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LEVELS OF COMPLEXITY IN THE MICROSTRUCTURE OF MAMMALIAN ENAMEL AND THEIR APPLICATION IN STUDIES OF SYSTEMATICS

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Abstract

Description and analysis of the complex structure of enamel can be facilitated through the application of a system of hierarchical levels of structural complexity. Five interdependent levels are distinguished. These are the levels of:

1) crystallites,
2) prisms,
3) enamel types,
4) schmelzmuster, and
5) dentition.

This system provides a basis for analysis of both variation of particular structures and variation of structural types throughout a mammal's dentition. Optimally, in wide ranging systematic and biomechanical studies, all levels of structural complexity should be considered, but lack of information about one level does not prevent significant analyses at other levels.

Introduction

The tempo of study of enamel microstructure has increased greatly during the last decade. Development and greater availability of scanning electron microscopes (SEM) has made it possible to shift from the study of thin sections to ground or etched surfaces and increased the quality of documentation. Additionally, this new technology has facilitated studies of much smaller structures, such as crystallites. However, easy access to larger magnifications has tempted workers to focus their investigations on the smallest structures and to lose sight of the total structural complexity of the enamel, which is the primary topic of this paper.

New data on enamel microstructure from different laboratories are, in some instances, difficult to compare. Differences in terminology are vexatious, but they can be overcome through clear, careful definition of terms. Use of different techniques for preparation of enamel reveals different levels of structural complexity. If this is recognized, comparable data on microstructure can be drawn from work carried out in different laboratories. The major stumbling block stems from the tendency of workers to concentrate their attention on a limited aspect of mammalian enamel structure, prism cross-sections, prism diameter, or prism directions, for example, and overlook the fact that the particular character selected for study is simply a description of only part of a very complex structure.

With increasing data on enamel microstructure and experience in its application in systematic studies, it has become apparent that the total complexity of enamel microstructure must be understood before successfully embarking on systematic analyses. Questions of relationships at different taxonomic levels usually are addressed with data drawn from different levels of structural complexity. For example, studies of variation in cross-sections and density of enamel prisms have

provided characters contributing significantly to our understanding of the membership and systematic interrelationships of suborders of multituberculates (Fosse et al. 1978; Krause and Carlson 1986). In contrast, data on the cross-sections of prisms have been notably uninformative in studies of the systematic interrelationships of families of rodents. At this taxonomic level, understanding of systematic relationships has been advanced by analyses not of prism cross-sections but of more complex schmelzmuster (Koenigswald 1980, 1982, Rabeder 1981).

Organization of information according to levels of structural complexity serves to facilitate comparisons between groups. Also, experience is showing that the applicability of the particular characteristics of the different levels of structural complexity is roughly inversely related to the taxonomic level of the systematic interrelationships being studied. Structural patterns at the crystallite or prism levels usually are applicable to questions of interrelationship at suprafamilial or higher taxonomic levels while patterns of complexity at the levels of the schmelzmuster or the entire dentition usually contribute to systematic studies at the specific or generic levels (Koenigswald, Martin, and Pfretzschner, in prep.).

The primary purpose of this paper is to discuss and categorize the levels of structural complexity of mammalian enamel. On the basis of our experience in studying many distantly related groups of mammals, including species of distinctly different adult sizes, we suggest a methodology for collecting and organizing data for use in systematic analyses of mammalian relationships.

This system of study is based on levels of structural complexity. It begins with crystallites, which are only a few angstroms wide, as the basic structural units of the enamel and builds upward to consideration of the entire suite of structural patterns found in a dentition, which can be several centimeters or decimeters in length. At each structural level, significantly different magnifications and areas of enamel studied are involved. These observations must then be brought together to provide an understanding of the total complexity of the enamel.

Preparation of study specimens

Both recent and fossil material can be effectively used in analyses of enamel microstructure. Post-mortem modification of the enamel has been observed to range from minor staining to, rarely, recrystallization that eradicates its original structure. These modifications of the structural complexity of the enamel can be easily recognized and do not influence the analysis.

Normally a series of sections are cut through the enamel. In addition to vertical and transverse sections (parallel and perpendicular to a dorsoventral plane of the crown), sections are cut tangentially to the surface of the enamel. Also, both worn and unworn areas of the outer surface of the crown can be studied.

A variety of different techniques for etching the surface of sections have been employed in studies of mammalian enamel (Carlson and Krause 1985). The specific etching technique used has to be adjusted to the level of structural complexity being investigated and, with fossils, the nature of their post-mortem modification, which can greatly affect the rates of etching. For example, studies of the orientation of crystallites normally require a very light etching of the surface. In contrast, for studies of prism orientation in different enamel types and schmelzmuster, etching must be heavier in order to remove more of the interprismatic matrix (IPM) and make the prisms clearly visible.

Etched surfaces can be studied with either a reflecting light microscope or a SEM. A reflecting light microscope (particularly with dark field illumination at magnifications of x 50 to x 500) is useful in studies at the schmelzmuster level, because the field of view is wide. A SEM is, of course, required for studies at all levels of structural complexity, but with increasing magnification the size of the field of view in the microscope is reduced. This limitation in field of view available for study can be overcome by the preparation of mosaics of SEM photographs documenting structural change through large areas of the enamel.

Embedding, grinding, and etching of the study specimens results in extensive modification and partial destruction of the material. These destructive techniques usually are only applied in studies of taxa known from large samples of material. Nondestructive techniques are also available. Cleaned but otherwise unaltered specimens can be studied with a Tandem Scanning Microscope (TSM), a technique developed by Boyde (Boyde et al. 1983). Its applicability is limited to studies of the morphology of prism cross-sections near the outer surface of the enamel, but these data can be of systematic importance as illustrated by comparative studies of species and genera of primates (Boyde and Martin 1987). Another nondestructive technique involves use of the light guide effect of prisms to study their orientations. Taking advantage of this physical property Koenigswald and Pfretzschner (1987) were able to trace the courses of Hunter-Schreger Bands (HSB) under a binocular light microscope at low magnifications (x 10 to x 50). These two nondestructive techniques have produced

data applicable to systematic studies at particular taxonomic levels; however, they do not provide a full spectrum of information about the structural complexity of enamel.

Levels of complexity

Hierarchy of microstructure

In order to be of use in systematic studies, the structural complexity of mammalian enamel must be partitioned in a way that will facilitate comparisons of structures. The hierarchical scheme suggested here is divided into five levels of complexity according to the size of the structures involved:

1. Crystallites: orientation of crystallites.
2. Prisms: cross-sections of prisms.
3. Enamel types: orientation of prisms relative to EDJ and differences in orientation of IPM crystallites relative to prisms. (Includes the subtypes: radial enamel, tangential enamel, Hunter-Schreger bands, and irregular decussation.)
4. Schmelzmuster: three-dimensional arrangement of enamel types.
5. Dentitions: variation in schmelzmuster throughout the dentition.

Obviously these levels of complexity are interdependent. Each level, however, provides a unique set of characters that can be used in comparisons between taxa. As examples from previous and new studies cited below demonstrate, the system reflects experience gained during the study of enamel of many, distantly related mammalian taxa and at very different scales of magnification. This classification is intended to serve as an operational scheme to help direct collection and analysis of data.

Crystallites

Crystallites of carbonate hydroxyapatite (dahllite) are the basic building blocks of both bone and enamel (Lowenstam and Weiner 1989). Unlike the minute, short crystallites of bone, the crystallites of dahllite in enamel are needle-like, narrow, and extremely long. Comparative studies of amphibians, reptiles, and mammals indicate that primitively the crystallites of enamel tend to be approximately parallel in orientation and extend radially outward from the enamel-dentine junction (EDJ) toward the surface of the tooth (Carlson 1990). This type of enamel is usually termed aprismatic or nonprismatic (Figs. 1 and 2).

A grade of increased structural complexity of mammalian aprismatic enamel is characterized by modification of the pattern of orientation of the crystallites. In the Early Jurassic mammal Morganucodon (Fig. 3), for example, the enamel crystallites are subdivided into columnar regions delimited by discontinuities in orientation of the divergent crystallites. In contrast, the enamel of another primitive mammal, the Late Jurassic docodont Haldanodon, also lacks prisms but is organized into internal, medial, and external layers distinguished by changes in crystallite orientation (Lester and Koenigswald 1989).

In "preprismatic" aprismatic enamel, the crystallites can be organized in columnar structures separated by distinct boundary planes; these are the so-called "pseudoprisms". The evolutionary and ontogenetic relationships of "pseudoprisms" and true prisms are uncertain. These structures can be distinguished by several characters. The boundary planes of the "pseudoprisms" tend to delimit polygonal, frequently hexagonal, cross-sections. In contrast, the cross-sections of prisms are demarked by sheaths that usually have curved outlines. Also, the "pseudoprisms" are in juxtaposition while the prisms of primitive prismatic enamel are widely separated by interprismatic matrix (IPM). In derived prismatic enamels, the IPM can be greatly reduced or lost.

Study of enamels characterized by regional differentiation in crystallite orientation but lacking discontinuities produced by prism sheaths is just beginning. Unfortunately enamels with these two microstructural characteristics have been dubbed with a wide variety of essentially synonymous names including "pseudoprismatic", "protoprismatic", "prismatic without prism sheaths", and "preprismatic". As an interim procedure we adopt, with a slight modification, Carlson's suggestion (1990) and use the term "preprismatic" for this advanced grade of structural organization, which is clearly an aprismatic enamel, i.e., lacks prisms. A reviewer of this paper noted that if one considers aprismatic enamels as structurally continuous enamels in contrast to prismatic enamels that are structurally discontinuous, "preprismatic" enamels are types of prismatic enamels. This observation helps highlight the current nomenclatorial confusion. Our choice of nomenclature is arbitrary.

The occurrence of aprismatic enamel in mammals is not limited to primitive, Mesozoic species. In some derived mammals, lipotyphlans, and carnivores (Koenigswald in press) and chiropterans (Lester and Hand 1987), the prismatic enamel is covered by a layer of aprismatic enamel in which the crystallites are oriented essentially in parallel. Lester and Hand (1987) named this aprismatic enamel in chiropterans "postprismatic" to distinguish it from primitive, aprismatic enamel (Fig. 4).

Finally, orientation of the crystallites plays a part in identification of structures at other levels of complexity.

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At the prism level, orientation of the crystallites within the prisms distinguishes different types of prisms (Helmcke 1967, Poole and Brooks 1961). At the level of enamel type, the orientation of the crystallites in the IPM, relative to the prisms, distinguishes different structural patterns (Martin 1990a, 1990b, in prep.) (Fig. 5 and 6).

In general, the fossil record documents an increase in complexity of enamel structure from the "preprismatic" aprismatic enamel of the earliest mammals to the oldest known occurrence of prism sheaths in Late Jurassic therians. Considerable research remains to be done in order to understand fully the functional significance of the increasing complexity in orientation of the enamel crystallites.

Prisms

Prisms are units or bundles of crystallites bounded, at least in part, by a major discontinuity in crystallite orientation, the prism sheath (Fig. 7). The cross-section of the sheath normally is rounded in contrast to the polygonal cross-section of the columnar "pseudoprisms". A minor discontinuity distinct from the prism sheath, the seam (Fig. 8), normally is oriented perpendicular to the cross-section of the prism, i.e., parallel to the sheath (Lester and Hand 1987). At the prism level, structural complexity of enamel can be increased by the development of tubules; passages radiating outward into the prisms and IPM. Tubules are found in the enamel of many marsupials (Boyde and Lester 1967, Lester et al. 1987) and multituberculates (Fosse et al. 1973, 1985) and are interpreted as primitive structures retained in the enamel of members of the Lipotyphla, Chiroptera, and even Primates (Lester et al. 1987).

The available fossil record indicates that the prismatic structure of enamel, apparently produced by the same ontogenetic processes, evolved at least twice in separate lineages of mammals. It appears first in the Upper Jurassic dryolestids (Lester and Koenigswald 1989) and later, independently, in late Early Cretaceous multituberculates (Fosse et al. 1985, Krause and Carlson 1986). Given the large number of Mesozoic mammals whose enamel has yet to be analyzed, additional examples of independent acquisition of prismatic enamel would not be surprising.

Sections of enamel displaying the cross-sections of the prisms have provided data for both quantitative and qualitative analyses. Prism diameter, prism density, and ratio of prism to ameloblast area have been investigated (Fosse 1968, Fosse et al. 1985, Krause and Carlson 1986). Prisms have been classified by morphological differences in their cross-sectional area, which is delimited by a prism

Complexity of the Enamel: Crystallite Level

Fig. 1. Aprismatic enamel of "preprismatic" grade in a molar of Varanus niloticus, Recent, Africa (Sa 2031), showing irregular, poorly defined, conical units of varying size. Not all of these units are continuous from the EDJ to the outer surface. Retzius-lines are very common.

Fig. 2. Aprismatic enamel of "preprismatic " grade in Placodus gigas, Middle Triassic, Germany (Sa 2003), with units of diverging crystallites that closely resemble those of Morganucodon (Fig. 3).

Fig. 3. Aprismatic enamel of "preprismatic" grade in Morganucodon watsoni, Early Jurassic, Wales (KOE 357). The columnar structure is characteristic of "preprismatic" aprismatic enamel, but the phylogenetic and ontogenetic relationships of these "pseudoprisms" to true prisms are still uncertain. - A nomenclatorial problem concerning the names Eozostrodon and Morganucodon bedevils the literature on enamel structure. Eozostrodon is the name for a mammal represented by two teeth found in England. Morganucodon is the name first given to an approximately contemporaneous mammal discovered in Wales. Some paleontologists argued these genera were synonymous and applied the name Eozostrodon to both. The teeth of Eozostrodon have not been duplicated in the immense collections of material from Wales. Apparently Eozostrodon and Morganucodon are distinct genera (Clemens 1979). The microstructure of the enamel of the two available teeth of Eozostrodon has not been studied. Enamel of Morganucodon has been described in many publications and in some misidentified as enamel of Eozostrodon.

Fig. 4. Aprismatic enamel forms the outer layer covering the prismatic enamel in a molar Ursus spelaeus, Upper Pleistocene, Germany (KOE 998).

Fig. 5. Prismatic enamel with thick interprismatic matrix in a lower molar of Microsyops, M. cf. M. augustidens, Lower Eocene, Wyoming (KOE 1154). The orientation of the crystallites of the IPM differs from that of the prisms by about 45°.

Fig. 6. Crystallites of the IPM are oriented in the third orthogonal direction between the decussating prisms of uniserial HSB in the portio interna of a lower incisor of Dicrostonyx torquatus, Recent, Banks Island, Canada (KOE 1003).
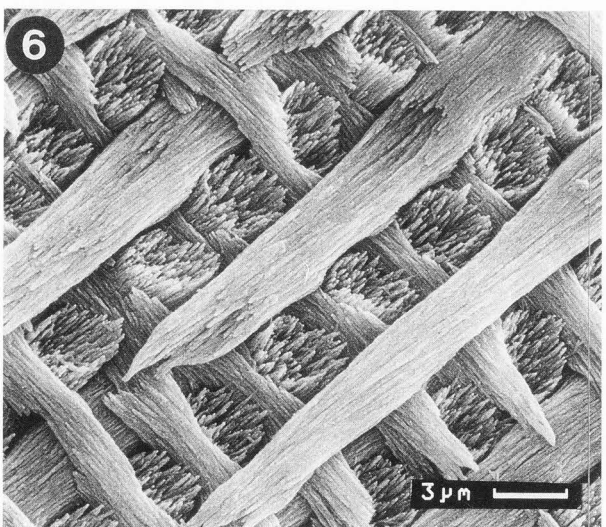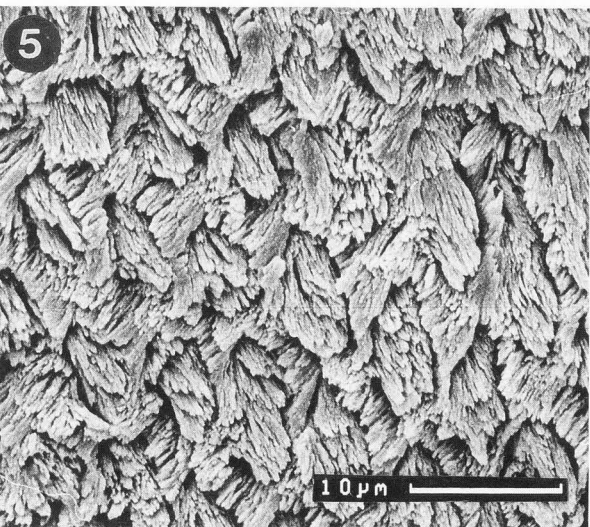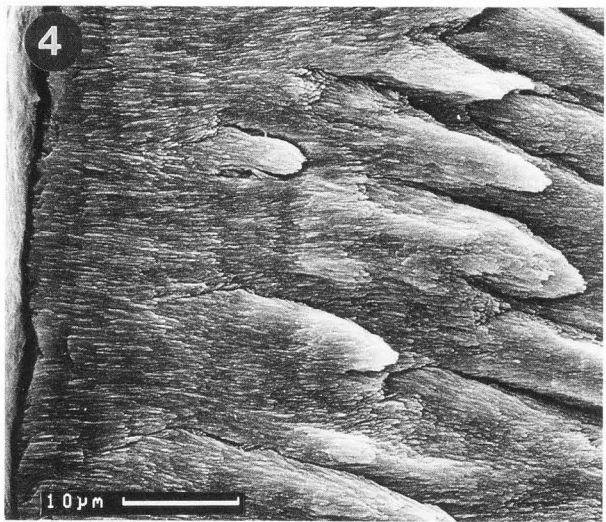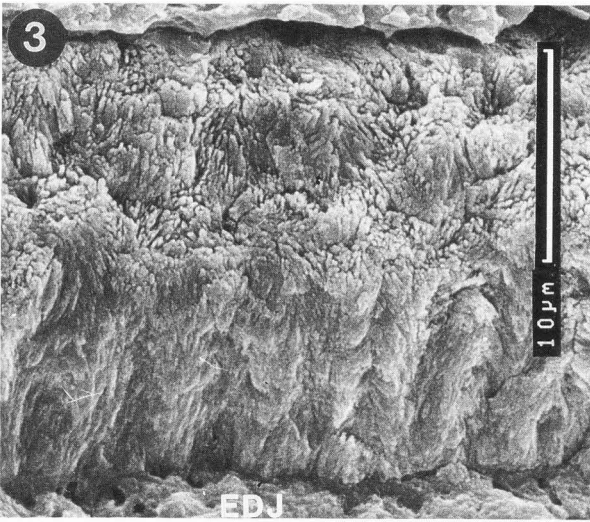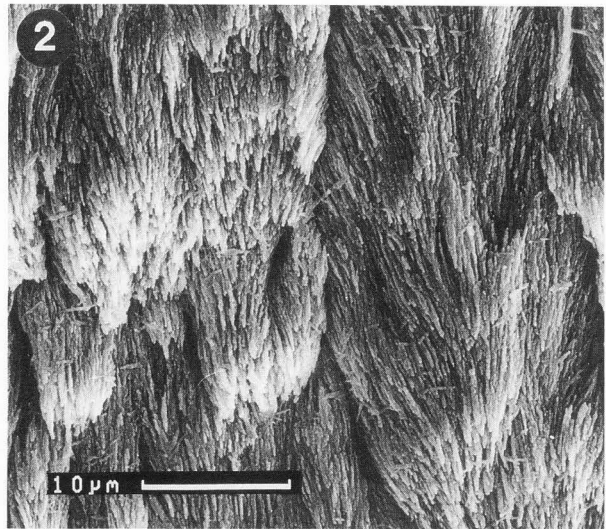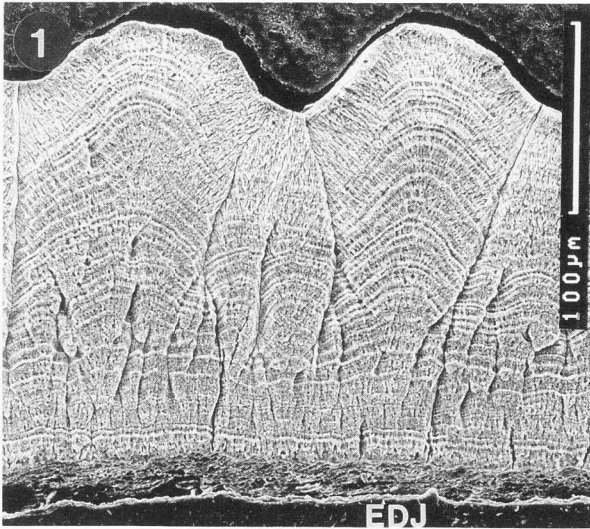
sheath. As Boyde (1964, 1965) has shown, the cross-sectional morphology of the prism sheath is determined by the shape of the Tomes process on the tip of the amelo-blast. Currently it is not known if the differences in morphology of the prism cross-sections have distinct functional significance.

Several investigators have analyzed the morphology of prism cross-sections and patterns of organization or packing of the prisms (e.g., Preiswerk 1894, 1895, 1896; Shobusawa 1952). The system of classifi-cation introduced by Boyde (1964) has been expanded and refined by him and, in some instances with important contradictions, by other workers (e.g., Gantt 1983, Fortelius 1985, Krause and Carlson 1986, Martin et al. 1988). Certainly this sys-tem, with its three basic prism types as a unifying feature, has greatly influenced the course of research on mammalian enam-el. However, with advances in knowledge of the diversity of prismatic enamels, limitations of the system have become ap-parent.

First, the system focuses on the three major types of prism cross-sections and thereby tends to limit analysis of variation to these categories. A number of suggestions for modification of the system introducing new categories have been made (e.g., Gantt 1983). Even with these additions, commonly occurring cross-sectional patterns, e.g., the lanceolate cross-sections frequently found in the enamel of various taxonomic groups, for example, marsupials (Fig. 9) or rodents (Fig. 16, left), are not easily cate-gorized.

Another limitation of the system stems from its application by many workers who have attempted to characterize taxo-nomic groups by occurrence of a specific prism type, but overlooked or deemphasized two different patterns of variation. First, not all enamels are characterized by prisms with morphologically uniform cross-sections. Variation in individual prism cross-sections within a limited area of the enamel can be extreme. For exam-ple, prism cross-sections of the primitive eutherian Purgatorius vary from irregular and sometimes infolded structures to horseshoe-shaped or ellipsoid structures (Fig. 7). Also, in the lipotyphlan insec-tivore Erinaceus its incompletely closed prisms are far from regular in shape (Fig. 10). This great variation in prism cross-sections is found consistently at different levels within the enamel in dif-ferent areas of the postcanine dentition.

In addition to this variation another type of genetically/ontogenetically con-trolled variability in prism cross-sections has been found in many mammals. During the ontogeny of prisms the shape of

their cross-sections can change in spe-cific, regular patterns. Layers within the enamel formed by different enamel types can have prisms with distinctly dif-ferent cross-sections. Even within a sim-ple enamel type, regular differences can occur. In the Hunter-Schreger bands of the carnivores Ursus (Fig. 11) and Felis, for example, the normally incomplete prism sheaths usually are complete in areas where prisms bend strongly as they change their orientation (Koenigswald 1980 and in press).

Also, Boyde's system of numbering prism packing patterns illustrates his initial interpretation of the polarity of evolution of prismatic structure (e.g., Boyde and Martin 1984a, 1984b). Type 1 prisms, characterized by closed, circular prism sheaths, were thought to be primi-tive and type 2 and type 3 prisms more derived. Subsequent discoveries indicate that not only is this interpretation of evolutionary interrelationships incorrect,

Complexity of the Enamel: Prism Level

Fig. 7. Variation of prism cross-sections in the enamel of a lower molar of Purgatorius unio, Early Paleocene, Montana (KOE 1118). The prism cross-sections, as shown by the strongly etched prism sheaths, are open on one side and vary from circular to irregularly bilobate. Individual crystallites are not visible in this section because of slight diagenetic recrystallization.

Fig. 8. Regular development of seams in the IPM of Prodiacodon crustulium, Early Paleocene, Montana (KOE 1113). The prism sheath is open on one side and the seam occurs within that opening.

Fig. 9. Prisms with lanceolate cross-sec-tions in Macropus rufus, Recent, Australia (KOE 995). Elongated apices of prisms commonly associated with bifurcations of the IPM. Note the tubule (T).

Fig. 10. Variation of prisms in Erinaceus europaeus, Recent, Germany (KOE 1074). The oblique section illustrates the irreg-ular outlines of the usually complete prism sheaths. Note the thick IPM.

Fig. 11. Circular prisms with complete prism sheaths as well as prisms open on one side and incompletely separated from the IPM occur together in Ursus spelaeus, Upper Pleistocene, Germany (KOE 998).

Fig. 12. The highly derived prisms with key-hole cross-sections are densely packed and show no IPM in contrast to the more primitive prisms, which are open on one side. Mammuthus primigenius, Upper Pleis-tocene, Germany (KOE 33).
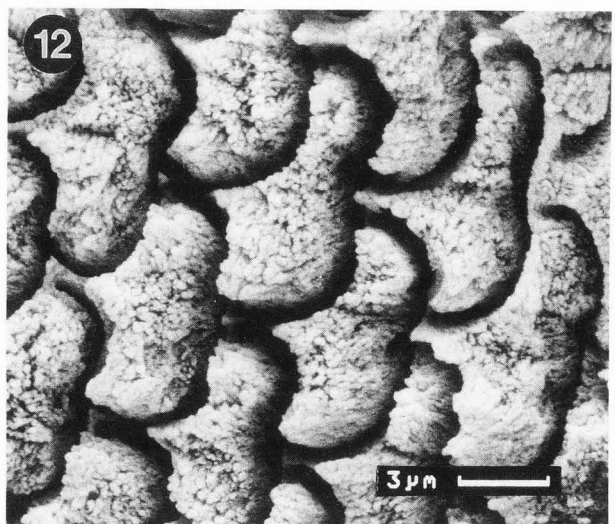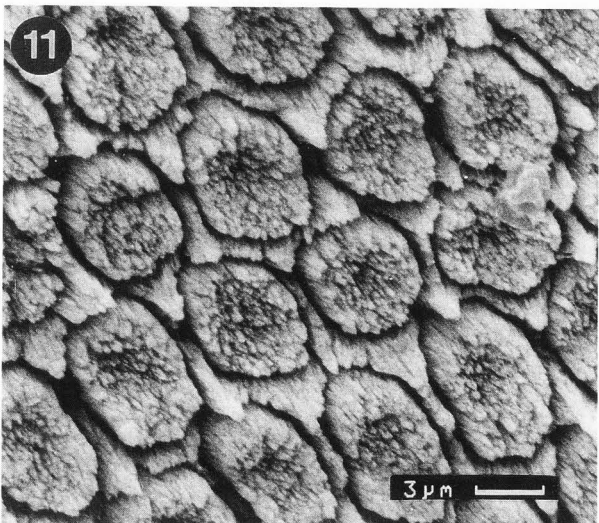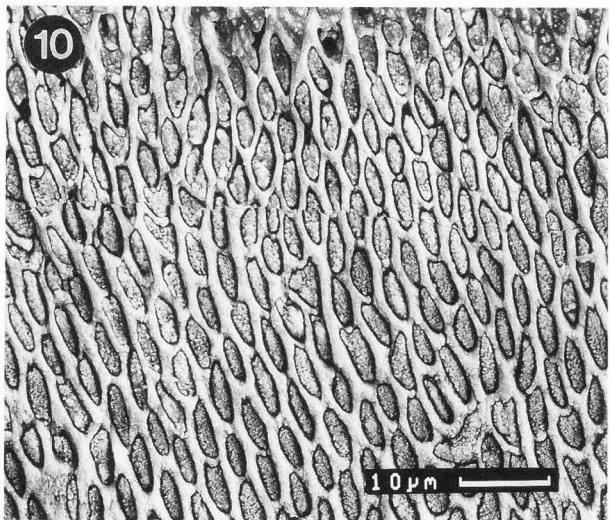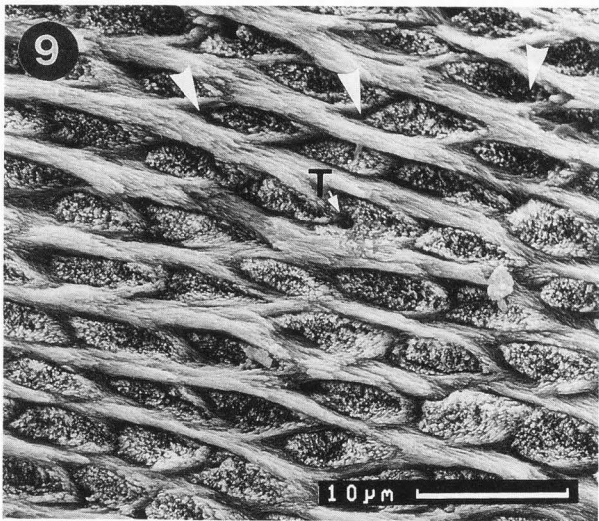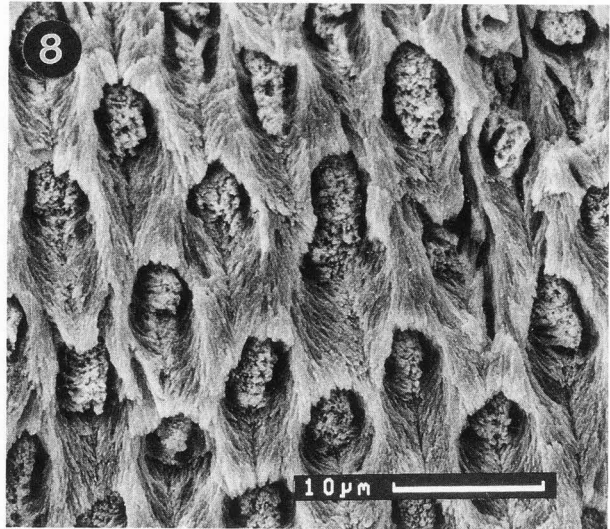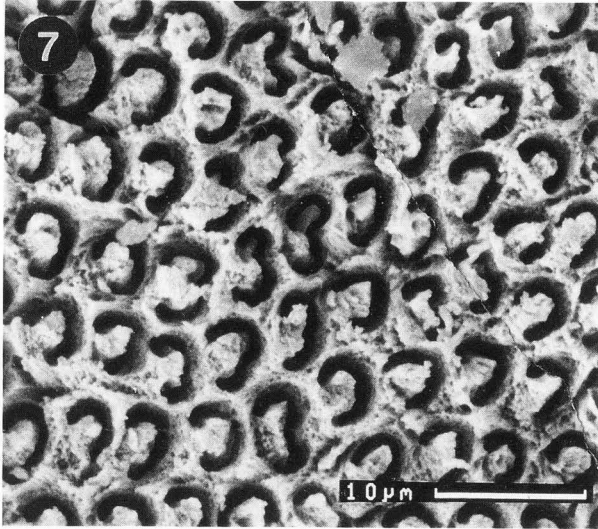
but also at least type 3 is an evolution-
ary grade, not a clade (Kozawa 1985, Clem-
ens and Wood, in prep.).

Both their occurrence in some pre-
tribosphenic and early tribosphenic mam-
mals and their earlier appearance in the
fossil record indicate that prisms with
broadly open, almost planar sheaths widely
separated by IPM probably are the most
primitive known mammalian prism type. A
dryolestid from the Late Jurassic illus-
trates this prism type, which most likely
characterized the last common ancestor of
eutherians and marsupials (Lester and
Koenigswald 1989).

Additionally, prism type 3 includes
not only prisms with simple, curved, in-
complete sheaths but also the highly de-
rived prisms with "key hole" pattern. The
latter pattern evolved independently in
primates and in several groups of tethy-
theres, for example, proboscideans (Fig.
12) and sirenians.

Prism cross-section is only one char-
acter of enamel microstructure. Orienta-
tion of prisms, the structural basis for
the next level of enamel complexity, pro-
vides another independent group of charac-
ters with different functional and adap-
tive values.

Enamel types

Units of enamel in which the prisms
have similar orientations are defined as
enamel types. The enamel of a tooth can
consist of but one enamel type, or two or
three enamel types can be present in a
specific, three dimensional order (a
schmelzmuster). In order to analyze and
describe the three dimensional orientation
of prisms, the enamel dentine junction
(EDJ) serves as a practical reference
plane. For systematic analyses usually it
is not necessary to follow the courses of
individual prisms from the EDJ to the ena-
mel's outer surface as Warshawsky and
Smith (1971) did in their study of a ro-
dent incisor. In most cases, the orienta-
tion of groups of prisms is of interest.

Different enamel types have charac-
teristic functional properties reflecting
their different prism orientations. These
functional properties appear to be inde-
pendent of the morphology, of the prism
cross-sections and thereby provide a dis-
tinct class of characters. Despite great
variability in tooth morphology the number
of enamel types is limited; so far four
basic types have been recognized: radial
enamel, tangential enamel, Hunter-Schreger
bands, and irregular decussation.

In **radial enamel**, the long axes of
the prisms are oriented radially from the
EDJ, as seen in a horizontal plane, and
rise occlusally toward the surface of the
enamel, as seen in a vertical plane
(Koenigswald 1977, 1980). The vertical
inclination of the prisms can vary through
the length of the prism. In most lipo-
typhlan insectivores, for example Talpa
(Figs. 13 and 14), the prisms rise from
the EDJ at an angle of about 45° and then
curve gently to intersect the outer sur-

Complexity of the Enamel: Enamel Types

Fig. 13. Radial enamel exposed in a hori-
zontal section through a molar of Talpa
europaea, Recent, Germany (KOE 1069).
Prisms are directed radially but change in
their inclination.

Fig. 14. Longitudinal section through the
radial enamel of a molar of Talpa
europaea, Recent, Germany (KOE 1069),
showing the changing inclination of the
prisms and the reduction of the angle be-
tween prisms and the crystallites of the
IPM. Close to the outer surface, the
prisms disappear in aprismatic ("post-
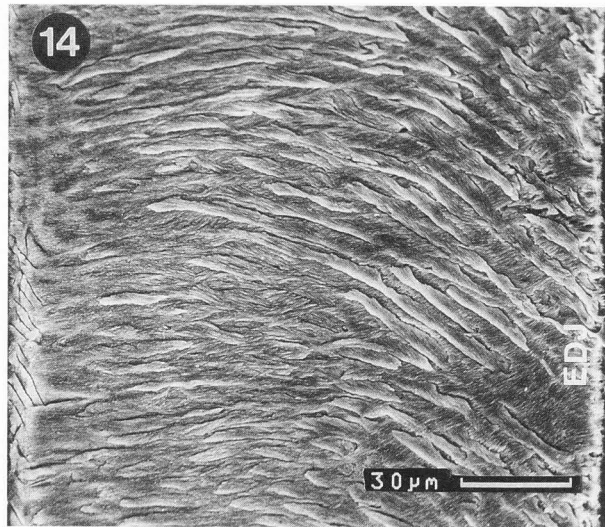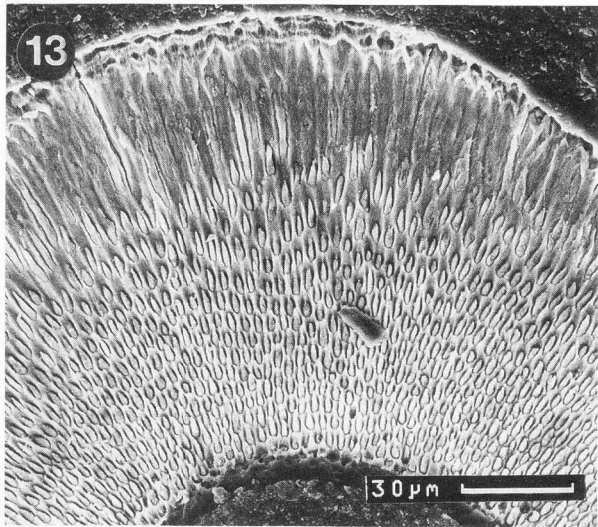prismatic") enamel.

Fig. 15. Modified radial enamel, a sub-
type of radial enamel, is characterized by
very thick layers of IPM ordering prisms
in rows. Horizontal section is from a
molar of Elephantulus infercens, Recent,
Tanzania (KOE 1090). The crystallites of
the IPM are oriented at right angles to
the direction of the prisms and do not
anastomose between them.

Fig. 16. Tangential enamel (right) over-
lying radial enamel (left) in a molar of
Mimomys sp., Pliocene, Germany (KOE
1470A). Horizontal section through the
trailing edge of a dentine triangle of a
molar (EDJ towards the left). The struc-
ture of the two enamel types is very simi-
lar in the relative orientation of the
prisms and the IPM. These remain constant
as the vertically rising prisms of the
radial enamel turn 90° into their horizon-
tal continuations in the tangential enam-
el. In this section, the prisms of the
radial enamel are deeply etched and only
the IPM is visible. In the tangential
enamel both prisms and IPM are visible.

Fig. 17. Hunter-Schreger bands composed
of decussating layers of prisms. Ursus
speleaus, Upper Pleistocene, Germany (KOE
998). In this vertical section through a
molar, the HSB vary in the number of
prisms per layer. The transition of prisms
from one band to the other and bifurcation
of bands is characteristic of most HSB.

Fig. 18. Irregular decussation of prism
bundles might have evolved from HSB. The
tangential section through the inner layer
of the enamel of an upper molar of
Hypolagus brachygranthus, (Pliocene, Po-
land, KOE 1062) shows decussating bundles
of a few prisms width. In addition, in
rodents uniserial HSB as well as thick HSB
independently evolved irregular decussa-
tion.
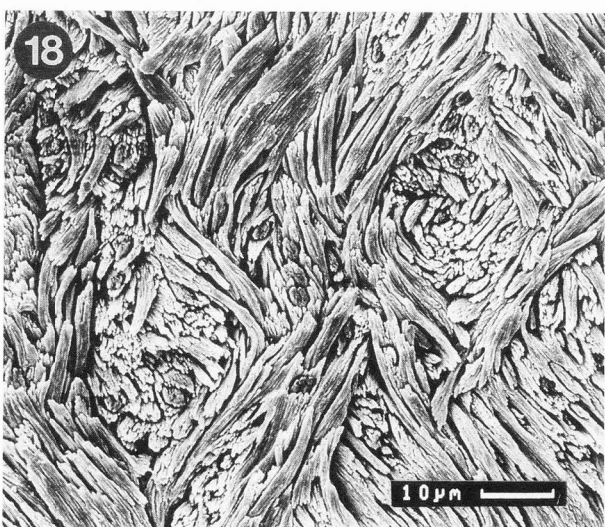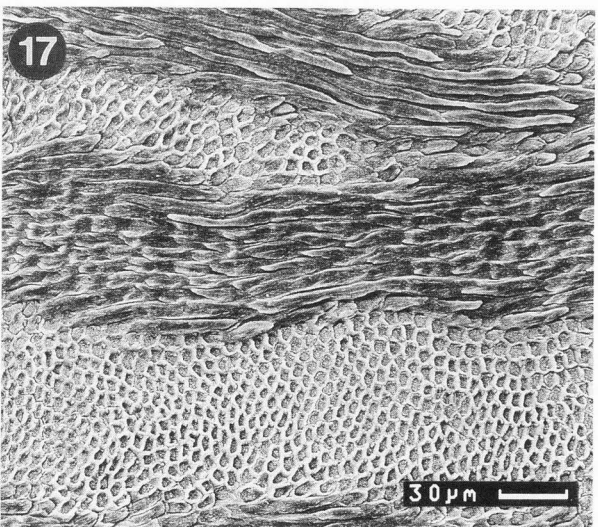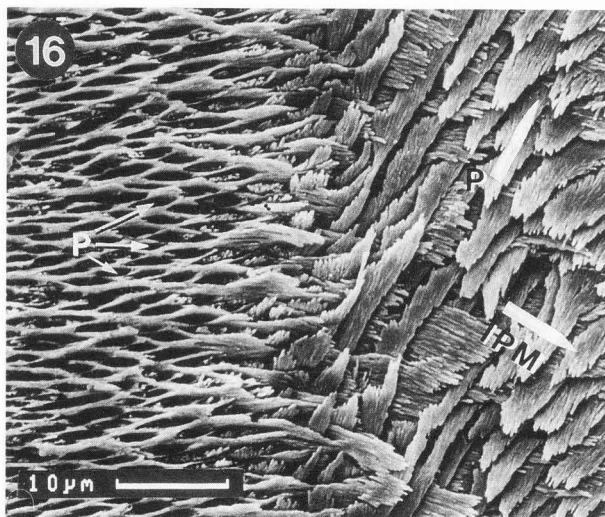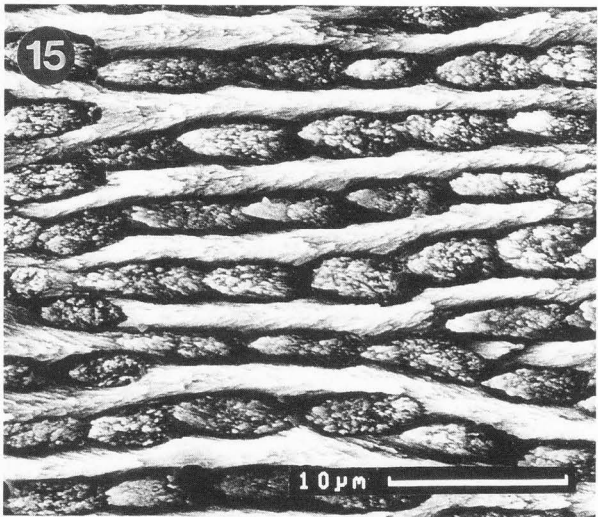
face almost at right angles, if they do not lose their sheaths and vanish into the interprismatic matrix. Radial enamel can consist of prisms with incomplete, complete, or "key hole" shaped cross-sections and can form the entire thickness of the enamel or only a distinct layer.

Different subtypes of radial enamel can be distinguished by differences in orientation of the IPM crystallites relative to the prisms, which can vary from almost parallel to intersections at angles of approximately 90°. If the angular difference is great, the IPM crystallites can anastomose between the prisms. In the most derived grade of complexity, these crystallites form thick layers between rows of prisms (Fig. 15). This modified radial enamel was classified by Shobusawa (1952) as "Huftierschmelz" and by Boyde as "type 2". It often forms the inner enamel layer of hypsodont teeth of large herbivores, for example, perissodactyls and artiodactyls, where it serves to resist radial tension forces (Pfretzschner 1991).

Orientation of enamel prisms is not restricted to a simple radial orientation; distinct lateral deviations can occur. In **tangential enamel** the prisms remain parallel as their outward course from the EDJ is laterally deflected from a simple radial orientation (Fig. 16). The vertical inclination of the prisms of tangential enamel tends to be very low (usually much less than 20° above the horizontal) and the crystallites of the adjacent IPM intersect the prisms at approximately right angles.

Tangential enamel frequently occurs adjacent to a layer of radial enamel. In the enlarged incisors of the extinct marsupial Groeberia and extant Macropus, a layer of tangential enamel lies between the EDJ and an outer layer of radial enamel (Koenigswald and Pascual 1990). Their positions are reversed in the molars of arvicolid rodents with radial enamel forming a layer adjacent to the EDJ and tangential enamel forming an outer layer.

Hunter-Schreger bands (HSB) are another derived type of enamel occurring more frequently than tangential enamel. Within each Hunter-Schreger band the prisms exhibit concordant changes in orientation (Fig. 17). The direction of change in orientation of the prisms in one band is opposite that in adjacent bands, thus producing decussations. The cross-sections of prism sheaths vary from incomplete to complete, including prisms with a "key hole" pattern. Usually HSB are oriented horizontally and most clearly visible in vertical sections. Kawai (1955) published an extensive survey of the occurrence of HSB in mammalian enamel and provided data on thickness of the bands.

In their course from the EDJ prisms regularly change from one band to another in a transition zone of variable thick-ness. Transition zones, up to three prisms in width, have been observed; Daubentonia provides an example (Koenigswald and Pfretzschner 1987). In these thick HSB, the characteristic bifurcation of the bands is produced by abrupt turns of the prisms before they reach the transition zone. Bifurcations also occur in uniserial enamel. Here prisms turn at an angle of 90°, immediately producing a bifurcation but leaving no transitional zone. These regular changes in orientation of the prisms were termed "aberrations" by Risnes (1979).

Koenigswald et al. (1987) argued that the Hunter-Schreger bands evolved in parallel in several groups and tended to occur when a body size roughly equivalent to that of a rabbit was achieved. This correlation probably results from the fact that larger body size results in larger jaw muscles and, thereby, the probability of greater maximum pressures (stresses) being exerted on the enamel of the teeth. Changes in configuration of the teeth or mechanical relationships of the jaws also can produce localized increases in pressure on the enamel and promote evolution of HSB without major increase in body size, for example in erinaceid lipotyphlans or plesiadapiform primates (Clemens and Koenigswald in prep.)

Hunter-Schreger bands have been studied most extensively in rodent incisors (e. g., Korvenkontio 1934, Wahlert 1968, Martin (1990a, 1990b, in prep.). In rodents, HSB can be differentiated according to thickness of the bands. They range from multiserial, the thickest, through pauciserial to uniserial HSB, which are but one prism in thickness. Differences in thickness of HSB coupled with differences in the orientation of crystallites of the IPM have been used to distinguish major taxonomic groups. For example, the most derived type of HSB, a one prism thick uniserial HSB, is found in Sciuromorpha and Myomorpha and clearly distinguishes them from the various groups of hystricomorphs, which have thicker, multiserial HSB. HSB of intermediate thickness characterize the pauciserial enamel of the extinct families of protrogomorphs (Korvenkontio 1934, Wahlert 1968, Boyde 1978).

Distinguishing multiserial and pauciserial HSB on the character of thickness alone does not provide a clear separation of the two types in the incisor enamel of some rodents. Martin (1990a, 1990b, in prep.) was able to overcome this difficulty and increase resolution by including orientation of the IPM crystallites in his diagnoses. In pauciserial enamel, the IPM crystallites are oriented in parallel to the prisms. In multiserial HSB, their orientations diverge. At an extreme, members of the Octodontoidea can be separated from members of the other superfamilies of

the Caviomorpha by an approximately 90° difference in orientation of the IPM crystallites and prisms.

Koenigswald (1980) previously argued that multiserial HSB were less derived than pauciserial HSB. Now, considering the orientations of IPM crystallites, this hypothesis has to be rejected (Martin 1990a, 1990b, in prep.). Also, Koenigswald (1990) found that pauciserial to multiserial HSB with intersecting IPM crystallites and prisms form an additional layer in the incisors of <u>Marmota</u>. These HSB evolved from the uniserial enamel with IPM crystallites oriented parallel to the prisms, which is characteristic of most of the sciurids studied to date.

Typically HSB are horizontally oriented, but in some eutherian mammals their orientation is vertical. For example, in members of the Rhinocerotidae (Rensberger and Koenigswald 1980) and some other large, herbivorous mammals (Fortelius 1985; Boyde and Fortelius 1986) the HSB are vertically oriented in some parts of the dentition. Likewise, in uniserial HSB of the incisors of some distantly related families of rodents, the HSB are oriented vertically (Korvenkontio 1934; Wahlert and Koenigswald 1985).
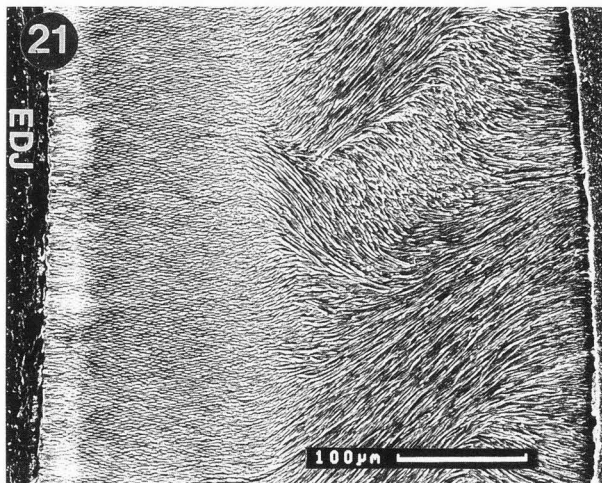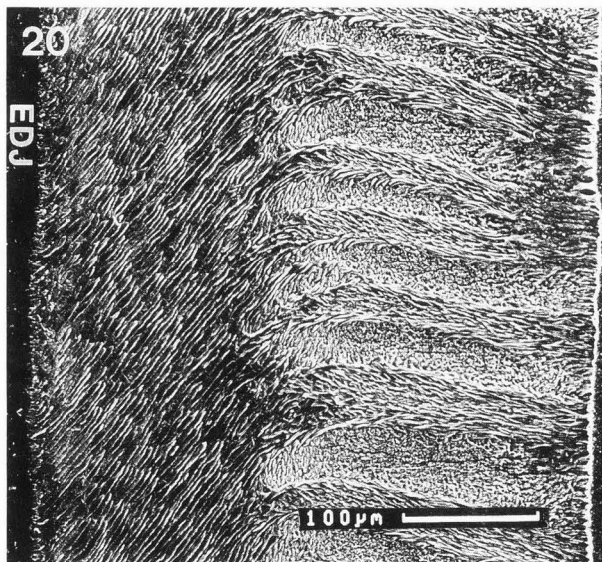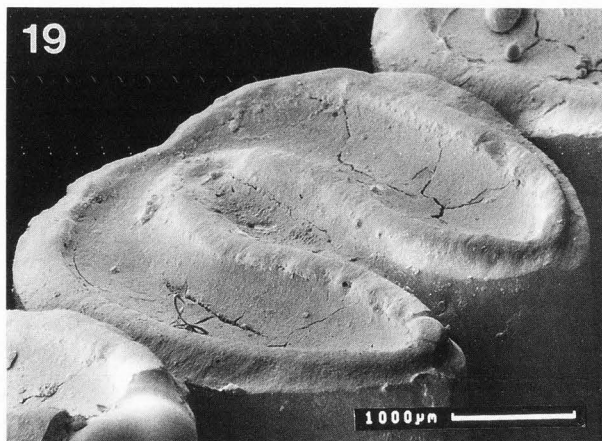

<u>Fig. 19.</u> On the occlusal surfaces of molars of <u>Pedetes cafer</u>, (Recent, Africa, KOE 158) the outer enamel is worn more intensively than the inner. This correlates with the different enamel types involved (see Figs. 21 and 22). Illumination with tangential light makes the horizontal HSB close to the outer surface visible.

<u>Fig. 20.</u> A vertical section illustrates the two enamel types in a molar of <u>Pedetes cafer</u>, Recent, Africa, KOE 158). The inner half is formed of radial enamel; the outer is made up of HSB of approximately equal thickness separated by very thin transitional zones. The strong inclination of the prisms of the radial enamel produces a greater resistance to wear than the horizontal prisms of the HSB (see Fig. 19).

<u>Fig. 21.</u> A horizontal section parallel to the occlusal surface of a molar of <u>Pedetes cafer</u>, Recent, Africa (KOE 158), shows the cross-sections of prisms in the radial enamel which forms approximately half of the thickness of the enamel band. In the outer layer several of the horizontal HSB intersect the plane of section. The prisms of adjacent bands decussate at almost right angles. The transition of prisms from one band to another is well illustrated.

Complexity of the Enamel:
Schmelzmuster

A fourth enamel type, **irregular decussation**, has been recognized. As the name indicates, enamels of this type consist of bundles of prisms that have irregular patterns of decussation (Fig. 18). Clearly these patterns evolved independently from HSB of different thicknesses. Irregularly decussating uniserial HSB form the "less ordered lamellar enamel" or "lemming enamel" found in members of the Lemminae (Koenigswald 1980, Koenigswald and Martin 1984). Multiserial HSB of the ochotonid lagomorph Prolagus (Fig. 18) show a similar irregular pattern (Mazza and Zafonte 1987). Interwoven bundles of thick HSB form the 3-D enamel of proboscideans (Remy 1976, Pfretzschner 1991). Distribution of enamel types among various lineages of Cenozoic eutherian mammals and time of their appearance in the fossil record suggests an evolutionary pattern involving many examples of parallel evolution. Radial enamel with the IPM crystallites oriented parallel to the prisms occurs in a large number of eutherians and marsupials, many of which would be characterized as primitive on the basis of analysis of other types of characters. Evolution of an angular intersection of prisms and IPM crystallites appears to be a derived character of radial enamel (CB Wood, in prep.).

Tangential enamel, which is known in marsupials, e.g., Macropus and Groeberia; eutherians, e.g., arvicolid rodents; and multituberculates, e.g., Ptilodus, clearly evolved more than once. In all known examples of tangential enamel, the angle of incidence of IPM crystallites and prisms is large. Whether this indicates that tangential enamels evolved from radial enamel with similar high angles of incidence or the orientation of the IPM crystallites and prisms was modified after the tangential reorientation of the prisms evolved is unknown.

Likewise, HSB definitely evolved more than once, probably from stocks characterized by different kinds of radial enamel. Increased angulation of IPM crystallites occurred in different lineages. The different subtypes of irregular decussation enamel appeared in lineages of mammals that had already evolved HSB of distinctly different thicknesses.

For a systematist, the message is clear. Similar patterns of structural complexity at the level of enamel types have evolved more than once in different mammalian lineages. For example, the occurrence of HSB in some lipotyphlan insectivores, primates, rodents, and ungulates as well as in at least one marsupial, the wombat, is certainly a product of parallel evolution and contributes little to understanding the phylogenetic interrelationships of these groups. On the other hand, as has been amply demonstrated in studies of the suborders of rodents (Korvenkontio

1934 and Martin 1990a, 1990b, in prep.), the pattern of occurrence of different derived enamel types has provided significant data elucidating phylogenetic interrelationships.
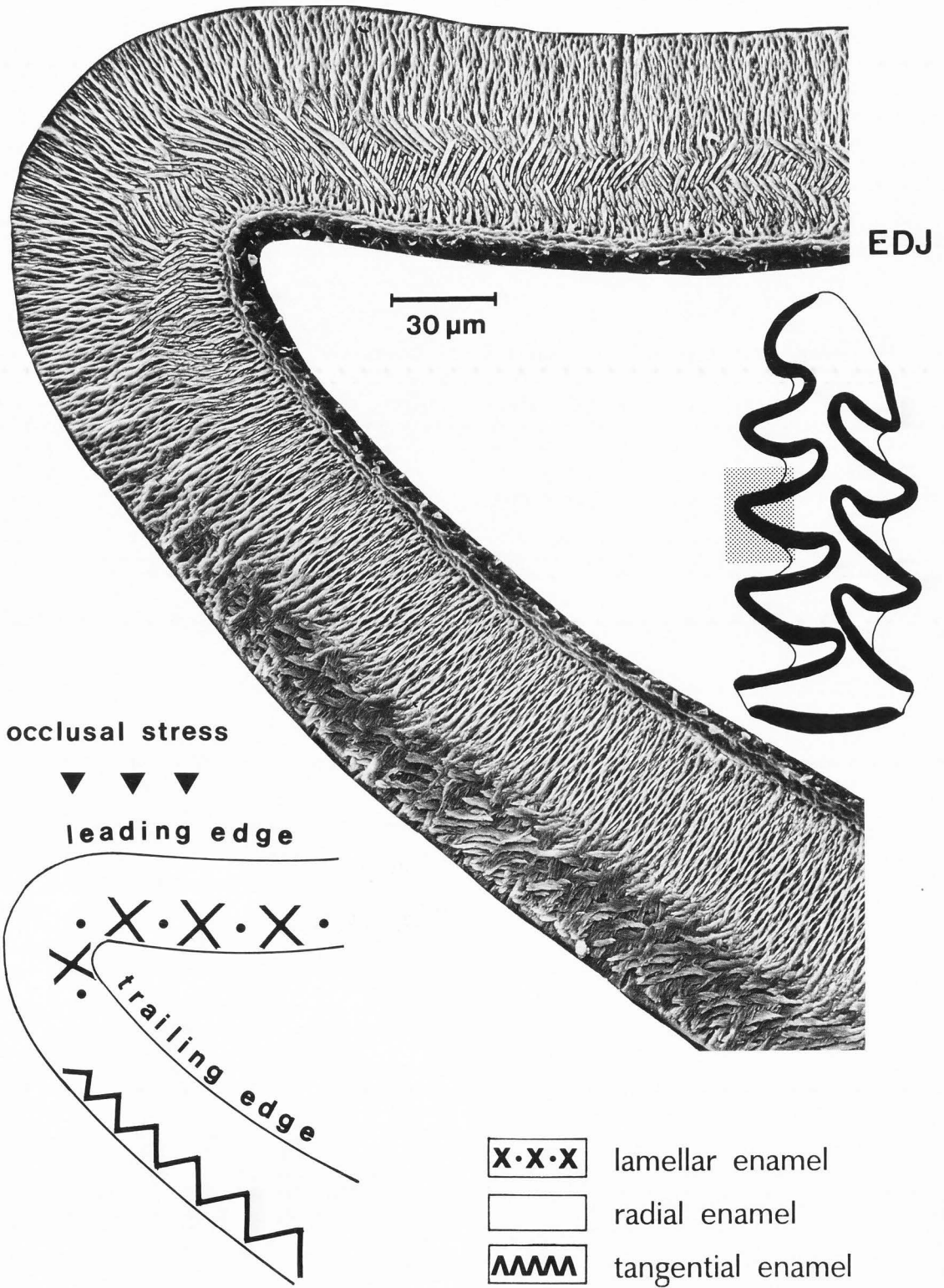
The functional significance of each of the various enamel types is not yet fully understood. A few generalizations, however, are warranted. Wear occurs at the slowest rate when the angle of incidence of the prisms with the occlusal surface is large (Rensberger and Koenigswald 1980, Stern, Crompton and Skobe 1989, Koenigswald and Pfretzschner 1991). Radial enamel tends to provide an optimal orientation of the prisms to minimize the rate of wear. This might provide an adaptive explanation for selection initially favoring this enamel type and its occurrence in many groups of primitive eutherians. Simple radial enamel is, however, prone to breakage because hair line cracks can penetrate the enamel following the straight boundaries of the prisms (Boyde 1976). A change in the direction of the prisms, such as in the transition to tangential enamel, tends to stop this cracking, for example note Groeberia (Koenigswald and Pascual 1990). Even greater protection from breakage is provided by the decussation of prisms in Hunter-Schreger bands (Koenigswald and Martin 1984, Pfretzschner 1988). Among the decussating prisms, however, many do not meet the wear surface at high angles of incidence. The price of protection against breakage is the potential for higher rates of wear of the enamel.

These different attributes indicate that there is no ideal enamel type suitable for all functional demands. Viewed from this functional perspective it is not surprising that different combinations and distributions of enamel types (schmelzmuster) evolved in various lineages of Cenozoic eutherians.

Complexity of the Enamel: Schmelzmuster

Fig. 22. Mosaic of part of the posterior end of a horizontal section of the lower P4 of Prolagus sardus, Pleistocene, Sardinia (KOE 1060). [D: dentine, C: cementum]. Basically the enamel has a two layered schmelzmuster with radial enamel internally and irregularly decussating enamel externally. The obvious variation in thickness of the enamel band is the result of loss of the external irregular decussating enamel followed by thinning of the radial enamel. Differentiation of leading and trailing edges is not developed.

23

EDJ

30 μm

occlusal stress

▼ ▼ ▼

leading edge

· X · X · X ·

X
·

trailing edge

X·X·X	lamellar enamel
	radial enamel
∧∧∧∧	tangential enamel

Schmelzmuster

Mammalian teeth capped with enamel composed of only one enamel type are rare. Normally two or more enamel types are present and have a characteristic distribution through the enamel of the crown. This three dimensional pattern of arrangement of enamel types has been designated "schmelzmuster" (Koenigswald 1977, 1980). The literal translation of the term is "enamel pattern", a phrase commonly used to describe distribution of enamel bands on occlusal surfaces of hypsodont teeth. To avoid confusion schmelzmuster is retained.

The schmelzmuster of rodent incisors regularly consists of two layers; the inner is composed of HSB and the outer of radial enamel. Some authors have used the term "rodent enamel" to refer to only the inner layer of uniserial HSB and have not considered other characters of the enamel.

Biomechanically a complex schmelzmuster brings together several enamel types with different functional properties, which can be clearly demonstrated in the molars of Pedetes. On the occlusal surfaces of the molars the enamel is restricted to a simply folded band. The enamel, however, has a two-layered schmelzmuster. The inner layer of radial enamel is more resistant to wear than the outer layer of HSB, which acts to prevent the formation of cracks (Figs. 19-21).

In Equus, Bison, or other mammals with hypsodont teeth a secondary occlusal surface is developed when wear exposes the dentine and enamel bands form cutting edges (Fortelius 1985). On any hypsodont, mammalian tooth the thickest areas of the bands of enamel exposed on a secondary occlusal surface usually consist of several layers. Thinning of the bands frequently is the product of loss of the outer layer (or layers). Therefore, in order to develop a total understanding of the complexity of the schmelzmuster of a tooth it is necessary to consider variation in structural complexity between thin and thick areas of the enamel bands (Fig. 22).

Schmelzmuster provide consistent characters for taxa at the generic or family levels. Individual variation often appears to be limited to minor changes in thickness of the constituent layers. A study of several hundred arvicolid molars (Koenigswald 1980) showed that in homologous areas composition and thickness of layers of different enamel types within the schmelzmuster are essentially constant.

Orienting hypsodont teeth of some ungulates and rodents in the direction of jaw movement when the upper and lower dentitions were occluded, Greaves (1973) and Rensberger (1973) distinguished the enamel bands forming the leading and trailing edges of the lophs by different patterns in relative wear of the enamel and dentine. These leading and trailing edges of the lophs also can differ in thickness. At an extreme, enamel is lost from the leading edge of cheek teeth of the wombat (Koenigswald and Pfretzschner 1991) and in some rodents. In the molars of some arvicolids, composition of enamel types can also differ between the leading and trailing edges of lophs (Fig. 23). Thus, variation in schmelzmuster can reflect the different biomechanical requirements of different parts of the crown (Koenigswald 1980, 1982)

Analyses of schmelzmuster have not only aided in characterization of taxa, particularly at the generic or familial levels, but also contributed to tracking the evolution of particular lineages. For example, primitively the base of the crown of cricetid molars is encircled by a layer of uniserial HSB (Fig. 24). A stratigraphically controlled sequence of Pliocene species of Mimomys documents the changes in extent of this layer on the leading edge of the tooth as it expands to cover the full height and width of the crown (Koenigswald 1980, 1982).

The evolutionary history of horses is one of the best known among fossil mammals. Pfretzschner (in press) studied the evolution of their schmelzmuster. He demonstrated that increase in height of the crown was accompanied by the introduction into the schmelzmuster of an inner layer of modified radial enamel characterized by thick plates of IPM. In some other lineages of large mammals a layer of similar modified radial enamel was added to the schmelzmuster as hypsodonty evolved.

The number of layers involved in a schmelzmuster can increase in more derived enamels. In their studies of the microstructure of multituberculate enamel, Krause and Carlson (1986) demonstrate that the gigantoprismatic structure (Fosse et al. 1978) of taeniolabidoids is probably more primitive than the smaller, complete prisms characteristic of ptilodontoids. Similarly, schmelzmuster of the incisors of the taeniolabidoid Taeniolabis is one-layered; the enamel is radial with the IPM crystallites intersecting the prisms at nearly right angles. In the ptilodontoid Ptilodus, the schmelzmuster is more com-

Complexity of the Enamel: Schmelzmuster

Fig. 23. Schmelzmuster of the first lower molar of Clethrionomys glareolus, Recent, Germany (KOE 1487). Each dentine triangle is surrounded by an enamel band differentiated into leading and trailing edges. The position of the radial enamel shifts from the outside to the inside of the enamel band during the change from the leading to the trailing edge.
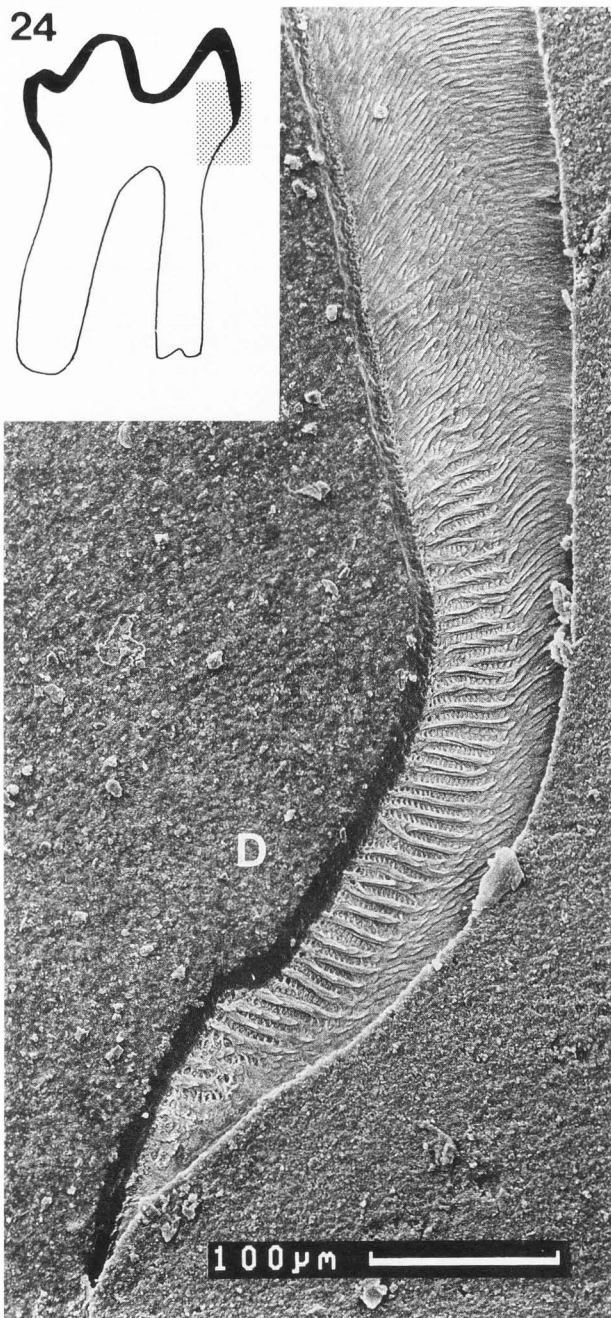
Complexity of the Enamel:
Schmelzmuster

Fig. 24. The schmelzmuster of molars of most muroids are vertically differentiated within the crown as illustrated here in <u>Cricetus cricetus</u>, Recent, Germany (KOE 100). The occlusal surface above top of micrograph. A band of uniserial enamel surrounds the base of the tooth; the remainder of the crown is formed by more primitive radial enamel.

Complexity of the Enamel: Dentition

Fig. 25 and 26. Orientation of the HSB in an incisor (Fig. 25, tangential view, tip of the incisor above the micrograph) and a molar (Fig. 26, oblique occlusal view) of the rhinocerotid <u>Chilotherium</u>, Miocene, Turkey (KOE 492). Light microphotographs of the natural surfaces with tangential illumination. In the incisor (Fig. 25) the HSB are oriented horizontally intersecting the vertical cutting edge on the side of the tooth. In the inner layer of molar enamel (Fig. 26) the HSB are oriented vertically, intersect the horizontal cutting edge, and are covered (bottom of fig.) by a thick layer of radial enamel.

Fig. 27 and 28. Longitudinal sections of the upper (27) and the lower (28) incisors of <u>Dicrostonyx torquatus</u>, Recent, Canada (KOE 1003), show differences in the enamel at the dentition level. The lower incisor is characterized by the large angle of incidence of the IPM in the inner layer with uniserial HSB. In the upper incisor the inner layer also is formed by uniserial HSB, but the crystallites of the IPM parallel the prisms.

as characters for systematic analyses is obvious. Many examples of use the complex schmelzmuster of arvicolid molars to characterize genera of voles and document their interrelationships at the subfamily level can be cited (Koenigswald 1980, 1989; Koenigswald and Martin 1984, and Rabeder 1981).

The significance of schmelzmuster has tended to be overlooked in SEM studies of enamel microstructure. In large part, this reflects the fact that at the magnifications needed to study enamel types, the SEM provides a view of a very limited area, one usually too small to adequately display the full development of the schmelzmuster. As already mentioned, this limitation can be overcome by making mosaics of pictures illustrating larger areas of the tooth (Fig. 22).

Dentition

Significant differences in the schmelzmuster of teeth in different areas of the dentition of an individual are well known in some groups of mammals. In all

plex and, therefore, probably more derived. The basal layer of radial enamel is covered by a layer of tangential enamel of approximately equal thickness (note Sahni 1979 and Carlson and Krause, 1985, fig. 7). In contrast, it appears unlikely that the one-layered enamel, made up of HSB, of leporid incisors is more primitive than the two-layered schmelzmuster of rodent incisors (Koenigswald 1985).

When fully described and analyzed, the great value of complex schmelzmuster
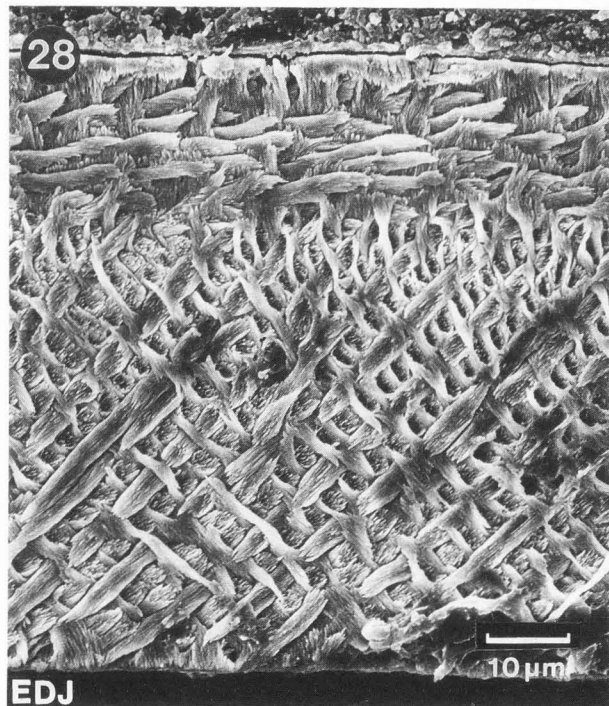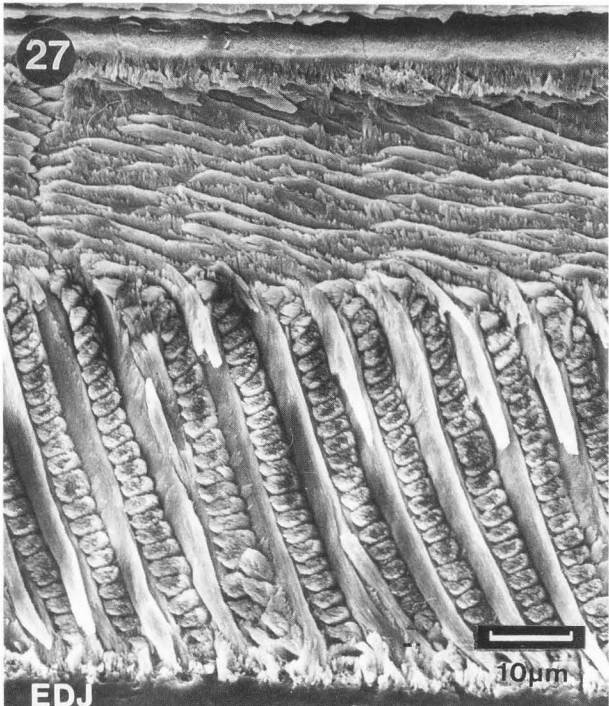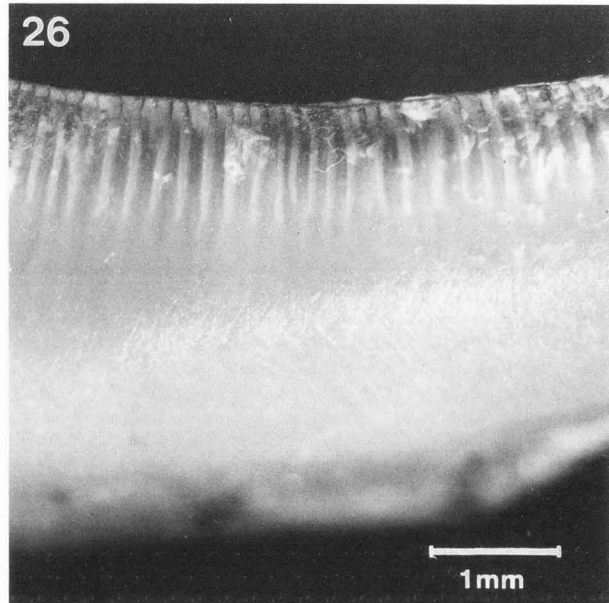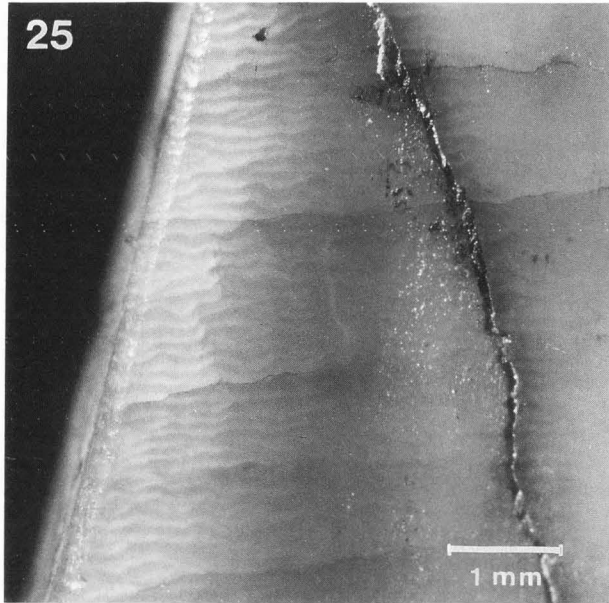
rodents, for example, the schmelzmuster of the incisors differs from that of the molars. In species of rodents with low crowned molars, the molar schmelzmuster is less derived than that of the incisors. In contrast, the schmelzmuster of hypsodont molars of other species can be more complex than that of the incisors. Koenigswald (1988) studied the enlarged front teeth of various mammals comparing their schmelzmuster with those of their molars and found marked differences in several taxa. In rhinocerotids, in contrast to the derived, vertical HSB characteristic of their molars, the HSB of the enlarged incisors are oriented transversely (Figs. 25 and 26).

The limited amount of information about regional differentiation of schmelzmuster within mammalian dentitions suggests that in some instances this regional differentiation can be linked to function-
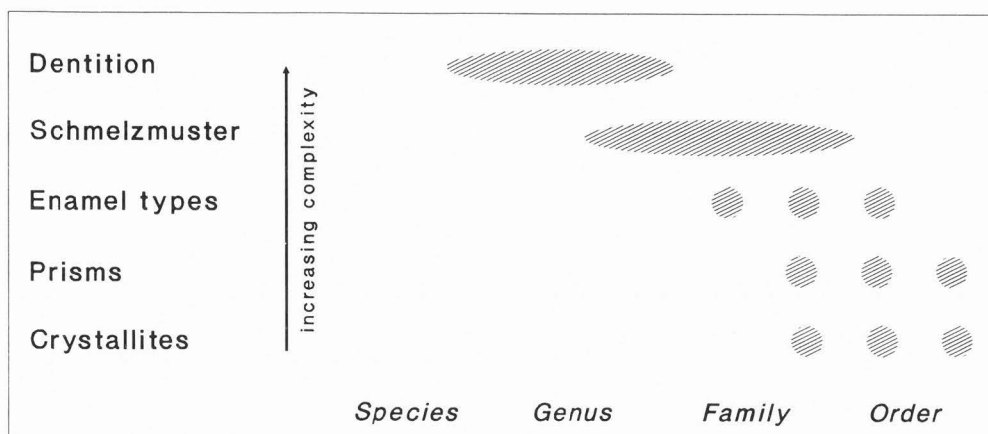
Fig. 29. Interrelationship of levels of structural complexity and the taxonomic rank at which the systematic significance of the various enamel characters is greatest. [Modified from Koenigswald et al. in press.]

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here, of course, does not cover all the areas of research on enamel pertinent to studies of systematic interrelationships or functional anatomy. Obviously missing are references to significant studies of patterns of dental wear both in the formation and morphology of the surface of wear facets (e.g., Grine 1987, Teaford 1988), and analyses of distribution of shearing and crushing surfaces as well as broader aspects of functional anatomy of the jaws and dentition (e.g., Crompton 1971, Butler 1990).

We have limited our discussion to the characters of mature, fully mineralized enamel because of our primary research interests and limitation of space. Obviously, data drawn from studies of ontogenetic patterns and their genetic background are pertinent fields. The sequence of enamel types forming a schmelzmuster, for example, is the product of changing ontogenetic patterns. As the ameloblasts move away from the EDJ the structure of the enamel deposited by each cell varies in a highly correlated fashion producing layers of enamel of similar structure over sometimes broad areas of the crown.

We also have not addressed the question of homology in structural patterns. Prisms, bundles of crystallites bounded, at least in part, by a major discontinuity in crystallite orientation, the prism sheath, have now been identified in marsupials and eutherians, multituberculates, and the agamid lizard, Uromastyx. Very probably the last common ancestor of marsupials+eutherians and multituberculates and certainly the last common ancestor of these mammals and Uromastyx had aprismatic

(including "preprismatic") enamel. If this hypothesis of phylogenetic relationships is correct, these structurally very similar prisms are analogous structures. To what extent is this structural similarity a product of the physical characteristics of dahllite and/or common developmental pathways of hard tissues in amniotes? A similar question, addressed by Zylberberg and Wake (1990), is to be found in the evolution of dermal ossifications in many groups of vertebrates.

Other aspects of the ontogeny of enamel have been addressed here. Increasing data on microstructure of mammalian enamel demonstrate that two aspects of morphological variation require careful analysis. As in any morphological character of a biological system, individual variation can be observed at every level of structural complexity of mammalian enamel, but their ranges of variation differ greatly. We have demonstrated that in some species the range of individual variation in morphology of prism cross-sections can be great. In contrast, at the schmelzmuster level of complexity, the small range of individual variation within many species is remarkable.

Turning from variation of particular characters at specific levels of complexity, we have stressed the need in both systematic and functional studies to consider the total pattern of structural variation in the dentition. To be sure, some information of value can be obtained in studies of particular groups through examination of the enamel at a similar depth in homologous areas of homologous teeth of each constituent species (note Grine et al. 1987). Here establishing a repeatable "depth" is best accomplished by reference to a particular level in the schmelzmuster rather than using a measurement. Although studies of this kind will produce data of value, we must argue that systematic and functional studies will be advanced more rapidly and thoroughly if attention is not focused on a particular area of a tooth

but emphasizes the variation throughout the dentition.

In her recent review article Carlson (1990:553) noted, "Unfortunately, too few comprehensive, empirical studies of intrataxon variation exist at the present time to inspire confidence in the patterns of variation within individual order or across the entire class of Mammalia". As research is advanced to fill these obvious gaps, it will be most efficient and fruitful to avoid limiting studies to a particular character at one level of structural complexity and focus on understanding the total complexity of the enamel in the dentition.

To reach this research goal, how many specimens need to be examined? Given the limitations of current technology, a full analysis of the patterns of structural complexity of enamel requires investigation of a series of teeth from different parts of the dentition of several individuals. As has been shown in some groups, the range of individual variation at some levels of complexity is small and valuable information can be obtained from single teeth, particularly when other members of the group are well known. Frequently, however, appropriate material is available in large samples of modern species or for extinct species represented in large quarry samples. Of course for rare or endangered modern species or extinct forms known only from one or a few specimens, destructive techniques of investigation of a number of teeth may not be appropriate or feasible.

Use of levels of complexity in the microstructure of mammalian enamel provides a system or framework for collecting and analyzing data for particular groups and facilitating comparisons between groups. We feel it will help overcome the difficulties raised when particular characters are not directly comparable. In their studies of multituberculate enamel at the level of complexity of prisms, Krause and Carlson (1986) found they could not apply Boyde's system of classification of prism shapes and packing patterns, which was developed for studies of eutherian and marsupial enamel. They used a primarily quantitative method for their descriptions and analyses. In contrast, as noted above at the level of schmelzmuster, informative comparisons can be made between the incisors of multituberculates and eutherians. Thus, the hierarchical system of analysis proposed here facilitates comparisons between distantly related groups and both highlights distinct differences and similarities. In its present form this system of analysis is basically designed for study of prismatic enamel and, no doubt, will require further development to facilitate study of aprismatic enamels.

Summary and Conclusions

Description and analysis of the complex structure of mammalian enamel can be facilitated through application of a system of hierarchical levels of structural complexity.

Like any biological structure, the microstructure of enamel exhibits individual variation, however significant structural differences distinguish taxa. Although, describing interdependent aspects of the total structural complexity, each hierarchical level provides unique characters significant in studies of systematic interrelationships and/or functional morphology.

a) Data on orientation and organization of the **crystallites** is significant in studies of the origin of the Mammalia and in the evolution of prismatic enamel.

b) **Prism** cross-sections are now known to show a wide range of absolute size and, in some groups, high levels of individual variation. In groups such as the multituberculates, prism size can be used to diagnose subordinal units.

c) **Enamel types** are characterized by the orientation of groups of prisms that can have very different cross-sections. Differences in orientation of the IPM crystallites relative to the prisms contribute to the further differentiation of enamel subtypes. The surprisingly small number of enamel types discovered so far repeatedly evolved independently in many, sometimes distantly related, lineages. Each type can be shown to have distinctly different functional characteristics.

d) **Schmelzmuster** are formed of one or more enamel types, and, in derived mammals, bring together their various functional attributes. Differences in schmelzmuster show a remarkably low range of variation in composition, but can often be used to characterize taxa at the family or generic level.

e) Differentiation of the structural complexity through a **dentition** usually appears to be an attribute of functional differentiation of the dentition often providing characters diagnostic at the generic level.

The system presented here provides a method for categorizing and studying both individual variation of particular structures and variation of structural types throughout a mammal's dentition.

Ideally studies of systematic interrelationships and functional anatomy should consider structural complexity at all hierarchical levels. Lack of information about one level of complexity does not prevent significant analyses at other levels of structural complexity.

Acknowledgments

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Discussion with Reviewers

J.M. Rensberger: You noted that the known distribution of HSB in lipotyphlan insectivores (absent except for weak development in the incisors and premolars in Erinaceus and Galerix) may not be functionally determined. What other factor might be involved?

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Authors: Our work on lipotyphlans and plesiadapiformes (close relatives of primates) strengthens the conclusion that HSB evolved independently (in parallel) in several groups of mammals (Koenigswald et al. 1987). Appearance of HSB is, in some instances, correlated with increasing body size, but this is not always the case; note the absence of HSB in large periptychid ungulates of the Paleocene. We hypothesize that the developmental pathways necessary for the formation of HSB are not a primitive character of mammalian amelogenesis, but evolved later in the radiation of mammals and only in some lineages. This could explain why HSB are not present in some mammals of relatively large body size with dentitions apparently adapted for crushing but present in other, relatively small mammals in which the dental battery is modified so as to increase pressure (stress) on specific areas of certain teeth.

J.M. Rensberger: You have emphasized the homoplasy of enamel structures at various levels of your hierarchical scheme in mammals, and the problems this presents to the use of these structures in systematics. I wonder if the enamel microstructures, if known completely, that is, throughout dentitions or even single teeth, would be much worse in this regard than many other characters, even dental cusp patterns, which have been used so extensively in systematics of many mammalian groups.

Authors: Obviously this important question can only be answered with data from research on variation of enamel structure in a greater variety of mammals than is available today. We recognize that cusps, such as the cusp we call the hypocone, have evolved more than once in various mammalian lineages, however, use of the character of presence or absence of a hypocone in investigating the phylogenetic interrelationships of some mammalian lineages has proven most useful.

The apparent high level of incidence of homoplasies in evolution of enamel microstructure has been an impediment to use of these characters in studies of mammalian phylogenetic interrelationships, but we feel this obstacle can be overcome. Already studies focused on prism size, density, and shape have advanced our understanding of the evolutionary history of multituberculates and studies of schmelzmuster have contributed to knowledge of the systematics of rodents.

Categorizing our observations on enamel microstructure according to their levels of structural complexity and then employing them in studies of phylogenetic interrelationships at specific taxonomic levels will enhance their usefulness in studies of mammalian systematics. When used in this fashion we are convinced that characters of enamel microstructure can be added to characters of cusp morphology and will help advance our knowledge of the patterns of mammalian evolution.

D.N. Stern: What significance do you attach to the outer layer of aprismatic enamel and what role do you think it plays relative to the biomechanical forces on the tooth?

Authors: Aprismatic enamel is a structural grade of enamel that certainly is the primitive condition and either appeared independently or was retained in the evolution of more complex enamels, for example, the frequent occurrence of aprismatic enamel adjacent to the EDJ and/or on the surface of the tooth. Whether the outer layer of aprismatic enamel is a retention of the primitive condition in the mammalian lineage or the later evolution of a specialized structure in many groups of derived mammals remains to be determined.

Likewise, we feel that we do not have enough data on the occurrence of surficial layers of aprismatic enamel to do more than generate hypotheses concerning its functional significance. Because it is quickly removed from areas undergoing heavy, rapid wear, probably surficial aprismatic enamel has little if any functional significance here. The possible functional significance of the presence of a layer of aprismatic enamel at the margin of major wear facets needs to be considered. We have noted that surficial aprismatic enamel often reacts to etching differently from prismatic enamel. Perhaps it might offer some protection against chemical destruction of areas of the tooth that are not undergoing heavy, rapid wear.

Z. Skobe: Do you find perikymata on the tooth surface of many mammals? I have not examined many species, but only see them on some, mostly primates. Their presence means there would be true lines of Retzius present also. Is this a parameter you have considered as part of the enamel prism pattern?

Authors: While Retzius lines (lines which reflect developmental stages in growth of the enamel) are frequently seen in small mammalian teeth, peri-kymata are found mostly in teeth with thick enamel. The joint presence of these characters, known in human teeth with a very thick enamel, does not occur in small mammals.