Construction and wear of mammalian teeth in terms of heterochrony

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Introduction

Heterochrony describes the elongation of a specific phase during ontogeny at the cost of others. Ontogeny includes the entire life history of an animal or its organs (Haeckel 1866). The ontogeny of a tooth includes two parts, early ontogeny and late ontogeny. During early ontogeny the tooth is formed in the crypt. During late ontogeny it is functioning and exposed to wear. Heterochrony during early ontogeny affects the final shape of the tooth and forms the basis for its function during late ontogeny that is characterized by wear. The result of tooth wear is not uniform with time. Only in a few tooth types the primary enamel surface function for a major part of the life span. In most other tooth types some initial wear is required to reach full functionality, when dentin is exposed and enamel ridges are carved out. When this functional surface is reached, further changes caused by continuing wear should be limited, allowing similar functionality to continue over a long time period. Some types of facets, in various mammalian groups, fulfill this requirement, and they stimulated the search for general patterns in the process of tooth wear. Examples are discussed here as "specialized wear facets". Their function is compared with common tools, such as scissors, guillotine cutters, rasps, or end-cutting pliers. This allows us to bypass the various inconsistent definitions of "cutting", "shearing", and "grinding".

The great variability of mammalian teeth and their different functions prohibit sophisticated and very detailed comparisons, but some more general thoughts are provided in this paper. Observing the life history of teeth offers a better understanding of the relationship between the wear-related changes in tooth morphology and function.

Teeth are formed almost completely in the crypt of the jaws, and after eruption they are exposed to wear. Wear, as a destructive and unrenewable process, causes changes in morphology and function.

The general life history of teeth is divided into several phases that allow some comparisons between various tooth types and wear patterns. The estimated length of these phases can be interpreted in terms of heterochrony (McNamara 1990, Smith 2003), because some phases are extended at the cost of others. The evolution of the different kinds of hypsodonty and various specialized wear facets can be used as examples of how heterochrony affects tooth morphology and the maintenance of function during wear.

This is a summary paper based on two earlier papers where additional discussion and citations are provided (Koenigswald 2011 and 2017).

Abbreviations of collections for figured specimens

BSPG   Bayerische Staatssammlung für Paläontologie und Geologie, München
CM   Carnegie Museum, Pittsburgh
GPIT   Institute of Geosciences, Paleontology Department and Museum, Universität Tübingen
HLMD   Hessisches Landesmuseum, Darmstadt
IGPB   Institute of Geosciences, Section Paleontology, Rheinische Friedrich-Wilhelms-Universität Bonn
LACM   Los Angeles County Museum
MNHN   Muséum national d'Histoire naturelle, Paris
NHMW   Naturhistorisches Museum, Wien
SLGM   Collection Frank Menger, Groß-Rohrheim
SMF   Senckenberg Forschungsinstitut und Naturmuseum Frankfurt
UF   University of Florida, Gainesville
UMZC   University Museum of Zoology, Cambridge
UW   Universität Wien
ZFMK   Zoologische Forschungsmuseum Alexander Koenig, Bonn

The life history of teeth

Various different heterochronies occur during early and late ontogeny. A most impressive example of heterochrony during early ontogeny is provided by the development of hypsodont teeth. In other words, the different kinds of hypsodonty can be explained by the heterochronic elongation of different phases during tooth formation. Similarly, specific stages of wear exist for a long time, while other phases are passed through rapidly. Such specializations for specific long lasting phases of wear can thus be interpreted

as examples of heterochrony as well. For comparison the various ontogenetic phases have to be defined.

Tooth mineralization starts from the top of the cusps and proceeds towards the base of the crown (see Ruf et al. 2019). This direction of growth is significant for the sequence of the four phases of early ontogeny. In brachydont teeth these phases are sequential but in euhypsodont teeth they may be compressed or even be eliminated (Fig. 9.1). The four phases are:

Ontogenetic phase I – formation of the cusped surface. If a tooth has several cusps, the formation starts with each cusp separately. The individual cusps merge later into a closed surface.

Ontogenetic phase II – formation of the side walls continues until the base of the crown is reached. There, the enamel formation comes to an end.

Ontogenetic phase III – formation of dentin-covered surface at the base of the tooth

Ontogenetic phase IV – formation of differentiated roots.

The root formation in phase IV does not end at a specific point. The continuous modification of roots helps to compensate for wear and corrects the position of the tooth within the tooth row. The horizontal tooth displacement occurring in some marsupials, some rodents, proboscideans and sirenians (Gomes Rodrigues et al. 2012) requires an intensive modification of roots throughout the lifetime. In other hypsodont teeth the peripheral enamel is reduced in dentin tracts, to allow periodontic ligaments an easier anchoring of the teeth. Solounias et al. (2019) drew attention to an additional function of hypsodont teeth. As long as a major part of them sticks in the jaw, they may serve as additional roots.

For the discussion of wear facets, life history is divided into generalized phases identified as A–G. Capital letters are used to discriminate this sequence from that used for early ontogeny. Late ontogeny, during which erupted teeth are exposed to wear, are discussed as wear stages C, D, E, F, and G. In this model, phases A and B summarize the early ontogeny, included here, because in hypsodont teeth tooth formation and abrasion during the wear stages C to G overlap in time. The wear stages C–G are discriminated by the degree of exposed dentin:

Wear stage C – The enamel cap is intact, providing facets within the enamel.

Wear stage D – Dentin is partially exposed.

Wear stage E – Dentin is widely exposed and dominant.

Wear stage F – Enamel is present only on one side.

Wear stage G – All enamel is worn away, but the dentin core is functioning.

Defining ontogenetic phases and wear stages is an artificial tool, especially when such phases are deduced from the tooth morphology, not the genetic background. This point of view was derived through discussions in the DFG (Deutsche Forschungsgemeinschaft) Research Unit 771 where these studies originated. This research group dealt mainly with fossil material that is not open for genetic analyses. However, the models derived from the fossil material may inspire other researchers to study teeth with their methods. That will widen the understanding of the variability in mammalian dentitions.

Heterochrony, the key to the various types of hypsodonty

High-crowned teeth are generally described as hypsodont. The use of this term, however, varies in different papers according to their authors. Some authors regard mainly or exclusively the cheek-teeth (e.g., Fortelius 1985, Fortelius & Solounias 2000, Kaiser et al. 2003), while others include enlarged incisors or canines (e.g., Hershkovitz 1962, Martin 1993). The most useful definition for hypsodonty compares the crown-height with the bucco-lingual width (e.g., White 1959, Van Valen 1960, Janis 1988). Comparing the height of a tooth to its length is applicable only if the same tooth position is compared.

Hypsodont teeth are rooted. Several lineages evolved rootless tooth types that are classified as euhypsodont (Mones 1982). The term euhypsodont is used in favor of hypselodont, a term that was controversially used and is easily mixed up (Koenigswald 2011).

Hypsodont teeth may occur in two kinds – external and internal hypsodonty. External hypsodont teeth protrude from the mouth like tusks or canines. Thus, they are restricted to the anterior part of the dentition. They are characterized by an eruption rate that exceeds wear. Their function is multifold; besides catching food items, they may be used for example as weapons or to demonstrate the social position of an individual.

In contrast, internal hypsodonty occurs in the postcanine part of the dentition. The true height of such premolars and molars is hidden within the jaw, because eruption rate and abrasion are in an almost perfect equilibrium. In fact, both control each other inconspicuously but fairly perfectly.

The function of internal hypsodont teeth is exclusively for breaking down food items.

An intermediate form between internal and external hypsodonty is seen in rodent incisors and the canines of pigs or *Hippopotamus*. Although they are characterized by an equilibrium of eruption rate and wear, these teeth in the anterior dentition have social functions as well.

Compensating intensive wear as in internal hypsodonty is an important reason for the evolution of hypsodont teeth, but not the only one. External hypsodont teeth offer other selective values.

There have been several attempts to define types of hypsodonty and to assign the great diversity of hypsodont teeth to them. However, most such classifications focus on specific mammalian groups (e.g., Hershkovitz 1962, 1967, Schmidt-Kittler 2002), and often only on specific tooth positions. A discussion of the various attempts and a comparison of the different terminologies was given in Koenigswald (2011).

The different types of hypsodont teeth (presented in Fig. 9.1) thus depend on which one of the various ontogenetic phases is extended to form the critical height of the tooth, the cusps, the sidewalls, or the dentin. Each of them can then be present to varying degrees in internal or external hypsodonty. These aspects allow us to describe the evolution from hypsodont to euhypsodont teeth.
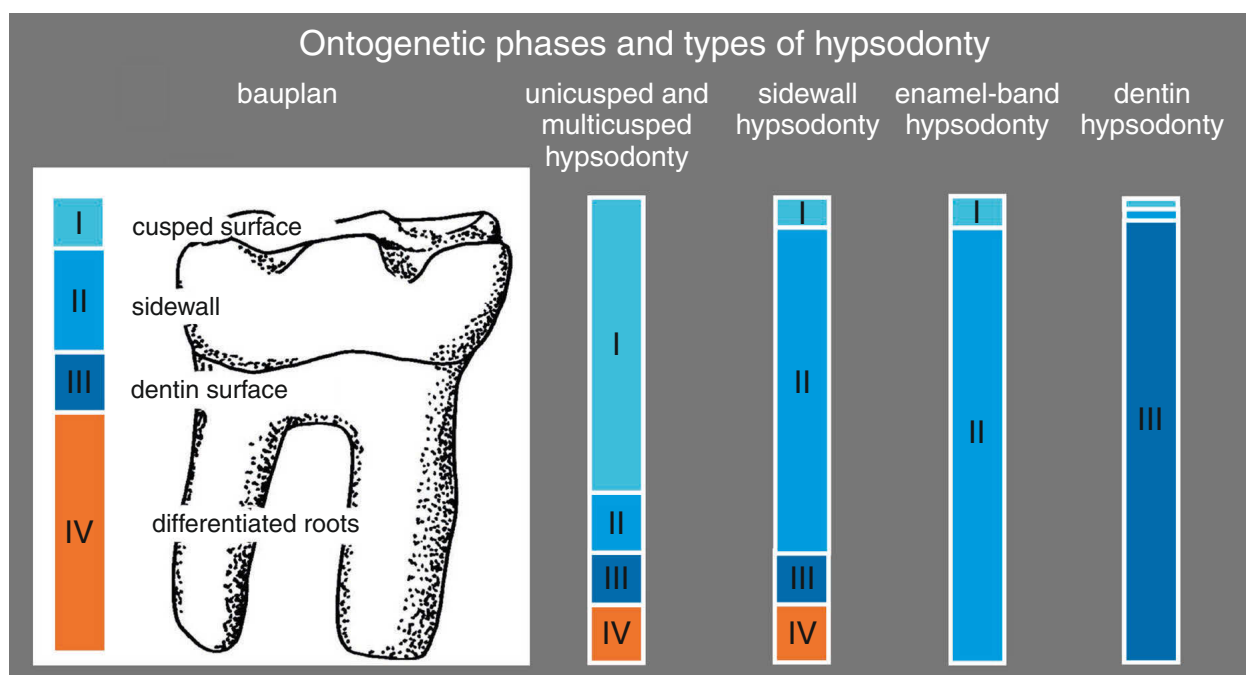
Fig. 9.1. Phases of the early ontogeny and types of hypsodonty: Idealized model of the ontogenetic phases I–IV during the early ontogeny, demonstrated in a lower murid molar. A heterochronic elongation of one of these ontogenetic phases leads to four different types of hypsodonty.

Elongation of ontogenetic phase I – "unicusped hypsodonty"

(Fig. 9.2)

Ontogenetic phase I starts with the forming of the cusp or cusps of a tooth. If this initial phase is significantly elongated, this cusp or cusps gain height and become uni- or multicusped hypsodont. These two types are differentiated, because teeth of unicusped and those of multicusped hypsodonty function differently, in addition to the differences in their morphological appearance.

Teeth such as canines with a high and pointed crown are regarded as unicusped hypsodont. The wear is generally small compared to the eruption rate. The enamel surface is of functional importance and dentin is exposed only rarely. Wear usually is limited to large teeth with an external hypsodonty. Therefore, such teeth occur in the anterior part of the dentition only. The most prominent examples of such unicusped hypsodont teeth are the enamel-covered canines of carnivores, creodonts, some artiodactyls (e.g., *Moschus*, *Deinohyus* Fig. 9.2A), most bats, and even in several primates (very prominent in *Papio*). Unicusped hypsodonty is not restricted to canines because enlarged incisors that are surrounded by enamel may be constructed in the same way (e.g. in Soricidae, lemurs, and diprotodont marsupials such as *Petaurus*). The main function of huge canines is catching prey, but the external hypsodonty facilitates a social significance too.

In the unicusped hypsodont teeth, it is difficult to separate the elongation of phase I from phase II that forms the side walls. Here, those teeth are regarded as unicusped hypsodont if their tips are of functional importance, in contrast to those teeth where the initial tips are worn away

rapidly. The reason for why the ontogenetic phase I (forming cusps) is separated from phase II (forming the sidewalls) becomes apparent in multicusped teeth.

Elongation of the ontogenetic phase I – "multicusped hypsodonty"

(Fig. 9.2)

An elongation of phase I occurs in multicusped teeth as well. These teeth are characterized by an equilibrium of wear with the tooth eruption rate. They occur in the postcanine region of the dentition. Due to intensive wear, the surface of the enamel is not of functional importance, but rather the exposed cross-section of the enamel surrounding the cusps is. The molars of *Phacochoerus* (Fig. 9.2C) form an outstanding example. Each of the individual cusps forms isolated columns that merge only on the base of the crown. This is an impressive example of phase I being extended with phase II being very short in comparison. Similarly constructed are the molars of desmostylids (Fig. 9.2B). The molars of *Elephas* and *Mammuthus* provide another variant of multicusped hypsodonty (Fig. 9.2E). The transverse lophs are as high as the molars but fused only at the base of the crown. The stability of these isolated elements is provided by the cementum between the lophs. A similar construction of molar teeth is found in several rodents, e.g., the Late Miocene giant dinomyid *Phoberomys*, the caviid *Hydrochoerus* (Fig. 9.2D), and the murid *Otomys*.

The molars of Elephantidae deliver an insight into the evolutionary sequence of how various characters were generated, as the initial cusps were aligned in transverse lophs prior to the acquisition of hypsodonty.

Fig. 9.2. Uni- and multicusped hypsodonty. **A,** *Deinohyus* sp., large upper canine with strong roots, where phases III and IV are continuous. **B,** *Hydrochoerus hydrochaeris*, M3 with equally spaced enamel crests, Recent, Argentina (IGPB M 5684). **C,** *Phacochoerus aethiopicus*, m3, Recent, Uganda, (IGPB1208). **D,** *Desmostylus hesperus*, Miocene, California, (BSPG 2009 I 50). **E,** *Mammuthus primigenius*, lower m3, occlusal surface, Late Pleistocene, Rhine River, Germany (IGPB M3287). Not to scale. Photos: G. Oleschinski.

Elongation of ontogenetic phase II – "sidewall hypsodonty"

The most frequent type of hypsodonty is sidewall hypsodonty which evolved in many herbivores independently. The high sidewalls are formed during an elongation of phase II (Fig. 9.1). The initial tips of the teeth formed during phase I are of minor functional significance and worn away rapidly. The subsequent phases including root formation are delayed. Mostly this tooth type occurs in the post-canine dentition and thus represents an internal hypsodonty.

Premolars and molars of *Bos* and *Equus* (Fig. 9.3 B, C) and many more herbivorous mammals are typical examples of teeth with sidewall hypsodonty. Despite the elongation of phase II, the later phases are postponed, but often present and continuous with the root formation. Some species evolve euhypsodont teeth, such as *Lepus europaeus* (Fig. 9.3D) and several rodents.

The intensive abrasion in these rasp-like grinding teeth is compensated by increasing hypsodonty. It allows faster eruption to replace abraded tooth material. Abrasion and eruption rates are in a perfect equilibrium with one another; if not, a pathological malfunction is the consequence.

Here, teeth in this category are only those whose sidewalls are predominantly covered by enamel, forming the ridges of the rasp. On the occlusal surface, the surrounding enamel forms the functional ridges of the rasp-like grinding tool. The number of ridges increases when the surrounding enamel is folded, such as in arvicolids (Fig. 9.3A), or when enamel islets are introduced.

The transition from hypsodonty to euhypsodonty was probably a relatively straight forward evolutionary step. It was observed in the phylogeny of Arvicolidae, where rooted molars show a gradual increase in hypsodonty due to an elongation of phase II (Koenigswald 1982, 1993, Chaline & Sevillia 1990). The short phase III and the root formation in phase IV are gradually delayed, allowing for a higher crown to be built during phase II. Therefore, rooted or unrooted molars are just a matter of the time when the animal dies. If individuals regularly die off before the root formation starts, then their teeth are euhypsodont. In essence, the root formation is delayed to a moment which is not outlived by the individuals. If this delay becomes part of the program, full euhypsodonty is achieved. That means that in terms of heterochrony, ontogenetic phase II continues until death in euhypsodont teeth, and the later phases III and IV are reduced or simply not present anymore (Koenigswald 1982). Therefore, the formation of euhypsodont teeth with surrounding enamel is assigned to ontogenetic phase II.

Increasing hypsodonty and the transition to euhypsodonty causes problems with the formation of enamel islets. The supply of the enamel organ forming the islets is interrupted as the rim of the islet becomes part of the occlusal surface (for details see Ruf et al. 2020, this volume). Lateral infolds of the enamel are not affected in the same way, they can be built continuously.
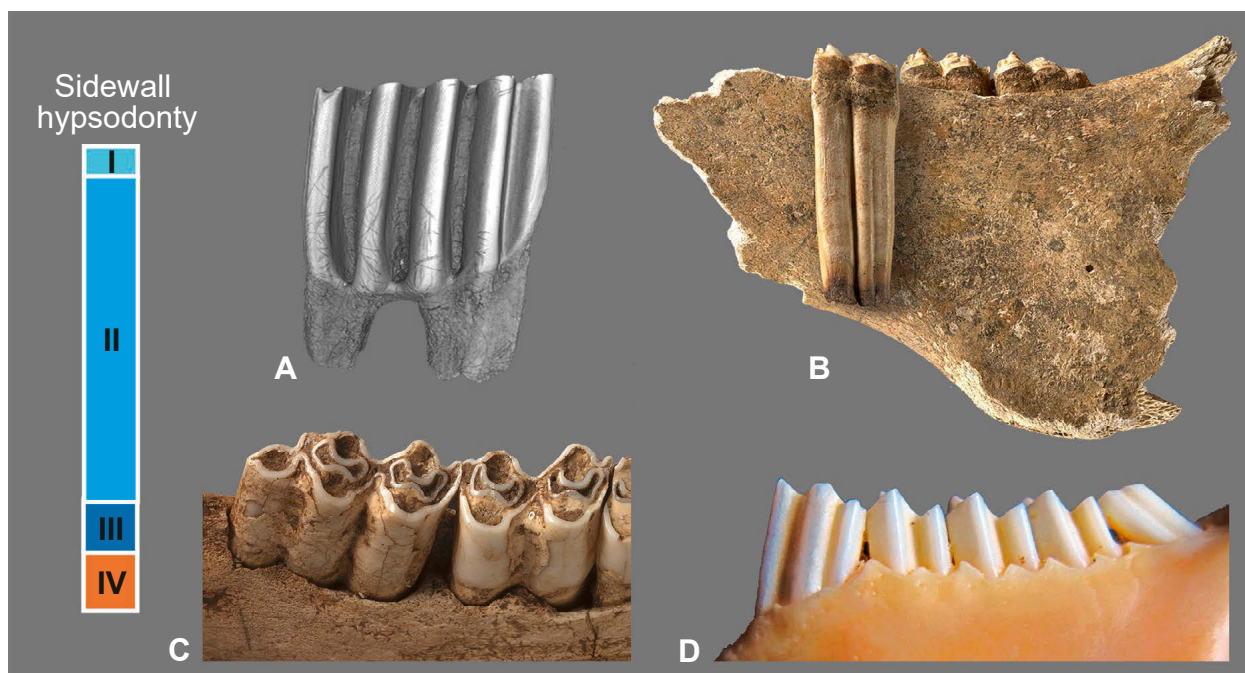
Fig. 9.3. Sidewall hypsodonty – extended ontogenetic phase II. Very common are teeth where the enamel of the elongated side walls forms the rasp-like grinding surfaces. **A,** *Mimomys reidi*, lower m1, Pliocene, Schambach, Germany (BSPG 11975 XXXI). The sidewall is deeply folded to provide proper ridges of the enamel band in the occlusal surface. **B,** *Equus caballus*, fragment of a mandible, subfossil, Germany (IGPB M589). The extracted m1 shows the hidden height of the crown and the postponed root formation. **C,** *Bos taurus*, m2 and m3 of the left mandible, subfossil, Germany. The enamel of the sidewalls and the islets form distinct ridges of the occlusal surfaces (IGBP). **D,** *Lepus europaeus*, Recent, Germany (IGPB 6241). Euhypsodont p4 and molars of the mandible. Not to scale. Photos B, C, D: G. Oleschinski.

Increasing hypsodonty retards the development of roots. The height of the tooth within the jaw may function to some degree as a substitute for a root. Dentin areas are preferred for periodontal ligament attachment, dentin tracts on hypsodont teeth are important for anchoring, their gradual extension has been observed in molars of arvicolines and other mammals (Rabeder 1981, Koenigswald et al. 2010b).

Elongation of ontogenetic phase II – "enamel-band hypsodonty"

The most prominent examples of euhypsodont teeth are the incisors of rodents and lagomorphs. They are formed during ontogenetic phase II, and they differ from the described sidewall hypsodonty by restriction of the enamel to one side or a limited part of the tooth. The presence of a preceding phase I with a tiny enamel cap can be assumed, and the later phases following are irrelevant in euhypsodont teeth. They are either totally reduced or the animal does not outlive them. The continuous formation of the enamel on one side implies an active enamel organ located on this side of the tooth. The growing tooth gradually passes along the enamel organ and gets a continuous cover of enamel. On the other side, the surface is formed by dentin.

Thus, the ontogenetic phases II and III are active at the same time, but locally separated. This modification does not invalidate the information deduced from the general scheme.

The most typical examples of the category of enamel-band hypsodonty are the large and strongly curved incisors of rodents (Fig. 9.4 A, B) and lagomorphs. In upper and lower teeth of these taxa, the enamel is restricted to the anterior and parts of the mesial sides. The occlusal surface of the enamel forms a sharp cutting edge because the dentin is abraded by the antagonist. The equilibrium between the eruption rate and wear is generally balanced, and lack of abrasion may cause severe functional difficulties or even death.

Enamel-band hypsodonty evolved in various mammalian lineages independently, e.g., in rodents, in the multituberculate *Taeniolabis*, and the marsupials *Diprotodon*, *Phascolonus*, and *Vombatus.* A similar construction of the incisors is known from hyracoids, tillodontids, pyrotheres, and the primate *Daubentonia* (Koenigswald 2011). The enamel band is generally placed on the anterior sides of the incisors, but the way in which the incisors occlude varies among species.

The canines of *Hippopotamus* (Fig. 9.4C) provide a special kind of enamel-band hypsodonty. In lower canines the enamel is situated on the anterior side, whereas in upper canines the enamel is on the posterior side. Because the occlusal surface is oblique, in both sides the cutting enamel is situated on the leading edge.

Another modification of hypsodont canines with a one-sided enamel is known from the marsupial *Thylacosmilus* and the cervid *Procervulus.* Both totally unrelated animals have enamel only on the buccal side of their large protruding upper canines which have no proper antagonist. The dentin on the lingual side is abraded by soft tissue to such a degree that the edges of the enamel are sharpened like a blade (Koenigswald & Goin 2000).
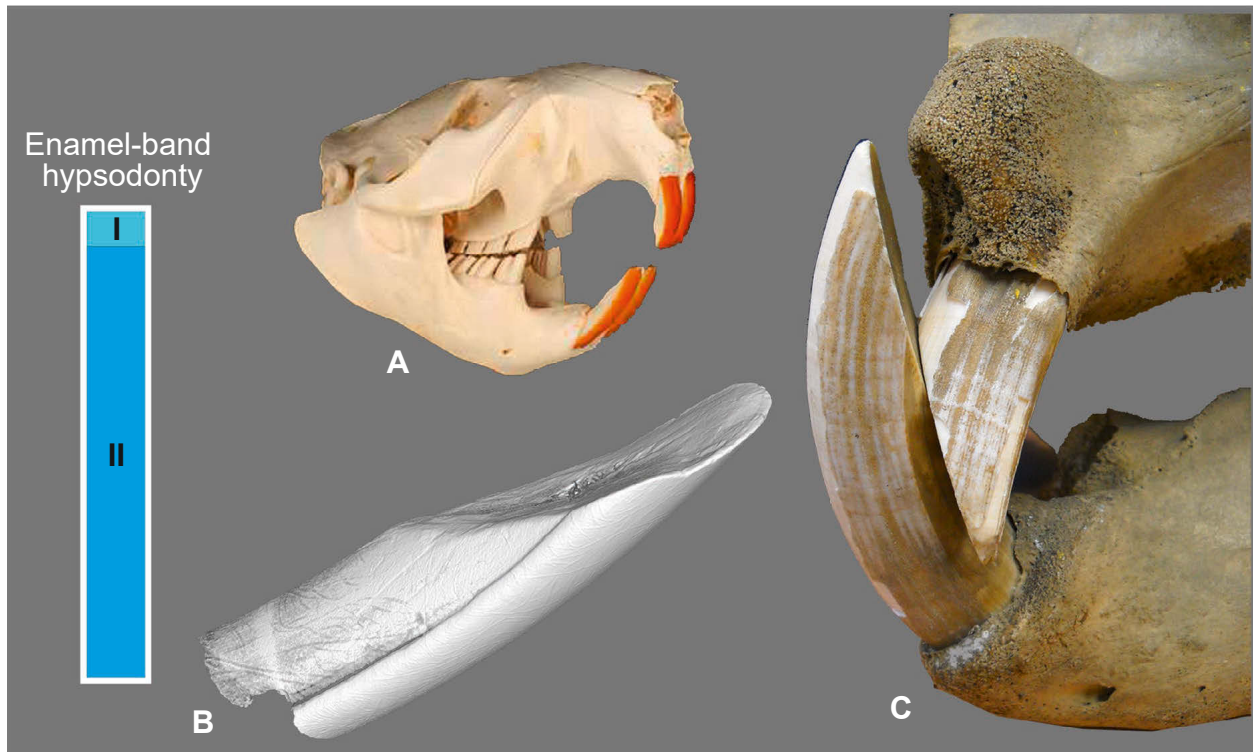
Fig. 9.4. Enamel band hypsodonty – extended ontogenetic phase III. Teeth characterized by enamel on one side are often euhypsodont and form nipper- or blade facets. **A,** *Castor canadensis*, cranium, Recent, Wyoming (IGPB MAÜ 2). Enamel on the anterior side of the teeth is pigmented red. **B,** *Dicrostonyx torquatus*, lower incisor, Pleistocene, Germany (IGPB KOE93). As typical in rodents, the thin enamel layer forms a sharp cutting edge. **C,** *Hippopotamus amphibius*, upper and lower canines in occlusion, Recent, Africa (IGPB M2365). In contrast to rodents, in *Hippopotamus* lower canine the enamel is on the anterior side and in upper on the posterior one, functioning as symmetrical blade facets. Not to scale. Photos: G. Oleschinski.

An atypical enamel-band hypsodonty without a functional context is present in some proboscidean tusks. In *Cuvieronius*, they form a spiral around the tooth, but have almost no functional significance and are a remainder of the former enamel cover.

Elongation of ontogenetic phase III – "dentin hypsodonty"

Dentin teeth that have no enamel occur in various mammalian orders and tooth positions, and include the euhypsodont tusks of elephants (Fig. 9.5B) and cheek teeth of xenarthrans (Fig. 9.5C). An assignment to phase III of the proposed ontogenetic sequence is rectified by tiny enamel caps that occur in various groups. They represent the preceding ontogenetic phases I and II, which are nearly entirely absent. Subsequent phase IV is also generally missing, for specific roots are not needed. Thus, dentin teeth represent an enormously expanded phase III.

Dentin teeth with an external hypsodonty may protrude from the mouth. Eruption rate is distinctly higher than abrasion by wear. In *Mammuthus*, erupting tusks, especially deciduous ones, show tiny caps of enamel (Fisher et al. 2014). Although they are functionally unimportant, they are still verifiable. Similarly, enamel caps were reported from the tusk of the cetacean *Monodon* and the canines of the fissiped carnivore *Odobenus* and suid *Babyrousa*.

Among whales, dolphins have enamel-covered teeth, whereas the dentin teeth of the sperm whale, *Physeter*, are well known as scrimshaws. The erupting teeth have an initial enamel cap as well, indicating reduction of the previously present ontogenetic phases I and II that were shortened during evolution.

It might be annotated that the large tusks of proboscideans that grow continuously throughout life and experience very little wear, document individual life history in their internal structure (e.g., Fisher et al. 2014).

Besides dentin teeth with external hypsodonty, dentin teeth with an internal hypsodonty occur in various xenarthrans where wear and eruption rates are in equilibrium. Most prominent are the premolars and molars of xenarthrans, e.g., *Megatherium* and *Glyptodon*. In a few xenarthrans, traces of an enamel cap have been observed (Simpson 1932, Ciancio et al. 2014, Green & Kalthoff 2015), indicating the presence of preceding ontogenetic phases I and II in this order.

Therefore, dentin teeth fit very well into the general sequence of ontogenetic phases, with the high specialization of an extremely extended phase III.
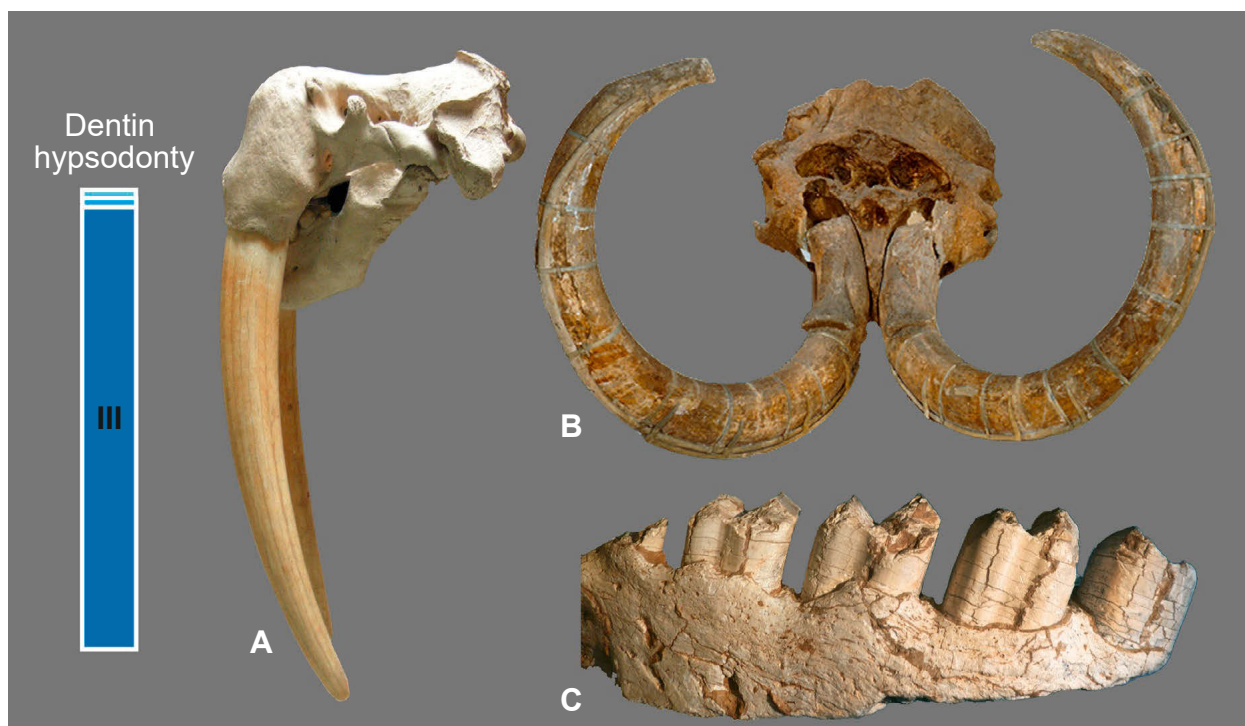
Fig. 9.5. Dentin hypsodonty – extended ontogenetic phase III. In dentin teeth, a primary enamel cap is often present but of no functional significance. **A,** *Odobenus rosmarus*, cranium with enlarged canines, Recent, Bering Sea (ZFMK94.138). **B,** *Mammuthus primigenius*, Pleistocene, Horb, Germany (GPIT/MA/2129). The strongly curved upper tusks of this male individual represent its social status. **C,** *Eremotherium* sp., part of the mandibular dentition, Late Pleistocene, South America (NHMW IX/21/3). The profile of the teeth originates of the different hardness of the dentin. The ridges of the lower teeth intercalate with those in the upper teeth. Not to scale. Photos: A and C by the author, B, I. Werneburg.

Heterochronic variability and evolution in the *bauplan* of hypsodont teeth

According to the observations above, the different types of hypsodonty can easily be interpreted as an elongation of a specific phase within a very general model of ontogenetic phases. Such an elongation of one phase occurs at the cost of the other phases. This is a typical pattern of heterochrony. In this way heterochrony modifies the *bauplan* of a normal brachydont tooth during the early ontogeny. In a similar way, the evolution from hypsodont into euhypsodont teeth can be understood.

Such an explanation illustrates the technical process during tooth formation, but it does not identify the reason why teeth become hypsodont or euhypsodont.

A chronological accordance of the expansion of grasslands and the increase of hypsodont teeth can be observed in herbivores during the Miocene. Grasses and the dust in an open habitat force a higher abrasion of teeth that is compensated by increased tooth material in hypsodont teeth. However, hypsodont teeth evolved in earlier periods as well; for example, Taeniodonta with euhypsodont teeth flourished during the Paleocene and Eocene epochs (Rose 2006).

The heterochronic expansion of phase I, II or III creates different types of hypsodonty. Functional selection may provide the explanation for why a specific phase of the ontogenetic sequence was elongated. But, in general, the achievement of hypsodonty has occurred relatively late in phylogeny, with the new character superimposed on a tooth morphology already present.

Discussing hypsodonty in terms of heterochrony is only one way of looking at this kind of teeth. Most of the other authors provided classifications concentrating on specialized tooth types or systematic groups (Koenigswald 2011). However, considering heterochrony as a useful guide allows an understanding of the evolution of specific modifications of tooth morphology.

Teeth adapted for specific wear stages, another type of heterochrony

Tooth wear is a destructive process that modifies the morphology of teeth. For estimating individual age, the wear of the entire tooth row has been considered and individual age stages (IDAS) have been described (Anders et al. 2011). Here the attempt is made to differentiate some general wear stages for individual teeth that allow comparisons of the specializations in various dentitions.

The second part of the life history of teeth starts when teeth are incorporated into the tooth row. The main purpose of teeth is breaking down food items, and this function
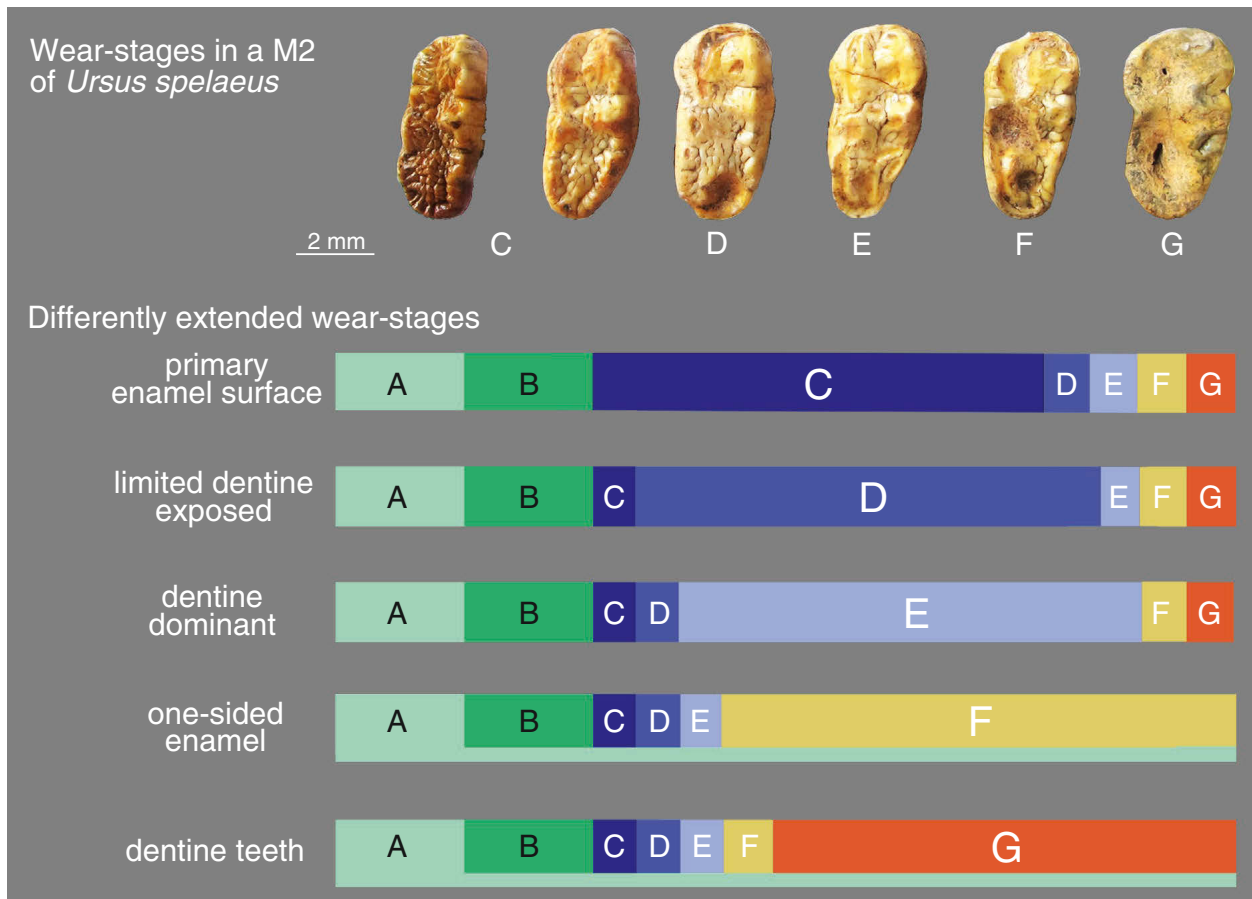
Fig. 9.6. Wear stages and heterochrony. Heterochronic differentiation of the wear stages in mammalian teeth. The stages are symbolized by capital letters C, D, E, F, and G. Wear stages A and B represent tooth formation in the crypt. During wear stage C the enamel surface is functioning. Wear stages D, E and F characterize wear stages with progressive exposure of dentin. In D, the dentin is partially opened. In E, the dentin becomes dominant. In F, only one side is covered with enamel. In wear stage G only dentin is left. Most teeth pass through these stages if the bearer lives long enough. For most teeth, the period of their optimal function can be attributed to a specific wear stage of this sequence. This phase is then often expanded, with earlier or later wear stages being reduced or missing. This allows for the characterizing of specialized wear facets that function in the same manner for a relatively long time. As an example for normal wear, various M2s of *Ursus spelaeus* (Late Pleistocene, Austria, UW collection without numbers) representing the stages C to G, are depicted in the top row.

causes destructive wear at different scales. The great variability of the morphology of mammalian teeth makes it difficult to identify comparable ontogenetic phases of wear if the scale is very detailed. In a more general aspect, when the main focus of wear is regarded, a model of wear stages can be established that seems to be generally applicable and informative. The phases of late ontogeny are indicated by capital letters C to G (Fig. 9.6), and are deduced from the amount of dentin exposed on the occlusal surface. As noted earlier, phases A and B cover early ontogeny. Introducing such wear stages allows to characterize and compare the different evolutionary trends that have occurred in order to cope with the destructive abrasion.

If teeth are functioning best with an intact enamel cover, they are attributed to wear stage C. Wear stages D, E, and F are characterized by different degrees of exposed dentin. As the exposure of dentin is affected by the different mechanical properties of enamel and dentin, these wear stages function in different ways and are described here as "specialized wear facets" (Koenigswald 2017). Their functions are comparable with those of common day tools. Teeth in which only dentin is left are added as wear stage G.

Teeth adapted to wear stage C, the primary enamel surface
(Fig. 9.7)

Using the enamel surface is common in most reptiles and several Mesozoic mammals, but it has also persisted in various mammalian groups. Therefore, not all such teeth can be regarded as specialized, but a specialization can be assumed, if the enamel is thickened in order to withstand abrasion for a longer time period.

The orientation of the enamel surfaces to one another during occlusion is of significance. In the molars of most Mesozoic mammals, the enamel surfaces of the antagonists slide along each other. A similar situation occurs in the enlarged canines of bats (Fig. 9.7A). The contact of the antagonists may cause facets within the enamel or even penetrate to the dentin. The different quality of these two materials does not affect the function in these types of movements. The molar of *Morganucodon* (Fig. 9.7B) provides an example.

The wide range of tribosphenic molars provides revealing insights. Generally, the triangles of the antagonistic
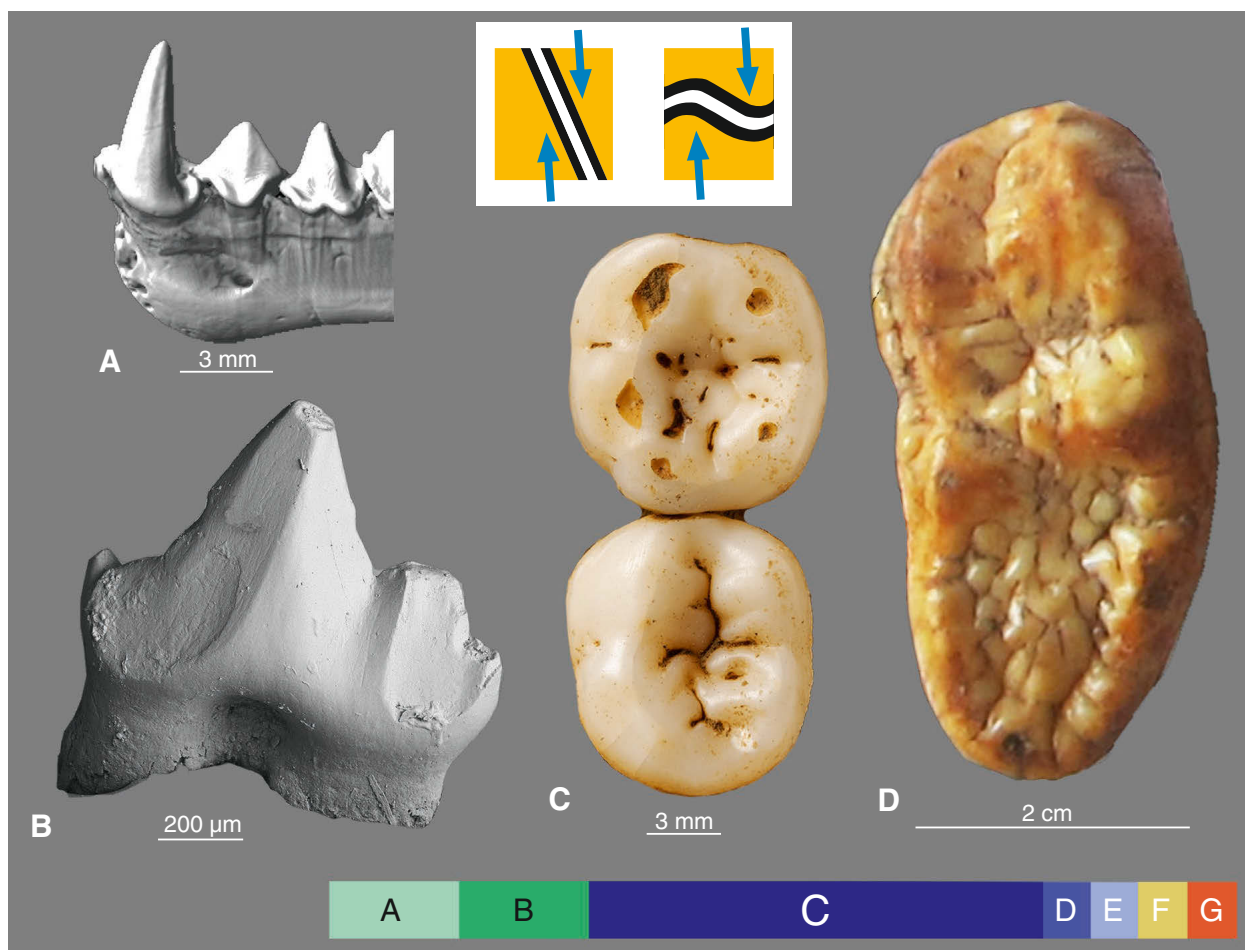
Fig. 9.7. Occlusal surfaces specialized for wear stage C. These teeth function best using their primary enamel surface. **A,** *Phyllostomus hastatus*, left dentary, Recent (ZMFK 59201). The canine and premolars function best when the enamel cover is intact (SEM micrograph). **B,** *Morganucodon watsoni*, lower m1, Late Triassic (UMZC EO.mr (Lr).32). The wear facet is parallel to the enamel surface. (SEM micrograph). **C,** *Homo sapiens*, lower m1 and m2, medieval times, Euskirchen, Germany. In the m1 wear stage D is just beginning, whereas the m2 shows stage C. The main function of these enamel covered teeth is compression. **D,** *Ursus spelaeus*, upper M2, Late Pleistocene, Austria (UW uncatalogued). Food items are compressed between the enamel covered surfaces. Photos: A, R. Hielscher; B, K. Jäger; C, G. Oleschinski.

trigons and trigonids interdigitate in a zig-zag line. As seen in pretribosphenic stem therians (Schultz & Martin 2011), the primary trigons and trigonids function like a punching die. The lateral enamel surfaces pass each other and process the food. Because these side walls are slightly curved, the contact area is reduced and the pressure raised. The enamel is very thin and does not form a functional crest when the dentin is exposed.

In the more derived molars of insectivorous mammals including Didelphidae, Soricidae, and Talpidae, the enamel functions slightly differently. Because the enamel is thicker, it forms sharp edges at the occlusal surface when it is exposed besides the dentin. It contributes to the effect of the punching die.

If the enamel-covered occlusal surface is more horizontal, food is mainly compressed or squeezed between the teeth. These teeth are often multicusped or crenulated, as in bears, humans, and other primates (Fig. 9.7 C, D). Abrasion reduces the enamel, and the exposing of the dentin is a measure of the individual's age. To compensate a more intensive wear, such as the crushing of hard shells, the enamel may be thickened, e.g. in the sea otter *Enhydra* or in australopithecines. A more derived way to cope with intensive wear is evolving a multicusped hypsodonty, as in *Phacochoerus*.

Teeth adapted to wear stages D, E, and F with partially exposed dentin
(Figs. 9.8, 9.9)

A great variety of teeth function best when part of the dentin is exposed in specific areas, and the exposed cross-section of the enamel functions as a ridge, across which the food items are squeezed. The difference in hardness of enamel and dentin contributes to the function. To reach this level, wear stage C has to be passed through. Wear stages D, E, and F are characterized by an increasing amount of exposed dentin during the time of their optimal function.

Each of these phases characterizes different types of teeth and is usually functioning over a long part of the life span. Teeth that have their optimal function in D or E may pass through the later wear stages with a limited functionality until the end of life.

In teeth specialized for wear stages D and E, the cross-sections of the worn peripheral enamel are of functional

significance and not the enamel surface as in teeth assigned to wear stage C. Of course, the exposure of the cross-sections of the enamel cover requires some opening of the dentin. The difference between the hard enamel and the softer dentin causes protruding enamel crests to be of significant functional importance.

Tooth morphology causes different types of facets that show a selective opening of the dentin. They are described as "specialized wear facets", and they can be related to the sequence of wear stages. "Blade facets", characterized by a single blade per facet, occur in two manners, as symmetrical or asymmetrical blade facets. But in either case, dentin is exposed in a limited area and of minor functional significance. Therefore, blade facets are assigned to wear stage D. "Rasp facets" generally have several enamel ridges, and thus more dentin is exposed. Rasp facets are assigned to wear stage E. In "nipper facets", representing wear stage F, the amount of dentin is highest, but functionally the narrow enamel band is most significant.

Symmetrical and asymmetrical blade facets

(Fig. 9.8)

"Blade facets" are facets formed by a single, well-sharpened enamel blade, forming a perfect cutting device. Due to the special morphology of the teeth, these blade facets are long-lasting and function continuously despite continuous wear. Two types of blade facets are distinguished, because they function slightly differently. The symmetrical arrangement of two blades in antagonistic teeth works like a pair of scissors. In the asymmetrical arrangement, one blade is sharp, but the antagonist is blunt and functions as an abutment. Thus, this structure is comparable to guillotine cutters. The blade facets are attributed to an expanded wear stage D.

Symmetrical blade facets

Carnassials function as typical symmetrical blade facets. The buccal side of the lower m1 slides along the lingual side of the upper P4. It requires some initial wear to expose and sharpen the antagonistic blades. The enamel blade is always on the leading edge of the facet. The edge of each enamel blade is sharpened by attrition and merges smoothly into a plane of exposed dentin. The occlusal plane is oblique, sloping on the buccal side.

The carnassials of Carnivora (Fig. 9.8B) and Hyaenodonta have typical facets forming symmetrical blades. The same tool is present in the marsupial lion *Thylacoleo carnifex*. In *Thylacoleo*, the margin of the blade is almost straight. In most Carnivora, the blade is characterized by a deep notch. This allows the cutting point to shift along the blade, which increases the applied forces and enables the dentin plane to control the exact fitting of the cutting edges. Cutting is more efficient if the subject is compressed beforehand. In carnassials, the compression is created by the general tooth morphology. The dentin is not involved specifically in this compression.

In carnivorous mammals, the symmetrical blades are mostly aligned along an anterior-posterior axis. The main function occurs during phase I of the chewing cycle. The power stroke is directed almost vertically with a slight transverse component in lingual direction. With increasing age, the angle of inclination becomes less steep, but the direction remains unchanged.

Symmetrical blade facets occur in the dentitions of herbivores as well, but the blades are oriented transversely in a bucco-lingual direction. Because they occur mostly in bilophodont molars, one may talk about 'bilophodont scissors' in contrast to the carnassials, although they function similarly. The well sharpened enamel blade is always on the leading side of the facet. During phase I of the power stroke, the food items are cut at the edges of the antagonistic enamel blades. Subsequently the food is compressed between the enamel surfaces of antagonistic lophs, when the teeth further interdigitate. The dentin platform controls this movement. Phase II of the power stroke is very limited or lacking. If present, such as in Macropodidae, it is directed in a lingual direction parallel to the lophs. But it has to be stressed that not all bilophodont teeth function with such bilophodont scissors, as, for example, the mastication pattern in *Papio* is very different.

Bilophodont scissors occur in various marsupials, such as *Diprotodon* and in almost all Macropodidae. Among extant Eutheria, only the tapirs have preserved this type of transverse blade facets. Among fossil herbivores, however, such bilophodont scissors with transverse blade facets are widespread. They occur in specific proboscideans (e.g., *Daouitherium* and *Deinotherium*), pyrotheres (*Pyrotherium*, Fig. 9.8C), xenungulates (e.g., *Carodnia*, Bergqvist & Koenigswald 2017), and of course fossil tapirs (e.g., *Lophiodon*, Koenigswald 2014) (Fig. 9.8A). Most of these teeth are brachydont, and only in *Arsinoitherium* (Embrithopoda) do bilophodont scissors occur in combination with hypsodonty.

Mastication with bilophodont scissors seems to have had limited evolutionary success; it was frequent among various mammalian groups in the Paleogene and faded gradually away, being almost extinguished in extant fauna (Hooker 2000).

Asymmetrical blade facets

A specific type of blade facets was found in the premolars and molars of *Dicerorhinus* (Fig. 9.8E–F). The ectoloph of the upper teeth forms a sharp cutting-edge without an equivalent blade in the lowers. An antagonist is required for applying any destructive forces to the food items: It is very inconspicuous and formed by the buccal edge of the lower premolars and molars. During the function of this structure, comparable with the rare guillotine cutters, the ectoloph of the upper tooth, and more precisely the cross-section of the buccal enamel, is cutting. It continues smoothly into the opened dentin. The enamel of the blade is often sharpened by attrition.

This type of blade facets was termed guillotine cutters or ectoloph-guillotine and occurs in a great number of early Perissodactyla: Brontotheriidae (e.g., *Megacerops*, Fig. 9.8G), Chalicotheriidae, and early Equoidea (e.g., *Palaeotherium*, *Anchitherium*, Fig. 98D). It was found as well in the South American Litopterna and Astrapotheria. This type of facet is rare in extant fauna, because the increasing grasses required more grinding than cutting.
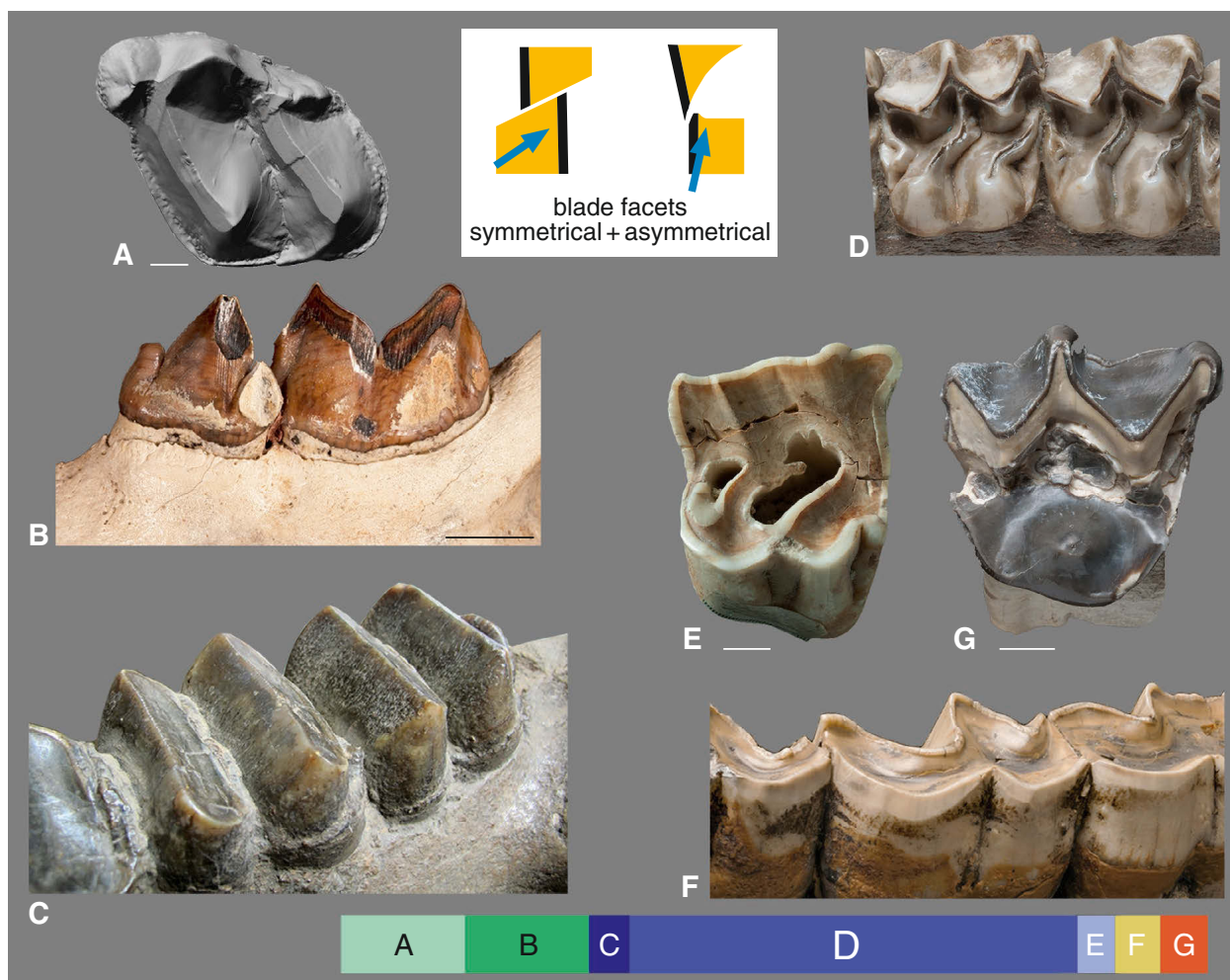
Fig. 9.8. Occlusal surfaces specialized for wear stage D. Symmetrical and asymmetrical blades are formed by the cross-section of the enamel. The dentin is partially exposed. **A,** *Lophiodon lautricense*, left upper M3, Eocene, Robiac, France (HLMD Ro 17c). The transverse lophs have symmetrical blades, that cut with the cross lophs of the lower molars. The function of the enamel blades requires an opening of the dentin that occurs after a short period of initial war. **B,** *Xenosmilus hudsonae*, left p4 and m1. Late Pleistocene, Florida (UF 60000). The dentin is opened in the blade facet with the enamel on the leading side. The functional surface of the upper molar is reciprocal. The optimal function of the symmetrical blades is provided by the exposed dentin. **C,** *Pyrotherium romeroi*, left m2 and m3, Deseadan, Rio Desado, Argentina (MNHN-F-DES 1238). The lophs have an enamel-covered anterior side, whereas the planar facet on the distal side is formed by dentin. The upper molars have a reciprocal orientation. Cutting of the food items occurs between the symmetrical blades at the enamel ridge, followed by compression against the enamel-covered surface. **D,** *Anchitherium aurelianense steinheimense*, right P4 and M1, Miocene, Steinheim am Albuch, Germany (BSPG 1897 XIII4a). The ectoloph forms the cutting facet for phase I of mastication, whereas proto- and metaloph show initial grinding facets for phase II of mastication. The lower molars carry mainly shearing facets. **E,F,** *Dicerorhinus* sp., upper M1, Pleistocene, Weimar-Ehringsdorf, Germany (IGPB M 4125) and lower molars, Pleistocene, Brüggen (IGPB 2863). The main mastication in rhinos occurs along asymmetrical facets. During phase I, the ectolophs of the upper premolars and molars form a cutting edge backed-up by dentin. The antagonistic lower premolars and molars have only a small facet as an abutment. During phase II the lower molars are in full function, grinding across the lingual part of the upper molars. The specialized facets of these teeth require a partial opening of the dentin. **G,** *Megacerops* sp., right M2, Orellan, Badlands, South Dakota (HLMD WT 735). The Brontotheriidae and Chalicotheriidae have a cutting device like that in the rhinos, but it is followed by compression against the ectoloph. Scale bars equal 10 mm. B, C, D, and F not to scale. Photos: G. Oleschinski.

The main power stroke with cutting is related to phase I of the chewing cycle and is oriented in Brontotheriidae in a strict lingual direction and stopped by the protocone. In Perissodactyla with an asymmetrical blade facet, the power stroke of phase I is usually directed in a mesio-lingual direction. It is followed by a phase II with grinding that increases during further evolution.

Rasp facets
(Fig. 9.9)

Teeth that are mostly grinding often have flat occlusal surfaces with enamel ridges that are separated by dentin and/or cementum. These enamel ridges are either formed by the surrounding side walls of the teeth, lateral infolds of the side walls, or by enamel islets. Antagonists in the lower and upper dentition are usually formed very similarly. Their
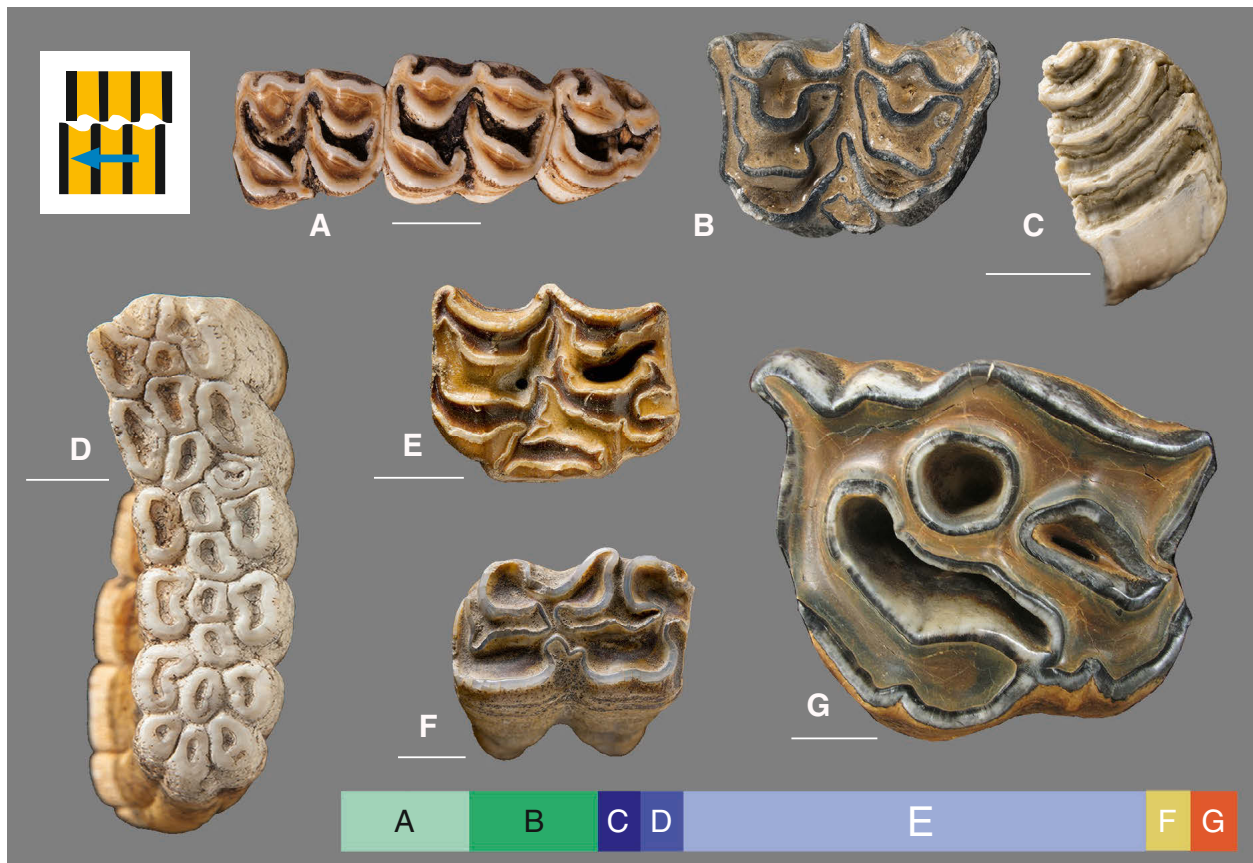
Fig. 9.9. Occlusal surfaces specialized for wear stage E. The enamel ridges between the widely exposed dentin form a rasp facet. The ridges are formed by the surrounding enamel, enamel islets and lateral infolds. Some of the teeth are hypsodont. **A,** *Rangifer tarandus*, left M1–M3, Recent, Banks Island, Canada (IGPB M 1508). The enamel islets of the low-crowned teeth are not filled with cementum. **B,** *Bison priscus*, Late Pleistocene, Groß-Rohrheim, Germany (SLGM). The enamel islets and the lateral infolds are filled with cementum. **C,** Dinomyidae indet., M3 sin., Late Miocene/Pliocene, Playa Arazatí, San José, Uruguay (IGPB KOE 4007). The enamel ridges occur on one side of the lophs only, but have exactly the same distance. **D,** *Phacochoerus aethiopicus*, Recent, Okavango, Botswana (IGPB-M 7028]. The rasp facet is formed by elevated cones that are surrounded by cementum. **E,F,** *Equus ferus*, subfossil, Adendorf near Meckenheim, Germany (IGPB-M 1850). Upper molar with enamel islets and lateral infolds and lower molar with lateral infolds only. **G,** *Coelodonta antiquitatis*, right M2 with enamel islets, Late Pleistocene, Bobenheim, Germany (SLGM). In comparison to earlier rhinos, the ectoloph of *Coelodonta* is lowered and incorporated into the flat occlusal surface. With progressive wear, the lateral infolds become when deeply worn enamel islets. Scale bars equal 10 mm, B not to scale. Photos: G. Oleschinski.

function is compared to a rasp. A great variety of teeth function in this way (Fig. 9.9), therefore the term rasp-facet is used here. In the sequence of wear stages presented here, a large amount of dentin is exposed between the enamel ridges, thus it is assigned to wear stage E.

The function of these teeth differs greatly from blade facets, because the food is compressed by the entire occlusal surface where the dentin plays a major role. The enamel ridges are thresholds where food items are squeezed across and broken. These enamel ridges mostly have a rounded surface and show striations only rarely. It is conspicuous that distances between the enamel ridges tend to be equal even though they may originate from different parts of the tooth morphology (Fig. 9.9A–G). That is especially obvious in *Mammuthus* (Fig. 9.2E) or rodents such as *Hydrochoerus* (Fig. 9.2D) and *Dinomys* (Fig. 9.9C). The occlusal surface is surrounded mainly by the side walls (e.g., *Cryptomys*, *Aplodontia*, *Thomomys*), or differentiated by enamel islets (Ruf et al. 2019). Such enamel islets, e.g. in *Mylagaulus* and *Castor* are traces of furrows

of the occlusal surface as in the gondwanathere *Vintana* (Krause 2014) or basal parts of lateral infolds, e.g., in the gondwanathere *Sudamerica* and in lagomorphs (Koenigswald et al. 2000, 2010a). Lateral infolds also occur on the molars of arvicolids and the rhinocerotoid *Elasmotherium*, and on lower molars of Equidae.

Of functional significance are the enamel ridges that tower above the enclosed dentin. It is the cross-section of the worn enamel, and not the primary enamel surface that forms the enamel crests. Lateral infolds and/or enamel islets enrich the number of enamel crests (Ruf et al. 2019). Very often, these ridges are oriented closely, but not exactly perpendicularly, to the direction of mastication (Maglio 1972, Koenigswald et al. 1994). With the increasing number of enamel ridges, the efficiency of the grinding teeth grows. Rasp facets are predominantly flat in the direction of the power stroke that varies between lingual and proal. It is nearly horizontal in some perissodactyl dentitions wherein the uniform power stroke is ultimately derived from a two-phased power stroke, where the direction and inclination of both phases have become more and more identical (Ruf et
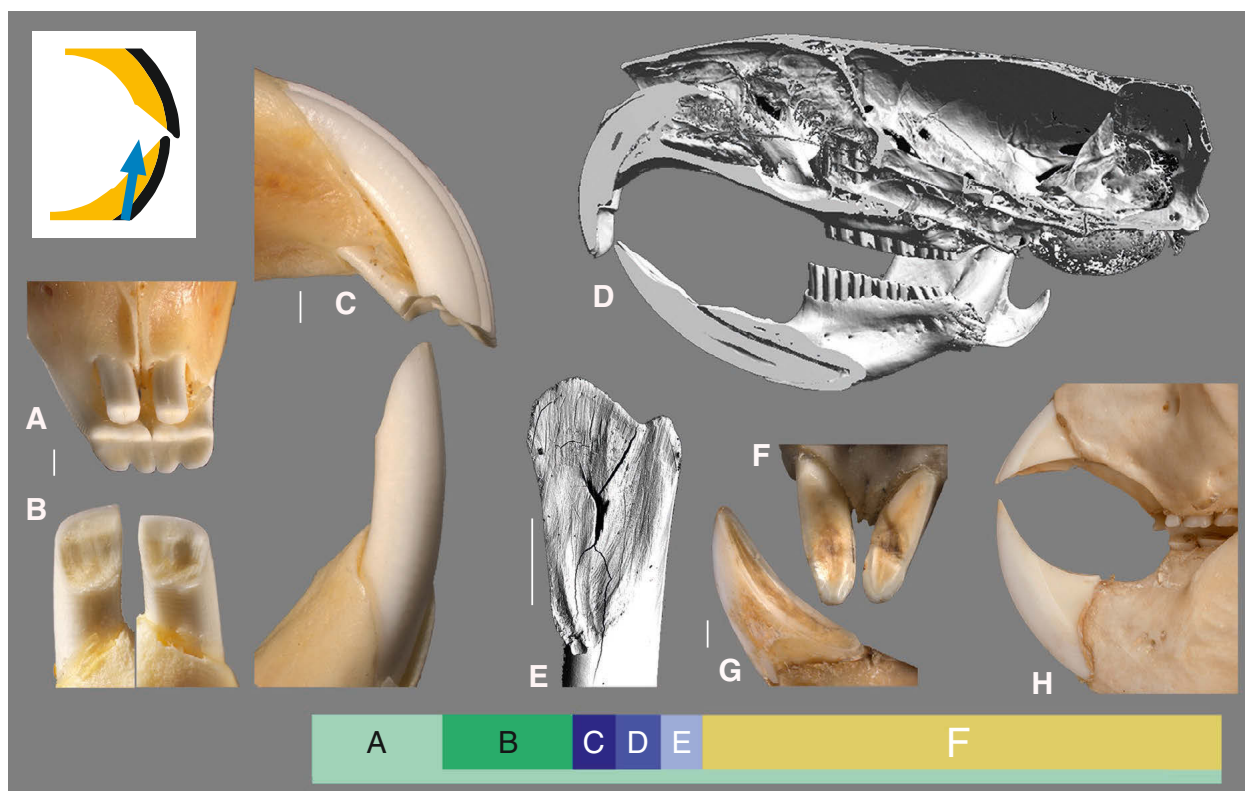
Fig. 9.10. Occlusal surfaces specialized for wear stage F. These teeth have enamel only on one side and may form nipper facets. The antagonist sharpens the blade by removing the dentin. **A–C,** *Lepus europaeus*, Recent, Germany (IGPB M 6241). **A,** wear facets on the upper incisors with a typical step caused by the lower incisor. **B,** lower incisors with marks caused by the upper ones during sharpening. Especially for sharpening the lower jaw is pushed forward so far that the upper incisors contact the posterior sides of the lower incisors. **C,** functional interaction of the two upper incisors with the lower incisor. **D,** *Microtus gregalis*, Recent, Fairbanks, Alaska (IGPB M 1005). Virtual section showing the interaction of lower and upper incisors when molars are well separated. **E,** *Otomys angoliensis*, Recent, Makapansgat, South Africa (IGPB-KOE 3356). Occlusal surface of lower incisor with scratches made by the upper incisor during sharpening. **F–H,** *Daubentonia madagascarienis*, Recent, Madagascar (SMF 1583). The nipper facets of upper (**F**) and lower incisors (**G**) are well polished and show no striations from the antagonists. They are very pointed due to the high-oval cross-sections. **F,** the upper facets grooves indicate where the tips of the lower incisors normally occlude. **H,** lateral aspect of the anterior dentition. The incisors occlude when the molars are very close. Scale bars equal 1 mm, D not to scale. Photos: G. Oleschinki.

al. 2019). Therefore, it is hard to decide whether the uniform power stroke represents phase I or phase II of the chewing cycle. Either the horizontal movement combines phases I and II with an adjusted inclination, or the horizontal grinding results from an expanded phase II found in teeth with an ectoloph-guillotine, as in most early Equoidea.

Nipper facets
(Fig. 9.10)

Nipper facets are best compared with a pair of end-cutting pliers. They are well known in rodent and lagomorph incisors. The one-sided enamel of the euhypsodont teeth is restricted more or less to the anterior side and forms a cutting edge, while the widely opened dentin is exposed on the lingual side. The two antagonistic blades cooperate like chisels, but during mastication they do not touch each other. Mostly the upper tooth is holding the item, whereas the lower one is cutting or gnawing into it. This type of blade facet is attributed to wear stage F because enamel is limited to one side and the dentin dominates intensively.

The teeth require a mutual sharpening by the antagonist. The cross-section of the incisors determines the shape of the cutting edge. It may be broad as in *Lepus* (Fig. 9.10A–C) or pointed as in *Glis*. The edge itself is formed by enamel. Because no attritional facets are recognizable on the enamel, it seems to break off. But the dentin has to be removed regularly to expose the enamel crest. During the sharpening process, the mandible with the incisor has to be shifted forward or backward in relation to the upper incisor. It has to be moved forward to such a degree that the cutting crest of the upper incisor can scrape its dentin the full length of the facet. Normally the upper incisor is positioned more anteriorly than the tip of the lower incisor. A distinct notch in the dentin of the upper incisors marking the contact with the lower incisors (Fig. 9.10A, C) occurs in some rodents and lagomorphs.

Besides lagomorph and rodent incisors, nipper facets occur in various other mammalian groups. The incisors of the primate *Daubentonia* have nipper facets mistakable for those of Glires (Fig. 9.10F–H).

Euhypsodont incisors with an enamel band occur in various mammalian orders, e.g., *Groeberia* and *Patagonia* (Gondwantheria), *Vombatus* (Marsupialia), *Tillodus* (Taeniodonta), and *Pyrotherium* (Pyrotheria), but not all form nipper facets due to the different orientation of the teeth.
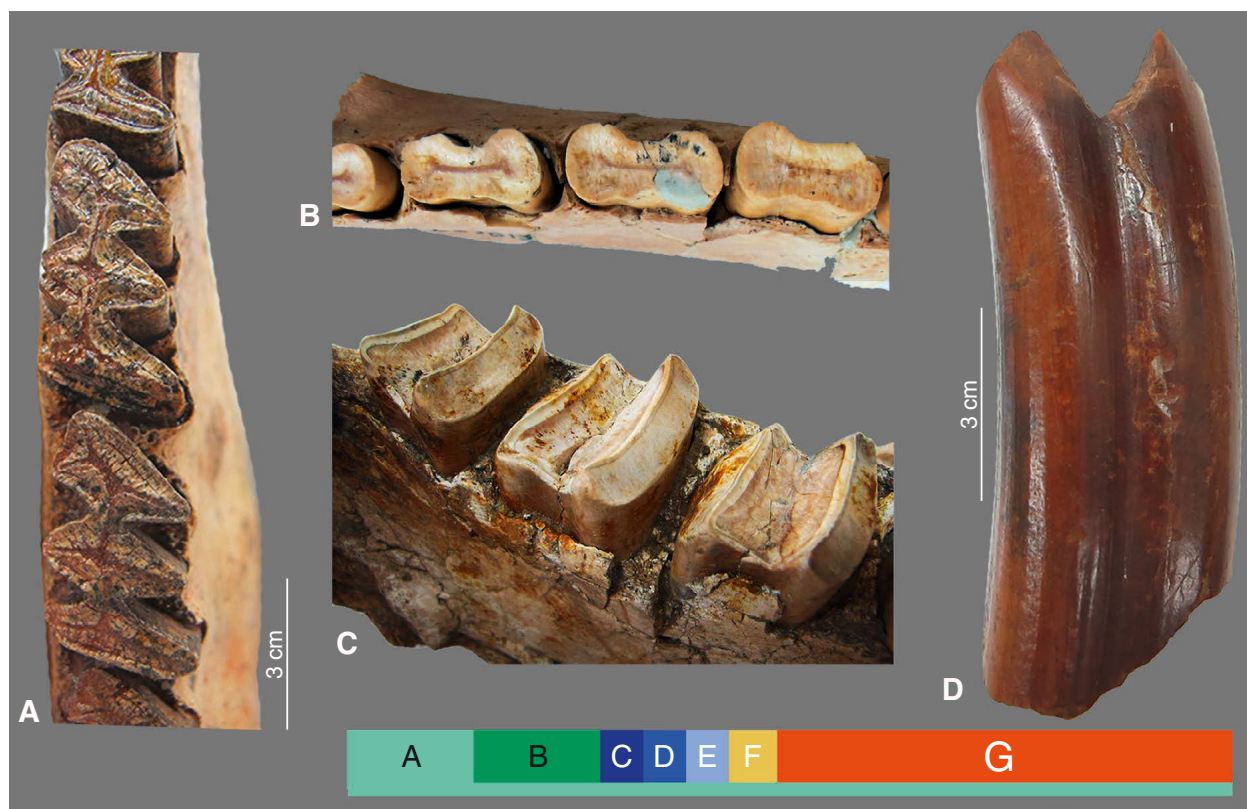
Fig. 9.11. Occlusal surfaces specialized for wear stage G. Dentin teeth may have had a primary enamel cap, but this is functionally insignificant. **A,** *Glyptodon* sp., part of the dentary, Pleistocene, Salta Prov., Argentina (LACM 64153). The cheek teeth show the differentiated dentin. **B,** *Holmesina floridanus*, cheek dentition of the mandible, Pliocene, Haile, Alachia Co., Florida (UF 223813). **C,** *Eremotherium*, part of the mandible, Pleistocene, Florida (UF). The ridges of the bilophodont occlusal surfaces are of dentin. **D,** *Eremotherium carolinense*, fragment of cheek tooth, Ecuador (LACM, no number). The entire tooth is formed by dentin, the crests are of orthodentin. B and C not to scale. Photos by the author.

Teeth adapted to function without enamel – dentin teeth
(Fig. 9.10)

In many teeth, the final wear stage (G) is reached, when all enamel is gone and only a stump of dentin may be left. Several mammals, however, evolved well-functioning dentin teeth. To complete the picture of wear stages, such dentin teeth are included here and briefly discussed. Due to a differentiation of the dentin, it may show distinct facets comparable with those of enamel.

Dentin teeth with external hypsodonty have almost always a significant function in the social environment that causes no regular wear.

In dentin teeth with an internal hypsodonty, the teeth are either abraded smoothly and form a well-rounded cusp, e.g., in *Physeter*. In Xenarthra, the dentin is not uniform but differentiated into orthodentin, osteodentin, and vasodentin. They differ somewhat in their physical properties, causing characteristic ridges on the occlusal surfaces in different patterns (Green & Kalthoff 2015). In armadillos, the outer layer is of relatively hard orthodentin surrounding a core of vasodentin. In Glyptodontidae, the trilobite cheek teeth have inner ridges where osteodentin surmounts the surrounding orthodentin (Fig. 9.11A). In contrast to the relatively flat occlusal surfaces seen in glyptodonts or *Holmesina* (Fig. 9.11B), Megatheriidae, (e.g., the giant *Megatherium* or *Eremotherium*, Figs. 9.11C,D) have bilophodont cheek teeth with a high profile. The crests are formed by orthodentin, whereas the slopes are of vasodentin or cementum. They allow a perfect self-sharpening of the euhypsodont teeth.

The correlation of the heterochrony of specialized wear facets with ontogenetic wear stages

Although limited in comparison with the vast variety of mammalian teeth, this survey shows that establishing general ontogenetic phases allows one to characterize the heterochrony of tooth formation and function, even if they are very divergent. Such a comparison illustrates the significance of heterochronies and general tendencies in the evolution of mammalian dentitions.

Tooth morphology allows to reconstruct the sequences and duration of ontogenetic phases. Although these ontogenetic phases of early life history remain theoretical, the evolution and variability of hypsodont teeth show a tight correlation between early ontogeny and the final tooth. They illustrate the manifold ways in which hypsodont teeth can be built in order to provide tooth material that compensates for intensive wear.

Another example of heterochrony in teeth occurs when tooth wear causes destructive abrasion. Only in some teeth is the primary enamel surface of functional importance. In many other teeth, for optimal function part of the enamel has to be worn away and the dentin has to be exposed in the secondary occlusal surface. The abrasion of the enamel occurs not randomly but in specific areas to prepare specialized facets. Although wear is very variable, a number of specialized wear facets can be defined. They are characterized by their long-lasting similar function, despite progressing wear. They are assigned to a series of subsequent wear stages, using the amount of exposed dentin as a guideline.

Thus, similar to the heterochrony in the ontogenetic stages, the functional duration of specific wear stages is extended at the cost of other (theoretical) wear stages.

Heterochronic shifts occur frequently in mammalian phylogeny because altering the duration of ontogenetic phases seems to be less problematic than inventing new characters. Thus, the life history of teeth is determined by different kinds of heterochrony.

Acknowledgments

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