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Specialized wear facets and late ontogeny in mammalian dentitions

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ABSTRACT

Many types of wear facets can be found in mammalian teeth. Some are related to the initial surface, others use the cross-section of the enamel as the main tool. In primary occlusal surfaces facets mark the gradual wear, that are related to a relatively late ontogeny. Facets in teeth with secondary occlusal surfaces, however, represent specific arrangements of crests of enamel and dentine. Such facets require some initial wear to become fully functional. The tooth morphology guarantees such facets to be effective for a long period of time. Therefore they can be discriminated as specialized facets. From the different types of facets three specialized ones were selected, blade facets, rasp-facets, and nipper-facets, because they ate widely distributed, function differently, and are comparable with mechanical tools. They are long lasting and differ in the amount of exposed dentine. The amount of dentine is used to differentiate phases during late ontogeny, the part of the life history, when teeth are exposed to wear. Consequently the various types of facets can be related to different ontogenetic phases. The relevant phases are prolonged at the cost of other ontogenetic phases. Therefore, the various specialized wear facets represent heterochronies within the ontogeny of teeth.

Introduction

Tooth wear is a destructive process and not much appreciated by most paleontologists that work in systematics, because wear eliminates details of tooth morphology that are useful for identification of species and furthermore for the study of their phylogenetic relationships. Tooth wear, however, is an immediate consequence of the main purpose of teeth, the acquiring and mechanical diminution of food items. Much work has been done on the homology of wear facets (e.g. Crompton 1971; Butler 1952, 1972, 1973; Maier 1980) and describing their precise orientation (Kullmer et al. 2009). These studies, however, concentrate mainly on primate teeth or tribosphenic molars (Ungar 2015) and much less on large herbivores that show interesting specializations as well.

This study concentrates on the occurrence, function and arrangement of three specialized wear facets that are formed by enamel and dentine. These facets are found to occur repeatedly in fossil and extant Marsupialia and Euplacentalia. The function of teeth that can be deduced from the study of wear facets. The job of teeth and their facets is the diminution of food. The great diversity of mammalian dentitions is like a toolbox full of implements for this purpose, therefore the aim of this paper is to better understand the mechanical function of tooth morphology. Good tools are invented by skilled craftsmen to fulfil specific functions in an optimal way. During evolution tooth morphologies have been selected that function well but not always in an optimally. In several functional complexes, however, initial wear corrects this discrepancy.

Two kinds of teeth can be differentiated in terms of function (Fortelius 1985). One group is formed by teeth that work sufficiently with their initial enamel cap, the primary occlusal surface. Most species with tribosphenic teeth having a high or low tooth profile represent this group, e.g. chiropterans, lipotyphlans, early primates. Among larger herbivores and mixed feeders those with brachydont and bunodont teeth belong to this group, too, e.g. *Phenacodus*, *Ursus*, *Sus*, and *Homo*. These teeth function well as soon as they are erupted and in position in the tooth row. The wear progressively modifies the occlusal surface continuously by reducing the profile and exposing the dentine gradually. In late stages the occlusal surface is flattened, and a rim of enamel surrounds the dentine field. In the very last wear stages only a dentine stump may be left, if the individual lives long enough. In dentistry, this procedure of gradual destruction is called *abrasion dentium* and *demastication* (Imfeld 1996) and obscures to some degree the importance of other kinds of wear.

A second major group of teeth requires some initial wear to reach full functionality in a secondary occlusal surface. The dentine is partially exposed and the cross-sections of the initial enamel cap form the most effective functional tools. Here the exposure of the dentine is not a sign of advanced individual age. The initial occlusal surface is of minor importance and the formation of specific facets is due to initial wear. Such specialized facets in secondary functional surfaces are the main topic of this paper. The architecture of the relevant teeth predetermines not only the position and the function of these facets but also their long lasting functional stability despite continuous wear.
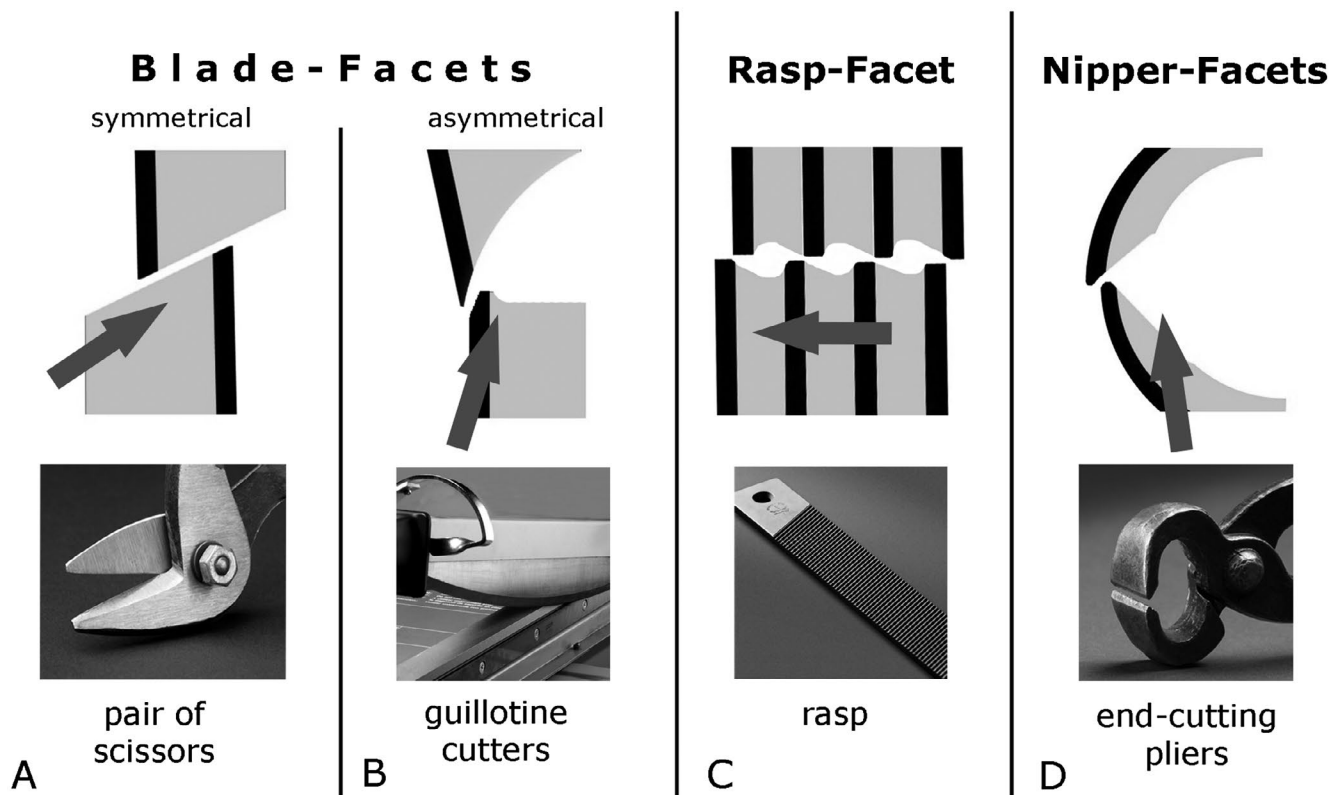
Figure 1. Schematic representations of three types of differentiated facets in combination with technical tools of similar functions. (A and B) Blade facets. (A) A symmetrical arrangement of two blades sliding past each other, comparable to a pair of scissors. Such a symmetrical pair of blade-facets occurs in two tooth types, carnassial and bilophodont-scissors. (B) An asymmetrical arrangement characterized by one blade-facet passing an antagonistic tooth of different morphology comparable to a guillotine-cutter. This arrangement is found in ectoloph-guillotine type facets. (C) Rasp-facets with alternation of enamel crests and excavated dentine or cementum fields occlude predominantly with rasp facets on an antagonist. (D) Nipper-facets in rodent incisors comparable with a pair of end-cutting pliers.

Such facets occur in carnivorous mammals as carnassial or in herbivores as grinding, shearing, or gnawing facets.

The function of the facets is compared to mechanical tools, such as scissors, guillotine cutters, and rasps. The function of teeth occurs mostly between antagonists. The corresponding facets may be similar or dissimilar in their construction, therefore the interaction between teeth has to be taken into account. The movement of the mandible that is achieved through the complex arrangement of the masticatory apparatus (e.g. Turnbull 1970; Crompton et al. 2010), is deduced from the wear facets and visualized in a mastication compass (Koenigswald et al. 2013).

The great diversity of mammalian teeth provides very different types of facets, some types are restricted to specific taxa (e.g. Lazzari et al. 2015; Engels 2011), and others evolved independently in various lineages. Differentiating all the various types of facets is beyond the aim of this paper, but three types of specialized facets that are wide spread are selected and discussed further. The first one (Figure 1(A) and (B)), the blade-facet, occurs mostly in brachydont molars. Blade-facets occur in a symmetrical arrangement in carnassials and bilophodont-scissors, and in an asymmetrical arrangement in what is here termed the ectoloph-guillotine. The second type of facet, the rasp-facet, occurs in brachydont and hypsodont molars, whereas the third one, the nipper-facet, occurs in euhypsodont incisors only. These three types were selected because they are wide spread among mammalian dentitions and share important functional similarities.

All of them require some initial wear to reach full efficiency in secondary functional surfaces. The three types of facets differ in the amount of exposed dentine which allows a correlation to a more general scheme of the ontogeny.

Wear occurs only when erupting teeth have reached the occlusal level of the tooth row. Thus, that part of tooth ontogeny when teeth are formed in the crypt is of minor significance here. Wear characterizes the second part of the life history of teeth and is referred to here as late ontogeny. This late ontogeny can be structured by a sequence of wear stages measured in relation to how far the dentine is exposed. In most teeth with primary occlusal surfaces without specialized wear facets, the various wear stages follow continuously one after the other. Such wear stages are used for discriminating of age groups. Using such wear stages as a guide line, the three groups of specialized facets in secondary occlusal surfaces represent different wear stages and their relationship to specific ontogenetic phases. This illustrates the different structural specializations and their evolutionary history.

Thus the approach of this paper differs distinctly from studies of tooth wear that employ methods of meso- and microwear that concentrate on dietary reconstruction (Fortelius & Solounias 2000; Kaiser et al. 2000; Solounias & Semprebon 2002; Solounias et al. 2010, Kalthoff 2011; Ungar 2015, 2016). A differentiated look at the various types of facets as well as the roles of enamel and dentine may contribute to a better understanding of meso- and microwear (Mihlbachler et al. 2016).

Materials and methods

This study concentrates on the occurrence, function and arrangement of three specialized wear facets that are formed by enamel and dentine. These facets are found to occur repeatedly in fossil and extant Marsupialia and Euplacentalia.

The main observations were made on original material while dealing with mammalian teeth in the field or during many visits to various museum collections throughout the last decades. Observations were made in the traditional way with hand lenses or binocular microscopes, but the SEM and µCT were applied as well. In addition to the tooth surface, sections available e.g. from studies of the schmelzmuster (Koenigswald 1980, 2004; Koenigswald et al. 2015) were considered.

The differentiation of enamel and dentine is important for understanding the function of the facets. In most fossil teeth, enamel and dentine were colored differently during fossilization and thus both materials can be differentiated easily. In recent teeth both materials are light, and the enamel is often opaque which sometimes hinders the differentiation of these materials making recognizing of facets more difficult. In some cases, if allowed, teeth were stained. After washing the teeth or jaws in H_2O_2, a solution of 1% Methylene blue was applied for one minute. After washing the bone and the dentine are bluish while the enamel remains lighter. Casts were investigated, if available. Generally they show facets well, but no striations, and differentiating enamel from dentine is often impossible.

Other data were collected from photos of mammalian dentitions provided by the Animal Diversity Web (Myers et al. 2016) and from pictures in the literature. The first choice was textbooks, although only a few have sufficiently detailed figures of the dentitions. Of great help was the extensively figured book on mammalian dentitions by Thenius (1989). These drawings indicate the facets, but details of their inclination or the direction of wear scratches were not available. Thus, even these figures do not provide sufficient information about the tooth function, as is true of most drawings in the literature on mammalian teeth. References to classification are only used here for easier orientation and characterizing the taxa – nomenclature follows the arrangement used by Rose (2006).

Lucas (2004) used 'mortar and pestle' as an analogy for describing a specific interaction of tribosphenic teeth. Here everyday tools such as scissors, rasps, nippers, end-cutting pliers, and guillotine-cutters are used to illustrate the specific function of facets. The movements of the left lower jaw are visualized by the mastication compass that differentiates between the two phases of the power stroke and the direction and the inclination during each phase (Koenigswald et al. 2013).

It is impossible to list all specimen studied or figures investigated, although they all contributed to the background knowledge, from which the ideas were developed. Therefore selected literature is cited to provide informative figures and detailed collection data are restricted to specimens figured in this paper.

Terminology of tooth morphology, tooth functions, tooth facets and life history of teeth

Tooth morphology

Occlusal surface is the working surface of a tooth. The primary occlusal surface describes the enamel cap of teeth that are fully functioning after eruption. Wear modifies the surface and reduces the functionality by leveling the cusps. The secondary occlusal surface is characterized by specialized facets that require a specific degree of wear to become fully functional (Fortelius 1985).

Enamel cover and enamel band: The enamel cover refers to the unmodified surfaces of the erupting tooth or the surfaces slightly modified by initial wear, as long as the dentine is not exposed. The term enamel band describes functional cross-sections of the enamel cap neighboring dentine. The enamel band may form a sharp edge of a blade or a crest surmounting the dentine field.

Molar wear gradient: The molar wear gradient compares the wear in the first and the last molar in a tooth row. If they are worn to a similar degree the gradient is low. If the m1/M1 are worn much more intensively than the last molars the gradient is high (Koenigswald 2014a). This use of the term 'molar wear gradient' differs from other usages (Teaford 2005; Fortelius & Solounias 2000).

Tooth functions

The scale on which the comminution of food is studied is of great importance for the terminology. In tribology considering mastication on a very detailed scale, the properties of the food are very important. In this paper the general shape of the facets and the tooth morphology is investigated at a much larger scale and therefore can be compared to mechanical tools.

There have been various attempts to differentiate the function of teeth in terms of piercing, cutting, grinding, and so forth (Rensberger 1973; Kay & Hiiemae 1974; Schultz & Martin 2011). Some of them used the angle of the functional plane between antagonists as a major criterion. Here the arrangement of facets between the antagonists and the distribution of enamel and dentine is used as are simple definitions for cutting, gnawing, and grinding as these seem to be sufficient for the aim of this study.

The term 'cutting' has been used in different ways. Here it is used in a very general way for the dissection of food items by one or two blades. Differentiation of the term is offered by the comparison to specific tools.

Knife-cutting: cutting with a single blade. It is equivalent to the cutting described by Rensberger (1973), who restricted the term cutting to the separation of food items by a single sharp edge, like a knife, that is pressed against another surface. This requires that the object to be dissected is fixed in one or the other way. Such cutting without an antagonist is rare in the context of teeth, but occurs, when the blade like canines of a saber-tooth cat (e.g. *Smilodon*, *Thylacosmilus*) penetrated into the prey.

Shear-cutting: cutting between two sharp scissor blades that slide past each other, exactly as in a pair of scissors (Figure 1(A)). Some compression occurs immediately before this cutting but

no parts of the occlusal surface are involved. The terms shearing and cutting were discussed by Schultz and Martin (2011) for tribosphenic molars. Rensberger (1973: Fig. 5b) figured a very similar model compared to Figure A, but he did not differentiate between enamel and dentine. He emphasized the lateral movement, and thus he regarded the comminution of the food as an initial phase of grinding.

Guillotine-cutting: cutting between one blade-facet and the (blunt) edge of an antagonist, as in the ectoloph of browsing rhinos. The antagonistic lower teeth may have support-facets on their buccal rim (Figure 1(B)). Ungar (2015) used the guillotine as a general analogy for the dissection of the food. Because a proper guillotine works with one blade only, the term guillotine is not well suited as an analogy if two blades are involved. Thus the term 'guillotine' is used in a different way as by Harris (1975) for the dentition of *Deinotherium*.

Grinding is used here for the comminution of food between two rough surfaces, similarly to Rensberger (1973). The roughness is given by two or more enamel crests that project somewhat above the remaining surface made up by eroded dentine or cementum. The cross-section of the enamel band forms crests surmounting the dentine (and cementum if present). These crests are rounded and have generally no distinct facets as in most blades. Therefore the illustrative term 'multi-blade-facet' (Fortelius 1985) does not fit exactly. The food is compressed by the entire occlusal surface and squeezed across the enamel crests and thereby disintegrated. Grinding occurs between the rasp-facets (Figure 1(C)).

Gnawing describes the cooperation of two enamel crests in anterior teeth working as antagonists. These blades do not slide past each other, but meet each other as in end-cutting pliers or a pair of nippers (Figure 1(D)). Gnawing occurs with nipper facets.

There are contradictory definitions for the term 'facet' or wear-facet (e.g. Fortelius 1985), especially in terms of whether facets are restricted to the enamel or include dentine areas as well. Such differences are often related to different taxa studied. In this paper, the term facet is used in a general sense describing facets as those parts of occlusal surfaces that are modified by wear, either by abrasion, by attrition, or by both. Consequently facets may be situated totally within the enamel surface or include enamel and dentine. Facets are related to specific sections of the power stroke. If mastication includes two phases separated by centric occlusion two distinct sets of facets may occur in different parts of the tooth. If no centric occlusion marks the margin between the two (possible) phases only one facet is present extending across the entire occlusal surface, as in many rasp-facets. Facets caused by interdental wear are of minor significance and damage on teeth caused by bruxism or individual pathologies are not considered here.

Facets cooperate with antagonistic facets, mostly. Therefore, the arrangement of antagonistic facets has to be considered. If these pairs are similarly constructed the arrangement is regarded as symmetrical, if not, as asymmetrical, as in the ectoloph-guillotine.

Tooth facets

Abrasional facets occur due to the removal of tooth material by food items and occasionally by detritus, i.e. tooth-food contact (Addey & Shellis 2006). Most often abrasion and attrition are combined. If abrasion is dominant, facets within enamel are often rounded and have no clear marginal edges. If the dentine is exposed abrasion creates the 'Greaves effect', an asymmetrical erosion of the dentine (Greaves 1973; Koenigswald 2016).

Attritional facets are more planar and often show striations. Generally they are regarded as predominantly formed by tooth-tooth contact. If the facet includes dentine, the dentine generally is not eroded deeper than the enamel. Striations are common in the enamel and occur occasionally in the dentine (Green & Kalthoff 2015). The differentiation between abrasional and attritional facets is not always easy since both factors may be involved.

Bilophodont-scissors describe the symmetrical arrangement of blade-facets on transverse lophs of upper and lower teeth. They occur predominantly in bilophodont dentitions.

Blade-facets are planar cutting facets with a single enamel blade on the leading side that is backed up by dentine. The blade is formed by the cross-section of a thick enamel band. The enamel is truncated by a planar (attritional) facet and has mostly a sharp edge. The facet continues from the enamel into the dentine smoothly, forming the sliding surface for the antagonistic tooth. Blade-facets occur in two arrangements, a symmetrical one that is formed by two similar blades and function like a pair of scissors (Figure 1(A)). The second arrangement is asymmetrical and resembles a guillotine-cutter with only one blade (Figure 1(B)). For details see below.

Ectoloph-guillotine describes an asymmetrical arrangement with one blade-facet on the ectoloph in uppers and a differently shaped antagonist in lower teeth. The contact area on lowers may be marked by a support-facet.

Nipper-facets occur in euhypsodont incisors and are characterized by one-sided enamel which forms the cutting edges. The cross-section of the tooth controls the shape of the enamel crest. This functional crest is backed up by a sloping dentine field covering the entire cross-section of the tooth. This sloping dentine field is mostly formed by attrition, but not used as a sliding plane. Nipper-facets occur always as pairs, and the enamel is situated in both antagonists on the anterior side. Therefore, this arrangement can be compared with end-cutting pliers (Figure 1(D)). One important function of nipper facets is gnawing.

Rasp-facets are grinding facets that mostly enclose several enamel crests between fields of dentine and cementum. The functioning crests are formed by the projecting cross-section of the enamel band. These enamel crests are mostly rounded by abrasion, but sometimes show an attritional facet. In the simplest form the enamel crest is formed by the surrounding enamel band only. In mechanically more derived facets the dentine core is structured by enamel islets or lateral in-folds of the enamel band. The dentine is generally somewhat eroded and shows the Greaves effect. Teeth may be brachydont, hypsodont, or even euhypsodont for compensating intensive wear. The rasp-facet may cover part of the occlusal surface or the entire one. A rasp-facet occludes with a similar facet in the antagonist, and thus the arrangement is always symmetrical. A technical equivalent of a single rasp-facet is the eponymous rasp or file (Figure 1(C)). The function of antagonistic rasp-facets is grinding as between mill stones. Effective grinding happens only in one direction – and not back and forth.

Support-facet: In the ectoloph-guillotine, the large blade-facet on the ectoloph requires some kind of an antagonist. A small facet, called here a support facet, may occur on the buccal rim of lower molars and premolars. Although such a support is important for the function of the blade-facet, not all taxa with an ectoloph-guillotine have a specific support-facet.

Life history of teeth

The term ontogeny was created by Haeckel in 1866 and describes the changes of individuals during their entire life history, from the fertilized egg to the individual death. Haeckel used this term for the development of individual organs as well. The term ontogeny is used here in this broad sense and applied to the life history of teeth including tooth formation as well as the various stages of wear. Tooth eruption marks the border between early ontogeny during which a tooth is formed and erupts, and a late ontogeny during which the tooth is worn down passing through different wear stages. These wear-stages can be estimated from the amount of dentine exposed as applied in some taxa for the estimation of the individual age (Freudenthal et al. 2002; Holland 2013). In teeth with a secondary occlusal surface and with a specialized facet, the phases of late ontogeny are not of equal duration and significance. Comparing and emphasizing these differences between the phases of late ontogeny, the term heterochrony can be applied here (McNamara 2001, McNamara & McKinney 2005; Renvoisé & Michon 2014).

Blade-facets

Various types of blade-facets are widely distributed in the postcanine dentition of carnivorous and herbivorous mammals, including the well-known carnassial. The term 'carnassial', however, cannot be extended to herbivores, where functionally similar blade-facets occur. Full functioning teeth with blade-facets are often characterized by a partial opening of the dentine that occurs after a relative short phase of initial wear.

A typical blade-facet is characterized by a single cutting edge formed by a relatively thick enamel band on the leading side (Figure 1(A)). The cutting edge is backed up by dentine. The truncated enamel band is well polished by attrition and often has a very sharp edge. The facet on the enamel band continues without a step into the dentine-platform on the trailing side. Thus enamel and dentine form one planar facet. The dentine is not excavated but forms the sliding surface for the antagonist. Thus blade-facets resemble mostly attritional facets. If an enamel-band is truncated at the trailing side, it is incorporated into the facet as well and thus has no functional significance. The inclination of the facet may vary from almost vertical to almost horizontal. The inclination is not regarded as a critical character. Blade-facets are mostly related to phase I of the power stroke.

The comminution of the food takes place mainly at the sharp tip of the blade. Together with the antagonist they form a self-sharpening system (Martin 1980; Anders 2011).

Blade-facets occur in different arrangements. Three of them are discussed here. Carnassials and the bilophodont-scissors are symmetrical arrangements with two blades that are sliding past each other. The ectoloph-guillotine is asymmetrical because the single blade passes a differently shaped antagonist.

Carnassials

The typical carnassial characterising Carnivora, is a symmetrical arrangement of two antagonistic blade-facets that are oriented in a longitudinal direction and function like scissors. After shear-cutting at the edges of the blades facets slide past each other. This very successful dental tool occurs in various mammalian groups, e.g. in Carnivora, e.g. *Miacis, Canis, Felis,* and *Hyaena* and in 'Creodonta', e.g. *Hyaenodon* and *Sinopa* (Figure 2). A very similar dental structure exists in the dentition of the diprotodont marsupial *Thylacoleo*.

Carnassials evolved several times in carnivorous mammals and thus in different tooth positions (Butler 1946). In Carnivora a single carnassial is situated at the locus of P4/m1 in the permanent dentition (Figure 2(B)–(F)) and in the deciduous dentition at DP3/dp4. In the fossil hyaenodontids several carnassials are developed in a more distal position. The principal carnassials occur at M2/m3 and M1/m2 (Figure 2(G)) and in oxyaenids at P4/m1 and M1/m2. Despite the different positions, the tooth elements forming these facets are the same. The lower blade-facet is homologized as the buccal sides of paraconid and protoconid, the upper blade-facet is the lingual side of metacone and metastyle (Bryant & Russel 1995). Thus the position of the carnassial is inherited from the primary occlusal pattern of the tribosphenic molar.

The initial surface of the teeth forming the carnassial are highly specialized and predetermine the exact position of the facets. The beginning of wear initiates the facets within the enamel. These initial facets form a sharp edge on the leading side (Figure 2(C)). The functional dominance of the leading side is due to the fact that the facet is slightly less inclined than the enamel surface of the trailing side. With progressive wear the dentine is exposed but the enamel tip of the blade remains sharp. The truncated enamel band on the leading side and the exposed dentine form a single planar facet. The enamel on the trailing edge usually contributes to this facet and does not form an additional crest (Figure 2(D)). The facet in the lower tooth slopes buccally while that of the upper slopes lingually. Thus the mastication movement of the lower jaw is not strictly orthal but slightly deviated to the lingual side and sometimes slightly in an anterior direction (Figure 2(C)). Only one side of the dentition occludes at a time.

During ontogeny intensive wear modifies the inclination of the facet. It is very steep in young animals and becomes gradually less inclined in old ones. This phaenomenon occurs in the carnassials of hypercarnivores to a lesser degree than in those of meso- or hypocarnivores (Anders 2011).

The antagonistic blades function like a pair of scissors. The cutting point is shifting along the blades that slide past each other. In carnassials the cutting points are shifting similarly. Both blades have a deep notch and thus the area of contact between the blades is strongly reduced. Therefore the strength made available by the musculature is effectively concentrated for disintegrating the prey (Popowics & Fortelius 1997). The planar facet behind the intersection forms a perfect sliding plane that contributes as a passive element to an optimal function of the scissor.

In hypocarnivore dentitions, e.g. in those of ursids and some mustelids, the cusps of the carnassials are lowered and the blade-facets partially reduced. Thus the wear pattern in these
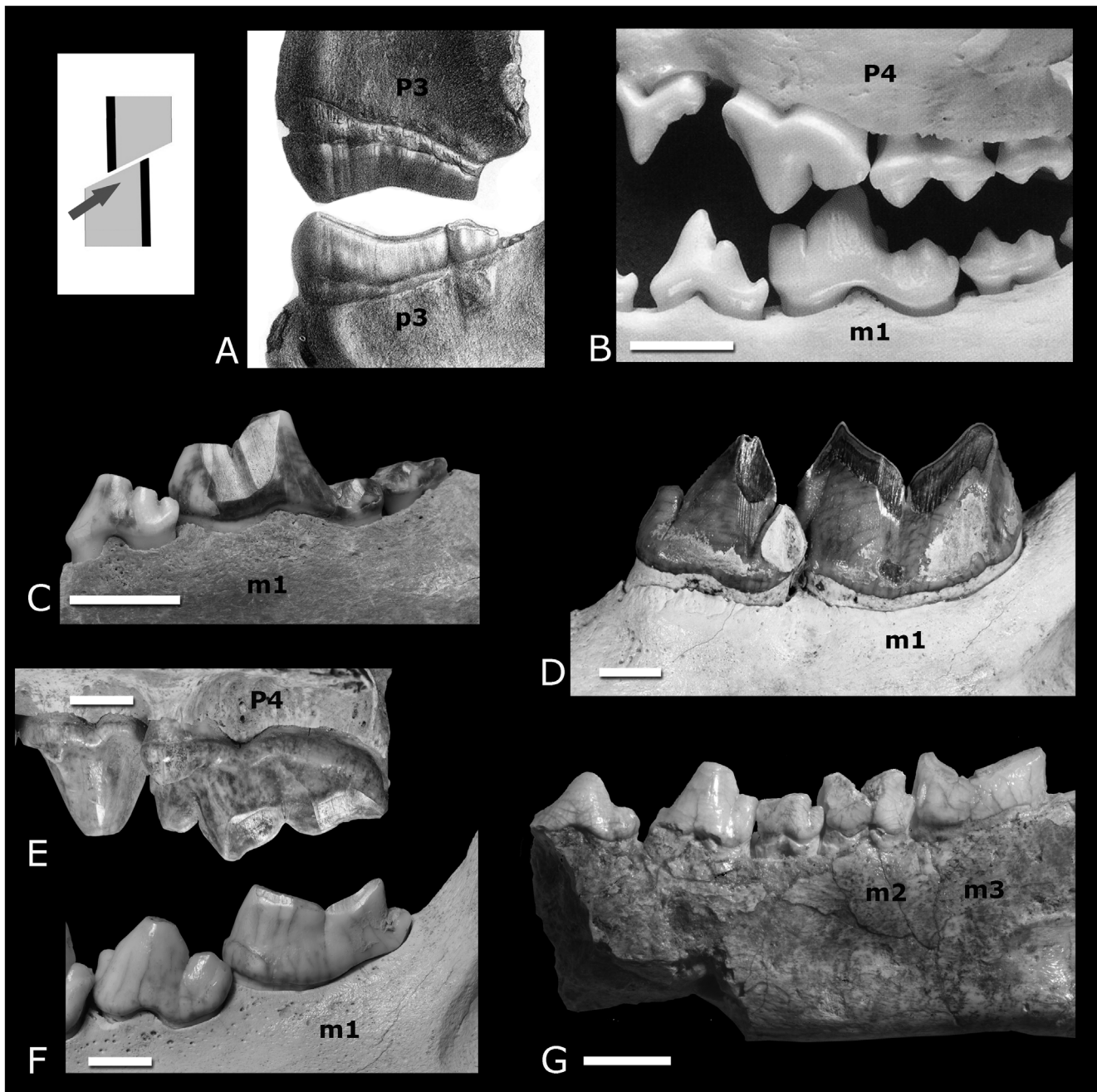
Figure 2. Symmetrical arrangement of blade-facets in carnassials. (A) *Thylacoleo carnifex*, Pleistocene, Australia (from Owen 1859 and 1871, inverse). The carnassial is situated between the upper and lower P3/p3 and has no notch. (B) *Vulpes vulpes*, Recent, Germany [STIPB-M 625]. In canids the trigonid of the m1 and the P4 form the carnassial. (C) *Canis lupus,* left mandible p3-m1; Upper Pleistocene, Germany, [STIPB- M528 inverse]. The blade facet in the enamel shows the striation of a not strictly orthal jaw movement. (D) *Xenosmilus hudsonae,* left p4 and m1. Upper Pleistocene, Haile, Aluacha Co. Florida USA, [UF 60000]. The dentine is opened in the blade facet and shows an almost orthal jaw movement. (E) *Crocuta crocuta spelaea* lingual aspect of right P3 and P4. Upper Pleistocene, Biggetal, Germany [STIPB M 404]. The blade of the carnassial is on the lingual side of the P4. (F) *Crocuta crocuta spelaea,* left lower p4 and m1, Upper Pleistocene, Aufhausen cave, Württemberg, Germany [SMNS 32658]. (G) *Hyaenodon leptorhynchus,* lower Oligocene, Gunzenheim, Bavaria, Germany [BSPG 1934 V 3, inverse]. The carnassials are in m2 and m3. - Scale bars equal 1 cm. Arrows indicate the mesial direction. - A from Owen (1859) inverted; Photos B, C, E, F by Georg Oleschinski; G from Kurt Heissig.

groups is more similar to bunodont dentitions, where the initial enamel surface is functionally more important.

In marsupials, *Thylacoleo carnifex*, the marsupial lion (Figure 2(A)), possesses a carnassial between the upper and lower P3/p3 that was compared to those of Carnivora (Owen 1859, 1871), although it evolved totally independently. Both teeth provide blade-facets in a symmetrical arrangement. In contrast to the carnassial in Carnivora the cutting blades are only slightly curved, and not deeply notched.

Bilophodont-scissors

A pair of symmetrical blade-facets on transverse lophs characterize this specialized facet arrangement. Functionally they are similar to carnassials but are oriented transversely and are less inclined. Bilophodont-scissors occur in the eponymous bilophodont dentitions on premolars and molars with two or three blades. The blades of the bilophodont-scissors are marked by a truncated enamel band on the leading edge that is backed up
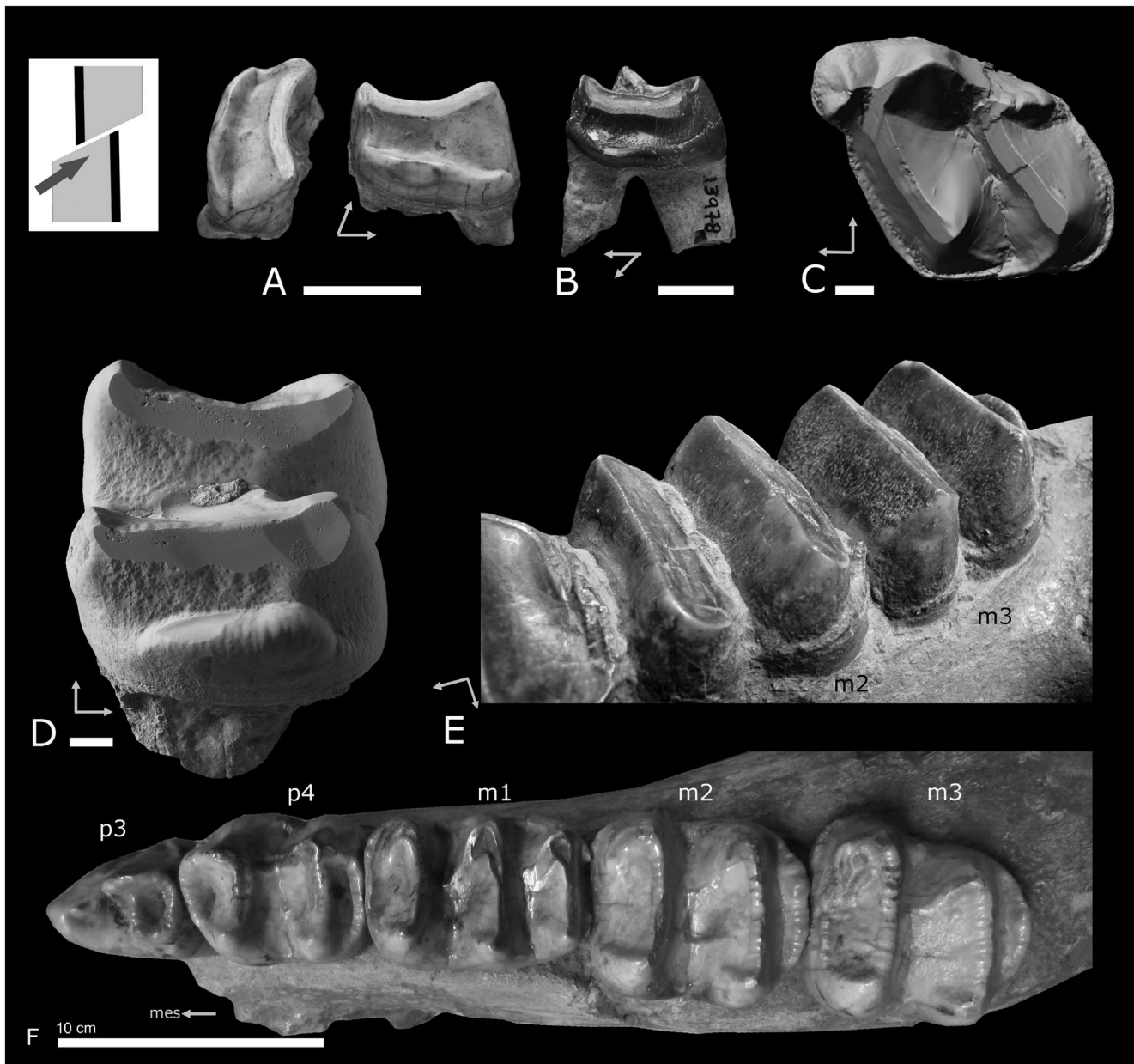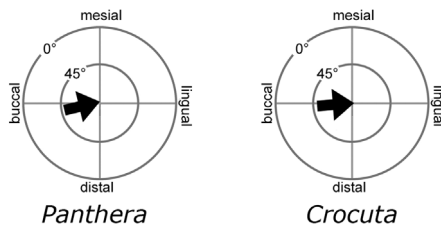
Figure 3. Symmetrical blade facets in bilophodont–scissors. (A) *Protemnodon* sp. (Macropodidae), Upper Pleistocene, Henschke's Quarry, South Australia [STIB-KOE 1729]. The blade-facet on the metalopid in two aspects. (B) *Bathyopsis fissidens* (Dinocerata), left M3, Wasatchian, Eocene, Sublette Co., Wyoming; USA [UM 13978] -KOE 1726]. In the blade facet on the protoloph the dentine is partially exposed. (C) *Lophiodon lautricense* (Lophiodontidae) left M3, Eocene, Robiac, France [HLMD-Ro4]. The blade facets are on the mesial side of proto- and metaloph, and include only small parts of the ectoloph. (D) *Prodeinotherium bavaricum,* right m2, Miocene, Pfaffenhofen, Bayern [BSPG 1953-I-542]. In lower molars the planar blade facets are on the distal sides of both lophs. (E) *Pyrotherium romeroi*, left m2 and m3, Deseadan, Rio Desado, Argentina [MNHN-F-DES 1238]. The planar facets on the distal sides include enamel and dentine, whereas the enamel surface on the mesial sides is used for compression at the end of phase I. (F) *Deinotherium* aff. *giganteum* left mandible with p3-m3, Mindelheim Bayern [BSPG 1958 I 185]. Note the three-lophed m1 and the crenulated carina on the last m3. - Scale bars equal 1 cm. Arrows indicate the mesial and buccal directions. - Photos A, B, C, D, and F by Georg Oleschinski.

by a planar dentine field. The dentine is not excavated, and the enamel band on the trailing side – if present – is incorporated into the facet and has only a minor functional significance. In lower teeth, the facets are sloping towards the distal side and in uppers to the mesial side. The arrangement of several transverse lophs in the tooth row modifies the function. In addition to the shear-cutting at the edge of the blades an intensive compression occurs subsequently between the lophs. Thus the arrangement of bilophodont-scissors differs distinctly from carnassials and the ectoloph-guillotine.
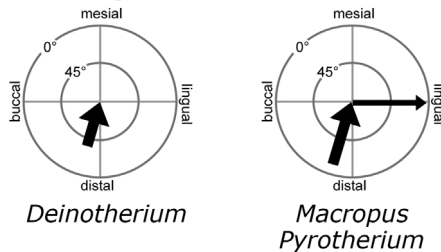
Bilophodont molars occur in various mammalian groups (Figure 3). Typical examples are among Marsupialia, the genera *Diprotodon* (Diprotodontidae) and *Macropus, Protemnodon* (Figure 3(A)), *Sthenurus* etc. (Macropodidae); among Euplacentalia in Pyrotheria: *Pyrotherium* (Figure 3(E)); in Xenungulata: *Carodnia;* in Perissodactyla: *Lophiodon* (Lophidontidae) (Figure 3(C)), *Tapirus* (Tapiridae); in Embrithopoda*: Arsinoitherium;* in Proboscidea: *Deinotherium* (Figure 3(D), (F)), *Phosphatherium, Daouitherium, Barytherium*; in Dinocerata (*Uintatherium, Bathyopsis* (Figure 3(B))) and in Pantodonta (*Coryphodon* where
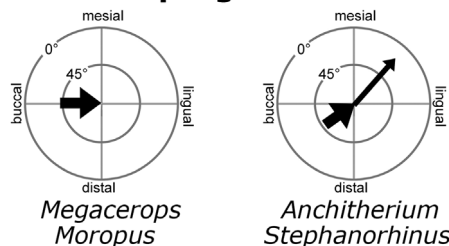
Symmetrical blade-facets

Carnassials

Panthera   *Crocuta*

Bilophodont-scissors

Deinotherium   *Macropus*
Pyrotherium

Asymmetrical blade-facets

Ectoloph-guillotine

Megacerops   *Anchitherium*
Moropus   *Stephanorhinus*

Rasp-facets

Sudamerica   *Elephas*
Vintana   *Arvicola*

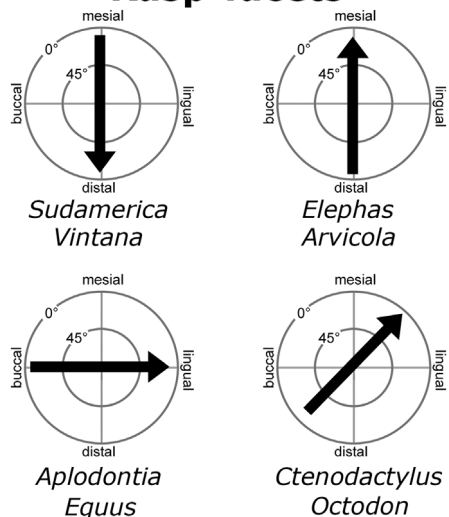*Aplodontia*   *Ctenodactylus*
Equus   *Octodon*

Figure 4. Mastication compass for molars with blade-facets and rasp-facets. The movement of the left lower jaw is depicted. The arrows show the direction, their length the inclination. Phase I ends in centric occlusion in center where phase II starts. The thickness indicates the functional significance. In dentitions with blade-facets the predominant function occurs during phase I, phase II is insignificant or absent. In dentitions with symmetrical blades the direction of phase I is roughly mesial, in those with asymmetrical blade-facets it is lingually directed. Because of the lack of centric occlusion in planar rasp-facets phase I and II cannot be differentiated. The direction of jaw movement varies. It is mostly almost perpendicular to the main enamel crests (see Figure 7 and 8).

the molars are not fully bilophodont and their lophs are oriented obliquely, but the symmetrical blade-facets function very similarly).

For full functioning the blade-facets have to be ground into the enamel. The position of the facets is determined by the morphology of the unworn teeth. The proper orientation and inclination, however, is induced by the first contact with the antagonist. In many cases the carina of the unworn loph is slightly overhanging and pointing in the direction of the later facet, e.g. in macropodids and *Diprotodon* among marsupials and in placentals, e.g. *Deinotherium, Tapirus,* and *Pyrotherium*. In some taxa, e.g. in *Deinotherium,* the overhanging carina is even crenulated (Cuvier 1836) (see m2 and m3 in Figure 3(F)). In *Pyrotherium, Daouitherium* and *Phosphatherium* the carina is crenulated but not overhanging. In all cases the surface area of the first contacts is reduced and eases the proper direction and inclination for the initial facet (Koenigswald 2014a, 2016).

Despite intensive wear the enamel and the dentine show mainly attritional and less abrasional marks. The facets last for a relatively long time, but the inclination of the facets becomes lower with increasing wear and leads to a final collapse of the lophs and the function of the lophs (Koenigswald 2014a; Koenigswald et al. 2015). When the lophs are fully collapsed, they function more or less as grinding facets. Some dentitions with bilophodont-scissors have a high molar wear gradient and thus the premolars may be worn flat whereas the last molar is still pristine, as in *Deinotherium*. In *Tapirus* the wear gradient is low and thus the lophs of the various molars show a similar wear stage. In the tapiroid *Lophiodon* the wear gradient is distinctly higher and thus the lophs in the m1 may be worn out while those in the m3 are in an initial stage (Koenigswald 2014a). In macropodids the wear gradient is even higher and is combined with a horizontal tooth displacement (Sanson 1989). Anterior teeth are worn off and sometimes expelled before the last molar comes into function and develops its blade-facets.

The function of blade-facets is related mainly to phase I of the power stroke. The lower jaw moves with a distinct inclination in a mesial direction. A slight deviation of the mesial direction towards the lingual side is possible, as seen in *Deinotherium* where the ectolophs in the premolars guide the jaw movement in this direction (Figures 3(F) and 4). The edges of the blades may be slightly curved, but there is no deep notch as is common in carnassials. The function during phase I is twofold. First shear-cutting at the edge of the blades occurs. Then the antagonist slides along the facets and the leading sides of the antagonistic lophs compress the food bolus until the lophs interdigitate in centric occlusion. This compression causes some abrasional polishing on the enamel surface of the subsequent lophs. This surface is slightly concave, preventing to some degree, lateral movement of the the compressed food. This doubled function during phase I is shared by most dentitions.

In contrast to *Deinotherium,* the upper molars of tapirs have a distinct metacone and paracone, but these cusps do not form a continuous ectoloph. The upper and lower lophs show the typical facets of phase I. Only with progressive wear do the blade-facets of the transverse lophs incorporate the lingual sides of the metacone and paracone. In the large *Lophiodon lautricence* from the Eocene, the ectoloph is somewhat more expressed but here too, the facets on the transverse lophs are formed first and expand onto the lingual side of the ectoloph (Figure 3(C)).

Facets representing a phase II are much smaller if present at all (Butler 1952, 1965; Koenigswald 2014a, and JJ Hooker personal communication).

A general feature of most bilophodont dentitions, e.g. in *Lophiodon* and *Deinotherium,* is that there are no facets representing phase II and therefore the jaw opens after centric occlusion without a distinct second phase II. In *Macropus* which has a central loph, a small facet for a transverse phase II was found (Sanson 1989) produced by a short movement in the lingual direction parallel to the lophs as documented by electromyography analysis (Crompton et al. 2010). In *Pyrotherium* (Figures 3(E) and 4) minute scratches represent a similar movement after centric occlusion (Koenigswald et al. 2015), but phase II certainly is not significant for the comminution of the herbaceous diet in dentitions with bilophodont-scissors.

Among Neogene proboscideans only *Deinotherium* has the typical bilophodont-scissors, but in some of Paleogene proboscideans similar bilophodont-scissors were observed, especially in *Phosphatherium, Daouitherium, Barytherium,* and *Numidotherium* (Gheerbrant et al. 2005). Parallel evolution within the different lineages cannot be excluded. In contrast to the proboscideans with bilophodont-scissors, the Mammutidae (e.g. *Zygolophodon borsoni* and *Mammuthus americanum*) have typical lophodont molars but no blade-facets at all (Koenigswald 2014b, 2016).

In unitathere *Bathyopsis* (Figure 3(B)) and pantodont *Coryphodon* the bilophodonty is less distinct, because the upper lophs are oriented obliquely, but not parallel and not of the same length. Nevertheless, the lophs have typical blade-facets on the distal side in lower lophs and the anterior side in uppers functioning as scissors. The edge of the blade is very sharp and striations mark the jaw movement in a mesio-lingual direction with a strong inclination. In *Coryphodon* the protolophid is much higher than the metalophid. Its facet is much more worn than that of the lower metalophid. Correspondingly the protoloph spanning between the protocone and parastyle carries a more distinct facet than the shorter loph between the paracone and metacone. An intensive molar wear gradient is seen in *Coryphodon armatus* from the San Juan Basin (UM21691) (Uhen & Gingerich 1995; Rose 2006). Thus Uintatheriidae and Pantodonta do not have typical bilophodont-scissors but resemble this arrangement.

The dentition of the embrithopod *Arsinoitherium* is very specialized (Court 1992) since the premolars and molars do not occlude at the same time and show different functions. The molars of *Arsinoitherium* are bilophed and have symmetrical blade-facets. They show similarities to bilophodont-scissors, but differ slightly because of hypsodont and curved molars. When the molars erupt, those parts where the later facets occur are free of enamel, thus the enamel cover is initially incomplete. The lophs function by having a planar occlusal surface with an enamel band on the leading side and a wide dentine field. The anterior enamel band of the hypolophid crosses the distal crest of the protoloph during phase I. According to the orientation of the facets and the enamel crests the jaw moves in a mesio-lingual direction with a low inclination. The stepwise arrangement of the facets causes a compression of the food at the end of phase I. There is no indication of a phase II. The premolars of *Arsinoitherium* function differently in a guillotine arrangement. In the related *Namatherium* (Pickford et al. 2008) the brachydont

molars function similarly, but owing to the more prominent paracone and metacone the jaw movement is almost horizontal and directed slightly more in a mesio-lingual direction.

Although the symmetrical blade-facets on transverse lophs seem to be an efficient tool for comminuting the diet it was found to be more frequent in Paleogene mammals than in recent ones. Hooker (2000) stressed the frequent occurrence of transverse lophs in the brachydont molars of early placental mammals as brachydont-transverse-lophodont teeth (BTL). He figured the uintathere *Prodinoceras*, the pantodont *Coryphodon*, and the condylarthran *Phenacolophus* as examples. They all have one or two pairs of symmetrical blade-facets.

In numerous rodents lophodont molars evolved, but none of them ever developed a blade-facet. Molars of derived lagomorphs (e.g. *Lepus europaeus*) are characterized by transverse lophs with sharp faceted enamel crests. These facets, however, are inclined to the outer side of enamel and not towards the dentine fields (Koenigswald et al. 2010). Thus, lagomorphs represent another type of functionally different blades. Thus, it seems to be noteworthy that not all taxa with two transverse lophs in their molars evolved bilophodont-scissors.

Ectoloph-guillotine

In molars and premolars with an accentuated ectoloph, a distinct blade-facet may occur that has a differently shaped antagonist (Figure 5). This asymmetrical arrangement is called ectoloph-guillotine, because there is only one blade. Strikingly the antagonist carries no or only a small facet identified as a 'support-facet'. The ectoloph-guillotine is oriented in a longitudinal direction and may be straight or W-shaped. The blade-facet is generally very sharp and backed up by dentine strongly sloping to the lingual side. The cutting function of the blade-facet is related to phase I of the power stroke, whereas the function during phase II differs in the various taxa. The occlusal surface of the lower antagonist is predominantly related to its function during phase II as it occludes with the lingual part of the upper teeth. The asymmetrical arrangement with only one blade characterizes this type of facet. The ectoloph-guillotine occurs in several mammalian orders, e.g. in: Arctostylopida: *Palaeostylops;* Notoungulata: *Pleurostylodon, Notopithecus, Nesodon*; Litopterna: *Diadiaphorus* (Figure 5(C)), *Macrauchenia*; Astrapotheria: *Astrapotherium* (Figure 5(D)), *Astraponotus;* Perissodactyla: *Palaeotherium, Plagiolophus, Mesohippus, Anchitherium* (Figure 5(B)) (Hippomorpha); *Hyracodon (Hyracodontidae); Rhinoceros, Stephanorhinus* (Figure 5(E)–(F)), *Dicerorhinus* (Rhinocerotidae); *Megacerops* (Figure 5(A)) (Brontotheriidae); *Chalicotherium, Moropus* (Chalicotheriidae); Hyracoidea: *Procavia*.

Browsing rhinos

In browsing rhinos (e.g. *Hyracodon, Rhinoceros* and *Stephanorhinus*) the ectoloph is fairly straight and its enamel on the buccal side is steep and forms an ectoloph-guillotine. In the crest of *Hyracodon* the paracone and metacone are more prominent than in *Stephanorhinus*, but that does not affect the function very much. During phase I of the power stroke the blade-facet of the ectoloph is met by the buccal enamel of the paralophid and the hypolophid of the lower teeth. As visible from the facet this movement is not strictly in a lingual direction, but slightly
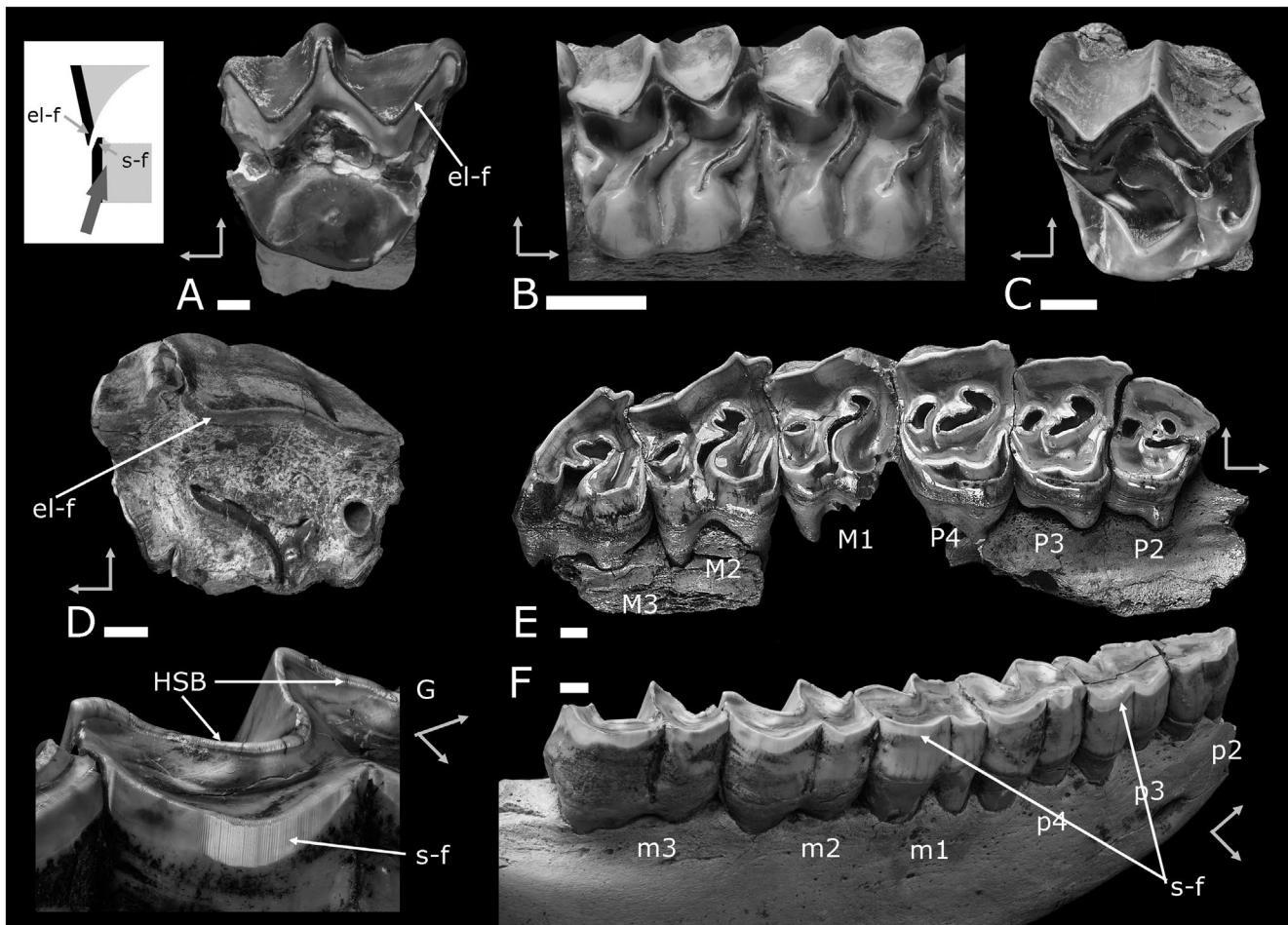
Figure 5. Asymmetrical blade-facets forming ectoloph-guillotines. (A) *Megacerops* sp. (Brontotheriidae), right M2, Orellan, Badlands South Dakota [HLMD WT735]. The blade-facet is W-shaped along the ectoloph. Phase I ends at the massive protocone as a bumper. (B) *Anchitherium aurelianese steinheimensis* (Hippomorpha), right P4 and M1 Miocene, Steinheim im Albuch, Germany [BSPG 1897 XIII4a]. The ectoloph forms the facet for phase I, whereas proto- and metaloph show initial facets for phase II. (C) *Diadiaphorus* sp. (Litopterna), left M2. Santacruzian, Santa Cruz, Patagonia [STIPB KOE 2847]. The blade-facet on the ectoloph is strongly folded. (D) *Astrapotherium magnum* (Astrapotheria), left upper molar, Santacruzian SALMA, Patagonia [STIPB KOE 3962]. The blade facet on the ectoloph is dominant. (E-G) *Stephanorhinus etruscus* (Rhinocerotidae), Early Pleistocene, Brüggen, Niederrhein, Germany [STIPG M 2826 and 2863]. (E) right upper and (F) lower dentitions with a typical ectoloph-guillotine. All premolars and molars have a blade-facet that articulates with the buccal side of the lower premolars and molars. In rhinocerotids a small support-facet occurs regularly (F and G, detail of m2). Striations of the facet indicate the steep inclination during phase I, whereas the flat occlusal surface of the lower teeth grindsagainst the lingual part of the uppers. (On these parts of the enamel band the vertical Hunter-Schreger bands are visible (Rensberger and Koenigswald 1980). – e-f: ectoloph blade-facet; HSB: Hunter-Schreger bands; s-f: support-facet. Arrows indicate the mesial and buccal directions - Scale bars equal 1 cm. - Photos A – G by Georg Oleschinski.

deviated to the mesial side. The antagonistic lower teeth provide only a small facet on the buccal rim of the lower teeth. This support-facet is steeply inclined to the buccal side and carries distinct striations (Figure 5(G)). It intersects the thickness of the enamel band only by half, or even less, but is seen on each of the lower molars and premolars in *Stephanorhinus etruscus* from Brüggen. This support-facet was observed regularly in the lower teeth of browsing rhinos. The remaining surface of the lower teeth and lingual parts of the uppers are flattened and more like rasp-facets for grinding (Figure 5(F) and (G)). During phase II the lower molar moves in a mesial or mesiolingual direction with a low inclination (Figure 4).

The grinding ability has increased during the evolution of some rhino lineages such that in the upper molars the grinding-facets expanded and the ectoloph-guillotines lost significance, e.g. *Ceratotherium, Coelodonta,* and *Elasmotherium* (Fortelius 1982).

Brontotheres and chalicotheres

In the upper molars of brontotheres and chalicotheres the buccal enamel is strongly inclined lingually and the parastyle and mesostyle are prominent. Thus, the facet of the ectoloph is W-shaped (Figure 5(A)) and its folded crest is truncated almost vertically. The functionally important cross-section of the enamel has a sharp tip and forms the leading edge of the facet. The surface of the dentine is very steep and curved towards the lingual side.

The lower antagonists have W-shaped buccal sides that fit perfectly into the folded ectoloph. During phase I the buccal side of the lowers passes the tip of the ectoloph of the upper molar in an almost vertical direction. In lower molars of *Megacerops* and other brontotheres a faint support-facet is cut into the enamel surface corresponding to the distinct facet found in *Stephanorhinus*, but is much more weakly formed. In the lower molars of *Chalicotherium* and *Moropus* no facets related to phase I were seen in the available material and figures. The jaw
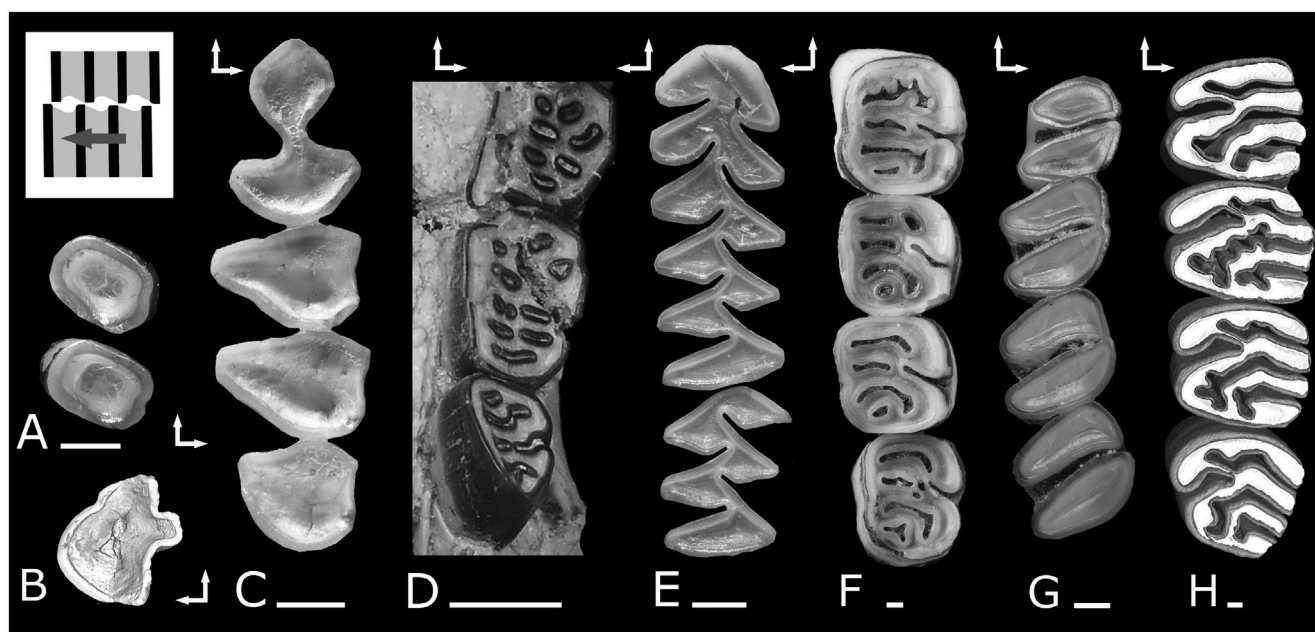
Figure 6. Rasp-facets differentiated by enamel islets and lateral infolds. (A-C) surrounding enamel, (D) enamel islets, (E) lateral infolds, (G) lophs, and (F and H) infolds and islets in combination. (A) *Cryptomys hottentotus,* li P4+M1, Recent Makapansgat South Africa [STIBO KOE 3360]. (B) *Aplodontia rufa,* left lower molar [STIPB-KOE 401 from UCMP]. (C) *Thomomys umbrinus*, lower jaw, Recent; California [STIPB M 3353]. (D) *Vintana sertichi,* left maxilla with Mf2-Mf4 with typical enamel islets, Upper Cretaceous, Madagascar [UA 9972]. (E) *Ondatra zibethicus*, right m1-m2, Recent, Germany (STIPB M 1062]. (F) *Dasyprocta agouti,* left P4-M3 [STIB-M1129]. (G) *Laonastes aeningmamus* left p4 – m3, Recent, Thakhet (Laos). The teeth are bilophed and worn flat. [AT 04]. (H) *Castor fiber* left P4-M3 [STIPB MaÜ02]. - Scale bars equal 1 mm. Arrows indicate the mesial and buccal directions - Photos C, E, F, G, by Georg Olescinski; D from Krause et al. 2014; drawing H by Anne Schubert.

movement of phase I ends with a compression of food against the protocone and hypocone, both of which are very voluminous . In moderately worn molars the surface of these cones is well polished but no distinct facets are detectable that might represent phase II (Figure 4).

Hippomorpha

Whereas the molars of *Hyracotherium* and *Propalaeotherium* represent typical primary occlusal surfaces, later hippomorphs developed secondary occlusal surfaces with specialized facets with blade-facets. In *Mesohippus* and *Anchitherium* (Figure 5(B)) the ectolophs are inclined somewhat in a lingual direction between the prominent parastyles and mesostyles. The triangular shape of the lingually protruding paracone and metacone indicate a browsing diet according to the mesowear method (Fortelius & Solounias 2000). When teeth are slightly worn, a folded functional crest continues from the parastyle to the metastyle. It is a typical blade-facet with the sharp tip on the leading side. The blade-facet on the ectoloph documents mesio-lingual jaw movement during phase I along with a very steep inclination. In *Mesohippus* this movement includes the distal side of the proto- and metaloph causing small blade-facets to develop there as well. In *Anchitherium* the proto- and metaloph show slightly excavated wear facets that indicate an initial grinding movement of phase II in a horizontal direction (MacFadden 2009) (Figure 4). This initial grinding during phase II also was observed in the lingual part of the upper molars in *Palaeotherium* and *Plagiolophus* (Butler 1952; Engels 2011). During the phyletic history of these taxa the relative length of the blade in comparison to tooth size increases demonstrating the increasing functional significance of the blade (Engels 2011).

Ectoloph-guillotines in other groups

Among the South America ungulates, most Not0ungulata, Litopterna, and Astrapotheria, possess well developed ectolophs in their upper molars. The buccal enamel of the ectoloph forms regularly developed, typical ectoloph-guillotines. The blade is very variable and may be almost straight e.g. in *Astrapotherium* (Figure 5(D)) and many notoungulates. In several litopterns, e.g. *Diadiaphorus* (Figure 5(C)), the ectolophs are strongly folded. The importance of phase I, is stressed by the long-lasting blade-facet of the ectoloph-guillotine. It persists even when the tooth elements in the lingual part are totally worn away, e.g. in astrapothere *Astraponotus* (Kramarz et al. 2011). The blade-facets of the guillotines articulate with the buccal surface of the lower molars that mostly lack a special facet. In the lingual part of the upper molars, the dentine field is structured by some lateral infolds and islets. They provide enamel crests for grinding during phase II of the power stroke. Grinding, however, does not seem to have been a dominant functional feature, because the lateral infolds and islets are worn off early in ontogeny or, in some cases, partially reduced.

Arctostylopina provide another example where upper molars have a prominent facet developed along the ectoloph that persists even in heavily worn teeth (Missiaen et al. 2012). The figured specimens in Missiaen et al. (2012) do not indicate whether or not grinding occurs on the lingual part of the upper molars.

In the premolars of the embrithopod *Arsinoitherium* the arrangement of facets is very similar to an ectoloph guillotine and differs distinctly from the bilophodont-scissor arrangement found in the molars. The premolars have well developed ectolophs with typical blade-facets and a steep dentine field. The blade occludes with the buccal sides of the lower premolars that move afterwards mainly in a lingual direction. Court (1992)
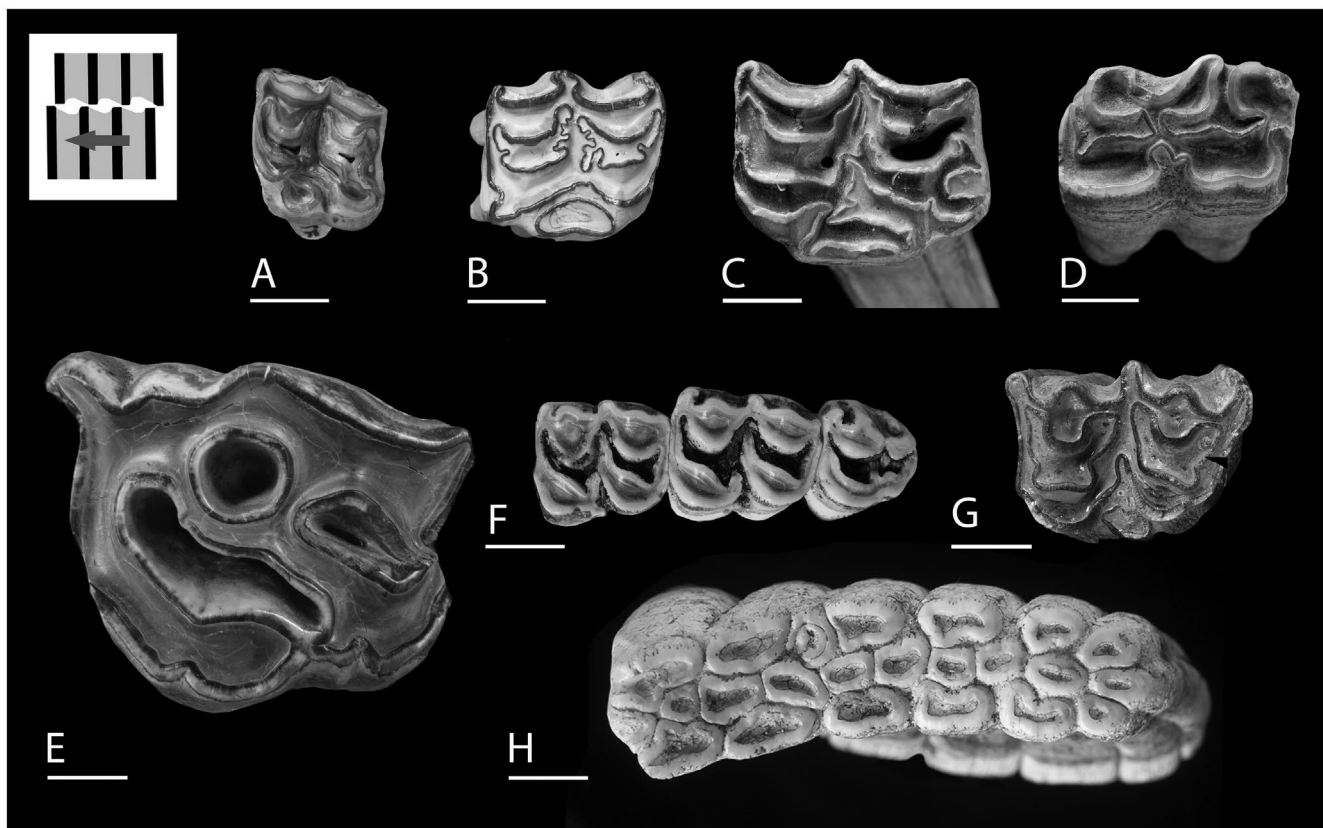
Figure 7. Rasp-facets with complicated occlusal surfaces. (A) *Parahippus leonensis*, left upper molar, early Miocene, Thomas Farm, Florida (UF 259476). A rasp facet on a low-crowned molar. (B) *Hipparion* cf. *dietrichi,* upper molar, Upper Miocene, Samos, [STIPB- M 586]. Cementum closes the gaps between the enamel bands. (C and D) *Equus ferus*, subrecent, Adendorf b. Meckenheim [STIPB- M 1850]. (C) Upper molar with enamel islets and lateral infolds and (D) lower molar with lateral infolds only. (E) *Coelodonta antiquitatis*, right M2, Upper Pleistocene, Bobenheim, [MENGER]. (F) *Rangifer tarandus* Banks Island [STIPB M 1508] left M1-M3. The enamel islets are not filled with cementum. (G) *Bison priscus,* upper Pleistocene*,* Groß-Rohrheim [MENGER]. The enamel islets and the lateral infolds are filled with cementum. (H) *Phacochoerus aethiopicus,* Recent, Okawambo, Botswana [STIPB- M 7028]. The rasp-facet is formed by elevated cones that are surrounded by cementum. - Scale bars equal 1 cm. – Photos A-H by Georg Oleschinski.

documented the fact that *Arsinoitherium* premolars and molars occlude differently owing to an angle in the tooth row between these two tooth fields. Molar occlusion is more similar to the bilophodont-scissors as discussed above.

In Hyracoidea the upper molars of *Procavia* have a distinct blade-like ectoloph indicating a steep phase I, whereas phase II is almost horizontal producing grinding across the lingual parts of the proto- and metaloph. The ectoloph-guillotine is even preserved when the teeth are heavily worn. *Procavia* differs distinctly from other hyracoids, e.g. *Megalohyrax*. There the para- and metacone are not fused and experience wear from their anterior and posterior sides, more similar to artiodactyls.

Rasp-facets

Rasp-facets are characterized by flat grinding surfaces with slightly projecting enamel crests as the main functional tools (Figure 1(C)). The dentine is widely exposed. Rasp-facets function only with an equivalent facet on the antagonist. Rasp-facets occur in some brachydont teeth, e.g. *Erethizon, Dasyprocta*, several cricetodontid rodents, and *Stegolophodon*, but mostly in hypsodont or euhypsodont teeth, because of the high abrasion during grinding. Primarily, the projecting crests are formed by the surrounding enamel band as soon as the initial enamel cap is worn off, e.g. in *Cryptomys* (Figure 6(A)). In morphologically

more derived taxa the dentine field is structured by enamel islets, lateral infolds, and narrow lophs (Figure 6(F), (H)) and in a few cases by numerous cusps. In some teeth, but by far not all, cementum surrounds the enamel and fills the enamel islets or the gaps between the tooth elements forming a closed occlusal surface. For the function of the rasp-facets it is important that the dentine and the cementum (if present) are slightly excavated between the projecting enamel crests. The dentine surface is often asymmetrically abraded. It indicates the direction of the jaw movement according to the Greaves-effect and the intensive compression between the rasp-facets prior to the comminution at the crests (Greaves 1973; Schmidt-Kittler 1984). The edge of the crests is generally rounded and only rarely has a facet similar to the edge of the blades.

The exposure of enamel crests requires some initial wear thus providing them with a secondary occlusal surface. As seen in teeth with an ectoloph-guillotine, rasp-facets may cover part of the teeth, but during evolution they tend to spread over the entire occlusal surface. The characteristics of rasp-facets are the same whether they cover part or the entire occlusal surface.

Rasp-facets extending over the entire occlusal surface occur in various mammalian orders, mostly with herbivorous diet, thus only a few examples are listed here: Marsupialia: *Vombatus*; Gondwanatheria: *Sudamerica, Vintana* (Figure 6(D))*;* Proboscidea: *Stegolophodon*, *Elephas* (Figure 7(A)), *Mammuthus*;
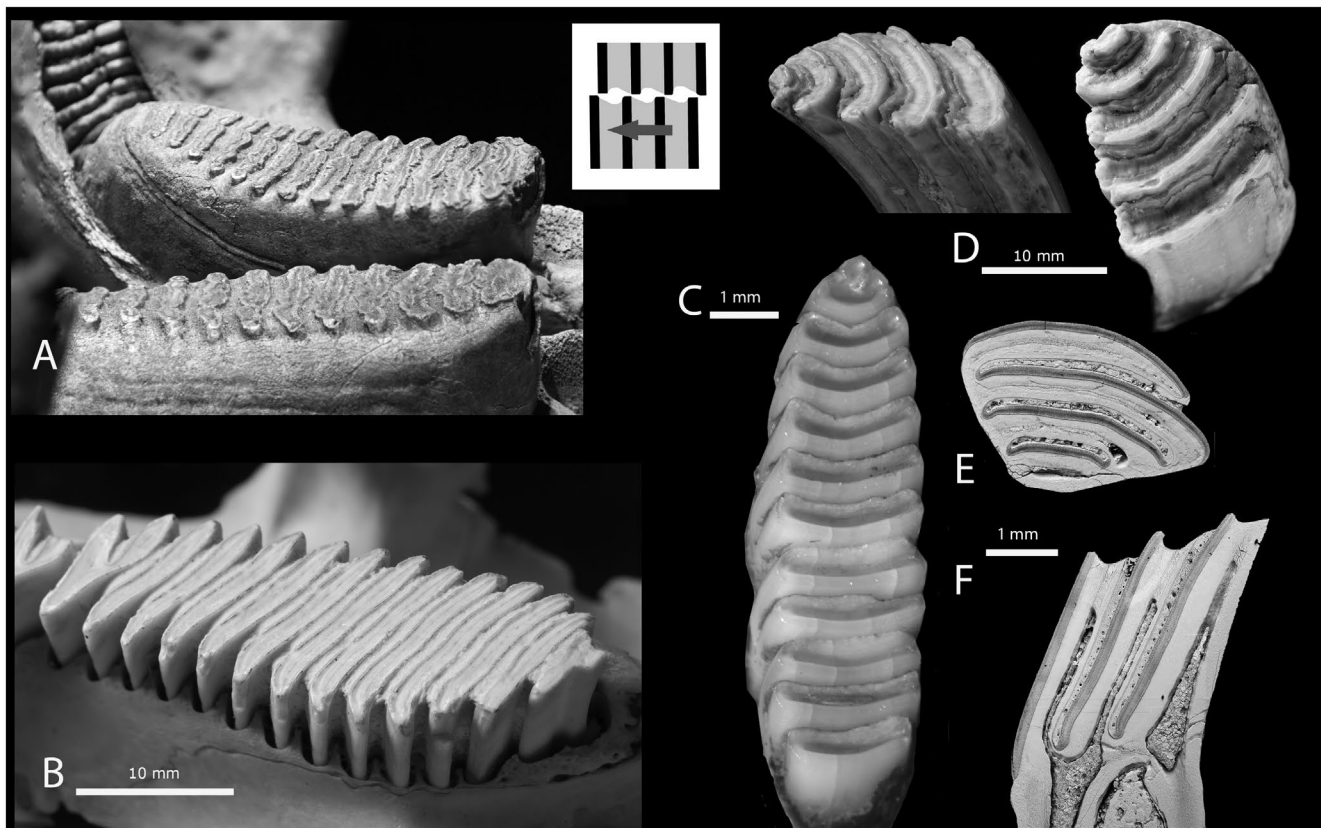
Figure 8. Rasp-facets with equally spaced enamel crests. (A and B) the enamel of both sides of the lophs form crests. The regular spacing is due to cementum between the lophs. (A) *Elephas antiquus,* lower jaw with m2, Upper Pleistocene, Crumstadt near Darmstadt, Germany [HLMD 3001]. (B) *Hydrochoerus hydrochaeris,* M3 with equally spaced enamel crests; recent, Argentina [STIPB M 5684]. (C-F) The slightly inclined lophs have enamel only on the trailing side, whereas that of the leading sides is reduced. (C) *Otomys angoliensis*, m1-m3 of the left mandible, Recent, Makapansgat, South Africa [STIPB-KOE 3356]). (D) Dinomyidae indet., M3 sin., Upper Miocene/Pliocene, Playa Arazatí, San José, Uruguay [STIPB KOE 4007]. (E-F) *Archaeomys* sp. Upper Oligocene, Gaimersheim, Germany [STIPB-KOE 381, 382]. SEM photos of (E) a lower molar in transverse section and (F) and of an upper molar in longitudinal section. - Photos A - D by Georg Oleschinski, E - F by Thomas Engler.

Rodentia: in almost all rodent families rasp-facets evolved, e.g. *Aplodontia, Thomomys* (Figure 6(C)), *Ondatra* (Figure 6(E)); *Dasyprocta, Laonastes* (Figure 6(G)), Castor (Figure 6(H)); Artiodactyla: *Rangifer, Camelus, Bos, Bison* (Figure 7(F) and (G)), *Phacochoerus* (Figure 7(H))*;* Perissodactyla: in horses: *Parahippus, Hipparion, Equus* (Figure 7(A)–(C)), and in rhinos: *Coelodonta* (Figure 7(E)), *Elasmotherium*, and *Ceratotherium*.

Rasp facets occur in the most derived stages of many groups. They evolve from very different tooth morphologies in ancestral forms, especially when these teeth become hypsodont.

If partial rasp-facets occur in the lingual part of upper molars together with ectoloph-guillotines, e.g. *Stephanorhinus* (Figure 5(E)), *Palaeotherium*, and *Procavia,* then they are related to phase II of the power stroke. In Artiodactyla partial rasp-facets related to phase II evolved as well, but there para- and metacones are separated and guide the jaw movement in a more transverse direction.

Wear stages during ontogeny

Fully functioning teeth with rasp-facets are characterized by a wide opening of the dentine that occurs after a relative short phase of initial wear. This process of initial wear does not require such an exact adjustment as in the blade-facets.

In *Equus* the molars erupt with a thick cover of cementum. The cementum and the underlying enamel is eroded when the tooth gets its final position in the tooth row.

Owing to tooth architecture rasp-facets are not temporary developments for most teeth. If abrasion is low, facets function in brachydont teeth for an appropriate time, e.g. in *Stegolophodon*. High abrasion often is compensated by hypsodonty or even euhypsodonty. Hypsodonty guarantees almost constant functioning of the occlusal surface during a long period of time, despite intensive abrasion. That is obviously one of apparent selective advantages of this tooth type (Koenigswald 2011). Nevertheless, during progressive wear some enamel islets disappear and lateral infolds may turn into enamel islets. Constructional constraints determine when the crests of enamel islets or lateral infolds disappear. During ontogeny wear reduces the enamel crests gradually, and rooted molars are ultimately worn down to the roots.

Differentiation of the dentine field

The simplest version of a rasp-facet is provided by teeth, in which the functional crest is just an enamel ring surrounding a dentine core. Several extant rodent families are characterized by such grinding teeth, e.g. in aplodontids (*Aplodontia* Figure 6(B)), bathyergids (*Cryptomys* Figure 6(A), geomyids (molars

of *Thomomys* Figure 6(C)), and the fossil Tsaganomyidae (Wang 2001). Several other families have molars where the circumference is curved, e.g. ctenodactylids, ctenomyids, and octodontids. Another way of structuring the dentine field is as deep lateral infolds. The euhypsodont molars of *Petedes* and *Dolichotis* are characterized by one infold. In many rodents the number of lateral infolds has increased. The lateral infolds may come from both sides, e.g. *Abrocoma, Agouti, Cavia, Cuniculus*, echymyids, and several cricetines, *Lemmus, Dicrostonyx, Arvicola, Ondatra* (Figure 6(E)).

The lateral infolds are often combined with enamel islets. Deep indentations from the surface characterize the molariform teeth of the gondwanatheres *Sudamerica* and *Vintana* (Figure 6(D)) and the enlarged premolar of *Mylagaulus*. Deep indentations from the occlusal surface that form enamel islets are typical for selenodont molars of artiodactyls, e.g. *Bos* or *Bison* (Figure 7(G)). There the islets occur in the upper and lower molars, in *Equus* however (Figure 7(C)), only in the upper teeth. The lowers are differentiated by lateral infolds only.

There is a third way how to increase the number of enamel crests within the rasp-facet. The occlusal surface may be modified into transverse lophs and additional lophs may be added, in various rodents, e.g. *Lophiomys, Cricetomys*, and *Laonastes* (Figure 6(G)), in dinomyids and in the caviid *Hydrochoerus* (Figure 8(B)). In large mammals the molars of elephantids are a paradigm (Figure 8(A)). Grinding facets formed by pillars instead of lophs are found in the hypsodont molars of *Desmostylus* and *Phacochoerus*.

A constructional constraint marks the difference between enamel islets and lateral infolds. Enamel islets are rings of enamel within rasp facets. They originate from depressions in the unworn occlusal surface. The depth of such depressions is limited because the enamel of the later islets has to be mineralized before the rim of the depression is closed by wear. At this moment the enamel organ loses contact to nourishing tissue (Koenigswald 1977; Koenigswald et al. 1999). In brachydont teeth the enamel formation is generally completed before the teeth erupt. In in hypsodont and especially euhypsodont teeth the enamel islets occur only in the upper most parts of the crown. In contrast the lateral infolds can be formed continuously, for the enamel organ is placed on the side and the growing tooth is passing by. In the phylogenetic evolution of the arvicolid genus *Mimomys* the enamel islets are gradually reduced and lateral infolds intensified. There is a second kind of enamel islet that occurs late in the ontogeny of rooted hypsodont molars. These are derived from the base of lateral infolds, e.g. in premolars and molars of *Castor* and in the gondwanatheres *Sudamerica* and *Vintana* (Koenigswald et al. 1999; Krause et al. 2014). The varying pattern of the occlusal surface during late ontogeny may impede systematic evaluation.

The functional advantage of the enamel islets and lateral infolds is in increasing the number of crests in the occlusal surface of a rasp-facet. Food is finely processed at these crests and their increasing number reflects increasing efficiency.

It is self-evident that the orientation of the crests in relation to the direction of the jaw movement is of great functional significance. Theoretically, those parts of the crests that are oriented perpendicular to the jaw movement have the maximal effect. However, each of these rasp-facets require an antagonistic rasp-facet. If the crests of the antagonistic facets were exactly perpendicular to the direction of the jaw movement and thus parallel to each other, large forces would be required to cross the full length of each crest simultaneously. Maglio (1972) demonstrated for elephant molars that the crests are slightly divergent from strictly perpendicular. Thus, a cutting point migrates along the crest and requires less energy. That explains the angled orientation between antagonistic rasp-facets in many rodent molars and their functional symmetry, e.g. in abrocomids and arvicolids (Figure 6(E)) (Koenigswald 1980; Koenigswald et al. 1994).

If rasp-facets cover the entire occlusal surface, adjacent teeth may form united functional areas. This is very obvious in dentitions, where the jaw movement is parallel to the length of the tooth row, either in a proal direction as in elephants, *Hydrochoerus, Cricetodon*, and arvicolids, or in a more palinal direction as in Gondwanatheria (Anders & Koenigswald 2013; Krause 2014; Krause et al. 2014) (Figure 4). Some small and several large herbivores, e.g. *Aplodontia, Hipparion, Equus*, or *Bison* with transverse jaw movements, have tooth rows that form a uniform grinding surface. The rasp-facets are located between these surfaces with crests obliquely oriented, e.g. *Dasyprocta* and *Myocastor* (Koenigswald et al. 1994, 2013; Schultz et al. 2014).

The general direction of jaw movement can be read from the orientation of the crests, but differentiation of phase I and phase II is more difficult or even impossible, because no centric occlusion can be identified during the power stroke. Partial rasp-facets that occur in combination with a blade-facet on the ectoloph indicate that the grinding is related to phase II after centric occlusion. This might be extended to a predominance of phase II in rasp-facets covering the entire occlusal surface. In contrast, if phases I and II have the same direction but differ in inclination, as in many herbivores, it is likely that the angle of inclination is adjusted and phases I and II are not discernable any more, as can be visualized in the mastication compass (Figure 4).

Equally spaced crests and the reduction of the length of crests

One other very obvious character is shared by many rasp-facets. In small and large teeth the enamel crests are more or less equally spaced. This is most obvious if transverse lophs form the rasp-facets, e.g. in *Elephas* (Figure 8(A)) and *Hydrochoerus* (Figure 8(B)). The cementum between the lophs correlates well with the thickness of the dentine core. The phenomenon of almost equally spaced enamel crests is even recognizable in much more complicated occlusal surfaces, if the main crests are considered e.g. *Dactylomys, Dasyprocta* (Figure 6(F)). Even in teeth with a combination of islets and crests, e.g. in *Equus* or *Bos* (Figure 7(B), (C), (E)) the distances between the main functional crests tend to be similar.

The total length of all crests is relevant for the efficiency of the facet (Rensberger 1973; Kay 1975). Within the high diversity of mammalian teeth, however, there are several counter-examples, where the total length of the crests are reduced, even when they are oriented properly. In several rodents, where the molars are formed by narrow transverse lophs, the thickness of the enamel band is drastically reduced asymmetrically on one side of the lophs. These sections are so thin that they are functionally negligible. These molars share a couple of characters. The lophs are slightly inclined, in lowers in a mesial, in uppers in a distal direction. This corresponds to the leading side according to the proal
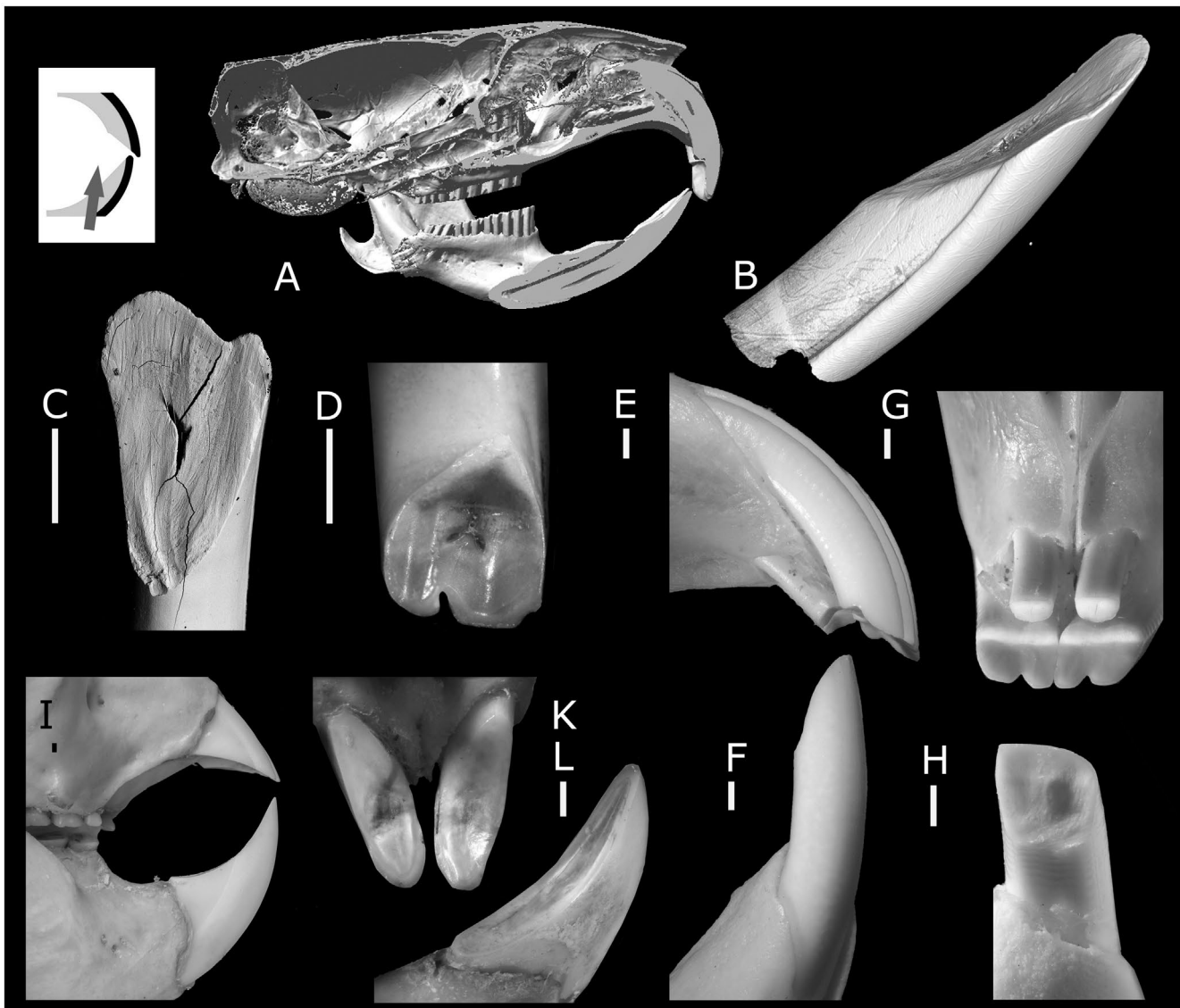
Figure 9. The Nipper facets in rodents, lagomorphs and primates. (A) *Microtus gregalis,* Recent, Fairbanks Alaska, USA [STIB M 1005]. Cranium and mandible in a sagittal section of a μCT model, showing occlusion and facets of upper and lower incisors and demonstrating that the incisors do not occlude simultaneously with the molars [STIPB- M1006]. (B) Nipper facet of the lower incisor of *Arvicola terrestris*, Recent, Germany). (C and D) Nipper facets of the lower and upper incisors of *Otomys angoliensis*, Recent, Makapansgat, South Africa, [STIPB-KOE 3356]. Longitudinal grooves in the enamel cause notches in the cutting edges. (C) Longitudinal scratches cover the total length of the facet in the lower incisor. They are caused by the antagonist during the sharpening process. (D) The occlusal surface of the upper incisor shows a step, where the lower incisors normally occludes. (E-H) Upper and lower incisors of *Lepus europaeus*, Recent, Germany [STIPB M 6241]. (E-F) Functional interaction of the lower incisor with the two upper incisors. (G) Wear facets on the upper incisors with a typical step and an incision of the longitudinal groove in the enamel cover. (H) The nipper facet of the right lower incisor has an almost straight cutting edge due to the flat external side and shows oblique scratches indicating irregular movements. (I-L) The specialized incisors of *Daubentonia madagascariensis,* Recent, Madagascar (SMF 1583). (I) Lateral aspect of the anterior dentition. The incisors occlude when the molars are very close. They are very pointed due to the high-oval cross-sections. The nipper facets of the (K) upper and (L) lower incisors are well polished and show no striations from the antagonists. In upper facet grooves indicate where the tips of the lower incisors normally occlude. - Scale bars equal 1 mm. – Photos by Georg Oleschinki.

jaw movement. The reduced part of the enamel band is always on the leading side of each loph except on the first loph in each tooth. The enamel bands of the trailing sides form the projecting grinding crests, and the reduced sections on the leading sides are hidden behind them. The reduced sections are functionally unimportant. Thus only half of the potential length of the enamel band is used for grinding.

This phenomenon evolved independently in several unrelated taxa, e.g. *Archaeomys* (Archaeomyidae) from the Oligocene in Europe (Figure 8(E), (F)), the extant African *Otomys* (Muridae) (Figure 8(C)). Several hystricomorph caviid rodents show a similar or even a complete reduction, e.g. *Chinchilla* and *Lagostomus* (Caviidae). Some of the fossil dinomyids that reached giant body sizes, e.g. *Amblyrhiza* from the Caribbean Islands and *Arazamys* from Uruguay (Figure 8(D)) (Antony 1918; Rinderknecht et al. 2011) show similar patterns.

Reasons why these species relinquished part of the enamel-band is not well understood. Nevertheless, the distances between the crests are perfectly alike. The extant *Dimomys* is related to *Amblyrhiza* and *Arazamys*. It might represent a less derived condition, because the enamel on the leading side is not reduced. The lophs are very close together without cementum in

between. Thus, the enamel of adjacent lophs are united into one functional crest that is broader. Therefore, the reduction of one side contributes to the sharpness of the crest.

The molars of some derived arvicolids reduced the length of the functional enamel crest in a slightly different way. Their molars are implanted vertically and have characteristic triangles. In some genera with euhypsodont molars the trailing edge of these triangles is so thin that they are abraded before they reach the level of the rasp-facet and thus they cannot contribute to the grinding function of the tooth. This phenomenon occurs in various lineages, e.g. *Microtus* and *Dicrostonyx,* but not in *Lemmus* (Koenigswald 1980). The partial reduction is a derived character, because many of the less derived taxa with rooted molars, e.g. *Mimomys*, *Clethrionomys* or *Ondatra* (Figure 6(E)), do not show such a reduction.

Partial rasp-facets

Rasp-facets that cover the entire surface of a tooth are very common, but in several taxa rasp-facets cover only part of a tooth surface and are combined with other types of facets. The upper molars of *Procavia* and *Stephanorhinus* (Figure 5(E)) combine an ectoloph-guillotine in the buccal half of with a partial rasp-facet on the proto- and metaloph on the lingual side. In these examples, grinding occurs during the phase II of the power stroke. In these cases the lower molars show mainly rasp-facets.

Nipper-facets

The facets of rodent and lagomorph incisors are included here, because they form a very specific type of functional relationship (Figure 9). The enamel is only on one side and almost the entire facet is formed by dentine. The functional surfaces of these teeth are described here as nipper-facets, because they can be compared with nippers or end-cutting pliers. Both upper and lower incisors have enamel only on their anterior sides. The cross-section of the enamel-band forms the sharp crest that is backed up by a large dentine field that is steeply inclined distally. The dentine field is not planar and never used as a sliding plane. Thus it differs distinctly from the arrangement in carnassials or bilophodont-scissors. Besides lagomorphs and rodents this type of facet occurs in the lemur *Daubentonia*, thus this will be discussed here as well.

Lagomorphs and rodents are well known for their remarkable ability to gnaw using their incisor teeth. The intensive wear produced on incisors is compensated for by development of euhypsodonty and fast eruption. Generally, the lower incisors grow and wear faster than the uppers, reflecting their greater activity during grinding. The amount of growth depends on various environmental factors and thus the eruption rate is much higher in chisel-tooth diggers, e.g. gophers, than in non-diggers (Hildebrand 1974).

For gnawing the enamel crest on the anterior side is highly important and always sharply exposed, because the dentine is deeply excavated. The enamel is relatively thin and thus normally no facet is recognizable on the enamel crest itself, in contrast to the much thicker enamel in blade-facets. The microstructure of the enamel in incisors is highly differentiated (Korvenkontio 1934; Wahlert 1968; Martin 1992; Kalthoff 2000) which may help prevent the enamel band from breaking; the loss of material owing to intensive wear does not seem to be a major problem because of the high eruption rate.

The shape of the cutting edge is controlled by the cross-section of the tooth. A straight cutting edge requires a flattened anterior side of the tooth, e.g. in the lower incisor of *Lepus* (Figure 9(H)) whereas a high oval cross-section results in a more pointed edge, e.g. *Glis*. Some incisors have one or two longitudinal grooves that create tips in the oblique facet tips. *Otomys* has two grooves in the upper and one groove in the lower incisor that generate differentiated cutting edges (Figure 9(C), (D)). Although the longitudinal grooves generate tips in the cutting crest, their functional importance remains unclear, because the resulting tips are fairly small.

The inclined dentine field behind the crest covers the entire cross-section of the incisors and owing to its oblique orientation is much longer than the antero-distal diameter of the tooth. In rodents and lagomorphs the dentine field is formed mainly by attrition during a specific sharpening process (Druzinsky 2015). Scratches formed by the antagonist were observed in the entire length of the dentine field, but some abrasion by food is possible too. The eroded surface of the dentine field reflects the cutting edge of the antagonist. If the blades are straight or rounded, the surfaces are smooth, but if the antagonist has a differentiated cutting edge, the dentine field is more irregular, as in *Otomys* (Figure 9(C)). Upper and lower incisors cooperate in various ways. Gnawing on various substrates is the main function. During the gnawing process the cheek teeth never come into occlusion. Basically the lower jaw is protruded so far that the crests of upper and lower incisors approach each other tip to tip, or the lower incisor passes just behind the crests of the upper one. The final position of the lower incisor is marked in the dentine field of the upper incisor by a step that occurs in several but not all taxa (Figure 9(D)). In lagomorphs this position is marked by a step and the second upper incisor. For effective gnawing the enamel crests have not to meet each other. For splitting a hard object, like wood, the chisel-like profiles of the upper and the lower incisors may push an initial split forward. In many cases the upper incisor secures an object, e.g. a nut, whereas the lower incisor gnaws out the hole and scraps out the fruit. The great maneuverability of the lower jaw offers many functions to the nipper facets.

For sharpening the nipper facets, the antagonists have to scrape each other through the full length of the dentine facets. To scrape the dentine field of the lower incisor, the mandible has be moved intensively forward. Scratches in the dentine reach the distal end of the facet and thus indicate the required protrusion. Although the mandibular joint is constructed differently in lagomorphs and rodents, a wide protrusion is possible in both (Druzinsky 2015). In the lower incisors of several caviomorph rodents, e.g. *Lagostomus*, transverse marks are related to the impact of the upper incisor. In *Lepus* and *Prolagus* mainly vertical scratches are observed in the lower incisors, but some diagonal ones are also present indicating that the teeth occasionally deviate to the buccal side. The nipper facet of the upper incisor is scraped similarly by the lower incisor. Even distally from the step marking the terminal position of the lower incisor during gnawing scratches caused by the lower incisor extend to the distal margin of the facet. At the distal end of the upper nipper-facets
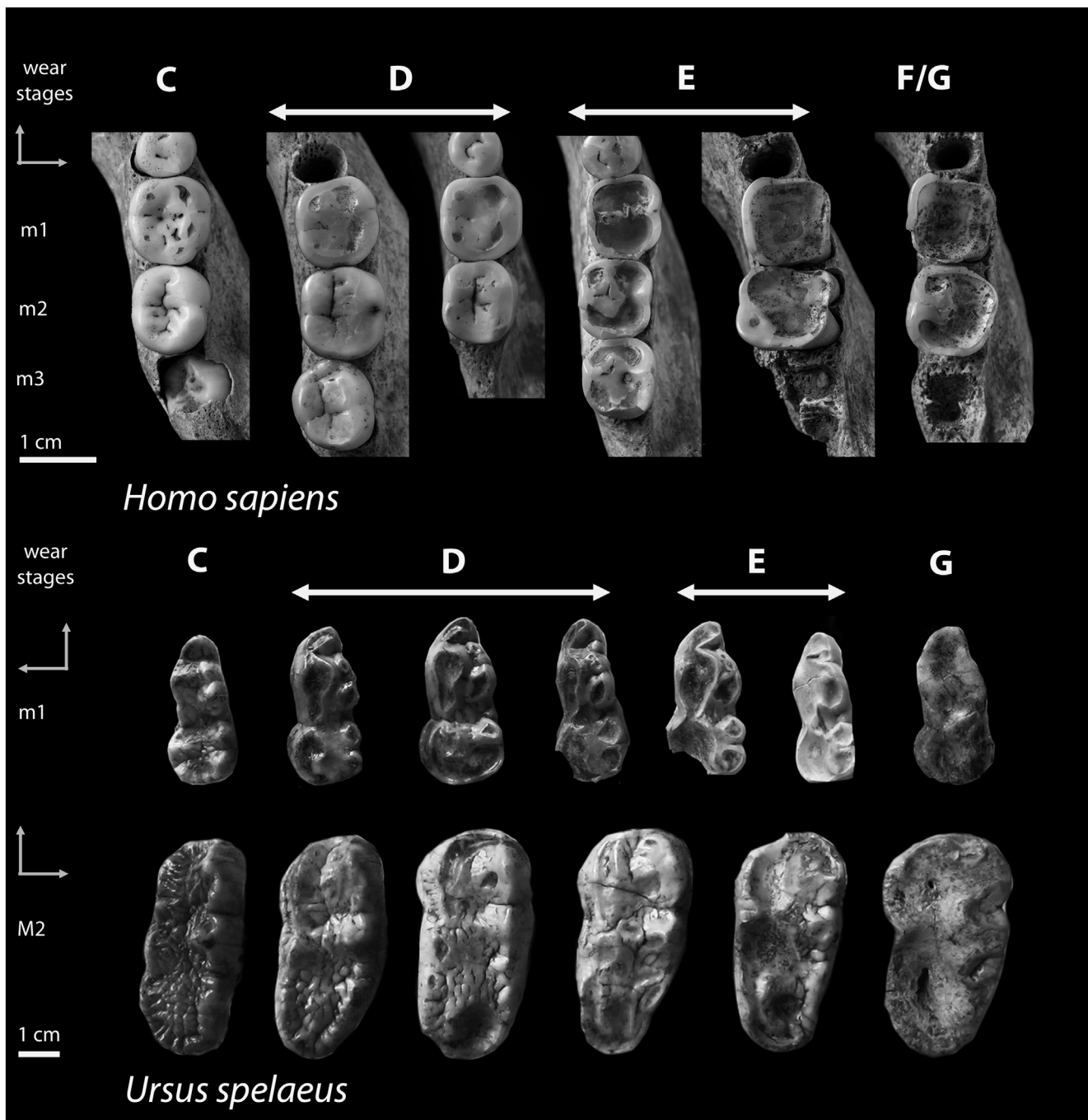
Figure 10. Wear stages of the late ontogeny in teeth in primary occlusal surfaces. Upper row: *Homo sapiens*, lower dentition (m1-m3) from medieval burials, Kreis Euskirchen, Germany [RLMB]. They represent gradual wear with increasing fields of exposed dentine. Lower two rows: *Ursus spelaeus*, left m1 and M2, Upper Pleistocene, Winden, Burgenland (Austria) [PIUW]. The various wear stages from fresh stage C to the badly worn stage E, demonstrate the gradual loss of the enamel cover and the increasing amount of exposed dentine. In stage G all enamel is gone, but the teeth are still able to process food to a sufficient degree. - C, D, E, F, and G indicate the association with the wear stages of late ontogeny. - Photos of the upper row by Georg Oleschinski, those of the lower by the author.

in *Otomys* small parts are splintered off and scratches are developed and oriented in an anterior-distal direction corresponding to movement of the lower jaw.

The incisors of the lemur *Daubentonia* (Figure 9(I), (K), (L)) are often compared with those of rodents. They are similarly constructed incisors but show significant differences in the sharpening process. Because of the highly oval cross-section, the incisors are very pointed. The dentine facet of the lower incisor

is generally more intensively curved than that of the upper, but individual variation is quite large.

Manipulating the cranium with the associated mandibles shows significant differences compared to rodents and lagomorphs. In rodents and lagomorphs the incisors are widely separated when the molars are in occlusion. In *Daubentonia*, however, the tips of the incisors are almost in contact when the molars are occluding. Thus for making use of the incisors in
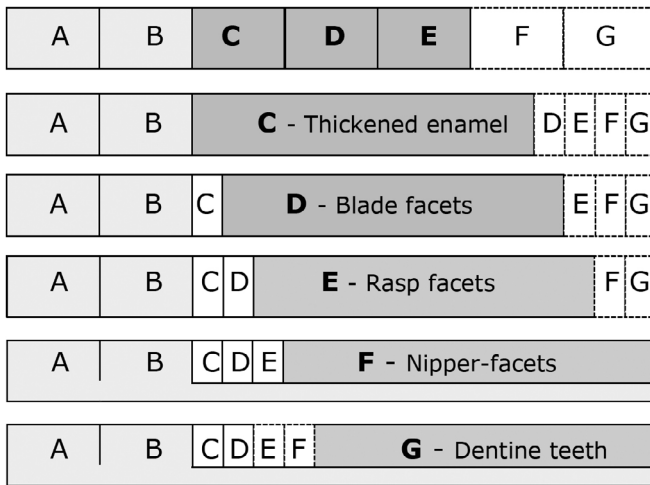
| A | B | **C** | **D** | **E** | F | G |

| A | B | **C** - Thickened enamel | D E F G |

| A | B | C | **D** - Blade facets | E F G |

| A | B | C D | **E** - Rasp facets | F G |

| A | B | C D E | **F** - Nipper-facets |

| A | B | C D E F | **G** - Dentine teeth |

Figure 11. Diagrammatic comparison of the heterochronic modification of ontogeny related to the various types of facets. Early ontogeny (phases **A + B**) is included for sake of completeness. In primary occlusal surfaces (uppermost line) the various wear stages **C** to **G** are more or less similar in length. In specialized teeth with secondary occlusal surfaces (thickened enamel, blade-facets, rasp-facets, nipper-facets, and dentine teeth) the relevant ontogenetic phases (**C, D, E, F,** and **G**) are temporally elongated at the expense of the others. Note that in euhypsodont teeth tooth formation and eruption (phases **A + B**) continue.

aye-ayes the mandibular joint does not have to be shifted as much as in lagomorphs and rodents (Druzinsky 2015).

The sharpening process seems to be different as well. The nipper-facets are well polished but not rounded at their margins. No scratches of the antagonist were found, except a little mark in the upper incisor just behind the cutting tip. The position corresponds perfectly to the step in the upper incisors of *Lepus* (Figure 9(E), (G)) or several rodents. Therefore, it is interpreted as being caused by the tip of the lower incisor when both incisors come into normal contact.

The dentine fields are so elongated that excavating by the antagonist would require unnatural movements of the mandible that exceed the movements observed in rodents by far. This, together with the lack of scratches in the dentine fields, leads to the conclusion that most of the dentine is eroded in another way. It is known that *Daubentonia* pulls its elongated fingers transversely through the mouth. The horny skin of the fingers may contribute to the erosion of the dentine.

Euhypsodont incisors are present in several other mammals as well (Thenius 1969) e.g. Gondwanatheria (*Groeberia, Patagonia);* Marsupialia (*Vombatus ursinus);* Taeniodonta (*Stylinodon);* Tillodontia (*Tillodus*); Glires (Lagomorpha: all members; Rodentia: all members); Primates (*Daubentonia* and some marmosets); Pyrotheria: *Pyrotherium*. Some but not all of them are gnawers with nipper facets. In many cases, the teeth oppose each other at different angles and do not strike each other more or less vertically, tip-to-tip.

A very special case is represented by the Pleistocene bovid *Myotragus balearicus* from the Balearic islands. The lower incisor is euhypsodont and very procumbent. It has enamel only on the anterior side. The dentine field is very wide. Because upper incisors are generally missing in bovids, there is no antagonist, and thus the enamel and dentine are abraded only by food items. Nevertheless, the enamel forms a sharp cutting edge at the anterior end of the tooth.

Correlation of specialized facets with ontogenetic wear stages

The ontogeny of teeth may be subdivided into two major sections: An early ontogeny containing tooth formation and eruption, and a late ontogeny when teeth are in use and wear occurs. Early ontogeny is indicated here as phases **A** and **B,** but they are not discussed because no wear occurs in these phases. Late ontogeny is differentiated into the phases **C** to **G** according to the amount of dentine that is exposed by wear. Although the demarcation of these phases is subjective, it is sufficient to demonstrate a general trend that is of interest here.

Phase A + B: Tooth formation in the crypt, eruption and integration into the tooth row

Phase C: Use of the initial enamel surface and first facets

Phase D: Dentine is partially exposed

Phase E: The dentine is widely exposed and dominant

Phase F: Enamel is present only on one side

Phase G: All enamel is worn away but a dentine core is still present

Most teeth with a primary occlusal surface pass gradually through all these phases one after the other, whereas in teeth with a secondary occlusal surface these ontogenetic phases differ distinctly in their length and thus in their functional significance.

Wear in primary occlusal surfaces

Teeth with a primary occlusal surface are wide spread. Tribosphenic and most bunodont molars pass through this sequence of ontogenetic phases gradually. Human teeth represent this group very well if they originate from a time prior to intensive dental care. Therefore our sample was selected from medieval graves in the Rhine area (Figure 10, upper row). Similar gradual tooth wear is found in mammals with brachydont and bunodont molars, e.g. *Phenacodus, Gomphotherium,* and *Ursus* (Figure 10, lower rows). First the tips of cusps are abraded, and the dentine becomes exposed. During further wear a gradual expansion of the dentine fields can be documented for *Ursus spelaeus, Apodemus,* and early hippomorphs (Holland 2013; Engels 2011; Morris 1972). Thus, these teeth pass gradually through phases C, D, and E. Phases F and G may follow, if the individual lives long enough. None of the phases is outstanding. In Figure 11 (first line) the various phases are symbolized as of equal length. Although this assumption is very simplistic, it is supported by various observations of gradual wear (e.g. Freudenthal et al. 2002; Holland 2013). It is used here merely to highlight the difference compared to teeth with secondary occlusal surfaces.

Besides those teeth that experience gradual wear, some others show specializations for phase **C,** because they depend on using the enamel surface for a very long time. This is possible if wear is limited, e.g. by the preference of a soft diet. Molars of glirids, e.g. *Glis, Muscardinus*, show very little tooth wear. Another way to enable the long-lasting use of the enamel cover is to increase enamel thickness. It is mostly interpreted as a specialization for feeding on hard objects that have to be cracked, as in the mollusk eating *Enhydra lutris* (Fisher 1941; Constantino et al. 2011). *Australopithecus* is characterized by thick enamel (Conroy 1991), but the specific function is under debate.

Wear is reduced in some teeth that are related to specific food gathering with procumbent incisors, as in, e.g. plesiadapids and soricids. These teeth generally show moderate wear and maintain their length to allow for precise grasping.

The crenulated cutting edges of the upper canines in some felids, e.g. *Homotherium* and *Smilodon*, are fully functional only with their initial enamel surface. These examples may be regarded as specializations of enamel surface that experience little or no wear and therefore represent a prolonged ontogenetic phase **C.** In these examples, the subsequent phases are of minor importance.

Teeth with secondary occlusal surfaces

Teeth with blade-facets
Teeth with secondary wear surfaces and specialized facets require specific initial wear to become fully efficient. If part of the dentine is exposed the cross-section of the enamel can be used as a functional tool. Thus phase **C** is a transitional phase and shortened, whereas ontogenetic phase **D** with a partial exposure of the dentine becomes dominant (Figure 11, third line). The various kinds of blade-facets, carnassials, bilophodont-scissors, and ectoloph-guillotines are typical examples for a specialization in an elongated phase **D**. The subsequent phases, e.g. **E** and **F**, show a reduced function but may occur in older age classes. An informative example is provided by the blade facets on transverse lophs in the molars of *Deinotherium* and *Lophiodon*. The blade-facets function well for a relatively long period of time, but at a specific grade of wear the lophs collapse, and afterwards the enamel crests function more like grinding facets (Harris 1975; Koenigswald 2014a, 2014b). In many dentitions such a functional shift from **D** to **E** is combined with a high molar wear gradient such that the shearing-cutting function shifts to more posterior molars that are less worn.

Besides these prominent examples in carnassials, bilophodont-scissors and guillotine-facets, different types with partially exposed dentine occur in other mammals, too. Murids have differentiated molars with such facets (Lazzari et al. 2015). In contrast to perissodactyls with an ectoloph-guillotine, several non-hypsodont artiodactyls developed a transverse guiding rail between paracone and metacone, e.g. in merycoidodontids and extant cervids. These two cones have facets on their mesial and distal sides. There the dentine is exposed between two bands of enamel. Thus, these facets differ distinctly from blade-facets and represent another type of facet that is related to ontogenetic phase **D**.

Molars with rasp-facets
Teeth specialized for grinding have rasp-facets and are attributed to ontogenetic phase **E.** These teeth pass quickly through phases **C** and **D,** because wear eliminates the enamel surface, and cross-sections of the more vertical enamel band are exposed. A large amount of exposed dentine characterizes phase **E.** Subsequent phases **F** and **G** are of minor significance (Figure 11, fourth line). The number of crests is multiplied by enamel islets and lateral infolds, and often the gaps are filled with cementum. Hypsodonty often counterbalances high abrasion in rasp-facet dominated dentitions. Therefore, the duration of rasp-facets and

thus ontogenetic phase **E** is extremely elongated. In euhypsodont teeth the phases **F** and **G** are never experienced before death.

The molars of elephants (Figure 8(A)) are specialized for grinding and demonstrate that the picture presented here of successive ontogenetic phases is somewhat simplistic. Because of horizontal tooth displacement all ontogenetic phases occur simultaneously but are locally well separated (Roth 1989; Tassy 1996). Nevertheless the general ontogenetic sequence can be recognized. During a moderate stage of wear the greatly enlarged M3/m3 of *Mammuthus primigenius* are worn down anteriorly while the last lophs are still developing (phase **A**). In the erupting area the lophs are still covered by cementum representing phase **B**. Further to the front the more worn lophs form the typical rasp-facet with an alternation of enamel, dentine, and cementum. Phase **E** grinding is concentrated on this rasp-facet. Owing to the oblique molar surface, it's most anterior part is worn down much more. The anterior lophs may be abraded down to the roots forming a dentine platform occasionally with some remnants of enamel that represent phases **F** and **G**. Only the rasp-facet related to phase **E** is of functional significance.

Incisors with nipper-facets
In the nipper facets of rodent incisors and similar teeth, the relative amount of exposed dentine is increased even more than in rasp-facets, because the enamel is restricted to one side only. These teeth are specialized for an extreme elongation of ontogenetic phase **F** (Figure 11 fifth line). Because of the euhypsodonty tooth formation is continuous and ontogenetic phases **A** and **B** persist. Intermediate phases **C, D,** and **E** may be present when the teeth erupt, but if so they are ontogenetically greatly condensed in duration. Owing to continuous growth final phase **G** is never reached. Even if the general pattern of the ontogenetic sequence is strongly modified, nipper facets can be regarded as a specialization for ontogenetic phase **F.** No other position within the ontogenetic sequence is reasonable. For a perfect gnawing function short enamel crests are enough to be most efficient.

There are several other types of facets in incisors and other teeth that are characterized by one-sided enamel and dentine that is widely opened. The canines of *Hippopotamus,* for instance, have an extremely large dentine field and fairly thin enamel that acts as a sharp crest. These teeth slide past each other along the large planar dentine facet and the enamel is on the leading sides in both antagonists. Thus, these teeth form a different type of facet, but are specialized for phase **F,** too. The upper incisor of *Procavia* has one-sided enamel and a similar sliding plane for the lower incisor, but the lower incisors being surrounded by enamel and having a flat occlusal surface are formed differently. Thus facets as those of *Hippotamus* and *Procavia* are different from the typical nipper arrangement, nevertheless they represent phase **F** as well.

One sided-enamel occurs in the molars of some animals as well, e.g. *Vombatus ursinus* and the caviid *Dolichotis.* In these teeth the enamel is on the trailing side behind widely exposed dentine. There are many variations of facets in front teeth and even in some molars that can be assigned to ontogenetic phase **F,** but differ from nipper-facets. However, not all teeth with one-sided enamel can be attributed to phase **F**. The tusks of various gomphotheres have a strip of enamel along the tooth.

In *Cuvieronius* it spirals around the tusk and has no obvious function. These teeth are more similar to dentine teeth that are related to phase **G**.

Dentine teeth

To complete the picture teeth composed only of dentine must be discussed as well. Because of the total exposure of dentine and the lack of enamel, they are regarded as specialized for phase **G** (Figure 11 – sixth line). Dentine teeth are known in xenarthrans and some other mammals. Dentine teeth deserve this position in the general ontogenetic sequence, because in fossil dasypodids *Astegotherium* and *Utaetus* traces of enamel have been identified (Simpson 1932; Ciancio et al. 2014) indicating the likely presence of enamel in former evolutionary stages. Erupting tusks of elephants are covered with a thin enamel cap that is worn off very quickly (Ungar 2016). During their later life these tusks experience only very little wear. Thus, much of their life history is recorded in the dentine layers (Fisher et al. 2008). The molars of xenathrans are formed by dentine and show intensive wear facets. Modifications of the dentine allow for a differentiated profile in the occlusal surface (Kalthoff 2011). Hence dentine teeth represent an enormous enhancement of ontogenetic phase **G.** It is the equivalent of the insignificant final part of the life history in more typical teeth

Heterochrony

In conclusion, late ontogeny of teeth can be roughly subdivided into ontogenetic phases measured by the exposure of the dentine. Teeth with specialized facets in secondary occlusal surfaces, however, can be correlated to specific ontogenetic phases that are expanded at the cost of other phases. Such an extension of one ontogenetic phase and the reduction of others is a typical example of heterochrony. Each of the facets discussed here shows an extension of a different phase and thus another kind of heterochrony. Heterochrony describes a very common pattern in evolution. It can be achieved by shifting the time proportions of ontogenetic phases (Gould 1977; McNamara 2001). Many morphological changes have been interpreted as heterochronic modifications. Heterochrony has been discussed in the evolution of teeth at different structural levels. The Evo-Devo perspective as well as the morphology of hypsodont and euhypsodont teeth were interpreted as heterochronies (Renvoisé & Michon 2014; Chaline & Sevilla 1990; Koenigswald 1982, 2011). The modifications of the enamel microstructure at the schmelzmuster level show typical heterochronies as well (Koenigswald 1993).

Conclusion

Tooth wear is not only a destructive phenomenon, but many teeth are constructed in a way, that wear is an important prerequisite for their full function. There is a significant difference between teeth specialized for primary or secondary occlusal surfaces (Fortelius 1985). Teeth with secondary occlusal surfaces often show specialized facets. The function of these facets can be compared with mechanical tools. By taking this approach systematic relationships are suppressed and frequent parallelism becomes obvious. The functional constraints and the limited number of different materials that are available for the formation

of teeth, lead to multiple convergences during evolution. Scissors are useful tools for the fragmentation of food items for both carnivores and herbivores. Of course differences exist but here the more common traits have been stressed.

The three types of tooth facets recognized here, blade-facets, rasp-facets and nipper-facets, represent only a small set of the possible wear facets occurring in a wide range of mammalian dentitions. They were selected to represent specializations to different phases in the late ontogeny of teeth.

Late ontogeny covers the part of the life history during which teeth are exposed to wear. The specialized wear facets selected for this paper can be correlated to specific wear stages that are preferentially elongated during late ontogeny. One of the surprising results of this study is that each of the described types of facets is related to a different ontogenetic stage. Thus the temporal elongation of specific phases is different for teeth characterized by different types of facets. If more general patterns of ontogeny provided by teeth with primary occlusal surfaces is taken as a standard, then their specialized wear facets can be interpreted as heterochronic modifications of this general pattern.

Many of the early representatives of evolutionary lineages show primary occlusal surfaces, e.g. *Cambaytherium* in Perissodactyla (Rose et al. 2014), stem equoids (Hooker & Dashzeveg 2004; Engels 2011), *Diacodexis* in Artiodactyla, or paramyids in Rodentia (Butler 1980; Rose & Koenigswald 2007). During their further evolution specialized facets are developed in each of these lineages. This enables the intensive differentiation observed within these various groups.

Abbreviations of collections

AMNH	American Museum Natural History New York
AT	Collection of Adrian Tröscher, Tübingen
BSPG	Bayerische Staatsammlung für Paläontologie und historische Geologie München
HLMD	Hessisches Landesmuseum Darmstadt
MENGER	Collection of Frank Menger, Groß-Rohrheim
MNHN	Museum National de Histoire Naturelle Paris,
NHMB	Naturhistorisches Museum Basel
PIUW	Paläontologisches Institut der Universität Wien
SMF	Forschungsinstitut und Museum Senckenberg Frankfurt
SMNS	Staatliches Museum für Naturkunde Stuttgart
STIPB	Steinmann Institut der Universität Bonn
STIPB-KOE	Schmelzsammlung des STIPB
UA	Université d'Antananarivo, Madagascar
UCMP	University of California, Museum of Paleontology, Berkeley
UF	University of Florida, Gainesville
ZFMK	Zoologisches Forschungsinstitut und Museum Alexander Koenig Bonn

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Disclosure statement

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