Introduction to terminologies of tooth enamel microstructures and a proposal for their standard Chinese translations (Postprint)

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Abstract

Tooth enamel is composed of elongated, hexagonal crystallites of hydroxyapatite. Some crystallites are arranged into various regual structures and futher formed a composite structure in a hierarchical manner. The hierarchical system can provide a basis for analysis different levels of structural complexity from varitaiton of particular crystallite strucutes to variation of structural types throughout a individual' s dentition. The size, orientation, distribution and the packing patterns of crystallites are gene-comtrolled and have limited range of intraspecific variability. Thus, these microstructures provide considerable and reliable morphological characters that help understanding of external dental morphology in context of both phylogeny and function in vertebrates. Because teeth are highly resistant to weathering, mainly owing to their enamel covering, so that they were commonly preserved as fossils. This organic system, particularly their microstructures, has attracted more and more attention from vertebrate paleontologists and other morphologists. However, as already recognized by many previous studies, some terminologies of the enamel microstructures have been complex and used inconsistently. Although considerable effort has been made to study enamel microstructures in China during the last few decades, a standard terminology of enamel microstructures in Chinese has not be formally brought into line with that in English literatures. Here we intend to introduce and systematize the relevant terminology used in the study of enamel microstructures and translate them into Chinese, in hoping that this systematic effort will enhance researches of enamel microstructures in China.

The microstructures of vertebrate tooth enamel exhibit abundant morphological characters bearing information on phylogeny, biomechanics, and other aspects. Based on previous research, this paper seeks to systematically introduce the fundamentals of enamel microstructure studies, propose Chinese translations for relevant terminology in enamel research, and provide brief explanations for some important terms, as a reference for relevant researchers, in hopes of promoting further development of enamel microstructure studies.

Full Text

Introduction to Terminologies of Tooth Enamel Microstructures and a Proposal for Their Standard Chinese Translations

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Abstract: Tooth enamel is composed of elongated, hexagonal crystallites of hydroxyapatite. Some crystallites are arranged into various regular structures and further form a composite structure in a hierarchical manner. This hierarchical system provides a basis for analyzing different levels of structural complexity, from variation of particular crystallite structures to variation of structural types throughout an individual' s dentition. The size, orientation, distribution, and packing patterns of crystallites are gene-controlled and have limited intraspecific variability. Thus, these microstructures provide considerable and reliable morphological characters that help understand external dental morphology in the context of both phylogeny and function in vertebrates. Because teeth are highly resistant to weathering, mainly owing to their enamel covering, they are commonly preserved as fossils. This organic system, particularly its microstructures, has attracted increasing attention from vertebrate paleontologists and other morphologists. However, as recognized by many previous studies, some terminologies of enamel microstructures have been complex and used inconsistently. Although considerable effort has been made to study enamel microstructures in China during the last few decades, a standard terminology of enamel microstructures in Chinese has not been formally brought into line with that in English literature. Here we introduce and systematize the relevant terminology used in the study of enamel microstructures and translate them into Chinese, hoping that this systematic effort will enhance research on enamel microstructures in China.

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The hard tissues of vertebrate teeth consist of two mineralized components: dentin, which forms the main body of the tooth, and enamel, which covers the crown surface. The central pulp cavity contains blood vessels and nerves that connect to periodontal tissues through the apical foramen and can produce dentin throughout life. Most mammalian teeth are surrounded by a thin layer of supporting connective tissue that envelops the root and attaches to the alveolar bone; this connective tissue is called cementum (Fig. 1 [Figure 1: see original paper]A) (Nanci, 2008). Tooth crown enamel is composed of ordered mineralized crystallites that form complex and diverse microstructures, characterized by low porosity and high inorganic content, making it the hardest tissue in the mammalian body and enabling it to resist enormous masticatory pressure and friction as well as chemical acid erosion in the oral environment (Boyde, 1964). The macroscopic morphology and microstructure of enamel-covered teeth are not easily deformed or altered after burial (Brudevold and Söremark, 1967) and are typically well-preserved in fossil materials, representing important content for paleontological research (Korvenkontio, 1934). Modern technological developments allow researchers to better extract taxonomic, paleontological, and histological information contained in tooth enamel, and studies on enamel microstructure have attracted increasing attention from scholars (Pfretzschner, 1992; Koenigswald, 1994a, b, 1997a, b, c, 2012; Martin, 1999; Stefen, 1999; Vislobokova and Dmitrieva, 2000).

Over recent decades, terminology for enamel structures has varied considerably among different biological groups and researchers, with some concepts prone to confusion. Many scholars have discussed these terms, their historical changes, and related issues (Boyde, 1964; Koenigswald and Clemens, 1992; Koenigswald and Sander, 1997; Sander, 1997, 1999). Chinese paleontologists have also conducted research on morphological classification, phylogeny, and ontogeny of fossil tooth enamel microstructures (Zhang and Ouyang, 1988; Ouyang and Huang, 1991; Ouyang and Xu, 1993; Zhao and Zhang, 1994; Ouyang, 1998; Wang and Ouyang, 1999; Zhao et al., 1999, 2003; Hu and Zhao, 2012; Li and Meng, 2013; Mao et al., 2014, 2015, 2016, 2017). However, these studies have not appropriately unified Chinese terminology with modern dental histology, and some inconsistencies and even misconceptions exist in paleontological research. Therefore, based on previous studies and comparing Chinese and international expert opinions, this paper systematically introduces the fundamental content of enamel microstructure, proposes Chinese translations for relevant terminology, and provides brief explanations for important terms as a reference for researchers, hoping to promote further development of enamel microstructure studies.

2. Sectioning Planes and Related Structures

The study of tooth enamel microstructure requires proper orientation. The current standard method involves obtaining information from three basic enamel sections—longitudinal, cross, and tangential—rather than limiting observation to two-dimensional planes, thereby comprehensively exploring and correctly understanding the three-dimensional structural organization of enamel (Koenigswald and Sander, 1997). In addition to these three basic sections, the enamel-dentine junction and outer enamel surface are also important for locating enamel microstructures. The basic definitions of these five surfaces (Fig. 1) are as follows:

Enamel Dentine Junction (EDJ): The interface between tooth enamel and dentin, representing the surface where enamel formation begins. The composition and crystallite structure of enamel and dentin differ significantly, making the interface distinct.

Outer Enamel Surface (OES): The outermost surface of the enamel layer, representing the surface where enamel formation terminates. This surface is usually smooth, though different ornamentations may appear in some taxa.

Longitudinal (=sagittal) Section: For incisors, canines, or single-cusped teeth, the longitudinal section is parallel to the long axis of the tooth, exposing the enamel layer from EDJ to OES at maximum depth and dividing the tooth into two halves (Wahlert and Koenigswald, 1985). For multicuspid heterodont teeth (such as molars), the longitudinal section is typically anterior-posterior or buccal-lingual, perpendicular to the tooth' s occlusal (crown) surface.

Cross (=transverse) Section: Typically perpendicular to the tooth' s long axis and longitudinal section, and parallel to the tooth' s crown surface (for molars), also exposing the enamel layer from EDJ to OES.

Tangential (=frontal) Section: A section parallel to both the OES and EDJ, passing only through the enamel layer without exposing dentin.

3. Aperiodic Microstructures

From a developmental perspective, tooth enamel exhibits two main structural categories: aperiodic microstructures, which are composed of crystallite arrangements containing substantial morphological, phylogenetic, and biomechanical information but essentially no ontogenetic information (Koenigswald and Clemens, 1992), and periodic incremental features that record individual developmental information (Smith et al., 2003), discussed in Section 4.

Tooth enamel can be broadly divided into two microscopic categories: prismatic enamel and prismless enamel. The former is common in mammalian teeth and was once considered a distinguishing feature between mammals and reptiles (Grine et al., 1979a, b; Grine and Vrba, 1980), while the latter is common in reptilian and early avian teeth (Sander, 1999; Wood et al., 1999; Abdala and Malabraba, 2007).

Koenigswald and Clemens (1992) categorized mammalian aperiodic prismatic enamel into five hierarchical levels of complexity based on different crystallite organizations, providing a framework for describing and analyzing morphological features from enamel microstructure to dentition-level variation. This hierarchical system defines the scope of discussion at different levels, applies to most descriptions and comparisons of mammalian enamel microstructure, and provides a series of detailed and comparable characters for phylogenetic and functional studies. Sander (1997, 1999) extended this hierarchy to reptilian prismless enamel after systematically studying enamel in 43 reptilian taxa (Fig. 2 [Figure 2: see original paper]), expanding its applicability while incorporating more detailed content and maintaining terminological continuity and consistency.

This paper synthesizes the basic terminological systems proposed in the aforementioned studies, supplemented by diagrams and images of incisor enamel microstructure in gliriform mammals, to introduce common features and structures at each enamel level, correlate Chinese translations with English terms, and provide brief explanations for major terms.

3.1 Crystallite Level

The main component of tooth enamel is hydroxyapatite, present as needle-shaped crystallites that are longer and larger than bone apatite crystallites (Lowenstam and Weiner, 1989). In enamel, crystallites align in specific directions to form basic units and structures. Sander (1999) classified crystallite patterns into three major categories based on their organization in different regions and orientation relative to the EDJ or OES (see Sander, 1999:fig. 3 [Figure 3: see original paper]):

(1) Parallel Crystallites: Crystallites arranged parallel to each other at a relatively simple and consistent angle to the EDJ. This arrangement generally occurs in the innermost layer of prismatic enamel near the EDJ, the outermost layer near the OES, and in much prismless enamel.

(2) Zones of Changing Crystallite Orientation: Crystallites continuously change direction within these zones without interruption. Based on their orientation relative to the EDJ and spatial constraints of the orientation zones, four types are recognized:

- **Elongate Zone of Convergence:** Crystallites extend along the tooth or along its sides, with adjacent crystallites converging.
- **Elongate Zone of Divergence:** Crystallites extend along the tooth or along its sides, with adjacent crystallites radiating.
- **Columnar Zone of Convergence:** Crystallites extend from EDJ to OES in a columnar shape, with adjacent crystallites converging.
- **Columnar Zone of Divergence:** Crystallites extend from EDJ to OES in a columnar shape, with adjacent crystallites diverging.

(3) Crystallite Discontinuities: Two groups of crystallites with inconsistent orientations form discontinuities at their junctions. Based on orientation relative to the EDJ and spatial constraints, four types are recognized:

- **Plane of Crystallite Convergence:** Adjacent crystallite groups converge along this plane.
- **Plane of Crystallite Divergence:** Adjacent crystallite groups diverge along this plane.
- **Lines of Crystallite Convergence:** Crystallites converge toward this line from all directions.
- **Lines of Crystallite Divergence:** Crystallites diverge from this line in all directions.

3.2 Module Level

This enamel hierarchical level describes how enamel crystallites arrange to form repeatable modules and their three-dimensional composition. The most common module is the prism (Fig. 3). Additionally, most synapsids form relatively regular but morphologically distinct enamel units. Module size can vary and exhibit complex nested patterns, with larger modules composed of smaller regular modules, ranging from several micrometers to several millimeters. Common module types include (see Sander, 1999:figs. 5, 9):

(1) Enamel Unit: The smallest regularly repeating enamel module, separated by crystallite discontinuity planes perpendicular to the enamel secretion surface. Generally, a unit is bounded by complete discontinuity planes; when these planes are indistinct, unit boundaries can be identified by high-angle crystallite intersection planes.

- **Columnar Divergence Unit:** A columnar enamel unit longer than wide, bounded by planes or zones of crystallite convergence. The cross-section is generally polygonal, with crystallites diverging from a central point, line, or plane within a single columnar unit. This is the most common component unit in prismless enamel.
- **Columnar Convergence Unit:** A columnar enamel unit longer than wide, bounded by planes or zones of crystallite divergence, with crystallites converging toward a central point, line, or plane.
- **Microunit:** A small enamel unit approximately 1–10 m in diameter and length, containing few crystallites that diverge at small angles from the unit center and connect with adjacent microunits. Definition is based primarily on divergent lines or planes at the unit center rather than bounding discontinuity planes, generally lacking growth lines. Microunits typically appear in the thin enamel layer immediately adjacent to the EDJ, oriented perpendicular to it, and can compose more complex structural units such as compound units.
- **Crystallite Bundles:** Enamel units intermediate in size between crystallites and microunits, where crystallites are parallel without divergence or convergence, usually possessing growth lines. They are generally located

near the EDJ or OES, formed by thin enamel matrix secreted by newly differentiated or late-stage ameloblasts before or after cell process formation, resulting in layered growth lines without prisms or enamel units due to ameloblast retreat.

- **Compound Unit:** A higher-order unit composed of many columnar units or microunits arranged regularly in space, bounded by crystallite discontinuity planes or zones of changing crystallite orientation. Unit composition shows considerable variation in arrangement, with divergence axes that may be central or offset, making compound units difficult to define and identify.

(2) Prism (or Enamel Rod): The most common regular enamel module in mammalian teeth, generally composed of extremely long parallel crystallites forming the prism body that extends regularly from EDJ to OES at a certain angle (Wood and Stern, 1997; Sander, 1997). The prism crystallite bundle is bounded externally by the prism sheath, a distinct crystallite discontinuity plane, generally a plane of crystallite convergence. In living extant mammals, the sheath contains abundant organic material that is replaced by minerals in fossils. During acid etching of histological sections, prism sheaths are typically easily etched and appear as seams. Short, non-bundled crystallites often exist between prisms, with orientations that differ from those within the prism body in derived types, forming the interprismatic matrix (IPM) that separates different prisms. Individual prisms typically do not bifurcate or fuse with other prisms. Additionally, a crystallite discontinuity convergence plane or line called a seam appears as a fissure on enamel cross-sections, extending from the prism sheath opening toward the EDJ into the IPM and often partially into interprismatic crystallites. Seams typically occur in some primitive types of prismatic enamel.

Modern dental histology considers prism formation to have a one-to-one correspondence with ameloblasts (Nanci, 2008), where one ameloblast produces one prism. Since this correspondence cannot be observed in fossils, some scholars suggest avoiding cell-prism correlations in paleontological research and defining prisms solely by morphological structure (Sander, 1997; Wood and Stern, 1997). Prism types are diverse, distinguished primarily by cross-sectional morphology defined by prism sheaths, including prism head, prism neck, prism tail, IPM morphology, and seam presence. Additional distinguishing features include absolute prism size, prism density, and crystallite orientation patterns within prisms and IPM. Common prism types include:

1) True Prism: Generally abbreviated as prism. In addition to basic prism features, true prisms typically exhibit: cross-sectional diameter of 4-5 m, lack of accessory structures such as seams, and relatively regular arrangement (Sander, 1997; Wood and Stern, 1997). True prisms are considered to appear only in mammalian lineages surviving the K/Pg boundary (Stern et al., 1989; Koenigswald et al., 1999; Wood et al., 1999; Wood, 2000; Wood and Rougier, 2005; Krause, 2013; Koenigswald and Krause, 2014; Mao et al., 2017). Their cross-sectional morphology and two-dimensional arrangement patterns are variable, leading some scholars to subdivide them into subtypes at the module level, such as Boyde’ s (1964) patterns 1, 2, and 3, and some derived subtypes (Schobusawa, 1952; Boyde, 1976; Boyde and Martin, 1984). However, these subtypes do not cover all mammalian prism types, and some contain higher-level information (Koenigswald and Sander, 1997). Therefore, this paper recommends dividing them into two main groups based on whether the prism sheath is open, discontinuing these subtypes without enumerating their subgroups; specific definitions can be found in relevant literature, with higher-level content briefly described in corresponding sections.

- **Closed Prism:** Approximates Boyde’ s (1964) pattern 1 morphology but excludes prism arrangement information (Fig. 3A). In cross-section, prisms are completely enclosed by prism sheaths without openings, separated by IPM, though the combination of prism body and IPM may form various shapes such as circular, hexagonal, or elongated forms (Schobusawa, 1952; Boyde, 1964).
- **Arc-shaped Prism:** Approximates Boyde’s (1964) patterns 2 and 3 morphology but excludes prism arrangement information. The prism sheath has an opening at its base in cross-section and is separated by IPM. Different morphologies form depending on opening size and IPM arrangement (Fig. 3A). For example, Boyde’ s (1964) and Gantt’ s (1983) pattern 3A features a near-semicircular enamel sheath at the prism head, with an uncontracted prism neck and contracted prism tail that fuses with IPM to form a “tadpole shape” (Shellis and Poolle, 1979; Zhao and Zhang, 1994). Boyde’ s (1964) pattern 3B and Meckel et al.’ s (1965) keyhole pattern features a prism head bounded by a greater-than-semicircular enamel sheath, with a contracted prism neck and divergent prism tail that fuses with IPM to form a “fish tail” shape.

2) Plesiomorphic Prism (Fig. 3) (Wood et al., 1999): Crystallites form bundles composing the prism body, with the prism sheath open toward the OES in cross-section. A crystallite discontinuity plane or line called a seam extends from the prism head or neck into the IPM. Prism diameter typically ranges from 2.5–6.5 m, surrounded and separated from other prisms by IPM, without bifurcation.

3) Transitional Prism (Wood et al., 1999; Mao et al., 2017): Defined primarily by rudimentary prism sheaths. In this enamel type, prism sheaths appear as crystallite discontinuity lines or planes, with a thin layer of short crystallites forming at the end near the EDJ that matches the sheath morphology. Crystallites within this layer intersect prism body crystallites at small angles. Transitional prisms have long seams, and the presence of a prism body within the sheath is not a necessary condition.

4) Gigantoprism: Similar to arc-shaped prisms but with larger prism diameters, typically exceeding 8 m. Gigantoprisms are found only in taeniolaboid multituberculates. The prism sheath at the prism head is arc-shaped, with variable neck and tail morphology among taxa and positions; some groups possess seam structures (Fosse et al., 1978; Carlson and Krause, 1985; Clemens, 1997; Mao et al., 2015).

3.3 Enamel Type

Enamel modules arrange parallel to each other, intersect regularly, or combine irregularly to occupy specific regions of the enamel layer, forming particular enamel types. This level shows parallel evolution across different mammalian lineages, with some subtypes occurring only in specific groups. Due to substantial differences between prismless and prismatic enamel (with prismatic including all subsets such as true, plesiomorphic, transitional, and gigantoprisms), we introduce them separately:

(1) Prismless Enamel (Sander, 1999)

- **Parallel Crystallite Enamel (PCE):** Composed of parallel crystallites without higher-order crystallite organization or more complex structures.
- **Wavy Enamel:** Formed by staggered crystallite arrangements where crystallites are not perpendicular to the EDJ but maintain a constant angle while continuously changing direction toward the OES, resulting in helical crystallite arrangements.
- **Microunit Enamel:** Composed of parallel microunits.
- **Columnar Enamel:** Composed of parallel columnar units, which can be subdivided into more subtypes based on columnar morphology and orientation.
- **Basal Unit Layer (BUL):** A thin layer near the EDJ composed of polygonal columnar units, approximately 5–15 m thick, with unit diameters typically 1–4 m.
- **Convergence Columnar Enamel:** Composed of parallel convergent columnar units.
- **Compound Unit Enamel:** Composed of parallel compound columnar units.

(2) Prismatic Enamel

1) Transitional Enamel (TrE) (Wood et al., 1999; Wood and Rougier, 2005; Mao et al., 2017): Initially defined as a transitional enamel structure or stage, here defined as an enamel type. Transitional enamel contains two module types: the main portion consists of columnar units inclined toward the cusp at angles typically not exceeding 45°; between adjacent columnar units appears another module type—rudimentary prism sheaths, mostly arc-shaped with unstable arrangement, morphology, size, and position. The sheath opening faces the OES, and the prism body may not develop within it. Long seams are located between columnar units, partially overlapping with crystallite convergence discontinuity planes between units but being wider and shorter, typically not extending to the OES.

2) Plesiomorphic Prismatic Enamel (PPE) (Wood et al., 1999; Wood

and Rougier, 2005): This enamel type features small prisms (2.5–5.5 m diameter), arc-shaped prism sheaths opening toward the OES, seams bisecting prisms, hexagonal prism arrangement, IPM separation, no prism decussation, and no obvious angular changes.

3) Radial Enamel: Prism long axes radiate from the EDJ toward the cusp and extend to the OES. The angle between prisms and EDJ may change during extension. Radial enamel refers only to prism arrangement; prism types within it may vary:

- **Primitive Radial Enamel:** Generally considered the primitive type of prismatic enamel, with prisms radiating roughly from EDJ to cusp toward OES, featuring large angles between prism bodies and IPM crystallites. The origin of primitive radial enamel in therians and marsupials is considered parallel evolution, developing different adaptive strategies: in marsupials, it evolved into other radial enamel subtypes to increase wear resistance, while in placentals, it evolved into Hunter-Schreger bands to resist stress and abrasion (Koenigswald, 2012).
- **Radial Enamel with Anastomosing IPM (Boyde, 1965):** A more derived radial enamel where prism body and IPM crystallites are not parallel but intersect at large angles, with IPM forming an anastomosing network.
- **Radial Enamel with Interrow Sheets (Boyde, 1965):** A more derived radial enamel where prisms arrange in rows and IPM appears as sheet-like structures running between prisms.
- **Modified Radial Enamel (MRE):** Prisms arrange in radial columns with thick, sandwich-like IPM between them (Pfretzschner, 1994; Koenigswald, 2012), commonly found in the innermost layer near the EDJ in high-crowned herbivorous ungulate teeth.
- **Arsinoitheriid Radial Enamel (ARE):** Adjacent bright and dark bands contain only one set with interrow sheets, while the other set is primitive radial. This enamel type is found only in *Arsinoitherium*.

4) Tangential Enamel (Koenigswald, 2000): Prisms are parallel to each other, differing from radial enamel in that they exhibit simultaneous prism deviation. In derived types, prisms do not incline toward the cusp but are strictly parallel to each other. Tangential enamel often occurs together with radial enamel; in the transition zone between the two types, the prism extension angle changes across an interface parallel to the EDJ, defined as simultaneous prism deviation (SPD).

5) Irregular Enamel (Koenigswald, 2000): Single or bundled prisms intersect irregularly without forming regular enamel layers. Irregular enamel occurs only in specific regions of particular teeth and typically appears together with radial enamel. It is thought to have different evolutionary origins in different groups: in placentals, it likely evolved from Hunter-Schreger bands, while in marsupials, it likely evolved from radial enamel (Koenigswald, 1997a, 2000).

6) Zipper Enamel (Koenigswald, 1994a): Occurs where radial enamel on both sides of a tooth meets to form a ridge, appearing as a very narrow band along the ridge where prisms regularly intersect at right angles to form thin layers. This enamel type differs from Hunter-Schreger bands primarily in its lack of lateral extension, appearing only in very limited areas at tooth margins. This type is found only in marsupials.

7) Hunter-Schreger Bands (HSB) (Koenigswald and Sander, 1997): Also called Schreger’ s bands, composed of one or several rows of alternating bright and dark bands. Prisms within each band are parallel to each other, while adjacent bands intersect at angles, creating alternating light and dark stripes on tooth sections (Hunter, 1778; Schreger, 1800). Hunter-Schreger bands show considerable variation among taxa, bearing clear taxonomic and phylogenetic information, relating to biomechanical factors, and exhibiting some parallel evolution. Common types in major mammalian lineages include:

a) In gliriform incisor studies, enamel type identification generally uses longitudinal sections of upper and lower incisors, with lower incisor sections being clearer. The enamel surface is typically divided into three layers from EDJ to OES: inner layer (portio interna, PI), outer layer (portio externa, PE), and prismless external layer (PLEX, also called aprismatic enamel). The prismless external layer is usually composed of parallel crystallites, though it may consist of crystallite bundles. The outer layer is radial enamel, but different radial enamel types may occur in different groups due to varying angles between IPM and prism body crystallites. The inner layer typically consists of Hunter-Schreger bands. Using features such as the number of prisms per band, angles between IPM and prism crystallites, inclination angle, intersection angle between bands, and presence of transition zones, rodent enamel inner layers are divided into three types: pauciserial, multiserial, and uniserial (Fig. 4 [Figure 4: see original paper]), with each type further subdividable (Wahlert and Koenigswald, 1985; Bruijn and Koenigswald, 1994):

- **Pauciserial HSB:** Bands contain 2-6 prisms, though this often varies within a single specimen. IPM is thick with crystallites parallel to prism direction. Inclination angles are minimal or absent, and transition zones are lacking. Outer layer IPM is thick, with prisms lowly inclined (25-55°). The entire incisor enamel layer is relatively thin (50–100 m). Pauciserial bands occur in primitive rodents and gliriforms such as paramyids, the eomyid genus *Cocomys*, and the mixodont *Rhombomylus*.
- **Uniserial HSB:** Band width is a single prism. IPM may be parallel to prisms (primitive type) or intersect at angles (derived type). Perpendicular intersection, which enhances three-dimensional stress resistance, is considered the most derived type. The primitive type first appeared in Middle Eocene rodents such as *Pappocricetodon antiquus* (Wang and Dawson, 1994). Primitive uniserial HSB occurs in Sciuromorpha, eomyids, some theridomyids, and anomalurids, while the perpendicular type appears in

later Myomorpha (Martin, 1997), also called lamellar enamel.

- **Multiserial HSB:** Also called multiserial (Wang and Ouyang, 1999), bands contain 3-10 prisms (mostly 3-7). In most cases, IPM intersects prisms at certain angles; in the most primitive taxa, they are roughly parallel but unlike pauciserial HSB, IPM is not thick and surrounding prisms. Transition zones occur between bands. Outer layer prisms are typically highly inclined (up to 80°). The earliest multiserial HSB appears in Middle Eocene cf. *Tamquammys*, while Hystricognathi, African Phiomorpha, South American Caviomorpha, Asian Hystricidae, and derived Ctenodactyloidea all possess multiserial HSB.

b) In perissodactyl cheek teeth, four common Hunter-Schreger band types are recognized based on their orientation relative to the occlusal surface and EDJ (see Koenigswald et al., 2011:fig. 4). This classification also applies to some artiodactyls and proboscideans (Rensberger and Koenigswald, 1980; Koenigswald, 1994b; Koenigswald et al., 2011). These four types contain phylogenetic information in perissodactyls, with transverse HSB considered the most primitive type having two evolutionary directions: one developing into curved HSB, the other evolving into vertical HSB via compound HSB:

- **Transverse HSB:** Bands parallel to the tooth occlusal surface and enamel crown base, often undulating or showing some variation but maintaining an overall transverse arrangement.
- **Curved HSB:** Also called U-shaped HSB. In some groups, transverse HSB bends toward the occlusal surface, forming an angle with the shearing surface. Curved HSB appears only in very limited areas, typically combined with transverse HSB. When bands bend in different directions, an interface forms at the convergence center, corresponding to obvious depressions on the tooth OES. Curved HSB usually occurs on high crests such as well-developed ectolophs and transverse crests.
- **Compound HSB:** Transverse HSB in the inner enamel layer and vertical HSB in the outer layer, with variable relative thicknesses. The appearance of vertical HSB may relate to enamel thickness rather than specific tooth morphology.
- **Vertical HSB:** Bands extend essentially vertically from the tooth basal cingulum to the occlusal surface, with minimal bending or undulation. Vertical HSB occurrence is not directly related to tooth morphology. Similar to transverse HSB, vertical HSB may show unidirectional bifurcation without band convergence and lacks interfaces. When vertical HSB intersects the occlusal surface, special banded structures called cross-ridges appear on the bands (Koenigswald et al., 2011).

c) In carnivores, including Carnivora, Creodonta, and some Condylarthra, most types possess Hunter-Schreger bands that nearly parallelly encircle the crown with some undulation, typically considered related to biomechanical factors (Stefen, 1997, 2010). Based on undulation amplitude in tangential sections, three subtypes are recognized with progressively increasing undulation (see Stefen, 2010:figs. 1, 2):

- **Undulating HSB:** A relatively primitive type where bands remain essentially straight with wave peak-trough angles greater than 140°, with bifurcation possible at any location.
- **Acute-angled HSB:** Increased undulation with greater irregularity than undulating HSB, with peak-trough angles of 140–70°. Bifurcation occurs mainly at peaks and troughs, representing a transitional type between undulating and zigzag HSB, often co-occurring with other enamel types in the same dentition type.
- **Zigzag HSB (Rensberger, 1995; Stefen, 1997):** Undulation amplitude increases progressively from EDJ to OES, becoming very obvious near the OES. The horizontal distance between undulation ridges is shorter than in the previous two types, while the vertical distance is greater. Adjacent bands may overlap vertically in a zigzag pattern, with peak-trough angles of 70–50° and bifurcation only at peaks and troughs. This enamel type possesses extremely high resistance to internal pressure from mastication and is typically found in bone-cracking carnivores such as hyaenids.

3.4 Schmelzmuster

This German-derived term was previously translated as "enamel structure."Since "enamel structure" is easily confused with various general enamel micro- and macro-structures, we translate this level as "schmelzmuster" to correspond with the lower classification level of enamel type. In enamel research, schmelzmuster is the most informative level (Koenigswald et al., 1994), referring to the three-dimensional spatial structure composed of enamel type(s) in a single tooth, which may consist of one or multiple enamel types (Koenigswald, 1980, 1982).

For example, in *Palaeomylus* lower incisors, enamel thickness is approximately 30 m, forming a single-layered radial enamel with a thin prismless external layer; prisms do not decussate and incline 15° toward the cusp. Prism cross-sections are irregularly circular to elliptical, with extremely thick IPM whose crystallites intersect prism long axes at certain angles, approximately perpendicular to the EDJ (Fig. 5). In contrast, incisor schmelzmuster in *Mimotona wana* and *Heomys orientalis* consists of outer radial enamel and inner Hunter-Schreger band enamel, with some differences (Fig. 6 [Figure 6: see original paper], 7). In *M. wana*, enamel thickness is approximately 90–130 m, forming double-layered enamel with a thin prismless external layer. The outer radial enamel layer occupies 40% of total enamel thickness, while the inner layer contains Hunter-Schreger bands 3–10 prisms thick (typically ~4 prisms) with an inclination angle of 50°. Prism cross-sections are irregularly circular in the inner layer and elongated in the outer layer, with relatively thick IPM intersecting prism long axes at certain angles. In *H. orientalis*, enamel thickness is approximately 125 m, double-layered, with the outer radial enamel layer occupying 30% of total thickness. The inner Hunter-Schreger bands are 2–11 prisms thick, with inclination angles of 10–30° and no transition zones. Prism cross-sections are irregularly circular in the inner layer, with IPM nearly parallel to prism long axes, while outer layer prisms are oval with IPM intersecting at larger angles; IPM is relatively thick.

Within an animal’ s dentition, different teeth such as incisors and molars have different morphologies and functions, and their schmelzmuster may differ accordingly. For example, rodent molars differ significantly from their incisors in schmelzmuster, which can be subdivided into three types (see Koenigswald, 2004:fig. 1):

- **P-Schmelzmuster:** In rodent molars, radial enamel forms the main body of enamel, with some prism decussation in some species but without forming any regular pattern.
- **S-Schmelzmuster:** Thick Hunter-Schreger bands, each composed of 4–10 prism rows, typically parallel to the occlusal surface, extending from crown base to occlusal surface throughout the entire lateral wall of molar enamel, as exemplified in the sciurid genus *Sciurus*.
- **C-Schmelzmuster:** The upper crown consists of radial enamel, while a ring of lamellar enamel at the crown base forms the basal ring of lamellar enamel (BRLE). Lamellar enamel consists of specialized Hunter-Schreger bands, each containing only one (single-layer) prism row, with adjacent layers having nearly perpendicular prism extension directions. It was first reported from the cricetid genus *Cricetus* (Koenigswald, 1980, 2004).

3.5 Dentition Type

This refers to the combination of all schmelzmuster types within an individual animal’ s dentition. Dentition type is crucial for higher-level comparative studies. Existing research shows that in homodont dentitions, enamel microstructure does not vary significantly across different teeth. However, in heterodont dentitions such as those of lagomorphs, rodents, and rhinocerotids, significant differences occur among different teeth. For instance, within the same individual, schmelzmuster differs between incisors and molars (Koenigswald, 1997c). In rodents with low-crowned teeth, molar schmelzmuster is typically less specialized than in incisors, whereas in high-crowned species, molar schmelzmuster is more specialized and complex than incisors. This marked difference in schmelzmuster between incisors and molars exists in many mammals and is generally attributed to functional differences among tooth positions, considered important for understanding tooth morphological differentiation (Koenigswald, 1988).

4. Periodic Enamel Microstructures

Tooth surfaces and interiors preserve periodic developmental records—enamel growth lines—that reflect the uninterrupted, incremental formation of enamel layers, recording rhythmic growth and developmental changes in the tissue (Koenigswald and Clemens, 1992). Two types of periodic growth lines are commonly used in tooth developmental studies: enamel prism cross-striations, a daily periodic growth line appearing as regularly spaced transverse lines along prism long axes; and Retzius lines, a long-period growth line appearing as a series of regularly spaced lines extending from the EDJ to the lateral OES (Fig. 8 [Figure 8: see original paper], Bromage et al., 1985). The regular lines formed where Retzius lines reach the enamel surface are called perikymata (Risnes, 1986).

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Note: Figure translations are in progress. See original paper for figures.