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Diversity and evolution of Hunter-Schreger Band configuration in tooth enamel of perissodactyl mammals

WIGHART VON KOENIGSWALD, LUKE T. HOLBROOK, and KENNETH D. ROSE

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Four different Hunter-Schreger Band (HSB) configurations were observed in the teeth of fossil and extant Perissodactyla. This variability exceeds that observed in Artiodactyla or Proboscidea. The four HSB configurations represent two different evolutionary pathways. Transverse HSB found in many mammalian taxa outside the Perissodactyla represents the most primitive HSB configuration. It occurs in several primitive perissodactyl families and is retained in Palaeotheriidae and extant Equidae. Curved HSB evolved from transverse HSB and occurs in Tapiridae, Helaletidae, and Lophiodontidae, as well as in Ancylopoda and Titanotheriomorpha. This likely indicates independent evolution of curved HSB in two or more lineages, but the number of instances of parallelism of this configuration is obscured by uncertainty in the relationships among these taxa and by a lack of data for some important basal taxa. A second evolutionary pathway leads from transverse HSB via compound HSB to vertical HSB. Compound HSB were detected in Hyrachyidae, Deperetellidae, and the early rhinocerotid *Uintaceras*. Vertical HSB configuration characterizes the molar dentition of other Rhinocerotidae, Hyracodontidae, Indricotheriidae, and Amynodontidae. Often, the incisors of rhinocerotids retain traces of compound HSB. Thus the HSB configuration reflects phylogenetic relationships to some degree. The selective value of the modified HSB configurations is interpreted functionally as a mechanism to reduce abrasion during mastication, assuming that the perpendicular intersection of prisms with the actual grinding surfaces resists wear better than prisms running parallel to the occlusal surface.

Key words: Mammalia, Perissodactyla, Hunter-Schreger Bands, HSB, tooth enamel microstructure, functional adaptation, phylogeny.

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Introduction

The shiny enamel of mammalian teeth is the hardest and most resistant material mammals can produce. The functional quality of the enamel is determined by the hardness of the material and by its internal structure. The decussating layers of prisms serve as a crack stopping mechanism (Pfretzschner 1988). Although the internal structures are of functional significance, they are genetically controlled, since the tooth is formed in the crypt where no mechanical forces are active. Despite the common occurrence of parallel and convergent evolution, variation in enamel microstructure may still provide insights into the phylogeny of particular groups of mammals, such as perissodactyls (Koenigswald 2004).

Most internal structures in the enamel are only visible using high magnification. The Hunter-Schreger Bands we discuss here for perissodactyls are visible under low magnification, as light and dark bands. They were originally figured by Hunter (1778) and Schreger (1800) for humans and bovids two centuries ago and accordingly are named Hunter-Schreger Bands (HSB). These bands occur in the enamel of most large mammals (Koenigswald et al. 1987).

The configuration of the HSB in perissodactyls shows an unusual extent of variation compared to other mammalian orders, though there is general consistency within perissodactyl clades. HSB are oriented vertically in rhinos (Rensberger and Koenigswald 1980; Fortelius 1984; Boyde and Fortelius 1986), a phenomenon originally observed and described in some detail by Quenstedt (1852). He illustrated the vertically oriented bands in molars of rhinoceroses (Fig. 1). The specific HSB configuration of chalicotheres and brontotheres was described as U-shaped (Koenigswald 1994). As shown below, different configurations occur in other perissodactyl clades. In this paper we concentrate on two aspects of HSB: the phylogenetic significance and the functional value of reoriented HSB.

The complex structure of the enamel can be studied on various levels (Koenigswald and Clemens 1992). The schmelzmuster describes the occurrence of different enamel types within a tooth. In this study, we concentrated on one aspect of

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the schmelzmuster, namely the configuration of HSB (as defined in the next section), and we surveyed the variability of this character in a wide diversity of perissodactyls. We focused on cheek teeth (molars and premolars), because these are best represented for the greatest number of taxa, but we also made observations on the anterior dentition (incisors and canines) whenever possible, since the schmelzmuster may differ in the various teeth at the dentition level. We then used these observations to make inferences regarding the evolution of HSB configurations in perissodactyls.

Institutional abbreviations.—AMNH, American Museum of Natural History, Department of Paleontology, New York, New York; BSPG, Bayerische Staatsammlung für Paläontologie und Geologie, München, Germany; CM, Carnegie Museum, Section of Vertebrate Paleontology, Pittsburgh, Pennsylvania; GMH, Geiseltalmuseum, Halle, Germany; HHZM, Zoologisches Museum der Universität Hamburg, Germany; HLMD, Hessisches Landesmuseum, Darmstadt, Germany; KOE, Koenigswald enamel collection of the STIPB, Bonn, Germany; MB, Museum für Naturkunde Berlin, Germany; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MR, Michael Rummel collection, Natur-Museum, Augsburg, Germany; NHMB, Naturhistorisches Museum, Basel, Switzerland; NHMW, Naturhistorisches Museum, Wien, Austria; PMM, Palaeontological Museum, Moscow, Russia; SDSM, South Dakota School of Mines, Museum of Geology, Rapid City, South Dakota; STIPB, Steinmann Institut, Paleontology, University of Bonn, Germany; UM, University of Michigan Museum of Paleontology, Ann Arbor Michigan; USGS, United States Geological Survey, Denver, Colorado, specimens now housed at USNM; USNM, National Museum of Natural History, Smithsonian Institution, Department of Paleobiology, Washington, D.C.; ZFMK, Zoologisches Museum Alexander Koenig, Bonn, Germany; ZSTÜ, Zoologische Sammlung Universität Tübingen, Germany.

Other abbreviations.—Br, Bridgerian; EDJ, enamel-dentine junction; HSB, Hunter-Schreger bands; if, interface between fields of HSB; OES, extend almost to the outer enamel surface; SEM, Scanning Electron Microscope; Wa, Wasatchian; Incisors, canines, premolars, and molars are designated as I, C, P, M for uppers, i, c, p, m for lowers.

The nature of Hunter-Schreger Bands

Hunter-Schreger Bands are an optical phenomenon produced by refraction of light due to the internal structure of the enamel. The term HSB is not only used for this phenomenon but is traditionally also used for the underlying structure formed by layers of decussating prisms. In the terminology related to enamel structures we follow Koenigswald and Sander (1997b). Enamel is a highly mineralized material. Several

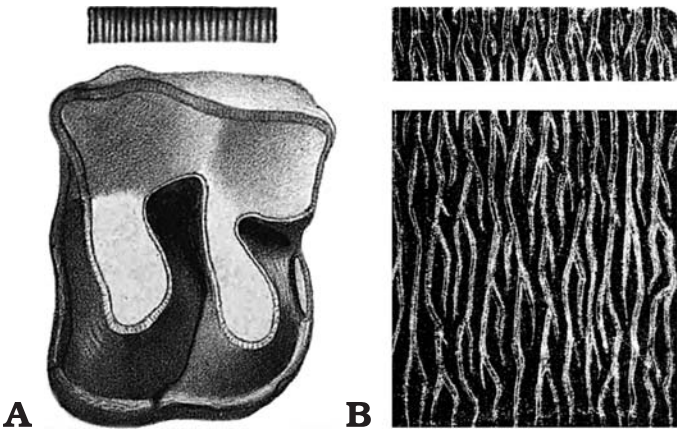


Fig. 1. Vertical HSB configuration as figured by Quenstedt (1852: pl. 2: 1 [A]; pl. 3: 35 [B]). **A**. Occlusial view with HBS in the extoloph. **B**. Orienation and bifiurcation of the HSB in tangential aspect.

structural levels must be differentiated to understand the phenomenon of HSB. The mineral hydroxyapatite forms very thin crystallites that are organized into rods, called enamel "prisms", although these structures are not prisms in the mineralogical sense. These prisms have a diameter on the order of 5 µm. Many studies have been devoted to the changing shape of the cross-section of the enamel prisms (e.g., Shobusawa 1952; Boyde 1965; Boyde and Martin 1984; Wood and Stern 1997). The enamel prisms start at the enamel-dentine junction (EDJ) and extend almost to the outer enamel surface (OES). They are normally arranged in groups with the same prism orientation or in a very symmetrical arrangement. Occasionally the orientation of the prisms is irregular, e.g., in proboscideans (Koenigswald 1997a; Tabuce et al. 2007; Ferretti 2008). The orientation of the prisms defines the various enamel types (Koenigswald and Sander 1997a, 1997b). The enamel cap of a tooth may be formed by two or three different enamel types. These can be arranged in layers within the thickness of the enamel band or occur in specific areas of the teeth. The arrangement of enamel types in a tooth was defined as schmelzmuster (Koenigswald 1980). The different tooth families within the same dentition may show differences in the schmelzmuster (Koenigswald and Clemens 1992).

The visual phenomenon of HSB (Fig. 2) is caused by the optical properties of the crystallites within the prisms. This effect would hardly be visible in single crystallites, but it is magnified when crystallites are packed in prisms and it is strongly increased when bodies of prisms are oriented in parallel. If the direction of the light coincides more or less with the long axis of the prisms it will disappear in the depth of the enamel. Thus the cross-section appears dark. Light falling perpendicular or at an angle to the prisms is reflected, and thus the prisms appear bright. Thus prisms effectively act in the same manner as fiber optic light guides.

The enamel type defined as HSB is formed by layers of enamel prisms which decussate at a high angle—often about 90°—with the prisms of the adjacent layer. The general biomechanical function of the layers of decussating prisms is to serve as an important crack-stopping mechanism, compa-

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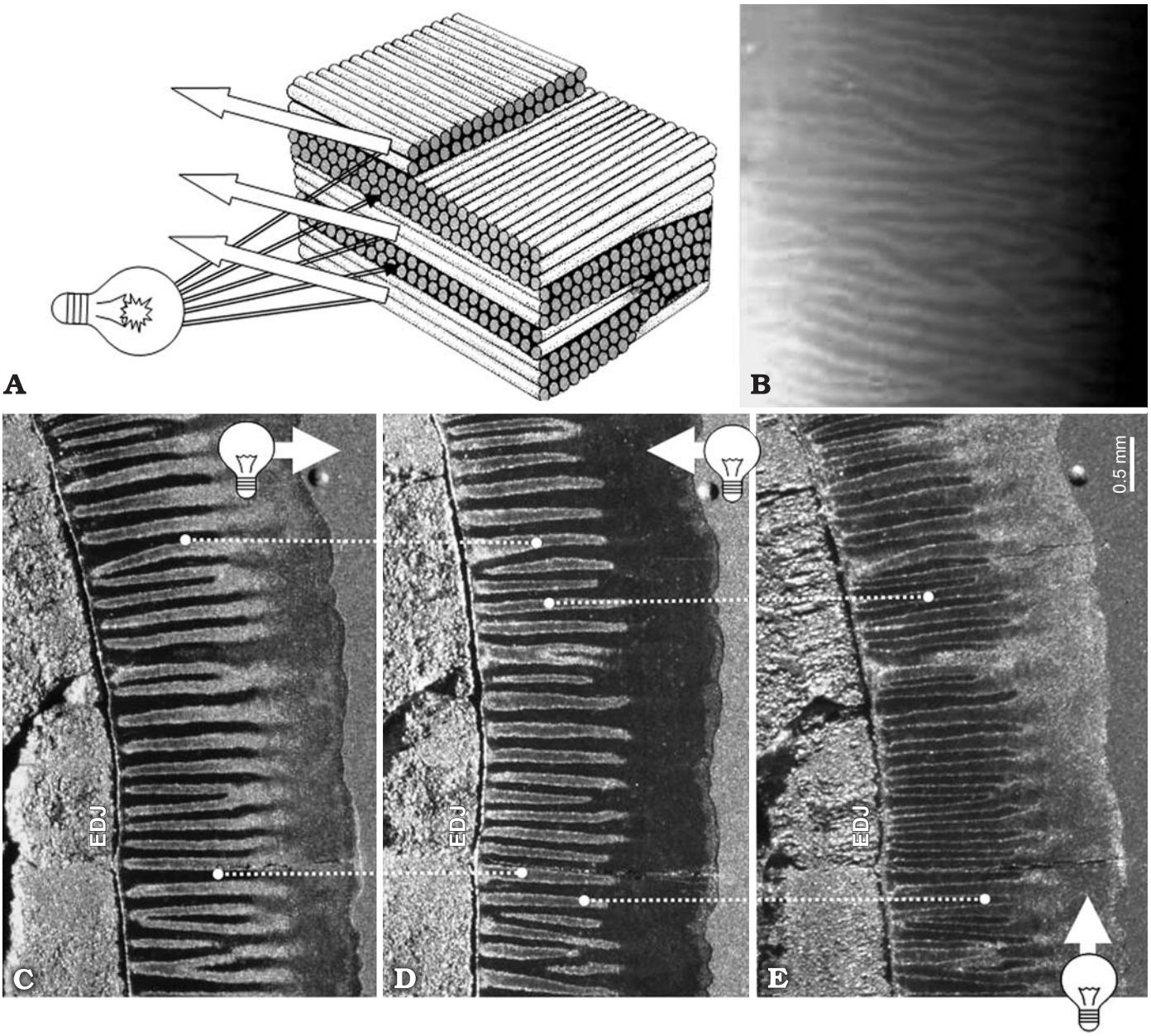


Fig. 2. Appearance of the HSB in variable light. **A**. Scheme of the fiber optic light guide effect of enamel prisms. Those prisms illuminated perpendicular to the long axis reflect brightly, while those illuminated parallel to the long axis appear dark. **B**. Transverse HSB illuminated from the left side in an incisor of the artiodactyl *Myotragus*. Note the regular bifurcation of the light bands to the left, of the dark bands to the right. **C**–**E**. Vertical HSB in an etched ground section of a molar of *Coelodonta antiquitatis* (Blumenbach, 1799) (Upper Pleistocene, Germany KOE 59) illuminated from different sides. Light source on the left (**C**), light source on the right (**D**), light source perpendicular to the direction of the bands (**E**), highlighting the transitional zones. White dotted lines connect identical spots.

rable to plywood structure (Koenigswald and Pfretzschner 1987; Koenigswald et al. 1993; Pfretzschner 1988, 1994).

The light or dark appearance of the bands depends on where the light source is situated. If this is changed from one side to the other, light bands become dark and vice versa (Fig. 2A, C). The thickness of these bands varies and is traditionally measured in the number of prisms per band. In rodent incisors the bands may be only one prism thick (Korvenkontio 1934). In most mammals with HSB, thickness is about 6 to 15 prisms, with larger mammals tending to have thicker HSB (Kawai 1955). In the vertical HSB of *Coelodonta antiquitatis* we counted 11 to 13 prisms per band.

The optical effect—the light and dark banding—is most obvious when the angle between prisms of adjacent bands is large and when the bands are thick and can be observed under low magnification. Quenstedt (1852) observed and figured vertical HSB in rhinocerotid molars using low magnification. He even correctly observed that these bands bifurcate and that intermediate layers occur between the light and dark bands. These layers are formed by prisms changing from one band to the next by a more or less sharp turn

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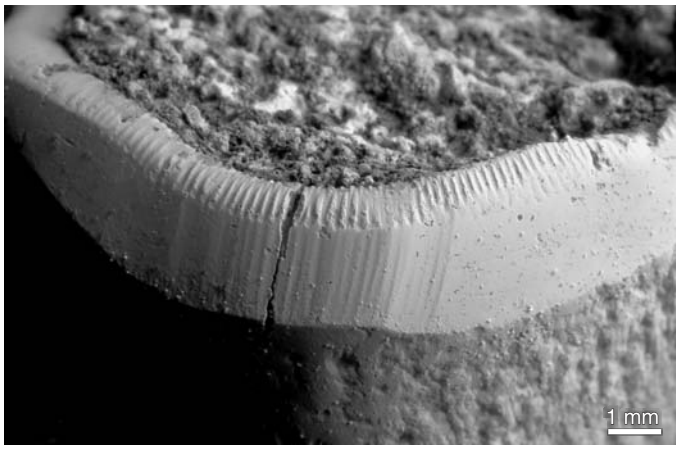


Fig. 3. Typical cross-ridges on the occlusal surface of the enamel band caused by vertical HSB in a lower molar of *Rhinoceros sondaicus* Desmarest, 1822 (KOE 71); Pleistocene, Saniran, Java. The vertical HSB are here superimposed by thick radial enamel.

(Rensberger and Koenigswald 1980). Under proper illumination this narrow transitional zone of turning prisms between two bands is visible as a thin reflecting line between the vertical bands (Fig. 2B).

The different prism orientation in HSB might cause differential wear resulting in a structure defined here as cross-ridges in the occlusal surface of the enamel band. They are most obvious in vertical HSB as in rhinocerotids, where they can often be felt when running a fingernail (Fig. 3) along the enamel band. Cross-ridges are not restricted to vertical HSB; they may occur wherever the HSB intersect the occlusal surfaces of the enamel band. On an oblique portion of the enamel band, even transverse HSB might create cross-ridges. Therefore, cross-ridges are not unequivocal evidence of vertical HSB.

Hunter-Schreger Bands have another important feature that differentiates them from other structural elements. The HSB bifurcate in a regular fashion, as was figured by Quenstedt (1852: table 3). One group of bands (such as the light ones) always bifurcates to one side while the other (the dark ones) bifurcates in the other direction. If the light comes from the other side the optical effect is reversed (Fig. 2B). This regular bifurcation of the HSB is related to the primary direction of prisms from the EDJ towards the OES (Koenigswald and Pfretzschner 1987: fig. 14).

We introduce the term "configuration of HSB" to refer to the course of HSB (as it intersects the OES or a tangential plane parallel to the EDJ) when viewed through the side of a tooth (buccal, lingual, mesial, or distal). This describes the orientation of HSB in relation to the growing direction of the tooth as seen from the outside or from tangential sections. The configuration often can be studied directly from the outside, but the layer of HSB is sometimes overlain by a thick layer of a different enamel type (such as radial enamel) that obscures the HSB. In such cases, a tangential section through the enamel (i.e., a section parallel to the OES and EDJ), passing through the layer with HSB, is required to see the HSB configuration. Specific types of configuration are described below. Configuration does not refer to the fact that HSB can run relatively straight or can be wavy in appearance, nor does it describe the angle of inclination defined by Korvenkontio (1934), which relates to the angle that the plane of the HSB forms with the EDJ in vertical sections.

Based on external observation and examination of tangential sections, we found four different configurations of HSB (Fig. 4):

Transverse HSB (Figs. 4, 5).—The HSB are generally parallel to the occlusal surface and the base of the enamel crown. This is essentially horizontal in premolars and molars. The HSB often undulate or show other minor differentiations but otherwise remain transverse. When the worn occlusal surface cuts obliquely through the enamel, these HSB intersect the enamel band.

Curved HSB (Fig. 4; see also Figs. 5–7, 11).—In several groups the basically transverse HSB curve toward the occlusal surface of the enamel band and thus intersect the shearing blades at a large angle. The curved HSB configuration is strictly related to specific areas of the tooth morphology and is always combined with transverse HSB in other parts of the teeth. Where HSB curve from different directions (what we refer to here as different "fields of HSB"), they may meet at a characteristic interface. The interface may be indicated by a distinct groove on the OES. These curved HSB occur mostly in prominent crests, such as well-developed ectolophs and crosslophs in upper and lower cheek teeth. Koenigswald (1994) described the most strongly curved HSB in chalicotheres and brontotheres and referred to them as U-shaped HSB. Fortelius (1985) mentioned curved HSB in several groups as "horizontal (concave)" HSB but did not describe them in detail.

Compound HSB (Fig. 4; see also Fig. 8).—We found a specific type of HSB configuration with transverse HSB as an inner zone and vertical HSB in an outer zone. The occurrence of vertical HSB may be related to enamel thickness but not to specific areas in the tooth morphology. The relative thickness of the inner and outer zones may differ, and this in turn affects how easily one can detect the corresponding HSB.

Vertical HSB (Fig. 4; see also Fig. 9).—In this configuration HSB are vertically oriented and are more or less straight, rather than wavy or curving, on all sides of the tooth from the

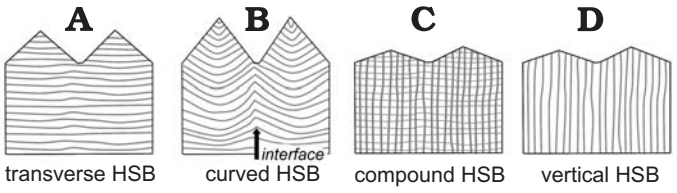


Fig. 4. Schematic illustration of the four configurations of Hunter-Schreger Bands (HSB) found in Perissodactyla: **A**. Transverse HSB configuration. **B**. Curved HSB configuration with interface. **C**. Compound HSB configuration with transverse HSB in an inner layer and vertical HSB in an outer layer. **D**. Vertical HSB configuration.

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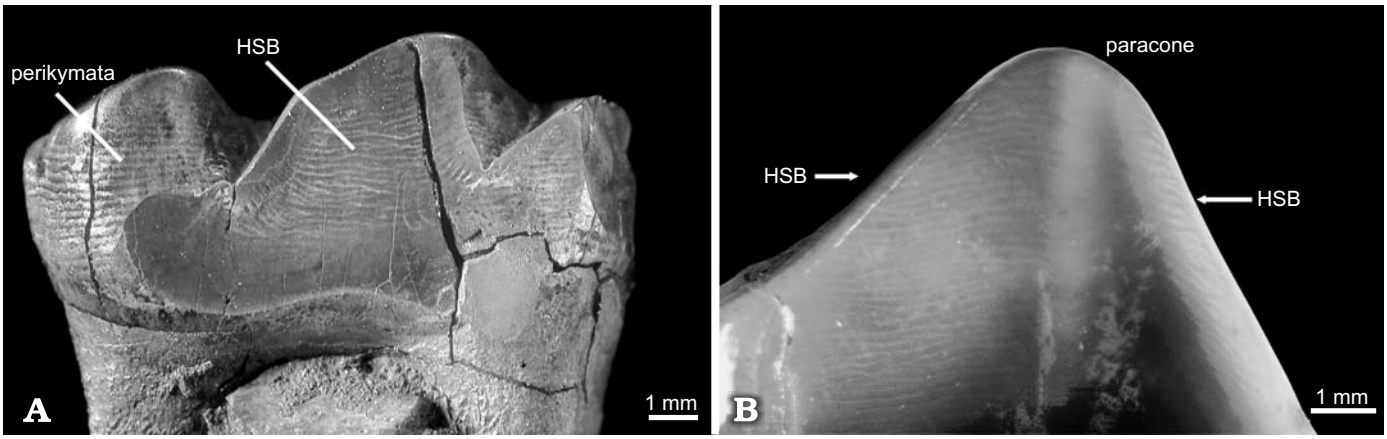


Fig. 5. Transverse HSB configuration in Equoidea. **A**. Lower molar of *Mesohippus* sp. (KOE 1509); late Eocene–early Oligocene, Toadstool Park area, Nebraska, USA. The transverse HSB are to be seen in the tangential section. Note also the transversely oriented perikymata on the outer enamel surface. Both structures are independent from each other. **B**. Upper molar of *Palaeotherium* sp. (KOE 4050); upper Eocene, Frohnstetten, Germany; transverse HSB visible in the translucent enamel of the paracone from the outside.

basal cingulum (where present) up to the occlusal surface. The occurrence of vertical HSB is not related to the tooth morphology. Like transverse HSB, they exhibit unidirectional bifurcation. Since the HSB do not converge, no interfaces are present, as are found regularly in the curved HSB configuration. Cross-ridges caused by the intersection of the HSB with the occlusal surface are very characteristic.

The configuration of the HSB may differ among the different tooth categories within the dentition, especially when dentitions are heterodont (Koenigswald and Clemens 1992). Thus incisors and canines may show a different HSB configuration than premolars and molars. Our survey shows that the presence or absence of differences between incisors and molars makes the characterization of different groups easier.

Methods of investigation

Appendix 1 lists the specimens investigated for this study. The specimens studied were selected to represent a wide spectrum of perissodactyl diversity, emphasizing the earliest members of the order and sampling the various lineages. In addition, several phenacodontid condylarths were examined as an outgroup.

Derived mammalian enamel is often composed of two or three different enamel types forming separate superimposed layers parallel to the EDJ (Koenigswald and Clemens 1992). The three-dimensional prism orientation is studied best from various oriented sections under the scanning electron microscope (SEM). The sections are polished and etched following procedures outlined by Koenigswald (2004). The configuration of HSB can be studied under the binocular microscope under low magnification and often sections are not necessary. Thus specimens do not need to be sacrificed. Most taxa studied here were examined in this way. However, if the layer with HSB is covered by another enamel type, or the enamel is not translucent, non-destructive methods may not be adequate for revealing HSB configuration. In such cases, whenever possible, sections were made. These sections were oriented tangentially—that is, parallel to the EDJ and the OES. Small teeth, such as those of several early perissodactyls, had to be sectioned as well, since the HSB are more difficult to identify in uneven and small areas.

HSB close to the OES can be investigated using the described fiber optic light guide effect of the prism layers. One of the various techniques is to hold the tooth in one hand with the enamel surface in focus under the binocular lens with varying magnification. The light source is held in the other hand. It is best to direct the narrow opening of a light tube of a fiber optic lamp from one side immediately beside the enamel. The light should be applied tangentially to a corner or fracture of the enamel. Most of the light should penetrate into the enamel tangentially. HSB show their light and dark pattern when the light falls at a very low angle onto the cross-section of the enamel band. It takes practice to turn the specimen until the best view is available. It is not easy, however, to document the results photographically.

A magnification of 10 to 20 times is most effective. In relatively clear enamel the bands may become visible at slight cracks within the enamel. There is no single way to make the HSB visible due to the modification of the enamel during fossil diagenesis, but with experience and persistence the orientation of HSB usually can be identified.

All tooth surfaces were studied in order to follow HSB throughout the enamel. HSB are best seen when they are close to the outer enamel surface. Transverse HSB often run parallel to the perikymata, superficial ridges on the OES that usually develop perpendicular to the growth axis, and which are related to time intervals of enamel formation. In contrast to perikymata, HSB of all configurations show very distinct unidirectional bifurcations (Koenigswald and Pfretzschner 1987). In rhinos, where HSB are vertical, the two structures may form a grid pattern (Koenigswald 2002).

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Observations

Our observations are arranged using the classification sequence given in Rose (2006), with the following exceptions. Lophiodontidae are placed after Tapiroidea based on the results of Holbrook (2009) that called into question a relationship with chalicotheres. Similarly, Deperetellidae are placed with rhinocerotoids because of the similarities of deperetellid schmelzmuster to that of *Hyrachyus*. We include *Colodon* within Tapiridae, following Colbert (2005). The results of our observations are summarized in the next section in the conclusions.

Phenacodontidae.—Only transverse HSB were observed in cheek teeth of *Phenacodus*, *Ectocion*, and *Meniscotherium*, as noted earlier for *Tetraclaenodon* (Koenigswald et al. 1987). Transverse HSB were observed in incisors of *Meniscotherium* and canines of *Meniscotherium* and *Phenacodus*.

Equidae.—Pfretzschner (1994) observed transverse HSB overlain by radial enamel in molars of *Hyracotherium* and *Palaeotherium*. Our own observations on various incisors, premolars and molars of *Hyracotherium* (sensu lato) confirm this orientation, but HSB are partially developed only weakly. In *Mesohippus* all investigated teeth show only transverse HSB (Fig. 5A). The outer layer of radial enamel presumably has been lost. Prominent perikymata may hide the HSB, but the refraction on cracks confirms the transverse orientation. In *Hippotherium* and *Equus* the transverse orientation of the HSB was confirmed.

In addition to the predominant transverse orientation of the HSB, some genera, e.g., *Anchitherium aurelianense*, present a specific convex bending in upper molars (Fortelius 1985). In the ectoloph HSB bend downwards from the tips of paracone and metacone to the parastyle and mesostyle, but do not form distinct interfaces. By this bending the HSB are almost parallel to the oblique shearing blades—in contrast to the curved HSB in brontotheres or chalicotheres. We regard this as a variation of the transverse HSB, as Fortelius (1985) used the classification "horizontal (convex)". Thus all studied members of the Equidae share a similar, transverse orientation of the HSB, regardless of whether they are hypsodont or brachydont. It occurs in upper and lower incisors, as well as premolars and molars.

Palaeotheriidae.—The Eocene *Propalaeotherium* from the Geiseltal and *Palaeotherium* from Frohnstetten, Germany, show well-developed transverse HSB in molars (Fig. 5B), premolars, partially combined with radial enamel. In canines and incisors HSB are dominantly transverse but we observed in one upper incisor a slight upward curvature at the lateral margin so that the HSB intersect the occlusal edge obliquely. In the pronounced ridge of the mesostyle and parastyle the HSB are slightly curved downwards. Fortelius (1985) listed the HSB of palaeotheres as "horizontal (concave)," as he did for brontotheres and chalicotheres. We did not observe a similar curvature in palaeotheres as in the other two groups, which we classified as curved HSB because of the distinct interface.

Isectolophidae.—*Homogalax protapirinus* was difficult to investigate externally because most of the material available was very dark. Thus the enamel of lower molars had to be sectioned tangentially. From these sections it is clear that the

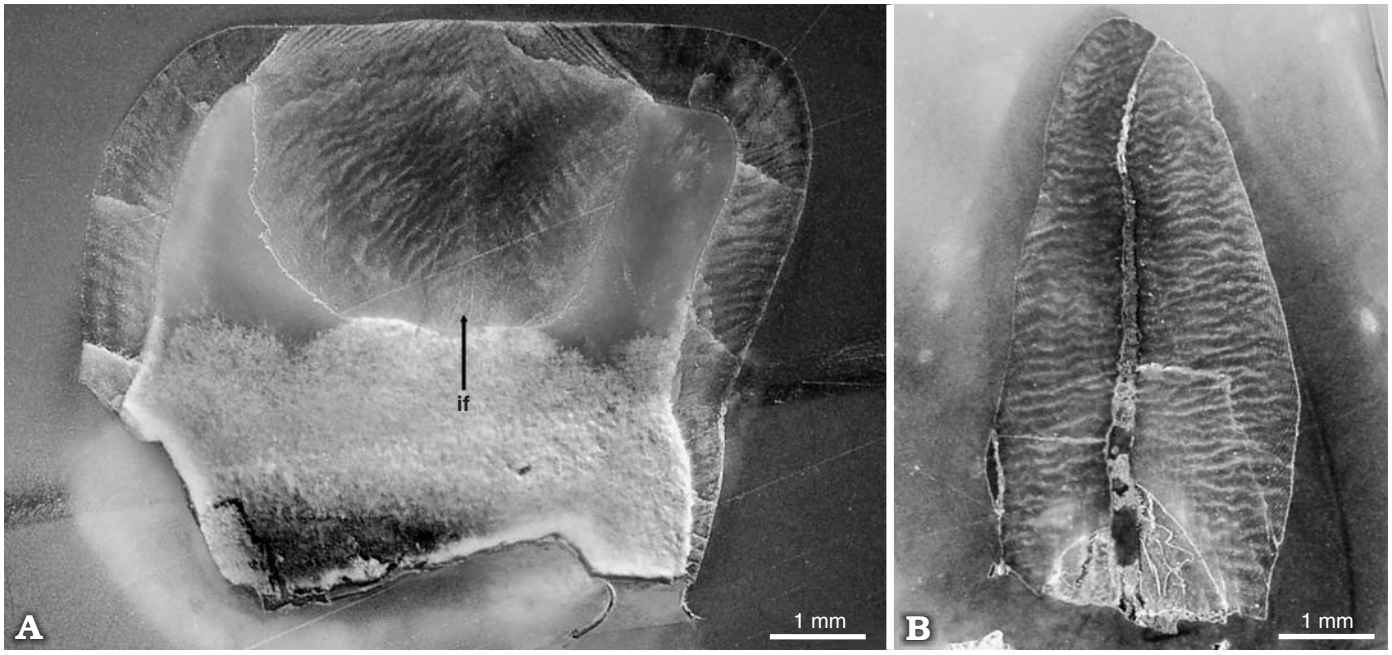


Fig. 6. Curved HSB configuration in *Heptodon calciculus* Cope, 1880 (KOE 4035, 4036); early Eocene, Willwood Formation, Bighorn Basin, Wyoming, USA. **A**. Tangential section of the posterior loph of a lower molar with two fields of curved HSB with the typical interface. **B**. Tangential section of the protoconid of a lower molar with the transverse HSB. Abbreviation: if, interface between fields of HSB.

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HSB are transversely oriented on the lingual and buccal sides. The cross-lophs of the lower molars were studied with special emphasis. No deviation from the transverse orientation could be identified in any of the several sections. Lower incisors and canines also exhibit transverse HSB.

Lower molars of *Cardiolophus* showed transverse HSB. Specimens of *Isectolophus annectens* have molars with transverse HSB that do not appear to exhibit the curved HSB.

Helaletidae.—The lower molars of *Heptodon calciculus* show curved HSB. The HSB are more transverse on the lingual and buccal sides of the cusps. In the cross-lophs the HSB rise diagonally towards the cutting edge, forming a clear interface in the middle of the loph. This is the typical curved HSB configuration as defined above, and was corroborated in a tangential section (Fig. 6). North American specimens of *Helaletes* exhibit the same curved HSB. Dashzeveg and Hooker (1997) erected the genus *Irdinolophus* for specimens previously referred to *Helaletes mongoliensis*, and they assigned another Mongolian species, *Helaletes fissus*, to the genus *Desmatotherium*. They considered *Irdinolophus* to be closely related to deperetellids, but we include it here in our discussion of helaletids, because its HSB configuration is more similar to that of helaletids than that of deperetellids. Fortelius (1985) listed "horizontal (concave)" HSB for Helaletidae.

Lower molars of *Selenaletes scopaeus*, which was originally placed in Helaletidae by Radinsky (1966), have only transverse HSB and do not exhibit the curved HSB. Therefore, the placement of this genus in Helaletidae may be questioned.

Lophialetidae and other endemic Asian "tapiroids" (except Deperetellidae).—Lophialetids (including *Lophialetes*, *Schlosseria*, and *Breviodon*) all exhibit transverse HSB in their cheek teeth without any of the curving toward the occlusal surface that is characteristic of the tapiroid condition. This is also true of *Rhodopagus* and *Pataecops*, two genera of Asian Eocene "tapiroids" of uncertain affinity.

Tapiridae.—Extant and Pleistocene *Tapirus* were studied from complete and partial dentitions. In the lower molars the buccal and lingual sides are characterized by curved HSB, which start as transverse on the cusps but curve upward in the cross-lophs from both lingual and buccal sides to meet the cutting surface almost vertically (Fig. 7A). Since the HSB of both fields curve in different directions, an interface between these two fields is present in the middle of the loph. The same structure is found on the mesial as well as on the distal side of the loph. In molars where the loph is heavily worn, this interface is less obvious. In upper molars the ectoloph also shows curved HSB, with an interface just mesial to the point where the ectoloph meets the metacone. The curved HSB are most evident closer to the occlusal edge, and the HSB are transverse near the root. Thus, wear may obscure the curved HSB on the ectoloph, giving the appearance of only transverse HSB. Upper and lower incisors and canines show transverse HSB only. In the upper molars the ectoloph and buccal sides

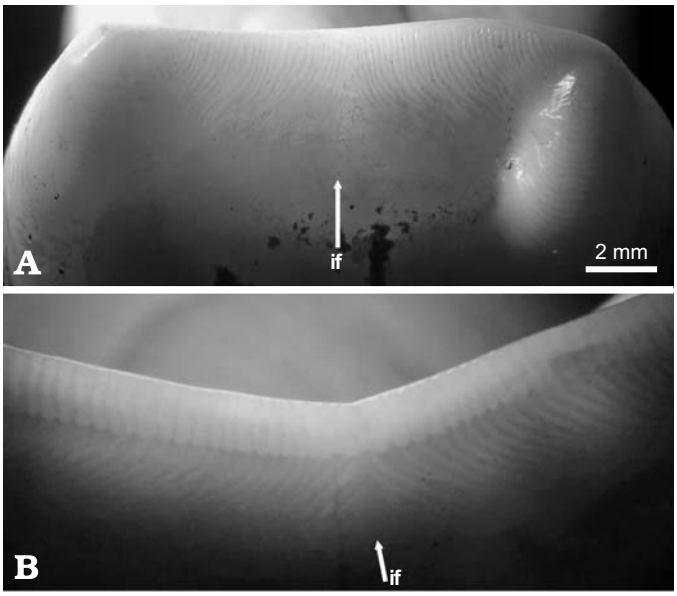


Fig. 7. Curved HSB configuration with the typical interface in the transverse lophs of lower molars in of tapirs. **A**. *Tapirus sinensis* Owen, 1870 (MB Ma 33219); Pleistocene, Junnan, China. **B**. *Lophiodon remensis* Lemoine, 1878 (KOE 4052); middle Eocene, Geiseltal, Germany. Abbreviation: if, interface between fields of HSB.

of protocone and metacone show transverse HSB. In the cross-lophs the HSB curve upwards from the buccal side. In the protoloph they cover the entire loph until it meets the ectoloph. In the metaloph the curved HSB do not extend as far to the ectoloph and meet the transverse HSB in the ectoloph before both lophs join, but there is no distinct interface between the two fields. Incisors and canines show dominantly transverse HSB, as do p2 and p3. In unworn incisors, however, curved HSB were evident at the occlusal tip.

In *Colodon occidentalis* the curved configuration is well developed in the lower molars. The p2 does not show two lophs like the other molariform premolars. Nevertheless a slight indication of the curved configuration was seen at the distal wall of the trigonid. Upper molars of *Colodon* exhibit curved HSB on both the cross lophs and the ectoloph, with a distinct interface present on the ectoloph. In *Colodon cingulatum* the incisors have transverse or slightly curved HSB. Molars of *Haagella peregrina* show very typical curved HSB with an interface in the cross-lophs of lower molars and one-sided curved HSB in the upper molars.

The curved configuration is also present in molars of *Tapiravus* from the upper Eocene and in lower molars and premolars of *Protapirus* from the lower Oligocene.

Lophiodontidae.—All studied species of *Lophiodon* show the typical configuration of curved HSB in the molar lophs (Fig. 7B). In the buccal and lingual sides of the lower premolars and molars the HSB are transverse; but in the lophs the bands curve upward at the ends, forming an interface between the fields of HSB from both sides. In the cutting edges of the lophs the cross-ridges are often visible. In the upper molars the ectoloph shows transverse HSB at the base and

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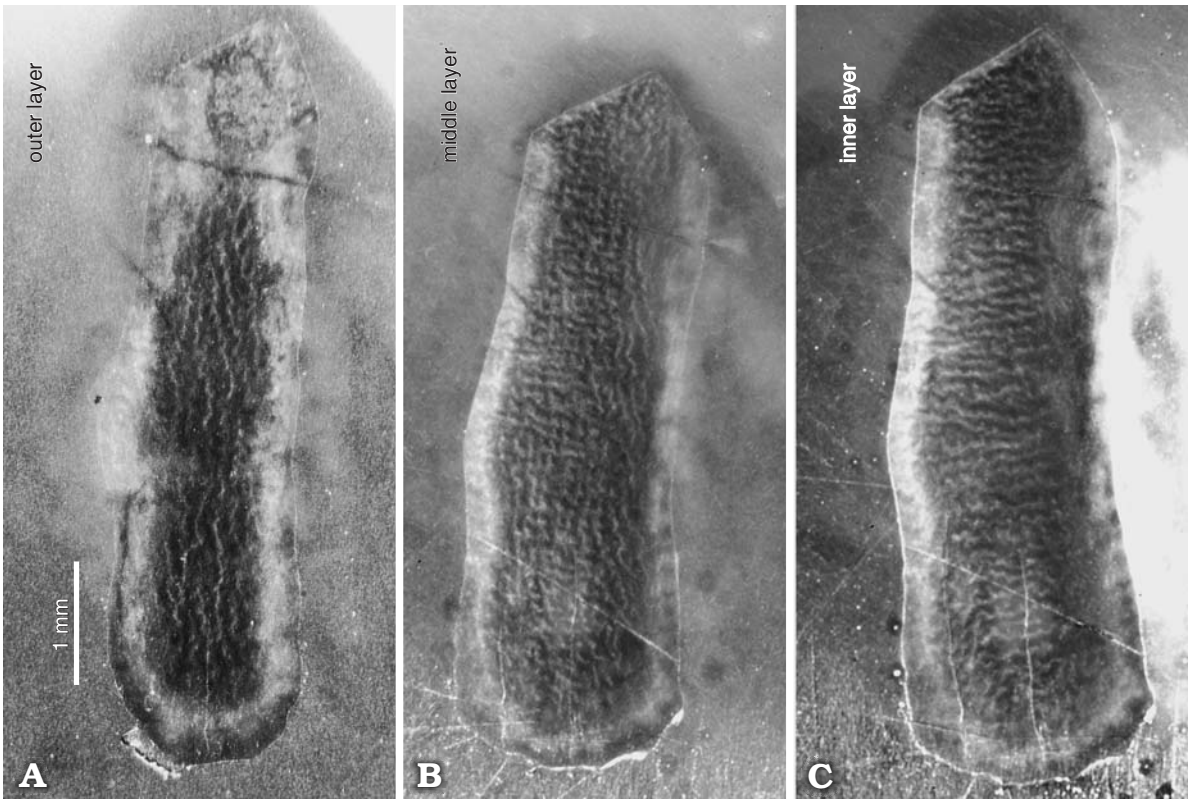


Fig. 8. Compound HSB configuration in *Hyrachyus minimus* (Fischer, 1829) (KOE 4050); middle Eocene, Geiseltal, Germany. Tangential section of the protoconid of a lower molar in three sequential levels. **A**. Outer layer with vertical HSB. **B**. Middle level with a transitional orientation of the HSB. **C**. Inner layer with transverse HSB.

slightly curved HSB in the upper part. There an interface was found between paracone and metacone. In the lophs the transverse HSB from the buccal side of the protocone and metacone bend upwards into the lophs to intersect the cutting edge, where they occur as cross-ridges. The field of curved HSB reaches almost to the ectoloph. In the thick part of the enamel, especially in *Lophiodon rhinocerodes* vertical elements originating from zigzag HSB were observed. Thus the transverse HSB partly are transitional to a compound HSB configuration. Lophiodontids are listed by Fortelius (1985) as having "horizontal (concave)" HSB.

In incisors and canines the HSB are oriented transversely. This is visible although the enamel has a rough surface texture.

Hyrachyidae.—*Hyrachyus* is characterized by the newly recognized compound HSB configuration in all tooth positions (Fig. 8). A superficial investigation of the outer surface of molar enamel indicated that European *Hyrachyus minimus* and North American *H. eximius* and *H. modestus* have vertical HSB. The vertical HSB are seen in all sides and lophs of the upper and lower molars. On the occlusal surface of the enamel band even the cross-ridges formed by the intersecting vertical HSB are visible. However, a more detailed investigation showed that these vertical HSB are only present in an outer layer, whereas transverse HSB form an inner layer. This combination was corroborated by a series of sections made parallel to the OES in molar teeth of *Hyrachyus*. It is difficult to observe this condition with low magnification and a light source, because the inner and outer layers can vary in thickness to a degree that one layer may be easily observed but not the other. Compound configuration was also observed in incisors and canines of *Hyrachyus*, with the vertical component appearing most strongly. Consequently, our observations do not confirm the classification of Fortelius (1985) as "horizontal (concave)" HSB.

Deperetellidae.—*Deperetella* was listed as having vertical HSB by Fortelius (1985). As reported by Holbrook (2007), specimens of *Deperetella* and *Teleolophus* exhibit cross-ridges on the occlusal surface of the enamel band that are characteristic of rhinocerotoids and their vertical HSB. Closer examination of AMNH specimens of *Deperetella* and *Teleolophus* confirm the presence of vertical HSB, but as part of the compound HSB configuration. Cheek teeth in these specimens clearly possess vertical HSB, but there also is evidence of horizontal HSB deep to the vertical layer, as observed in *Hyrachyus*. The horizontal component is most evident in specimens of *Teleolophus* and in the enamel closest to the root. Thus cheek teeth of both genera are characterized by the compound HSB configuration.

Hyracodontidae.—*Hyracodon nebraskensis* was represented by all tooth positions. The vertical HSB are present in the ectoloph as well as in the buccal side of the protocone and the

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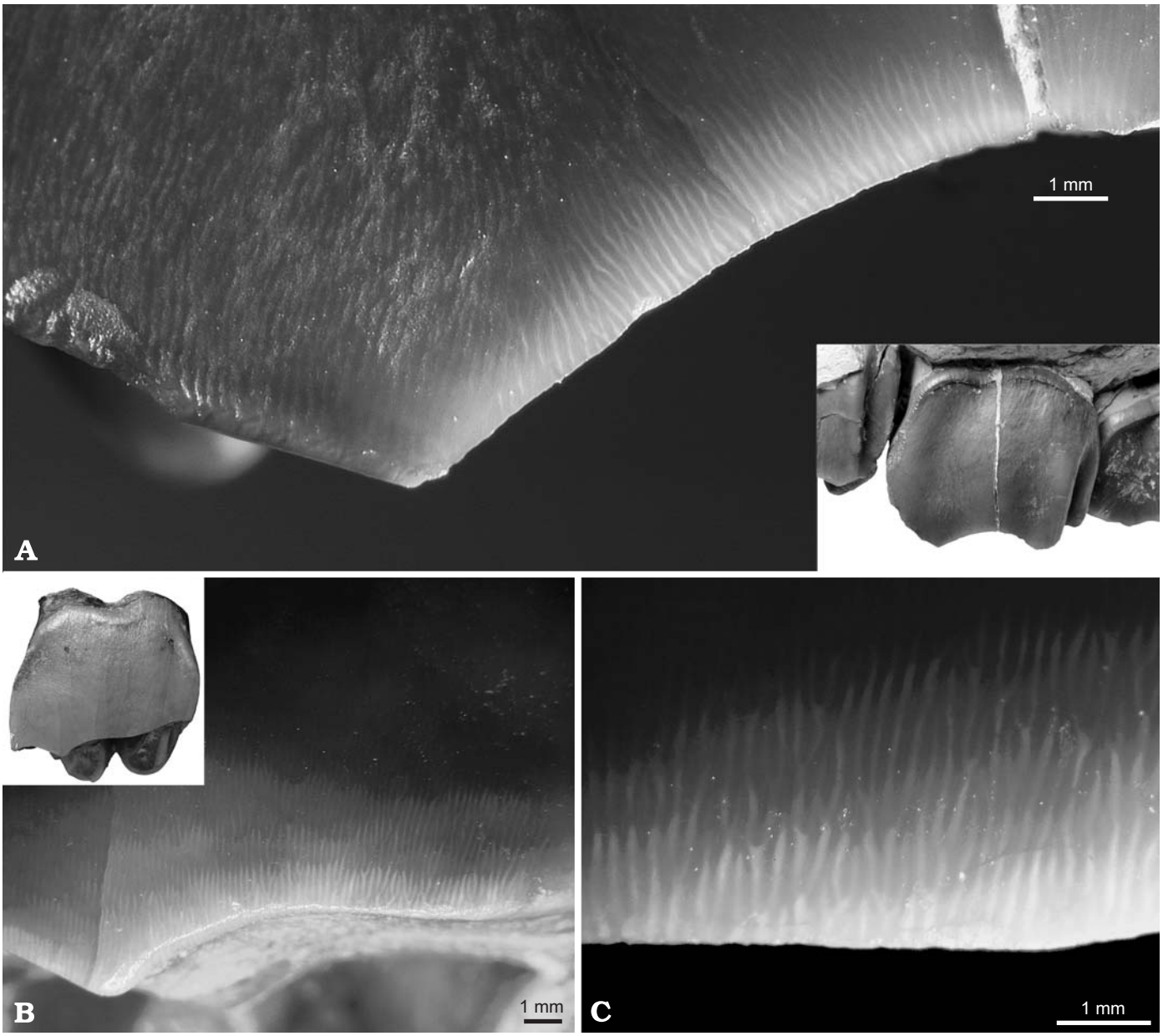


Fig. 9. Vertical HSB configuration in Rhinocerotoidea. **A**. *Hyracodon nebrascensis* (Leidy, 1850) (STIPB M 1772); late Eocene–early Oligocene, White River Group, Toadstool Park area, Nebraska, USA. Vertical HSB in the shearing blade of the ectoloph in the right M1. Note the bifurcations of the HSB. **B**. *Floridaceras whitei* Wood, 1964 (KOE 357); early Miocene, Gilchrist County, Florida, USA. Strictly vertical HSB in the shearing blade of the ectoloph of the upper P3. **C**. Detail of B.

metacone (Fig. 9A). The HSB tend to continue to the outer surface. There vertical ridges are visible which correlate with the HSB. In some areas—especially on the buccal side—these ridges in the outer surface are crossed by transverse perikymata. Special care was taken to examine incisors and canines available from a juvenile mandible; vertical HSB showing the typical bifurcations were found in all tooth positions. The same is true for all tooth positions of the genus *Ardynia* from Mongolia.

In *Eggysodon* from the Oligocene of Germany and Switzerland the molars show vertical HSB, but—in contrast to *Hyracodon*—in the lower incisor only transverse HSB were detected. *Triplopus proficiens* exhibits vertical HSB in the molars; other teeth could not be assessed. Cheek teeth assigned to *Epitriplopus uintensis*, as well as a specimen assigned to *Triplopus* sp. (CM 11955), exhibit the combination of transverse and vertical HSB observed in *Hyrachyus,* described as compound HSB above.

Indricotheriidae.—*Forstercooperia* exhibits vertical HSB on the molars and premolars. An isolated incisor assigned to *Forstercooperia totadentata* (AMNH 20118) appears to have transverse HSB. *Juxia sharamurenense* also has vertical HSB in the cheek teeth, but on incisors certainly vertical HSB occur

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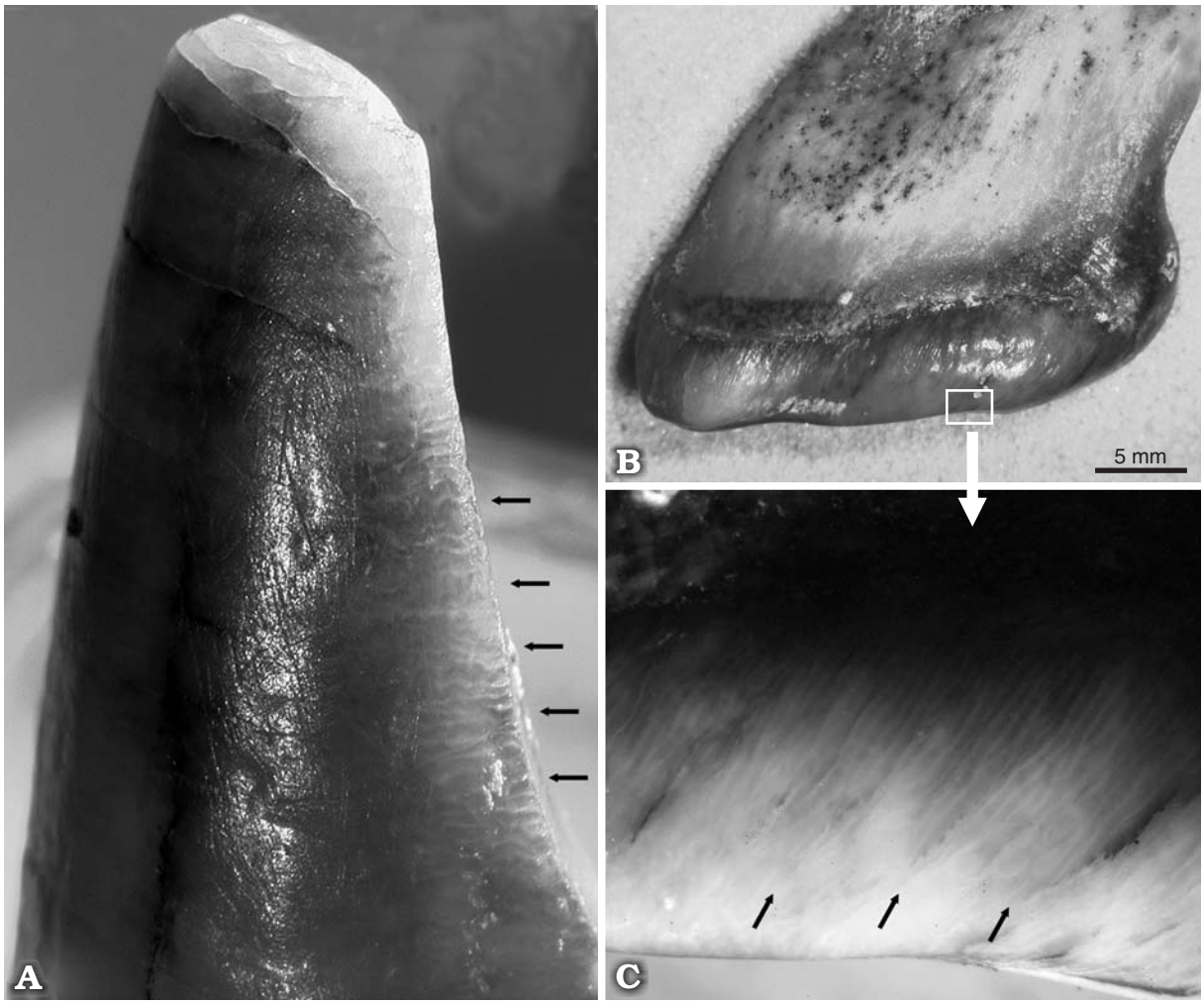


Fig. 10. HSB configuration in the incisors of the rhinocerotid *Menoceras arikarense* (Barbour, 1906) (USNM 412981); early Miocene, Arikaree Formation, Agate, Nebraska, USA. **A**. The lower incisor with an almost vertical shearing blade has transverse HSB. **B**, **C**. In the upper incisor with a shearing blade oblique to the growing axis the HSB are almost vertical.

(AMNH 20286 and AMNH 20287). The HSB configuration of the canines varies between these two specimens. The first one has transverse HSB, whereas the second one appears to have vertical HSB. One other anterior tooth of AMNH 20287, possibly a P1 or p1, also exhibits transverse HSB.

Amynodontidae.—In *Metamynodon* and *Cadurcodon* the massive canines of the mandible show transversely oriented HSB, whereas vertical HSB are evident in the worn tip of an isolated i1 (AMNH 1092). Vertical HSB are found in the enamel of all upper and lower cheek teeth. They form an inner layer of the schmelzmuster, covered by an outer layer of radial enamel. On the occlusal surface of the enamel band the characteristic cross-ridges of the HSB, formed as the vertical HSB intersect the occlusal plane, are evident to the naked eye. Molars of *Amynodon advenum* and *Caenolophus promissus* also exhibit vertical HSB.

In the Asian *Armania asiana*, we found vertical HSB, although the enamel is partially corroded in the available material. The outer enamel surface is characterized by slight vertical ridges, indicating that the vertical HSB extend to the outer enamel surface (and therefore radial enamel is absent). Perikymata observed on the lingual side are oriented transversely, forming a grid pattern with the vertical HSB.

Rhinocerotidae.—Details about the various rhinocerotids studied are summarized in Table 1. All rhinocerotids are characterized by vertical HSB in premolars and molars (Fig. 9B, C; Rensberger and Koenigswald 1980), including very strong cross-ridges in most specimens. The milk dentition of *Rhinoceros unicornis* also showed vertical HSB in the deciduous premolars and transverse HSB in the incisors.

Incisors, however, differ in the HSB configuration and may have transverse, vertical, or compound HSB configuration. Compound HSB were found in *Trigonias* and in *Subhyracodon* lower and upper incisors, especially where the enamel is thin. In thicker parts of the enamel, especially in the enlarged upper incisors, the HSB tend to change from undulating into a zig-zag structure. Since these zig-zag HSB are parallel, the aligned crests and troughs give the appearance of vertical structures, which are different from the strictly vertical HSB in the cheek teeth. In *Menoceras* from Agate

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Table 1. The HSB configuration in molars and incisors of the studied Rhinocerotidae.

Taxon	Age	HSB in cheek teeth	HSB in incisors
Eocene			
Uintaceras radinskyi	Middle Eocene, Myton Pocket, Utah, USA	compound	vertical
Trigonias osborni	Late Eocene, Weld Co. Colorado, USA	vertical	compound
Penetrigonia dakotensis	White River Badlands, USA	vertical	
Oligocene			
Subhyracodon occidentale	lower Oligocene, Toadstool Park area, Nebraska, USA	vertical	compound
Epiaceratherium magnum	Oligocene MP 22, Möhren 13, Germany	vertical	transverse
Ronzotherium filholi	Oligocene, Möhren 7, Germany	vertical	transverse
Miocene			
Menoceras arikarense	Miocene, Agate, Nebraska, USA	vertical	compound
Aceratherium incisivum	upper Miocene MN 11, Eppelsheim, Germany	vertical	compound
Aceratherium tetradactylum	middle Miocene, MN 6 Sansan, France	vertical	compound
Aceratherium cf. *tetradactylum*	middle Miocene MN 5, Münzenberg near Leoben, Austria	vertical	compound
Aceratherium sp.	middle Miocene MN 7, Steinheim im Albuch, Germany	vertical	transverse
Chilotherium sp.	Miocene, Asia (no more data)	vertical	transverse
Floridaceras whitei	lower Miocene, Gilchrist Co. Florida, USA	vertical	
Plesiaceratherium fahlbuschi	middle Miocene MN 5, Sandelzhausen, Germany	vertical	compound
Dihoplus (= *Dicerorhinus*) *schleiermacheri*	Mainz Mombach, Germany	vertical	compound
Lartetotherium sansaniense	middle Miocene MN 5, Sandelzhausen, Germany	vertical	transverse
Brachypotherium brachypus	middle Miocene MN 7, Steinheim im Albuch, Germany	vertical	compound
Prosantorhinus germanicus	middle Miocene MN 5, Sandelzhausen, Germany	vertical	compound
Pliocene			
Teleoceras fossiger, upper and lower dentition	Pliocene, Janna Hills, Kansas, USA	vertical	transverse
Quaternary			
Rhinoceros unicornis	Recent	vertical	transverse
Dicerorhinus kirchbergensis, maxilla	Upper Pleistocene, Burgtonna, Germany	vertical	
Coelodonta antiquitatis, tooth fragments	Upper Pleistocene, Urspringhöhle, Germany	vertical	no incisors
Elasmotherium sibiricum, molar fragment	Pleistocene, Russia	vertical	

Springs in Nebraska, both upper and lower incisors exhibit differentiation in the compound HSB configuration. In I1, the vertical component is dominant, whereas in the i2 the transverse component is strongest (Fig. 10).

Uintaceras radinskyi differs from other rhinocerotids in its schmelzmuster. The molars of the type specimen, CM 12004, display clear vertical HSB, but the upper molars also clearly exhibit an inner enamel layer that displays transverse HSB, and thus exhibit compound HSB configuration. The lower molars are not clear with regard to any horizontal HSB. The anterior teeth are isolated and their exact loci are not clear, but some that appear to be upper incisors clearly

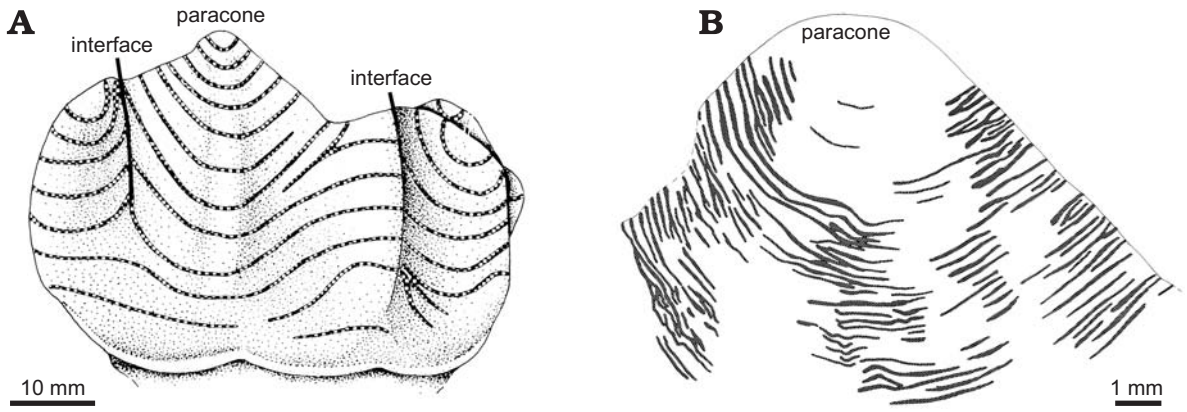


Fig. 11 Curved HSB configuration in *Moropus elatus*. **A**. Buccal aspect of M2. **B**. detailed mapping of visible HSB in the paracone (modified from Koenigswald 1994).

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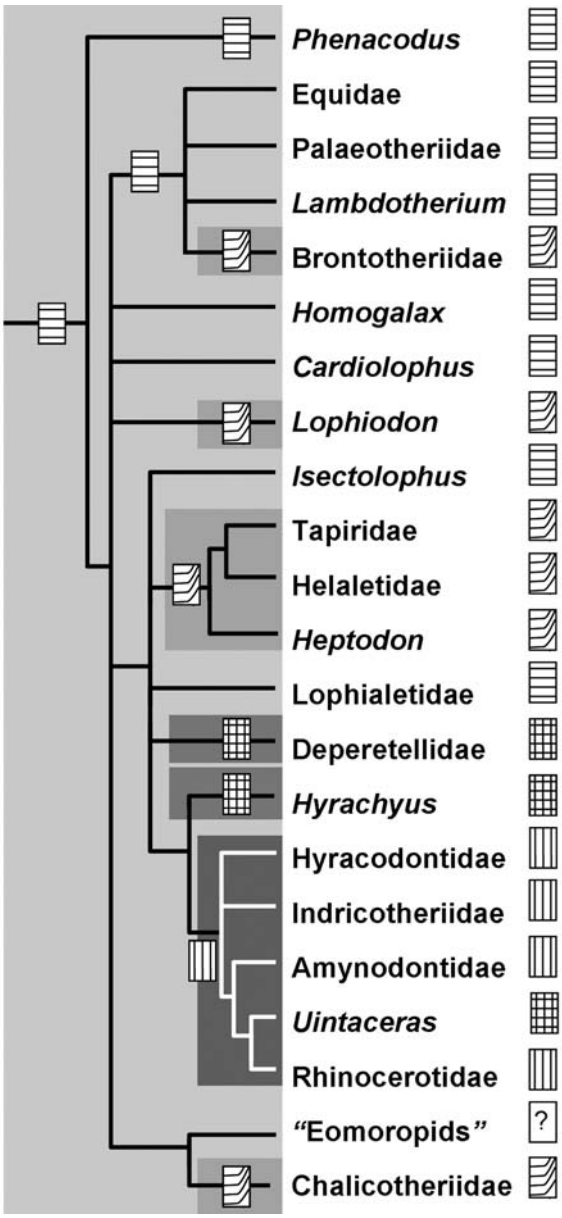


Fig. 12. Cladogram summarizing relationships among major lineages of Perissodactyla and the evolution of various HSB configurations. Boxes on the right indicate HSB configurations in various perissodactyl taxa. Boxes on the tree itself indicate changes in HSB configuration, as inferred from the distribution of HSB configurations given this phylogeny. The phylogeny is a conservative estimate of perissodactyl relationships drawn from Hooker (1989, 1994), Froehlich (1999), and Holbrook (1999, 2009).

have vertical HSB. The other conical teeth that might represent the canines and lower incisors are either inconclusive or show some evidence of horizontal HSB.

Eomoropidae.—In *Eomoropus* and *Litolophus*, there is evidence of transverse HSB, but in no specimen could the HSB be followed into the lophs to ascertain whether it is curved. The m3 of the holotype of *Eomoropus amarorum* has what could be interpreted as a groove representing the interface between two U-shaped fields of HSB, but even this is questionable.

Chalicotheriidae.—The curved configuration of HSB in the molars of *Moropus elatus* from Agate Springs (Fig. 11) was described in detail by Koenigswald (1994) and was confirmed by the investigation of additional material of *Chalicotherium*, *Ancylotherium pentelicum*, *Nestoritherium sinense*, and *Metaschizotherium* from Europe. The thick protocone has transverse HSB, whereas in the ectoloph the HSB are strongly curved on either side of the paracone. In the upper molars, one interface on the ectoloph occurs on the preparacrista close to the parastyle, and another occurs distal to the mesostyle. In the lower molars, two interfaces are very close, on either side of the twinned metaconid. In addition, there are interfaces in the middle of the protolophid and hypolophid, as mentioned by Koenigswald (1994). He used the term "U-shaped HSB" for this extreme form of curved HSB. In contrast to the premolars and molars, the incisors show only transverse HSB. Fortelius (1985) listed chalicotheres as having "horizontal (concave)" HSB, which in this case is a synonym of our curved configuration.

Lambdotheriidae.—*Lambdotherium*, from the late early Eocene (biozone Wa-7) of Wyoming, has clearly transverse HSB in various upper and lower molars and premolars. In some upper molars, however, a slight curvature of the HSB was observed. Thus these bands intersect the occlusal facet at a high angle. No interface as in the more derived brontotheriids could be detected. No information on incisors was available, but the canines have transverse HSB.

Brontotheriidae.—The lower molars of *Eotitanops* show transverse HSB on the lingual side. The HSB on protoconid and hypoconid are transverse but curve upwards in the lophids, forming the typical curved HSB configuration. In upper premolars and molars of *Palaeosyops* transverse HSB were seen on the lingual side. The buccal side of the upper molars is formed by two cones with an angled cutting edge. Here the HSB are clearly curved with a distinct interface. Fortelius (1985) listed brontotheres as having "horizontal (concave)" HSB.

The large brontothere *Megacerops* from the upper Eocene, including several genera synonymized by Mihlbachler (2008), has curved HSB in upper and lower molars with distinct interfaces. The canines and incisors both show transverse HSB.

Discussion

Perissodactyl phylogeny in the light of HSB configuration

In addition to documenting the HSB configuration in fossil and Recent Perissodactyla, a major goal of this paper is to trace the evolution of HSB configuration in this order of mammals (Fig. 12). Because this goal is obviously dependent on our understanding of perissodactyl phylogeny, a brief review is given here. Schoch (1989) provided a more de-

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Table 2. Generalized HSB configuration in cheek teeth, canines and incisors of the various perissodactyl families.

	premolars and molars	incisors	canines
CONDYLARTHRA			
Phenacodontidae	transverse	transverse	transverse
PERISSODACTYLA			
EQUOIDEA			
Equidae	transverse	transverse	transverse
Palaeotheriidae	transverse	transverse	transverse
TAPIROMORPHA			
Isectolophidae	transverse	transverse	transverse
CERATOMORPHA			
TAPIROIDEA			
Helaletidae	curved	transverse	transverse
Lophialetidae and other endemic Asian "tapiroids"	transverse	transverse	
Tapiridae	curved	transverse	transverse
Lophiodontidae	curved	transverse	transverse
RHINOCEROTOIDEA			
Hyrachyidae	compound	compound	compound
Deperetellidae	compound		
Hyracodontidae	vertical	compound	compound
Indricotheriidae	vertical	transverse	compound?
Amynodontidae	vertical	? compound	transverse
Rhinocerotidae	vertical	compound and transverse	
ANCYLOPODA			
Eomoropidae	transverse/ curved		
Chalicotheriidae	curved	transverse	transverse
TITANOTHERIOMORPHA			
Lambdotheriidae	transverse		transverse
Brontotheriidae	curved	transverse	transverse

tailed review of the history of perissodactyl systematics prior to 1989, and we refer the reader to that paper and to Hooker (2005) for more information.

Wood (1934) divided perissodactyls into two suborders: Ceratomorpha, including "tapiroids" (sensu lato) and rhinocerotoids; and Hippomorpha, including equoids, chalicotherioids, and brontotherioids. While the general concept of a close relationship between the tapir and rhinoceros clades relative to the horse clade has been generally accepted (and even corroborated by molecular studies; Norman and Ashley 2000), the relationships among the so-called "hippomorph" taxa, as well as the relationships of certain putative fossil members of Ceratomorpha, are unclear or controversial.

Hooker (1989, 1994) published the first computer-generated cladistic analyses of early perissodactyl interrelationships, based primarily on Eurasian taxa and dental characters. Hooker concluded that (i) what was then called *Hyracotherium* actually represents multiple genera, and that the holotype of the type species, *Hyracotherium leporinum*, is actually a palaeotheriid, (ii) lophiodontids, historically classified as "tapiroids" sensu lato, are closely related to chalicotherioids, and are grouped together with them in the clade Ancylopoda (Hooker 1984), and (iii) Hooker's Ancylopoda formed a clade with an emended Ceratomorpha and Isectolophidae, which he called Tapiromorpha. Froehlich (1999) came to similar conclusions in a study that focused on North American taxa, but Holbrook (1999, 2001) was not able to recover Hooker's concept of Tapiromorpha from data emphasizing characters from the cranial and postcranial skeleton. Hooker (Hooker and Dashzeveg 2003, 2004; Hooker 2005) subsequently modified his view of Ancylopoda, retaining the lophiodontid-chalicotherioid relationship, but allying this group with a ceratomorph-equoid clade he called Euperissodactyla; Euperissodactyla and Ancylopoda form a larger clade, Lophodontomorpha, to the exclusion of Brontotherioidea.

Within specific groups of perissodactyls, there are other phylogenetic issues relevant to this study. *Lambdotherium*, known from the early Eocene of North America, has historically been interpreted as the earliest brontotherioid, but some studies have challenged this and suggested that this taxon is more closely allied with palaeotheriids (Mader 1989; Lucas and Holbrook 2004).

Tapiroidea is a term that was historically applied to all non-rhinocerotoid ceratomorphs (Radinsky 1963), but more recently this taxon has been restricted to a more exclusive monophyletic group including tapirids and helaletids (Colbert and Schoch 1998; Holbrook 1999, 2001). As a result, "isectolophids," including the Wasatchian *Homogalax* and *Cardiolophus* as well as the Bridgerian *Isectolophus*, have been removed from the Tapiroidea and probably do not represent a monophyletic family (Holbrook 1999, 2001). In addition, the relationships of a variety of endemic Asian "tapiroids"—specifically lophialetids and deperetellids—to other perissodactyls are no longer clear (Holbrook 1999).

Within Rhinocerotoidea, the main phylogenetic issues concern the relationships among various taxa assigned to the Hyracodontidae. Radinsky (1966) broadened Hyracodontidae to include any rhinocerotoids that could not be assigned to Rhinocerotidae or Amynodontidae. These included small, cursorial forms like *Hyracodon* from North America and *Eggysodon* from Eurasia, as well as the large to gigantic indricotheres of Asia. Though Hyracodontidae was clearly a wastebasket taxon, others adopted Radinsky's (1966) composition of the family when attempting to establish it as monophyletic (Prothero et al. 1986, 1989). Some recent studies have cast doubt on the monophyly of this concept of Hyracodontidae, especially with regards to the inclusion of indricotheres (Holbrook 1999, 2001). Thus, we here treat indricotheres as a separate family (Indricotheriidae) and consider North American hyracodontines and Eurasian eggysodontines separately.

Given the current state of knowledge of perissodactyl phylogeny, and considering the distribution of HSB configuration observed in this study, several of the unresolved phylogenetic issues impact our ability to trace the evolution of HSB config-

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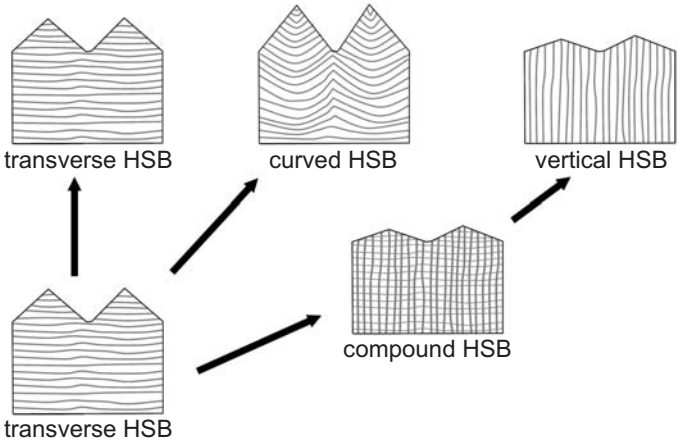


Fig. 13. Schematic hypothesis of the evolutionary interrelationship of the four configurations of Hunter-Schreger Bands (HSB) found in Perissodactyla. From the basal transverse HSB configuration evolved the curved HSB configuration on the one hand. On the other hand the compound HSB configuration evolved and gave rise to the vertical HSB configuration in Rhinocerotidae.

uration. In particular, the phylogenetic positions of lophiodontids, chalicotherioids, and brontotherioids are important for interpreting HSB evolution. Even with these limitations, we can still make some inferences regarding HSB evolution, and we summarize these below (Fig. 13).

The ancestral HSB configuration.—Phenacodontids exhibit the tranverse HSB configuration, which is consistent with the notion that this configuration is the ancestral condition for perissodactyls. Equids and palaeotheriids consistently exhibit the transverse configuration throughout their history, effectively retaining the ancestral condition from bunolophodont forms in the early Eocene through hypsodont forms right up to Recent times (Pfretzschner 1993). Other taxa that appear to have retained the ancestral condition include *Lambdotherium*, *Homogalax*, *Cardiolophus*, lophialetids, *Rhodopagus*, and *Pataecops*. Unfortunately, the retention of the ancestral condition does not clarify the relationships of these taxa to other perissodactyls.

The evolution of curved HSB.—Curved HSB generally occur together with transverse HSB and thus presumably originated from transverse HSB. They are evident in chalicotheriids, brontotheriids, lophiodontids, and tapiroids sensu stricto (i.e., helaletids and tapirids) (Figs. 13, 14). The nature and extent of the curving differs among these groups, though this is at least partly due to the differences in the development of specific lophs. Chalicotheriids and brontotheriids, for instance, have very strong ectolophs and weaker cross lophs, whereas the opposite is true for tapiroids. Lophiodontids have strong cross lophs and fairly strong ectolophs. Thus, it is much easier to detect curved HSB in the ectolophs of chalicotheriids and brontotheriids than in the cross lophs, and vice versa for tapiroids. Consequently, it is difficult to ascertain whether observed differences in HSB are due to distinct HSB patterns or to molar morphology. In any case, it seems certain that curved HSB arose independently from the transverse HSB configuration at least twice, since no recent phylogenies place all of these taxa together. However, on the basis of these observations, we cannot rule out either of the two proposed affinities of lophiodontids (either with tapiroids, or with chalicotheres). The number of times that the curved HSB arose could be more easily determined if we could determine (i) the HSB configuration of eomoropids and (ii) the position of some putative basal members of these lineages, such as *Lambdotherium*, *Homogalax*, and *Cardiolophus*.

The compound HSB configuration and the origin of vertical HSB.—Arguably the most interesting issue arising from these data is the evolution of HSB configurations. In rhinocerotoids we see a close linkage between the compound HSB configuration (transverse HSB in the inner zone and vertical HSB in the outer zone) and the vertical HSB configuration. These configurations are similar in that they are not restricted to specific functional areas of the dentition. The evolution of the more derived vertical configuration probably occurred by reducing the inner layer of transverse HSB (Fig. 13). The previous interpretation (Rensberger and Koenigswald 1980)—that vertical HSB derived from a tapir-like configuration—must be rejected.

Vertical HSB have long appeared to be a distinctive feature of rhinocerotoids and a synapomorphy uniting all members of the superfamily, from the basalmost *Hyrachyus* to modern forms. The observation of vertical HSB in deperetellids (Fortelius 1985; Holbrook 2007) suggested that these unusual endemic Asian "tapiroids" might actually be rhinocerotoids as well. Recognition of the compound HSB configuration, however, calls into question any simple interpretation. The compound HSB configuration is found in *Hyrachyus*, *Uintaceras*, and deperetellids.

Holbrook and Lucas (1997) described *Uintaceras radinskyi* from the Uintan of North America as the sister-group to Rhinocerotidae, and later analyses considered it to be the basalmost member of the family (Holbrook 1999, 2001; Prothero 2005). The presence of compound HSB in *Uintaceras* is interesting because, if *Uintaceras* is a basal rhinocerotid, it suggests that one of the following is true: (i) The vertical HSB configuration evolved from the compound condition independently in rhinocerotids and in the other main families of rhinocerotoids (Hyracodontidae, Amynodontidae, and Indricotheriidae) or (ii) the vertical HSB configuration characterizes all of these families, and a reversal to the compound configuration occurred in the lineage leading to *Uintaceras* (Figs. 12, 14).

The presence of the compound HSB configuration in deperetellids may very well be evidence of a unique relationship with rhinocerotoids. Considering that deperetellids share very few other characters with rhinocerotoids and are otherwise quite derived dentally, this may indicate that deperetellids are a derived offshoot of the lineage that led to conventional Rhinocerotoidea. It would also indicate an Asian origin for the superfamily.

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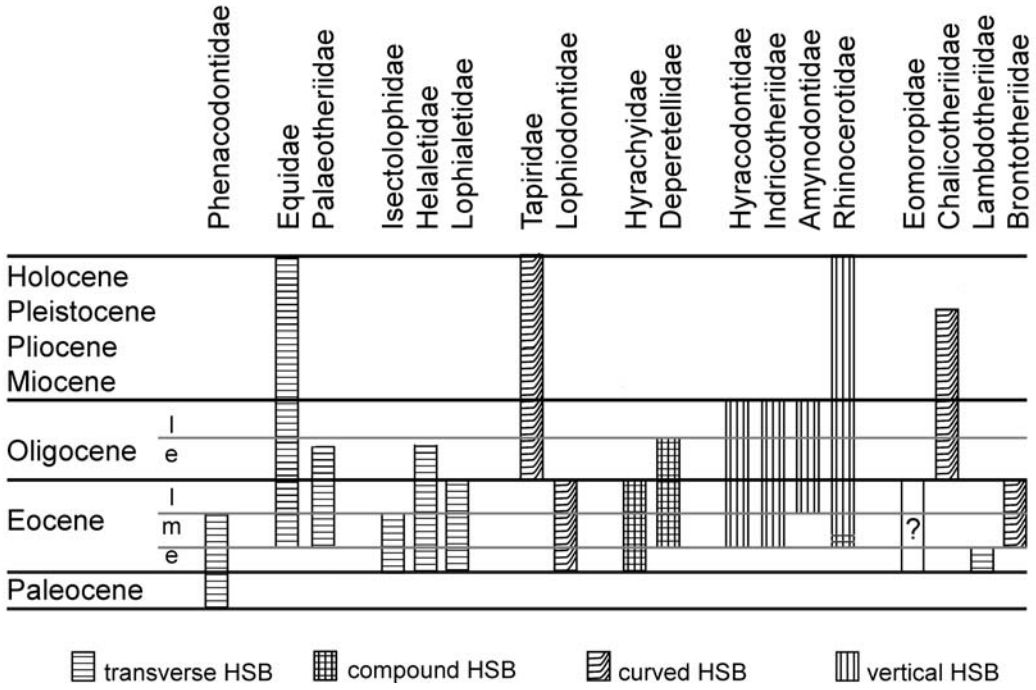


Fig. 14. Schematic diagram of the stratigraphic occurrence of the four configurations of Hunter-Schreger Bands (HSB) found in the various perissodactyl families. The range data of the families are taken from McKenna and Bell (1997). All four types occurred during the Paleogene in several families. The compound HSB configuration did not reach the Neogene. The three other types are represented by one family each in the extant fauna: the transverse HSB configuration in Equidae, the curved HSB configuration in Tapiridae, and the vertical HSB configuration in Rhinocerotidae.

In contrast to the vertical HSB in rhinocerotoid cheek teeth, some genera with enlarged incisors modified the compound HSB configuration in a very different way. Functional reasons, as described below, led to the reduction of the vertical HSB in the outer layer and gave preference to the transverse HSB of the inner layer.

Functional interpretation of HSB configurations found in Perissodactyla

HSB are an optical phenomenon, but they reflect the arrangement of enamel prisms, which is important for the biomechanical properties of the enamel. Although prisms change direction on their way from the EDJ to the OES, thus passing through various HSB, the sections of the prisms within a band share the same direction. The functional interpretation offered here is not based on the course of individual prisms but rather on the major structural units, represented by the HSB, in which the prisms are oriented parallel to each other.

Cracking and abrasion reduce the functionality of the enamel. HSB are recognized as an effective crack-stopping mechanism in enamel. The decussating prisms cause an initial crack to radiate, reducing its strength, and thus stopping the progression (Fortelius 1985; Pfretzschner 1988). HSB occur in most placental mammals in which the adult body size exceeds 1–2 kg (Koenigswald et al. 1987). Among insectivores only the largest erinaceids have this structure, and in primates early and small forms lack HSB. This restriction of HSB to larger mammals, together with the distribution in the fossil record, indicates that HSB evolved in various placental lineages independently. But there is no strict relationship between body size and the occurrence of HSB (Maas and Thewissen 1995). For example, rodents are a prominent exception; they have HSB in their incisors regularly. Very few large placental mammals lack HSB. In perissodactyls HSB are regularly present, although they may be developed only weakly in the small *Hyracotherium*.

Abrasion is affected by the prism direction. Several indications and preliminary measurements indicate that enamel is more resistant to abrasion when prisms intersect the occlusal surface at an almost right angle. Prisms with their long axis more or less parallel to the occlusal surface are abraded more easily (Osborn 1965; Rensberger and Koenigswald 1980; Boyde 1984).

An impressive example, illustrating this correlation, is provided by the euhypsodont molars of the rodent *Pedetes*. In the occlusal surface the cross-section of the enamel band is exposed around the dentine core. In the inner layer formed by radial enamel, the steeply rising prisms intersect the occlusal surface almost at a right angle. The outer layer is formed by transverse HSB and here the prisms are oriented almost parallel to the occlusal surface. In most naturally worn teeth the inner layer is distinctly higher and less abraded than the outer layer (Koenigswald and Clemens 1992).

The transverse configuration.—Of the various HSB configurations, transverse HSB is the most common one and occurs in most placental lineages. Even in wombats, the only extant marsupial with HSB, they are transversely oriented (Koenigswald 2000).

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The transverse orientation reflects a basic functional requirement as a crack-stopping mechanism in teeth covered with an enamel cap and loaded from the occlusal surface during mastication (Pfretzschner 1988; Koenigswald and Pfretzschner 1991). The vertical load causes tensile stresses in a horizontal plane and thus the transverse HSB with their layers of decussating prisms have the optimal orientation to withstand the tension. Although this biomechanical model is somewhat simplistic, it serves well to explain some observations. Muroid molars are characterized by a basal ring of lamellar enamel (very thin HSB) at the base of the crown, while the enamel in the upper part of the crown does not show this differentiation. The ring of HSB occurs exactly where the intensity of the transverse stresses is at a maximum according to this simple model, since the stresses increase towards the base of the crown (Pfretzschner 1988; Koenigswald 2004).

This initial model for teeth covered with an enamel cap must be modified when the dentine core is exposed due to abrasion, as in hypsodont teeth. Then the surrounding enamel band is loaded from the cross-section. Besides compensating for tension stresses, resistance to abrasion gains increasing significance in order to maintain the functional properties. In transverse HSB most prisms are often more or less parallel to the occlusal surface and thus less resistant to abrasion. Abrasion can be reduced by the modification of the prism direction Thus only the reorientation of the HSB may combine the benefit of the crack-stopping mechanism related to decussating prisms and a steep angle of the prisms when they penetrate the occlusal surface.

Transverse HSB are widely distributed among early perissodactyls. Most perissodactyl clades, however, tend to modify the orientation of the HSB. Equoids are the only group within the Perissodactyla that retains the transverse prism orientation into the Neogene. Their phylogenetic success may be related to the development of hypsodont teeth and specific modification of the radial enamel within the enamel (Pretzschner 1994).

Curved HSB configuration.—We recognized curved HSB in tapirs, lophiodontids, chalicotheres, and brontotheres. The curved HSB are conspicuously developed in the main functional shearing blades. These are the transverse lophs of tapirs and lophiodontids and the ectolophs in chalicotheres and brontotheres. In the latter the curved HSB evolved to the U-shaped pattern (Koenigswald 1994). The functional significance of these curved HSB is probably to bring as many prisms as possible in a steep angle to the shearing blade, reducing abrasion. Consequently the lophs can function for a longer time.

Compound HSB configuration.—The compound HSB configuration is composed of an inner layer with transverse HSB and an outer layer of vertical HSB. This compound HSB is dominant in the cheek teeth of early Hyrachyidae, Deperetellidae, and *Uintaceras*. It occurs in all sides of the teeth and seems not to be related to the tooth morphology as with the curved HSB configuration. The compound HSB evolved from transverse HSB. The functional advantage of the two layers with a different orientation of the HSB is twofold: first, it forms an additional protection against cracks, and second, prisms of either the inner or the outer layer are oriented nearly perpendicular to horizontal or strongly inclined shearing blades, thus reducing abrasion.

The advantage of prisms oriented almost perpendicular to shearing blades can be tested in the rhinocerotid incisors (Fig.10). In *Trigonias* and *Subhyracodon* both layers of the compound HSB are present, whereas the derived rhinos with large incisors show some differentiation. In *Menodus*, *Aceratherium, Chilotherium*, and many other genera, the enlarged lower incisors are covered by enamel on the mesial side while the dentine is exposed on the posterior side. The enamel forms a sharp edge beside the exposed dentine on both sides. The shearing blades formed by the cross-section of the enamel band are almost parallel to the growing axis. The transverse HSB are dominant and only a few "vertical structures" suggest the outer layer of the compound HSB configuration. Due to the dominance of transverse HSB, most of the prisms are oriented perpendicular to the shearing blade.

The upper incisors are shaped very differently. The teeth are short and the shearing blade is oriented at an oblique angle or perpendicular to the growing axis. Both layers of the compound HSB configuration are present in several areas of the tooth. In the shearing blade the vertical HSB dominate, thus most of the prisms form a large angle with the shearing blade.

The contrasting differentiation of the compound HSB configuration in rhinocerotid upper and lower incisors seems to be related to the advantage of having prisms (and HSB) perpendicular to the actual shearing blade in order to reduce abrasion. The compound HSB configuration offers an adequate layer of prisms in the inner or the outer layer. The layer which is less advantageous tends to be the one reduced.

The compound HSB configuration occurs sporadically in various perissodactyls. Traces of this type were found in a canine of *Hyracotherium* and as a minor component of the schmelzmuster in *Lophiodon rhinocerodes*, especially where the enamel was thick.

Comparable compound HSB configurations are also known in some carnivores (Stefen 1995, 1997a, b, 1999). Especially in the robust, cone-shaped premolars of hyaenids the transverse HSB undulate only slightly at the EDJ. The amplitudes increase with the distance from the EDJ and form a "zig-zag HSB." With increasing amplitudes the vertical sets of prisms gain significance, eventually forming vertical HSB. This structure obviously is suited to cope with high pressure during bone-cracking, but comparable structures have also been observed in some other mammals that were clearly herbivorous, such as the Eocene pantodont *Coryphodon* (Koenigswald and Rose 2005).

Vertical HSB configuration.—The vertical HSB configuration is characteristic for cheek teeth of the Rhinocerotidae (Ta-

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ble 1). The shearing blades of these teeth are mostly parallel to the occlusal plane. Due to the vertical arrangement of the HSB a great number of prisms intersect the occlusal surface at high angles. Therefore the prisms are oriented very suitably for reducing abrasion. The small differences in the angle of the prisms of adjacent bands are often accentuated by differential wear. They form the characteristic cross-ridges in the cross-section of the enamel band (Quenstedt 1852; Rensberger and Koenigswald 1980). Fortelius (1985) is correct in stressing the point that a decussation of the prisms between the bands in the HSB structure would not be necessary to increase wear resistance. Certainly radial enamel would have been appropriate as well, but the HSB was an inherited structure. The bend of the HSB brought prisms into a much more effective direction than prisms in transverse HSB. Whether this functional property, however, caused the reorientation of the HSB remains an open question.

Vertical HSB do not occur exclusively in Rhinocerotidae but are also found in a few other non-related mammalian taxa, e.g., in *Astrapotherium*, *Carodnia*, and *Pyrotherium* (Fortelius 1984, 1985; Lindenau 2005; Line and Bergqvist 2005; Rensberger and Pfretzschner 1992). The functional advantage of vertical HSB is probably the same as in rhinocerotoid cheek teeth, reducing the abrasion by an optimum prism orientation perpendicular to the occlusal surface. Vertical HSB were detected also in the incisors of some rodents (Bruijn and Koenigswald 1994; Kalthoff 2000; Koenigswald 1993).

Conclusion

Early in their evolution, perissodactyls modified the orientation of the transverse HSB inherited from phenacodontids. The four types of HSB configuration were fully developed during the Eocene, but several of the perissodactyl families vanished at the end of the Eocene or during the Oligocene. In the extant fauna the transverse HSB configuration is retained in Equoidea, the curved HSB configuration is preserved only in *Tapirus*, and the vertical HSB configuration characterizes the Rhinocerotidae. The compound HSB configuration is not present in any living perissodactyls (Fig. 14).

Of the various HSB configurations found in Perissodactyla the transverse HSB are the least derived form. These transverse HSB are retained in equoids, palaeotheriids, and isectolophids. Most other perissodactyl lineages modified this basal pattern. From the transverse HSB configuration the curved HSB configuration arose in helaletids, tapirs, lophiodontids, chalicotheres, and brontotheres. It is characterized by curved fields of HSB with distinct interfaces. The fields of curved HSB are closely correlated with tooth morphology. The evolution of the curved HSB configuration may have occurred several times independently.

A second way of reorganising the transverse HSB is found in the compound HSB configuration, where a second layer of vertical HSB is superimposed on an inner layer of transverse HSB. These vertical HSB characteristically occur on all sides of the teeth and are not related to the tooth morphology. We found this HSB configuration in hyrachyids, deperetellids, and *Uintaceras*. We infer that the vertical HSB configuration typical for the cheek teeth of hyracodontids, amynodontids, rhinocerotids, and indricotheriids evolved from the compound HSB configuration.

The analysis of the HSB configuration provides new evidence for the phylogenetic position of some genera and higher taxa of perissodactyls, but it also leaves some of these questions still very much unanswered. Lophiodontids show similarities in HSB to both tapiroids and chalicotheres, though all three groups are distinct from rhinocerotoids and equoids. The presence of compound HSB in deperetellids is very suggestive of a close relationship between this family and rhinocerotoids, since the compound and vertical HSB configurations are likely closely related.

This study also raises a number of new phylogenetic questions. Are the various instances of curved HSB homologous, and, if so, does this indicate a close relationship between brontotheres, chalicotheres, lophiodontids, and tapiroids? Since rhinocerotoids are thought to be closely related to tapiroids, how are the evolution of curved HSB on the one hand and compound and vertical HSB on the other related? Better sampling should provide more insights, especially data on Eocene chalicotherioids and endemic Asian "tapiroids".

The adaptative value of the reorganization of the HSB configuration in perissodactyls is interpreted functionally as an efficient reduction of the abrasion during mastication, assuming that prisms intersecting the actual grinding surfaces almost perpendicularly resist wear better than prisms parallel to the occlusal surface. It should be mentioned that the enamel microstructure is formed in the crypt, an area free of external stresses. Enamel is not remodelled under stress like the structure of bones. In Perissodactyla various types of HSB configurations were selected for in different clades, but all of them share this specific relationship between the prisms and the occlusal surface. The various HSB configurations are not related to specific diets, but rather to phylogenetic lineages.

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References

Boyde, A. 1965. The structure of developing mammalian dental enamel. *In*: M. Stark and R. Fearnhead (eds.), *Tooth Enamel*, 163–194. Wright, Bristol.

Boyde, A. 1984. Dependence of rate of physical erosion on orientation and density in mineralised tissues. *Anatomy and Embryology* 170: 57–62. [CrossRef]

Boyde, A. and Fortelius, M. 1986. Development, structure and function of rhinoceros enamel. *Zoological Journal of the Linnean Society* 87: 181–214. [CrossRef]

Boyde, A. and Martin, L. 1984. The microstructure of primate dental enamel. *In*: D. Chivers, B. Wood, and A. Bilsborough (eds.), *Food Acquisition and Processing in Primates*, 341–367. Plenum Publishing, New York.

Bruijn, H. de and Koenigswald, W. von 1994. Early Miocene rodent faunas from the eastern Mediterranean area. Part V. The genus *Enginia* (Muroidea) with a discussion of the structure of the incisor enamel. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen* 97: 381–405.

Colbert, M. 2005. The facial skeleton of the early Oligocene *Colodon* (Perissodactyla, Tapiroidea). *Palaeontologia Electronica* 8 (12A): 1–27.

Colbert, M. and Schoch, R. 1998. Tapiroidea and other moropomorphs. *In*: C. Janis, K. Scott, and L. Jacobs (eds.), *Evolution of Tertiary Mammals of North America, Vol. 1: Terrestrial Carnivores, Ungulates, and Ungulate-like Mammals*, 569–582. Cambridge University Press, Cambridge.

Dashzeveg, D. and Hooker, J. 1997. New ceratomorph perissodactyls (Mammalia) from the middle and late Eocene of Mongolia: their implications for phylogeny and dating. *Zoological Journal of the Linnean Society* 120: 105–138. [CrossRef]

Ferretti, M. 2008. Enamel structure of *Cuvieronius hyodon* (Proboscidea, Gomphotheriidae) with discussion on enamel evolution in elephantoids. *Journal of Mammalian Evolution* 15: 37–58. [CrossRef]

Fortelius, M. 1984. Vertical decussation of enamel, prisms in lophodont ungulates. *In*: R. Fearnhead and S. Suga (eds.), *Tooth Enamel IV*, 427–431. Elsevier, Amsterdam.

Fortelius, M. 1985. Ungulate cheek teeth: developmental, functional and evolutionary interrelations. *Acta Zoologica Fennica* 180: 1–76.

Froehlich, D. 1999. Phylogenetic systematics of basal perissodactyls. *Journal of Vertebrate Paleontology* 19: 140–159.

Holbrook, L. 1999. The phylogeny and classification of tapiromorph perissodactyls (Mammalia). *Cladistics* 15: 331–351. [CrossRef]

Holbrook, L. 2001. Comparative osteology of early Tertiary tapiromorphs (Mammalia, Perissodactyla*). Zoological Journal of the Linnean Society* 132: 1–54. [CrossRef]

Holbrook, L. 2007. Rhinocerotoid affinities of Deperetellidae (Mammalia, Perissodactyla) based on enamel microstructure. *Journal of Vertebrate Paleontology* 27: 90A.

Holbrook, L. 2009. Osteology of *Lophiodon* Cuvier, 1822 (Mammalia, Perissodactyla) and its phylogenetic implications. *Journal of Vertebrate Paleontology* 29: 212–230. [CrossRef]

Holbrook, L. and Lucas, S. 1997. A new genus of rhinocerotoid from the Eocene of Utah and the status of North American "*Forstercooperia*". *Journal of Vertebrate Paleontology* 17: 384–396.

Hooker, J. 1984. A primitive ceratomorph (Perissodactyla, Mammalia) from the early Tertiary of Europe. *Zoological Journal of the Linnean Society* 82: 229–244. [CrossRef]

Hooker, J. 1989. Character polarities in early perissodactyls and their significance for *Hyracotherium* and infraordinal relationships. *In*: D. Prothero and R. Schoch (eds.), *The Evolution of Perissodactyls*, 79–101. Oxford University Press, New York.

Hooker, J. 1994. The beginning of the equoid radiation. *Zoological Journal of the Linnean Society* 112: 29–63. [CrossRef]

Hooker, J. 2005. Perisssodactyla. *In*: K. Rose and J. Archibald (eds.), *The Rise of Placental Mammals*, 199–214. Johns Hopkins University Press, Baltimore.

Hooker, J. and Dashzeveg, D. 2003. Evidence for direct mammalian faunal interchange between Europe and Asia near the Paleocene–Eocene boundary. *Geological Society of America Special Paper* 369: 479–500.

Hooker, J.J. and Dashzeveg, D. 2004. The origin of chalicotheres (Perissodactyla, Mammalia). *Palaeontology* 47 (6): 1363–1386. [CrossRef]

Hunter, J. 1778. *The Natural History of Human Teeth: Explaining their Structure, Use, Formation, Growth, and Diseases*. Second edition. 128 pp. Johnson, London.

Kalthoff, D. 2000. Die Schmelzmikrostruktur in den Incisven der hamsterartigen Nagetiere und anderer Myomorpha (Rodentia, Mammalia). *Palaeontographica Abteilung A* 259: 1–193.

Kawai, N. 1955. Comparative anatomy of bands of Schreger. *Okajimas Folia Anatomica Japonica* 27: 115–131.

Koenigswald, W. von 1980. Schmelzstruktur und Morphologie in den Molaren der Arvicolidae (Rodentia). *Abhandlungen Senckenbergische Naturforschende Gesellschaft* 539: 1–129.

Koenigswald, W. von 1993. Die Schmelzmuster in den Schneidezähnen der Gliroidea (Gliridae und Seleviniidae, Rodentia, Mammalia) und ihre systematische Bedeutung. *Zeitschrift für Säugetierkunde* 58: 92–115.

Koenigswald, W. von 1994. U-shaped orientation of Hunter-Schreger Bands in the enamel of *Moropus* (Mammalia: Chalicotheriidae) in comparison to some other Perissodactyla. *Annals of Carnegie Museum* 63: 49–65.

Koenigswald, W. von 1997a. Brief survey of the enamel diversity at the schmelzmuster level in Cenozoic placental mammals. *In*: W. von Koenigswald and P. Sander (eds.), *Tooth Enamel Microstructure*, 137–161. Balkema, Rotterdam.

Koenigswald, W. von 1997b. Evolutionary trends in the differentiation of the mammalian enamel ultrastructure. *In*: W. von Koenigswald and P. Sander (eds.), *Tooth Enamel Microstructure*, 203–235. Balkema, Rotterdam.

Koenigswald, W. von 2000. Two different strategies in enamel differentiation: Marsupialia versus Placentalia. *In*: M. Teaford, M. Smith, and M. Ferguson, (eds.), *Development, Function, and Evolution of Teeth*, 107–118. Cambridge University Press, New York.

Koenigswald, W. von 2002. Besonderheiten der Schmelzoberfläche bei Säugetieren. *Lynx N.S.* 32 (2001): 171–181.

Koenigswald, W. von 2004. The three elementary types of schmelzmuster in rodent molars and their occurrence in the various rodent clades. *Palaeontographica Abteilung A* 270: 95–132.

Koenigswald, W. von and Clemens, W. 1992. Levels of complexity in the microstructure of mammalian enamel and their application in studies of systematics. *Scanning Microscopy* 6: 195–218.

Koenigswald, W. von and Pfretzschner, H. 1987. Hunter-Schreger-Bänder im Zahnschmelz von Säugetieren (Mammalia): Anordnung und Prismenverlauf. *Zoomorphology* 106: 329–338. [CrossRef]

Koenigswald, W. von and Pfretzschner, H. 1991. Biomechanics in the enamel of mammalian teeth. *In*: N. Schmidt-Kittler and K. Vogel (eds.), *Constructional Morphology and Biomechanics*, 113–125. Springer, Berlin.

Koenigswald, W. von and Rose, K. 2005. The enamel microstructure of the early Eocene pantodont *Coryphodon* and the nature of the zigzag-enamel. *Journal of Mammalian Evolution* 12: 419–432. [CrossRef]

Koenigswald, W. von and Sander, P. (eds.) 1997a. *Tooth Enamel Microstructure*. 280pp. Balkema, Rotterdam.

Koenigswald, W. von and Sander, P. 1997b. Glossary. *In*: W. von Koenigswald and P. Sander (eds.), *Tooth Enamel Microstructure*, 267–280. Balkema, Rotterdam.

Koenigswald, W. von, Martin, T., and Pfretzschner, H. 1993. Phylogenetic interpretation of enamel structures in mammalian teeth: possibilities and problems. *In*: F. Szalay, M. Novacek, and M. McKenna (eds.), *Mammal Phylogeny*, 303–314. Springer, New York.

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Koenigswald, W. von, Rensberger, J., and Pfretzschner, H. 1987. Changes in the tooth enamel of early Paleocene mammals allowing increased diet diversity. *Nature* 328: 150–152. [CrossRef]

Korvenkontio, V.A. 1934. Mikroskopische Untersuchungen an Nagerincisiven unter Hinweis auf die Schmelzstruktur der Backenzähne. Histologisch-phyletische Studie. *Annales Zoologici Societatis Zoologicae-Botanicae Fennicae – Vanamo* 2: 1–274, Helsinki.

Lindenau, C. 2005. *Zahnschmelzmikrostrukturen südamerikanischer Huftiere*. 193 pp. Ph.D. thesis University Bonn, Bonn. http://hss.ulb.unibonn.de/2005/0557/0557.htm

Line, S. and Bergqvist, L. 2005. Enamel structure of Paleocene mmammals of the São José de Itaboraí Basin, Brazil. *Journal of Vertebrate Paleontology* 25: 924–928. [CrossRef]

Lucas, S. and Holbrook, L. 2004. The skull of the Eocene perissodactyl *Lambdotherium* and its phylogenetic significance. *New Mexico Museum of Natural History and Science Bulletin* 26: 81–87.

Maas, M. and Thewissen, J. 1995. Enamel microstructure of *Pakicetus* (Mammalia: Archaeoceti). *Journal of Paleontology* 96: 1154–1163.

Mader, B. 1989. The Brontotheriidae: a systematic revision and preliminary phylogeny of North American genera. *In*: D. Prothero and R. Schoch (eds.), *The Evolution of Perissodactyls*, 458–484. Oxford University Press, New York.

McKenna, M.C. and Bell, S.K. 1997. *Classification of Mammals Above the Species Level*. 631 pp. Columbia University Press, New York.

Mihlbachler, M. 2008. Species taxonomy, phylogeny, and biogeography of the Brontotheriidae (Mammalia: Perissodactyla). *Bulletin of the American Museum of Natural History* 311: 1–475. [CrossRef]

Norman, J. and Ashley, M. 2000. Phylogenetics of Perissodactyla and tests of the molecular clock. *Journal of Molecular Evolution* 50: 11–21.

Osborn, C. 1965. The nature of the Hunter-Schreger Bands in enamel. *Archive of Oral Biology* 10: 929–933. [CrossRef]

Pfretzschner, H. 1988. Structural reinforcement and crack propagation in enamel. *Mémoirs Muséum national d'Histoire naturelle* (sér. C) 53: 133–143.

Pfretzschner, H. 1993. Enamel microstructure in the phylogeny of Equidae. *Journal of Vertebrate Paleontology* 13: 342–349.

Pfretzschner, H. 1994. Biomechanik der Schmelzmikrostruktur in den Backenzähnen von Grossäugern. *Palaeontographica Abteilung A* 234: 1–88.

Prothero, D. 2005. *The Evolution of North American Rhinoceroses*. 218 pp. Cambridge University Press, Cambridge.

Prothero, D., Manning, E., and Hanson, C. 1986. The phylogeny of the Rhinocerotoidea (Mammalia, Perissodactyla). *Zoological Journal of the Linnean Society* 87: 341–366. [CrossRef]

Prothero, D., Guerin. C., and Manning, E. 1989. The history of the Rhinocerotoidea. *In*: D. Prothero and R. Schoch (eds.), *The Evolution of Perissodactyls*, 321–340. Oxford University Press, New York.

Quenstedt, F. 1852. *Handbuch der Petrefaktenkunde*. 792 pp. Laupp and Siebeck, Tübingen.

Radinsky, L. 1963. Origin and early evolution of North American Tapiroidea. *Peabody Museum of Natural History, Yale University, Bulletin* 17: 1–106.

Radinsky, L. 1966. The families of the Rhinocerotoidea (Mammalia, Perissodactyla). *Journal of Mammalogy* 47: 631–639. [CrossRef]

Rensberger, J. and Koenigswald, W. von 1980. Functional and phylogenetic interpretation of enamel microstructure in rhinoceroses. *Paleobiology* 6: 477–495.

Rensberger, J. and Pfretzschner, H. 1992. Enamel structure in astrapotheres and its functional implications. *Scanning Microscopy* 6: 495–510.

Rose, K. 2006. *The Beginning of the Age of Mammals*. 428 pp. Johns Hopkins University Press, Baltimore.

Schoch, R. 1989. A brief historical review of perissodactyl classification. *In*: D. Prothero and R. Schoch (eds.), *The Evolution of Perissodactyls*, 13–23. Oxford University Press, New York.

Schreger, D. 1800. Beitrag zur Geschichte der Zähne. *Beiträge zur Zergliederkunst* 1: 1–7.

Shobusawa, M. 1952. Vergleichende Untersuchungen über die Form der Schmelzprismen der Säugetiere. *Okaijamas Folia Anatomica Japonica* 24: 371–392.

Stefen, C. 1995. *Zahnschmelzdifferenzierungen bei Raubtieren. Carnivora, im Vergleich zu Vertretern der Dreodonta, Arctocyonidae, Mesonychidae, Entelodontidae (Placentalia), Thylacoleodontidae Dasyuridae und Thylacinidae (Marsupialia)*. 190 pp. Unpublished Ph.D. thesis, Universität Bonn, Bonn.

Stefen, C. 1997a. The enamel of Creodonta, Arctocyonidae, and Mesonychidae (Mammalia), with special reference to the appearance of Hunter-Schreger Bands. *Paläontologische Zeitschrift* 71: 291–303.

Stefen, C. 1997b. Differentiations in Hunter-Schreger Bands of carnivores. *In*: W. von Koenigswald and P. Sander (eds.), *Tooth Enamel Microstructure*, 123–136. Balkema, Rotterdam.

Stefen, C. 1999. Enamel microstructure of recent and fossil Canidae (Carnivora: Mammalia). *Journal Vertebrate Paleontology* 19: 576–587.

Tabuce, R., Delmer, C., and Gheerbrant, E. 2007. Evolution of the tooth enamel microstructure in the earliest proboscideans (Mammalia). *Zoological Journal of the Linnean Society* 149: 611–628. [CrossRef]

Wood, H. 1934. Revision of the Hyrachyidae. *Bulletin of the American Museum of Natural History* 67: 181–295.

Wood, C., and Stern, D. 1997. The earliest prisms in mammalian and reptilian enamel. *In*: W. von Koenigswald and P. Sander (eds.), *Tooth Enamel Microstructure*, 63–83. Balkema, Rotterdam.

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Appendix 1

Phenacodontidae

Phenacodus vortmani, USGS 26100 (incisors, canines); early Eocene, Willwood Formation, Bighorn Basin, Wyoming.

Phenacodus almiensis, USNM 16691 (maxillae with canines and cheek teeth); late Paleocene (Clarkforkian), La Barge area, western Wyoming.

Phenacodus sp., UM 66761 (dentaries); early Eocene, Willwood Formation, Bighorn Basin, Wyoming.

Phenacodus primaevus, KOE 3668 (fragment of upper molar); early Eocene, Wyoming.

Ectocion parvus, USNM 525599, 525600, 527656 (dentaries); earliest Eocene, Willwood Formation, Bighorn Basin, Wyoming.

Ectocion osbornianus, USNM 494921, 487874, 487875 (dentaries and maxillae); early Eocene, Willwood Formation, Bighorn Basin, Wyoming.

Ectocion sp., KOE 4058 (lower molar); early Eocene, Willwood Formation, Bighorn Basin, Wyoming.

Meniscotherium chamense, USNM 22699, 22712, 22725 (skulls and dentaries); early Eocene, Wasatch Formation, Sublette County, Wyoming.

Meniscotherium robustum, USNM 19508, 19510 (skull and mandibles); early Eocene, Wasatch Formation, Sublette County, Wyoming

Equidae

Hyracotherium sandrae, USNM 511099, 527653, 533617, (dentaries and maxilla), earliest Eocene, Willwood Formation, Bighorn Basin, Wyoming.

Hyracotherium vasacciense, USNM 336136, 336137 (dentary and rostrum); early Eocene, Wasatch Formation, Huerfano, Colorado.

Hyracotherium sp., KOE 1022, 3669, 3670 (various upper and lower molars); early Eocene, Willwood Fm, Wyoming.

Xenicohippus grangeri, holotype: USNM 531628 (= USGS 292) (mandible with premolars); early Eocene, Willwood Formation, Wyoming.

Mesohippus bairdii, SDSM V 9626 (cranium and mandible); early Oligocene (Orellan), Brule Formation, White River Badlands, South Dakota.

Mesohippus sp., STIPB 6522 (jaws and isolated teeth); late Eocene–early Oligocene, Toadstool Park area, Nebraska.

Anchitherium aurelianense, STIPB M 3301 (lower molar), Middle Miocene, Petersbuch, Germany.

Anchitherium aurelianense, BSPG, not catalogued, (upper molar); Middle Miocene, Sandelzhausen, Germany.

Equus caballus, KOE 38, 3365 (various dentitions); Recent, Germany.

Palaeotheriidae

Propalaeotherium sp., GMH uncataloged, KOE 4047 (left upper molar); middle Eocene (MP 13), Geiseltal, Germany.

Palaeotherium sp., STIPB M2106, M2111; KOE 60, 1255, 1665 (isolated teeth from all tooth positions, and fragments); late Eocene, Frohnstetten, Germany.

Isectolophidae

Homogalax sp., KOE 881, 1301, 3671 (jaw fragments and isolated teeth); early Eocene, Willwood Formation, Bighorn Basin, Wyoming.

Homogalax protapirinus, USGS 5034, 25032 (partial skulls and mandibles); early Eocene, Willwood Formation, Bighorn Basin, Wyoming.

Isectolophus annectens, CM 2337, 3043, 11752 (maxillae and mandibles with cheek teeth and canine); middle Eocene (Uinta C), Myton Pocket, Uinta Basin, Utah.

Isectolophus latidens, AMNH 12221 (skull with P3–M3); early middle Eocene (Bridgerian), Twin Buttes, Henry's Fork Lone Tree, Wyoming.

Helaletidae

Heptodon calciculus, KOE 4035, 4036, and USNM 522718-KOE 4037 (isolated teeth and fragments); early Eocene, Willwood Formation, Bighorn Basin, Wyoming. AMNH 294, 4850, 4855, 14868 (maxillae and dentaries with almost all tooth positions); early Eocene, Wind River Formation, Wind River Basin, Wyoming. USNM 22782 (skull and dentary); early Eocene, Wasatch Formation, Sublette County, Wyoming.

Heptodon posticus, AMNH 14874, 14971 (maxilla and mandibule); early Eocene, Wind River Formation, Wind River Basin, Wyoming.

Selenaletes scopaeus, AMNH 8229 ,8230 (holotype), 8231, 8232 (lower dentitions); early Eocene, Wind River Formation, Wind River Basin, Wyoming.

Helaletes nanus, AMNH 12130, (maxilla); middle Eocene (Bridgerian), Bridger Formation, Middle Cottonwood Creek, Wyoming. AMNH 12663, 13125 (dentary and isolated teeth); middle Eocene (Bridgerian), Bridger Formation, Granger area, Wyoming.

Desmatotherium fissum, AMNH 20161, 81804 (maxilla and dentary); early middle Eocene (Bartonian), Irdin Manha, Camp Margetts, Mongolia.

Irdinolophus mongoliensis, AMNH 19161 (holotype, maxilla with P2–M2); middle Eocene, Irdin Manha, Iren Dabasu, Nei Mongol, China.

Lophialetidae and other endemic Asian "tapiroids"

Lophialetes expeditus, AMNH 21569, 81675 (maxilla and mandibule); middle Eocene, Ulan Shireh beds, Shara Murun region, Nei Mongol.

Schlosseria magister, AMNH 20241 (holotype, maxilla and lower jaw), AMNH uncatalogued (maxilla); early middle Eocene (Bartonian), Irdin Manha, Telegraph Line Camp, Nei Mongol, China.

Breviodon acares, AMNH 26113 (holotype, mandible); middle Eocene, Ulan Shireh beds, Shara Murun region, Nei Mongol.

Breviodon minutus, AMNH 20139 (holotype, upper molar, probably M2); early middle Eocene (Bartonian), Irdin Manha, Telegraph Line Camp, Nei Mongol, China.

cf. *Breviodon* sp., AMNH 81751 (skull with cheek teeth); early middle Eocene (Bartonian), Irdin Manha, Telegraph Line Camp, Nei Mongol, China.

Pataecops parvus, AMNH 21747 (holotype, maxilla with P2–M3), 21746, 81861 (maxilla and dentary); middle Eocene, Kholobolchi Formation, Orok Nor, Mongolia.

Tapiridae

Colodon sp., USNM uncatalogued (field no. Wy 71-358); middle Eocene–early Oligocene, Wyoming.

Colodon cf. *occidentalis*, MB Ma 33150 (lower molars); early Oligocene, White River Group, South Dakota. AMNH 42893 (m3); middle Oligocene (Whitneyan), *Protoceras* beds, South Dakota.

Haagella peregrina, BSPG 1975 XXII (holotype) and BSP1974 XXIV (fragments of mandible and maxilla); early Oligocene, Möhren 19 and 20, Germany.

Protapirus bavaricus BSPG1949 I 9, 1952 II 176a (mandible and maxilla); late Oligocene (MP 28), Gaimersheim, Germany.

Dilophodon minusculus, USNM V17826, V17827 (maxillae); middle Eocene (late Bridgerian), Bridger Formation, Wyoming.

Tapirus terrestris, ZSTÜ 7135, HH ZM Mam 351, ZFMK 79450 skulls and mandibles of different ontogenetic ages); Recent, South America.

Tapirus sinensis, MB Ma 33219, 33222, 33244 (teeth); Pleistocene, Junnan, China.

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Tapirus sp., USNM uncatalogued (isolated teeth); Pleistocene, Melbourne, Florida.

Lophiodontidae

Lophiodon remensis, KOE 4052 (several dentitions, isolated teeth and tooth fragments); middle Eocene (MP 13), Geiseltal, Germany.

Lophiodon rhinocerodes, MB Ma 33179, HLMD-RO 1–17 (maxillae, mandibule, and isolated teeth); upper Eocene (MP 14–16), Robiac, St. Mamert, Gard, France.

Hyrachyidae

Hyrachyus eximius, AMNH 1645 (skull and jaws); early middle Eocene (Bridgerian), Twin Buttes, Wyoming. AMNH 12355 (mandible); early middle Eocene (Bridgerian), Twin Buttes, Cat-Tail Springs, Wyoming. AMNH 12362 (holotype of "*Methyrachyus troxelli*," maxilla); early middle Eocene (Bridgerian, Bridger C), Henry's Fork, Wyoming. AMNH 12364 (skull); early middle Eocene (Bridgerian, Bridger D), Henry's Fork, Wyoming. AMNH 12371 (skull); early middle Eocene (Bridgerian), Bridger Formation, Summers Dry Creek, Wyoming.

Hyrachyus modestus, AMNH 12359 (holotype of "*Ephyrachyus cristalophus*," maxilla); early middle Eocene (Bridgerian, Bridger C), Twin Buttes, Wyoming. AMNH 12664 (skull and jaws); early middle Eocene (Bridgerian, Bridger B2-3), Grizzly Buttes West, Wyoming. AMNH 12667 (mandible); early middle Eocene (Bridgerian, Bridger B), Millersville, Wyoming. USNM nos. 417319 (mandible), 417328 (right dentary); early Eocene (early Bridgerian), Sheep Pass Formation, Elderberry Canyon, Nevada.

Hyrachyus minimus, GMH XXXVI 52 and 265, XXII-87 and 401, XIV-497, and KOE 4049, 4050 (various dentitions, isolated teeth and tooth fragments); middle Eocene (MP 13), Geiseltal, Germany.

Hyrachyus affinis, USNM 365033 (maxilla with upper molars); early middle Eocene (Bridgerian, Bridger C), Bridger Basin, Wyoming.

Hyrachyus sp., KOE 882 (upper molar); middle Eocene (Bridgerian), Cedar Mountain, Sweetwater Co., Wyoming. UM 32989-KOE 4033 and UM 32989-KOE 4034 (lower and upper molar); middle Eocene (Bridgerian Br-2), Green River Basin, Wyoming. USNM 487381 (maxilla); middle Eocene (Bridgerian), Bridger Basin, Wyoming.

Fouchia elyensis, USNM 417339 (holotype, dentary), 417340, 417341, 417342 (maxillae and dentaries); early Eocene (early Bridgerian), Sheep Pass Formation, Elderberry Canyon, Nevada.

Deperetellidae

Teleolophus magnus, AMNH 26063 (holotype, maxillary fragment and mandible); late Eocene or early Oligocene, "Ulan Gochu" beds, Urtyn Obo, Shara Murun region, Nei Mongol.

Teleolophus medius, AMNH 20166 (holotype, dentary with p1–m3); early middle Eocene (Bartonian), Irdin Manha, Telegraph Line Camp, Nei Mongol, China.

cf. *Teleolophus medius*, AMNH 81799, 81853, 81854 (mandibles and M2–3); early middle Eocene (Bartonian), Irdin Manha, Camp Margetts, Mongolia.

Teleolophus medius?, AMNH 26128 (M3), 26129 (M3), 26286, 26287, 81797 (maxillae); middle Eocene, Ulan Shireh beds, Shara Murun region, Nei Mongol.

Deperetella cristata, AMNH 20290 (holotype, right maxilla), 20292 (mandible); early middle Eocene (Bartonian), Ula Usu, Mongolia.

Hyracodontidae

Hyracodon nebrascensis, STIPB M 1778, M 1779, M 6513, M 6606 (jaws); late Eocene–early Oligocene, White River Group, Toadstool Park area, Nebraska (skull and dentary); Oligocene?, "near Harrison," Nebraska. 42911 (skull and dentary); Oligocene, Sioux County, Nebraska.

Triplopus proficiens, AMNH 26123 (mandible); middle Eocene, Chimney Butte North Mesa, Ulan Shireh beds, Shara Murun region, Suiyan Province, Nei Mongol, China.

Triplopus sp., CM 3240 (upper molar, probably M1), 11955 (skull and jaw fragments); middle Eocene (Uinta C), Uinta Formation, Myton Pocket, Uinta Basin, Utah.

Epitriplopus uintensis, CM 3007 (juvenile skull and jaw fragments); middle Eocene (Uinta C), Uinta Formation, Myton Pocket, Uinta Basin, Utah.

Ardynia praecox, AMNH 26039 (skull and mandible); middle Eocene (Ludian), Urtyn Obo, Nei Mongol, China.

Ardynia kazachstanensis, AMNH 26183 (mandible); middle Oligocene, Baron Sog beds, Nom Khong Obo, Nei Mongolia, China.

Eggysodon osborni, BSPG 1972 XI 1951 (lower incisor); Oligocene (MP 22), Möhren 13, Germany. NHMB KB18 (upper and lower molars); Oligocene, Kleinblauen, Switzerland.

Indricotheriidae

Forstercooperia totadentata, AMNH 20116 (rostrum with premolars and anterior teeth), 20118 (maxilla); middle Eocene, Irdin Manha, Telegraph Line Camp, Nei Mongol, China.

Juxia sharamurunense, AMNH 20286, 20287 (dentaries); middle Eocene, Shara Murun, Mongolia.

Amynodontidae

Amynodon advenum, CM 3107 (maxillary); middle Eocene (Uinta C), Uinta Formation, Myton Pocket, Uinta Basin, Utah.

Metamynodon planifrons, HLMD-WT 515 (mandible), AMNH 1092 (isolated i1); late Eocene, White River Group, South Dakota. USNM 6719 (dentary); early Oligocene, Brule Formation, South Dakota.

Cadurcodon sp., PMM 473 707-KOE 486 (ectoloph of P3); late Eocene–early Oligocene, Mongolia. AMNH 19155 (juvenile skull); middle Eocene, Ardyn Obo Formation, Ardyn Obo, Dorono Gobi Province, Mongolia.

Cadurcotherium cayluxi, MB Ma 26318 (upper molars); late Eocene, Caylux, Quercy, France.

Armania asiana, KOE 3648 (from Dashzeveg field no. 1991 No. 17-31), (two right upper premolars); late Eocene, Ergilin-Dzo Formation, Mongolia.

Caenolophus promissus, AMNH 20297 (holotype, maxilla with P3–M3); early middle Eocene (Bartonian), Ula Usu, Mongolia.

Rhinocerotidae

Eocene

Uintaceras radinskyi, CM 12004 (holotype, most of the dentition); middle Eocene, (Uinta C), Uinta Formation, Myton Pocket, Uinta Basin, Utah.

Trigonias osborni, USNM 4815 (mandible); latest Eocene (Chadronian), South Dakota.

Penetrigonias dakotensis, MB Ma 42545 (cranium); late Eocene, White River Badlands, South Dakota.

Oligocene

Subhyracodon occidentale, STIPB M 1781, M 6576 (lower deciduous and permanent molars); early Oligocene, Toadstool Park area, Nebraska. USNM 16826 (skull); early Oligocene (Orellan), Brule Formation, Niobrara County, Wyoming. MCZ uncatalogued-KOE 556 (M3); early Oligocene, Brule Formation, Torrington, Wyoming.

Subhyracodon sp., USNM 15967 (skull); early Oligocene (Orellan), Brule Formation, Niobrara County, Wyoming. USNM uncatalogued field no. 213-42 (dentition including incisors); horizon and locality unknown.

Epiaceratherium magnum, BSPG 1972 XI 1912 (upper and lower incisors and molars); Oligocene (MP 22), Möhren 13, Germany.

Ronzotherium filholi, BSPG 1969 XXIV 153 (lower incisor); Oligocene, Möhren 7, Germany

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Miocene

Menoceras arikarense, USNM 412981 (incisors); early Miocene, Arikaree Formation, Agate, Nebraska.

Aceratherium incisivum, MB Ma 26302 (enlarged lower incisor), STIPB 1690 (cranium with molar dentition); late Miocene (MN 11), Eppelsheim, Germany.

Aceratherium tetradactylum, MB Ma 42562 (two enlarged lower incisors); middle Miocene (MN 6), Sansan, France.

Aceratherium cf. *tetradactylum*, MB Ma 26430 (incisors); middle Miocene (MN 5), Münzenberg near Leoben, Austria.

Aceratherium sp., MB Ma 28030 and 28029 (a small and a very large lower incisor); middle Miocene (MN 7), Steinheim im Albuch, Germany.

Chilotherium sp., PMM-KOE 492 (lower incisor and molar fragments); Miocene, Asia.

Floridaceras whitei, MCZ 4052-KOE 357 (lower and upper premolars); early Miocene, Gilchrist County, Florida.

Plesiaceratherium fahlbuschi, BSPG 1959 II and KOE 452 (several lower and upper incisors and molars); middle Miocene (MN 5), Sandelzhausen, Germany.

Gaindatherium vidali, BSPG 1956 II 263 (lower incisor); late Miocene, Nagri Formation, northern India.

Dihoplus schleiermacheri, STIPB M 1787 (fragmentary lower molars); Mainz Mombach, Germany.

Lartetotherium sansaniense, BSPG 1959 II 4977, 3912 (upper and lower dentitions); middle Miocene (MN 5), Sandelzhausen, Germany.

Brachypotherum brachypus, MB Ma 26348 and 26347 (upper molars and premolars); middle Miocene (MN 7), Steinheim im Albuch, Germany.

Prosantorhinus germanicus, BSPG 1959 II 3582, 2542, 5183 (several dentitions); middle Miocene (MN 5), Sandelzhausen, Germany.

Pliocene

Teleoceras fossiger, MB Ma 228165 (upper and lower dentition); Pliocene, Janna Hills, Kansas.

Quaternary

Rhinoceros unicornis, ZMFK VIII 1935 (skull with mandibles); Recent.

Dicerorhinus kirchbergensis, MB Ma 32 (maxilla); late Pleistocene, Burgtonna, Germany.

Coelodonta antiquitatis, KOE 52 (tooth fragments); late Pleistocene, Urspringhöhle, Germany.

Elasmotherium sibiricum, PMM-KOE 1253 (molar fragment); Pleistocene, Russia.

Eomoropidae

Eomoropus amarorum, AMNH 5096 (holotype, skull and mandible); early middle Eocene (Bridgerian), Mammoth Buttes, Wyoming. CM 3109 (holotype of "*E. annectens*," maxillae); middle Eocene (Uintan, Uinta A), Wagonhound Member, Uinta Formation, Utah.

Litolophus gobiensis, AMNH 26644, 26645, 26647, 26648, 26649–26652 (skulls and mandibles); early middle Eocene (Bartonian), Irdin Manha, Camp Margetts, Mongolia.

Chalicotheriidae

Moropus sp., CM 1831, 1740-KOE 1638 (several dentitions); early Miocene, lower Harrison Formation, Agate Springs Quarry, Sioux County, Nebraska.

Chalicotherium grande, NHMB C 53, NHMW C25a, B4 (upper and lower dentitions); middle Miocene (MN6), Neudorf, Slovakia.

Chalicotherium goldfussi, HLMD Din 3168 (left maxilla); late Miocene (MN11), Eppelsheim, Germany.

Metaschizotherium fraasi, MR P 239A-003 and 004 (upper dentition); middle Miocene (MN6), Petersbuch 71, Germany.

Ancylotherium pentelicum, AMNH uncatalogued (left dP4 and dp4); late Miocene (Turolian), Samos, Greece.

Nestoritherium sinense, AMNH 18453 (lower molar); Pleistocene, Chung-King-Foo, Szechuan, China.

Lambdotheriidae

Lambdotherium popoagicum, KOE 4032 (upper molars); late early Eocene ("Lostcabinian," Wa-7), Willwood Formation, Bighorn Basin, Wyoming. AMNH 4863 (mandible), 4880 (M1 and M2); early Eocene (Wasatchian, Wa-7), Wind River Basin, Wyoming. USNM 19761,19772 (skulls and mandible); late Wasatchian (Wa-7), Knight Formation, Wyoming.

Lambdotherium sp., UM 78903-KOE 4027 (fragmentary lower and upper molars); early Eocene, Wasatch Formation, Daniel, Wyoming.

Brontotheriidae

Palaeosyops fontinalis, UM 111893-KOE 4029, 4030, (upper premolars); late early Eocene (Gardnerbuttean, Br-1a), Wasatch Formation, Green River Basin, Wyoming.

Palaeosyops robustus, AMNH 11710 (maxillary); early middle Eocene (Bridgerian, Bridger C), Twin Buttes, Wyoming. USNM 13466, 26138, 26303 (maxillae and dentary); middle Eocene (late Bridgerian), Bridger Formation, Wyoming.

Palaeosyops sp., KOE 3894, (left P4 and M3 fragment); late early or middle Eocene, Bridger Formation road cut near Lonetree, Wyoming.

Eotitanops borealis, UM-KOE 4028 (m1); late early Eocene (Gardnerbuttean, Br1a), Wasatch Formation, Green River Basin, Wyoming.

Eotitanops gregoryi, AMNH 14887 (holotype, maxillary and mandible); late early Eocene (Wasatchian), Wind River Basin, Wyoming.

Eotitanops minimus, AMNH 17439 (holotype, left p4–m3); late early Eocene (Wasatchian), Huerfano B, Colorado.

Eotitanops sp., AMNH 4772 (lower molar); early Eocene (Wasatchian), Wind River Formation, Wind River Basin, Wyoming.

Telmatherium cf. *cultridens*, USNM V13463 (dentary), middle Eocene (late Bridgerian), Bridger Formation, Wyoming.

Megacerops proutti, HLMD uncatalogued (cranium and upper and lower molars); late Eocene, Big Badlands, South Dakota.

Megacerops sp., UM10999 (upper premolars); late Eocene, Big Badlands, South Dakota.

Incertae sedis

Toxotherium hunteri, USNM 244352 (dentary), 244359 (maxilla with molars), 244361 (dentary with p4–m2); late Eocene (Chadronian), Flagstaff Rim, Wyoming.

Toxotherium woodi, AMNH 42901 (dentary fragment), late Eocene (Chadronian), White River Formation, Wyoming.

Rhodopagus pygmaeus, AMNH 21554 (holotype, maxilla), 26112 (mandible), 20391, 20392 (assorted jaw fragments and isolated molars); middle Eocene, Ulan Shireh beds, Shara Murun region, Nei Mongol.

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