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THE SPECIALIZED STRUCTURE OF HYAENID ENAMEL: DESCRIPTION AND DEVELPOMENT WITHIN THE LINEAGE - INCLUDING PERCROCUTIDS

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Abstract

The tooth enamel of hyaenas has a highly specialized structure adapted to their diet. Hyaenid enamel is characterized by a type of Hunter-Schreger-Bands (HSB) with a complex 3-dimensional structure showing a zigzag pattern when viewed tangentially. This structure, also found in other carnivorous mammals of different phyletic affinities in which it must have evolved independently, is described and its distribution among hyaenid taxa is documented. Hyaenids also have another specialization: in the shearing blade of the carnassials the HSB turn upwards more strongly than in other carnivorans to intersect the cutting edge at roughly a right angle. This bending of the HSB occurs on the buccal side of the paracone and posteriorly through the metastyle in the upper P4 and at the lingual side of the protoconid and the paraconid of the lower M1. The zigzag pattern may be derived from undulating HSB, judging from the taxo-nomic distribution of these structures and the phyletic relationships of the taxa. The extensiveness of zigzag HSB increased within the dentition during the evolution of hyaenids. The occurrence of the zigzag pattern in as-sociation with bone-eating habits in living taxa suggests that this structure strengthens the enamel to resist the high stresses accompanying the fracturing of hard, tough objects such as bones. The restriction of upturned HSB to the carnassial blades in the dentitions of hyaenids and the upturning of less specialized HSB in the same region in other carnivorous taxa suggests that this structure maintains the sharp edge required for this function.

Key Words: Enamel microstructure, Hunter-Schreger-Bands, zigzag HSB, prism decussation, ossiphagy, bone-crushing, Hyaenidae, Percrocutidae, Mammalia

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Introduction

Phylogenetic and taxonomic associations of certain enamel structures have been recognized for many years (e.g. Korvenkontio, 1934; Kawai, 1955; Boyde, 1965; Martin, 1992). But recently it has become clearer that some enamel microstructural morphologies also have functional roles in the chewing mechanism (Von Koenigswald, 1980; Rensberger and Von Koenigswald, 1980; Pfretzschner, 1986, 1994; Young *et al*., 1987; Von Koenigswald and Pfretzschner, 1991; Rensberger and Pfretzschner, 1992; Marx, 1994), which makes the selective factors involved in the origins of enamel microstructures more readily determinable and provides additional information about the feeding behaviours of extinct taxa.

Differences in enamel microstructure are known to correlate with factors involved in the processing of food. Microwearstudies demonstrate correlations between the striae and pit characteristics and food type (O'Leary and Teaford, 1992; Hojo, 1996). Enamel surfaces are anisotropic in their rates of wear, which depend on the direction of prisms (Rensberger and Von Koenigswald, 1980; Boyde and Fortelius, 1986; Young, McGowan, and Daley, 1987). Prism decussation is better developed in mammals with strong chewing musculature and high occlusal stresses (Von Koenigswald *et al*., 1987); it is weakly developed in primates that eat soft foods but more pronounced in species that include hard foods in their diets (Maas, 1986). Prism decussation is organized differently in teeth with ellipsoidal cusps compared with teeth in which lophs are developed (Pfretzschner, 1986; Rensberger and Von Koenigswald, 1980; Fortelius, 1985). These differences have been shown to be related to the differences in directions of chewing-induced stresses in the enamel (Pfretzschner, 1986; Rensberger and Pfretzschner, 1992, Rensberger, 1993).

Most of the data in the above studies are based on the enamel of herbivorous mammals. Carnivore enamel has been rarely studied except for an early preliminary description of carnivores of different systematic affinities by Tomes (1906) and descriptions of some single species (e.g. Reif, 1974: *Canis familiaris* and *Cynodictis*; Skobe *et al*. 1985: *Canis familiaris* and *Felis domestica*; Von Koenigswald, 1992: *Ursus spelaeus*). An overview of carnivore enamel is given by Stefen (1997). References to the specialized hyaenid enamel have been made several times in recent literature (Von Koenigswald, 1992; Rensberger, 1993, 1995) and it may have been observed by other workers too. Rensberger (1995), using a 3-dimensional finite element model of the canine, showed that the most highly folded HSB of the canine in *Crocuta crocuta* are developed only in the region where the highest tensile stresses are likely to occur.

The structure of hyaena enamel has not been described for the other teeth of the dentition, including the posterior premolars where the primary bone-crushing occurs in hyaenas. In the present paper we present a detailed interpretation of the structure for the entire dentition in *Crocuta crocuta* and describe how these structures are distributed in the other members of the Hyaenidae.

The specialized structure, here termed zigzag HSB (Hunter-Schreger-Bands, layers of decussating prisms) has first been thought to be characteristic for the Hyaenidae, but this is not the case as has been shown by Stefen, 1995, 1997). Zigzag HSB occur in different families of Carnivora (Mustelidae, Amphicyonidae, Ursidae, Canidae, Felidae, Hyaenidae and Otariidae), Condylarthra (Mesonychidae) and Artiodactyla (Entelodontidae).

Our discussion of the Hunter-Schreger-Bands here emphasizes their three dimensional configuration and how the structure varies through the thickness of the enamel and in different regions of the posterior teeth. We also discuss the phylogenetic implications of the distribution of these structures in the Hyaenidae. In a paper in preparation, we will analyze the functional implications of the various enamel microstructural specializations of hyaenas.

Some parameters, for example prism shape and the thickness of the Hunter-Schreger-Bands, could only be determined for *Crocuta* and *Proteles* because material from other taxa was not available for sectioning. However, the HSB of several other fossil and recent hyaenid taxa are described on the basis of light microscopic methods and interpreted with regard to phylogenetic and taxonomic associations.

Abbreviations

AMNH	American Museum of Natural History, New York
BSP	Bayerische Staatssammlung für Paläontologie, München
F:AM	Frick American Mammals Collection, AMNH, New York
FMNH	Field Museum of Natural History Zoology Collection, Chicago
GPIBO	Geologisch und Paläontologigsches Insititut der Universität, Bonn
SMNS	Staatliches Museum für Naturkunde, Stuttgart
ZFMK	Zoologische Forschungsanstalt Museum Koenig, Bonn
KOE	Enamel sample collection of Prof. W. von Koenigswald, Inst. für Paläontologie, Bonn

Materials

The 3-dimensional structure of hyaenid HSB is based on teeth of *Crocuta crocuta* that were obtained from several sources. For light microscopic studies, we examined full dentitions in Recent specimens from ZFMK, FMNH, a partial dentition from the Zooarchaeology collections of the Transvaal Museum, South Africa, isolated teeth from GPIBO (Pleistocene cave specimens) and specimens provided by several individuals (see Acknowledgements). For scanning electron microscopy, we examined KOE specimens 1234 and 1183; specimen A3650 from the Zooarchaeology collections of the Transvaal Museum, South Africa.

Methods

Where HSB are close to the surface they can be observed by light-optical methods without preparation of the teeth (Von Koenigswald, 1980). Most specimens in curated museum collections were studied in this way. Examining sections made in different planes is important for understanding the 3-dimensional arrangement of prisms. When material for sectioning was available, teeth were embedded in polyester resin or epoxy resin and sectioned in horizontal, vertical and tangential planes. Tangential sections were made by grinding either from the outer surface or from the dentinal surface in order to reveal the structure at varying distances from the enamel-dentine junction (EDJ). Ground sections were etched with 2N HCl, cleaned in an ultrasonic bath, dried and sputtered with gold or gold-palladium for 3 to 12 minutes, sometimes in separate coating episodes in which the specimen was rotated. These sections were examined by both light and scanning electron microscopy.

In the descriptions, the terms undulating HSB, acute-angled HSB, and zigzag HSB are used, which are briefly explained in Fig. 1 (for further details see Stefen 1997).

If several types of HSB are present in one tooth, undulating bands usually occur at the enamel base and more acute-angled HSB in the middle region and zigzag HSB near the tip. Because the transition from undulating HSB to zigzag HSB always involves a few acute-angled bands, this is not repeated in each description.

Results

In the enamel of *Crocuta crocuta*, a conspicuous feature is a strongly sculptured surface of furrows (Fig. 2). Ridges and troughs of these furrows are aligned parallel to

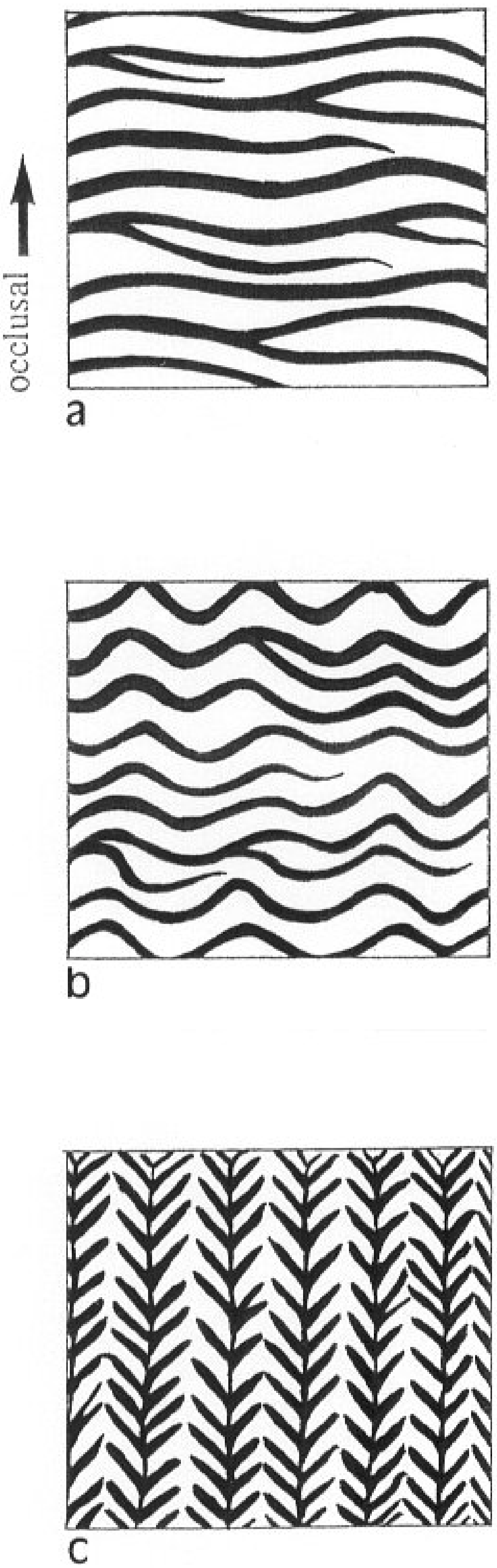

Figure 1: Schematic drawing of the appearance of different HSB types of carnivores. View of the outer surface. **a**) undulating HSB, horizontal bands with a slightly wavy course; **b**) acute angled HSB represent a transitional form between undulating and zigzag HSB with acute angles at wave crests and troughs; **c**) zigzag HSB, horizontal HSB with extremely acute angles of ca. 50° at wave crests and troughs.

the long axis of the tooth. Individual ridges vary in length and neighbouring ones may merge toward the tips. This rugosity sometimes renders light microscopic analysis of the HSB difficult.

Specialized HSB of hyaenids

The given description is based on observations on *Crocuta*.

Tangential section. To show the 3-dimensional morphology, we initially describe the structure as seen in tangential section, then in vertical (radial), horizontal and oblique sections. In tangential sections and in unprepared teeth, the HSB are characterized by a very pronounced waviness in the horizontal course, with wave crests and troughs bending through angles of about 50-70 degrees, giving them a zigzag appearance (Fig. 3, 4, 6). All teeth of *Crocuta* display these zigzag HSB, which usually are oriented horizontally around the teeth. Bifurcations, which are typical for HSB in general, occur at wave crests or troughs only (Fig. 5). The most remarkable feature that can be seen from the outside of a tooth, are vertical connections of wave crests and troughs of adjacent bands (Fig. 3, 4, 6). These can be followed over a varying number of crests or troughs. Toward the tip of the tooth, as the diameter of the tooth decreases, the connections merge at several sites (Fig. 3). With oblique illumination, even the horizontal course of HSB seems to be interrupted at wave crests and troughs, depending on the angle of incoming light. This is a result of the differential light-conducting property of prisms.

At wave crests the connections are built by prisms of the same direction and at wave troughs the prisms all run in a direction opposite that of the crests. In wave crests the prisms point outward and in the direction of the crest; in wave troughs the prisms point outward and in the direction of the trough.

Vertical section. In vertical sections the HSB are frequently bent in different directions on their way from the EDJ to the outside (Fig. 7). They may start with varying inclinations at the EDJ and neighboring bands are not necessarily aligned parallel to one another. Some show inclinations toward the tip of the tooth, others toward the base. Also the number of curves a single band shows on its way to the surface varies. Some cannot be followed from the EDJ to the outside in one section. Toward the outside, the angle between prisms of adjacent bands decreases.

Horizontal section. In horizontal sections (Fig. 8, 9), sometimes two regions can be distinguished: in the inner region only a slight decussation of prisms is observable, whereas toward the outside the boundaries of bands become clear cut. These are oriented perpendicular to the EDJ and run straight to the outside. Nevertheless, the structure is not a regular one because the bands usually start as thick and poorly defined areas near the EDJ. Further out they have clear cut boundaries and are straight, radial bands. Toward the outside they thin out. Some bands cannot be followed through the whole thickness of the enamel in one section. This change in appearance of the HSB in the section is due to a more horizontal decussation of prisms near the EDJ and a more vertical decussation further out.

The appearance of horizontal sections is especially dependent on the angle of the section to the EDJ, which may not easily be perpendicular in premolars and molars, but more so in canines (Fig. 8). If the angle of the section deviates much from 90° the HSB appear clear cut from the EDJ onwards and the enamel does not appear to be twolayered.

Oblique section. Oblique tangential sections from the EDJ (Fig. 10) help to show the 3-dimensional arrangement of HSB in one section and help to interpret the structures seen in separate vertical and horizontal sections. In the oblique section it can be seen that the HSB start at the EDJ as slightly undulating bands and increase their waviness toward the outer margin of the tooth. The increased waviness is accompanied by more acute-angles at wave crests and troughs. Additionally, the vertical distance (amplitude) between wave crests and troughs increases and the horizontal distance (wave length) in the circumferential direction between crests and troughs decreases. This leads to an overlapping of bands in the horizontal (circumferential) direction.

From the information in the different sectioning planes, a 3-dimensional model of zigzag HSB can be created (Fig. 11). It is apparent that this type of HSB contains both horizontal and vertical directional elements: disregarding the undulations the individual HSB make, horizontal is the general course of the HSB and dominates at a position close to the EDJ where the undulations are low, and the vertical direction dominates further out, where the HSB have connections from wave crest to crest and trough to trough.

Course of the HSB through the teeth. As in most other mammals, the zigzag HSB of hyaenas usually run horizontally around the teeth. However, an exception occurs in the carnassial blades, where the HSB turn from their horizontal course to a nearly vertical course. In the upper carnassial (P4), the HSB are aligned in such a way that they intersect the cutting edge at right angles and are parallel to the axis of the opposing tooth and the direction of its relative movement (Fig. 12). They bend in the buccal enamel of the metastyl and paracone. In the lower carnassial (M1), the HSB bend in the lingual enamel between the paraconid and protoconid to also intersect the cutting edge at right angles.

Figure 2: Light-optical photograph of furrowed surface of *Crocuta crocuta* premolar. Ridges and troughs do not run continuously from the base of the crown to the tip, but merge at several sites toward the tip (see arrow). Tip of the tooth is to the top. Bar = 0.1 mm.

Figure 3: Light microscopic photograph of zigzag HSB under oblique lighting in a tangential section in the outer enamel of a *Crocuta* premolar. The horizontal course of the HSB seems to be interrupted and the vertical connections at wave crests and troughs can be seen. c - wave crest, t - wave trough of HSB. Tip of the tooth is to the top. Bar = 0.1 mm.

Figure 4: Scanning electron micrograph showing the vertical connections between adjacent zigzag HSB in a *Crocuta* incisor. Tooth is only etched from the outside. One vertical connection can be followed over several adjacent bands. Tip of the tooth is to the right upper corner. Bar = 100 µm.

Figure 5: Scanning electron micrograph of tangential section of *Crocuta* premolar showing bifurcation of HSB at a wave crest. Tip of the tooth is to the top. Bar = 100 µm.

Figure 6: Scanning electron micrograph with enlarged view of a vertical connection in zigzag HSB in *Crocuta* incisor. Tip of the tooth is to the top. Bar = 100 µm.

Figure 7: Vertical (radial) section of enamel in *Crocuta* premolar. The bent course of HSB from the EDJ (at the left side) to the outer surface (right) is noticeable. The arrow points to the tip of the tooth. Bar = 300 µm.

Distribution of HSB types as seen under light microscopy

Protictitherium Kretzoi, 1938

Protictitherium praecurrens Dehm, 1950 (= "*Progenetta praecurrens*"; Werdelin, pers. com. 1994) Material: P^{3}-^{4}, locality Wintershof West, zone MN3, Orleanian Stage, Miocene, BSP.

Undulating HSB are present but difficult to see in the transparent enamel.

Protictitherium gaillardi (Forsyth Major, 1903) Material: right P_2-fragment, P_3-M_2, locality Langenau 1, black layer, zone MN4, Orleanian Stage, Miocene, SMNS.

Undulating HSB are present but difficult to trace in the poorly preserved fossils.


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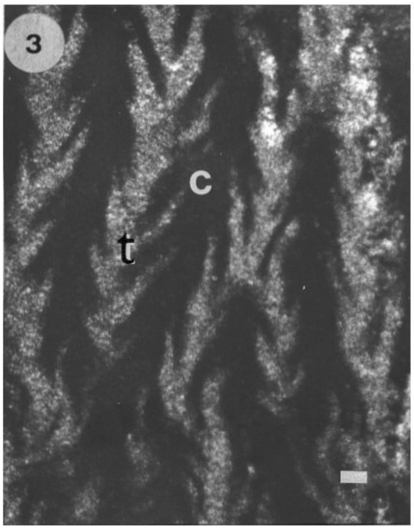
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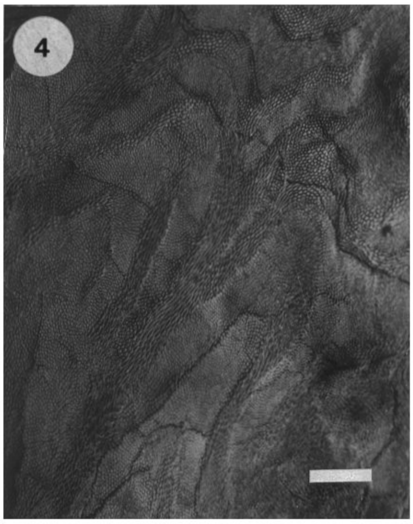
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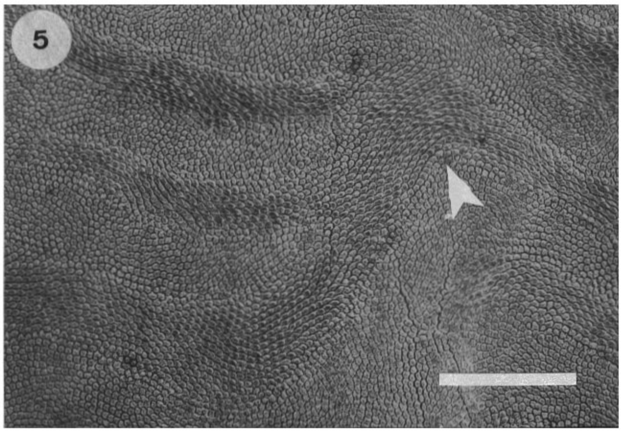
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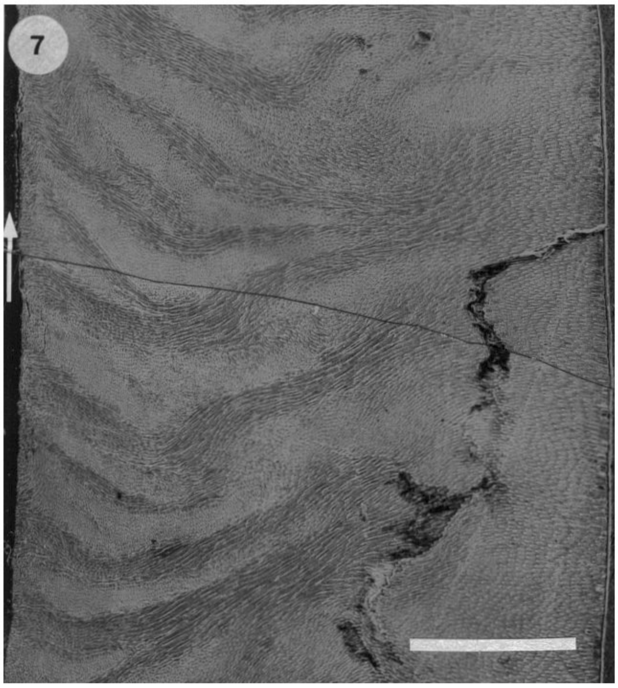
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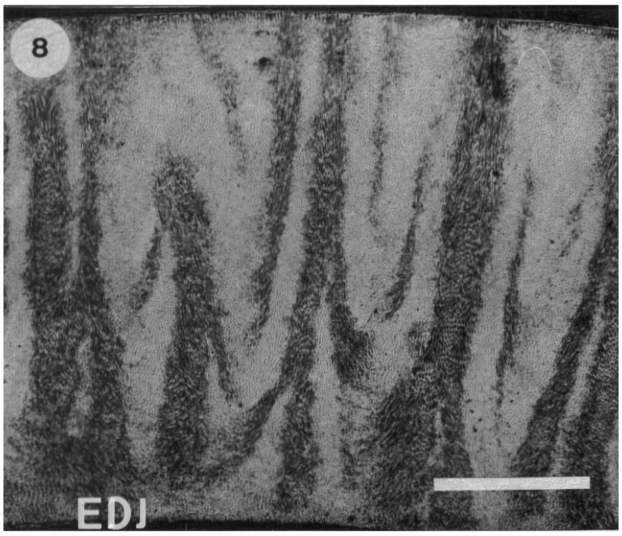
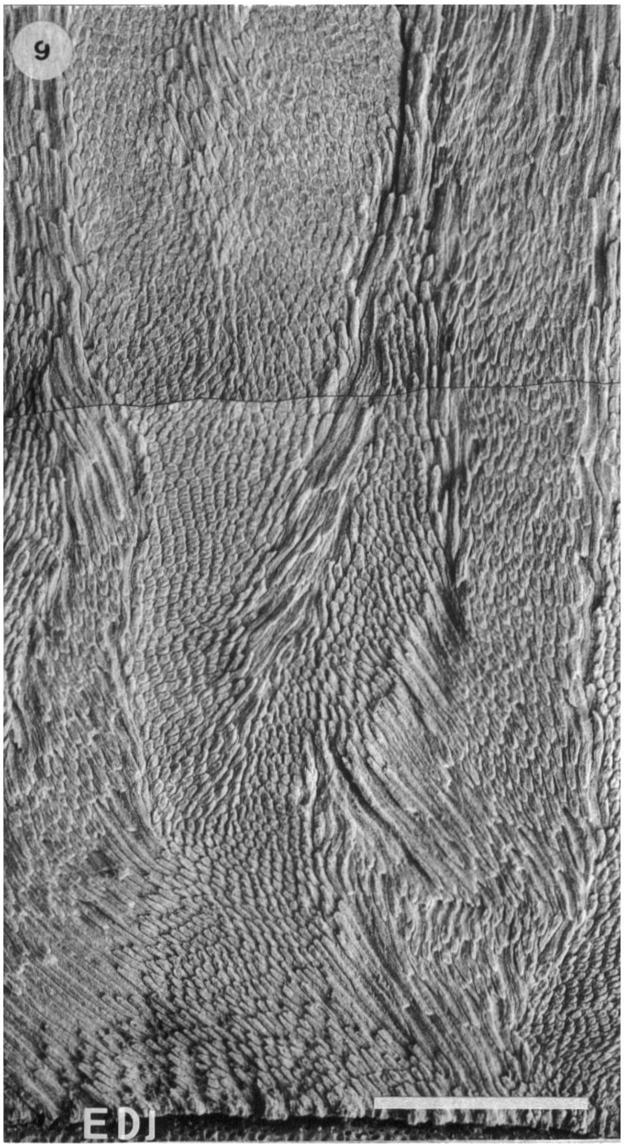




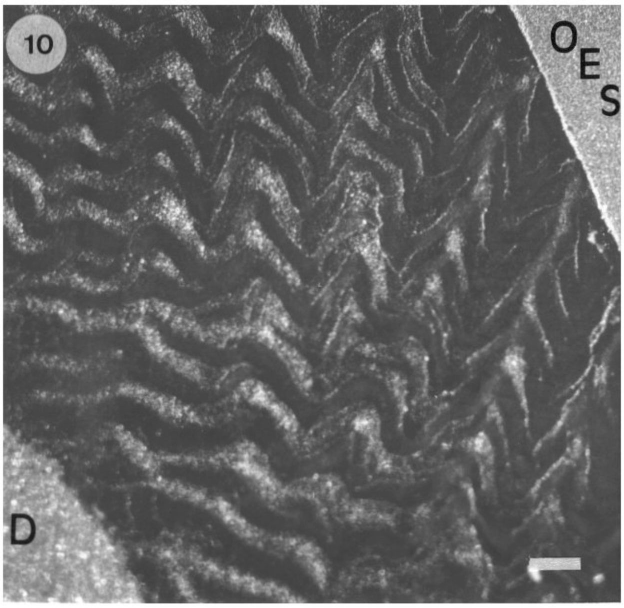


Figure 8: Scanning electron micrograph of horizontal section of enamel in *Crocuta* canine. A gradual change from inner enamel, where the borders between the HSB are not so clear, to the outer enamel with clear cut HSB can be seen. Bar = 300 µm.

Figure 9: Scanning electron micrograph of *Crocuta* canine showing detail of horizontal section and the transition in structure from inner to outer enamel. Bar = 100 µm.

Figure 10: Light micrograph of oblique tangential section from the dentine (D lower left corner) to the outer enamel surface (OES) in a premolar of *Crocuta*. From the EDJ where the bands are only slightly bent (undulating bands) the wave amplitude increases toward the outer surface of the enamel. Bar = 0.1 mm.

Protictitherium crassum (Deperet, 1892) (= "*Progenetta crassa*" according to Werdelin and Solounias, (1991)) Material: left P_2-M_1. Vindobonian Stage, Miocene, Scofa, BSP; premolar, middle Miocene, La Grieve, St. Alban, BM.

The surface of the teeth is smooth and a transition from undulating to zigzag HSB can be observed.

Plioviverrops Kretzoi, 1938 cf. *Plioviverrops*, Material: P^4-M^1, Turolian Stage, Miocene, Samos, AMNH.

As far as can be seen in the very transparent enamel the HSB are undulating.

Proteles Geoffroy, 1824.

Figure 11: Schematic drawing of zigzag HSB. The arrow is placed at the EDJ and points to the tip of the tooth. In this model the vertical connections are left out to depict the overlapping of bands in the horizontal plane. c - wave crest, t - wave trough.

Proteles cristatus (Sparrman, 1783) Material: whole dentition, Recent, SMF.

Undulating HSB are present in the thin enamel of the reduced teeth.

Thalassictis Gervais and Nordmann, 1850.

Thalassictis montadai (Villalta and Crusafont, 1943) (= "*Miohyaena montadai*"; according to Werdelin and Solounias, 1991) Material: right C, M_1-$_2$, left I_1-P_3, M_1, Vindobonian, Miocene, Yeni Eskihisar, Turkey, BSP.

A transition from undulating to zigzag HSB occurs. All HSB run horizontally around all analysed teeth.

Ictitherium Wagner, 1848.

Ictitherium viverrinum (Roth and Wagner, 1854) Material: Right upper P^4, Miocene, Tone Pikermi, Turkey, BSP; right mandible, Hipparion beds, Turolian Stage, late Miocene, China, AMNH.

Only few undulating HSB occur at the enamel base of all teeth and a transition to zigzag HSB occurs toward the tips. The surface of the chinese teeth is furrowed. In the lower carnassial (M_1), bending of the HSB as described in *Crocuta* occurs toward the shearing edge in the lingual enamel at the paraconid and protoconid.

Hyaenotherium Semenov, 1989. "*Hyaenotherium* sp". Material: right P_2-M_1, zone MN10, Vallesian Stage, Miocene, Asia, BSP.

A transition from undulating to zigzag HSB occurs from the tooth bases toward the tips, but is difficult to observe owing to surface corrosion.

"*Palhyaena aff. hipparionum*" (Gervais, 1846); represents *Hyaenotherium* according to Werdelin (pers. com., 1994). Material: right M_1, Miocene, Shansi, China, BSP.

The surface of the enamel is furrowed. Zigzag HSB can be seen in the enamel. In the lingual enamel the HSB bend near the paraconid and protoconid.

Hyaenotherium wongii (Zdansky, 1924) (= "*Thalassictis wongii*"). Material: lower left mandible and maxillary, Turolian Stage, China, AMNH; premaxillary and maxillary, Yang Mu Kou, Turolian Stage, upper Miocene, AMNH.

With the exception of the incisors and canines and where the HSB cannot be observed due to bad preservation, zigzag HSB occur with pronounced vertical connections. In the buccal enamel of the upper carnassial, the HSB bend as described in *Crocuta*. The HSB of vertical course are undulating.

Hyaenictitherium Kretzoi, 1938.

Hyaenictitherium namaquensis (Stromer, 1931) (= "*Hyaena namaquensis*" according to Werdelin and Solounias (1991)). Material: P_2-M_1, Pliocene, Schotter, Klein Zsee, south of Port Nolloth, Klein Namaqualand, SW Afrika, BSP.

The surface is furrowed and the HSB are difficult to see in the transparent enamel. The HSB are acute-angled to zigzag. In the M_1 the HSB bend in the lingual enamel of the paraconid and protoconid.

Hyaenictitherium hyaenoides (Zdansky, 1924) (= "*Thalassictis hyaenoides*" (Zdansky) according to Werdelin and Solounias, 1991). Material: P_3-M_1, maxillary, P^4, Hipparion Beds, Turolian, late Miocene, AMNH.

Due to poor preservation, the HSB can only be observed in P^4 and M_1 where they are zigzag. Both carnassials show the described bending of HSB in the lingual and buccal enamel respectively.

Lycyaena Hensel, 1862.

Lycyaena chaeretis (Gaudry, 1861). Material: right mandible, Hipparion beds, Turolian, late Miocene, China, AMNH.

The enamel surface is furrowed. Zigzag HSB are present. In the M_1 the HSB in the lingual enamel bend in the region of the paraconid and protoconid to intersect the cutting edge at right angles (Fig. 13).

Chasmaporthetes Hay, 1921.

Chasmaporthetes lunensis (Del Campana, 1914) (= "*Chasmoporthetes kani*" Galiano and Frailey) Material: right mandible, post-Turolian, Ma Tzu Kou, China; maxillary, Shou Yang Pist, China; maxillary, post-Turolian, China, AMNH.

The surface of the enamel is slightly furrowed and

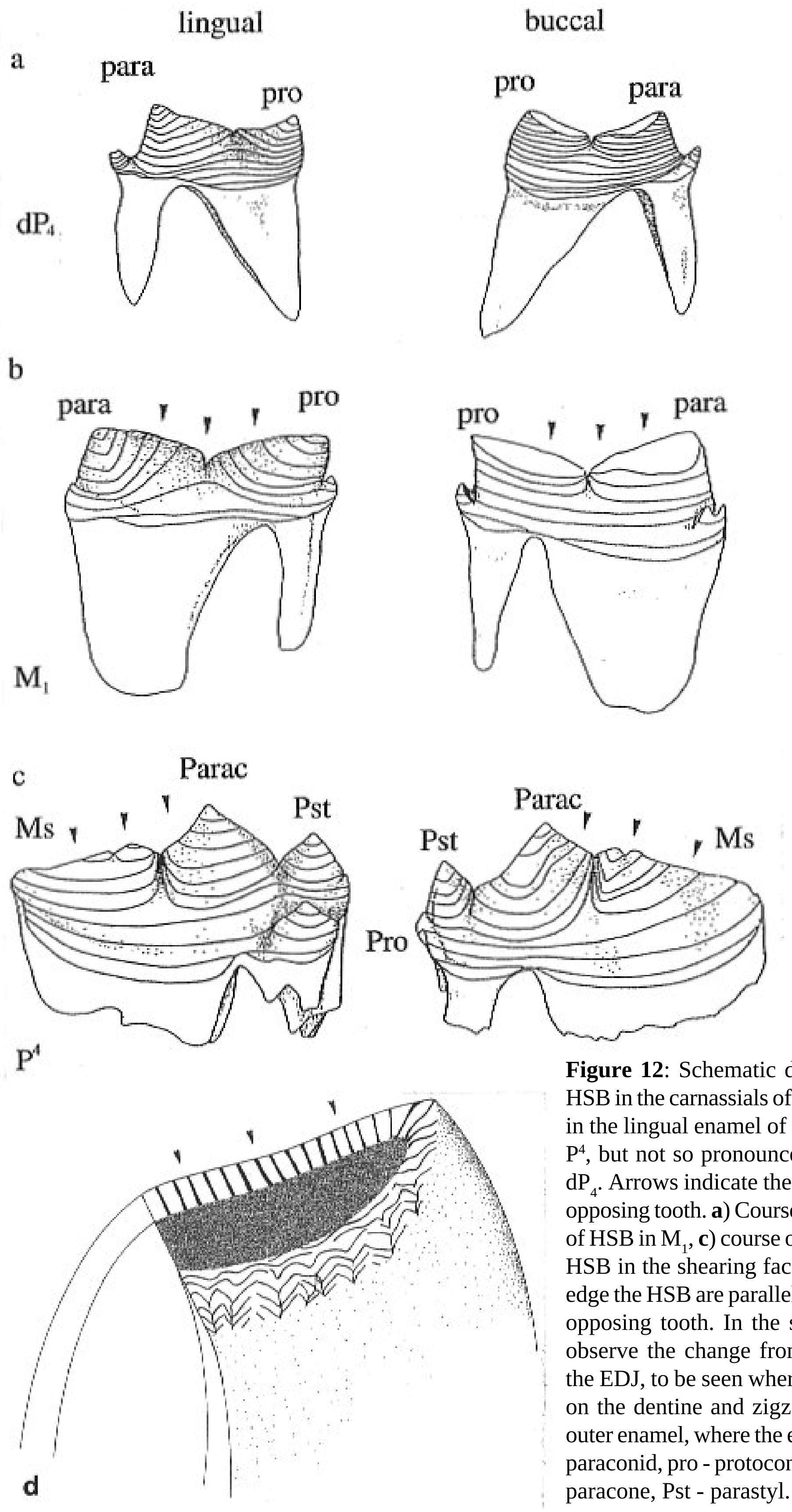


Figure 12: Schematic drawing of the course of HSB in the carnassials of *Crocuta*. Bending occurs in the lingual enamel of M_1 and buccal enamel of P^4, but not so pronounced in the cutting edge of dP_4. Arrows indicate the shearing direction of the opposing tooth. **a**) Course of HSB in dP_4, **b**) course of HSB in M_1, **c**) course of HSB in P^4. **d**) Course of HSB in the shearing facette of M_1. In the cutting edge the HSB are parallel to the vertical axis of the opposing tooth. In the shearing facette one can observe the change from slight undulation near the EDJ, to be seen where only thin enamel is left on the dentine and zigzag as can be seen in the outer enamel, where the enamel is still thick. para - paraconid, pro - protoconid, Ms - metastyl, Parac - paracone, Pst - parastyl.

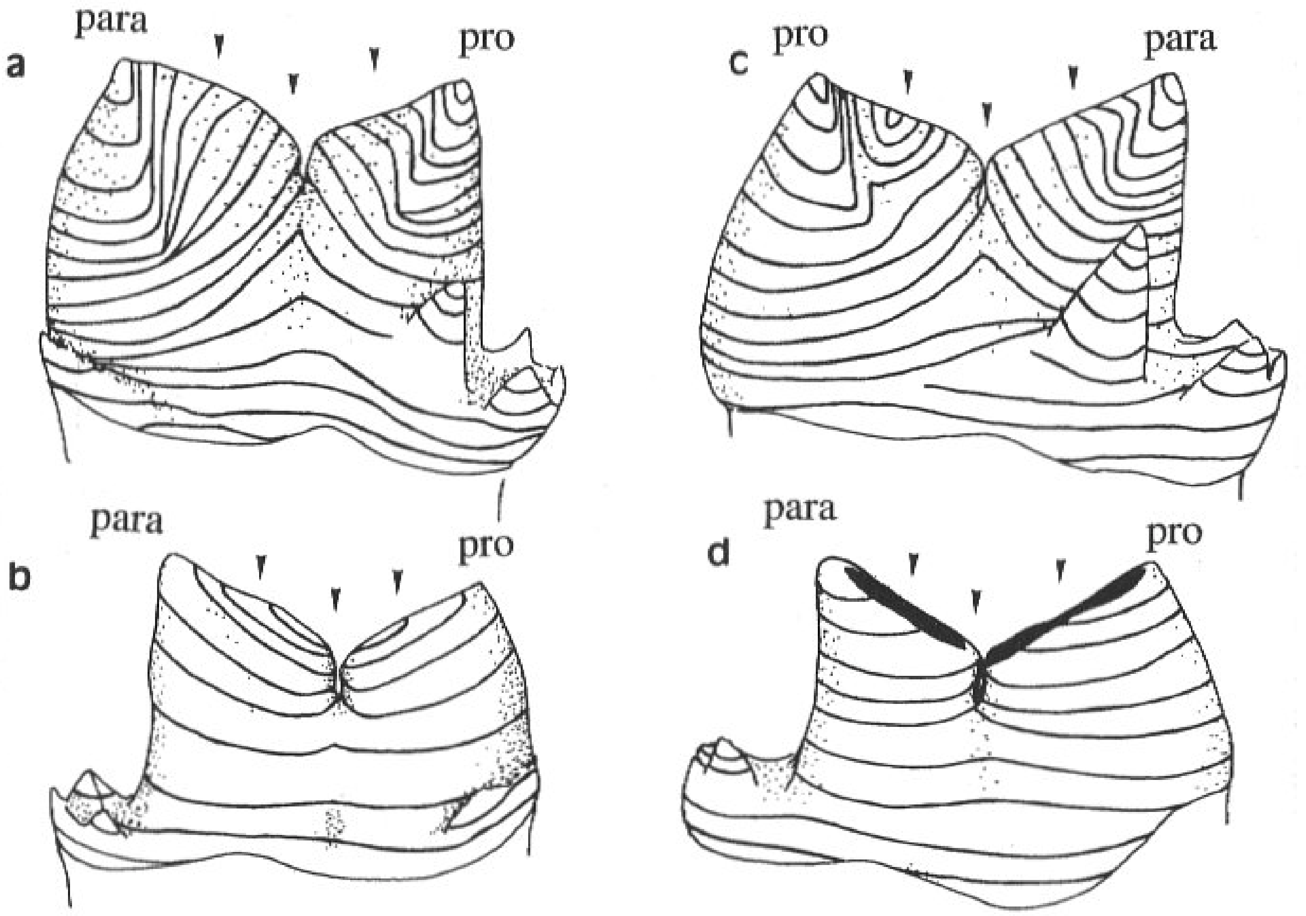


Figure 13: Slight differences in the bending of HSB in the carnassials occur in different species. Course of the HSB in the lingual and buccal enamel of M_1 of *Belbus* (**a**, **b**) and *Lycyaena* (**c**, **d**). para - paraconid, pro - protoconid.

the premolares are strongly worn. Except for a few undulating HSB at the enamel base, HSB are zigzag. The HSB follow a horizontal course in all teeth, including the carnassials.

Chasmaporthetes exitelus (Kurten and Werdelin, 1988). Material: P^4-M^1, Hipparion Beds, late Miocene, China, AMNH.

The surface of the enamel is slightly furrowed. HSB are zigzag, except for a few undulating bands near the enamel base. The exact course of the bands in P^4 could not be seen.

Chasmaporthetes cf. ossifragus Hay, 1921. Material: C, Blancan near Benson, Arizona, F:AM; posterior half of P_4, Blancan, F:AM.

In both teeth a transition from undulating to zigzag HSB is present in the lower third of the crown.

Belbus Werdelin and Solounias, 1991.

Belbus beaumonti (Qiu, 1987). Material: I_1-fragm., I_2-C erupting, P_1-P_2, M_2, Samos, Turolian, late Miocene, SMNS.

The surface is furrowed. Except for a few undulating bands at the enamel base, the HSB are zigzag and have an irregular appearance. In the lingual enamel of M_1 the HSB bend near the paraconid and protoconid to intersect the cutting edge at right angles (Fig. 13).

Parahyaena Hendey, 1974.

Parahyaena brunnea (Thunberg, 1820) (= ”*Hyaena brunnea*” Thunberg). Material: whole dentition, Recent, ZFMK.

The surface of the enamel is furrowed and the premolars are strongly worn. The HSB are zigzag except for a few undulating bands at the enamel base. The vertical connections are very pronounced and the HSB seem to be thin. The carnassials have the typical bending of the HSB toward the cutting edge.

Hyaena Brisson 1762 / Zimmermann 1777.

Hyaena hyaena (Linnaeus 1758). Material: whole dentition, Recent, adult, juvenile, ZFMK

The deciduous teeth show undulating HSB, which become acute-angled toward the tip of the tooth. In all deciduous teeth, including the milk-carnassials, the HSB are oriented horizontally. Only a slight tendency for bending was observed at the metastyle of P^4 sup.

The adult teeth are furrowed and mostly worn. All teeth show zigzag HSB with a few undulating bands at the enamelbase. The incisors have more undulating bands than the other teeth. In the carnassials the HSB bend in the way described for *Crocuta* (Fig. 14) to intersect the cutting edge at right angles.

Pachycrocuta Kretzoi, 1938.

Pachycrocuta brevirostris (Aymard, 1846). Material: upper right jaw, Pleistocene, Chou Kou tien, China, AMNH.

The teeth are furrowed and the premolars are strongly worn. Nevertheless in all teeth an abrupt transition from undulating to zigzag HSB occurs. In the P^4 the HSB bend in the described way.

Pliocrocuta Kretzoi, 1938.

Pliocrocuta perrieri (Croizet and Jobert, 1828) (= "*Pachycrocuta perrieri*" Croizet and Jobert, 1828). Material: right P_4-M_1, Hsia Chuang, late Pliocene, F:AM; P_4, deciduous teeth, F:AM.

The enamel of the deciduous molars is slightly furrowed and the teeth are worn. The HSB here are mostly undulating and become acute-angled toward the tips.

The enamel of the adult teeth is furrowed and shows zigzag HSB. Some deviations from the horizontal course of the HSB occur in the tip of P_4. The carnassials show the bending of HSB described for *Crocuta*.

Adcrocuta Kretzoi, 1938.

Adcrocuta eximia (Roth and Wagner, 1854) (= "*Hyaena eximia*" Roth and Wagner, 1854). Material: left P^1-P^4, early Pliocene, Samos, BSP; P4, Miocene, Pikermi, BSP; right I_3-M_1, Vallesian Stage, Garkin, Tyrkey, BSP; mandible, Yang Mu Kou, China, AMNH; right P^2-^{4}, Tu Kou, China, AMNH; deciduous teeth: lower right jaw, Pontian Stage, Samos quarry 5, AMNH; dP_4, lower Turolian Stage, Samos, AMNH. In the deciduous teeth, undulating HSB dominate but become acute-angled toward the tips. In the deciduous carnassials only a slight tendency for bending can be seen.

The adult teeth from Samos show undulating HSB at the enamel base and zigzag HSB elsewhere. The enamel of P^4 is furrowed and on the buccal side the HSB bend toward the carnassial edge. The lower teeth from Turkey are badly preserved so that the exact course of the HSB cannot be followed. The Chinese teeth have furrowed enamel and are strongly worn; the HSB are zigzag and it is not clear whether undulating bands occur at the enamel base; the carnassials show the bending of HSB as described in *Crocuta*.

Crocuta Kaup, 1828.

Crocuta crocuta (Erxleben, 1777) (= "*Crocuta spelaea*" Goldfuss; according to Werdelin and Solounias, 1991). Material: whole dentition, Recent, ZFMK,; "*C. spelaea*" from Gailenreut cave, Pleistocene, GPIBO; several isolated teeth, caves of southern Germany, late Pleistocene; Vogelherdhöhle, Pleistocene, Erlangen, Prof. Groiß; deciduous teeth: lower C, dP_4, Tronewton Cave, Pleistocene, KOE 1230.

In the thin enamel of the deciduous teeth undulating HSB are present. The bending of the bands in the milk-carnassials is not as pronounced as in the adult teeth of

Figure 14: Light microscopic photograph of the HSB with near vertical course in the carnassial of *Crocuta*. The white arrow indicates the direction of the opposing tooth. In several hyaenas the bent HSB which run perpendicular to the cutting edge seem undulating, probably because the more extremely folded HSB and the connections can not be seen, owing to light direction. Bar = 0.1 mm.

Figure 15: Horizontal section of *Proteles cristatus* canine enamel. Undulating HSB are characterized by slight prism deviations in horizontal sections, as shown here and in Figure 5; acute angled and zigzag HSB are characterized by strong deviations in prism direction with respect to the plane of section, as shown in figures 6 and 9. Notice the varying layer of aprismatic enamel (a) at the outer surface. Different orientations of prisms are indicated by arrows. Bar = 30 µm.

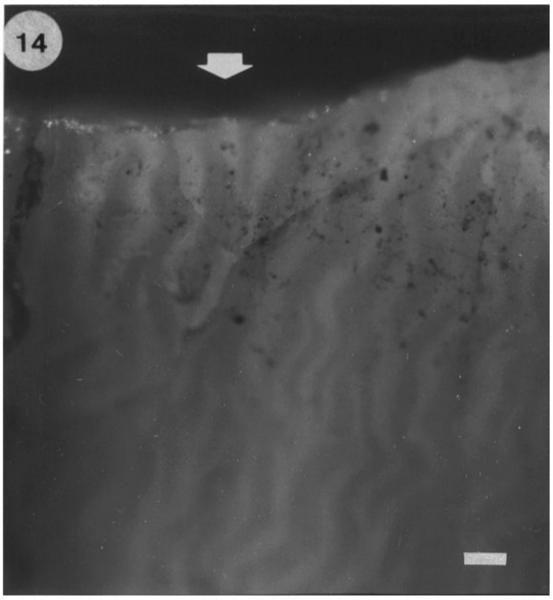
Figure 16: Light microscopic photograph of enamel in the lower milk premolar of *Crocuta*, showing undulating HSB and only a slight tendency to bending of the bands toward the cutting edge. Bar = 0.1 mm.

Figure 17: Vertical section of the enamel of *Proteles* canine. The angles between prisms of adjacent HSB is very small and often hardly noticeable in such a small part of a vertical section. Note also the thinness, which is characteristic of *Proteles* enamel. Arrow at the EDJ points to the tip of the tooth. Bar = 10 µm.

Figure 18: Tangential section at the outer surface of *Crocuta* premolar, showing dominantly polygonal prisms with complete prism sheaths. Bar = 30 µm.

Figure 19: Tangential section at the inner surface of the enamel of *Crocuta* premolar, seen from the EDJ. The prisms here are rounded and often occur with open prism sheaths. Bar = 10 µm.

Figure 20: Tangential section at the outer surface of *Proteles* canine, showing circular prisms with complete prism sheaths. Bar = 10 µm.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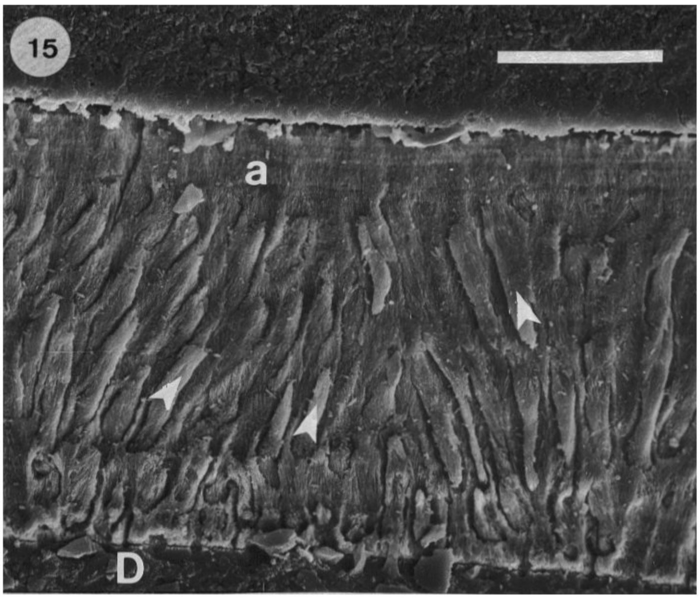
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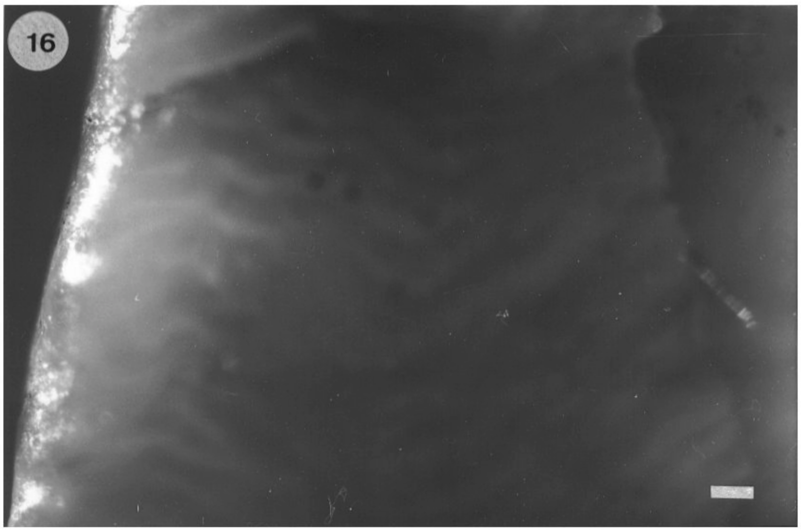
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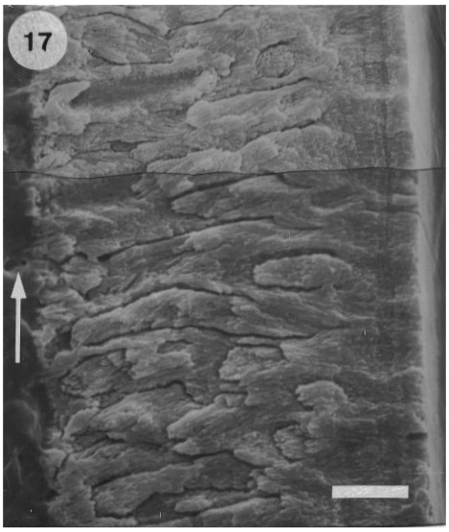
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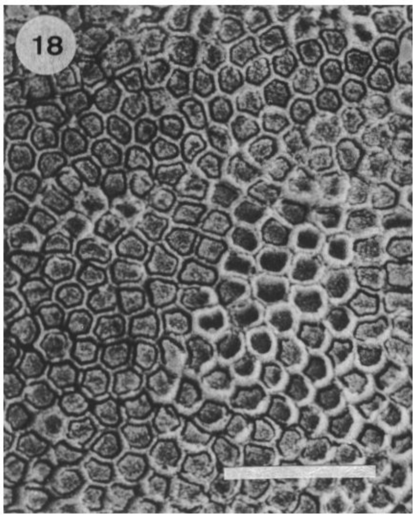
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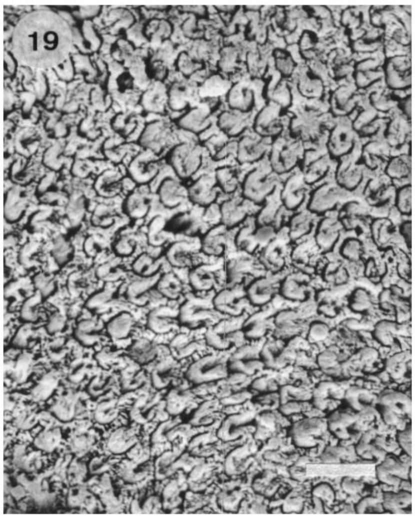
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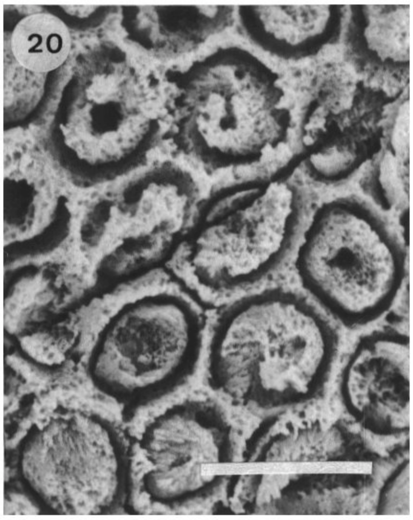
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Recent *C. crocuta* (Fig. 16).

The enamel surface of the adult teeth is furrowed and the teeth are worn, especially the premolars. All teeth show zigzag HSB with pronounced vertical connections; a few undulating bands occur at the enamel base. The wave length and amplitude of the undulations varies around the canines (see Rensberger, 1995, for further details). The carnassials show the described bending of the HSB toward the cutting edge.

Percrocutidae Werdelin and Solounias, 1991.

Percrocuta Kretzoi, 1938.

Percrocuta tungurensis (Colbert, 1939). Material: right mandible, Vindobonian Stage, Tung Gur Fm., Miocene, below Wolf Camp, Ga Tung Khara Usu, AMNH.

The enamel surface is furrowed. All premolars are heavily worn. The HSB are zigzag but the course in the M_1 could not be seen.

Percrocuta aff. tungurensis (Colbert). Material: left P^4, Vindobonian Stage, Miocene, Candiar, Turkey, BSP

The enamel surface is furrowed, and the furrows are more pronounced toward the tip of the tooth. The HSB are zigzag with a few undulating bands at the enamel base.

Percrocuta miocenica Pavlovi and Thenius, 1965. Material: left P_4-M_1, Vindobonian, Miocene, Paslar, Turkey, BSP.

The enamel surface is smooth and the transparent enamel shows zigzag HSB with pronounced vertical connections. Due to the poor preservation, the course of the HSB in the M_1 cannot be seen.

Dinocrocuta Schmidt-Kittler, 1976.

Dinocrocuta gigantea (Schlosser, 1903) (= "*Hyaena gigantea*" Schlosser, 1903). Material: left M^1, left P_4, early Pliocene, Shansi, China, BSP.

The enamel surface is furrowed. The teeth show zigzag HSB from very near the enamel base upward. Bending of the HSB does not occur in these carnassials.

Structure in SEM

Proteles cristatus, KOE 1207, KOE 1240, canine (Fig. 15, 17, 20).

The HSB are perpendicular to the EDJ and run straight toward the outer surface; near the outer surface the HSB are terminated by a variably developed layer of aprismatic enamel (up to 1/4 of the enamel thickness). The enamel of *Proteles* is only about 50 micrometers thick, very thin for hyaenids. Individual HSB consist of 5 to 18 prisms. The angle between the prisms of adjacent bands is about 30-50 degrees and transitional directions of prisms between bands are rare. The prisms are round to slightly polygonal in cross-section and have a complete prism sheath. The crystallites of the interprismatic matrix (IPM) is about parallel to the crystallites of the prisms and surrounds them with equal thickness in all directions.

Crocuta crocuta, KOE 1183, isolated teeth, premolar, canine, incisor (Figs. 4-10, 18, 19).

Figure 21: Cladogram of the *Hyaenidae* after Werdelin *et al*. (1994). The occurrences of undulating HSB (u), zigzag HSB (z) and the bending of HSB toward the carnassial cutting edge (b) are marked for the studied species. Indications in brackets mean that undulating HSB are present but only at the enamel base. The question marks for *Chasmoporthetes exitelius* and *C. lunensis* indicate that the presence of bending could not be verified with the available material. The extant species are typed in boldface letters.

The HSB start at the EDJ with varying inclinations and curve frequently on their way toward the outer surface. Toward the outer surface of the teeth the angle between the prisms of adjacent bands decreases and near the outer surface the HSB end at an irregularly thin layer of aprismatic enamel.

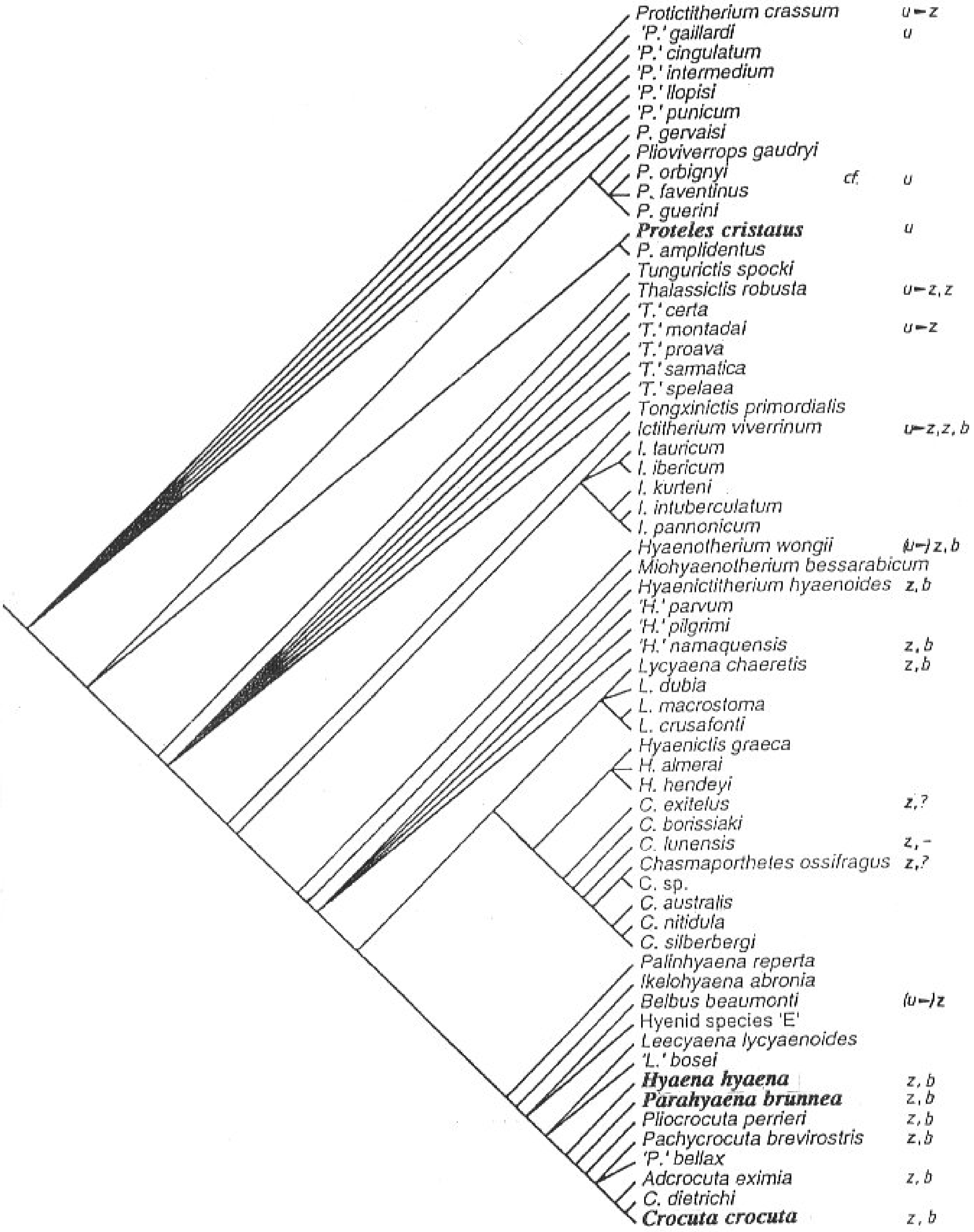
Transitional zones between bands consist of 1 to 3 prisms and the angle between prisms of adjacent bands ranges from 30 to 80 degrees. Due to the curving and irregular appearance of HSB in vertical sections, the number of prisms per HSB is difficult to determine but appears to be about 11 plus or minus 4 (n=21) in the canine. Near the outer surface of the enamel the prisms are hexagonal to polygonal (Fig. 18) but hardly ever rounded and show complete prism sheaths. But at the EDJ the prisms are rounded to oval and most show incomplete prism sheaths (Fig. 19). The IPM crystallites are almost parallel with the prisms, but deviations of 40(-45) degrees occur rarely. The enamel of the middel part of the canine is about 600 micrometers thick, but varies within the teeth.

Discussion

Phylogenetic and taxonomic relationships

The inclusiveness of the family Hyaenidae is problematic because no morphological feature or combination of features have been demonstrated to define the family clearly (Werdelin and Solounias, 1991). The concept of Werdelin and Solounias (1991), which includes *Protictitherium* and *Plioviverrops* in the family, is used here although it is not unquestioned. The Hyaenidae are derived from viverrid-herpestid stock (Schmidt- Kittler, 1977). It has been debated whether *Herpestides* is close to the ancestory of hyaenids (Schmidt-Kittler 1977; Hendey, 1978). Generally the paraphyletic group *Protictitherium* is considered the most primitive group of hyaenas (Werdelin and Solounias, 1991).

The phyletic distribution of the different microstructures in the Hyaenidae (Fig. 21), suggests that the occurrence of zigzag HSB is a derived condition and has


Protictitherium crassum u–z
'P.' gaillardi u
'P.' cingulatum
'P.' intermedium
'P.' llopisi
'P.' punicum
P. gervaisi
Plioviverrops gaudryi
P. orbignyi cf. u
P. faventinus
P. guerini
Proteles cristatus u
P. amplidentus
Tungurictis spocki
Thalassictis robusta u–z, z
'T.' certa
'T.' montadai u–z
'T.' proava
'T.' sarmatica
'T.' spelaea
Tongxinictis primordialis
Ictitherium viverrinum u–z, z, b
I. tauricum
I. ibericum
I. kurteni
I. intuberculatum
I. pannonicum
Hyaenotherium wongii (u–) z, b
Miohyaenotherium bessarabicum
Hyaenictitherium hyaenoides z, b
'H.' parvum
'H.' pilgrimi
'H.' namaquensis z, b
Lycyaena chaeretis z, b
L. dubia
L. macrostoma
L. crusafonti
Hyaenictis graeca
H. almerai
H. hendeyi
C. exitelus z, ?
C. borissiaki
C. lunensis z, –
Chasmaporthetes ossifragus z, ?
C. sp.
C. australis
C. nitidula
C. silberbergi
Palinhyaena reperta
Ikelohyaena abronia
Belbus beaumonti (u–) z
Hyenid species 'E'
Leecyaena lycyaenoides
'L.' bosei
Hyaena hyaena z, b
Parahyaena brunnea z, b
Pliocrocuta perrieri z, b
Pachycrocuta brevirostris z, b
'P.' bellax
Adcrocuta eximia z, b
C. dietrichi
Crocuta crocuta z, b

evolved from undulating HSB (undulating HSB characterize *Herpestides* and *Leptoplesictis* as well as most other viverrids and herpestids (Stefen, 1997)). Among the two examined *Protictitherium* species, one shows undulating HSB and the other a transition from undulating to zigzag HSB. Because the genus *Protictitherium* is paraphyletic it is difficult to predict the enamel structure in the other species. The data from the species *P. crassum* and *P. gaillardi* demonstrate that zigzag HSB occur even in the most primitive hyaenid genus. From *Hyaenotherium* through most of the more advanced hyaenid taxa, the enamel structure is dominated by zigzag HSB (Fig. 21).

Enamel structure has been interpreted as a taxonomic characteristic at different levels. The size of prisms differentiates groups of multituberculates (Krause and Carlson, 1986); HSB have become vertical in rhinocerotoids, astrapotheres and a few other extinct ungulates (Rensberger and Von Koenigswald; 1980; Fortelius, 1984) but are horizontal in many other mammals.

Because zigzag HSB are very striking and easily observable with light microscopy without sectioning the teeth, it had been speculated in the early stages of hyaenid enamel research that this feature may be characteristic of the family. Our results, however, indicate that this is not the case, because the hyaenid *Proteles* lacks zigzag HSB and other species of different systematic affinities, such as creodonts, condylarths and entelodonts, contain taxa with zigzag HSB (Stefen, 1997). Thus this aspect of the HSB type may have little taxonomic specificity and may have originated as a result of selective factors related to similar adaptations.

The bending of HSB from horizontal to vertical in the carnassials occurs in the rather primitive *Ictitherium* and in most of the more advanced taxa. However, bending appears to be absent in *Chasmoporthetes lunensis*; the presence or absence of bending of the HSB in the carnassials of the other species of *Chasmoporthetes* could not be checked due to the absence of carnassials in the study. It is unclear why *Chasmoporthetes lunensis* lacks the bending of the HSB in the carnassials. The fact that the bending is absent in the primitive genera *Protictitherium* and *Pliovirrops* strongly suggests that it is a derived feature.

Functional implications

The ecology and feeding habits of Recent hyaenas is well known. As Flower (1869) states already Sparman noted in 1786 that *Proteles* feeds on termites. *Proteles* also takes insects and their larvae as well as eggs of ground nesting birds (Ketelholdt, 1966). The other living hyaenas, *Crocuta*, *Hyaena* and *Parahyaena* are carnivorous to ossiphagous. Hyaenas usually consume their entire prey and leave only the teeth and horns behind (Kruuk, 1975). In South Africa hyaenas are the only carnivores that chew bones regularly (Richardson *et al.*, 1986). The species differ in the percentage of intake of large vs. small mammals (Kruuk, 1966, 1975; Mills, 1987, 1990). For brown hyaenas 10% of diet consists of large mammals (> 100 kg), 5% on medium size mammals (80-100 kg) and 10% on small mammals (1-12 kg). On the contrary for spotted hyaenas 48% of the diet consists of large mammals, 32% on medium sized mammals and only 2% on small mammals (Mills, 1987).

For several fossil hyaenas feeding habits and ecological adaptations have been assumed through morphological analysis and comparison with living taxa. *Plioviverrops* is considered to occupy the omnivore-insectivore niche, as indicated by a low trigonid and high metaconid; *Ictitherium* has similarities to jackals (*Canis aureus*), *Hyaenictitherium* to wolves and *H. hyaenoides* in particular to *Canis dirus* and *Lyacon pictus* (Werdelin and Solounias, 1991). For wolves, jackals and african hunting dogs (*Lyacon pictus*) a diet mainly on meat and nonvertebrates is stated by Van Valkenburgh (1989). But wolves also consume bones occasionally (Mech, 1974) and *Lyacon pictus* is known to crush bones as well (Van Valkenburgh, 1996). *Canis dirus* also was able to chew bones (Van Valkenburgh, 1989). So one can assume the tendency to chew bones for the similar form *Hyaenictitherium*. And as species of *Canis* which feed on meat mainly, use bones as food resource sometimes as well, one can probably assume a similar habit for *Ictitherium*.

Galiano and Fraily (1977) give the following indications of ecology and feeding habits of some fossil hyaenas: *Crocuta* and *Pachycrocuta brevirostris* - bone-crushing carnivores; *Lycyaena*, *Euryboas* and *Chasmaporthetes* - grasping carnivores with strong jaws, which implies a carnivorous diet with less bone consumption as in the first group. Werdelin and Solounias (1991) state that *Chasmoporthetes* was not specifically adapted to bone crushing. These authors divide the hyaenas into two major groups, one of hypercarnivorous (reduced M_2 and elongated P^4), crusorial forms where “the shearing component of the dentition is stressed on expense of the bone crushing component” as *Lycyaena*, *Hyaenictis* and *Chasmaporthetes* and a second group where “the bone crushing component in the dentition is stressed on expense of the shearing component” as *Belbus*, *Parahyaena*, *Hyaena*, *Pliocrocuta*, *Pachycrocuta*, *Adcrocuta* and *Crocuta*. But they nevertheless stress (page 85) that a division into bone-crushing and non-bone-crushing forms is arbitrary because the overall evolution of the hyaenids shows increasing adaptation toward fuller use of the prey and thus more and more use of bones as well.

Considering the distribution of HSB types among hyaenas in connection with their food preferences, there appears to be an association between bone eating and zigzag HSB. The omnivore-insectivore *Plioviverrops* (Werdelin and Solounias, 1991) and the specialized insectivore *Proteles cristatus* have undulating HSB. The wolf- and jackal-like and thus probably carnivorous to ossiphagous forms *Ictiterium* and *Hyaenotherium* show a transition from undulating to zigzag HSB, as do living wolves and coyotes (Stefen, 1995). Both canids show a transition from undulating to zigzag HSB in the dentition.

All species tending towards ossiphagy in the hyaenid cladogram above *Hyaenotherium* have dominantly zigzag HSB in their enamel. The living representatives above this genus are well adapted bone-crushers and the extinct forms show a tendency to fuller use of prey and thus use of bones (Werdelin and Solounias, 1991).

These associations of bone-eating and derived morphology, including zigzag HSB, suggests that the enamel microstructure in the family of *Hyaenidae* evolved in correlation with an increase in bone consumption. The same correlation of bone eating or more generally spoken of feeding on hard matter with presence of zigzag HSB also occurs in several families of other carnivorous mammals, like *Carnivora*, *Creodonta* and *Condylarthra*. In the studied *Carnivora* there is also a correlation between the percentage of bones consumed and the extensiveness of zigzag HSB (Stefen, 1997).

Percrocuta has recently been separated from the *Hyaenidae* (Chen and Schmidt-Kittler, 1983; Werdelin and Solounias, 1991). The teeth of *Percrocuta* are similar to those of hyaenids in gross shape, suggesting similar food preferences (Werdelin, pers. comm. 1994). The percrocutids we examined have zigzag HSB which, together with the evidence showing an association between zigzag HSB and ossiphagy, suggests that the *Percrocutidae* were also bone eaters.

Biomechanic considerations of zigzag HSB

There are mechanical reasons for linking zigzag HSB and bone-eating. It can be expected that fracturing bone requires higher stresses than fracturing most other types of food, and that the teeth of bone-eating taxa must therefore withstand higher stresses than teeth of most other taxa. Data supporting this hypothesis and showing how the morphologies of hyaena enamel are mechanically related to fracture resistance will be presented in another paper (Rensberger and Stefen, in preparation). Data concerning the functional role of enamel structure in the canine in *Crocuta crocuta* has been described briefly in Rensberger (1995).

As described above zigzag HSB have a complex three dimensional structure with horizontal and vertical elements and an irregular overlapping in the horizontal plane. As Pfretzschner (1986) has demonstrated decussation of prisms renders the enamel more resistant to tensile stresses. Horizontal bands can divert horizontal stresses, vertical bands can divert vertical stresses. The overlapping in different direction resists radial stresses. So zigzag HSB are resistant to stresses in different directions (for further detail see Rensberger and Stefen, in prep.).

Bending of HSB from horizontal to vertical

The bending of HSB from a horizontal to nearly vertical course only occurs in the carnassials and here only at certain sites: in the buccal enamel of paracone and metastyle in the P^4 and in the lingual enamel of paraconid and protoconid in M_1. This leads to a special arrangement of bands (Fig. 12). In the cutting edge the bands are parallel to the opposing tooth and at right angles to the opposing tooth in the shearing facet. As Rensberger and Von Koenigswald (1980) have shown, HSB which are parallel to the abrasive force are more resistant to abrasion than such alined at right angles to the force. So the special course of HSB in the carnassial of hyaenids probably helps to maintain a sharp and slender cutting edge. The bands in the cutting edge are more resistant to wear than those at the shearing facette. A similar bending of HSB which has been assumed to have the same function occurs in Chalicotheriidae and Brontotheriidae (Von Koenigswald, 1994).

Within carnivores this pronounced bending of HSB to the cutting edge only occurs in hyaenids. The reason why it is much more pronounced in this group and not e.g. in the ecological similar but extinct borophagines which have zigzag HSB as well (Stefen, 1995) is probably that only hyaenas developed a clear separation of bone crushing and meat cutting functions within their dentition. In some non-hyaenid genera of Carnivora tendencies to this bending in metastyle of p^4 is observable, but there is variability in this and it is nowhere as pronounced as in hyaenids.

Difference in the HSB in milk and adult teeth

The HSB of deciduous teeth were examined in a few taxa (*Crocuta*, *Hyaena* and *Adcrocuta*). It is striking that in the milk teeth the HSB are dominantly undulating and become acute-angled toward the tip but are not zigzag. Bending of HSB in the carnassials is poorly developed or absent in deciduous teeth. These differences in the enamel structure correlate again with the different feeding habits of young versus adult hyaenas. Sutcliffe (1970) describes the difference between juvenile and adult *Crocuta*: the adults can fracture bones, whereas juvenile animals with milk teeth can only chew on bones but not fracture them.

Conclusions

Zigzag HSB have a threedimensional complex structure which renders the enamel more resistant to tensile stresses from different directions than other types of HSB.

The occurrence of zigzag HSB is correlated with a diet requiring high biting forces as in bone crushing or more generally spoken with a diet on hard matter.

Within the lineage of *Hyaenidae* an increase of the amount of HSB could be observed correlating with an increase of bone consumption.

Another specialization of some hyaenas is the bending of the HSB in the carnassials to intersect the cutting edges with right angles. In functional terms this can be explained to help to maintain a sharp and slender cutting edge.

Milk and adult teeth of bone crushing hyaenas differ in their HSB: milk teeth show undulating to acute angled bands and no pronounced banding whereas adult teeth show dominantly zigzag HSB and bending of HSB in the carnassials.

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Discussion with Reviewers

M. Maas: You state that "all teeth of *Crocuta* display these zigzag HSB" — is this true for incisors as well? Can you speculate as to why teeth not involved in bone-eating would show these derived features (note that one possibility is suggested by Van Valkenburgh`s observation (J. Mamm. **77**:240-254) that carnivores sometimes used teeth other than "specialized" teeth for certain functions, including bone-cracking)? Are there other instances where derived enamel structure features (for example, vertical HSB) are present in some teeth of the dentition but not others?

Authors: Incisors were not accessible for many species. Where incisors could be studied (*Thalassictis*, *Belbus, Parahyaena*, *Hyaena*, *Adcrocuta* and *Crocuta*) they display the same HSB types and distribution as the other teeth of these species. Differences seem to occur in the amount of undulating HSB present at the enamel base, but to study this in detail is beyond the scope of the present paper.

As to why the incisors, usually not involved in bone-eating show these derived zigzag HSB, we thought that teeth of species which consume a lot of bones are very likely to come into contact with bones accidentally. That would increase the risk of fracturing even in these teeth not usually involved in bone crushing. The fact that hyaena sometimes "break bones, such as ribs and scapulae, with their incisors or carnassials (Van Valkenburgh, 1996 p. 250) shows the necessity for hyaenas to strengthen the enamel of incisors to reduce the danger of crackformation and -propagation.

As to the distribution of vertical HSB within the dentition, only few other observations than stated in the paper were made in carnivores. Most felids show tendencies to bend the HSB in a way described for *Crocuta*, but this is nowhere so obvious as in hyaenids, where we interpret it as a feature to keep a sharp and slender cutting edge in the carnassials. Also in one creodont tooth, an upper M1 of *Oxyaena* a similar bending of HSB towards the cutting edge was observed (Stefen, 1995).

There are examples within Carnivora where specialized zigzag HSB are present in some teeth of the dentition and not in others (e.g. *Indarctos*, *Canis lupus familliaris*, *Pliocyon*). In these cases usually the following schmelzmuster can be observed: incisors and canines show a transition from undulating HSB to acute angled and/or zigzag HSB toward the tip, the anterior premolars have undulating HSB only and toward the carnassials, the amount of acute-angled and/or zigzag HSB in the tips of the teeth increases (Stefen, 1997). Here again, in the species were incisors were accessible, the incisors show the more derived HSB types as the carnassials and not undulating HSB only as the anterior premolars.

M. Maas: Are there any data on differences in fracture frequency of carnassials with and without zigzag HSB, or with and without bending HSB? What are your predictions?
Authors: Concerning the fracture frequency of carnassials with and without zigzag HSB or with and without bending HSB we have no data and are not aware of any in the literature. A study on tooth breakage in large carnivores by Van Valkenburgh and Hertel (1993) showed that *Crocuta crocuta* had the highest fracture frequency as would be expected in a habitual bone-cracker. A comparison of the fractures of carnassials with or without zigzag HSB or any other enamel feature is difficult, because species showing different enamel structures have other dietary adaptations and therefore different tensile stresses are implied to the enamel. And to determine the influence zigzag HSB or bending of HSB have on the fracture frequency of teeth, they would have to be tested under the same stresses, which is impossible *in vivo*. Also the morphology of the teeth would have to be considered.

We assume that the carnassials of *Crocuta* would break more easily if they would not have zigzag HSB and the cutting blade would be more easily worn if they had no bending of HSB.