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Tooth enamel of the cave bear (*Ursus spelaeus*) and the relationship between diet and enamel structures

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In the enamel of *Ursus spelaeus*, prisms with incomplete prism sheaths dominate, although prisms with complete prism sheaths are also present. The Schmelzmuster consists of two indistinctly separated layers. Dominant is the inner layer characterized by well developed Hunter-Schreger bands. The outer layer, varying in thickness, is formed by radial enamel. Aprismatic enamel was found in a few areas close to the enamel-dentine junction but occurs more frequently on the outer surface. The crystallites of the interprismatic matrix are parallel to the prisms or form a slight angle (max. 45°). Although *Ursus spelaeus* preferred a vegetarian diet, its teeth show typical carnivore enamel and have no similarities with herbivore enamel. In many herbivores, crystallites of the IPM are oriented at wide angles (about 90°) to the prisms and frequently form "inter-row sheets". In comparison to the enamel in carnivores, herbivore enamel is derived and often combined with a secondary occlusal surface. Examples, however, show that both characters are independent. The enamel of *Ursus spelaeus* demonstrates that a specialization of diet over a short period of time does not have an immediate influence upon enamel structure. Only during longer phases of evolution does selection result in an almost perfect correlation of the Schmelzmuster and stress patterns during mastication.

1. Introduction

The paleontological work of Björn Kurtén, to whom this memorial volume is dedicated, was devoted to the study of carnivores. It may be that his parents predetermined his interest by giving him the name Björn (bear). His thesis and several of his papers (Kurtén, e.g. 1955, 1958, 1967, 1969, 1972, and the "Cave bear story" of 1976) deal with the upper Pleistocene cave bear, *Ursus spelaeus* Rosenmüller & Heinroth, 1794. Because of the great amount of scientific literature on *Ursus spelaeus*, this species is often cited as being the best known fossil mammal. Kurtén's scientific contributions and subsequent studies by Rabeder (e.g. 1983, 1989) demonstrate that there are many more aspects still to be studied in this species.

The structure of the enamel in *Ursus spelaeus* was touched on by B. Kurtén only very marginally in a co-authored paper (Gantt et al. 1980) in which previously supposed hominid teeth from Petralona were identified as cave bear teeth. The structure of the enamel of *Ursus spelaeus* will be

described in the present paper. It is known that great differences occur in the ultrastructure of the enamel in various groups of mammals. This character can be used to identify mammalian taxa of higher orders and to reconstruct their phylogenetic relationships. On the other hand, in many dentitions, a close relationship between the ultrastructure of the enamel and the biomechanical stress patterns within the tooth has been demostrated (von Koenigswald 1980, 1982; Pfretzschner in press). The question may thus be raised whether enamel structure is determined primarily by phylogeny or by functional demands caused by different diets. A preliminary survey of the enamel of carnivores and herbivores has shown distinct structural differences, especially in the orientation of the interprismatic matrix.

Traditionally in palaeontology one tends to differentiate between characters that are clearly functionally determined and those determined mainly by phylogeny. This delineation is certainly not reasonable as most phylogenetical characters also have functional aspects, even if they are not obvious. Most functional characters are determined by the genome as well. Enamel formation is determined mainly by the genome and shows distinct functional correlations. In this discussion, *Ursus spelaeus* may be illustrative because it is mainly herbivorous, despite belonging to the order Carnivora.

2. Material and methods

Teeth of *Ursus spelaeus* are frequently found in upper Pleistocene cave deposits of Central Europe. Incisors, canines and various molars studied here were collected from the Kartstein cave near Eiserfey in the Eifel mountains about 25 km southwest of Bonn. This cave was excavated by Rademacher (1911) early in this century, and collections from the unstratified spoil heaps of his excavations were appropriate for this investigation. Although the material is unstratified, it is most probably early or middle Weichselian in age.

The fragments were embedded in artificial resin, sectioned in various directions and polished. In order to study the microscopic structure of the enamel, the surface of each section was etched for 2–5 s with 2N HCl. The structures are then visible under a reflecting light microscope, especially when using darkfield equipment. After sputtercoating, the sections were studied with a scanning electron microscope (SEM), in which the details of the structure become visible (Fig. 1). Longer etching allows the course of prisms to be studied more easily since the interprismatic matrix (IPM) is preferentially removed from the surface. To study the IPM, selected sections were etched only for a short time. The degree of fossilization can vary and affect the appropriate time of etching as well.

3. The enamel of *Ursus spelaeus*

3.1. Prism types, interprismatic matrix, and aprismatic enamel

Boyde (1964) described different prism packing patterns in his unpublished thesis. Later papers by him and his students (e.g., Boyde 1965, 1969a, 1969b, Boyde & Martin 1984, Gantt 1981, Gantt et al. 1980, Fortelius 1985, Grine et al. 1987) referred to this first description but gave somewhat divergent definitions. The prism-packing pattern was defined according to the cross-sections of the prisms as well as their relationship to the forming ameloblasts.

As stressed by Grine et al. (1987) the spatial arrangement of the prisms cannot be applied to all enamels (Carlson & Krause 1985).

In most differentiated teeth, the enamel structure in cross-sections shows a great variation between the enamel-dentine junction (EDJ) and the outer surface. In order to fully describe the regularities of the complex stuctures in enamel, von Koenigswald (1980) distinguished three levels in the organization of the enamel: the level of "prism types", defined by the cross-section of the prisms, the level of the "enamel types", defined by the direction of the prisms and the interprismatic matrix and, as a third level, the "Schmelzmuster", describing the combination of different enamel types within a tooth.

With the exception of very small areas of prism-free enamel close to the EDJ and the outer surface, the enamel of *Ursus spelaeus* is prismatic. The prisms are generally densely packed

in a hexagonal packing pattern which is frequently found in carnivores (e.g. in *Canis* Reif 1974). However, the prisms delimited by the prism sheaths are not in contact with one another, but are separated by a thick layer of IPM. In vertical sections prisms intersect at different angles due to their arrangement in Hunter-Schreger bands (Fig. 1). Even when the prisms are not cut ideally, it can be shown in most cases that the prism sheaths are incomplete (Figs. 2 and 3), a character of prism type 3 in Boyde's classification. In some areas, they even come very close to the "key-hole pattern" (prism type 3B) found in many higher primates (Gantt et al. 1977, Boyde & Martin 1984). In some areas, however complete, prism sheaths are present, as in prism type 1 (Fig. 4).

Crystallites within the prisms are almost parallel to the axis of the prism. Orientation of the crystallites of the IPM vary to some extent. They may be parallel to the prisms or deviate up to an angle of about 45° (Figs. 5 and 6). It is not yet possible to give a three-dimensional model for the arrangement of the crystallites in the IPM.

Lester & Hand (1987) named an additional structural character, the "seam". It is a minor discontinuity of crystallites, independent of the prism sheath. Seams were occasionally found as an exception in some prisms close to the outer surface. They are by far not as regular as in *Felis* or *Smilodon* (Lester & von Koenigswald 1989).

Aprismatic enamel was found in some restricted areas close to the enamel dentine junction (EDJ). However, in others the prisms start almost directly from the EDJ. The patchy occurrence of aprismatic enamel on the outer surface of the enamel (Figs. 7 and 8) is not related to wear. While the crystallites of the prisms and the IPM continue, the prism sheaths disappear. This does not occur at a specific distance from the outer surface but vary irregularly; thus the thickness of the aprismatic enamel varies over short distances. In the aprismatic enamel close to the outer surface, some of the Retzius-lines are usually visible (Fig. 7).

3.2. The course of the prisms

Mammalian enamel is not only characterized by the shape of its prisms, but the number of significant characters is greatly increased if the course of the prisms is considered as well. Two layers can be distinguished in the Schmelzmuster of *Ursus spelaeus*.

The inner layer, which is about 3/4 of the enamel thickness, shows up under a light microscope as light and dark bands formed by thick layers of decussating prisms, called Hunter-Schreger bands (HSB) (Figs. 9, 10 and 11). In vertical sections, the HSB are orientated at almost 90° to the EDJ or show only slight inclination towards the occlusial surface. In tangential view, the orientation of the HSB is basically transverse, which in molars is parallel to the base of the crown. However, the bands undulate irregularly and quite often split (Fig. 10). Splitting is typical of HSB (von Koenigswald & Pfretzschner 1987) and undulation was observed in several carnivores such as canids and hyaenids. The irregular deviation of the HSB from any plane causes difficulties in determining the maximum angle between the prisms of different bands. Sections almost always truncate the bands instead of being almost parallel, which would be ideal for measurements. Even though it is difficult to demonstrate in optimal pictures, the angle between the prisms of different bands approaches 90°. At the margins between the bands, in narrow transitional zones prisms change from one band to the next, as described for *Daubentonia* (von Koenigswald & Pfretzschner 1987). The thickness of the HSB varies between 6 and 16 prisms, averaging out at about 12 prisms.

In the outer layer the angle between prisms is greatly reduced. Using the light-guide effect of the prisms (von Koenigswald & Pfretzschner 1987) under a reflecting light microscope, a small angle between the prisms becomes obvious, even though the prisms appear almost parallel under the SEM (Fig. 11). Aprismatic enamel, present in a few spots close to the EDJ and more pronounced in several areas close to the outer surface, does not form a continuous layer.

The wrinkled occlusal surface of the molars characterizing the Ursidae is composed of two layers as well; an inner layer with HSB and a more distinct outer layer with radial enamel prisms lying only parallel. In this part of the molars, however, the HSB are less pronounced and are usually visible close to the EDJ. There is not a clear boundary between the enamel with

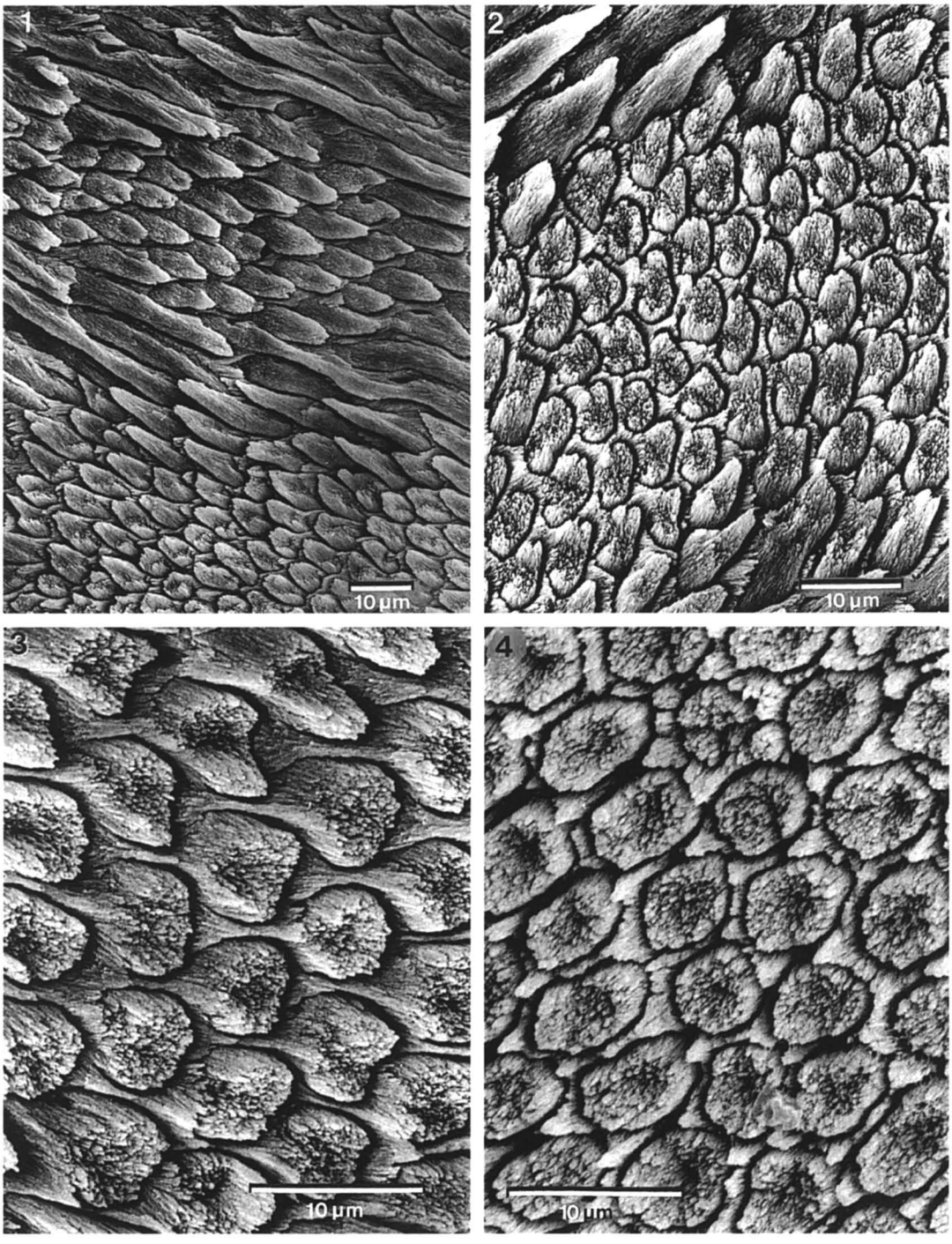

Fig. 1–4. Various prism types in the enamel of *Ursus spelaeus*. — 1: Depending on the angle at which the prisms are seen in the section, the prisms have different appearances. — 2: Dominant prism type with an incomplete prism sheath (type 3). — 3: "Key hole" shaped prisms (type 3B). — 4: Prisms with closed prism sheaths (type 1). Bar length 10 µm.

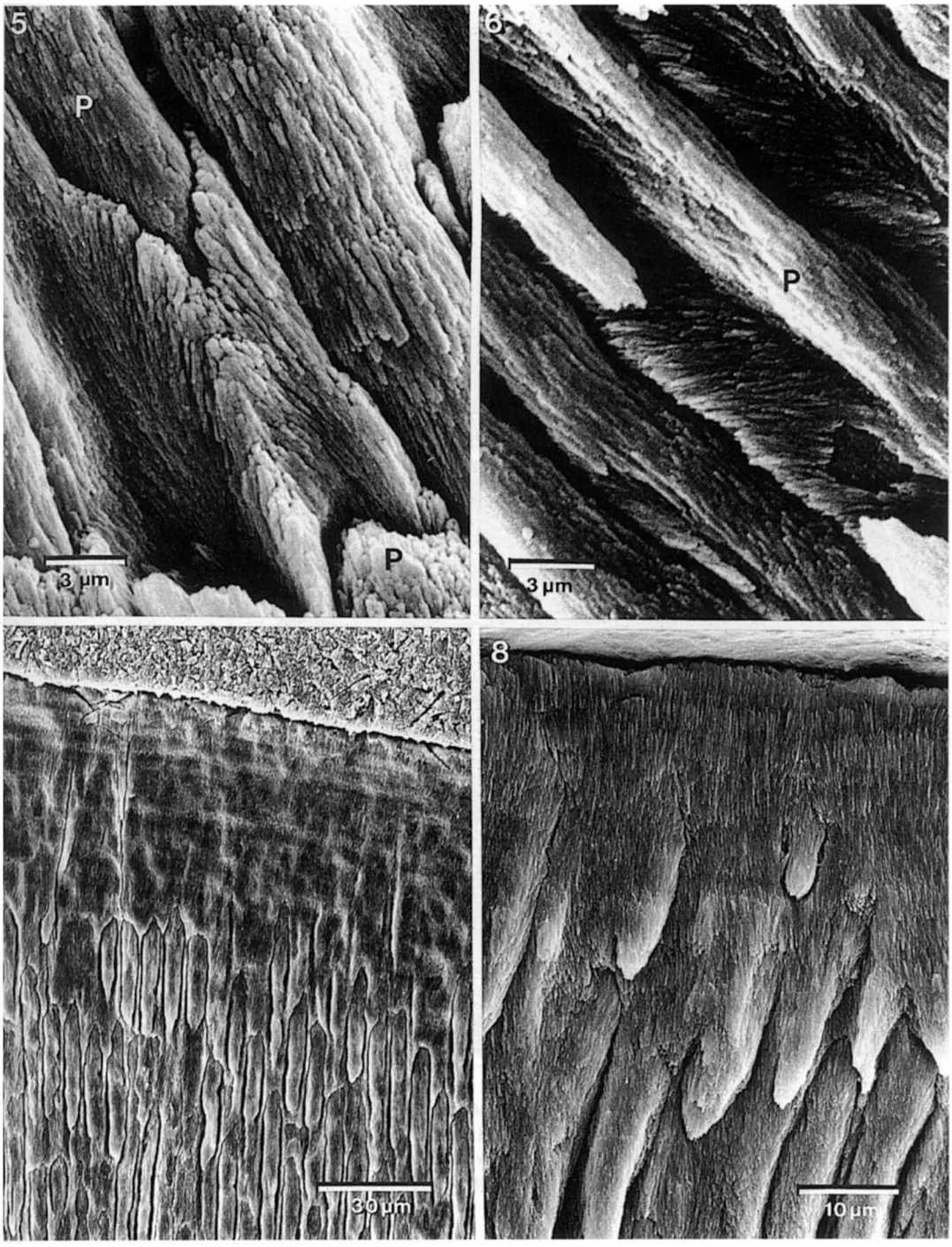

Fig. 5–6. Interprismatic matrix (IPM) in *Ursus spelaeus*. The crystallites of the IPM are almost parallel (Fig. 5) or at an angle smaller than 45° (Fig. 6) to the prisms (P). Bar length 3 µm.
Fig. 7–8. Aprismatic outer enamel in *Ursus spelaeus*. The thickness of the aprismatic enamel varies greatly. Note the Retzius lines in Fig. 7. The crystallites of the prisms run straight into the aprismatic enamel (Fig. 8). The outer surface of the enamel is above. Bar length in Fig. 7 30 µm and in Fig. 8 10 µm.

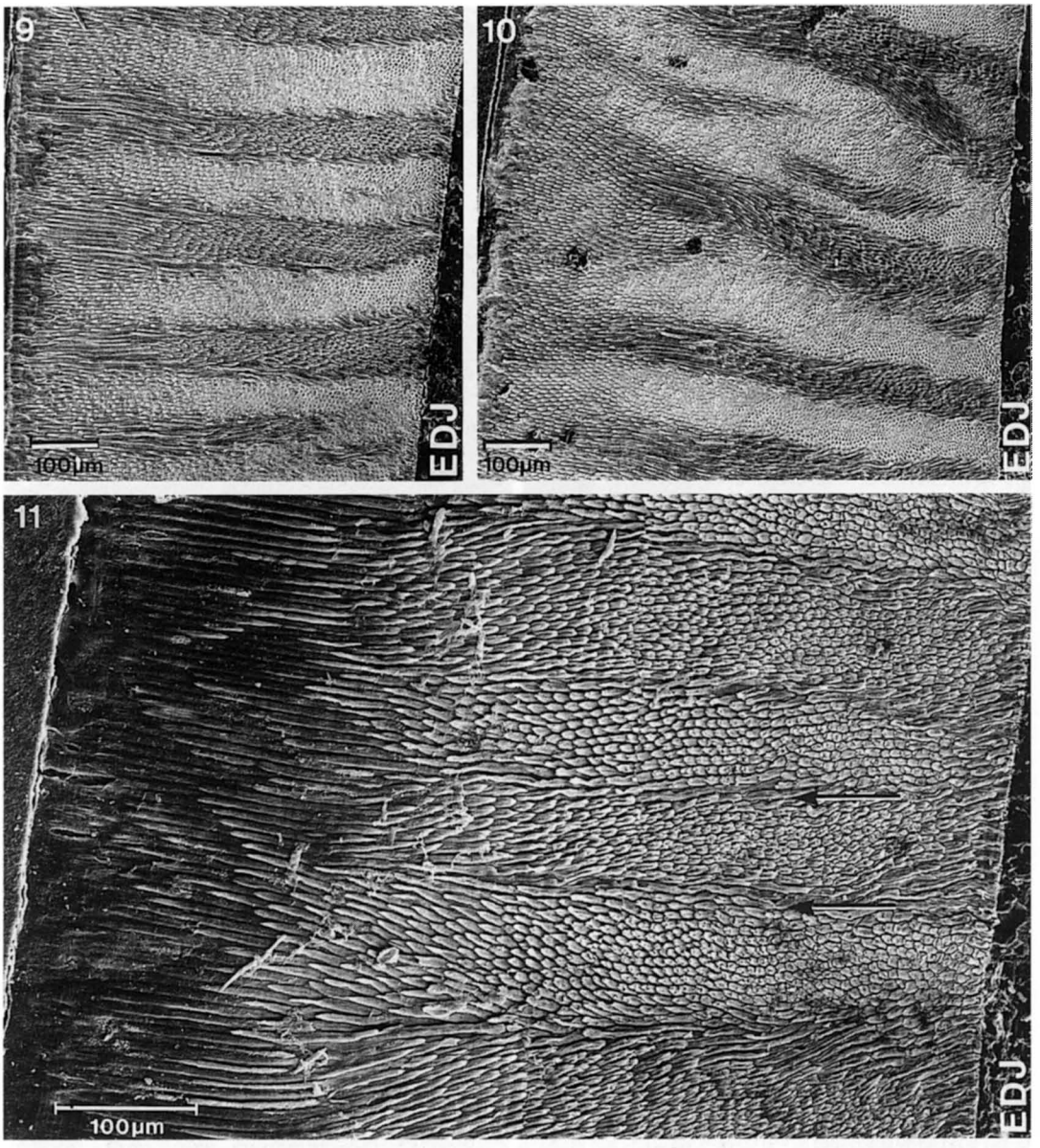

Fig. 9–11. Hunter-Schreger bands (HSBs) in *Ursus spelaeus*. The HSB are more pronounced in the inner part of the enamel. The thickness of the outer part varies and has little or no decussation. Note the bifurcation of the HSB in Fig. 10. In Fig. 11, the transitional zones between bands are dominant. The enamel-dentine junction (EDJ) is to the right, and the occlusial surface above. Bar length 100 µm.

HSB and the outer radial enamel, because the angle between the prisms of adjacent bands is continuously reduced towards the outside. The portion of the outer layer with radial enamel is generally thicker than that in the side walls. The little cusps forming the wrinkled occlusal surface are not indicated at the EDJ but are formed by a thicker enamel, and here radial enamel occupies the main portion.

4. Discussion

4.1. Prism cross-section

The variabilty of prisms in cross-section is not unusual and may only terrify those who consider prism types as the only character in mammalian enamel. It is important to note that the cross-sections of the prisms are not necessarily uniform within a single taxon, especially when several different enamel types are involved in the Schmelzmuster. Boyde (1964, 1969b, Boyde & Martin 1984, Wakita & Shioi 1984) showed how the cross-sections of prisms are dependent upon the shape of the Tomes process of the ameloblast. In terms of enamel formation, changing prism cross-sections can be understood as reflecting changing shapes of the Tomes process during the passage of the ameloblasts from the EDJ towards the outer surface. A prism free-enamel close to the EDJ, as observed in *Ursus spelaeus* close to the outermost surface of the enamel, indicates that the Tomes process is almost flat when forming these enamel areas. Such distinct changes of the Tomes process were previously assumed in the description of the enamel of some Mesozoic mammals (Lester & von Koenigswald 1989).

As yet in *Ursus spelaeus*, a close correlation between the occurrence of various prism types in specific morphological positions has not been identified. However, as in *Felis catus*, it seems that prisms with complete sheaths are situated more commonly in the middle of HSB, while those with incomplete sheaths occur where prisms are strongly curved in the transitional zones between bands (von Koenigswald 1989).

In *Ursus spelaeus* prism type 3 is dominant as is usually the case in Carnivora (Boyde & Martin 1984). Gantt et al. (1980) describes prism type 1 in an hexagonal arrangement as typical for the early cave bear (*Ursus deningeri*), but the figures in this paper show many prisms with incomplete sheaths.

Reif (1974) described the dominance of prism type 1 *Canis*, in contrast to prism type 3 as described by Boyde & Martin (1984). Prism types 1 and 3 are closely related in having a hexagonal packing pattern in common and having the IPM almost parallel to the prisms. Their basic difference from prism type 2 is more clearly expressed by the orientation of the IPM rather than only by the spatial arrangement. The crystallites of the IPM are orientated at almost right angles to the prisms and may anastomose between the prisms or form "inter-row sheaths". The cross-section should always be incomplete according to Boyde's classification. However, fully closed prism sheaths are common too, e.g. in rodents. Additional investigation is needed to establish a comprehensive system for describing the complexity of prism cross-sections.

The natural occurrence of different prism types within a taxon must be kept in mind when tooth fragments or teeth with few morphological characters are to be attributed to a specific taxon. Errors have occurred several times, especially when questionable human remains were detected in an archeological context. The experience with *Ursus spelaeus* shows that not only should a single section of a tooth be considered but also the general appearance of the enamel must be taken into account (Gantt et al. 1980).

4.2. Hunter-Schreger bands (HSB)

The irregular and undulating character of HSB as found in *Ursus spelaeus* appears to be a widespread character among the Carnivora. It was also observed in canids, felids and, in a very specialized form, in hyaenids. The thickness of about 12 prisms per band is common among carnivores as well, whereas these bands in herbivores tend to be somewhat thicker (Kawai 1955). HSB were convergently developed in various lineages of larger eutherian and metatherian mammals, but are usually missing in smaller insectivores. The earliest occurrences observed so far are those in the Paleocene arctocyonids (von Koenigswald et al. 1987). Therefore, the occurrence of HSB in *Ursus spelaeus* cannot be related to any particular specialization of its diet.

The enamel of carnivores has not been sufficiently studied, but according to my preliminary survey, the basic characters found in *Ursus spelaeus* seem to be general and widespread in this order. This does not exclude the possibility of minor differences characterizing various groups within the carnivores. For instance the seam appears to be more regular in felids.

4.3. Interprismatic matrix (IPM)

The Schmelzmuster of most carnivores, as it is in *Ursus speleaeus*, is less derived than in most herbivores, such as equids, bovids, lagomorphs and many rodents, where a greater differentiation is marked by a combination of more distinct enamel types with more regular borders between them. But this difference between carnivores and herbivores is less obvious than a second one: many carnivores, like *Ursus spelaeus*, have only a small angle between the prism and the IPM. This may be regarded as a less derived character than in most herbivores where the crystallites of the IPM and the prisms are at almost right angles (Figs. 12 and 13) instead of the maximum of 45° found in *Ursus spelaeus* and other carnivores. Greater difference in the orientation of fibres gives more strength to the enamel.

The crystallites of the IPM may anastomose between single prisms of radial enamel, as in many rodents, or in more derived character states may include series of prisms. In areas with HSB the IPM can grow in a third direction between the decussation prisms, thus reducing the danger of crack propagation (von Koenigswald 1988, 1989). In multiserial HSB, the network is not as obvious and dense as in the uniserial HSB found in the lower incisors and molars of arvicolids. Much work is still needed to define the various arrangements. Certainly they include what Boyde calls prism type 2, characterized by "inter-row sheets". Grine et al. (1987: fig. 5) figure major differences in the appearance of prism type 2 in a caprine molar from the interior to the exterior and Pfretzschner (in press) identified the biomechanical significance of the innermost layer, the "modified radial enamel".

In comparison to carnivores, it is sufficient to state that most herbivores were able to use the large angle between prisms and the IPM in the differentiation of the enamel. However, some major exceptions can be cited. Rhinoceroses and a few other lophodont herbivores have modified their enamel with the development of vertical HSB (Rensberger & von Koenigswald 1980; Fortelius 1984; Boyde & Fortelius 1986). Elephants developed prism type 3 in which most IPM is incorporated into the prisms so that it is not available to form an additional structural element (Shobusawa 1952, Kozawa 1985).

Because enamel containing "inter-row sheets" is frequently combined with a secondary occlusal surface (Fortelius 1985) in the tooth morphology it is of interest whether there is any functional correlation between these two characters.

On a secondary occlusal surface, which is a prerequisite for hypsodonty and ever-growing teeth, the exposed enamel band is loaded differently on the trailing and leading edge, respectively, of each dental element (Greaves 1973). Correlated with this mechanical difference, the thickness of the enamel band is modified in many small and some medium-sized herbivores. In wombats, for example, the enamel is totally missing on the leading edge of the lower and upper molars. In some hypsodont rodents like the arvicolids even the Schmelzmuster of the molars is obviously differentiated between the leading and the trailing edges (von Koenigswald 1980, 1982, von Koenigswald & Pfretzschner 1991).

The hypothesis of correlation of both characters, enamel modification and tooth morphology, could be supported if one character always antedates the other in phylogeny. However, there are conflicting examples. In the incisors of some sciuromorph rodents, we find the less derived-orientation of crystallites in the IPM, that is, parallel to the prisms, together with a secondary occlusal surface (von Koenigswald 1990). By contrast, *Sus* (Fig. 10) developed typical interrow sheets in low crowned teeth with a primary occlusal surface. Therefore both characters found most often together do not require the other as a basic prerequisite.

None of these important characters of enamel structure found in most herbivores are present in *Ursus spelaeus*. The enamel of *Ursus spelaeus* does not differ basically from that in other carnivores, retaining the more primitive character state in spite of a specialization to a mainly vegetarian diet. If diet were to have an immediate influence on the enamel structure, some changes should be found in the enamel of *Ursus speleaus*. This vegetarian carnivore, however, retains the enamel typical of its phylogenetic group. In the Artiodactyla, the omnivorous *Sus scrofa* shows the enamel characteristic of its group although the molars of *Ursus* and *Sus* show some morphological similarities.

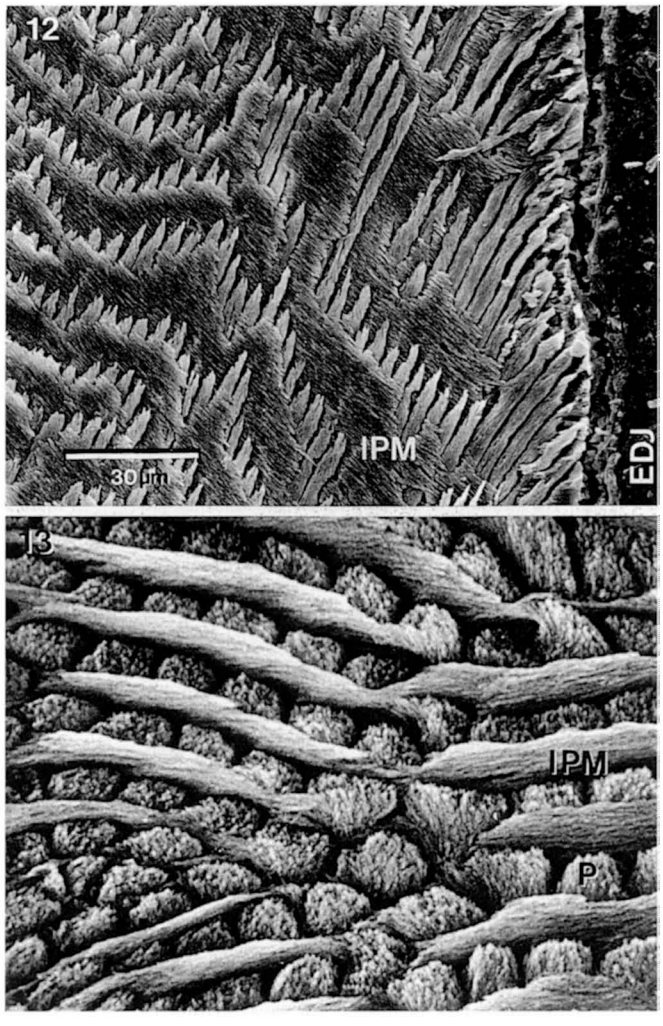

Fig. 12–13. Enamel in herbivores with crystallites of the interprismatic matrix (IPM) at an angle of about 90° to the direction of prisms (P). — 12: "Modified radial enamel" in *Equus caballus* near the enamel-dentine junction (EDJ). — 13: Prisms and "inter-row sheets" in *Sus scrofa*. Bar length 30 µm.

The enamel of the molars of *Ursus spelaeus* impressively demonstrates that the correlation between diet and enamel structure is not close enough for a change of diet to lead to an immediate change in enamel structure. Nevertheless, during a longer period of evolution, strong selection for structures of optimal functional properties can be observed. On the one hand this causes multiple examples of convergence and parallelism between groups (von Koenigswald & Pascual 1990) and, on the other hand, great differences in the Schmelzmuster may occur even within a single dentition, when it is sharply divided into different functional areas. Enlarged incisors may require a different Schmelzmuster than modified molars (von Koenigswald 1988). In *Ursus speleaus* no significant differences between the various tooth types were discovered.

Difficulties occur in the interpretation of enamel modifications between these two extremes of phylogenetic inheritance and functional adaptation. We assume that there is a range of minor changes in enamel structures that is genetically controlled, like enamel structures in general, but which is functionally unimportant in the initial phase. During subsequent evolution, however, minor changes may be a valuable preadaptation. Examples could include modified orientation of the crystallites of the IPM, as well as a secondary occlusal surface. These features together and es-

pecially in combination with increasing hypsodonty form the basic prerequisites for specific structures of high mechanical significance, like modified radial enamel (Pfretzschner in press.).

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