28).

Proportionate amount of prismatic matrix

The percentage areas occupied by prism core matrix (PM) within the deep, intermediate, and superficial enamel fields of the *Ovis* and *Capra* sample are recorded in Table 29. In both samples the average contribution of prismatic matrix to each field increased from the deep to the superficial enamel, the relative amount of interprismatic matrix being notably greater in the deep than in either the intermediate or superficial levels.

Table 29. Proportionate prismatic matrix (PM) values recorded for deep, intermediate, and superficial enamel (values as percentages)

Sample/depth	*n*	$\bar{x}$	SD	SE	CV%
Ovis aries					
Deep	10	48.82	9.33	2.96	19.11
Intermediate	10	79.15	10.54	3.33	13.32
Superficial	10	82.38	11.50	3.64	13.96
Capra hircus					
Deep	10	47.59	9.98	3.16	20.97
Intermediate	10	71.96	20.26	6.41	28.15
Superficial	10	75.93	16.24	5.13	21.39

Interindividual (that is, intraspecific) variability in the PM values was highest for the deep enamel in the *Ovis* sample, whereas in the *Capra* sample the CV obtained for the intermediate enamel was higher than those pertaining to the deep and superficial levels. Whereas the *Ovis* and *Capra* sample CVs recorded for deep enamel were similar, the coefficients of variation for the intermediate and superficial levels were notably higher in the *Capra* sample.

Discussion and summary

Recently, aspects of mammalian tooth enamel structure have been used with increasing frequency in taxonomic and phylogenetic studies. Most of these analyses have been based on observations of qualitative features, with little (if any) attention having been paid to the question of individual (intraspecific) variability. Moreover, even in those few instances in which quan-

Table 28. One-way analysis of variance (between species) of prism area (PA) for deep, intermediate, and superficial enamel

	Welch statistic		Standard ANOVA	
Depth	W	*p*	F	*p*
Deep	4.25	=0.057	4.25	=0.054
Intermediate	2.50	=0.140	2.50	=0.131
Superficial	0.03	=0.865	0.03	=0.865

titative parameters of enamel structure have been analyzed, the question of variability has not been assessed adequately.

If ultrastructural traits of tooth enamel are to be of any use in arguments concerning taxonomy, phylogeny, and, indeed, functional adaptation, it is imperative that the variability of these traits be established. The present study considers the degree of variability expressed by mensurable parameters of molar enamel structure at three different enamel depths (deep, intermediate, and superficial) in samples of two closely related caprine taxa (*Ovis aries* and *Capra hircus*). Each species sample comprises a single mandibular first permanent molar (M_1) from 10 different animals.

A total of nine parameters, comprising the primary d, y, and x diameters between adjacent prism centers, the average computed central distance (CD), the apicocervical compression/distention value (K), the average cross-sectional ameloblast secretory area (ASA), the cross-sectional prism head area (PA), and the proportionate or relative contribution of prismatic matrix to a given field area (PM), were variously assessed in terms of the variability evinced (i) at a given depth within a single individual, (ii) between different individuals comprising a species sample, and (iii) between species samples.

Because 10 separate d, y, and x dimensions and 10 separate PA values were recorded at each enamel depth for every individual, these four parameters could be evaluated in terms of both relative variability (as expressed by the coefficient of variation (CV)) and absolute variability at the individual, intraspecific, and interspecific levels. Inasmuch as the other parameters (CD, K, EPD, ASA, and PM) are each represented by a single value calculated for each animal at a certain enamel depth, their variance is amenable to evaluation only at the intraspecific and interspecific hierarchical levels.

Levene's robust test for homogeneity of absolute variability among individuals of a given species shows interesting differences between *Ovis aries* and *Capra hircus*. Rejection of the null hypothesis of homoscedasticity is warranted for the x diameter at all enamel levels in the *Ovis* sample but only at the superficial level in the *Capra* sample. In contrast, rejection is warranted for the d diameter at all levels in *Capra* but at none of the three levels for *Ovis*. Whereas acceptance of the null hypothesis is indicated for the y dimension at the deep level of *Ovis*, this is the case in *Capra* only at the intermediate level. Nevertheless, significant differences among individuals within each species exist for all parameter means (the y diameter in *Ovis* deep enamel is equivocal).

The results of the present study also indicate that in both caprine species, relative variability in structural parameters is not equivalent at different enamel depths. For the nine metrical features examined, relative variability tends to be higher at deep and superficial levels than in the intermediate enamel. At the same time, however, the degree of relative variability shown by these parameters at each enamel depth is comparable among conspecific individuals and between species samples.

Variability in mensurable parameters of enamel structure of the mandibular first molars of these closely related caprine taxa appears to be of nearly equivalent magnitude at intraindividual, intraspecific, and interspecific levels. For example, the hypothesized equality of interspecific variances could be rejected only for the y diameter at the superficial level and for the prism area at the intermediate level. In addition, equality of species means could not be rejected for the d, y, and x diameters or for the prism area at the superficial level. Significant differences are commoner at deep and intermediate levels.

Whereas the results of this study of variability in quantitative parameters of enamel pertain strictly to the molars of the two species examined, they would appear to indicate that caution should be exercised in taxonomic comparisons of mammalian enamel structure—especially those that utilize mensurable data. With regard to the variables for which individual specimen means were calculated (that is, the d, y, and x dimensions and the PA values), it is evident that not only are there significant differences in absolute variance among individuals in most instan-

ces, but also the hypothesis of equality of conspecific individual means can be rejected in all instances. Even within the comparatively thin-enamelled caprine species examined here there exist pronounced differences among deep, intermediate, and superficial prism fields in the degrees of both absolute and relative variability. Absolute individual variances tend to be equivalent only at intermediate enamel depth, and measures of relative variability tend to be lower for parameters of intermediate depth than for either deep or superficial enamel. Generally, whereas the degrees of absolute and relative variability tend to be lowest for enamel of intermediate depth, superficial enamel fields tend to evince the greatest amount of variability.

In view of the differences displayed among conspecific individuals and among various enamel depths, it is evident that taxonomic comparisons that utilize such metrical data must be made at equivalent relative enamel depths. Studies that rely on quantitative analyses of variables such as prism size and ameloblast secretory area must first adequately address the question of individual variability before quantitative data on enamel structure can be used with any degree of reliability in taxonomic and/or phylogenetic analyses.

The tendency for superficial caprine enamel to display more variability than deep and especially intermediate enamel may be related (developmentally) to the observation that, whereas only pattern 2 prisms were encountered in the deep and intermediate fields, prism packing patterns 2 and 3 were found in some superficial fields. Inasmuch as the superficial fields that were examined were very close to the outermost crown surface, it is possible that the increased variability at this level may be related to the terminal phase of ameloblastic activity. At the same time, whereas only pattern 2 prism packing was observed in the deep enamel fields (demonstrating that pattern 1 enamel is not necessarily a developmental precursor of other packing patterns), the higher degrees of variability displayed by them in comparison with the fields of intermediate depth may be related to the initial onset of ameloblastic secretory activity. This initiation and the final stage of amelogenesis may well act to impart a greater degree of variability to prismatic enamel structure; certainly, the present results suggest that quantitative assessments of deep and superficial enamel that are used in comparative phylogenetic analyses should be viewed with circumspection.

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References

1. Tomes J. On the structure of the dental tissues of the order Rodentia. Phil Trans R Soc Lond 1850;140:529–67.
2. Carter JT. The structure of the enamel in the primates and some other mammals. Proc Zool Soc Lond 1922;1922:599–608.
3. Shobusawa M. Vergleichende Untersuchungen über die Form der Schmelzprismen der Saugetiere. Okajimas Folia Anat Jpn 1952;24:371–92.
4. Kawai N. Comparative anatomy of the bands of Schreger. Okajimas Folia Anat Jpn 1955;27:115–31.
5. Boyde A. The structure and development of mammalian enamel [Thesis]. London: University of London, 1964.
6. Boyde A. The structure of developing mammalian dental enamel. In: Fearnhead RW, Stack MV, eds. Tooth enamel: its composition, properties and fundamental structure. Bristol: Wright, 1965:163–7.
7. Boyde A. The development of enamel in mammals. In: Blackwood JJ, Owen M, eds. Calcified tissues. New York: Springer-Verlag, 1965:276–80.
8. Boyde A. Electron microscope observations relating to the nature and development of prism decussation in mammalian dental enamel. Bull Groupe Int Rech Sci Stomatol Odontol 1969;12:151–207.
9. Boyde A. Comparative histology of mammalian teeth. In: Dahlberg AA, ed. Dental morphology

and evolution. Chicago: University of Chicago Press, 1971;81–94.
10. Shellis RP, Poole DFG. The calcified dental tissues of primates. In: Lavelle CLB, Shellis RP, Poole DFG, eds. Evolutionary changes to the primate skull and dentition. Springfield, Ill.: Thomas, 1977:197–279.
11. Boyde A, Martin LB. Enamel microstructure determination in hominoid and cercopithecoid primates. Anat Embryol 1982;165:193–212.
12. Ishiyama M. Comparative histology of tooth enamel in several toothed whales. In: Fearnhead RW, Suga S, eds. Tooth enamel. Vol. IV. New York: Elsevier, 1984:432–6.
13. Gantt DG, Pilbeam DR, Steward GP. Hominoid enamel prism patterns. Science 1977;198:1155–7.
14. Boyde A. Development of the structure of the enamel of the incisor teeth in the three classical subordinal groups of the Rodentia. In: Butler PM, Joysey KA, eds. Development, function and evolution of teeth. New York: Academic Press, 1978:43–58.
15. Vrba ES, Grine FE. Australopithecine enamel prism patterns. Science 1978;202:890–2.
16. Gantt DG. Implications of enamel prism pattern for the origin of the New World monkeys. In: Ciochon RL, Chiarelli AB, eds. Evolutionary biology of the New World monkeys and continental drift. New York: Plenum, 1980:249–98.
17. von Koenigswald W. Enamel structure in the molars of Arvicolidae (Rodentia, Mammalia), a key to functional morphology and phylogeny. In: Kurten B, ed. Teeth: form, function and evolution. New York: Columbia University Press, 1982:109–22.
18. Gantt DG. The enamel of Neogene hominoids: structural and phyletic implications. In: Ciochon RL, Corruccini RS, eds. New interpretations of ape and human ancestry. New York: Plenum Press, 1983:249–98.
19. Boyde A, Martin LB. A non-destructive survey of prism packing patterns in primate enamels. In: Fearnhead RW, Suga S, eds. Tooth enamel. Vol. IV. New York: Elsevier, 1984:417–21.
20. Marcus H. Zur Phylogenie der Schmelzprismen. Z Zellforsch 1931;12:395–429.
21. Eisenberg MJ. A microscopic study of the surface enamel of human teeth. Anat Rec 1938;71:221–6.
22. Fosse G. A quantitative analysis of the numerical density and the distributional pattern of prisms and ameloblasts in dental enamel and tooth germs. III. The calculation of prism diameters and numbers of prisms per unit area in dental enamel. Acta Odontol Scand 1968;26:315–36.
23. Fosse G. A quantitative analysis of the numerical density and the distributional pattern of prisms and ameloblasts in dental enamel and tooth germs. IV. The vertical compression of the prism pattern on the outer enamel surface of human permanent teeth. Acta Odontol Scand 1968;26:545–72.
24. Boyde A. Correlation of ameloblast size with enamel prism pattern: use of scanning electron microscope to make surface area measurements. Z Zellforsch 1969;93:583–93.
25. Fosse G, Eskildsen O, Risnes S, Sloan RE. Prism size in tooth enamel of some Late Creataceous mammals and its value in multituberculate taxonomy. Zool Scripta 1978;7:57–61.
26. Sahni A. Enamel ultrastructure of certain North American Cretaceous mammals. Paleontographica 1979;166:37–49.
27. Carlson SJ, Krause DW. Enamel ultrastructure in multituberculate mammals: an investigation of variability. Contrib Mus Paleont Univ Mich 1985;27:1–50.
28. Fosse G, Kielan-Jaworowska Z, Skaale SG. The microstructure of tooth enamel in multituberculate mammals. Palaeontology 1985;28:435–49.
29. Grine FE, Krause DW, Martin LB. The ultrastructure of *Oreopithecus bambolii* tooth enamel: systematic implications. Am J Phys Anthropol 1985;66:177–8.
30. Grine FE. Effects of different etching agents on bovid tooth enamel. S Afr J Sci 1986;82:265–70.
31. Levene H. Robust tests for equality of variance. In: Olkin I, ed. Contributions to probability and statistics. Palo Alto, Calif: Stanford University Press, 1960:278–92.
32. Brown MB, Forsythe AB. Robust tests for the equality of variances. J Am Stat Assoc 1974;69:364–7.
33. Van Valen L. The statistics of variation. Evol Theory 1978;4:33–43.
34. Dixon WJ. PFD. Description of groups (strata) with histograms and analysis of variance. BMDP statistical software. Berkeley, Calif.: University of California Press, 1983:105–22.
35. Brown MB, Forsythe AB. The small sample behavior of some statistics which test for the equality of several means. Technometrics 1974;16:129–32.

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