Built to Last: The Structure, Function, and Evolution of Primate Dental Enamel

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The teeth of every primate, living and extinct, are covered by a hard, durable layer of enamel. This is not unique: Almost all mammals have enamel-covered teeth. In addition, all of the variations in enamel structure that occur in primates are also found in other groups of mammals. Nevertheless, the very complexity of enamel and the variation we see in it on the teeth of living and fossil primates raise questions about its evolutionary significance. Is the complex structure of primate enamel adaptive? What, if anything, does enamel structure tell us about primate phylogeny? To answer these questions, we need to look more closely at the characteristics of prismatic enamel in primates and at the distribution of those characteristics, both in relation to our knowledge of primate dental function and feeding ecology and from a phylogenetic perspective.

THE STRUCTURE AND COMPOSITION OF ENAMEL

Enamel is the strongest tissue in the body. It is not only *hard* (resistant to permanent surface deformation), but

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tough (resistant to crack propagation and brittle fracture). Its durability means that enamel can potentially be preserved, unaltered, for literally millions of years. Moreover, because it is not remodeled during life, enamel is unique among mammalian tissues in that it preserves a permanent record of its ontogeny.

Enamel is composed of fiber-like mineral crystals and a small nonmineral fraction of water and protein that holds the mineral fibers together. The resulting composite material is much tougher than mineral alone. The mineral and nonmineral components are organized in a complex fabric that dissipates forces traveling through teeth and protects them from fracture.

Mineral is the dominant component of enamel, which is much more highly mineralized than the two other calcified dental tissues, dentine and cementum. The enamel mineral is a form of carbonate hydroxyapatite $[Ca_{10}(PO_4)_6(OH)_2]$. The Ca:P ratio of enamel apatite is slightly lower than that of hydroxyapatite.¹⁻³ In human teeth, enamel is densest (96% apatite) close to the outer surface and less dense (84% apatite) near the enamel-dentine junction.⁴

Though water and protein comprise only a minor part of mature enamel,

they are crucial to its development (see Box 1) and are important in understanding its structural organization and physical properties. Abundant hydrophobic proteins called amelogenins dominate developing enamel, but as the mineral crystals grow in size during maturation, amelogenins disappear so that only the less abundant, acidic proteins, enamelins and tuftelins remain.5-8 This remnant protein fraction is contained in the spaces between mineral crystals, where it serves as a "glue" between crystallites.9 Most of the water within enamel is tightly bound to the mineral phase¹⁰ and serves to influence enamel's compressibility and permeability.11,12 Although the high mineral content accounts for enamel's hardness, it is the arrangement and organization of its mineral and nonmineral constituents (enamel structure) that modulates the way enamel responds to stress.

Enamel structure can be visualized through a simple hierarchical model of increasing complexity and scale.13-16 The least complex and smallest structural units are apatite crystallites. In most mammal teeth, crystallites are grouped into more complex and largerscale structures known as prisms. The arrangement of groups of prisms determines the next most complex unit, enamel types. On a still larger and more complex scale, the different enamel types within a tooth define its schmelzmuster; this German term is preferred over its literal English translation, "enamel pattern," which is a specialized description of the arrangement of enamel types on occlusal surfaces of hypsodont teeth.¹⁵ The most complex and largest-scale hierarchical level is that of the *dentition*, which describes the variation of schmelzmus-

Box 1. Enamel Development

The first stages of tooth development consist of a series of epithelialmesenchymal interactions that define the enamel-dentine junction.¹¹¹ As is the case in many other morphological systems, both morphogen gradients and the products of homeobox genes appear to play significant roles in determining the location and timing of tooth development.^{112–114} The mesenchyme within tooth germs is derived from the neural crest and gives rise to cells known as odontoblasts. The onset of dentine secretion by odontoblasts induces enamel formation. The epithelium within tooth germs differentiates into ameloblasts. the cells that secrete the enamel matrix proteins in which hydroxyapatite crystals grow. It is not entirely clear whether dental epithelium is ectodermal or endodermal in origin.8,111

At some point in the life cycle of most mammalian ameloblasts, the secretory surface develops a protrusion called a Tomes process, which is surrounded by a flattened area called an ameloblast shoulder (A). Both of these structures secrete enamel matrix proteins. During enamel mineralization, hydroxyapatite crystals within the secreted enamel matrix proteins grow perpendicular to Tomes processes and ameloblast shoulders.^{115,116} Because of the fixed relationship of the crystallites growing perpendicular to ameloblast secretory surfaces, the shape of the secretory poles of ameloblasts determines the orientation of mature crystallites and, therefore, the formation of either prismless or prismatic enamel (A). At both the beginning and end of enamel deposition in mammals, ameloblasts lose their Tomes processes. This results in a very thin layer (sometimes less than a micron) of parallel crystallite enamel near the enamel-dentine junction and usually a thicker layer at the outer surfaces of teeth. Tomes processes form and assume a variety of shapes during the middle phase of ameloblast secretion, leading to the different enamel prism types seen in mid-thickness enamel.¹¹⁷ (see Fig. 1).

The movement of ameloblasts relative to one another and the local mechanical environment surrounding Tomes' processes determines the enamel type—in primates, either radial or decussating enamel. Though all agree that complex movements of ameloblasts result in prism decussation, the specific mechanisms mediating it remain a source of debate.^{8,23,43,87}

The activity of ameloblasts, like that of other secretory cells, varies in regular cycles. Ameloblasts exhibit both circadian (daily) and circaseptan (approximately weekly) variation in the rate at which enamel matrix proteins are deposited. A record of daily and weekly fluctuations in depositional activity are visible in fully mineralized enamel as two types of incremental lines: prism cross-striations (B) and (Brown) striae of Retzius, respectively. In most primate teeth (but not necessarily all mammal teeth), some striae of Retzius are expressed at the tooth surface as *perikymata* (see Fig. 4).

The relationship between cross striations and circadian variation in enamel deposition has been demonstrated experimentally.^{118,119} Studies documenting longer depositional cycles are based on counts of cross striations between adjacent striae of Retzius. These cycles have been called circaseptan, but the seven-day interval implied by this name is certainly not universal, even among primates. Although the interval between striae and their expression on the tooth surface as perikymata is approximately seven days in humans,120 it varies both within¹²¹⁻¹²³ and among¹²⁴⁻¹²⁷ species. Nevertheless, many studies have made use of the relatively constant (roughly weekly) time intervals represented by striae of Retzius and perikymata to investigate comparative rates of growth and development in fossil hominoids and hominids.¹²⁸⁻¹³² Such studies may ultimately go a long way toward illuminating how growth rates and patterns constrain prism patterns and enamel types and, in doing so, have influenced the evolution of primate enamel microstructures.



A. The relationship between ameloblast shape and the orientation of hydroxyapatite crystallites in parallel crystallite prismless enamel (top) and prismatic enamel (bottom). Hydroxyapatite crystals (short dashed lines) always grow perpendicular to the secretory faces of ameloblasts. Thus, parallel crystallite enamel is formed when ameloblasts lack Tomes processes and prismatic enamel is formed when the secretory poles of ameloblasts have Tomes processes and ameloblast shoulders.



B. Prism cross striations appear under backscattered scanning electron microscopy as dark bands (arrows) perpendicular to prism long axes. The dark bands indicate regions of increased carbonate concentration that form during daily periods of decreased deposition. In the scanning electron microscope, cross striations usually, but not always,¹²² appear to be associated with so-called prism varicosities, or alternating swellings and constrictions along prism long axes. Several studies have demonstrated an association between crossstriation repeat interval and enamel prism type.^{9,41}



Figure 1. Scanning electron micrographs of primate prism morphology. A: Longitudinal section through a lower incisor of *Varecia variegatus* showing inner layer of radial prismatic enamel (PE) and outer layer of prismless parallel crystallite enamel (PCE). Enamel-dentine junction at bottom. B: Surface-tangential section through a *Loris tardigradus* molar showing the arrangement of prisms (P) and interprismatic enamel (IP). In some primates and other mammals, crystallites within the prisms and contiguous interprismatic enamel converge, forming a linear discontinuity called an enamel seam (arrows). C: Longitudinal section through a *Loris tardigradus* molar shows that crystallites in the prisms (P) are oriented roughly parallel to the prism long axis and at an angle to crystallites in the interprismatic (IP) enamel. D: Surface-tangential section through a *Tarsius syrichta* molar showing cross sections of enamel prisms demarcated from interprismatic and interprismatic regions is gradual at the bottom (cervical direction) of most prisms, so the prism sheath is arc-shaped. However, some prisms have closed prism sheaths, and there is considerable variation in prism shape and their arrangement. Scale bars = $10 \,\mu$ m.

ter from tooth to tooth. Some of these structural levels are unique to mammalian teeth, although many other vertebrates have teeth with complex enamel or enamel-like organization.^{14,17,18}

Enamel Crystallites

The apatite crystals in enamel are called crystallites because of their submicroscopic dimensions. Like all crystalline structures, enamel crystallites have a short dimension, the a-axis, and a longer dimension, the c-axis or optical axis. Reports of crystallite length vary from a fraction of a micron to 100 microns,¹⁹ but most agree that they are very long compared to the short crystals that characterize bone. Early in enamel development, crystallites are flat and ribbon-like,²⁰ but fully mineralized crystallites are hexagonal¹⁹ or rhomboidal²¹ in cross section. Complicating their description is the likelihood that crystallite shape differs between species and may become more irregular as crystallites increase in size during enamel maturation.²² Small groups of adjacent crystallites are arranged in *subparallel crystallites* are aligned parallel to one another.²³

Although there is some evidence of interspecific differences in crystallite composition, size, and shape,²² most comparative studies have focused on interspecific variation in their arrangement and orientation. These criteria are used to define the two major classes of mammalian enamel: prismless and prismatic enamel. (The terms "aprismatic enamel," "nonprismatic enamel," and "preprismatic enamel" have been used extensively in the literature to refer to various types of prismless enamel, but confusion has arisen from inconsistent application of these concepts.14 The most recent synthesis of enamel terminology recommends abandoning their use.13). The simplest arrangement of enamel crystallites is a type of prismless enamel called parallel crystallite enamel. In parallel crystallite enamel, the crystallites are oriented with their long axes roughly parallel to one another and perpendicular to the outer tooth surface and to the enamel-dentine junction (Fig. 1A). Parallel crystallite enamel is found in at least some regions of most mammal teeth, most prominently close to the outer surface of the tooth. Some reptiles and early mammals have a slightly more complex type of prismless enamel. This enamel, termed columnar unit enamel, is characterized by a regular pattern of gently diverging crystallites.¹⁷ Prismless enamel (either parallel crystallite enamel or columnar unit enamel) is the only type of enamel found in reptile teeth, with the single exception of the agamid lizard, Uromastyx. 14,17,24 In primates, as in most mammals, prismless enamel is a minor component of the schmelzmuster. The bulk of primate enamel has a more complex organization, known as prismatic enamel, in which the primary structural units are enamel prisms.

Enamel Prisms

These are both more complex and larger in scale than crystallites. Whereas crystallites are a fraction of a micron in diameter, the diameter of prisms ranges from two to ten microns. *Enamel prisms* are rod-shaped (cylindrical) bundles of crystallites (Fig. 1B–D). The crystallites within a bundle, or prism, are oriented roughly parallel to the prism long axis, though in some prism types they fan out from the center toward the edges (Fig. 2A).



Figure 2. Schematic block diagrams of prismatic enamel (above), showing the relationship of prismatic (P) and interprismatic (IP) crystallites. Crystallites in interprismatic regions are oriented at an angle to crystallites within prisms. In this prism pattern, the change in crystallite orientations between prisms and IP enamel is abrupt adjacent to the prism sheaths, but gradual at the open, cervical ends of the prisms. If enamel is sectioned at different angles, as a result of either artifacts produced during specimen preparation or the formation of differently angled wear facets during normal tooth use, this will produce different orientations of prismatic and interprismatic crystallites relative to the sectioned surface (above, right) and differences in the size and shape of prism cross-sections¹⁰⁸ (below).

The long axes of individual prisms extend from the enamel-dentine junction to the outer surface of a tooth. The crystallites that lie outside the prisms are called *interprismatic* enamel. Prismatic and interprismatic enamel differ only in the arrangement and orientation of its crystallites; their composition is identical. The boundaries of a prism are defined by submicroscopic gaps formed by the change in orientation between prismatic and the interprismatic crystallites. Because protein and water accumulate in these gaps, prism boundaries appear as distinct structures called prism sheaths (Fig. 1D).

Prism patterns are two-dimensional descriptions of cross-sectioned prisms (sectioned perpendicular to their long axes). They are defined by the shapes of prism sheaths and differences in prism packing, or the way prisms and interprismatic enamel are arranged relative to one another. Boyde^{9,25–27} proposed an influential scheme of enamel classification based on observations of the developing enamel sur-

face that correlated with differences in the size, shape, and arrangement of mature enamel prism cross-sections. Although many other workers have investigated interspecific variation in prism structure,^{28–33} no other descriptive scheme for tooth microstructure has been so broadly used in primate dental studies.

Boyde's scheme distinguished three major classes and several subclasses of prisms in mammalian enamel. (Fig. 3). He demonstrated that many species are characterized by the predominance of a single prism pattern. He and others went on to characterize entire families and even orders of mammals by prism pattern.^{14,26,27,34} In reality, prism cross sections show far more variability in shape and alignment than is evident from schematic diagrams of prism packing arrangements (Fig. 1D). Indeed, many species show a combination of all three prism patterns. Moreover, the appearance of prism cross sections can change dramatically depending on the angle at which they intercept tooth surfaces

(Fig. 2B). Because of this, confusion arises over distinguishing prism patterns in primate teeth, especially variants of the basic patterns.35,36 Some researchers have advocated a simpler classification that distinguishes only between "closed" prisms (as in Pattern 1) and "open" or "arc-shaped" prisms (as in Patterns 2 and 3).^{14,37–39} Despite the practical drawbacks to applying Boyde's prism classification scheme within Primates, that scheme has been almost universally adopted in the literature on primate enamel. We report those designations here (Table 1 and Table 2), with the important caveat that they have not necessarily been applied consistently among different studies.

Enamel types are independent of prism patterns, and thus represent a separate class of characters as well as a distinct level of organization. The type of prismless enamel found in primate teeth, like that of all mammals, is parallel crystallite enamel.

Enamel Types

Much of the variation in enamel occurs not at the level of crystallites or prisms, but at the more complex level of enamel type. Enamel types are independent of prism patterns, and thus represent a separate class of characters as well as a distinct level of organization.¹⁵ The type of prismless enamel found in primate teeth, like that of all mammals, is parallel crystallite enamel. The two prismatic enamel types that occur in primate enamel are radial enamel and decussating enamel (Fig. 4). In radial enamel, all prisms are roughly parallel to one another as they extend out from the enameldentine junction to the surface. In



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and most other mammals, the layers are usually several prisms thick (known as multiserial enamel or pluriserial enamel), but in some rodents each layer is only one prism thick (uniserial enamel). The most common type of decussating enamel is *horizon*tal decussation, in which Hunter-Schreger bands are stacked on top of one another from crown to root, with long axes of prisms in adjacent horizontal layers of prisms extending toward the outer enamel surface at different angles (Fig. 5). This is the type of decussating enamel found in primate teeth.^{32,35,38,41,42}

"Hunter-Schreger bands" and "prism decussation" (literally, "crossing of prisms") are sometimes used synonomously. However, complete crossing of prisms at 90° to those in adjacent groups ("true decussation"⁴³) does not

Simple radial enamel is the only type of prismatic enamel that occurs in the teeth of the earliest mammals and many small-bodied living mammals, including many of the smaller primates.

occur in all species. More typically, the angle between prisms in adjacent bands is less than 90°, and changes as prisms pursue a slightly sinuous course from the enamel-dentine junction to the outer tooth surface. There is often a gradual change in the orientation of prisms from the center of one band to the center of the next, giving the impression of a transitional zone between bands (Fig. 4E). Most descriptions of Hunter-Schreger bands are based on the appearance of prisms in sectioned teeth. Bands of prisms sectioned more or less parallel to their long axes are called *parazones*; those sectioned more or less perpendicular to their long axes are called *diazones*.

There is considerable interspecific variation in Hunter-Schreger bands, including the numbers of prisms in

Figure 3. Diagram of Boyde's prism patterns.^{9,26} Pattern 1 prisms are usually small (3 to 5 µm) and have complete, roughly circular, boundaries. Prisms are completely separated by interprismatic enamel and are arrayed in offset horizontal rows. Close to the outer enamel surface, the prisms of most mammals are Pattern 1. Boyde's Pattern 2 and Pattern 3 defined two major classes of prisms with incomplete prism boundaries and arc-shaped prism sheaths. In both of these prism patterns, the open side of the prism is toward the cervix (root-crown junction) of the tooth. Pattern 2 prisms are small 2 to 4 µm in diameter and are arranged in longitudinal columns from the apex to the cervix. Pattern 2 variants (Patterns 2, 2A, and 2B) differ in the amount and distribution of interprismatic enamel and packed in horizontally offset rows, like Pattern 1 prisms. The variants (Pattern 3, 3B, and 3C) differ in the shape of the prism sheath and the amount and distribution of interprismatic enamel. Although Boyde's scheme has been widely used in primate enamel studies, prism patterns in many primate species are so variable that it may be more practical to distinguish only between ``closed'' (Pattern 1) and ``open'' (Pattern 2 and 3) prisms.

decussating enamel, prisms are arranged in regularly organized, alternating layers or groups that extend out from the enamel-dentine junction to the surface at different orientations. Decussating enamel produces the optical phenomenon referred to as Hunter-Schreger bands, which are a result of the different refractive properties of differently oriented prisms in adjacent layers. Other prismatic enamel types that do not occur in primates include *irregular* or *3-D enamel*, which consists of complexly interwoven bundles of prisms,¹⁶ and *tangential enamel*, which consists of prisms with a strong lateral deviation, so that prism axes are oriented tangential to the tooth surface.15,40

Radial enamel is the prismatic enamel type most common among mammals.⁴⁰ In simple radial enamel, the orientation of interprismatic crystallites deviates only slightly from that of prismatic crystallites. Simple radial enamel is the only type of prismatic enamel that occurs in the teeth of the earliest mammals and many smallbodied living mammals, including

many of the smaller primates. A derived variant of radial enamel, modified radial enamel, is characterized by very high angles between prismatic and interprismatic crystallites (close to 90° in some cases) and by interprismatic crystallites that are arranged in sheets as thick as the prisms themselves. Modified radial enamel occurs in many hypsodont ungulates and many marsupials. It has not been found in primate teeth. Although some primate enamels show high angles between prismatic and interprismatic crystallites, the interrow sheets are not as thick as those in the modified radial enamel of ungulates and tend to anastomose between adjacent rows rather than maintaining the sheet-like arrangement of the interprismatic crystallites of modified radial enamel.

Decussating enamel, (or Hunter-Schreger bands) like radial enamel, is common in primates. In decussating enamel, layers of prisms extend outward from the enamel-dentine junction to the tooth surface at an angle to prisms in adjacent layers. In primates

TABLE 1. Summary of Prism Patterns and Enamel Types for Living Primates							
	Mass (gm) ⁹⁶	Prism	Enamel Types				
Taxon	(F/M)	Patterns	(From enamel-dentine junction to surface)				
Hapalemur ariseus	670/748	1 3 ³⁸	Radial prismless ³⁸				
lemursp.	0,0,,,,0	1,0	HSB. radial ³²				
Lemur catta	2.210	1, 3 ³⁸	HSB, radial, prismless ³⁸				
Eulemur fulvus	2,250/2,180	1, 3 ³⁸	HSB. radial, prismless ³⁸				
Eulemur macaco	1,760/1,880	1, 3 ³⁸	HSB, radial, prismless ³⁸				
Varecia varieaata	3,520/3,630	1, 3 ³⁸	HSB. radial, prismless ³⁸				
Indriidae	-,,-,	., -	,				
Propithecus verreauxi	2,950	1, 3	HSB. radial, prismless				
Cheirogaleidae							
Microcebus murinus	63/59	1, 3	Radial, prismless				
Cheirogaleus medius	282/283	1, 3	Irregular HSB, radial , prismless				
Daubentoniidae			č				
Daubentonia madagascariensis	2,490	2 ⁸⁰	HSB ^{72,80}				
Lorisidae							
Nycticebus coucang	626/679	1, 3	Radial, prismless ⁵⁴				
			Irregular HSB (canine only)				
Loris tardigradus	269/264	1, 3	Radial, prismless				
Perodicticus potto	836/830	1, 3 41	Radial, prismless ⁴¹				
Galagidae							
Otolemur garnetti	734/794	1, 3	Radial, prismless				
Galago senegalensis	199/227	1, 3 ⁴¹	Radial, prismless ⁴¹				
Otolemur crassicaudatus	1,110/1,190	1, 3 ³⁷	Radial, prismless ³⁷				
Tarsiidae							
Tarsius syrichta	117/114	1, 3	Radial, prismless				
Tarsius spectrum	108/125	335	Radial, prismless				
Tarsius bancanus	117/128	3 ³⁹	Radial, prismless				
Atelidae							
Alouatta sp.		2A; ⁸¹ 1, 3 ³⁶	Radial , weak HSB, prismless, radial ³²				
Alouatta seniculus	5,210/6,690	1, 2, 3 ³⁵	Radial ⁵⁴				
Alouatta fusca	4,350/6,730	1, 2, 3 ³⁵					
Ateles sp.		2A; ⁸¹ 1; ³⁵ 1, 3B ^{41,82}	irregular HSB, radial, prismless ^{32,41}				
Ateles belzebuth	7,250/8,290		HSB ⁵⁴				
Lagothrix lagotricha	7,020/7,280	1, 3; ³⁶ 1, 2, 3 ³⁵	HSB ⁵⁴				
Brachyteles arachnoides	8,070/9,610	330	HSB ⁵⁴				
Callicebus moloch	956/1,020	2B; ⁸¹ 2, 3; ³⁰ 1, 2, 3 ³⁵	Radial, prismless ⁵⁴				
Cacajao melanocephalus	2,710/3,160	342	HSB, prismless ^{42,54}				
Chiropotes satanus	2,580/2,900	2;35 3;42 1, 336	HSB, prismless ⁴²				
Pithecia sp.	1 500 (1 0 40	1, 300					
Pithecia pithecia Ditte e das as as hus	1,580/1,940	335					
PITNECIA MONACIUS	2,110/2,610	300	HSB, prismiess, HSB ³⁴				
	70//010	00.81 00.82 1 035	Develiert versionelle er 54				
Aotus trivirgatus	/30/813	2B; ⁰¹ 3C; ⁰² 1, 3 ⁰⁰	Raaiai, prismiess ³⁴				
Cebus sp.	0 500 /2 / 50	ZB;° ¹ I, 3°°	Develorit LICD reviewelle and 2.54				
Cebus apella	2,320/3,030	1, 3 1, 2 35	Radial, HSB, prismiess ^{22,04}				
Cebus capacinas	2,340/3,060	1, 300	Radial USP , prismiess ²				
	2,290/3,100	1 20.41 82 035	Radial, nsb, prismiess -				
Callithriven	000/779	1, 3C, 11,02 Z ⁰⁰					
Callithrix argontata	360/333	1, //or 3C, or 200					
Callithrix bumoralifor	A70/A75						
Callithrix iacchus	304/317	1 2 249	HSB prismlose ^{32,46,49}				
Cebuella pyamaea	1224/01/	1, 2, 3 3,35 1 2 3 49	HSB prismless ^{46,49}				
Leontonitheous rosalia	508/620	1 2 3·35 1 2 349	Padial prismless ^{46,49,54}				
Saauinusso	0707020	1, 2, 0, 1, 2, 0	Padial HSB ⁸²				
Saguinus fuscicollis	358/3/3	1, 35 1 2 349	Padial, irregular HSB, prismless ^{46,49}				
Saquinus aeoffrovi	502//82	1 2 3 ⁴⁹	Radial irregular HSB prismless ⁴⁹				
Saquinus imperator	475/171	1 2 3 ⁴⁹	Radial irregular HSB prismless				
Saauinus inustus	2803/585	i, 2, 0	Radial irregular HSB prismless ⁴⁶				
Saquinus labiatus	539/490	1, 2 , 3 ⁴⁹	Radial, irregular HSB, prismless ^{46,49}				
Saguinus leucopus	490/494	· <i>/</i> _ , _	Radial, irregular HSB ⁴⁶				

TABLE 1. (Continued)					
	Mass (gm) ⁹⁶	Prism	Enamel Types		
Taxon	(F/M)	Patterns	(From enamel-dentine junction to surface)		
Saguinus midas	575/515		Radial, irregular HSB, prismless ⁴⁶		
Saguinus mystax	539/510	1, 2, 3 49	Radial, irregular HSB, prismless ^{46,49}		
Saguinus nigricollis	484/468		Radial, irregular HSB, prismless ⁴⁶		
Saguinus oedipus	404/418	1, 2, 3 49	Radial, irregular HSB, prismless ^{46,49}		
Callimico goeldii	468/499	1, 2, 3 49	Radial, irregular HSB, prismless ^{46,49}		
Cercopithecidae					
Cercocebus torquatus	6,230/11,000	2 , 3 ³⁵	HSB, radial, prismless		
Cercopithecus mona	?/5,100	2, 3 ³⁵			
Cercopithecus neglectus	4,230/7,350	2, 3 ³⁵			
Cercopithecus pygerythus		3B ^{41,81}	HSB, radial, prismless ⁴¹		
Chlorocebus aethiops	2,980/4,260	2, 3 ⁸³			
Colobus angolensis	7,570/9,680	1, 3 ³⁵			
Colobus polykomos	8,300/9,900	1, 3 ^{35,83}			
Erythrocebus patas	5,770/10,600	1, 2; ⁹ 3B ⁸²			
Lophocebus alibgena	6,020/8,250	2, 3 ³⁵	HSB, radial, prismless		
Macaca fasciculata	3,590/5,360	341	HSB, radial, prismless ^{32,41}		
Macaca mulatta	5,370/7,710	3; ^{41,83} 1, 2, 3 ^{9,25,35}	HSB, radial, prismless ⁴¹		
Macaca nemestrina	6,500/1,120	2 , 3 ³⁵			
Macaca speciosa		341	HSB, radial, prismless ⁴¹		
Macaca sylvanus	11,000/16,000	2, 3 ³⁵			
Nasalis larvatus	9,820/20,400	3 ⁸³			
Papio anubis	1,330/25,100	2, 3 ⁸³			
Papio cynocephalus	12,300/21,800	3; ⁴¹ 2, 3 ³⁵	HSB, radial, prismless ⁴¹		
Papio hamadryas	9,900/16,900	3 ⁸³			
Papio sphinx		2 , 3 ³⁵			
Presbytis obscura		1, 2 ³⁵			
Semnopithecus entellus	9,890/13,000	1, 2, 3 ^{35,83}			
Trachypithecus cristatus	5,760/6,610	1, 3 ³⁵			
Hominoidea					
Gorilla gorilla	>70,000	1; ⁹⁰ 1, 2, 3 ^{9,35,85}	Radial; ⁴¹ weak HSB, radial, prismless ³⁵		
Homo sapiens	>40,000	1, 2, 3 ^{9,35,85}	HSB, radial, prismless ³⁵		
Pan troglodytes	>33,000	1; ⁹⁰ 1, 2, 3 ^{9,35,85}	HSB, radial, prismless ³⁵		
Pongo pygmaeus	35,600/77,900	1 ; ⁹⁰ 1, 2, 3 ^{9,35,85}	HSB, radial, prismless ^{32,35}		
Hylobates sp.	5,500-11,900	1, 2, 3 9	HSB ³²		

Bold type indicates the predominant prism pattern or enamel type reported in the literature; contradictory or alternative interpretations are discussed in the text. Unreferenced data are from unpublished work of the authors. Prism patterns follow the convention established by Boyde,²⁵⁻²⁷ but descriptions such as ``closed'' (as in Pattern 1) or ``open'' (as in Patterns 2 and 3) more accurately reflect the variability of prism patterns in many primate species. HSB = Hunter-Schreger bands.

each band, the width of the transitional zone, the extent of the bands from the enamel-dentine junction, and the orientation of bands. However, there are problems in documenting this variation. In many primates, Hunter-Schreger bands vary in different parts of the teeth, such as cusp tips, basins, and near the root-crown junction. In addition, the appearance of Hunter-Schreger bands is strongly influenced by the plane of section, a factor that is almost impossible to control because there is no precise correlation between orientation of the microscopic, subsurface structure of enamel and the gross features of teeth. Some attempts have been made at systematic documentation of interspecies variation in horizontal Hunter-Schreger bands using quantitative^{32,42,44,45}

or qualitative assessments,38,45-50 but no generally accepted scheme has been devised. One important distinction is between enamel in which discrete parazones and diazones can be distinguished and enamel in which it is impossible to identify discrete Hunter-Schreger bands, although the prisms are not parallel to one another as in radial enamel. Instead, sectioned teeth show poorly demarcated, irregular clusters of differently oriented prisms. This type of enamel occurs in several primate species and has been called irregular decussation⁴⁹ or irregular Hunter-Schreger bands (Fig. 4B). This type of enamel differs from irregular (3-D) enamel (3-D enamel) because the clusters of prisms are not interwoven in a complex fashion.

More derived variants of decussating enamel have evolved in some groups of mammals, but not primates. Some bone-feeding Carnivora, such as hyenas, have evolved zig-zag Hunter-Schreger bands, with the undulations of prism layers being so extreme that these layers are vertical in some regions.⁵¹ In vertical Hunter-Schreger bands, layers of alternately oriented prisms are oriented vertically from crown to root so that, in transverse section, zones appear to radiate outward from the central axis of the tooth. Such bands occur in many hypsodont ungulates.^{23,52}

Schmeltzmuster and Dentition

The enamel of most mammalian teeth consists of more than a single

			Schmelzmuster	
	Estimated	Prism Pottern	(from enamel-dentine	
Taxon	Mass ⁹⁶ (am)			
	Mass (gill)	ranom	Janonon to Sanacoy	
ORDER PLESIADAPIFORIVIES				
Chiramyoidanan ³⁹	150, 200	1.0		
Chirornyoldes sp. ³⁰	150-300	1, 3		
Nannoaectes Intermealus"	221	1, 3	Radiai, prismiess	
Plesiaaapis cooker ⁹	3,055	1, 3	HSB, prismiess	
Plesiadapis rex ³⁹	506	1, 3	HSB, prismless	
Plesiadapis tricuspidens	759	1, 3	HSB, prismless	
Purgatorius unio ¹⁵	92	1, 3		
Paromomyidae				
Ignacius frugivorus ³⁹	96	1, 3	Radial, prismless	
Ignacius graybullianus ³⁹	152	1, 3	Radial, prismless	
ORDER PRIMATES				
Adapidae				
Adapis parisiensis	1,300	1; ³⁹ 3	Radial, prismless	
Adapis sudrei	1,400	2, 3	Radial, prismless	
Cantius ralstoni ⁴⁵	1,300	1, 3	Radial, prismless	
Cantius mckennai ⁴⁵	1,600	1, 3	Radial, prismless	
Cantius trigonodus ⁴⁵	2,000	1, 3	Irregular HSB, radial , prismless	
Cantius abditus ⁴⁵	3,000	1, 3	HSB. radial, prismless	
Cantius venticolis ⁴⁵	3,000	1, 3	HSB, radial, prismless	
Copelemur praetutus ⁴⁵	1,300	1.3	Radial, prismless	
Furonalemur dunfei	1,360	1,3	Radial, prismless	
Lentadanisso	1.300-4.000	2.3	Radial	
Periconodon ideaeri	920	1.3		
Notharatus pupiensus ⁴⁵	2 000	1,0	Irregular HSB radial prismless	
Notharctus robinson ⁴⁵	4 700	1,3	HSB radial prismless	
Notharatus no 45	3,000	1, 3	HSB, radial, prismless	
Omenyidae	3,000	1, 3	H3B , Tadiai, prisiriless	
	200 500	1 2	Dadial prismlass	
Anapioniorphus sp.	200-500	1, 0		
Omomys sp.	300	1, 3		
Snosnonius sp.	150	1, 3	Radiai, prismiess	
Ielinaraina americana ³⁷	120	3		
Ietonius sp. 39	100-300	3		
Washakius sp. 39	150	1, 3	Radial, prismless	
Hemiacodon sp.	1,005	3		
Parapithecidae ⁷⁸				
Apidium moustafai	850	1, 3	Radial, prismless	
Apidium phiomense	1,600	1, 3	Radial, prismless	
Parapithecus grangeri	3,000	1, 3	HSB, radial, prismless	
Oligopithecidae				
Catopithecus browni ⁹⁷	900	1, 3	Radial, prismless	
Propliopithecidae				
Aegyptopithecus zeuxis ⁷⁸	6,700	1, 3	HSB, radial, prismless	
Cercopithecoidea				
Mesopithecus pentelicus ⁸⁴	8,000	3		
Hominoidea				
Oreopithecus sp. ³⁵	30.000	3		
Proconsul sp. ^{93,94}	>17,000	3A		
Proconsul major ⁹⁹	50.000	1	HSB	
Proconsul africanus ⁹⁹	27 400	1	HSB	
Dryonitheous sn 99	>20,000	3		
Otovinitheousen ⁹⁹		13		
Ciurpiniecus sp.	14,000-20,000 < 40,000	1,0		
$Ciacaptopithoousop ^{93.94}$	~40,000	34		
Australopithoous spire and 35.02	> 190,000	3A 2		
Australopinecus afficanus ^{33,92}	>30,000	3		
Paranthropus robustus ^{33,92}	>32,000	3		

Bold type indicates the predominant prism pattern or enamel type; contradictory or alternative interpretations are discussed in the text. Unreferenced data are from unpublished work of the authors. Prism patterns follow the convention established by Boyde, $^{25-27}$ but descriptions such as ``closed'' (as in Pattern 1) or ``open'' (as in Patterns 2 and 3) more accurately reflect the variability of prism patterns in many primate species. HSB = Hunter-Schreger bands.



Figure 4. Scanning electron micrographs of prismatic enamel types that occur in primate teeth. A: Longitudinal section through a cusp of a Nycticebus coucang molar showing radial enamel. In radial enamel, prisms extend outward from the enamel-dentine junction (bottom) in straight, curved, or sinusoidal paths, but are always parallel to one another. Scale bar = 10 µm. B: Longitudinal section through lateral enamel of a Cheirogaleus medius molar, with enamel-dentine junction at bottom. Irregular Hunter-Schreger bands appear as clusters of prisms (cl) oriented at angles to adjacent prisms, but do not form discrete zones. Scale bar = 10 µm. C: Longitudinal section through lateral enamel of a Cebus apella molar showing broad Hunter-Schreger bands extending in a sinusoidal course from the enamel-dentine junction (right) to the outer surface. Adjacent Hunter-Schreger bands are sometimes referred to as diazones and parazones. Prisms in diazones (dz) are sectioned perpendicular to their long axes; prisms in adjacent parazones (pz) are sectioned parallel to their long axes. Scale bar = 100 μ m. D: Longitudinal section through lateral enamel of a Chiropotes sp. molar showing narrow, well-organized Hunter-Schreger bands extending straight from the enameldentine junction (bottom right) to the tooth surface (left). Perikymata (left arrows) visible on the outer tooth surface are the surface manifestations of the incremental striae of Retzius (horizontal arrows), which mark the place at which the ameloblasts along the developing enamel front appear to have undergone decreased activity.^{1,122} Scale bar = 100 µm. E. Longitudinal section through lateral enamel of a Cacajao molar showing gradual change in the orientation of prisms between adjacent Hunter-Schreger bands. Because the change in prism orientation between parazones (pz) and diazones (dz) is gradual, there appears to be a transitional zone (tz) where prisms are sectioned oblique to their long axes. Striae of Retzius are visible in the outer, parallel crystal enamel (right). The enamel-dentine junction is at left. Scale bar = 100 µm. F: Longitudinal section through buccal enamel of a Lemur catta premolar with the enamel-dentine junction at bottom. The schmelzmuster consists of Hunter-Schreger bands, radial enamel, and prismless parallel crystal enamel (PCE) at the outer surface (top). Relative proportions of enamel types may vary in different regions of a tooth crown, such as at the tip of a cusp and the root-crown junction. Scale bar = $100 \,\mu m$.

enamel type. As noted, *schmelzmuster* refers to the arrangement of these enamel types within a tooth (Fig. 4F). In molars of small-bodied primates,

for example, the schmelzmuster typically consists of an inner layer of radial enamel and a much thinner outer layer of prismless parallel crystal-

lite enamel. In larger primates, the schmelzmuster typically includes an inner layer of horizontal Hunter-Schreger bands, a middle radial layer, and an outer prismless layer. Thorough characterization of the schmelzmuster is facilitated by examination by light microscopy, since the differences in prism orientation and arrangement that characterize the different enamel types are sometimes most easily distinguished by their different refractive properties. The considerable variation in schmelzmuster among primate species is expressed as presence, absence, or differences in proportions of some enamel types, but has not been studied systematically.

The *dentition*, or variation in schmelzmuster among different teeth in the tooth row, is the highest level of enamel



Figure 5. A: Simplified mechanical model of loads and stresses in a mammal tooth cusp, adapted from Pfretzschner.⁶⁹ Vertical chewing loads (vertical arrows at top) produce horizontal tensile stresses (horizontal arrows) that increase in magnitude toward the base of the cusp. Tensile stresses can pull prisms apart and thus form vertical cracks (wavy lines). These cracks are resisted by the alternating orientation of prism long axes in adjacent Hunter-Schreger bands. B: Simplified diagram of prism decussation, adapted from Rensberger.⁴⁴ Prism long axes have different orientations in adjacent Hunter-Schreger bands. Vertical cracks created by tensile stresses generated during chewing follow the planes of least resistance, which are parallel to prism long axes and perpendicular to the horizontal plane of decussation. Extension of the cracks in a vertical direction is resisted by the change in prism orientation between adjacent Hunter-Schreger bands, which thus serve as ``crack stoppers.'





Figure 6. Scanning electron micrographs of *Lemur catta* molar showing experimentally airpolished wear facets in functionally distinct regions of molars (A and B) and the enamel microstructure of those regions etched with dilute HCI (C and D) to show the underlying differences in crystallite orientation relative to the surface. Air polishing highlights the differences in wear resistance between a cuspal facet (A) where interprismatic enamel has been preferentially removed and an adjacent chewing facet (B) where there is no difference in rate of removal of prismatic and interprismatic enamel. C: At the cuspal facet, prisms intercept the wear surface so that the interprismatic crystallites (IP) are nearly parallel to the surface and prismatic crystallites (P) are nearly perpendicular; the latter are therefore more resistant to abrasion. D: In contrast, at chewing facets prisms (P) and interprismatic (IP) crystallites intercept the surface nearly perpendicular to their long axes, and thus are equally resistant to wear. Scale bars = $10 \,\mu$ m.

complexity. Dentition-level differences in schmelzmuster may be expressed as markedly different proportions of the same enamel types, different arrangements of the same enamel types, or the absence of some enamel types in some teeth. Dentition-level variation in enamel microstructure has received little attention. Most rodents have different incisor and molar schmelzmuster, as do rhinoceroses and some insectivores; in some rodents, schmelzmuster even differs between upper and lower incisors.15 Some of these differences are clearly related to tooth function, but in other cases the explanation is not obvious. Among primates, there appears to be relatively little variation in enamel microstructure at the dentition level. We have observed that lemurs, lorises, and tarsiers all have similar schmelzmuster in incisors, canines, and cheek teeth, despite the very different gross morphologies, enamel thicknesses, and functions of those teeth. Baboon incisors, canines, and premolars also show similar schmelzmuster, despite differences in tooth morphology and enamel thickness.53 Ceboid microstructure also is reported to be consistent throughout the dentition.42,54 Callitrichids have the same schmelzmuster in incisors and cheek teeth despite the pronounced functional differences between those teeth.^{46,49}

TOOTH ENAMEL AND DENTAL FUNCTION IN PRIMATES

Most nonhuman primates acquire their permanent teeth early in life. Enamel functions to control tooth wear, thereby maintaining the functional shape of tooth cusps and crests, and to protect teeth from catastrophic damage so that they can continue to process food throughout an animal's life. Enamel structure facilitates these functions in two important ways. First, it affects the way that chewing surfaces wear by mitigating the process

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of abrasion. Second, it enhances tooth durability by inhibiting brittle fracture of the enamel cap.

The resistance of enamel to abrasion and brittle fracture depends on structural features expressed at two different scales. Tooth *abrasion*, the loss of enamel by food-on-tooth wear,⁵⁵ occurs at a microscopic scale and is influenced by small-scale structural elements, especially the orientation of crystallites. In contrast, *brittle fracture*, failure of a material resulting from crack propagation, is a largerscale process and is mitigated by larger-scale structural elements, especially enamel types.

Enamel Structure and Abrasion

Experimental studies show that abrasion, or small-scale wear, removes enamel in units of crystallites or, perhaps, subparallel crystal groups, and that the primary structural constraint on rate of wear is the orientation of crystallites.56-58 Crystallites that are parallel to a wear surface and force vector are less resistant to abrasion than are those perpendicular to the surface. This can be explained by the fact that perpendicularly intercepted crystallites are largely enclosed by adjacent crystallites and present only a small area for abrasive contact, whereas those intercepted parallel to their long axes are less protected and present a larger area for contact. In vitro studies also show that enamel is least resistant to abrasion in areas where crystallites are parallel to the wear surface, but only if the abrasive vector also is directed parallel to the tooth surface.^{23,52,53,56,57} A similar relationship between crystallite orientation and wear resistance also has been demonstrated for naturally worn tooth surfaces.59-61

This relationship between crystallite orientation and abrasion has implications for dental microwear studies. The shape of microwear featuresthat is, scratches vs. pits^{62,63}—mostly depends on the direction and magnitude of chewing forces. There is little evidence that enamel microstructure influences the shape of microwear features. However, there is evidence that the size of some microwear features, especially the width of microscopic scratches, is affected by the orientation of underlying crystallites.^{57,60} This means that, all other things being equal, abrasion of predominantly surface-parallel crystallites will produce broader striations than will abrasion of surface-perpendicular crystallites. Though this phenomenon is unlikely to overpower the signal of diet in most instances, it probably accounts for the lack of discriminatory power of some microwear variables.

Crystallite density, or how closely crystallites are packed, also influences

the way enamel responds to abrasion. Prismless enamel is more resistant to abrasion than is prismatic enamel. This is because prismatic enamel crvstallites are less densely packed along prism boundaries. In vitro abrasion of prismatic enamel has demonstrated that low-energy mechanical etching preferentially removes crystallites from prism boundaries.^{56,23} This same phenomenon can be observed on naturally worn teeth. It is especially pronounced if interprismatic crystallites are parallel to the surface and crystallites within prisms are perpendicular to the surface (Fig. 6). However, if occlusal forces are higher or if food contains hard, abrasive particles, these structurally constrained patterns will be swamped. This was illustrated in the seminal study of microwear in browsing and grazing hyraxes⁶⁴: In the browsing species, low-energy polish-

Tooth wear is a complex interaction among chewing forces, tooth shape, food properties, the quantity of enamel (enamel thickness), and enamel structure.

ing wear preferentially removed the interprismatic crystallites, but in the grazing species abrasion by harder phytoliths obscured this structurally dependent wear.

Of course enamel structure is not the only thing that affects how teeth wear. Tooth wear is a complex interaction among chewing forces, tooth shape, food properties, the quantity of enamel (enamel thickness), and enamel structure. Enamel may wear at different rates depending on how hard food particles are, how much chewing force is generated, and the direction of chewing force relative to enamel crystallites and the tooth surface. Because of this, enamel may wear at different rates in different parts of teeth, even though the enamel structure is the same, or wear at the same rate in different parts of teeth, even though its structure is different.^{23,37,59,61,65} (See Box 2.)

Enamel Structure and Fracture

Wear also takes place on a much larger scale. Large-scale enamel loss can occur if a crack passes through the enamel and fractures the tooth crown, and this can have catastrophic effects on tooth function. Most mammals have powerful chewing muscles and can generate enough force during normal food processing to fracture a brittle material such as enamel. The extent of the damage depends on the magnitude of force an animal generates (and thus on the animal's muscular capacity), the physical properties of the food that the animal is chewing, and the structure of its enamel.

Prism boundaries represent natural planes of weakness in enamel and constrain the path through enamel that cracks will travel. This is because the energy required to generate a crack (work of fracture) is lower along prism boundaries, where crystallites are less densely packed, than through prisms.^{66,67} At the same time, because prism boundaries form a convoluted path, more total energy is needed for a crack to travel between two points than if it could follow a straight path. This is one way that the structure of prismatic enamel inhibits crack propagation. Many mammals, however, generate enough force to overcome the crack resistance offered by prism structure.47 In these mammals, prism decussation, and thus structural variation at the level of the enamel type, can inhibit crack propagation47,66,67-71 (Fig. 5).

Prism decussation is common in mammal teeth. Enamel with Hunter-Schreger bands first appears in the mammalian fossil record in the Paleocene, soon after the beginning of the major Cenozoic radiation of mammalian herbivores. The mechanical relationship between stress and crack propagation suggests that prism decussation evolved in response to increased chewing stresses associated with larger body size, and thus larger chewing muscles.47 Horizontal Hunter-Schreger bands occur in some species of almost every family of living primates (Table 1).^{32,37,38,41,43,46,54,72} They occur in teeth

Box 2. Enamel Microstructure and Wear Facets

Do differences in enamel structure correspond to differences in the gross morphology of primate teeth? Variation in the arrangement of prisms and crystallites across the surface of some primate molar teeth suggests that this may be the case. The three functionally important and mechanically distinct areas of primate molars are cusp tips, cusp slopes-including both more vertically oriented shearing surfaces and more horizontally oriented grinding surfaces-and crushing basins. Cusp tips are especially important during initial puncture-crushing of food. All three functional regions are involved during the subsequent chewing cycle. Different occlusal forces, such as shearing (surface-parallel force) and crushing (surface-perpendicular force) dominate at different functional regions because of their different geometries and differences in jaw movements during different phases of the chewing cycle.¹³³

Many mammals with low-crowned tribosphenic molars develop flat horizontal wear surfaces at cusp tips (apical facets) and more vertically oriented Phase I and Phase II chewing facets along cusp slopes. Because these surfaces are angled differently relative to enamel prisms, they intercept prismatic and interprismatic crystallites at different angles as well, although there are no enamel structural differences between the two regions (A). Scanning electron microscopy of naturally worn cheek teeth of the greater galago shows differences in crystallite orientations between these functionally distinct wear facets.37 At apical facets, interprismatic crystallites intercept the wear surface parallel to their long axes and prismatic crystallites intercept the surface more perpendicular to their long axes. According to

the mechanics of enamel wear, this arrangement should be resistant to compressive force (forces perpendicular to the wear surface) generated during puncture-crushing, but less resistant to abrasion by shearing forces that also act at cuspal facets. In contrast to the surface of apical facets, interprismatic and prismatic crystallites intercept the Phase I and Phase II facets slightly oblique to the wear surface, and thus should be optimally resistant to shearing abrasion. This same configuration has been observed in some lemur molars (those of Lemur, Hapalemur. and Eulemur but not Varecia) and in molars of the marmosets Callithrix and Saguinus⁴⁹ (Fig. 6).

Can this arrangement of crystallites and wear surfaces be considered an adaptation in these primates? The evidence is equivocal. Mammals as functionally diverse as the opossum,65 musk shrew,¹⁰² and koala^{59,60} show a similar pattern of different orientations of crystallites relative to cuspal and shearing facet surfaces. In these animals, differential resistance to abrasion between the two regions accounts for the creation and maintenance of sharp cutting edges along the leading edges of crests at the interface between apical facets and shearing facets. In fact, this potential for differential wear conferred by prism or crystallite orientation is thought by some to be the major factor driving the innovation of prismatic enamel among the earliest mammals.¹⁰² But while the primates studied thus far resemble primitive mammals with respect to the differences in crystallite and prism orientation between apical and chewing facets, they do not develop sharp cutting edges between cusp tips and slopes. This suggests that the mechanical association between prism



A. Schematic diagram of a longitudinal section through a primate molar cusp tip and adjacent wear facet showing the orientation of enamel prisms and crystallites relative to functionally distinct wear surfaces. Prisms extend outward from the enamel-dentine junction at a uniform angle, but because the two wear surfaces are oriented differently, the prismatic crystallites (black lines) and interprismatic crystallites (gray lines) intercept the surface at different angles in the two regions. At the apical facet, formed by abrasion of the cusp tip during puncture-crushing, interprismatic crystallites lie parallel to the surface and prismatic crystallites intercept the surface nearly perpendicular to their long axes. At the shear facet, formed by abrasion along cusp slopes during chewing, both the interprismatic and prismatic crystallites intercept the surface nearly perpendicular to their long axes.

and crystallite orientation and abrasion has been exapted to enhance tooth durability in mammals such as primates, in which the functionally diverse bunodont molars are very different from those of the early mammals. In these teeth, the surface-parallel crystallites at surfaces of apical facets and more perpendicular crystallites at chewing facets are both optimally arranged to resist the different loading regimes that predominate in each region.³⁷

of hard object *and* soft-object feeders and in primates with thick *and* thin enamel. Although, for the most part, they are found only in the teeth of primates weighing more than about 2,000 gm, there are some puzzling exceptions.^{32,35,49} (Fig. 7). The occurrence of Hunter-Schreger bands in primates with thick and thin enamel also raises questions regarding the functional interpretation of enamel thickness. Thick enamel has been invoked as part of a suite of morphological features that includes tooth occlusal shape and cranial architecture and that is associated with hard-object feeding in primates.^{73–76} However, the relationship between enamel thickness and diet seems to be more complex. While there is some support for the hypothesis that pri-

Hylobates spp. Pongo pygmaeus Pan troglodytes Homo sapiens Gorilla gorilla Papio cynocephalus Macaca spp. Lophocebus albigena Cercocebus torquatus Callimico goeldii Saguinus spp. Leontopithecus rosalia Cebuella pygmaea Callithrix spp. Saimiri sciureus Cebus spp. Aotus trivirgatus Pithecia monachus Chiropotes satanus Cacajao melanocephalus Callicebus moloch Brachyteles arachnoides Lagothrix lagotricha Ateles belzebuth Alouatta spp. Tarsius spp. Galago senegalensis Otolemur spp. Perodicticus potto Loris tardigradus Nycticebus coucang Daubentonia Cheirogaleus medius Microcebus murinus Propithecus verreauxi Varecia variegata Eulemur spp. Lemur catta Hapalemur griseus



Tarsius, his work generated little interest among anthropologists. Although some primates were included in broad comparative surveys of mammalian enamel,^{31,32} the enamel microstructure of primates was generally ignored until the late 1970s, when Boyde's^{26,27,43} pioneering application of scanning electron microscopy to enamel development and structure heralded a renewed interest in mammalian enamel. Over the last 20 years, the enamel microstructure of many living and fossil primates has been sampled (Table 1 and Table 2) as a result of increased interest in functional as well as phylogenetic aspects of enamel structure.

Prosimians

Recent studies of prosimian enamel^{37–39,79} have demonstrated that

... the schmelzmuster of almost all small prosimians (species weighing less than about 2,000 gm), including tarsiers, consists of radial enamel overlaid by a variably thick outer prismless layer. There are two known exceptions.

Figure 7. Predominant prismatic enamel types for some living primates. Body masses⁹⁶ for dimorphic species are for the larger sex, and average weights are used for congeneric species with the same dominant enamel type. The dashed line indicates the size (about 1,500 to 2,000 gm) above which most herbivorous mammals have Hunter-Schreger bands; radial enamel is dominant in teeth of smaller herbivores.⁴⁷ The strong Hunter-Schreger bands of callitrichine primates are a puzzling exception to this ``rule.'

mate hard-object feeders have relatively thicker enamel than do *closely* related soft-object feeders, there is no evidence that a threshold value of enamel thickness separates hard-object feeders from soft-object feeders.77 Other dietary factors, including acidity and the abrasiveness of foods, need to be considered in testing functional explanations of enamel thickness in primates. Another important factor may be schmelzmuster. Schmelzmuster differences among thick-enameled primate species demonstrate that all thick enamels are not mechanically identical.78 It may be that increase in thickness of certain enamel types such as Hunter-Schreger bands may be more important than increase in total thickness for protecting the teeth of some hard-object feeders.

ENAMEL STRUCTURE IN LIVING AND FOSSIL PRIMATES

Primate dental enamel was first surveyed in the 1920s by Carter.29 Although Carter reached some intriguing conclusions, for example that the adapids Notharctus and "Pelycodus" were linked to the Malagasy prosimians and the omomyid Hemiacodon to

the schmelzmuster of almost all small prosimians (species weighing less than about 2,000 gm), including tarsiers, consists of radial enamel overlaid by a variably thick outer prismless layer (Table 1). There are two known exceptions: We have observed irregular Hunter-Schreger bands in upper and lower canines of the Nycticebus and throughout the dentition in Cheirogaleus medius (Fig. 4B). In contrast, all larger prosimians have horizontal Hunter-Schreger bands overlaid by radial and prismless enamel, though the Hunter-Schreger bands are more distinct and more extensive in some species than in others.38

We now know that most prosimians, including Tarsius, have predomi-

nantly Pattern 3 prisms but that, as is the case for many mammals, Pattern 1 prisms appear throughout the enamel from the enamel-dentine junction to the outer surface, and are common close to the tooth surface. This clarifies the sometimes conflicting descriptions of earlier studies^{35,39} (see Table 1). The aye-aye (Daubentonia madagas*cariensis*) appears to be unique among prosimians in that its incisors are characterized by distinctive Pattern 2 prisms with very broad interrow sheets and pronounced, narrow Hunter-Schreger bands.^{72,80} It is not known whether this prism pattern and schmelzmuster are also found in its cheek teeth, though dentition-level variation does not appear to be characteristic of primates.46,49,53,54

New World Monkeys

These monkeys, like prosimians, are characterized by a variety of prism patterns and enamel types. The enamel literature abounds with contradictory descriptions of platyrrhine enamel, especially prism patterns (Table 1). Gantt⁸¹ thought that platyrrhines resembled Old World monkeys in having a predominance of Pattern 2 prisms, but Shellis^{41,82} interpreted New World monkey prisms as a variable combination of Pattern 1 and Pattern 3. Propst⁴⁹ documented all three major prism patterns among callitrichines and concluded that prism patterns were not unique to genera or species. Likewise, Martin and colleagues35 reported that most platyrrhines they studied show some combination of all three prism patterns. They also noted unusual "Vshaped" prism cross-sections in a specimen of Leontopithecus, but most prisms are the more typical arc-shape. The V-shaped prisms also occasionally occur in other callitrichines.49

While prism type does not appear to characterize subgroups of platyrrhines, variation in enamel types and schmelzmuster may be distributed in a more meaningful way. All of the largerbodied species have Hunter-Schreger bands (Fig. 7), but the arrangement and appearance of the bands can be strikingly different (Fig. 4C–E). Pitheciines, though not very large, all show well-defined decussation zones that extend straight from the enamel-dentine junction to the outer enamel sur-

face. Cebus has well-defined bands with a more sinusoidal course to the outer surface; the much larger Alouatta has Hunter-Schreger bands, but they are difficult to distinguish. As expected on the basis of their body size, the small cebids Saimiri, Aotus, and Callicebus have only radial and prismless enamel. But remarkably, some of the tiny callitrichines weighing less than 500 gm have well-developed prism decussation. Hunter-Schreger bands are well-developed in all teeth of both Callithrix^{32,35,41,46,49,54} and the pygmy marmoset, Ce*buella*.^{46,49,54} Irregular Hunter-Schreger bands occur in Saguinus and Cal*limico*. Contrary to a previous report³⁶ of pronounced Hunter-Schreger bands in Leontopithecus, lion tamarins are the only callitrichine that shows the expected small-mammal schmelzmus-

While prism type does not appear to characterize subgroups of platyrrhines, variation in enamel types and schmelzmuster may be distributed in a more meaningful way.

ter of radial and prismless enamel.^{46,49} Propst⁴⁹ offered two hypotheses that are not mutually exclusive to account for the presence of decussation in marmosets: one, that they retain prism decussation from a larger-bodied ancestor (e.g., the phyletic dwarfing hypothesis) and the other that prism decussation is part of an adaptivefunctional complex related to treegouging and exudate feeding.

Old World Monkeys

Enamel microstructure has been described for relatively few of the more than 80 species of living Old World monkeys (Table 1).^{32,35,36,41,81,83,84} Most of these reports have focused exclusively on prism patterns, but a few include brief descriptions of enamel types and schmelzmuster.

Cercopithecoids all appear to have a combination of radial and decussating enamel with a thin but variable prismless layer. This is not surprising, given their relatively large body sizes. Because schmelzmuster has been described for so few species, we do not know whether Old World monkeys, like New World monkeys, show any variation in the appearance of Hunter-Schreger bands that might be of either functional or phyletic importance. Variation in enamel among different parts of the dentition also has been neglected. However, it is likely that the schmelzmuster is similar throughout the dentition, given that this seems to be the case for other primate species. Moreover, the canines, premolars, and incisors of Papio all show well-developed Hunter-Schreger bands.53

Initial descriptions of cercopithecoid prism patterns raised hopes that prism morphology could be used to distinguish this group of primates, and perhaps to determine affinities of problematic species. Large areas of Pattern 2 prisms were reported to predominate in many cercopithecid species, though Patterns 1 and 3 also were observed.^{25,35,85,86} But, as is the case for other primate groups, there has been disagreement about the interpretation of prism patterns (see Table 1). Shellis and Poole⁴¹ argued that despite its superficial resemblance to "Type II" (Pattern 2), Macaca enamel lacked interrow sheets. Shellis⁸² later concluded that all cercopithecines are characterized by Pattern 3 prisms. Similarly, Gantt's⁸¹ descriptions of Pattern 2A prisms in Macaca and Papio enamel were later interpreted as Pattern 3.35 Detailed studies of colobine and cercopithecine prism patterns^{83,84} illustrate both Pattern 2 and Pattern 3 arrangements, but predominantly the latter for cercopithecines and colobines. Dostal^{83,84} pointed out that most cercopithecine prisms are slender and elongate with shapes varying from pointed to parallel-sided with flat, truncated tops, whereas colobine prisms characteristically are broader and more rounded. (The broad, rounded prisms of Papio hamadryas and the parallel-sided truncated prisms of Nasalis are exceptions). These interesting observations have never been followed up, though metrical studies suggest that both Pattern 2 and Pattern 3

prisms of cercopithecoids are more elongate than those of hominoids.³⁵

Hominoidea

Relative to their taxonomic diversity, hominoids have received a disproportionate amount of attention with regard to their enamel microstructure. In a way, this is understandable, for much of what we know about enamel structure, function, and development has been driven by interest in human dental health.^{87,88} Evolutionary studies of nonhuman hominoid enamel, however, have largely focused on what prism patterns can tell us about hominoid phylogeny.

Although all three major prism patterns can be recognized in some regions of human teeth,35 there is general agreement that human enamel is characterized by the predominance of key-hole-shaped prisms (Pattern 3B) and well-developed Hunter-Schreger bands.⁸⁹ Characterization of ape enamel has been more controversial. Shellis and Poole⁴¹ thought that Gorilla enamel, but not that of other hominoids, consisted entirely of Pattern 1 prisms. Gantt^{90,91} initially argued that recent and fossil hominids had Pattern 3 prisms and thus were distinguished from other hominoids with Pattern 1 prisms. But, responding to concerns about preparation methods and adequacy of sampling,9,85,92 he modified his conclusions and reported that extant pongids have Pattern 3A prisms, in contrast to the predominantly keyhole-shaped Pattern 3B hominid enamel prisms.93,94 Others, however, maintain that there is no evidence for a hominid-pongid dichotomy based on prism patterns.35 In any event, the preponderance of evidence indicates that all hominoids have a combination of prism patterns, dominated by Pattern 3.

The schmelzmuster of most hominoids is also similar, consisting of radial enamel and Hunter-Schreger bands, usually with an outer prismless layer of varying thickness; the report that *Gorilla* lacks Hunter-Schreger bands⁴¹ is incorrect.^{9,85,86} Though some variations in the pattern and extent of Hunter-Schreger bands have been noted, the functional or phyletic significance of this variation has yet to be investigated.

Enamel Structure of Fossil Primates

Because of its high mineral content, the structure of enamel is preserved virtually unaltered in the fossil record. Therefore, we can directly observe the enamel of many of the most primitive primates and even compare the enamel structures of problematic fossil forms to those of living species. The availability of fossil material not only affords insights into the evolution of primate enamel, but provides samples with which to test functional hypotheses generated from the study of living species.

Plesiadapiformes, though no longer classified in Primates, are almost certainly close to the origins of the order. The earliest plesiadapiform, *Purgatorius*, has radial enamel with some

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Pattern 1 but mostly Pattern 3 prisms, all widely separated by interprismatic enamel.39,95 Later plesiadapiforms (microsyopoids, paromomyids, carpolestids, plesiadapids, and picrodontids) also have both Pattern 1 and, predominantly, Pattern 3 prisms.³⁹ Most plesiadapiforms have radial enamel, but Hunter-Schreger bands have been reported in molars of some species39 and in the enlarged incisors of at least one plesiadapid, *Plesiadapis tricuspidens*⁹³ (Table 2). Interestingly, these species probably were smaller⁹⁶ than most living mammals with Hunter-Schreger bands.

The enamel of the earliest primates, like that of the plesiadapiforms, consists of Pattern 3 prisms, with Pattern 1 prisms largely confined to surface enamel (Table 2). The North American adapids have been studied in detail. In these species, including Cantius ralstoni, one of the earliest and most primitive primates, the prisms are relatively small and widely separated by interprismatic enamel.^{39,45} The European adapids also have mostly Pattern 3 prisms, though at least one species, Adapis parisiensis, appears to have Pattern 1 prisms throughout its enamel.39 The early Eocene North American omomyids also show a combination of Pattern 1 and, most commonly, Pattern 3 prism cross sections. The distribution of enamel types among the Eocene adapids and omomyids largely follows the predictions of the bodysize dependent model (Table 2). The smallest adapids and omomyids have radial enamel and prismless enamel, but Hunter-Schreger bands occur in the larger species.

Nothing is known of enamel structure of the earliest anthropoid fossils, from the middle Eocene of China, but the more diverse and better known radiation of late Eocene to early Oligocene primates from the Favum of Egypt has been studied in detail (Table 2). Like the North American and European adapids and omomyids, all five species studied thus far (Apidium phiomense, A. moustafai, Parapithecus grangeri, Aegyptopithecus zeuxis, and Catopithecus browni) have mostly arcshaped prisms with fairly broad interprismatic regions (comparable to Pattern 3A), but also some Pattern 1 prisms, especially in the outer enamel.97,98 The larger species have extensive Hunter-Schreger bands, whereas the smaller ones have only radial and prismless enamel. Apidium phiomense represents a unique combination of characters, at least among primates. Its molar enamel is among the thickest, relative to body size, of any living or fossil primate, but, unlike other primates with thick enamel, it lacks Hunter-Schreger bands. This extremely thick radial enamel, along with analysis of microwear patterns, has led researchers to reconsider ideas about the diet of this enigmatic anthropoid.96

Enamel has been described for a few fossil members of later primate radiations, mostly with reference to phyletic relationships. Thus, the predominance of Pattern 3 prisms in the problematic Miocene *Oreopithecus*

may support its affinity with Hominoidea rather than Cercopithecoidea, though only if the absence of Pattern 2 prisms is derived.³⁵ Prism morphology of the Miocene cercopithecoid Mesopithecus supports its systematic position within the Colobinae.83 In the case of the Miocene hominoid Otavipithecus, confocal microscopy revealed a predominance of Pattern 1 prisms,99 leading to speculation that *Otavipithecus* might be more closely related to extant African apes than to other Miocene hominoids. However, restriction of the sample to surface enamel and the contradictory reports of the predominant prism patterns of extant apes (see Table 1) make this conclusion problematic. Gantt^{93,94,100} argued that predominance of Pattern 3A prisms, which he found in the Miocene hominoids Proconsul, "Ramapithecus," Sivapithecus, and Gigantopithecus, and in the living apes, are primitive for hominoids, whereas the fossil hominids *Australopithecus* and *Homo* erectus share with humans the derived keyhole-shaped Pattern 3B prisms. Others, however, dispute this distinction.35 More recent investigations of the enamel structure of fossil hominoids have moved away from phylogenetic interpretations of prism patterns. These studies have focused almost exclusively on the functional implications of enamel thickness and Hunter-Schreger bands¹⁰¹ and especially on the ontogenetic evidence for the evolution of dental development patterns contained in microstructural features such as incremental lines (see Box 1).

FUNCTIONAL AND PHYLOGENETIC SIGNAL IN PRIMATE ENAMEL

At the beginning of this paper, we posed two questions: Is the structure of primate enamel adaptive? What, if anything, does enamel structure tell us about primate phylogeny? The evolution of primate enamel, like that of other morphological systems, has been driven by a combination of developmental constraints, functional influences, and phylogenetic history. Much, though not all of the developmental basis of enamel structure, is well understood,^{1,8,22} but to decipher the functional and phylogenetic signals, a grasp of two key elements is essential. The first is an understanding of the levels of structural complexity at which both influences are played out. The second is an understanding of the levels of the taxonomic hierarchy where they are manifest.

It is clear that components of primate enamel structure representing several levels of structural complexity have important functional associations. At the smallest scale, crystallites intersect functionally distinct tooth surfaces at angles that enhance resistance to wear. At the level of the prism, prismatic enamel inhibits crack propagation, but only under relatively low loads. At the level of the enamel type,

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radial and prismless enamel optimize abrasion resistance (a larger-scale expression of the crystallite-level phenomenon). Also at the level of the enamel type, Hunter-Schreger bands function as a crack-stopping mechanism in cases where occlusal loads are high. This typically occurs in largebodied species weighing more than about 2,000 gm, but among primates Hunter-Schreger bands also are found in some small exudate feeders, perhaps because they experience high occlusal loads during bark gouging. At the level of the schmelzmuster, enamel types combine to optimize function and protection for the whole tooth.

Change in either total enamel thickness or in the thickness of one or more enamel types, also acts at the schmelzmuster level to protect teeth. What is significant from a phylogenetic perspective, however, is that none of the functionally important enamel features at any structural level is unique to primates.

In all mammals with prismatic enamel, crystallites and prisms intersect different tooth surfaces at different angles. This is, at least in part, a direct result of the way in which enamel is deposited during development. Also, among mammals in general Hunter-Schreger are a common solution to the problem of dealing with increased occlusal loads. Likewise, the schmelzmuster variation in proportions of enamel types and enamel thickness that we see in primates duplicates mechanical solutions in other mammals. In other words, primate enamel is not characterized by a key innovation that promoted the evolution of the variety of tooth morphologies within the order. Indeed, the earliest primates had relatively simple enamel composed mostly of Pattern 3 and some Pattern 1 prisms, both with fairly broad interprismatic regions, and a schmelzmuster consisting of radial enamel with a prismless surface layer. This enamel structure is typical of many primitive mammals.^{15,102} We see similar enamel patterns in many extant lipotyphlans and chiropterans,⁴⁰ as well as many living small primates. Early in primate evolution, Hunter-Schreger bands appear in conjunction with increased body size. Again, this echoes evolutionary patterns in other mammals. Essentially, the evolution of primate enamel, like that of the enamel of many other mammals, was a process of using existing structures and developmental pathways and, perhaps, making relatively minor adjustments to them.

The distribution across Mammalia of the functionally important features also expressed in primate enamel, as well as the variations in these features, suggest that they have been acquired independently many times, are relatively plastic, and thus are most likely to carry phylogenetic information across limited clades and at low levels of the taxonomic hierarchy. There is some evidence that this is the case for

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primates. For example, Hunter-Schreger bands have clearly been acquired many times within primates. The different patterns of decussation that seem to characterize pitheciines, cebines, and atelines may reflect their independent origin within each group and, at that taxonomic level, carry some phylogenetic signal. On a still lower taxonomic level, enamel thickness varies among species within genera in conjunction with dietary adaptations for soft or hard food items⁷⁷ and, perhaps, other dietary specializations.⁹⁸

In sum, the answer to the question, "Is the structure of primate enamel adaptive?" is a qualified "yes." Some elements of primate enamel structure serve specific functional roles, but are best understood as exaptations, or morphological innovations that have been co-opted for some new function. This is certainly the case for the smallscale structural variation in crystalliteto-surface orientation. This phenomenon, common among mammals, is largely a by-product of the way that mammalian enamel develops, but it is a functionally plastic feature that has been co-opted in some species to enhance differential wear and in others to resist wear. Other elements of enamel structure, including largerscale features such as Hunter-Schreger bands and variation in both enamel thickness and schmelzmuster, require significant alterations of primitive developmental pathways, and probably originated independently in different primate taxa in association with evolution of special adaptations in those clades.

To fully answer the question of what enamel structure tells us about primate phylogeny we need to consider variation in prism cross-sectional morphology, the only enamel feature that has been investigated from a phylogenetic perspective but that is without clear functional correlates. Until the mid 1980s, most phylogenetic studies of primate enamel focused on placing prisms into discrete categories based on qualitative, descriptive criteria. More recent work has incorporated quantitative criteria. The impetus for this shift came from three different arenas. The first was the development of efficient, high-magnification electron and confocal microscopy, which increased potential sample sizes and made statistical assessments of variation feasible. The second was the demonstration that enamel prisms of closely related species (domestic sheep and goats) could be distinguished by metrical criteria so long as comparisons were made at homologous depths within the enamel.¹⁰³ The third development, the most intriguing to systematists, was the successful use of prism size, shape, and spacing to test phylogenetic hypotheses of relationships among multituberculates, an extinct order of mammals.^{104,105} Unfortunately, the attempts to use either qualitative or quantitative descriptions of prisms to answer questions about primate phylogeny were stymied by their

... enamel prisms and patterns do not distinguish among hominoids, living or extinct; they are not phylogenetically informative. Attempts to apply qualitative prism morphology criteria to questions of primate subordinal systematics were equally unsuccessful.

inherent variation and homoplasy. Rather than providing clear solutions to phylogenetic questions, these studies have primarily served to point out the practical limitations of enamel prism data at a variety of taxonomic levels.

One of the first modern attempts to use prism patterns in primate systematics focused on hominoid phylogeny and evolution, a family-level taxonomic problem. The initial report that hominids could be distinguished from other hominoids on the basis of prism morphology⁹⁰ generated considerable polemics.^{9,35,85,92,94} But it is now clear that enamel prisms and patterns do not distinguish among hominoids, liv-

ing or extinct; they are not phylogenetically informative. Attempts to apply qualitative prism morphology criteria to questions of primate subordinal systematics were equally unsuccessful. Initial reports that lemurs were characterized by Pattern 1 prisms led some to speculate that the presence of prism patterns other than Pattern 1 might characterize haplorhines (anthropoids plus tarsiers).9,35 In fact, Pattern 3 prisms are common among all primates, both haplorhines and strepsirhines,^{32,37-39,41,82,106} and prism patterns simply do not contribute meaningful information to the debate regarding primate subordinal relationships.79

These studies, however, stimulated careful assessments of preparation and sampling techniques, including appropriate etching regimes for different types of specimens,^{85,86,107} control for sectioning artifacts, 37, 38, 108 and control for enamel depth to reduce the problem of within-sample variation.¹⁰¹ As a result, most recent studies have employed a rigorous protocol and produced thoroughly documented, replicable results.^{37,39,40,49,79} But even when methodological factors are taken into account, attempts to distinguish species, genera, and subfamilies on the basis of prism patterns have been unsuccessful. In lemurids,38 callitrichines,49 and cercopithecids,83 prism morphology failed to distinguish unequivocally among taxa.

Even at the ordinal level, prism morphology has proved an intractable means of distinguishing primate phyletic relationships. Dumont106 investigated the utility of enamel prism size, shape, and spacing for testing the monophyly of Archonta (primates, tree shrews, bats, and flying lemurs). This study, implementing careful controls for preparation artifacts and intraand interindividual variation, coded prism metrical and shape variables for 17 archontan and insectivoran (the outgroup) species into character states, but the results were equivocal. Parsimony analyses using species as terminal taxa demonstrated that homoplasy was rampant; orders and even families were consistently rendered paraphyletic. In other words, as for lower-level taxonomic analyses, enamel prisms are phylogenetically uninformative.

The failure of these studies of prism

patterns to elucidate phylogenetic signal in primate enamel highlights a critical flaw in their approach: ignoring other levels of structural complexity (crystallite, enamel type, and schmelzmuster) obscures the fundamental nature of prism variation, and thus obscures enamel's phylogenetic signal. In other words, one "can't see the forest for the trees": you cannot characterize enamel solely on the basis of prism cross-sections any more than you can characterize a forest on the basis of the shapes of tree trunks. Investigations of enamel structure in other groups of mammals that have adopted a more holistic concept of enamel have produced some intriguing functional and phylogenetic insights.^{16,40,51,109,110} It is not vet clear whether this will be the case for primates.

After almost 80 years of primate enamel studies, we conclude that the question of what, if anything, enamel structure tells us about primate phylogeny, has yet to be answered fully. Our current understanding is largely limited to what the functional features of enamel can tell us about primate evolution; to date, phylogenetic assessments of the nonfunctional enamel characters, prism shape and size, have not been successful. While the technical constraints on preparing and viewing enamel and the presence of variation in its structure contribute to this failure, it primarily reflects the lack of a clear phylogenetic signal in primate prism pattern and size. We suspect that phylogenetic analyses of primate enamel, and perhaps even most mammalian enamel, must take into account the functional influences at the level of the enamel type and schmelzmuster if they are to meet with success. It may be that enamel will only be useful in defining clades that are characterized by common functional adaptations. In the case of enamel, functional and phylogenetic signal are so strongly associated that perhaps they are one and the same.

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