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Article

Diversity of hypsodont teeth in mammalian dentitions – construction and classification

by

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with 9 text-figures and 3 tables

This paper is dedicated with great respect to Prof. em. Dr. Adolf Seilacher of Tübingen and Yale. Dolf successfully inspired many students with his understanding of 'Constructional Morphology.' He opened many eyes, mine included, to the trade-offs of history, function, and construction that constrain morphology.

Zusammenfassung

Hypsodontie, so wie der Begriff hier gebraucht wird, beschreibt Zähne, deren Krone parallel zur Wachstumsrichtung verlängert ist. Diese Zahnform kann in allen Zahnpositionen auftreten. Die Hypodontie wird als die heterochrone Verlängerung bestimmter ontogenetischer Phasen während der Zahnbildung auf Kosten der anderen Phasen interpretiert. Mit drei Kriterien lässt sich die Vielfalt hypsodonter Zähne unterscheiden: zum einen geht es darum, welche Phase (oder Phasen) in der Ontogenie verlängert sind, zum anderen um den Grad der Hypsodontie (zunehmende Kronenhöhe bis zur Euhypsodontie) und drittens um die Art der Abkauung (ein ausbalancierter Abrieb, bei dem Nachwachsen und Abrieb im Gleichgewicht stehen, oder ein freies Größenwachstum). Die Unterteilung der Ontogenie in vier Phasen (I = Zahnspitzen; II = Seitenwände, III = Dentinoberfläche (Zahnhals) und IV = differenzierte Wurzeln) ist zwar künstlich, ermöglicht aber, die Diversität hypsodonter Zähne in sechs Kategorien zu gliedern. 1. Vielspitzen-Hypsodontie (verlängerte Phase I); 2. Spitzen-Hypsodontie (verschmolzene Phasen I und II); 3. Seitenwand-Hypsodontie (verlängerte Phase II); 4. Schmelzband-Hypsodontie (Phasen II und III bilden den Zahn gleichzeitig); 5. Partielle Hypsodontie (Phasen II, III und IV sind gleichzeitig aktiv) und 6. Dentin-Hypsodontie (Dominanz von Phase III). Eine Gegenüberstellung der bislang benannten Typen von hypsodonten Zähnen wird gegeben. Die neue Klassifizierung ist generell anwendbar, eröffnet den Blick in erster Linie auf die Bauweise der hypsodonten Zähne und ermöglicht auch einen Vergleich unter evolutionären Aspekten.

Schlüsselwörter: Heterochronie, Vielspitzen-Hypsodontie, Spitzen-Hypsodontie, Schmelzband-Hypsodontie, Partielle Hypsodontie, Dentin-Hypsodontie

Summary

Hypsodonty, as used here, describes a specific type of tooth with the crown elongated parallel to the growing axis, a condition which can occur in any tooth position. Hypsodonty is interpreted as the elongation of specific ontogenetic phases during tooth development at the cost of all others in a heterochronic mode. Three parameters are used for differentiation: the specific elongated ontogenetic phase or phases; the degree of hypsodonty (increasing hypsodont and euhypsodont); and the kind of abrasion (balanced wear by an antagonist or free growth). The first parameter is regarded as the most important one. Although the separation of the four ontogenetic phases (I - cusps, II - sidewalls, III - dentine surface, and IV - differentiated roots) is artificial, it allows characterization of the great diversity of hypsodont teeth in six categories: 1) multicusped hypsodonty (extended phase I); 2) unicuspid hypsodonty (confluent phases I+II); 3) sidewall hypsodonty (extended phase II); 4) enamel band hypsodonty (phases II+III synchronous); 5) partial hypsodonty (phases II+III+IV synchronous); and 6) dentine hypsodonty (phase III dominant). A synopsis with previously defined types of hypsodonty is given. The new classification is comprehensive, opens the view to the construction of hypsodont teeth, and allows a comparison under evolutionary aspects.

Keywords: heterochrony, multicusped hypsodonty, unicuspid hypsodonty, sidewall hypsodonty, enamel-band hypsodonty, partial hypsodonty, dentine hypsodonty.

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Content

1. Introduction

Hypsodonty is a widespread phenomenon in mammalian dentitions. The term hypsodonty describes those teeth in which the enamel-covered crown is higher than wide or long (White 1959; Van Valen 1960), as occurs e.g., in the premolars and molars of horses. The horse example is often used in textbooks, and many papers dealing with hypsodonty consider only cheek teeth of ungulates (e.g., Fortelius 1985; Janis 1988; Fortelius & Solounias 2000; Kaiser et al. 2003). This might evoke the impression that hypsodont teeth are restricted to cheek teeth. But teeth of similar construction occur in the anterior dentition as well. Hershkovitz (1962) and Martin (1993) discussed as hypsodont the enlarged canines in carnivores, rodent incisors and elephant tusks. Later Janis & Fortelius (1988); Bargo et al. (2006); and Fields (2009) did not hesitate to talk about the hypsodonty in xenarthran molars although they have no enamel. Thus, the term hypsodonty was expanded from cheek teeth with an enlarged crown covered with enamel to elongated teeth of the entire dentition including dentine teeth without enamel. This extended use of the term makes sense, because it focuses the discussion of hypsodonty on the structural aspect. In this study the term hypsodonty is used in this broad sense. The constructional and functional similarities lead to an all-embracing classification of the great variety of hypsodont teeth, although hypsodonty evolved independently in various mammalian lineages.

This is not the first attempt in classifying the great diversity of hypsodont teeth. White (1959) surveyed the molar hypsodonty of a great variety of fossil mammals and suggested three types of hypsodonty: "cusp hypsodonty", "tooth-base hypsodonty", and "root hypsodonty". Hershkovitz (1962, 1967) could not apply these categories to rodents from South America. Observing that different parts of the crown are elongated, he created the term "coronal hypsodonty" for an expansion of the superficial part, and "tubercular hypsodonty" for an expansion of the base of the crown. Schmidt-Kittler (2002) interpreted hypsodonty in rodents as a stretching of particular ontogenetic growth programs, but he did not aim at a more comprehensive system.

The classification proposed here is based on a set of three independent parameters and is intended to be applicable to all teeth that are elongated parallel to the growing axis, no matter which region of the dentition they occur in. It pays special attention to whether the teeth are covered with enamel totally, partially or if they lack enamel altogether. The main factor of the classification is related to the specific ontogenetic phase during which the predominant part of the tooth is formed. This requires a definition of four distinct ontogenetic phases. The second factor differentiates hypsodont teeth according to their wear. The third factor is the degree of increasing hypsodonty.

The categories established here refer to the hypsodonty of single tooth positions or tooth families, thus different types may occur within the dentition of the same individual. In *Sus scrofa*, for instance, the premolars and molars are brachydont, the canines are euhypsodont, but show a highly differentiated enamel cover. The upper incisors are brachydont, the lower incisors are hypsodont, but, in contrast to the canines, are rooted.

The classification proposed here shall primarily draw attention to a better understanding of the formation and different constructions of hypsodont teeth. This approach differs widely from the application using hypsodonty primarily as an indicator for palaeoecological conditions (e.g., Kaiser et al. 2003; Damus & Janis 2011).

Several of the existing terms together with the new ones are compiled in Table 1. The relationship and concordance of the different types of hypsodonty proposed by the various authors will be discussed later (see also Table 2).

2. Materials and methods

This classification is based on traditional tooth morphology. Tooth morphology was often discussed in detail in the traditional literature, but specific characters used here e.g., enamel thickness or dentine fields, are often described incompletely or figured inadequately. Thus besides an extensive study of the literature, original material of extant and fossil taxa was reinvestigated, as far as possible. In fossil teeth the various materials of a tooth (enamel, dentine, cementum) often differ in colour and enable an easy differentiation.

In extant teeth it is often very difficult to distinguish the various materials, especially when they are fresh and bright. Most zoological collections provide skulls with dentitions, but rarely isolated teeth that allow a better investigation of the root formation. The extraction of hypsodont teeth for investigation is rarely advisable, due to the value of the material. CT-scans and/or micro CT scans offer an adequate method for the investigation of the unerupted parts of teeth as well as the distribution of enamel. Thus, this study is based on a wide mixture of information. Due to the great diversity of hypsodont teeth in mammalian dentitions only a limited number of taxa could be investigated, but this survey seems to be extensive enough to outline the main features. A selection of taxa investigated and the classification of their hypsodont teeth in various tooth positions is listed in the Table 3.

Abbreviations for collections

AMNH – American Museum Natural History, New York
BSPG – Bayerische Staatsammlung Paläontologie und Geologie, München
CM – Carnegie Museum, Pittsburgh
GPIT- Geologisch-Paläontologisches Institut der Universität Tübingen
MB – Museum für Naturkunde Berlin

Table 1. Attempt of a synopsis of various systems of hypsodont teeth.

This paper	Schmidt-Kittler 2002	Herschkovitz 1962/1967	White 1959
Multicusped hypsodonty ontogenetic phase I dominant	stretching of only the relief of the tooth (his No. 3)	Tubercular hypsodonty	Cusp hypsodonty
Unicuspid hypsodonty ontogenenetic phases I and II	proportional stretching of all its parts (perhaps his No. 1)		
Sidewall hypsodonty ontogenetic phase II dominant	stretching of only the basis of the crown (his No. 2)	Coronal hypsodonty	Tooth base hypsodonty
Partial hypsodonty ontogenetic phases II, III and IV occur simultaneously	asymmetrical stretching of the relief (his No. 4)	--	--
Enamel-band hypsodonty ontogenetic phases II and III	?	Tubercular hypsodonty	Root hypsodonty
Dentine hypsodonty ontogenetic phase III			
Root differentiation ontogenetic phase IV no hypsodont teeth	--	--	--

NHMB – Naturhistorisches Museum Basel
STIPB – Steinmann-Institut (Paläontologie) der Universität Bonn
ZMFK – Zoologisches Museum und Forschungsinstitut Alexander Koenig, Bonn
ZMK – Zooogical Museum Kopenhagen

3. The three parameters characterizing hypsodont teeth

3.1. First parameter: The ontogenetic phases (Text-fig. 1)

Mammalian teeth are mostly formed in the crypt and mineralization starts at the tip and migrates down towards the root. The enamel is formed by odontoblasts on the outer side of the basement membrane. Osteoblasts form the dentine on the inner side of the basement membrane (Keil 1966; Peyer 1968; Hildebrand 1974). For comparison an idealised sequence of four ontogenetic phases is adequate, beginning with the tip of the cusps. The four ontogenetic phases distinguished here are:

Phase I – the primary occlusal surface characterized by the cusps

Phase II – formation of the enamel covered sidewalls

Phase III – formation of the dentine covered surface around the tooth

Phase IV – formation of the separated roots

In brachydont teeth these phases are subsequent to each other, and the tooth formation proceeds in ring like growing zones that are mostly perpendicular to the growing axis of the tooth. All types of hypsodonty are characterized by the heterochronic expansion of one of these phases at the costs of the others (Text-fig. 1A–E).

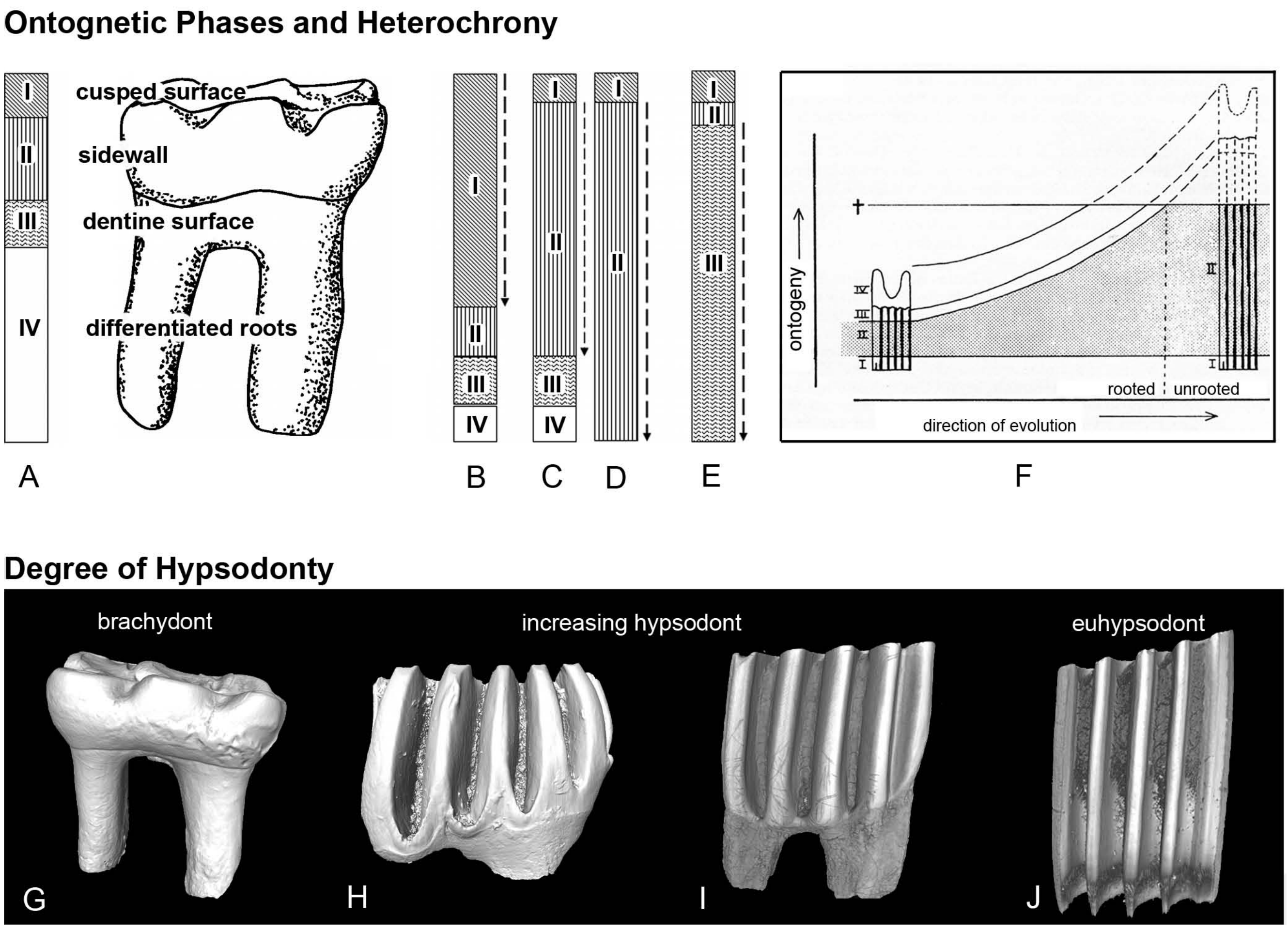
This idealized differentiation of these phases needs some interpretation for hypsodont teeth, especially since subsequent phases may overlap in time to various degrees. During the ontogenetic phase I the cusps are formed individually. At the end of this phase they merge into the primary surface of the crown. During the subsequent phase II the sidewalls are formed prior to tooth eruption. Both phases are easily distinguishable when the crown is broadened and contains several cusps, as is true of most molars. In unicuspid teeth, however, phase I and phase II are often confluent and cannot be separated. The enamel covered sidewalls are formed during the phase II are more or less vertical in hypsodont teeth. Deep enamel islets related to the tooth surface, and thus to phase I may be formed simultaneously with the sidewalls during phase II. These enamel islets and their relation to intensive re-entrant folds of the sidewalls will be discussed separately. The end of phase II is marked by the end of enamel formation. But in many hypsodont teeth the lower margin of the enamel undulates intensively, forming dentine tracts, especially in rodent teeth (Hibbard 1954). Rabeder (1981) coined the term "linea sinuosa" for the undulating enamel margin in arvicolids. In the ring like growing zone of tooth formation, some parts are covered with enamel (phase II), while in other parts the dentine surface (phase III) is formed. Thus both phases occur simultaneously in the growing zone but on different sides of the tooth. The ontogenetic phase III is primarily subsequent to the enamel formation and marked by the formation of the dentinal surface in the entire circumference of the tooth. This area is often called the neck of the tooth. It occurs prior to the formation of separated roots during phase IV.

These four ontogenetic phases were shaped for the description of the great variability of hypsodont teeth. Although they may overlap in parts they turn out to be very useful as shedding light on the construction of hypsodont teeth and their evolutionary changes.

During each of the proposed phases several genetic programs are active simultaneously, e.g., forming enamel and dentine. They are related to much more complex interactions of the dental epithelium and the odontogenetic mesenchyme at a distinctly more delicate scale. Thus the phases defined here are not identical to the various genetic cascades of gene expression. The tooth morphology demonstrates that the different genetic programs are correlated at a higher level. Nevertheless the defined ontogenetic phases seem not to contradict with the genetic programs for enamel and/or dentine formation as described for arvicolid molars (Tummers & Thesleff 2003; Renvoisé et al. 2009).

3.2. Second parameter: Increasing tooth height (Text-fig. 1)

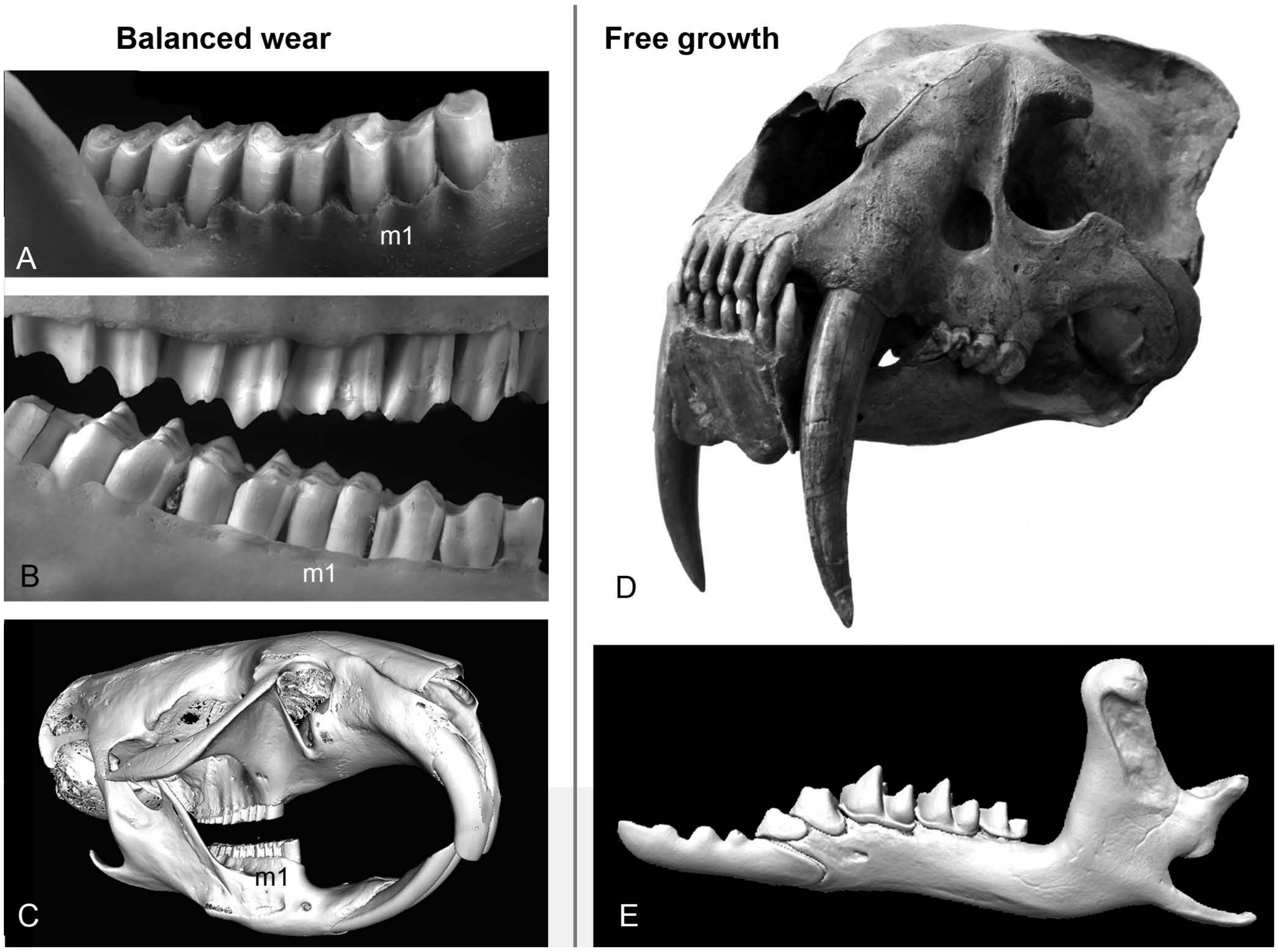
In the evolution of several mammalian lineages an increasing height of teeth can be observed leading from brachydont teeth to hypsodont teeth and even rootless teeth (Text-fig. 1 G–J). The degree of hypsodonty is one of the three parameters used here. Several terms describe the transition from brachydont to hypsodont teeth (mesodont, prohypsodont, protohyp-



Text-fig. 1. The four ontogenetic phases in the tooth formation:
A–E – Schematic models fort he ontogenetic phases and the heterochronic extension of one phase at the costs of the others: **A** – Brachydont molar; **B** – Extended phase I as in multicusped and unicuspid hypsodonty; **C** and **D** – Extended phase II as in sidewall hypsodonty, in D the euhypsodonty is reached, while phases III and IV are suppressed; **E** – Extension of phase III as in dentine hypsodonty, phase IV is suppressed.
F – An early attempt explaining the transition from rooted to rootless (euhypsodont) arvicoline molars by the extension of phase II, during which the sidewalls are formed. The death of the animal occurs (mostly) before the phases III and IV become activated (Koenigswald 1982).
G–J: Increasing hypsodonty in rodent molars (m1): **G** – *Apodemus sylvaticus* m1, Recent, Germany (STIBG – M1069); **H** – *Microtia* sp., m1, Late Miocene, Mte. S. Gargano, Italy (STIPG – KOE 276); **I** – *Mimomys reidi*, m1, Late Pliocene, Schambach, Germany (BSPM 1075 XXXI 18); **J** – *Arvicola terrestris*, m1, Recent, Germany (STIPG M 6623). – (G-J virtual 3D models based on Micro CT scans).

sodont) Most of these terms were used with varying definitions or are applicable only for specific groups (e.g., Schmidt-Kittler & Vianey-Liaud 1987; Vianey-Liaud 1991 for theridomyids). Fewer terms describe the increasing height of hypsodont teeth. White (1959: 233) regards a tooth as being "full hypsodont" when the crown is twice as high as wide. But the term "full hypsodont" is used for teeth which are rootless (Tobien 1976, 1978). Martin (1993) used the term "superhypsodont". Rootless or continuously growing teeth are often described as "hypselodont", and Janis & Fortelius (1988) differentiated between "crown hypselodont" and "root hypselodont" in molar teeth. But the term hypselodont was used in different ways and sometimes for hypsodont, as shown by Mones (1982). Thus, he coined the term "euhypsodont" for continuously growing teeth. This term is preferred here.

Several indices for hypsodonty were created to indicate the height of the unworn tooth and these indices were successfully used for palaeoecological reconstructions. But such indices were defined for the various mammalian groups in different ways (e.g., Artiodactyla: height to length of lower m3 in Janis 1988; Equidae: relation between different measurements of upper molars in Kaiser et al. 2003; Arvicolidae: relation of the height of specific dentine tracts in Weerd 1976; Xenarthra: relation of mandibular height and tooth row length in Bargo et al. 2006; Fields 2009). Thus these hypsodonty indices are suitable for a comparison within an evolutionary lineage or in closely related groups. For ecological interpretations the data base NOW (Neogene of the Old World) uses the tooth shape for herbivores calculated from the relation between height and length of the second upper or lower molars. Brachydont teeth have a ratio below 0.8, mesodont a ratio between 0.8 and 1.2. A ratio above 1.2 is regarded as hypsodont (Fortelius et al. 2002). An increasing hypsodonty index correlates in ungulates with an increasingly open environment and thus is an important indicator of the paleoenvironment (Janis 1995; Jernvall & Fortelius 2007; Mendoza & Palmquist 2007). For our purpose it is sufficient to realize the increasing hypsodonty without



Text-fig. 2. Types of wear in hypsodont teeth, balanced wear (A–C) and free growth (D–E): **A** – *Vombatus ursinus,* right lower jaw, Recent, Australia (STIPB M542); **B** – *Ovis ammon*, right upper and lower jaw, Recent, Germany (STIPB M6642); **C** – *Microtus geregalis*, cheek teeth and incisors show balanced wear, Recent, Alaska (STIPB M1004); **D** – *Smilodon fatalis*, cranium with hypsodont upper canine representing free growth, Pleistocene, Califormia; **E** – *Sorex araneus*, left mandible with extended lower incisor, Recent, Germany (STIPB MaÜ 156). – Figures are not to scale. (A, B: photos G. Oleschinski, STIPB; D: photo © Wallace63 / GFDL; C and E virtual 3D models based on Micro CT scans).

quantification and be aware of the multiple transitions from hypsodonty to euhypsodonty. Tooth height is one, but not the only parameter important for characterizing hypsodont teeth.

3.3. Third parameter: Relation between tooth eruption and wear (Text-fig. 2)

Most brachydont teeth erupt in a fairly short time and then form the roots. Hypsodont teeth erupt for a much longer time before they form roots, or they erupt continuously when rootless. In relation to wear, hypsodont teeth are attributed here to two distinct categories: "balanced wear" (Text-fig. 2A–C) and "free growth" (Text-fig. 2D–E).

"Balanced wear" is characterized by a constant position of the occlusal surface, although the teeth erupt for a long period or even continuously (Martin 1993). The intensive wear by an antagonist is in a perfect equilibrium with the tooth eruption. Any disturbance of the balanced wear results in severe malfunctions (Keil 1966). In cheek teeth the occlusal surface is mostly very close to the alveolar border, in the anterior dentition those teeth showing balanced wear may surmount the alveolar border significantly. The presence of a similarly constructed antagonist is the prerequisite of balanced wear. Hypsodont or euhypsodont teeth with balanced wear occur in cheek teeth, e.g., in many herbivores, and/or in the anterior dentition e.g., in rodent or lagomorph incisors, and in several notungulates.

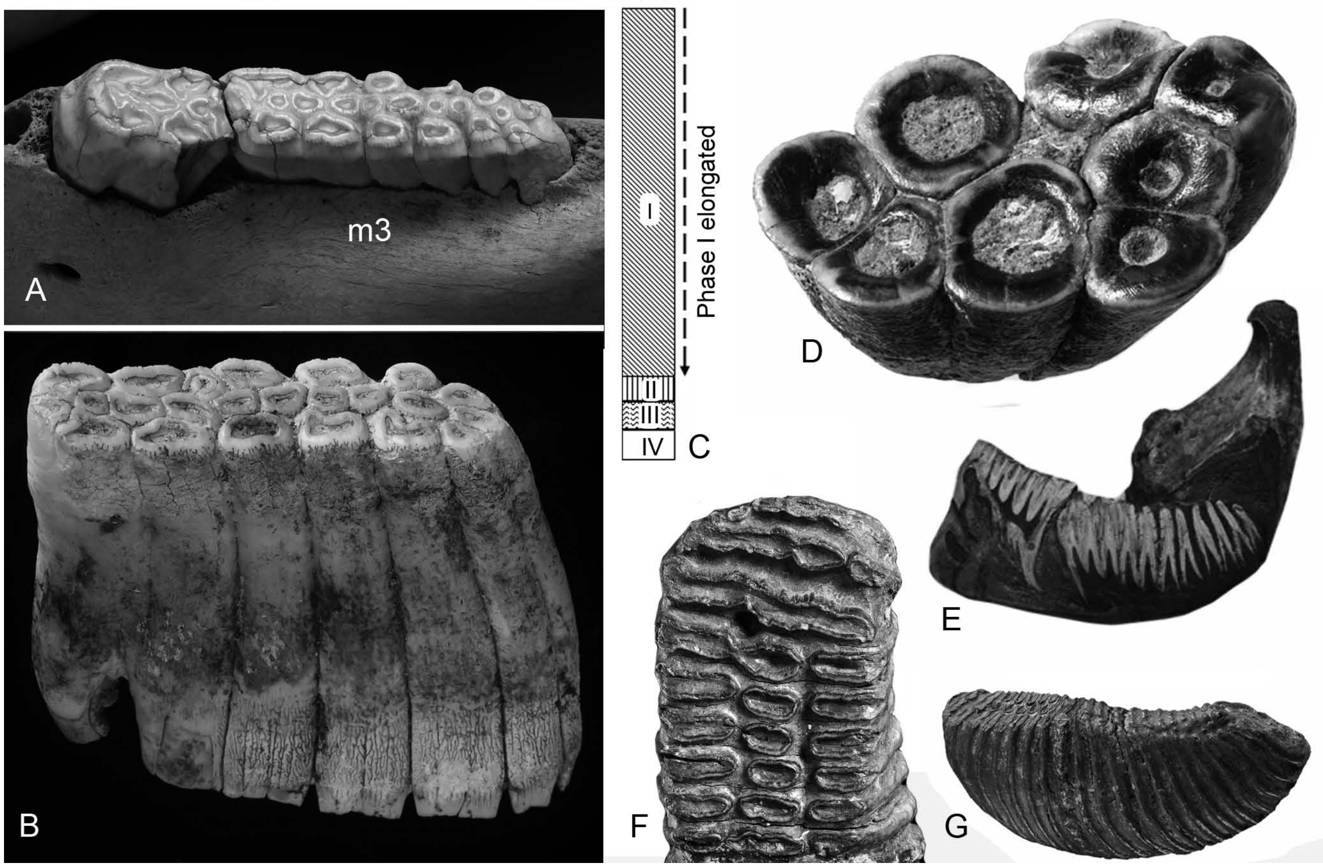
"Free growth" is characterized by the lack of wear compensating for tooth eruption in hypsodont teeth. The visible length of such teeth is not limited by the wear of an antagonist, and they often protrude from the mouth. The teeth erupt to full size if hypsodont or may erupt continuously if euhypsodont. Teeth with free growth are restricted to the anterior dentition. The primary tip is often preserved but may show irregular wear as well. More often wear facets occur on their sides. Such teeth are found in canines of several mammalian groups (e.g., carnivores, bats, suids and several primates (Text-fig. 2D, 4F, 8B, 8E), or as enlarged incisors (e.g., macropodids, apatemyids, plesiadapids, and lemurs (Text-fig. 2E, 4D–E, G). Most spectacular examples are the tusks of elephants (Text-fig. 8D) or the whale *Monodon*.

Balanced wear and free growth exclude each other almost totally. A few exceptions, however, may occur. The insular bovid *Myotragus* and the rhino *Chilotherium* have greatly enlarged lower incisors, but no antagonist in the premaxilla. They fall in the category of free growth, but their length is regularly shortened by soft tissues or horny plates, and thus the result is similar to a balanced wear.

4. The heterochronic approach of interpretation

The rich fossil record of rodent dentitions and the multiple transitions from rooted to rootless molars required an evolutionary explanation that is more informative than the "loss of roots". Koenigswald (1982) differentiated ontogenetic phases for the tooth formation in arvicolid molars and explained the loss of roots by a heterochronic shift of ontogenetic phases, assuming that the phase during which the sidewalls are built, was elongated to such a degree that the animal would not live long enough to experience the formation of roots (Text-fig. 1F). This model was based on own observations in the extant gerbillid *Rhombomys opimus* from Central Asia, which is regarded to have euhypsodont molars (Pavlinov 1982). But in very old individuals the initial formation of the crown base could be observed in several individuals. Such an unbalanced elongation or reduction of specific ontogenetic phases is typical for heterochrony (McNamara 1990; Smith 2003).

Chaline & Sevillia (1990) interpreted some evolutionary changes in *Mimomys* using the term heterochrony explicitly. Agusti et al. (1993) described the evolution of specific arvicolid genera and distinguish between lineages following peramorphic and paedomorpic tendencies. Schmidt-Kittler (2002: 143) interpreted hypsodonty in rodent molars as a stretching of particular ontogenetic growth programs and differentiated: "(1) proportional stretching of all its parts, (2) stretching of only the base of the crown, (3) stretching of only the relief of the tooth, and (4) asymmetrical stretching of the relief and expansion of the size of particular elements of the crown at the cost of other elements". While we did not find any instance of a stretching of all ontogenetic phases, the expansion of one phase (or two subsequent ones) at the cost of all others is the general way in which hypsodont teeth are constructed. The various types of hypsodont teeth can be characterized by the specific phase that is expanded. In addition the degree of hypsodonty and the type of wear have to be recognized to understand the great diversity of hypsodont teeth.



Text-fig. 3. Multicusped hypsodont teeth: **A** – *Phacochoerus aethiopicus,* mandible with m2 and m3, Recent, Uganda, (STIPG M1208); **B** – *Phacochoerus aethiopicus,* m3, Recent, Botswana, (STIPG M7028); **C** – Schematic model for the heterochronic extension phase I at the costs of the other phases; **D** – *Desmostylus hesperus*, Miocene, California, (BSPG 2009 I 50); **E** – *Elephas maximus*, sectioned mandible, Recent (Tübingen collection). **F-G** – *Mammuthus primigenius*, lower m3, occlusal surface and lateral aspect, Upper Pleistocene, Rhine River (STIPG M3287). – Figures are not to scale. (A, B, F, G: photos G. Oleschinski, STIPB; D: photo BSPG Munich).

5. The categories of hypsodont teeth

5.1 Multicusped hypsodonty (Text-fig. 3)

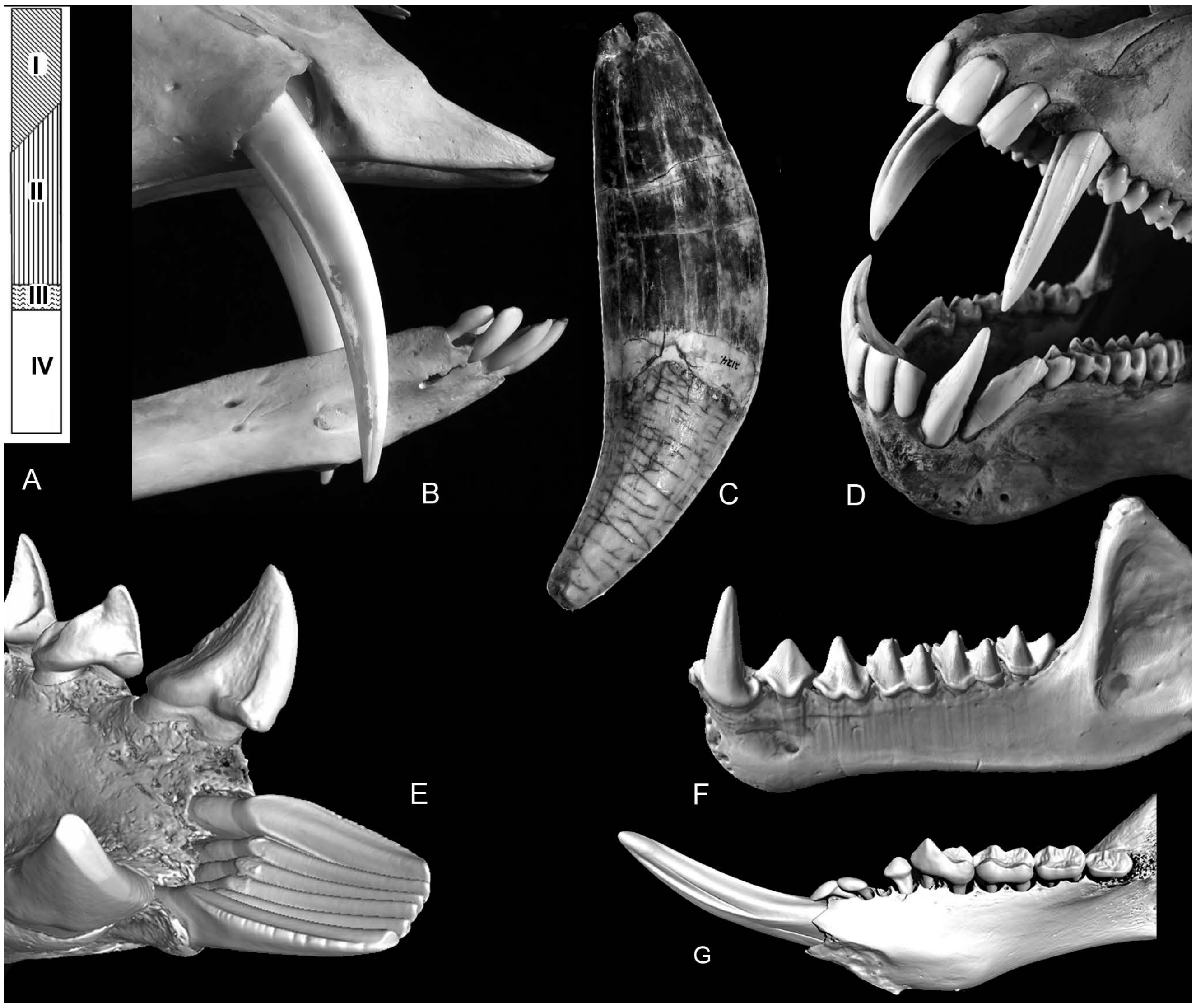
In several hypsodont teeth the cusps of the occlusal surface are elongated and dominate the tooth morphology (Text-fig. 3C). The sidewalls are very low. Thus in these teeth the ontogenetic phase I is dominant, and the subsequent phases II, III and IV are relatively short. Multicusped hypsodont teeth occur in the posterior dentition only and show a balanced wear. So far no examples for euhypsodonty are known.

Typical examples are the molars of *Phacochoerus* or *Desmostylus* (Text-fig. 3A–B, D). The isolated cusps form columns that are linked by enamel only at the very base. Among the huge diversity of rodent molars, such multicusped hypsodonty is fairly rare. We found only some molars of *Microtia* fitting into this category.

To the same category belong those teeth with elongated, transverse lamellae formed by confluent cusps. The molars of *Elephas*, *Loxodonta* and *Mammuthus* are examples (Text-fig. 3E–G). The individual lamellae merge only at the very base. The stability of these teeth is not related to sidewalls but to cementum between the cusps or lamellae.

5.2. Unicuspid hypsodonty (Text-fig. 4)

The category "unicuspid hypsodonty" refers to elongated single cusped teeth, as the large canines of carnivores. Wear may occur on the tip or on the sidewalls, but the length is not primarily controlled by wear.



Text-fig. 4. Unicuspid hypsodont teeth: **A** – Schematic model of the ontogenetic phases with the smooth transition from phase I to phase II; **B** – *Moschus moschiferus,* anterior dentition with enlarged upper canines (adult male), Recent, Siberia (ZMFK 97.664); **C** – *Deinohyus* sp., large upper canine with strong roots, where phases III and IV are continuous, Miocene, Agate Springs, Nebraska (CM 2124); **D** – *Papio ursinus*, upper and lower canines are hypsodont, Recent, Namibia (STIPB M 280); **E** – *Lemur fulvus albifrons*, all teeth of the tooth comb can be classified as unicuspid, Recent, zoo specimen (ZMFK 87.649), hypsodont with free growth; **F** – *Phyllostomus hastatus*, mandible with enlarged canine, Recent, Ecuador (ZFMK 59.201); **G** – *Petaurus breviceps*, mandible with enlarged incisor that is rooted and surrounded by enamel, Recent, Tübingen breed (STIBG KOE935). – Figures are not to scale. (B, D: photos G. Oleschinski, STIPB; E-F: virtual 3D models based on Micro CT scans).

The single cusp and the sidewalls are confluent, thus both ontogenetic phases I and II contribute to the height of the tooth crown. In unicuspid hypsodont teeth the phase II is often marked when the sidewalls show longitudinal grooves or a basal cingulum. The subsequent phases III and especially IV (root formation) are usually present (Text-fig. 4A).

Such elongated unicuspid teeth that are restricted to the anterior dentition are generally characterized by free growth. When fully erupted, these teeth normally develop strong roots.

Typical examples are the enlarged canines of bats, primates, creodonts, and carnivores (Text-figs. 2D, 4D–F). The upper canines of some artiodactyls (e.g., *Moschus* or *Deinohyus* (Text-fig. 4B–C) have to be included here as well.

Many mammalian lineages evolved a pair of elongated procumbent lower incisors that work against several upper incisors of very different shape. Such hypsodont teeth occur e.g., in soricids, apatemyids, plesiadapids and diprotodontid marsupials, e.g., *Petaurus* (Text-fig. 4G) or *Macropus.* These teeth share the characteristic that the main functional surface is the sidewall directed upwards due to the horizontal orientation of the tooth. The characteristic tooth comb in lemurs (Text-fig. 4E) is formed by the incisors and canines. Each tooth fulfils the characteristic of a unicuspid hypsodont tooth.

The lower margin of the enamel cap may show an undulating linea sinuosa. In some teeth, especially incisors and canines, the dentine areas may extend into the crown and form dentine tracts. The increasing width of the dentine tracts forms a morphological transition from teeth that are clearly unicuspid hypsodont to those that are here classified as sidewall or enamel-band hypsodont.

The term "unicuspid hypsodonty" covers partly the cusp hypsodonty as defined by White (1959), but we differentiate between multicusped hypsodonty, usually occcuring in cheek teeth with balanced wear, and unicuspid hypsodonty, common in the anterior dentition with free growth. The unicuspid hypsodonty covers a section of the wide realm of "tubercular hypsodonty" of Hershkowitz (1962), but his unit includes other unicuspid teeth as well, here attributed to the categories enamel band hypsodonty or dentine hypsodonty. Only unicuspid teeth with strong roots come close to what Schmidt-Kittler (2002) described as a "proportional stretching of all parts". However, he referred mainly to rodent molars. In well rooted unicuspid teeth, phases I and II as well as III and IV are not easily discernable, and thus their proportional elongation cannot be tested.

5.3. Sidewall hypsodonty (Text-fig. 5)

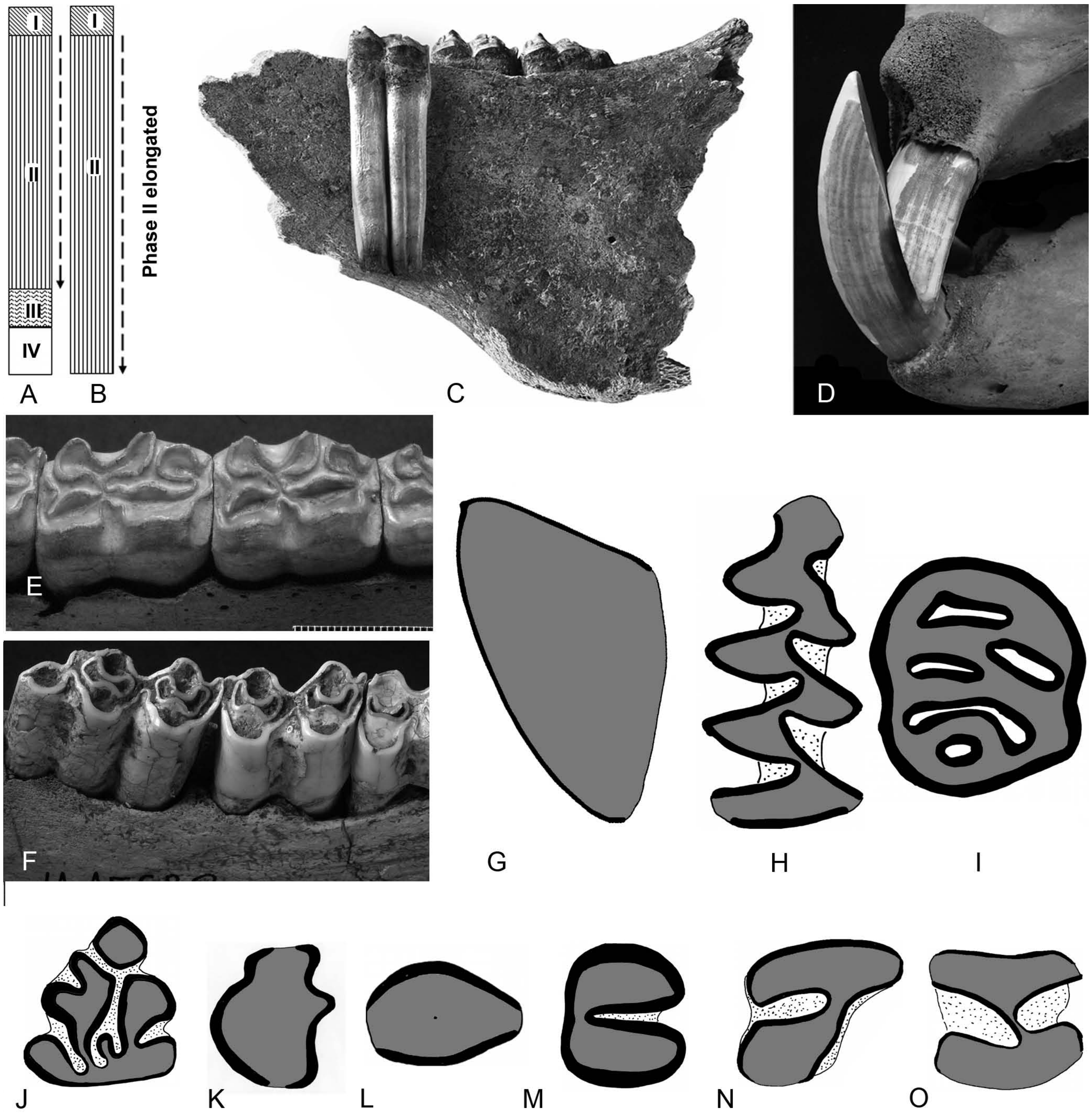
Teeth of the category "sidewall hypsodonty" are dominated by high sidewalls that are covered with enamel and formed during the ontogenetic phase II (Text-fig. 5A–B). The primary occlusal surface, related to phase I, is functionally insignificant and worn away quickly after tooth eruption. Balanced wear is dominant in molars. The enamel covered sidewalls form cutting edges surrounding a dentine field (Text-fig. 5B-O). The phases III and IV may be present, but in many evolutionary lineages euhypsodonty was achieved and thus the phases are postponed. Sidewall hypsodonty is widespread among placental mammals and occurs in the anterior and posterior dentition. In the posterior dentition it is always linked with balanced wear.

In the anterior dentition, sidewall hypsodonty occurs e.g., in spatulate incisors of *Lama* and *Camelus* or elongated ones in *Sus*. These teeth have enamel-covered sidewalls and are abraded but have no explicit balanced wear. They are not regarded as unicuspid hypsodont because of their differentiated and broadened shearing blade.

The examples for sidewall hypsodonty in the posterior dentition are innumerable. Most hypsodont or euhypsodont cheek teeth of derived equids (Text-fig. 5C, E), bovids (Text-fig. 5F), camelids, notungulates, and some rhinos, belong to this category. In small mammals the cheek teeth of some macroscelids, of many rodents, e.g., pedetids, hystricids, geomyids, arvicolids, and various other species (Text-fig. 5H–I, K–O) have sidewall hypsodonty. Sidewall hypsodonty certainly is the most frequent form of hypsodonty. Since the primary occlusal surface is lost in early wear stages, several authors talk about a simplification or even a degeneration of the occlusal surface, when only a ring of enamel surrounds the dentine (Hershkovitz 1967; Thenius 1989; Schmidt-Kittler 2002). *Aplodontia* and geomids are typical examples. More often, however, the secondary occlusal surface is differentiated by enamel islets and/or re-entrant folds that increase their efficiency (Text-fig. 5H–I).

Examples for teeth with distinct enamel islets (related to phase I) are e.g., cheek teeth of bovids (Text-fig. 5F) and those of many rodents e.g., *Castor* and *Hystrix* (Text-fig. 5I). Examples for lateral re-entrant folds (related to phase II) are the lower cheek teeth of *Equus* (Text-fig. 5E), several rodents (Text-fig. 5H, M–O), including the geomyoid *Entoptychus* (Rensberger 1971, 1975), or lagomorphs (Text-fig. 5J) (Koenigswald et al. 2010a). Both structures are functionally very important since they are increasing the shearing ability of the secondary occlusal surfaces, but there is a significant difference in the formation of these two structures.

Teeth attributed to the category of sidewall hypsodonty are mainly covered with enamel on the various sides. Hibbard (1954) drew attention to the dentine tracts in rodent molars, e.g., in arvicolids and geomyids. Dentine tracts are narrow, vertical stripes of dentine extending from the lower margin of the enam-



Text-fig. 5. Sidewall hypsodont teeth: **A**–**B** Schematic models for the heterochronic extension phase II; A – retaining phases III and IV (= rooted) and B – reduced phases III and IV (= euhypsodont); **C** – *Equus caballus* mandible with hypsodont lower molar, subfossil, Germany (STIPB M589); **D** – *Hippopotamus amphibius*, occlusion of canines, the enamel band in lowers on the anterior side in uppers on the posterior side, Recent, Africa (STIPB M2365); **E** – *Equus caballus*, occlusal surface of lower molars surrounded by enamel with deep re-entrant folds, Recent, Germany; **F** – *Bos taurus*, lower molars with enamel islets, Recent, Germany (STIPB M1568); **G** – *Sus scrofa*, cross-section of lower canine with on e side free of enamel, Recent, Germany (STIPB 2163); **H** – *Mimomys savini,* m1 dex., with intensive lateral re-entrant folds, Pleistocene, Cromer, Britain (STIPB KOE19); **I** – *Hystrix* sp., molar with enamel islets, Pleistocene, China (STIPB KOE74); **J** – *Prolagus sardus*, euhypsodont p4 with complicated re-entrant folds, Pleistocene, Sardinia (STIPB KOE1060); **K** – *Aplodontia rufa*, m1 with dentine tracts, Recent, Washington (STIPB KOE591); **L** – *Thomomys bottae*, M2 sin., with dentine tracts, Recent, Chile (STIPB KOE1612); **M** – *Pedetes cafer*, m1, Recent, Africa (STIPB KOE158); **N** – *Octodon degus*, M2 with lateral infold, Recent, Chile (STIPB KOE976); **O** – *Abrocoma benetti*, upper M1with lateral infolds from both sides, Recent, Chile (STIPB KOE619). – In cross-sections: black = enamel, gray = dentine, stippled = cementum. – Figures are not to scale. (Photos G. Olschinski STIPB).

el cap far up into the crown and their progressive evolution has been documented in Oligocene geomyoids (Rensberger 1971). Thus these dentine tracts are related to phase III, but these molars are dominated by the surrounding enamel of phase II. For practical reasons such dentine tracts up to 1/3 of the circumference of the tooth are tolerated in the category of sidewall hypsodonty. If the dentine fields exceed this value, as in rodent incisors, the hypsodont teeth are classified as enamel-band hypsodont.

In the anterior dentition sidewall-hypsodonty may occur in teeth of free growth. In contrast to enlarged incisors and canines attributed to unicuspid hypsodonty, these teeth are characterized by distinct dentine tracts. The upper and lower canines of *Astrapotherium* are triangular, and a dentine tract covers the posterior side that is narrower than 1/3 of the circumference of the tooth. Thus this tooth represents sidewall hypsodonty (Scott 1937).

In *Hippopotamus* the massive canines have distinct dentine tracts. In the lower teeth thick enamel covers the anterolingual and anterobuccal sides, while the posterior side is free of enamel. In upper canines the anterior side shows the dentine tract while the grooved posterior side is covered by enamel. The dentine tracts are less than 1/3 of the circumference of the teeth and thus they can be classified as sidewall hypsodont. The occlusion of upper and lower canines is characterized by balanced wear. The lower canine passes the upper on the anterior side (Text-fig. 5D). Thus the enamel forms a sharp cutting edge anteriorly on the almost vertical occlusal surface. In the upper canine the steeply ascending occlusal surface forms a sharp cutting edge on the posterior side. Thus the orientation of the dentine tracts has a significant function.

The impressive lower canines of *Sus scrofa* (Text-figs. 5G, 9L) and several other suids have a dentine tract on the posterior side. It covers less area (about 1/3 of the circumference) of the tooth. Thus these teeth are classified as sidewall hypsodont. They are euhypsodont and represent a free growth, although they show intensive wear. But the wear is from the side and leaves a sharp tip which becomes larger with individual age.

5.4. Enamel-band hypsodonty (Text-fig. 6)

The category "enamel-band hypsodonty" comprises hypsodont teeth that have enamel only on one or two sides, while the dentine surface covers more than one third of the circumference of the tooth. Teeth with smaller dentine tracts are included in sidewall hypsodonty. Both ontogenetic phases II and III are forming the tooth simultaneously in its dominant part, in euhypsodont teeth throughout the entire life span. In all of these teeth a small enamel cap may be formed during phases I, but it is relatively small and functionally insignificant. Many teeth showing an enamel band hypsodonty are euhypsodont, which means the phases III and IV are missing (Text-fig. 6A).

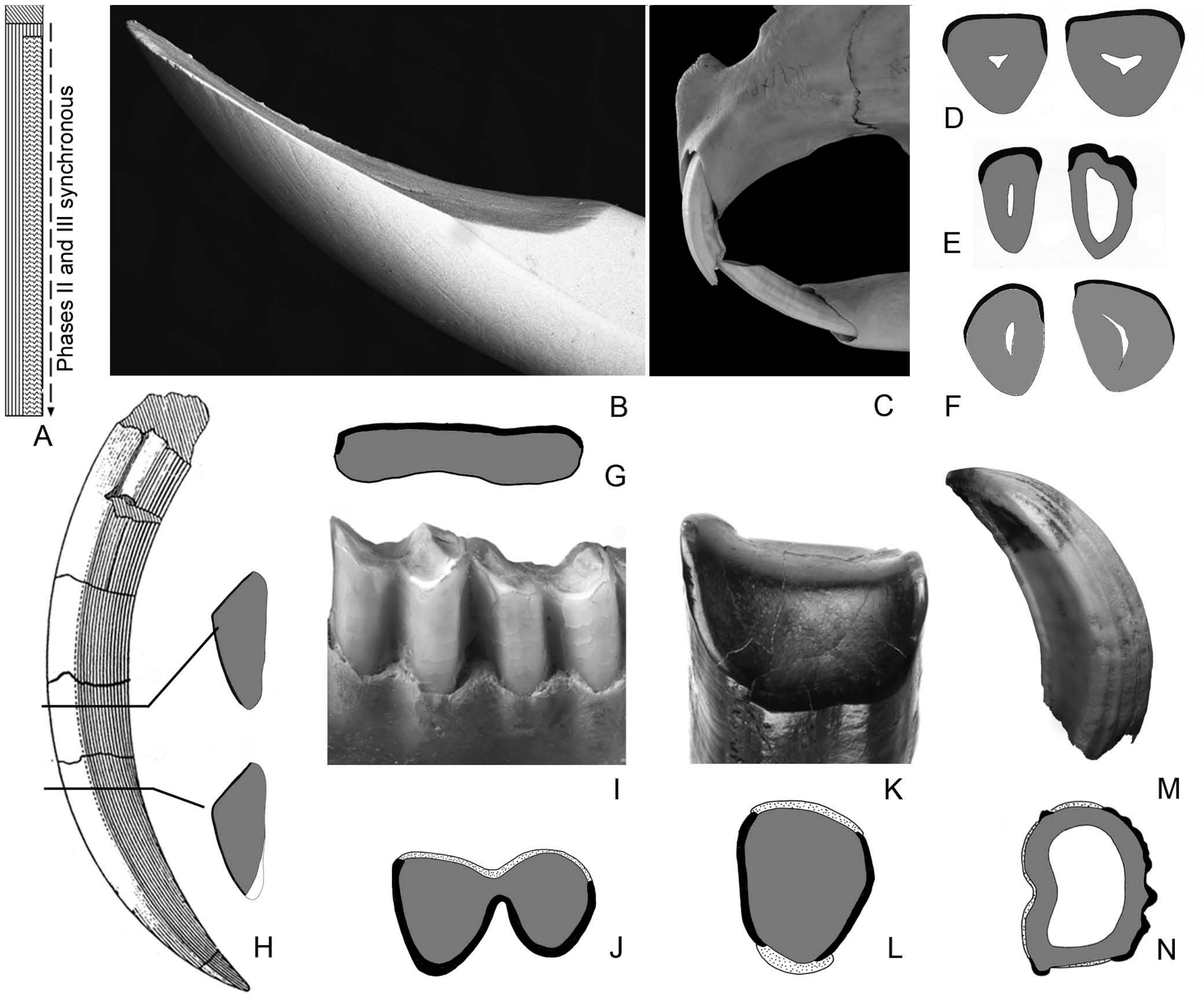
The most typical examples for the category of enamel-band hypsodonty are the large incisors of rodents (Text-fig. 6B–F) and lagomorphs. Upper and lower incisors are euhypsodont and the enamel band covers the anterior side regularly and parts of the mesial side. The length of these teeth is strictly controlled by balanced wear.

Very similar constructions of incisors evolved independently in lagomorphs, the multituberculate *Taeniolabis*, the primate *Daubentonia*, hyracoids, tillodonts, taeniodonts, pyrotheres, and even in few marsupials (e.g., the fossil *Diprotodon* and *Phascolonus* (Text-fig. 6G), and the extant *Vombatus* and *Lasiorhinus* (Text-fig. 6I–J).

In *Hippopotamus amphibius* upper and lower incisors, with exception of the dentine hypsodont lower first incisor, have a distinct lateral band of enamel. These teeth are euhypsodont and have a rounded cross-section. The tip is worn, but irregularly. Thus they are classified as enamel-band hypsodont with free growth.

The insular bovid *Myotragus balearicus* is special in having a pair of euhypsodont lower incisors, with a typical enamel band on the anterior side. Although this incisor has no antagonist, it is intensively worn by food and the horny plate covering the premaxilla.

The upper canines of *Sus scrofa* are euhypsodont and intensively curved, therefore the geometry of these teeth covered only partially with enamel is complex. At the alveolar rim a broad enamel band is found at the lower side. A just erupted permanent upper canine shows the unworn enamel cap (Text-fig. 6M–N). This cap continues into the wide enamel band on the lower side and two narrow ones on the opposite sides. These bands separate the dentine tracts, which are confluent in a later stage, covering three sides of the tooth. In contrast to lower canines, the uppers have enamel band hypsodonty.



Text-fig. 6. Enamel-band hypsodont teeth: **A** – Schematic model for the heterochronic extension of phases II and III with suppression of phase IV, if euhypsodont; **B** – *Dicrostonyx torquatus* lower incisor, Pleistocene, Germany (STIPB KOE93); **C** – *Hydrochoerus hydrochaeris*, occlusion of rodent incisors, Recent, Argentina (STIPB M5684); **D** – *Tachyoryctes splendens*, cross-sections of lower and upper incisors, Recent, Kongo (STIPB KOE2382); **E** – *Meriones shawi,* cross-sections of lower and upper incisors, Recent, Morocco (STIPB KOE44); **F** – *Ondatra zibeticus*, cross-sections of lower and upper incisors, Recent, Germany (STIPB KOE2807); **H** – *Thylacosmilus atrox,* euhypsopdont upper with enamel on the buccal side only. Wear sharpens the blade; **G** – *Phascolonus gigas*, cross-section of upper incisor, Pleistocene, New South Wales (STIPB KOE1684); **H–I** – *Vombatus ursinus*, lower molars with enamel on the buccal side only, Recent, Australia (STIPB M542). **K–L** – *Stylinodon mirus* cheek tooth with enamel on buccal and lingual sides, Eocene, Wyoming (USNM 16664); **M** *Sus scrofa*, Recent, Germany (STIPB M 1212), freshly erupted upper canine, distal aspect of the unworn tip with the wide dentine band to the right and one narrow to the left; **N** – Cross-section of the same tooth -section with the wide enamel band on the lower side and three dentine tracts; due to the freshly erupted tooth the pulpa is very wide. – In cross-sections: black = enamel, gray = dentine, stippled = cementum. – Figures are not to scale. (D–F: from Kalthoff 2000; H: from Koenigswald & Goin 2000; C, I, K, M: photos G. Oleschinski, STIPB).

Other canines attributed to this category are more bladelike. The large, euhypsodont canines of the marsupial *Thylacosmilus* (Text-fig. 6H) is an impressive example (Turnbull 1978). The canine is covered with enamel only on the lateral side, while dentine is exposed on the lingual side. Although there is no antagonist the dentine is abraded by the horny skin covering the mandible. The exposed rims of the enamel form sharp cutting edges (Koenigswald & Goin 2000). Several early cervids (e.g., *Muntiacus, Pomelomeryx)* have very similarly constructed upper canines.

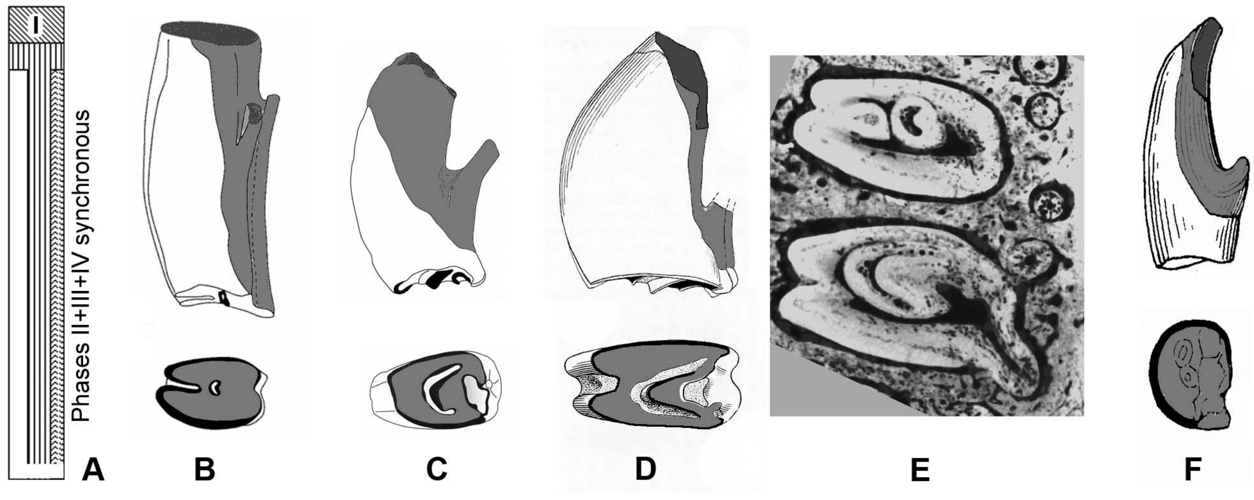
In the posterior dentition, enamel-band hypsodonty is rare since the surrounding enamel is of great functional importance. Therefore, dentine tracts exceeding 1/3 of the circumference are found only in a few cheek teeth. The wide dentine tracts in *Stylinodon* (Text-fig. 6K–L) were observed previously by White (1959). Broad dentine tracts with cementum cover the anterior and the posterior side (Koenigswald et al. 2010b). The euhypsodont cheek teeth of the extant marsupials *Vombatus* (Text-fig. 6I–J) and *Lasiorhinus* are covered with enamel only on one side. Lowers show enamel on the buccal side, uppers on the lingual side. Such a distribution is related to the chewing direction and thus to the pattern of functional symmetry found in many cheek teeth (Rensberger 1973; Koenigswald et al. 1994). The euhypsodont lower molars of the rodents *Geomys* and *Pappogeomys* then fall into the same category, having an enamel band on the distal side only, while uppers are characterized as sidewall hypsodont with narrower dentine tracts free of enamel.

5.5. Partial hypsodonty (Text-fig. 7)

The category "partial hypsodonty" as defined by (Tobien 1963, 1974, 1976, 1978) is represented by strongly curved upper cheek teeth that are dominated by a hypsodont enamel band on the lingual side, while tiny roots anchor the tooth on the buccal side (Text-fig. 7B–F). During the long lasting tooth eruption, the tooth rotates in a buccal-lingual direction around the anchoring roots.

Such teeth have a primary occlusal surface formed during phase I. The dominant enamel on the lingual side is related to phase II. Simultaneously, the dentine surface of phase III is built more buccally and the small roots on the buccal side represent phase IV (Text-fig. 7A). Thus the phases II, III, and IV are involved simultaneously in the formation of this type of tooth.

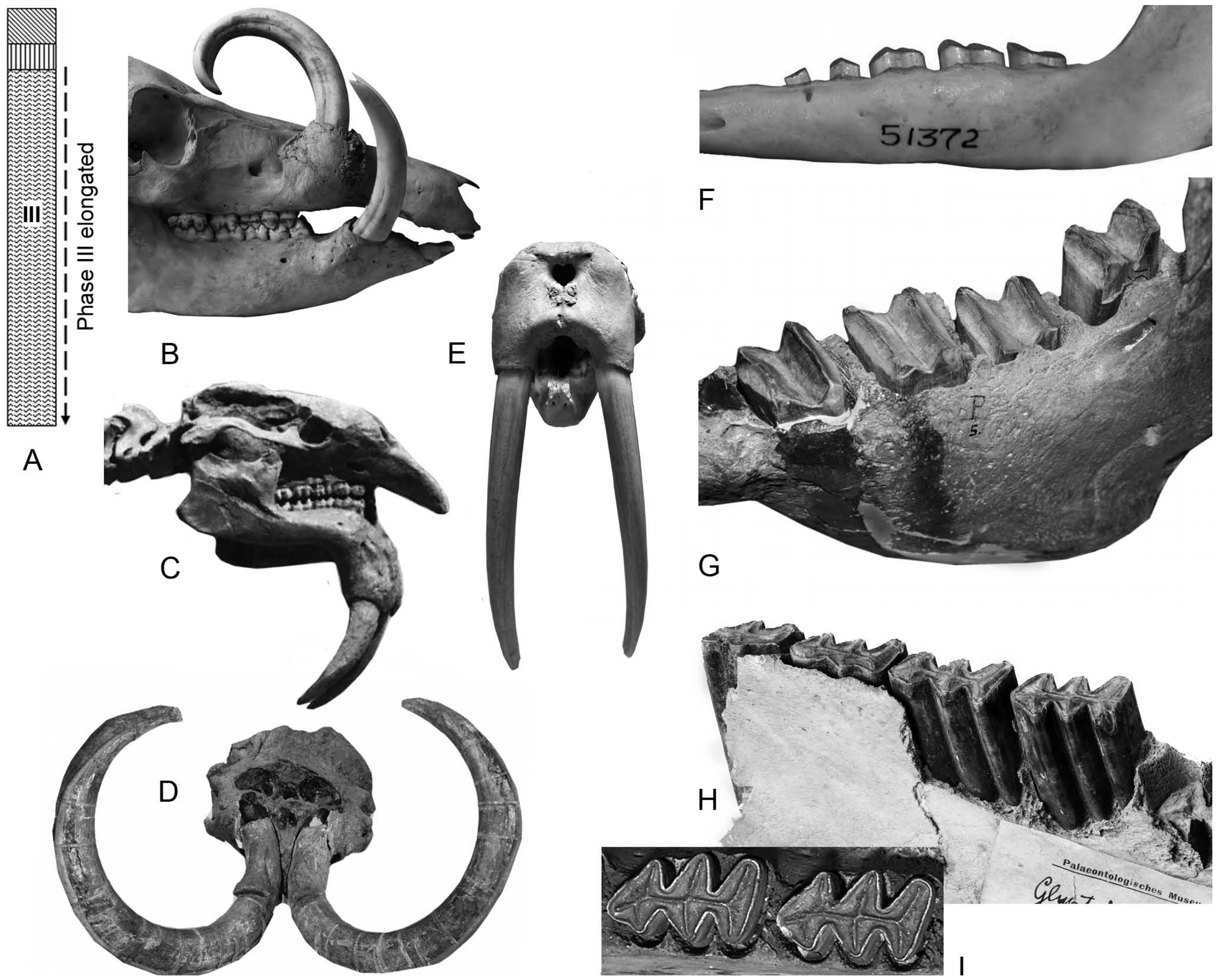
The most prominent examples of partial hypsodonty are the upper cheek teeth of some lagomorphs (e.g., *Palaeolagus*, *Amphilagus*, *Piezodus, Titanomys*, and *Mytonolagus*) (Text-fig. 7B–E) (Forsyte Major 1899; Tobien 1963, 1976, 1978; Dawson 1958, 1967; Bair 2007; Fostowicz-Frelik & Tabrum 2009; Koenigswald et al. 2010). An almost identical construction is found in theridomyids (Schmidt-Kittler & Vianey Liaud 1987), tsaganomyids



Text-fig. 7. Partial hypsodonty in upper cheek teeth of lagomorphs (B–E) and rodents (F). **A** – Schematic model for the heterochronic extension of phase II; phases III and IV occur simultaneously on the buccal side. **B** – *Palaeolagus* sp., M1 with lateral roots, middle Eocene, Montana (STIPB KOE 668); **C** – *Mytonolagus ashcrafti*, P4, middle Eocene, Montana; **D** – *Amphilagus ulmensis*, P4 , Miocene Germany; **E** – *Amphilagus antiquus*, MicroCT of P4 and M1 showing the pair of buccal roots in cross-section, upper Oligocene, France (NHMB Cod 377); **F** – *Cyclomys lohensis*, early Oligocene, Mongolia. In drawings: black = enamel, gray = dentine, stippled = cementum. – Figures are not to scale. (B and C: from Fostowicz & Tabrum 2009; D: from Tobien 1974; F: from Wang 2001).

(Text-fig. 7F) (Wang 2001), and several other rodents. During wear, the secondary occlusal surface is rotating around the buccal rim. Due the increasing obliquity with the growing axis the buccal-lingual extension of the occlusal surface becomes larger (Bair 2007). The lower cheek teeth of the same taxa are less curved and represent sidewall hypsodonty.

Bair (2007) studied the geometrical aspect of the partial hypsodonty in the ochotonids *Desmatolagus* and *Hesperolagomys*. She compared the strongly curved upper molars with incisors of the rodent *Ondatra*. Despite similarities in the geometry both tooth types are related here to different categories of hypsodonty. Neither in rodent incisors nor in any of the



Text-fig. 8. Dentine hypsodonty: **A** – Schematic diagram for the heterochronic extension phase III. Phase I and II may be present, phase IV is regularly suppressed. **B** – *Babyrussa babyrussa*, euhypsodont upper and lower canines are dentine teeth, Recent, Sulavesi (ZMFK 39.136); **C** – *Prodeinotherium bavaricum*, Miocene, Ulm (SMNS 41562); **D** – *Mammuthus primigenius*, Pleistocene, Horb, Germany (GPIT/MA/2129); **E** – *Odobenus rosmarus*, cranium with enlarged canines, Recent, Bering Sea (ZFMK 94.138); *Mamuthus primigenius* tusk, Pleistocene, Siberia; **F** – *Orycteropus afer,* mandible with euhypsodnt dentine teeth, Recent, Africa (AMNH 51372); **G** – *Megatherium americanum,* mandible with lophed cheek teeth, Pleistocene, Buenos Aires province, (MLP 2-56); **H** – *Glyptodon reticularis,* mandible with euhypsodont cheek teeth, Pleistocene, San Alberto, Bolivia (MB Ma. 33514); **I** – *Glyptodon typus,* cheek teeth showing the dentine differentiation of the dentine, Pleistocene, Escrivanta Huelen, Brazil (ZMK 1845/1:9250). – Figures are not to scale. (Photos B: G. Olschinski, STIPB; C: H. Lumpe, SMNS; D – W. Gerber, GPIT; E: R. Hutterer, ZMFK; F: T. Lehmann, SMF; G: S. Bargo, MPL; H: O. Hampe, MB; I: K.L.Hansen, ZMK).

strongly curved cheek teeth occurring in notungulates or vombatids, roots restricted to the buccal side are present or can be assumed for earlier phylogenetic stages.

5.6. Dentine hypsodonty (Text-fig. 8)

The category "dentine hypsodonty" comprises elongated teeth with a surface that is dominated by dentine and thus attributed to ontogenetic phase III (Text-fig. 8A). A small enamel cap formed during phases I and II may be present but is normally insignificant. The teeth of dentine hypsodonty are generally euhypsodont and thus a formation of differentiated roots during phase IV does not occur. Dentine hypsodonty occurs in anterior dentitions showing free growth as well as in posterior dentitions with balanced wear. The most impressive examples are the ivory tusks in the whale *Monodon,* the canivore *Odobenus,* or in proboscideans (*Elephas, Mammuthus* and *Deinotherium*) (Text-fig. 8C–E).

In the posterior dentition, typical dentine hypsodonty can be observed in *Orycteropus* (Text-fig. 8F) and fossil and extant xenarthrans e.g., *Megatherium* and *Glyptodon* (Text-fig. 8G–H). These teeth show balanced wear and are regularly surrounded by cementum. The dentine structure provides various modifications of different resistance to wear (Kalthoff 2011).

Traces of the initial enamel cap are known from fossil and even some extant dasypodids (Sprugin 1904; Simpson 1932), indicating that the ontogenetic stages I and II were present in earlier phylogenetic stages but have been reduced. Similarly the narrow enamel band present in the entire length of gomphotherian tusks (e.g., *Cuvieronius* and *Gomphotherium*) can be interpreted as a rudiment (Göhlich 2010).

In *Hippopotamus amphibius,* only the massive lower central incisor is a dentine tooth, while the other incisors represent enamel-band hypsodonty. In the suid *Phacochoerus,* the upper canines are heavy dentine teeth: In *Babyrussa* not only the upper canines are free of enamel but the lowers as well.

6. Discussion

6.1. Comparison with previously described types of hypsodonty

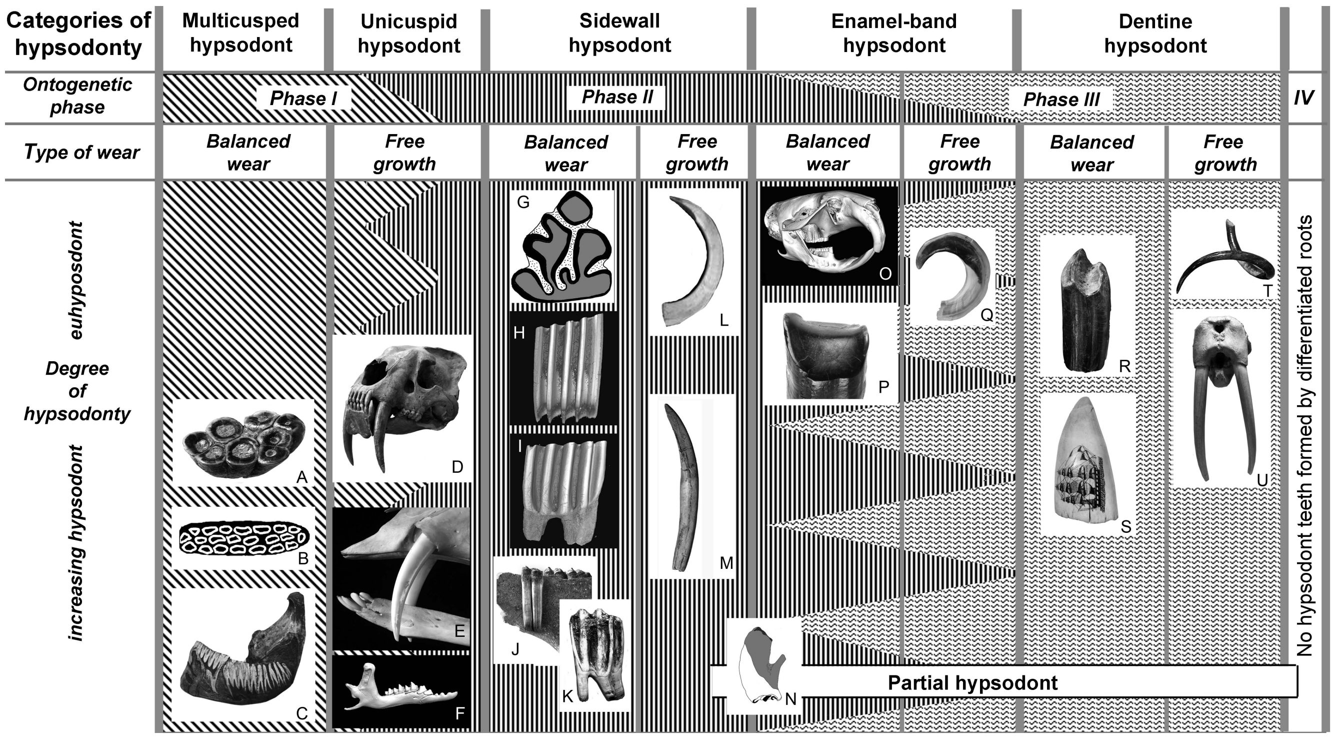
In contrast to the previous classifications, the types of hypsodonty defined here are based on three different and independent parameters: the extended ontogenetic phase, the degree of hypsodonty, and the type of wear. One parameter alone is not enough to characterize the great diversity of hypsodonty in mammalian dentitions. That this classification is applicable to the great diversity of hypsodont teeth in mammalian dentitions is shown by the arrangement of examples in the field between the three selected parameters, as shown in Text-fig. 9. A single dentition may contain several types of hypsodont teeth. In Table 3 various mammalian taxa having hypsodont teeth are listed, and the various tooth positions are classified. This list demonstrates the occurrence of hypsodonty in almost all mammalian orders and the wide applicability of the proposed system. Any such kind of classification is like a Procrustean bed, into which some intermediate stages have to be squeezed in. The large array of taxa listed in Table 3 shows that the new system is broad enough to include almost all teeth. Certainly the attribution to a specific type does not give all the required information nor replaces a detailed description. But with additional comments these basic types of hypsodonty can easily be differentiated.

The more traditional way to look at hypsodont teeth dealt mainly with cheek teeth of balanced wear and thus excluded all other hypsodont teeth, despite their very similar construction.

As mentioned in the introduction this is not the only approach classifying hypsodont teeth. The system proposed by White (1959) covers the morphology of a great number of hypsodont cheek teeth in mammalian families, but his types are not comprehensive and do not include all tooth types. Hershkowitz (1962) concentrated on rodent teeth and created a system with only two types. Thus teeth attributed to one of his types may show a highly diverse ontogenetic history. Nevertheless these types can be correlated with the system proposed here (Table 2), but some of them cover several types distinguished here.

6.2. Evolutionary aspects

All categories of hypsodonty differentiated here are based on the critical condition that primarily one of the ontogenetic phases is extended at the cost of others. Thus all categories can be deduced from this basic pattern alone. But any classification is more or less static and does not reflect the evolutionary changes. The widespread tendency for hypsodonty to increase can be expressed within the parameter of the degree of hypsodonty.



Text-fig. 9. Categories of hypsodonty characterized by three parameters: 1. dominant and extended ontogenetic phase (phase I, II, and III), 2. type of wear (balanced wear or free growth), and 3. degree of hypsodonty (increasing hypsodont to euhypsodont). **A** – *Destmostylus* (molar); **B** – *Phacochoerus* (molar); **C** – *Loxodonta* (molars); **D** – *Smilodon* (upper canines); **E** – *Moschus* (upper canines); **F** – *Sorex* (lower incisor); **G** – *Prolagus* (premolar); **H** – *Arvicola* (euhypsodont molar); **I** – *Mimomys* (rooted molar); **J** – *Equus* (molar); **K** – *Bos* (molar); **L** – *Sus scrofa* (euhypsodont lower canine); **M** – *Protaceratherium minutum* (rooted lower incisor); **N** – *Mytonolagus* (upper molar with partial hypsodonty); **O** – *Microtus gregalis* (upper and lower molars and upper and lower incisors); **P** – *Stylinodon mirus* (euhypsodont molar); **Q** – *Sus scrofa* (euhypsodont upper canine); **R** – *Megatherium* (molar); **S** – *Physeter* (molar); **T** – *Mammuthus primigenius* (tusk); **U** – *Odobenus* (upper canines). – Figures are not to scale.

But whether categories change within lineages when the teeth are modified during evolution needs to be discussed. One striking result from this survey is that cheek teeth seldom change from one category to the other during their evolution in the fossil record. One exception is the rodent *Microtia*, classified as multicusped hypsodont. It seems to develop enlarged sidewalls and might end up in the sidewall hypsodont category. Others may develop central longitudinal ridges connecting the cusps.

The enlarged teeth in the frontal region are more likely to change category by increasing the dentinal part of the tooth surface. Apatemyids are an example. The enlarged lower incisor of *Stehlinella* from the Uintan (Middle Eocene) of Utah is enlarged but well rooted. The elongated cusp is covered with enamel on all sides and thus is classified as unicuspid hypsodont. In the more derived *Sinclairella* from the Oligocene of Dakota, the crown is elongated and covered by enamel mainly on the lower side (Jepsen 1934). The European genus *Heterohyus* from the Eocene of Messel and Egerkingen has achieved a full euhypsodont lower incisor with an enamel-band on the anterior side (Stehlin 1916; Koenigswald 1990). Although this is not a phylogenetic lineage, these teeth demonstrate the possible evolutionary pathway.

Canines of suids provide another example. Although the upper canines are massive, the enamel bands, present in *Sus*, are reduced in *Phacochoerus* while the pointed lower canine retains the enamel forming sharp cutting edges. In *Babyrussa* the enamel of upper and lower canines is reduced to produce essentially dentine teeth, although these teeth are very impressive in size. It seems that enamel is less important in teeth mainly used as display organs. Perhaps the stiff enamel is less favored in large tusks that need

Table 2. Terms related to hypsodonty with abbreviated explanations and comments about their interrelationships.

Balanced wear (this paper)	Hypsodont or euhypsodont teeth with a stable position of the occlusal surface due to a constant equilibrium between a long lasting tooth eruption and abrasion by a structurally similar antagonist.
Coronal hypsodonty (Hershkovitz 1962 and 1967: 834)	"Coronal hypsodonty results in vertical elongation of the entire crown of the tooth at the expense of the root ... in molariform teeth" [equivalent to multicusped- and mainly sidewall hypsodont teeth in this paper]
Crown hypselodonty (Janis & Fortelius 1988)	"(Cheek-) teeth with indefinite suppression of root formation, and the crown continues to grow after eruption." [Such euhypsodont teeth are part of sidewall hypsodonty in this paper]
Cusp hypsodonty (White 1959:243)	Molars with elevated crowns, rooted or unrooted. [Comprises multicusped -, unicuspid-, and partly sidewall hypsodonty of this paper]
Dentine hypsodonty (this paper)	Hypsodont teeth mainly formed by dentine, usually euhypsodont (ontogenetic phase III dominant)
Dentine tracts (e.g., Hibbard 1954)	Narrow stripes of dentine reaching from the *linea sinuosa* up into the crown
Enamel-band hypsodonty (this paper)	Hypsodont teeth with enamel and dentine exposed in the sidewalls, the dentine part is more than 1/3 of the circumference, simultaneous activity of phases II and III in the dominant part of the tooth
Euhypsodont (Mones 1982)	Rootless or continuously growing teeth (equivalent to hypselodont)
Free growth (this paper)	Hypsodont or euhypsodont teeth that may protrude from the mouth and are not limited in length by regular abrasion.
Hypselodont	Synonym of euhypsodont (see Mones 1982)
Hypsodont (as used in this paper)	Teeth higher than wide or long (Van Valen 1960: 531), being rooted or unrooted (euhypsodont), occur in the entire dentition, and may have enamel or not.
Hypsodonty index (various authors)	Relationship between the height of freshly erupted, hypsodont teeth and the width or length, defined for restricted taxa and special purposes
Linea sinuosa (Rabeder 1981)	Undulating lower margin of the coronal enamel, often forming dentine tracts
Multicusped hypsodonty (this paper).	Hypsodont teeth with several elevated cusps or transverse lophs, and low sidewalls; balanced wear is dominant.
Partial hypsodonty (Tobien 1963, 1974, 1978)	Hypsodont cheek teeth in lagomorphs with an oblique lower enamel margin and growing zone. They are strongly curved in lingual-buccal and often rooted on one side. The enamel cover is predominantly on the side with the greater radius [simultaneous activities of phases II, III, and IV], partly equivalent to unilateral hypsodonty.
Root hypsodonty (White 1959: 243)	"In this type the principal growth of the tooth takes place in the roots....the enamel depositing may or may not persist or may be limited to certain areas". [Thus this type comprises enamel-band hypsodont, and dentine hypsodont cheek teeth]
Root hypselodonty (Janis & Fortelius 1988)	"Teeth with true crown lost through wear in an early stage and the root continue to grow and erupt as a dentine peg." [equivalent to cheek teeth with dentine hypsodonty]
Sidewall hypsodonty (this paper)	Teeth that are dominated by extended sidewalls. They may be rooted or euhypsodont. The primary occlusal surface is functionally insignificant. Ontogenetic phase II dominants at the costs of other parts. Enamel islets and lateral re-entrant folds may be present. Dentine tracts up to 1/3 of the circumference are tolerated. Thus ontogenetic phase I and III may be partially involved. [Cheek teeth of this type are fall in the category "tooth-base hypsodonty" of White (1959). Euhypsodont cheek teeth fall into "crown hypselodonty" of Janis & Fortelius (1988)]
Superhypsodonty (Martin 1993:210)	Another term for euhypsodont or hypselodont
Tooth-base hypsodonty (White 1959:243)	"In this type the principle growth of the tooth takes place between the base and the root and the cusps or crests are usually low." [Comprises sidewall hypsodont cheek teeth in this paper.]

Table 2. Continued.

Tubercular hypsodonty (Hershkovitz 1962 and 1967: 834)	"Tubercular hypsodonty results in elongation of the coronal tubercle, or tubercles, at the expense of the remainder of the tooth, including the root." [He explicitly includes rodent incisors, elephant tusks, but molariform teeth as well. Thus it comprises multicusped, unicuspid, and enamel band-, and dentine hypsodont teeth of this paper]
Unicuspid hypsodont (this paper)	Hypsodont teeth with simple (unicuspid) enamel cap that continues into the sidewalls, thus the ontogenetic phases I and II are not distinguishable. As in some canines, roots may be larger than crowns.
Unilateral hypsodont (Burke 1934, 1941)	Hypsodont molars, where the lower rim of the enamel cap is at different height on the lingual and buccal sides (Wang 2001; Candela et al. 2007). [A synonym of partial hypsodonty Tobien 1963.] – Bair (2007) expanded this term (unfortunately) to rodent incisors.

to be somewhat elastic to prevent breakage. This relationship is not applicable to dentine teeth in the posterior dentition.

Teeth with partial hypsodonty are a final example. Tobien (1976) assumed that the ochotonid lagomorphs achieved euhypsodonty in their upper molars by passing through a stage of partial hypsodonty in which the curvature of the upper cheek teeth was gradually straightened. The two buccal roots are possibly replaced by dentine ridges located in exactly the same position. Such ridges are present in several derived ochotonids. Thus these teeth changed from the category of partial hypsondonty to sidewall or enamel-band hypsodonty.

A similar evolutionary change presumably occurred in the upper molars of theridomyid rodents (Schmidt-Kittler 2002) and may have occurred in hystricids as well. Partial hypsodonty seems to be one way to reach the level of euhypsodonty, but certainly it is only one of several ways, for it is not applicable to rodent or lagomorph incisors.

A transition from one hypsodont category to the other is possible through partial hypsodonty. The impression of our study, however, is that the interchange between the various types of hypsodonty is limited. Neither so far convincing examples for any evolutionary reversals were found, neither in reduction of the degree of hypsodonty nor in closure of dentine tracts or fields by enamel.

6.3. Simultaneous activity of different ontogenetic phases

The ontogenetic phases are not strictly sequential but distinct interactions between the various phases occur. In unicuspid hypsodonty, phase I cannot be differentiated from phase II. This is a simple interaction. More complicated is the formation of enamel islets. If they originate from the primary occlusal surface, they are related to phase I and are formed – to some degree – simultaneously with the sidewalls of phase II. The formation of such an enamel islet is, however, only possible until the margins of the islet have reached the occlusal surface, for the enamel forming epithelium can only be supported from outside of the basement membrane. Thus, such islets are limited in depth to the maximal tooth height before the eruption. This may be the reason why enamel islets disappear when teeth become euhypsodont. Perhaps this specific limitation is the reason why bovid molars are hypsodont but never became euhypsodont. However, lateral reentrant folds from the sidewalls do not have this structural limitation. The preference for lateral infolds is well documented in the evolutionary history of arvicolids. The relationship between islets and the ontogenetic phase II can be a bit more complicated. Some lateral infolds often end with a final deepening that take the form of enamel islets when the tooth is worn. Such enamel islets have been observed in the molars of the multituberculate *Sudamerica* and the upper cheek teeth of the lagomorph *Palaeolagus* (Koenigswald & Goin 2000; Koenigswald et al. 2010a). This specific topic requires a more detailed investigation.

The simultaneous activity of the ontogenetic phases II and III characterizesenamel-band hypsodonty and occurs to a minor degree in teeth of the category sidewall hypsodonty with narrow dentine tracts. In contrast to brachydont teeth, where the ontogenetic phases are more or less subsequent, in hypsodont teeth different genetic programs are active in different areas. In teeth representing partial hypsodonty as many as three phases are active simultaneously.

In euhypsodont teeth, the heterochronic expansion of the phases II or III suppresses the formation of differentiated roots. It is not known, so far, whether the genetic information for the root formation is totally lost or present but no longer expressed. Certainly it is a question of time until genetic information becomes unavailable due to mutations, when the expression of such genes is not controlled by natural selection.

6.4. Function and selective value of hypsodont teeth

The different types of wear in hypsodont teeth open the view to the selective value of hypsodonty. The function of teeth with free growth ranges from gathering food e.g., the large canines in carnivorous mammals to social interactions e.g., weapons in pigs, or demonstration of superiority in elephants. Some enlarged canines show a significant sexual dimorphism e.g., canines in primitive cervids (Text-fig. 9E).

Hypsodont teeth with balanced wear occur in the anterior and posterior dentition. They all are related to food acquisition or comminution. Those in the anterior dentition may have many other functions as well, e.g., rodent incisors for digging, fighting or giving signals.

The advantage of hypsodont teeth with balanced wear is often regarded as its provision of increased durability (Janis & Fortelius 1988) because of the additional tooth material that can be used for comminuting food. Van Valen (1960) assumed that hypsodont teeth might allow a longer life span. However, a prolonged life span does not seem to have a selective value (Fortelius 1985). The additional tooth material provided by hypsodont teeth allows feeding on more abrasive food (Rensberger 1971) and thus expands the range of available resources.

Despite an intensive abrasion the occlusal surface of molars belonging to this type of hypsodonty remains almost unchanged. Thus the effectiveness of these teeth remains constant for a very long period during the life span. That seems to be one of the major advantages of this very widely spread type of hypsodonty. It is very common in environments characterized by siliciferous grasses and the correlation is intensively discussed (e.g., MacFadden 1992, Janis 2008, Sanson et al. 2007, Hummel et al. 2010).

The progressing hypsodonty is combined with an accelerated tooth eruption. When molars become euhypsodont the eruption rate may be accelerated even more. In arvicolid molars first comparative data of tooth eruption could be obtained (Koenigswald & Golenischev 1979). In *Clethrionomys*, with rooted molars, the eruption rate reaches only about 10% of the eruption rate measured for *Lagurus, Microtus,* and *Dicrostonyx*, which have euhypsodont teeth. The highly increased costs required for the formation of hypsodont and euhypsodont teeth does not seem to be a limiting factor for the animal. The worn-off tooth material passes together with the food through the gut and might be partially digested and thus recycled by the animal itself. Nevertheless enlarged teeth mainly used as display organs tend to become dentine hypsodont, relinquishing the enamel.

6.5. The building material in hypsodont teeth

The building materials are crucial for the function and durability of hypsodont teeth (Janis & Fortelius 1988). During mammalian evolution the building materials of teeth, enamel, dentine and cementum are partly modified. Thus the question may be raised whether the evolution of hypsodonty requires specific structural changes in these materials. Many hypsodont teeth show cementum on the enamel surface, and some of them have an especially rough enamel surface for the attachment of the cementum (Koenigswald 2002). Cementum on the enamel surface is known as early as the late Cretaceous on the hypsodont molars of the multituberculate *Sudamerica ameghinoi* from Patagonia (Koenigswald et al. 1999). White (1959) highlighted the combination of cementum and euhypsodonty in the molars of the Paleogene taeniodont *Stylinodon* (Text-fig. 6G). Cementum occurs frequently in hypsodont teeth, e.g. in the molars of bovids, horses, and elephants. Arvicolids demonstrate that euhypsodont molars can have cementum on the crowns (*Ondatra*, *Microtus*, *Arvicola, Lemmus*) but also may lack it (*Dicrostonyx, Lagurus*).

Some specific variations of the dentine structure occur in the euhypsodont dentine teeth. The high elasticity in elephant tusks is related to the presence of Schreger bands that create the typical ivory pattern (O'niel Espinoza & Mann 1993). The dentine of *Orycteropus afer* has a highly specialized prismatic structure, although these teeth are poorly loaded when the animal is crushing ants (Heuser 1913; Keil 1966). Modified types of dentine with different physical properties cause the differential wear in the molars of the xenarthrans *Glyptododon* and *Megatherium* (Text-fig. 8G–I) (Kalthoff 2011).

The various modifications in the enamel microstructure evolved in brachydont teeth to reinforce the enamel against breakage. But two examples indicate that the degree of differentiation is especially high in euhypsodont teeth. The enamel in marsupials is generally formed by underived radial enamel. A notable example occurs in the euhypsodont wombats, which have very distinct Hunter-Schreger bands (HSB) in their incisor and cheek tooth enamel (Beier 1981; Koenigswald 1994). The hypsodont and euhypsodont molars of arvicolids have a much more differentiated pattern of enamel structures than in the related but brachydont cricetids (Koenigswald 1980). In conclusion, the building material of hypsodont teeth is often highly derived, but – perhaps with exception of the dentine – these structures occur prior to and independent of the development of hypsodonty.

7. Conclusions

Hypsodont teeth are regarded as a morphological group of teeth elongated parallel to the growing axis, regardless of the tooth position or the presence of enamel. This goes beyond the traditional usage of the term, in which generally cheek teeth with balanced wear are discussed. This extension of the term was anticipated by Hershkovitz (1962), Martin (1993), and others. The construction of teeth may differ in the various tooth positions. Thus different teeth from a single dentition may represent very different types of hypsodonty. The aim of this new classification is a better understanding of the construction and the evolution of hypsodont teeth. The ecological significance of hypsodonty for herbivorous mammals is not discussed here.

Three independent parameters are used to distinguish different types of hypsodont teeth:

1) The extension of specific ontogenetic phases,
2) The degree of hypsodonty, and
3) The type of wear.

Mammalian teeth have a basic pattern of tooth formation, which is divided here into four more or less subsequent ontogenetic phases. The various types of hypsodont teeth can be characterized by the dominant ontogenetic phase which is extended at the cost of the others. This can be described as heterochrony.

The expansion of the first phase, the formation of tooth cusps, leads in molars to multicusped hypsodont teeth, with low sidewalls, as in *Phacochoerus* or *Elephas*.

In canines the cusp is not discernable from the subsequently formed sidewalls, thus such teeth, if hypsodont, are regarded as unicuspid hypsodont.

In most hypsodont teeth, the primary occlusal surface is worn away and the elongated sidewalls are the most functionally important. Those teeth are regarded as sidewall hypsodont and are formed usually during ontogenetic phase II. The worn occlusal surface is often differentiated by enamel islets or re-entrant folds that increase their efficiency. This category is represented by the teeth of many herbivorous mammals from rodents to ungulates. They may be rooted or euhypsodont. The enamel covered sidewalls may be interrupted by dentine tracts related to the next ontogenetic phase.

If the dentine tracts do not cover more that 1/3 of the circumference, the teeth are regarded as sidewall hypsodont, but if the dentine covers more than 1/3, the next category, they represent enamel band hypsodonty. Rodent incisors and many other similarly built teeth represent this category, in which phase II and III are forming the tooth simultaneously.

Hypsodont teeth formed dominantly during phase III are dentine teeth and range from xenarthran molars to elephant tusks. They represent dentine hypsodonty and are mainly euhypsodont. Differentiated roots never cause the hypsodonty of a tooth.

The dominance of extended ontogenetic phases sets the framework for this classification, but adding the two other aspects, increasing hypsodonty and the type of wear, allows a much better description of the great diversity of hypsodonty. All three features evolved independently and parallel in many mammalian lineages. They indicate the constructional limitations in tooth formation.

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Table 3. Diversity of hypsodonty in different tooth positions in selected taxa from various mammalian orders.

TAXON	UPPER MOLARS	LOWER MOLARS	UPPER CANINE	LOWER CANINE	UPPER INCISOR(S)	LOWER INCISOR(S)
MULTITUBERCULATA						
Sudamerica ameghinoi[1] Paleocene Argentina	sidewall hypsodont - with islands and folds rooted balanced wear	sidewall hypsodont - with islands and folds rooted balanced wear			unknown	enamel-band hypsodont euhyposodont ? balanced wear
Mesodma formosa[2] Upper Createceous Montana						unicuspid hypsodont - with dentine tract rooted free growth
Taeniolabis sp.[3] Paleocene New Mexico					enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear
MARSUPIALIA						
Thylacosmilus atrox[4] Pleistocene South America			enamel-band hypsodonty - enamel only on one side euhypsodont free growth			
Thylacoleo carnifex Pleistocene, Australia						unicuspid hypsodont rooted free growth
Macropus giganteus Recent, Australia						unicuspid hypsodont rooted free growth
Petraurus breviceps Recent, Australia						unicuspid hypsodont rooted free growth
Vombatus ursinus Recent, Australia	enamel-band hypsodont - enamel only lingually euhyposodont balanced wear	enamel-band hypsodont - enamel only buccally euhyposodont balanced wear			enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear
Diprotodon opatum Pleistocene Australia					enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear
XENARTHRA						
Megatherium americanum Pleistocene South America	dentine hypsodont - differentiated dentine euhypsodont balanced wear	dentine hypsodont - differentiated dentine euhypsodont balanced wear				
Glyptodon sp. Pleistocene South America	dentine hypsodont - differentiated dentine euhypsodont balanced wear	dentine hypsodont - differentiated dentine euhypsodont balanced wear				

Table 3. Continued.

TAXON	UPPER MOLARS	LOWER MOLARS	UPPER CANINE	LOWER CANINE	UPPER INCISOR(S)	LOWER INCISOR(S)
Dasypus novemcinctus Recent Texas	dentine hypsodont euhypsodont balanced wear	dentine hypsodont euhypsodont balanced wear				
MACROSCELIDEA						
Myomygale spiersi[5] Pleistocene East Africa	sidewall hypsodonty rooted balanced wear	sidewall hypsodonty rooted balanced wear				
Myohyrax oswaldi Miocene East Africa	sidewall hypsodonty - with enamel islets rooted balanced wear	sidewall hypsodonty - with enamel islets rooted balanced wear				
LAGOMORPHA						
Palaeolagus temnodon[6] Oligocene Nebraska	partial hypsodont - with lagicone structure rooted balanced wear	sidewall hypsodont - deep buccal fold rooted balanced wear			enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear
Mytonolagus ashcrafti[7] Eocene Montana	partial hypsodont - with lagicone structure rooted balanced wear	sidewall hypsodont - with two columns rooted balanced wear			enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear
Amphilagus antiquus[8] Miocene Europe	partial hypsodont - with lagicone structure rooted balanced wear	sidewall hypsodont - with two columns rooted balanced wear			enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear
Prolagus sardus Pleistocene Mediterranean	sidewall hypsodont euhypsodont balanced wear	sidewall hypsodont - with two columns euhypsodont balanced wear			enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear
Ochotona pusilla Pleistocene Europe	sidewall hypsodont - deep lingual fold euhypsodont balanced wear	sidewall hypsodont - with two columns euhypsodont balanced wear			enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear
Lepus europaeus Recent Europe	sidewall hypsodont - deep lingual fold euhypsodont balanced wear	sidewall hypsodont - deep buccal fold euhypsodont balanced wear			enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear
RODENTIA						
Aplodontia rufa Recent North America	sidewall hypsodont - with dentine tracts euhypsodont balanced wear	sidewall hypsodont - with dentine tracts euhypsodont balanced wear			enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear

Table 3. Continued.

TAXON	UPPER MOLARS	LOWER MOLARS	UPPER CANINE	LOWER CANINE	UPPER INCISOR(S)	LOWER INCISOR(S)
Sciurus vulgaris Recent Europe					enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear
Castor fiber Recent Europe	sidewall hypsodont - with enamel islets rooted balanced wear	sidewall hypsodont - with enamel islets rooted balanced wear			enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear
Cricetus cricetus Recent Europe					enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear
Ondatra zibethicus Recent Europe	sidewall hypsodont - with re-entrant folds rooted balanced wear	sidewall hypsodont - with re-entrant folds rooted balanced wear			enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear
Arvicola terrestris Recent Europe	sidewall hypsodont - with re-entrant folds and dentine tracts euhyposodont balanced wear	sidewall hypsodont - with re-entrant folds- and dentine tracts euhyposodont balanced wear			enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear
Rhombomys opimus Recent Central Asia	sidewall hypsodont - with re-entrant folds rooted balanced wear	sidewall hypsodont - with re-entrant folds rooted balanced wear			enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear
Geomys bursarius Recent Kansas	sidewall hypsodont - with dentine tracts euhypsodont balanced wear	enamel-band hypsodont euhypsodont balanced wear			enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear
Pappogemys castanops[9] Pleistocene Texas	sidewall hypsodont - with dentine tracts euhypsodont balanced wear	enamel-band hypsodont euhypsodont balanced wear			enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear
Thomomys bottae Recent Nevada	sidewall-hypsodonty - with enamel tracts euhypsodont balanced wear	sidewall-hypsodonty - with enamel tracts euhypsodont balanced wear			enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear
Tsaganomys altaicus[10] Eocene Mongolia	partial hypsodont rooted balanced wear	sidewall hypsodont rooted balanced wear			enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear
Hystrix cristata Recent Africa	sidewall hypsodont - with enamel islets rooted balanced wear	sidewall hypsodont - with enamel islets rooted balanced wear			enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear

Table 3. Continued.

TAXON	UPPER MOLARS	LOWER MOLARS	UPPER CANINE	LOWER CANINE	UPPER INCISOR(S)	LOWER INCISOR(S)
Cavia porcellus Recent South America	sidewall hypsodont - with re-entrant folds euhyposodont balanced wear	sidewall hypsodont - with re-entrant folds euhyposodont balanced wear			enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear
Dolichotis patagomum Recent South America	sidewall hypsodont - lingual re-entrant fold euhyposodont balanced wear	sidewall hypsodont - buccal re-entrant fold euhyposodont balanced wear			enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear
Hydrochoerus hydrochaerus Recent South America	sidewall hypsodont - with re-entrant folds euhyposodont balanced wear	sidewall hypsodont - with re-entrant folds euhyposodont balanced wear			enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear
Ctenodactylus gundi Recent N-Africa	sidewall hypsodont euhyposodont balanced wear	sidewall hypsodont euhyposodont balanced wear			enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear
Abrocoma bennetti Recent Chile	sidewall hypsodont euhyposodont balanced wear	sidewall hypsodont euhyposodont balanced wear			enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear
Pedetes cafer Recent South Africa	sidewall hypsodont - buccal re-entrant fold euhyposodont balanced wear	sidewall hypsodont - lingual re-entrant fold euhyposodont balanced wear			enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear
APATOTHERIA						
Apatemys chardini[11] Eocene Wyoming						enamel-band hypsodont rooted free growth
Heterohyus nanus[12] Eocene Germany (Messel)						enamel-band hypsodont euhyposodont free growth
TAENIODONTA						
Stylinodon mirus[13] Eocene Wyoming	enamel-band hypsodont - wide dentine tracts euhypsodont balanced wear	enamel-band hypsodont - wide dentine tracts euhypsodont balanced wear	enamel-band hypsodont euhypsodont balanced wear	enamel-band hypsodont euhypsodont balanced wear	enamel-band hypsodont euhypsodont balanced wear	enamel-band hypsodont euhypsodont balanced wear
TILLODONTA						
Trogosus sp.[14] Eocene Wyoming					enamel-band hypsodont euhyposodont balanced wear	enamel-band hypsodont euhyposodont balanced wear

Table 3. Continued.

TAXON	UPPER MOLARS	LOWER MOLARS	UPPER CANINE	LOWER CANINE	UPPER INCISOR(S)	LOWER INCISOR(S)
PANTODONTA						
Coryphodon sp. Eocene Wyoming			unicuspid hypsodont rooted free growth			
CREODONTA						
Hyaenodon cayluxi Oligocene France			unicuspid hypsodont rooted free growth	unicuspid hypsodont rooted free growth		
CARNIVORA						
Canis lupus Pleistocene Europe			unicuspid hypsodont rooted free growth	unicuspid hypsodont rooted free growth		
Smilodon fatalis Pleistocene California			unicuspid hypsodont rooted free growth			
Homotherium crenatidens Pleistocene Europe			unicuspid hypsodont rooted free growth			
Odobenus rosmarus Recent circumpolar Arctic			dentine hypsodont euhypsodont free growth			
LIPOTYPHLA						
Sorex araneus Recent Germany						unicuspid hypsodont rooted free growth
CHIROPTERA *Phyllostomus hastatus*			unicuspid hypsodont rooted free growth	unicuspid hypsodont rooted free growth		
PRIMATES						
Plesiadapis tricuspidens[15] Paleocene Europe						unicuspid hypsodont rooted free growth
Eulemur fulvus Recent Madagaskar			unicuspid hypsodont rooted free growth	unicuspid hypsodont rooted free growth	unicuspid hypsodont rooted free growth	unicuspid hypsodont rooted free growth
Daubentonia madagascariensis Recent, Madagascar					enamel-band hypsodont euhypsodont balanced wear	enamel-band hypsodont euhypsodont balanced wear

Table 3. Continued.

TAXON	UPPER MOLARS	LOWER MOLARS	UPPER CANINE	LOWER CANINE	UPPER INCISOR(S)	LOWER INCISOR(S)
Papio ursinus Recent Africa			unicuspid hypsodonty rooted free growth	unicuspid hypsodonty rooted free growth		
UINTATHERIDA						
Uintatherium anceps [16] Eocene Wyoming			unicuspid hypsodont rooted free growth			
TUBULIDENTATA						
Orycteropus afer Recent subsaharian Africa	dentine hypsodont - differentiated dentine euhypsodont balanced wear	dentine hypsodont - differentiated dentine euhypsodont balanced wear				
CETARTIODACTYLA						
Monodon monoceras Recent Arctic Ocean					dentine hypsodont euhypsodont free growth	
Sus scrofa Recent Germany			enamel-band hypsodont - with wide dentine tract euhypsodont free growth	sidewall hypsodont - with wide dentine tract euhypsodont free growth		sidewall hypsodont - with dentine tracts rooted free growth with wear
Phacochoerus africanus Recent subsaharian Africa	multicusped hypsodont - with isolated cusps rooted balanced wear	multicusped hypsodont - with isolated cusps rooted balanced wear	dentine hypsodont euhypsodont free growth	sidewall hypsodont euhypsodont free growth		sidewall hypsodont - with dentine tracts rooted free growth with wear
Babyrussa babyrussa Recent Celebes			dentine hypsodont euhypsodont free growth	?dentine hypsodont euhypsodont free growth		i1-i2 dentine hypsodont euhypsodont free growth with wear
Hippopotamus amphibius Recent Africa			sidewall hypsodont euhypsodont balanced wear	sidewall hypsodont euhypsodont balanced wear	enamel band hypsodont euhypsodont free growth	i1 dentine hypsodont i2 enamel band hypsodont euhypsodont free growth
Bos primigenius Recent Germany	sidewall hypsodont - with enamel islets- rooted balanced wear	sidewall hypsodont - with enamel islets rooted balanced wear				
Camelus bactrianus Recent, domesticated Teneriffa	sidewall hypsodont - with enamel islets rooted balanced wear	sidewall hypsodont - with enamel islets rooted balanced wear				sidewall hypsodont rooted wear without antagonist

Table 3. Continued.

TAXON	UPPER MOLARS	LOWER MOLARS	UPPER CANINE	LOWER CANINE	UPPER INCISOR(S)	LOWER INCISOR(S)
Vicungna vicugna Recent Chile	sidewall hypsodont - with enamel islets rooted balanced wear	sidewall hypsodont - with enamel islets rooted balanced wear				sidewall hypsodont rooted wear without antagonist
Myotragus balearicus Pleistocene Baleares	sidewall hypsodont - with enamel islets rooted balanced wear	sidewall hypsodont - with enamel islets rooted balanced wear				enamel-band hypsodont euhypsodont wear without antagonist
NOTUNGULATA						
Astrapotherium magnum[17] Miocene Patagonia	sidewall hypsodont - with enamel islets rooted balanced wear	sidewall hypsodont rooted balanced wear	sidewall hypsodont - wide dentine tract euhypsdont balanced wear	sidewall hypsodont - wide dentine tract euhysodont free growth with wear		
PYROTHERIA						
Pyrotherium macfaddeni[18] Oligocene Bolivia						enamel-band hypsodont euhypsodont ? free growth with wear
PERISSODACTYLA						
Hippotherium gracile Miocene Germany	sidewall hypsodont - with enamel islets rooted balanced wear	sidewall hypsodont - with re-entrant folds rooted balanced wear				
Equus zebra Recent Africa	sidewall hypsodont - with enamel islets rooted balanced wear	sidewall hypsodont - with re-entrant folds rooted balanced wear				
Rhinoceros unicornis Recent zoo specimen						enamel band hypsodont rooted free growth with wear
Prosantorhinus germanicus Miocene Germany						sidewall hypsodont rooted free growth with wear
Chilotherium sp. Miocene China						sidewall hypsodont rooted free growth with wear
Diceros bicornis Recent Africa	sidewall hypsodonty - with islets and folds rooted balanced wear	sidewall hypsodonty rooted balanced wear				

Table 3. Continued.

TAXON	UPPER MOLARS	LOWER MOLARS	UPPER CANINE	LOWER CANINE	UPPER INCISOR(S)	LOWER INCISOR(S)
Elasmotherium sibiricum Pleistocene Russia	sidewall hypsodonty - with re-entrant folds euhypsodont balanced wear	sidewall hypsodonty - with re-entrant folds euhypsodont balanced wear				
EMBRITHOPODA						
Arsinoitherium zitteli Oligocene Egypt	sidewall hypsodonty rooted balanced wear	sidewall hypsodonty rooted balanced wear				
HYRACOIDEA						
Procavia capensis Recent South Africa					enamel-band hypsodont euhypsodont balanced wear	sidewall hypsodont rooted balanced wear
DESMOSTYLIA						
Desmostylus sp. Pleistocene Japan	multicusped hypsodont - with isolates cusps rooted balanced wear	multicusped hypsodont - with isolates cusps rooted balanced wear			insufficient data	
PROBOSCIDEA						
Deinotherium giganteum Miocene Germany						dentine hypsodont euhypsodont free growth
Elephas maximus Recent Africa	multicusped hypsodont - with transverse lophs rooted balanced wear	multicusped hypsodont - with transverse lophs rooted balanced wear			dentine hypsodont euhypsodont free growth	
Mammuthus primigenius Pleistocene Germany	multicusped hypsodont - with transverse lophs rooted balanced wear	multicusped hypsodont - with transverse lophs rooted balanced wear			dentine hypsodont euhypsodont free growth	

1 Koenigswald et al. (1999)
2 Clemens & Kielan-Jaworowska (1979)
3 Clemens & Kielan-Jaworowska (1979)
4 Turnbull 1978; Koenigswald & Goin (2000)
5 Butler (1984)
6 Dawson (1958); Koenigswald et al (2010a)
7 Fostowicz-Frelik & Tabrum (2009)
8 Tobien (1974)
9 Koenigswald et al. (1994)
10 Wang (2001)
11 Koenigswald et al. (2005)
12 Koenigswald (1990)
13 Koenigswald et al. (2010b)
14 Rose (2006)
15 Gingerich (1967)
16 Turnbull (2002)
17 Scott (1937), Thenius (1989)
18 Shokey & Daza (2004)