Case studies on functional aspects and constraints in early and late tooth ontogeny

Irina Ruf, Anne M. Schubert, and Wighart v. Koenigswald

Introduction

Despite the immense diversity of mammalian dentitions in morphology and function, the great majority of teeth share the same basic elements in their ontogeny. The term "ontogeny" covers the entire life history from the fertilized egg to the individual's death (Haeckel 1866). Haeckel applied the term to individuals as well as individual organs. We differentiate two periods in the life history of teeth: an early ontogeny when teeth are formed deep in the crypt, and a late ontogeny when teeth are erupted, and exposed to wear. These phases are deduced from the tooth morphology.

The mineralization of tooth material starts at the cusps of the occlusal surface and proceeds continuously towards the base of the crown (Alt & Türp 1997). This orientation is elementary to understand the ontogenetic constraints of complex teeth. Similar to the uniform formation of teeth the subsequent life history passes through similar stages during the wear process, when teeth are incorporated into the tooth row and start with their function e.g., comminution of food objects by cheek teeth. This function continues until the deciduous tooth is replaced by a permanent one, or the tooth is totally worn off, or the animal dies. During late ontogeny wear causes loss of material and gradual destruction of the tooth. This basic pattern of ontogeny occurs in most teeth although modified in various ways during ontogeny. Heterochronies are the most common way to alter this general pattern as demonstrated by the ontogenetic phases and types of hypsodonty (high-crowned teeth) in herbivores (see Koenigswald 2020, this volume). Only few teeth do not share this life history, especially those that are in specific tooth positions. For instance, proboscidean tusks are one of the rare exceptions, where wear is minimal and the continuously growing dentin tooth documents the entire life history of the animal (Fisher et al. 2014).

Herbivorous mammals have to cope with intensive abrasion of tooth material due to phytoliths and grit intake and have evolved certain adaptations in their dentition; however, the extent to which phytoliths or grit contribute to tooth abrasion is still discussed (e.g., Fortelius 1985, Williams & Kay 2001, Strömberg 2006, Mendoza & Palmqvist 2008, Hummel et al. 2011, Merceron et al. 2016, Martin et al. 2019). Some herbivorous species that retain brachydont (low-crowned) cheek teeth show a complex occlusal surface adapted to comminution and abrasion. Another strategy to cope with high abrasion is the evolution of hypsodont or euhypsodont (ever-growing) teeth with more or less complex occlusal surface e.g., rodent incisors, equid and rodent check teeth; in high-crowned teeth growth and abrasion are balanced (Thenius 1989, Schmidt-Kittler 2002, Koenigswald 2016, Martin et al. 2019). Variations in enamel thickness in the tooth crown can be associated with functional adaptations. For instance, in Equus quagga thinner coronal enamel areas allow fast exposition of enamel ridges, whereas in primates the relative thick enamel may provide a greater resistance to abrasion (Janis & Fortelius 1988, Winkler & Kaiser 2015).

Function and performance enhancement in mammalian dentitions, the major task of the DFG Research Unit 771, can only be elucidated by a deeper understanding of dental adaptations and constraints in extant as well as fossil species. One major key to this is a deeper understanding of dental ontogeny - from early development of dental tissues via timing of tooth eruption and replacement to modifications of the occlusal surface caused by wear. In this chapter, first the general framework of tooth ontogeny is outlined followed by the presentation of three specific aspects of dental ontogeny and function that represent different approaches. Each topic is exemplified by a case study that originated in the DFG Research Unit 771. The first case study deals with the enamel islets in rodent molars, a specialization of the occlusal surface formed by deep indentations that resemble fingers of a glove, and the limitations to the way they are formed. The second case study discusses perinatal tooth eruption in precocial versus altricial Rodentia and Lagomorpha. The third case study specifies individual wear stages in placental mammals that allow comparison of ontogenetic stages across species boundaries. Thus, the presented research topics concern individual teeth as well as the functional unit of the entire postcanine dentition including the morphological and functional changes of the occlusal structures during wear and life.

Ontogeny of individual teeth

In the last two decades the investigation of early development and genetic control of teeth increased our knowledge of dental patterns and evolution significantly (e.g., Aberg et al. 1997, Jernvall et al. 2000, Jernvall & Thesleff 2000, Tummers & Thesleff 2003, Harada & Ohshima 2004, Kavanagh et al. 2007, Harjunmaa et al. 2014). As the process of tooth formation and tissue genesis (amelogenesis, dentinogenesis, cementogenesis) as well as the morphology

T. Martin & W. v. Koenigswald (eds.): Mammalian Teeth - Form and Function. Pp. 102-124, 18 figs. © 2020 by Verlag Dr. Friedrich Pfeil, München, Germany - ISBN 978-3-89937-266-3

DOI: http://doi.org/10.23788/mammteeth.07 Published 22 December 2020



Fig. 7.1. Interdependence between tooth formation, enamel islets, lateral infolds, and abrasion. **A**, detailed aspect of a developing tooth: the enamel is formed in the crypt by the inner epithelium, whereas the dentin is formed by the mesenchyme. **B**, tooth formation and mineralization start at the top of the tooth and move continuously in apical direction. **C**, in hypsodont or euhypsodont teeth the enamel organ (cervical loop area) is still active after eruption and can add outer enamel. **D**, several hypsodont teeth have deep depressions of enamel from the coronal to the apical part of the tooth (small arrow). These are formed simultaneously with the external walls of the crown by a part of the enamel organ that sticks into the depressions. **E**, when the tooth erupts the connection between the surrounding enamel organ and the part in the depression gets lost and the enamel formation within the depression is stopped (X). **F**, the former depression becomes an enamel islet by abrasion. **G**, the connection between the enamel organ and the part in the depression is open to one side (lateral infold). As long as a connection to the enamel organ is preserved – even through a narrow slit – the enamel formation and the deepening of the lateral infold can continue.

of mammalian teeth is presented in many textbooks and publications in detail (e.g., Teaford et al. 2009, Ungar 2010), we selected those structures and events that are related to the presented case studies for further discussion. In order to evaluate the complex tooth morphology of herbivorous mammals, that is often characterized by enamel islets and infoldings as well as hypsodonty or euhypsodonty, a deeper understanding of the early tooth formation is demanded.

The tooth morphogenesis from bud stage to bell stage comprises the development of the dental follicle, enamel organ, and dental papilla. The ameloblasts, cells of the enamel organ, develop in the inner enamel epithelium from oral epithelial cells and produce the enamel matrix along the basal membrane, the later enamel-dentin junction (EDJ); the ameloblasts induce the maturation of the enamel matrix to form enamel. This is triggered by enamel knots (epithelial signaling centers) along the inner enamel epithelium that determine the formation of later cusps; mechanical forces and constraints during growth of the cell layers may also affect tooth morphogenesis. In parallel, the odontoblasts, that are derived from ectomesenchymal cells, are creating dentin along the EDJ inside the dental follicle (Fig. 7.1 A, B). The complex process of tooth formation is controlled by so-called bone morphogenetic proteins (BMPs) that are multi-functional growth factors playing a crucial role during the entire ontogeny; BMPs are not restricted to the development of teeth but are also involved in the development of many further structures and organs e.g., cartilage, bone, heart, neural structures, and ectodermal appendages. Especially BMP7 acts as a central mediator of epithelial-mesenchymal interactions in tooth development. BMP signal cascades as well as expression of antagonists are involved in several stages of the entire tooth development including the development of enamel, dentin, roots, pulp cavity, and periodontal ligaments. For instance, in later stages BMP expression in the tooth epithelium induces enamel formation whereas in enamelfree areas antagonistic genes are expressed (Aberg et al. 1997, Chen et al. 2004, Osborn 2008, Zouvelou et al. 2009, Graf & Mitsiadis 2013). Msx2 from the muscle segment homeobox gene family plays a major role in enamel formation by controlling proliferation and differentiation of ameloblasts. This gene regulates laminin5a3 expression in enamel knots and therefore is also involved in cusp formation (Bei et al. 2004).

The notch signaling pathway genes FGF 10 control the crown formation and the transition from the crown to the root. The formation of roots is delayed in hypsodont teeth and skipped totally in euhypsodont teeth (Tummers & Thesleff 2003). Absence of this signaling induces growth stop of the tooth and the development of roots. At the cellular level the area where inner and outer enamel epithelium join, the so-called cervical loop, is responsible for apical growth of the tooth crown (Fig. 7.1A–C). In brachydont teeth the stellate reticulum of the cervical loop is lost and the respective tissue switches to root fate. In contrast, in hypsodont and euhypsodont teeth the production of ameloblasts from the stellate reticulum of the cervical loop is maintained and thus allows prolonged or even permanent growth of the tooth (Tummers & Thesleff 2003). Ontogenetically, the evolution of hypsodont and euhypsodont teeth is regarded to be a heterochronic effect (see Koenigswald 1982, 2020, this volume).

The differentiation and mineralization of the tooth occurs from the tip of the cusps to the roots, and after eruption the tooth becomes part of the functional unit of the tooth row. Therefore, the formation of specific occlusal structures is limited as they need to be completely mineralized before tooth eruption and consequent interruption of amelogenesis as well as dentinogenesis after root formation (Fig. 7.1 C, E) (Janis & Fortelius 1988, Koenigswald 2011). However, heterochronic events can compensate these restrictions (see Koenigswald 2020, this volume). Generally, occlusal morphology is determined by the shape of the enamel epithelium and mesenchyme that show specific folding during tooth development, and activators and inhibitors within these tissues control the cusp size and tooth size; the number of cusps is also co-regulated by the tooth size and cusp size as demonstrated by a tooth patterning study in rats and mice (Cai et al. 2007). A recent study on Myodes glareolus demonstrates that mechanical constraints from the growing jaw bones also influence molar tooth morphogenesis (Renvoisé et al. 2017). From an evolutionary perspective cusp size and number can be also explained by linking tooth development and population-level variation as a patterning cascade mode of cusp development as proposed for the postcanine dentition of seals (Jernvall 2000).

On the genetic level, expression patterns are obviously correlated with specific tooth phenotypes and heterotopic and iterative processes may be major drivers of the diversity of mammalian molar patterns. Asymmetric BMP expression affects the shape of the tooth itself and patterns of Fgf4, Lef1, p21, and Shh genes are correlated with lateral cusp topography (Aberg et al. 1997, Jernvall et al. 2000, Chen et al. 2004, Zouvelou et al. 2009, Graf & Mitsiadis 2013).

Rasp facets in herbivore dentitions

The above described developmental patterns impose limitations for adaptations in the teeth of herbivores. The physical disaggregation of tough plant material by mastication requires enamel ridges working as shearing edges on the occlusal surface of the postcanine dentition that Koenigswald (2016) defined as rasp facets. These grinding facets have evolved independently from various different tooth morphologies in ancestral forms. Several herbivorous taxa have evolved hypsodont or even euhypsodont teeth e.g., various rodent families, Rhinocerotidae, Equidae, Proboscidea and selenodont Artiodactyla such as Cervidae and Bovidae (Thenius 1989, Koenigswald 2016). Most of these dentitions are characterized by rasp facets that are flat grinding surfaces with projecting enamel crests between dentin fields. To achieve such a fully-functioning occlusal surface these teeth need to be exposed to wear in order to remove the covering enamel of the primary occlusal surface and sharpen the enamel crests in the secondary occlusal surface. The dentin between the enamel structures is widely exposed and gaps may be filled with cementum. The simplest pattern comprises an enamel crest that is formed by the surrounding enamel band only e.g., in cylindrodont rodents. This basic pattern may be optimized by additional enamel crests that occur as lateral infolds (flexus, flexids) or enamel islets (fossettes, fossettids). They increase the mechanical performance of the rasp-facet (Koenigswald 2016). A combination of enamel islets and lateral folds is common because many lateral infolds are transformed sooner or later into islets when wear continues (e.g., Koenigswald et al. 1999 and see below). Examples of such complex teeth are manyfold in Rodentia, Rhinocerotidae, Equidae, and selenodont ruminants (Fig. 7.2) (Rensberger 1973, Janis & Fortelius 1988, Thenius 1989, Koenigswald et al. 1994).

A specific ontogenetic limitation occurs when during evolution teeth become hypsodont or euhypsodont. The lower part of the erupting tooth may laterally still be covered with enamel by the surrounding enamel organ while the upper penetrates the gingiva and is already functioning (Fig. 7.1C-G). At this stage lateral infolds can be continuously formed as the cervical loop is still active. Enamel



Fig. 7.2. Enamel islets and lateral infolds in selected extant and fossil species. **A**, enamel islets in the P4 of *Hystrix cristata* (Rodentia), Recent, Mt. Elgin, Kenya (IGPB KOE 25); **B**, lateral infolds in the M1 of *Ondatra zibethicus* (Rodentia), Recent (IGPB, no number); **C**, lower molar of *Equus caballus* (Perissodactyla) with lateral infolds, subfossil, Rhineland (IGPB, no number); **D**, upper molar of *Equus caballus* with enamel islets, subfossil, Rhineland (IGPB, no number); **E**, upper molars in the Late Pleistocene *Coelodonta antiquitatis* (Perissodactyla), Groß Rohrheim, Germany (SLGM, no number), showing how the lateral infold (median sulcus, still present in M3) forms an enamel islet (mediofosset, present in M2 and M1) due to the progressive wear. Abbreviations: IGPB, Institute of Geosciences, Section Paleontology, Universität Bonn; IS, enamel islet; LIF, lateral infold; M1–3, upper molar 1–3; SLGM, collection Frank Menger, Groß Rohrheim, Germany.

islets which originate from the occlusal surface, however, cannot be deepened and produced anymore, because the enamel epithelium responsible for the enamel islets is cut-off from tissue supply, as soon as the surrounding enamel is incorporated into the functional occlusal surface (Fig. 7.1 E, F). Thus, the growth of enamel islets is definitely restricted to the developmental phase before the tooth erupts (Janis & Fortelius 1988, Tummers & Thesleff 2003, Koenigswald 2011, Koenigswald 2020, this volume).



Fig. 7.3. Upper molars of the extant muroid rodent *Otomys* sp., Recent, Makapansgat, South Afrika (IGPB KOE 3355). The occlusal surface is made up by transverse enamel ridges on the trailing side, whereas those of the leading side are reduced asymmetrically. Abbreviations: IGPB, Institute of Geosciences, Section Paleontology, Rheinische Friedrich-Wilhelms-Universität Bonn; M1–3, upper molar 1–3.

Enamel islets can be found in brachydont and hypsodont teeth; in euhypsodont teeth they are restricted to juvenile stages. However, the height of hypsodont dentitions with enamel islets is limited to the space available in the jaw because these structures need to be mineralized within the crypt before tooth eruption (Koenigswald 2011). The upper and lower premolars and molars of Equus caballus are hypsodont and provide an interesting difference: lower cheek teeth have lateral infolds, uppers islets (Fig. 7.2C, D). Thus, the lower teeth would allow a transition to a euhypsodont architecture, but the upper teeth not. That might have stopped the increasing hypsodonty in horses. Rhinocerotidae provide another informative example as enamel islets are common in the upper molars as observed in Coelodonta antiguitatis (Fig. 7.2E). In Ceratotherium simum hypsodont molars evolved with deep lateral infolds. These folds end up as enamel islets when teeth are almost worn out. The Pleistocene Elasmotherium from Siberia has evolved euhypsodont molars (Brandt 1864). This was possible due to the lack of enamel islets in the flat grinding surface of its teeth, but the lateral infolds are highly complicated in order to increase the rasp function.

In contrast, enamel islets are rare in euhypsodont dentitions, and if present they are restricted to the coronal part of the teeth. In the molars of arvicolid rodents, the loss of enamel islets in combination with the accomplishment of euhypsodonty can be observed. In the hypsodont but still rooted molars of *Mimomys savini* an enamel islet is still present in m1, but in the euhypsodont m1 of *Arvicola* it is lost (Koenigswald 1982, Koenigswald & Kolfschoten 1996).

In grinding surfaces, the length of the enamel ridges is directly related to the efficiency of the mastication process, as a high amount of enamel ridges allows a faster disintegration of food particles with fewer power strokes during mastication (Rensberger 1973, Kay 1975). Teeth with hypsodont lophs show enamel ridges that are almost equally spaced either by dentin or cementum e.g., in Elephantidae, especially in *Mammuthus primigenius*. Even in teeth with a combination of islets and crests (e.g., *Equus, Bos*) the distances between the main functional enamel ridges tend to be similar. Too dense enamel ridges on the occlusal surface and thus a decrease in possible mastication force of the rasp facets would lead to insufficient disintegration

of food particles (Schmidt-Kittler 1984). In these teeth the thickness of the enamel does not vary significantly. In some species, mainly in rodents, however, the thickness of the enamel band may be significantly reduced on one side of the lophs and lophids resulting in functional units that are correlated with the direction of jaw movement, the so-called leading and trailing edges (Greaves 1973). This asymmetry is mainly related to the position of the enamel at the leading or trailing side of the dentin, because it occurs especially in those teeth where the enamel crests are transverse to the chewing direction. This pattern evolved independently in several unrelated rodent taxa such as the archaeomyid Archaeomys from the Oligocene in Europe, the extant African murid Otomys, and fossil and extant South American caviomorphs like Chinchilla and Lagostomus (Koenigswald 1980, 2016, Rinderknecht et al. 2011, Ubilla & Rinderknecht 2016). In these teeth, the lophs are slightly inclined towards the chewing direction. Mostly, the leading side is reduced in thickness or totally missing (Fig. 7.3). The gap to the next loph is filled by cementum. As only part of the enamel band is functioning in the grinding process, it might reduce the effectiveness of the tooth. However, as the rhythm of the mastication is another component determining the efficiency of the teeth it could serve the compensation of effectiveness reduction. A similar phenomenon of an asymmetrical reduction of the enamel has been observed in the lingual infold of the upper molars of extant and fossil Lagomorpha by Koenigswald et al. (2010).

Case study 1: Ontogeny and function of enamel islets in rodents

The occlusal surface of a tooth represents only a snapshot in the ontogeny of the individual life history, because wear modifies the occlusal surface continuously. It may be assumed, that selection favors occlusion surface patterns that stay functional at least until the end of the reproductive lifespan.

In order to test how the occlusal surface changes due to progressive wear and how the enamel islets change with progressing wear, a major study was executed by one of the authors (Schubert 2019) in the DFG Research Unit 771. This study intended to clarify the basic formation and fate of enamel islets, using the great variety of rodent molars. The variability in various ontogenetic stages can be investigated and used for comparative morphological studies as well as morphofunctional analyses.

Rodents show a high diversity that is also reflected in their dentitions, and enamel islets evolved independently in several herbivorous species of the three major clades, the Ctenohystrica, mouse-related clade, and squirrel-related clade (see Thenius 1989 and Koenigswald 2016). Previous studies on these structures are based on the comparison of the occlusal surface of teeth in different wear stages (e.g., Hagmann 1907: *Cuniculus paca* and *Dasyprocta leporina*, Rusconi 1930: *Myocastor coypus*, van Weers 1990, 1993: Hystricidae, Calede & Hopkins 2012: Mylagaulidae) or on teeth that were artificially ground down (e.g., Rusconi 1934: *Cuniculus paca*, Hünermann 1966: *Castor* sp.). The former method allows an investigation of various wear stages in



Fig. 7.4. Definition of general wear stages A-H based on rodent dentitions with enamel folds and islets. Not all wear stages (schematic sketches) can be found in each of the investigated species due to different morphologies. Modified from Schubert (2019).

one species, but does not decipher the entire ontogeny of an individual and species, respectively. The artificial grinding is a destructive method and not always applicable. Non-invasive high-resolution computed tomography (µCT) and virtual 3D reconstructions reveal the relationships of internal dental structures as shown in the Late Cretaceous gondwanatherian Vintana sertichi (Krause 2014). Furthermore this approach allows elucidation of future occlusal surfaces along the entire crown reflecting major parts of the life history in a single individual as already demonstrated for the fossil castorid Steneofiber siamensis (Suraprasit et al. 2011). Most former studies concentrated on one or very few closely related species in order to understand their variability but contributed only to a limited degree to the general understanding of tooth ontogeny and functional changes by wear.

The changes of enamel islets by progressive wear were investigated by μ CT and virtual 3D reconstructions in ten extant and three fossil rodent species. The sample covers a wide range of the morphological diversity of enamel islet patterns encountered in Rodentia: extant Caviomorpha (*Cuniculus paca, Dasyprocta azarae, Dasyprocta leporina, Myocastor coypus, Erethizon dorsatum*), extant Old World Hystricognathi (*Thryonomys swinderianus, Hystrix cristata, Hystrix indica*), extant Castoridae (*Castor fiber, Castor canadensis*), fossil Castoridae (*Steneofiber eseri, Steneofiber depereti*), and fossil Aplodontidae (*Mylagaulus elassos*).



Fig. 7.5. 3D model and standardized nomenclature for enamel folds and islets as exemplified by the M2 of *Dasyprocta leporina.* **A**,**B**, 3D model of enamel (dark gray) and dentin (light gray); **C**, enamel portion only. Color code of enamel folds and islets: blue, enamel islet 1; green, enamel islet 2; yellow, enamel islet 3; orange, enamel islet 4; red, enamel fold V. **A** and **C** in buccal view, **B** in occlusal view.

Based on the 3D models virtual occlusal surfaces over the complete height of the enamel portion of the tooth were created. For the comparison of the generated occlusal surfaces several wear stages (A to H) were defined based on appearance and disappearance of folds and/or islets (Fig. 7.4). The traditional nomenclature for the enamel folds and islets was standardized as enamel elements are numbered from I–V (folds) and 1–5 (islets) from mesial to distal (Fig. 7.5).

Origin and splitting patterns of enamel islets

Some enamel islets occur in the occlusal surface immediately after a short period of wear, other islets are formed later. Based on hypsodont molars of the gondwanatherian Sudamerica, Koenigswald et al. (1999) differentiated three types of enamel islets. Type 1 comprises islets that originate from enamel invaginations from the occlusal surface. Type 2 refers to islets that derive from lateral infolds, which still exist in later wear stages. Type 3 comprises islets that are formed by complete transformation (isolation) of lateral infolds, mostly close to the base of the crown. In Sudamerica all three types occur in the same molar (Fig. 7.6). Enamel islets of type 1 were observed in Mimomys, a basal arvicoline rodent. Enamel islet type 3 occurs in many rodents (e.g., Hystrix and Castor) and in early lagomorphs such as Palaeolagus (Tobien 1974, 1975, Koenigswald et al. 1999, 2010). Schubert (2019) differentiated the enamel islets of type 2 in enamel islets originating from splitting of enamel folds (type 2a) and enamel islets developing from splitting of enamel islets (type 2b). Rodent molars often show a combination of enamel islets of different origins: in



Fig. 7.6. The three types of enamel islets and their relation to lateral infolds. Cross sections (right) of a cheek tooth (left) of the Paleocene gondwanatherian *Sudamerica ameghinoi*. Enamel is black, dentin is white, the pulp cavity is hatched, and cementum is indicated by stippled areas. Abbreviations: IS1-3, type of enamel islets; LIF, lateral infold. Modified from Koenigswald et al. (1999).

the upper dentition of *Erethizon dorsatum* and *Thryonomys swinderianus* type 1 and type 3 occur together. In most investigated species enamel islets of type 2 (2a and/or 2b) and type 3 were found.

Splitting of enamel islets during further abrasion i.e., one enamel islet/fold splits into two islets, was postulated previously for e.g., *Hystrix* (van Weers 1990, 1993, 2005) and Mylagaulus (Black & Wood 1956, Kitts & Black 1959, Baskin 1980, Calede & Hopkins 2012), but their intra- and interspecific variability caused problems in the systematic evaluation. However, beside these variations the present study revealed also some stable patterns e.g., the sequence of isolation of the enamel folds. This sequence can be the same in all tooth positions as in the upper dentition of Myocastor coypus or the lower dentition of Cuniculus paca (Fig. 7.7). The splitting pattern of enamel islets is also comparable in all tooth positions of certain species e.g., in Dasyprocta or Steneofiber (Fig. 7.7B). In one specimen of Myocastor coypus under study and Thryonomys swinderianus no splitting of enamel elements was observed (Fig. 7.7C). In the dentition of both species of Castor only minor changes can be detected over most part of the crown height. Enamel folds get separated late in ontogeny in Castor and splitting of enamel islets occurs rarely (Fig. 7.7E), but older individuals can show crenulation of enamel structures (Hünermann 1966, Piechocki & Stiefel 1977, Mayhew 1979). This was also confirmed in later wear stages of both species by Schubert (2019).

In most investigated species the enamel elements split once or twice. Three or four splittings are very rare but occur in e.g., *Cuniculus paca* (M2 with four splittings and m1 with three splittings) or in *Mylagaulus elassos* (four splittings in one p4). If more than one splitting is present, they mostly occur from buccal to lingual in the upper and from lingual to buccal in the lower dentition. In contrast to the splitting of enamel islets, a fusion in apical direction was never observed as it is ontogenetically impossible. A comparison of upper and lower cheek teeth reveals only slight differences in the morphology of splitting of enamel folds and islets in the specimens under study. However, more splittings of enamel elements can be found in the lower dentition (Fig. 7.7D). Since upper and lower dentitions do not differ in their function in rodents and thus their morphology often is similar (functional symmetry after Koenigswald et al. 1994), the observed differences cannot be related to function. This is also true for differences in left and right teeth, which do not differ in their function either.

In some investigated specimens (e.g., *Dasyprocta* and *Hystrix*) the enamel islets are completely closed apically but some of which are not fully mineralized in the apical part (Fig. 7.8). This may not be due to developmental constraints as not always the deepest part of the enamel islet is affected by incomplete mineralization. Instead it seems that the mineralization was stopped too early, leaving the apical part of the islet unmineralized.

Density and alignment of the enamel crests formed by enamel islets

Splitting of enamel elements is apparently a common feature among certain rodent clades and it is likely that this pattern is functionally constraint. However, there seems to be no correlation between the amount of splitting of enamel elements as well as the diet of a species or crown height of its teeth. This feature occurs in the frugivore *Cuniculus* as well as in the grazer *Mylagaulus*, in the relatively low crowned *Steneofiber* as well as in the relatively high crowned *Hystrix*.

As the above described morphological changes during ontogeny of the occlusal surface might have an impact on their functional performance, two functional parameters were tested. Functionality of the dentition can be quantified with the length of functional enamel ridges in relation to the area of the occlusal surface (functional structural density (D_a), Schmidt-Kittler 1984). A high D_a equals a high number of enamel ridges and thus a better functionality for communition as it allows a faster disintegration of food particles with fewer power strokes during mastication (Rensberger 1973). Additional enamel folds can therefore increase the functionality (Koenigswald 1980, 1982). However, too high values for D_e would mean too dense enamel ridges on the occlusal surface leading to a decrease in functionality (Schmidt-Kittler 1984). Another parameter for functionality is enamel ridge alignment (e.g., Herrmann 2002, Schmidt-Kittler 2002). The highest functionality in an evenly grinding tooth can be achieved by enamel ridges aligned mainly perpendicularly but slightly inclined to the chewing direction, leading to minimal contact area but increasing the duration of the contact of the shearing edges (Maglio 1972, Koenigswald 1980). Enamel ridges parallel to the chewing direction cannot disintegrate food particles and thus are functionless.

For the morphofunctional analyses of this study the generated occlusal surfaces were aligned in chewing direction and the functional length of the enamel ridges (all ridges not parallel to chewing direction) were measured. By this, changes in functionality by progressive wear can be detected within the investigated individuals (for details see Schubert 2019).



Fig. 7.7. Splitting pattern of enamel islets in upper and lower cheek teeth of selected extant and fossil rodent species. View through the transparent outer enamel portion onto colored internal enamel elements. Upper teeth in buccal view, lowers in lingual view. **A**, *Cuniculus paca*; **B**, *Dasyprocta azarae*; **C**, *Myocastor coypus*; **D**, *Hystrix indica*; **E**, *Castor fiber*, **F**, *Steneo-fiber eseri* (buccal view); **G**, *Steneofiber eseri* (buccal view, mirrored); **H**, *Steneofiber eseri* (mesial view); **I**, *Steneofiber eseri* (distal view); **J**-**K**, *Mylagaulus elassos* from lingual (**J**) and buccal (**K**, mirrored); **L**-**M**, *Mylagaulus elassos* from lingual (**L**) and buccal (**M**, mirrored). Color code A-I: blue, enamel fold I; green, enamel fold II; yellow, enamel fold III; orange, enamel fold IV; red, enamel fold V. Color code J-M: blue, enamel islet 1; dark green, enamel islet 2; light green, enamel islet 3; yellow, enamel islet 4; orange, enamel islet 5; red, enamel islet 6. Mesial to the left, in **H** and **I** buccal to the left. Arrows indicate splitting of enamel elements. Modified from Schubert (2019).



Fig. 7.8. Incomplete mineralization (arrows) deep inside the enamel islets of rodents as revealed by μ CT images (cross sections). Thus, these structures show a less X-ray density and appear darker. **A**, *Cuniculus paca*, left M1. **B**, *Dasyprocta leporina*, left m1. **C**, *Hystrix cristata*, right m1. Not to scale. Modified from Schubert (2019).

In order to maintain a high functionality during the lifetime of the animal, D_e and the concentration of enamel ridge alignment should remain constant despite progressive wear. Most of the investigated species show similar values for D_e around 5–6, although they are characterized by slight differences in morphology of the occlusal surface as well as in their degree of hypsodonty. In many groups of rodents D_e decreases with increasing hypsodonty e.g., Aplodontidae, Ctenodactylidae and Heteromyidae. In euhypsodont taxa the rather fast abrasion due to the low amount of enamel ridges gets compensated with life-long growth of the dentition (Schmidt-Kittler 2002). In some of the investigated species D_e as well as the concentration of enamel ridge alignment decreases only in latest wear stages. Other

species show decrease of D_e constantly with progressive wear and the enamel ridges are less concentrated (Figs. 7.9, 7.10). Though most of the investigated species show the same trend in upper and lower dentition, D_e and concentration of enamel ridge alignment are not necessarily correlated. Like in the upper dentition of Dasyprocta azarae, D_e can decrease with progressive wear but enamel ridge alignment stays more or less constant. In Hystrix cristata D_e of the upper dentition decreases constantly, whereas in the lower dentition D_e remains constant with progressive wear. Species with enamel folds and/or islets present into high age (late wear stages), as Cuniculus paca or Castor, show a more or less constant D_e with progressive wear. Only in late wear stages (E-H) enamel elements get lost and the remaining elements significantly reduce in length, leading to a decrease of D_e and thus reduction of functionality of the dentition. In species with continuous loss of enamel elements by progressive wear, as Dasyprocta azarae or Hystrix indica, De decreases continuously during ontogeny (Fig. 7.9).

Conclusions about functional compensation and dietary adaptations

Most of the investigated species possess a rather high functionality of their dentition during lifetime. In those species with continuously decreasing values for D_e and/ or decreasing concentration of enamel ridge alignment eruption of M3/m3 and P4/p4 (if present) leads to com-



Fig. 7.9. Decrease of the functional structural density (D_e) with progressive wear in *Cuniculus paca* (**A**,**B**) and *Hystrix indica* (**C**,**D**). **A**,**C**, upper cheek teeth; **B**,**D**, lower cheek teeth. *Cuniculus paca* represents species with reduction of enamel islets only in late wear stages and *Hystrix indica* shows continuously reduction of enamel islets with progressive wear. From Schubert (2019).



Fig. 7.10. Comparison of enamel ridge alignment with progressive wear. **A**, species with straight enamel folds (example of *Cuniculus paca*); **B**, curved enamel folds (example of *Dasyprocta azarae*). Future occlusal surfaces (S) are numbered consecutively (number next to S) defined by changing in wear. Wear stage categories (see also Fig. 7.4) are given. Values of 0° and 180° indicate ridge alignment parallel to chewing direction. Colored bars show enamel ridge alignment in steps of 5°; length of bars indicate amount of enamel ridges in percentage aligned in specific direction. Light blue: upper M2; dark red: lower m2. From Schubert (2019).

pensation of abraded material of the M1/m1 and M2/m2. In some investigated species like *Cuniculus paca, Dasyprocta leporina,* and *Hystrix indica* the occlusal surface and/or crown height of the P4/p4 are greater than those of the molars and thus increase functionality (Janis & Fortelius 1988). However, we should keep in mind that wild individuals seldom reach an age where the dentition gets worn down to wear stages that would show very low D_e and concentration of the angles.

The investigated rodent taxa can be divided in two groups after their pattern of enamel ridge alignment. For enamel ridge alignment the angles of an enamel ridge to the chewing direction were measured on several points along the enamel ridge; measurements were taken only on the leading edges (see Schubert 2019). The first group (taxa with parallel, straight enamel folds and islets as Cuniculus paca and Castor) possess a high concentration of enamel ridges around specific angles. The shearing edges are aligned roughly perpendicular to the chewing direction with a deviation up to 20°, and the inclination of upper and lower jaw is rather small (e.g., 20-30° in Cuniculus paca) (Fig. 7.10A). In the second group (e.g., Dasyprocta, Hystrix) not all elements on the occlusal surface are parallel and some enamel folds and islets are curved, leading to a higher deviation to 90°, and the enamel ridges are oriented in a wider range (e.g., 50-70° in the upper, 120-130° in the lower dentition of Dasyprocta azarae); the inclination of shearing edges of upper and lower jaw is 50-80° (Fig. 7.10B). It seems as if functionality is lower in the second group, but with curved enamel ridges food particles can be trapped more easily and a greater inclination of antagonistic shearing edges is possible (Rensberger 1973, Schmidt-Kittler 1984). To avoid the lateral movement of food particles that occurs in dentitions with straight enamel ridges, the inclination of the enamel ridges has to be less than 45°. Thus enamel ridge alignment gives only limited information about efficiency; other parameters as food particle transportation or the kind of food are also important (Rensberger 1973,

Schmidt-Kittler 1984). Abrasive and tough food like grass needs higher values for D_e and straight, parallel shearing edges; for less abrasive food such as leaves or fruits lower values for D_a and curved enamel ridges are sufficient (Herrmann 2002). However, curved ridges may be more efficient to trap certain food items like fruits. This pattern could not be confirmed among the investigated species. Although the morphology of the occlusal surface seems to follow this tendency in most species (e.g., straight, parallel enamel ridges in tough-fiber eating taxa as Castor, *Myocastor* and the potential grazer *Mylagaulus* and curved elements in fruit-eating *Dasyprocta*), the values for D_e are approximately the same in most species (ca. 5-7 in first wear stages). Although Cuniculus paca feeds on fruits and leaves (Dubost & Henry 2006, Townsend & Croft 2008) the morphology of the dentition resembles a grazer. The relatively low-crowned teeth of Thryonomys swinderianus have rather low values for D_e (3-4) and enamel ridges that are not aligned perpendicular to the chewing direction. Both features do not indicate a grazer diet but Thryonomys strictly feeds on tough grasses. This is possible because of the highly specialized feeding procedure of Thryonomys *swinderianus*, in which the grass mostly gets disintegrated with the incisors and only afterwards with the cheek dentition (Ewer 1969). The diet of a species can differ from that of its ancestor, but as long as the inherited morphology of the dentition fulfills the required amount of functionality it does not need to be optimally adapted to the diet (Schmidt-Kittler 1984, Gailer et al. 2016).

Surprisingly, in the present case study the results for functional structural density (D_e) and enamel ridge alignment indicate no significant influence of splitting of enamel folds and islets on the masticatory function. The splitting of enamel folds and islets can increase the number of enamel elements on the occlusal surface, but as demonstrated not D_e and thus functionality, as splitting obviously only affects the number of elements but not the length of shearing blades.

Ontogeny and tooth replacement

Teeth are rarely functioning as isolated individuals but mostly within the tooth row. Therefore, the coordinated eruption of teeth into the tooth row is of selective value in placental mammals. Most eutherian mammals have a diphyodont dentition. In contrast marsupials replace only the third premolar as all other teeth are permanent (e.g., Ungar 2010). The tooth eruption sequence of the permanent dentition has been investigated in many species and can show quite different patterns among orders constrained by phylogeny as well as function and size (e.g., Shigehara 1980). For example, the eruption of all molars before permanent premolars observed in several extinct and extant clades of Artiodactyla is regarded to present a plesiomorphic condition of this group (Monson & Hlusko 2018, Gomes Rodrigues et al. 2019). Size differences among teeth may also cause sequence differences like observed in Primates, in which the enlarged canines erupt relatively late (Smith 2000). Delayed eruption and completion of the permanent postcanine dentition has been observed in Afrotheria, which is regarded to be a synapomorphic pattern of this taxon (Asher & Lehmann 2008). Another exceptional pattern of tooth eruption is linked to the horizontal tooth replacement, where the eruption of the last molars is delayed like in Elephantidae, *Trichechus* and even in Macropodidae (Domning & Hayek 1984, Sanson 1989, Gomes Rodrigues et al. 2012). Such a delay of erupting teeth allows the presence of fresh teeth even at a high individual age. The functional area of the dentition (FAD) can grow parallel to the increasing body size as observed in Elephantidae (Anders & Koenigswald 2013). Continuous tooth replacement in combination with supernumerary teeth like in the African rodent *Heliophobius argenteocinereus* is rare in mammals (Gomes Rodrigues et al. 2011).

Tooth eruption is controlled by hox gene Msx2 that targets the growth factor BMP4 (see above) as well as the osteoclast differentiation pathways in the alveolar bone (e.g., Aïoub et al. 2007). Marks & Schroeder (1996) give



Fig. 7.11. Transversal histological serial sections through the dentition of altricial muroid rodents showing the eruption of specific tooth position in neonatal to early postnatal stages. **A**,**B**, *Micromys minutus*, 4 days, 14 mm head length, slices 10-5-4 (A, oral fissure) and 20-4-1 (B, oral cavity behind diastema). **C**,**D**, *Mesocricetus auratus*, neonate, 15 mm head length, slices 5-2-6 (C, oral fissure) and 6-2-3 (D, oral fissure slightly behind (C). **E**, *Mesocricetus auratus*, 7 days, 19 mm head length, slice 21-4-2 (oral cavity behind diastema). **F**, *Mesocricetus auratus*, 11 days, 23 mm head length, slice 25-3-2 (oral cavity behind diastema). Arrows refer to erupting teeth. Not to scale. Abbreviations: de, dentale; dl/i2, deciduous upper/lower incisor 2; dnp, ductus nasopharyngeus; ey, eye; M/m1, upper/lower molar 1; mx, maxillare; nc, nasal cavity; pm, praemaxillare; tn, tongue.

a detailed overview on the tooth eruption mechanisms and pathways in primates, dogs and rodents. During the pre-eruptive phase bone formation and root growth (brachydont and hypsodont teeth) occur at the base of the dental alveoli while the bone above and/or root of the respective deciduous tooth are resorbed until the tooth completely penetrates the gingiva. The speed of pre-eruptive movements of developing teeth and the eruption speed are stage and species specific and depend on tooth position. In *Homo sapiens* premolars the speed of eruption from gingival emergence to the complete occlusal plane can be up to 75 µm/day (Proffit et al. 1991).

While the timing of eruption of permanent teeth can easily be investigated for comparative morphofunctional and systematic purposes (e.g., Asher & Lehmann 2008, Anders et al. 2011a,b, see case study 3), the study of pre- and perinatal eruption of deciduous teeth especially in placentals is a matter of technical limitations although the development of one of the major metabolic tools, the dentition, is an important key to the understanding of life history of a species. Thus, most studies on tooth eruption focus on the permanent dentition in postnatal stages, especially in primates (e.g., Smith et al. 1994, Jekl et al. 2011).

Case study 2: Perinatal tooth eruption in rodents and lagomorphs

Growth rates differ significantly in precocial (born relative mature) and altricial (born naked with closed eyes) mammals. The former have their growth rate peak earlier in development than the latter (Gaillard et al. 1997). Perinatal eruption of teeth in placental mammals is therefore also expected to be highly constrained by the mode of postnatal development in terms of precocial versus altricial adaptations.

Rodentia and Lagomorpha are suitable case studies as both orders comprise altricial as well as precocial species (Nowak 1991). Because lagomorphs and especially rodents use their incisors not only for gnawing but also for exploration, early eruption is advantageous in order to explore their surroundings early in life. Furthermore, in altricial species tooth eruption of check teeth may be delayed well into postnatal stages compared to precocial species as the former require initially intense care and nursing. To date, only few species of rodents and lagomorphs have been investigated in terms of tooth eruption in early ontogeny



Fig. 7.12. Transversal histological serial sections through the dentition of precocial ctenohystric rodents showing the eruption of specific tooth position in fetal stages. **A**,**B**, *Octodon degus*, late fetal, 24 mm head length, slices 14-2-2 (A, oral fissure) and 19-2-5 (B, oral fissure slightly behind A). **C**, *Thryonomys swinderianus*, late fetal, 38 mm head length, slice 48-2-1 (anterior oral cavity). **D**, *Cavia porcellus*, late fetal, 19 mm head length, slice 67-1-1 (oral cavity behind diastema). Arrows refer to erupting teeth. Not to scale. Abbreviations: de, dentale; dl/i2, deciduous upper/lower incisor 2; nc, nasal cavity; dP/p4?, ambiguous deciduous upper/lower premolar 4; mx, maxillare; pm, praemaxillare; tn, tongue.



natal stages. **A**, **B**, *Oryctolagus cuniculus*, 1 day, 35 mm head length, slices 22-2-3 (**A**, oral fissure) and 70-2-1 (**B**, oral cavity behind diastema). **C**–**G**, *Lepus europaeus*, late fetal, 39 mm head length, slices 15-1-1 (**C**, oral fissure), 18-1-2 (**D**, oral fissure slightly behind C), 19-2-1 (**E**, oral fissure slightly behind D), 67-1-1 (**F**, oral cavity behind diastema), and 75-1-2 (**G**, oral cavity slightly behind F). Arrows refer to erupting teeth. Not to scale. Abbreviations: de, dentale; dl2–3, deciduous upper incisor 2–3; di2, deciduous lower incisor 2; dP/p3-4, deciduous upper/lower premolar 3–4; 13, permanent upper incisor 3; nc, nasal cavity; mx, maxillare; pm, praemaxillare; tn, tongue.

and correlations with their reproductive biology were only rarely considered (e.g., Jekl et al. 2011).

For the present study perinatal stages of altricial and precocial Rodentia and Lagomorpha were investigated some of which are represented by several ontogenetic stages. The altricial rodent species are members of the Muroidea (*Mesocricetus auratus, Peromyscus maniculatus, Mus musculus,* and *Micromys minutus*), the precocial ones belong to the Ctenohystrica (*Petromus typicus, Thryonomys swinderianus, Octodon degus, Chinchilla lanigera, Myoprocta pratti,* and *Cavia porcellus*). Lagomorpha are represented by the altricial *Oryctolagus cuniculus* and the precocial *Lepus europaeus*. The histological sections are housed in the Institut für Evolution und Ökologie (formerly Lehrstuhl für Spezielle Zoologie), Eberhard-Karls-Universität Tübingen, Germany. Dental eruption is defined here according to previous studies (e.g., Jekl et al. 2011) in that any portion of the tooth crown is penetrating the gingiva. Therefore, information on the soft tissue structures is demanded for the precise identification of eruption of deciduous as well as permanent teeth. This can be best achieved by histological serial sections.

G



Fig. 7.14. Relative timing pattern of perinatal tooth eruption in altricial and precocial rodents and lagomorphs. Precocial species are born with all tooth types erupting whereas in the altricial species under study cheek teeth start erupting not until after birth. Interestingly among the altricial rodents only *Mesocricetus* is born with erupting incisors. In general, incisors erupt before cheek teeth except for *Cavia* and *Chinchilla* in which it is vice versa.

In all investigated altricial rodents, except for Mesocricetus auratus, eruption of incisors and molars is restricted to postnatal stages (Fig. 7.11). Peromyscus maniculatus nicely exemplifies this pattern: a neonate shows no erupted teeth whereas an early juvenile stage (25 mm head length) has a fully erupted dentition. However, a neonatal stage of Mesocricetus auratus shows erupted upper and lower incisors which clearly indicates prenatal eruption of the incisors (Fig. 7.11C,D). This pattern is surprising but may be explained by the species' peculiar reproduction biology. Mesocricetus auratus has the shortest gestation period (15-17 days) among placentals but its development and craniogenesis are accelerated and therefore mostly comparable in their timing to all other investigated muroids (Soderwall et al. 1960, Ruf 2020). This species starts nibbling food eight days after birth and after three weeks weaning is completed (Nowak 1991). However, a seven days old specimen shows no further erupted teeth; in an eleven days stage M1 and m1 have erupted. Thus, the observed eruption pattern correlates with the above described postnatal development but a fully erupted dentition is obviously not necessary after weaning.

The precocial rodents under study are generally characterized by a longer gestation period than in altricial species (Nowak 1991). Though this does not necessarily affect the timing of tooth eruption, tooth development seems to be more advanced at time of birth compared to altricial

rodents. In the investigated precocial species the incisors erupt in prenatal stages before or at the same time as the premolars or first molars and this happens before birth (Fig. 7.12). As shown by a recent study in Octodon degus none of the premolars and molars erupts before the second day after birth. Functional occlusion of the first two cheek teeth does not start before the ninth day after birth. Eruption of lower molars is somewhat delayed compared to the upper dentition and full occlusion of all cheek teeth is accomplished on days 58-72 after birth (Jekl et al. 2011). This pattern, slower development of teeth in the lower jaw, has been also described for Cavia (Harman & Smith 1936, Berkovitz 1972). However, some variation can be observed in Octodon degus as in our sampling a neonatal specimen already shows erupting deciduous premolars. Prenatal tooth eruption has already been described in caviomorphs and the prenatal occlusion can even result in attritional tooth wear before birth as described for Cavia and Myocastor (Ainamo 1971, Sone et al. 2008).

In general the sequence of cheek tooth eruption in the investigated rodents is from anterior to posterior. However, the investigated specimens of *Cavia porcellus* and *Chinchilla lanigera* show a deviating pattern as the first molar is already erupting while the premolar is still covered by gingiva. Unfortunately, it is not clear if these premolars are deciduous or permanent as no younger or older stages of these species are at hand. At least in *Cavia* it is known

that the deciduous premolar becomes resorbed in prenatal stages (Harman & Smith 1936). Surprisingly, in a late fetal *Cavia porcellus* the incisors are still covered by gingiva though the premolars, M1–2, and m1–2 are in different stages of eruption. Although intraspecific variation in the timing of tooth formation and eruption, even within the same litter, has been observed in *Cavia* (Harman & Smith 1936), a delayed eruption of the incisors has not been mentioned yet. Due to the time consuming preparation of histological serial sections and the fact that the sampling of prenatal stages is restricted in most species, analyses of intraspecific variation of perinatal tooth eruption are still pending.

The lagomorphs under study reveal that all deciduous incisors already erupt well before birth (Fig. 7.13A, C-E). However, Nagy & Daniel (1992) describe the beginning of incisor eruption for the neonate New Zealand white rabbit (*Oryctolagus cuniculus*); intraspecific variation could explain this discrepancy. In the neonatal stage of the altricial *Oryctolagus cuniculus* the cheek teeth have not pierced the gingiva yet (Fig. 7.13B). The premolars are observed to erupt after one week, the first molar after two weeks, the second after 3.5 weeks and the third molar after four weeks (Nagy & Daniel 1992). In contrast, the investigated

late fetal stage of the precocial *Lepus europaeus* already shows partially erupted dP3-4 and dp3-4 (Fig. 7.13F,G). Obviously the first upper cheek tooth (dP2) shows a delayed eruption compared to all other deciduous premolars. A study on *Lepus brachyurus brachyurus* reveals that at birth all deciduous premolars and the first and second molars are erupted (Yamada et al. 1990).

Though in both lagomorph species under study the incisors erupt before birth, there is evidence for a different timing of cheek tooth eruption in the two reproduction types. This pattern is comparable to the observations in rodents, in which altricial species show postnatal eruption of cheek teeth in contrast to precocial species that are born with at least partly erupted cheek teeth (Fig. 7.14). This confirms the hypothesis that the mode of development at birth is also reflected in the development of the dentition of Rodentia although further altricial and precocial members of the mouse-related clade as well as the squirrel-related clade need to be investigated to exclude a phylogenetical effect. As many altricial muroids reach their sexual maturity within a few weeks and therefore need a functional dentition for optimal energy supply, their relative delayed tooth development is obviously compensated by highly accelerated tooth eruption.

Age differentiation and life history

Unlike bones, teeth are not remodeled during the life history. Therefore at least a limited amount of time markers in the dentition is available to reconstruct the life history of a mammal. However, classifications of age stages based on tooth wear can be used for ontogenetic and (paleo) ecological interpretations of single species as well as species communities as demonstrated in our case study below. In contrast, life history is also documented in teeth that are not affected by wear i.e., in the tusks of elephants a major part of the life history is recorded. For Mammuthus primigenius major events, such as severe traumata or diseases, malnutrition, giving birth in females, or rush in males, are recognizable by the changes of microstructure in the dentin (Fisher et al. 2014). Based on the carbon and nitrogen isotope analyses of a juvenile Mammuthus primigenius from Wrangel Island evidence of weaning has been documented (Rountrey et al. 2007). Perhaps the large dentin teeth with limited abrasion of Monodon monoceros or Odobenus rosmarus may provide similar data.

The formation of enamel during the early ontogeny of teeth contains other time markers. On the outside of teeth, perikymata (incremental growth lines) mark subsequent steps of the mineralization of the enamel. Within the enamel they are seen as Retzius lines that cross the individual prisms. The prisms themselves have a rhythm, regarded as daily, and thus the progress of tooth formation can be compared between different taxa. In dentin a comparable daily incremental pattern can be observed, the von Ebner lines (Dean et al. 1993). This topic is discussed especially in early hominins (e.g., Smith et al. 2015).

In many mammal species the degree of tooth wear is used as an indicator of individual age, especially in domesticated animals and game (Baumann 1949, Habermehl 1975,

Chapter 7. I. Ruf et al.: Functional aspects and constraints in tooth ontogeny

1985). Already at medieval fares, horses were evaluated according to the wear stages of the incisors (Kroon 1929). Unfortunately, these approaches can be applied only to a limited degree on extinct species. The methods used for extant mammals aim at individual ages measured in years but are often restricted to the investigated species. For instance, the dental wear age classes that refer to the absolute age of the animals defined by Grau et al. (1970) for Procyon lotor (classes I-V) and by Goddard (1970) for Diceros diceros (classes I-XX) are not comparable or consistent. General age stages as "infantile", "juvenile", "mature", "adult", or "senile" were often used in various ways by different authors, such as Schultz (1935, 1960) and Smith (2000) for primates in general, and Knußmann & Martin (1988) for humans. Therefore the general application of these definitions to a wide range of extant and fossil taxa has been difficult to date. However, related to the aim of a study specific and detailed classifications of ontogenetic stages are still demanded as shown above by Schubert (2019).

Case study 3: Individual dental age stages

Anders et al. (2011a,b) provide an age classification for eutherian mammalian dentitions based on the tooth eruption and wear of the postcanine teeth. The "individual dental age stages" (IDAS) are independent of the occlusal morphology and the absolute age and can be applied to almost all fossil and extant eutherian species. Taxa with horizontal tooth replacement, expanded or reduced tooth formula (e.g., elephants, manatees, hyenas) can be considered by slight adaptations of the IDAS system (see Anders et al. 2011a,b).



Fig. 7.15. Individual dental age stages (IDAS) 1–5 examplified in the lower dentition of two extant Artiodactyla: the bundont *Sus scrofa* and the selenodont *Capreolus capreolus*. The vertical lines refer to the position of the lower first molar (m1). Modified from Anders et al. (2011a).



Fig. 7.16. Distribution patterns of individual dental age stages (IDAS) 1–5 in relation to the life span of selected extant cervids (top) and bovids (bottom). Compared to the maximum life span (100 %) the average life span (vertical bars) is longer in bovids (around 82 %) than in cervids (around 54 %). The elongated phases IDAS 2, 3, and 4 reflect the hypsodonty in Bovidae. Variation of the IDAS 3 and 4 is indicated by the oblique edges of the bars. Modified from Anders et al. (2011a).



Fig. 7.17. Mortality of Cainotheriidae in three fossil communities deduced from individual dental age stages (IDAS) of the respective samples. **A**, IDAS of *Caenomeryx filholi* from the Upper Oligocene of Gaimersheim showing the predominance of IDAS 2 and 3. **B**, Left maxilla with P4-M3 (IDAS 3) of *Caenomeryx filholi* from the same locality (IGPB 7395). **C**, *Cainotherium* sp. from Saulcet (Lower Miocene) is also mostly represented by IDAS 2 and 3. **D**, *Cainotherium huerzeleri* from Steinberg im Ries (Lower Miocene) shows a different pattern in being represented by only IDAS 1 and 2. Abbreviations: IGPB, Institute of Geosciences, Section Paleontology, University of Bonn; M3, upper molar 3; MN, Mammal Neogene zone; MP, Mammal Paleogene zone; P4, upper premolar 4. Modified from Anders et al. (2011a).

The IDAS cover the entire life span from prenatal to senile stages and can be correlated to traditional terms as e.g., juvenile, adult or senile. They comprise six stages that are defined as follows (Fig. 7.15):

- IDAS 0 (prenatal) The prenatal stage of tooth development cannot be determined in the teeth directly. However, this stage has been included in order to allow comparison and characterization of prenatal specimens. In the fossil record, independent evidence for the prenatal death of the individual is needed.
- IDAS 1 (infant) This stage refers to the period from birth to the first attritional facets on the erupting first molar. The deciduous dentition dominates and the eruption of the first molar approximately marks the time of weaning in many placentals (e.g., Smith 2000, Kelley & Smith 2003).
- IDAS 2 (juvenile) This stage refers to the period from the first facets through wear on the first molar to the fully erupted permanent dentition.
- IDAS 3 (adult) This stage refers to the period from full eruption of the dentition until the loss of the inner profile of the first molar, so the occlusal surface is free of interior enamel but the outer enamel band is not

119

broken down. IDAS 3 is supposed to be the time of maximum activity and reproduction in most Eutheria. In the fossil record this stage is common.

- IDAS 4 (late adult) This stage lasts from the loss of the inner profile of the first molar until the loss of the inner profile of the second molar.
- IDAS 5 (senile) This stage lasts from the loss of the inner profile of the second molar to the complete breakdown of the dentition by wear and/or tooth loss. The nutrition may be compromised.

The varying duration of different stages in the IDAS pattern during the life history forms an additional way to characterize mammalian species and groups by the ontogeny and wear of their dentition. The late eruption of the third upper and lower molar is discussed to be related to longevity (e.g., Smith 2000). The length of the single IDAS stages differs in the various species that were studied by Anders et al. (2011a,b). A comparison between Cervidae and Bovidae shows that the former reach IDAS 5, the senile stage, earlier in their maximal life span than the latter (Fig. 7.16). This difference might be due to the fact that bovids have hypsodont cheek teeth. The higher amount of material in these teeth can compensate the loss of



Fig. 7.18. Distribution of individual dental age stages (IDAS, left) and species composition (right) among fossil perissodactyls and artiodactyls from Höwenegg, Upper Miocene, Germany. The sampling is dominated by IDAS 3. Modified from Anders et al. (2011a).

dental material caused by chewing of highly abrasive plant matter. Therefore, these teeth function for a longer part of the average life span. This result supports the hypothesis that the functional performance of the dentition impacts the longevity of an animal (compared to similarly sized species). This is especially the case in herbivores as the functional efficiency of their cheek teeth is a key limiting factor to energy harvest, and the loss of shearing blades or blade sharpness reduces the grinding capacity of the dentition (Popowics & Fortelius 1997).

A major advantage of the IDAS is the application to fossil specimens, characterizing the mortality in monospecific populations or of entire fossil communities composed of various species. Even if no extant relatives exist from which the individual age in years could be deduced by comparison, functional age groups can be classified and used to elucidate fluctuations in population size or age structures in correlation to climatic or seasonal parameters. Anders et al. (2011a,b) provide IDAS analyses of the placental fauna of several fossil sites. One striking example refers to Cainotheriidae, extinct rabbit-sized artiodactyls from the Eocene/Miocene of Europe from three investigated localities. Caenomeryx filholi from Gaimersheim (Upper Oligocene fissure fillings, Germany) and Cainotherium sp. from Saulcet (Lower Miocene freshwater limestones, France) are represented by IDAS 1-5 (Fig. 7.17A-C). Juvenile and adult individuals are clearly dominating and IDAS 3 makes up at least 50 % of the population. This pattern resembles a stable population indicated by the dominance of individuals of reproductive age (Klein & Cruz-Uribe 1983). In contrast the fossil site Steinberg im Ries (Lower Miocene freshwater deposits, Germany) provides a quite different pattern (Fig. 7.17D). *Cainotherium huerzeleri* is mostly represented by IDAS 1 and 2. This accumulation of infant and juvenile stages might be best explained by a taphonomic phenomenon caused by birds of prey that might have nested in that area and preferred smaller prey animals (Heizmann & Fahlbusch 1983).

The lake deposits of Höwenegg (Upper Miocene, Germany) exemplify the application of IDAS to a fossil assemblage in order to elucidate age classes and mortality in a fossil mammal fauna represented by different taxa. The 46 investigated specimens comprise Perissodactyla as well as Artiodactyla (Fig. 7.18). Again the investigated sampling is dominated by IDAS 3 (about 80 %). IDAS 1 is represented by only one specimen of *Hippotherium* and IDAS 2 by one *Aceratherium*, one *Dorcatherium*, and three individuals of *Miotragocerus*. IDAS 4 and 5 are completely missing in the sample.

IDAS 0 is represented theoretically by three fetuses. A pregnant mare of *Hippotherium* shows one fetus and twins can be observed in the abdomen of a *Miotragocerus* specimen. The teeth of the fetuses are not well documented (Anders et al. 2011a,b). As both pregnant females belong to IDAS 3, these finds support the hypothesis that IDAS 3 definitely coincides with reproductive activity, although reproduction could also occur in IDAS 2 or 4. However, the observed IDAS pattern in the fossil perissodactyl and artiodactyl assemblage from Höwenegg does not reflect a natural population composition of neither of the investigated species because not all IDAS are represented. Predominance of IDAS 3 might be due to a so far unidentified selection.

Conclusion

Premolars and molars play an important role in food communition and their reliability is correlated with longevity of the respective species. Especially in herbivorous mammals enhancement of efficiency during the power stroke is a major key to cope with abrasive materials in their diet, such as phytoliths or grit. Therefore, specialized occlusal patterns (e.g., enamel elements) and compensatory constructions (e.g., hypsodonty) evolved. These features are generally correlated to but also constrained by ontogeny. Only the deeper understanding of tooth ontogeny i.e., from pre-erupting to late adult stages are crucial to elucidate the evolution and functional performance of postcanine dentitions in herbivorous mammals.

The case studies presented in this chapter meet general research questions investigated in the DFG Research Unit 771 and clearly demonstrate how ontogeny in a single tooth as well as in a tooth row representing a functional unit can be interpreted from extant as well as fossil dentitions.

Hypsodonty and euhypsodonty guarantee the efficiency or a prolonged function of rasp facets in the dentition. This is often in concert with additional enamel crests of the occlusal surface like enamel folds and/or islets. Enamel islets can increase the length of shearing ridges on the occlusal surface. There are, however, limitations in the development of teeth with enamel islets such as the possible crown height. Especially in Rodentia enamel islets often split with progressive wear, thus an increasing amount of enamel elements functions on the occlusal surface. As shown in case study 1, these splittings are highly variable but may not directly contribute to an increase or preservation of functionality of the teeth during progressive wear. Even if the stimulus of the splitting is so far unknown, this pattern evolved several times independently.

Loss of functionality of worn teeth can be compensated to a certain degree by the normal tooth replacement of the deciduous dentition or by a horizontal tooth replacement. The latter allows a function for a longer period, the compensation of a possible increase of body size, and enhances the lifespan of an individual. The sequence and timing of tooth eruption can vary in different species. Case study 2 indicates the correlation of the tooth eruption sequence and its timing with the reproduction mode in rodents and lagomorphs. In these orders, precocial taxa show an eruption of the first cheek teeth prior to birth, whereas in altricial species cheek teeth erupt after birth. Accordingly, this heterochronic pattern allows the more mature newborn pups of precocial species to have a functional dentition and to cope with food particles relatively early after birth.

Due to the differences in tooth eruption and wear the determination of the age of an individual is only possible when the dentition can be compared to an individual of the same species with known age. This is not only difficult in many wild living species, but almost impossible for extinct mammals. An estimation of the relative age (e.g., juvenile, adult, senile) can be accomplished with the eruption pattern and wear stages of the dentition. Case study 3 provides the definition of several individual dental age stages (IDAS), which can be applied for almost all living and extinct mammal species. Furthermore, by means of IDAS a direct comparison of different species as well as the age composition of a fossil population is possible.

In systematic studies of fossil and extant mammals, unworn or only slightly worn teeth are preferred. But they gain access only to a very limited aspect of mammals. If attention to the entire ontogeny is included, as clearly demonstrated in the three case studies, many more aspects become visible that reflect adaptations to specific functions or the requirements of specific environments.

Acknowledgments

We thank Ulrike Anders and Leonie Schwermann, who provided data from their PhD theses that were executed in the DFG Research Unit 771. The case studies were part of several projects in this research group (KOE 627/36-1, RU 1496/5-1).

We are grateful to Philip D. Gingerich (University of Michigan, Ann Arbor, MI), Ernest L. Lundelius (University of Texas, Austin, TX), Kenneth D. Rose (Johns Hopkins School of Medicine, Baltimore, MD), Richard C. Hulbert Jr. (Florida Museum of Natural History, Gainesville, FL), Thomas Mörs and Daniela Kalthoff (Naturhistoriska Riksmuseet Stockholm), Thomas Kaiser (Universität Hamburg), Wolfgang Maier (Universität Tübingen) as well as the citizen scientists Frank Menger (Groß-Rohrheim), Walter and Christian Keller (Ginsheim) who provided access to fossil and extant specimens for our studies. Adrian Tröscher (Universität Tübingen, Senckenberg-HEP) assisted with histological data, Georg Oleschinski (Universität Bonn) took the photographs. Last but not least we thank the reviewers Vincent Lazzari (Université de Poitiers) and Madeleine Geiger (Universität Zürich) who helped to improve the manuscript.

References

* indicates publications that originated from the DFG Research Unit 771.

- Aberg, T., Wozney, J. & Thesleff, I. (1997): Expression patterns of bone morphogenetic proteins (Bmps) in the developing mouse tooth suggest roles in morphogenesis and cell differentiation. Developmental Dynamics 210: 383–396.
- Ainamo, J. (1971): Prenatal occlusal wear in guinea pig molars. European Journal of Oral Sciences 79: 69–71.
- Aïoub, M., Lézot, F., Molla, M., Castaneda, B., Robert, B., Goubin, G., Néfussi, J. R. & Berdal, A. (2007): Msx2 -/- transgenic mice develop compound amelogenesis imperfecta, dentinogenesis imperfecta and periodontal osteopetrosis. Bone 41: 851–859.
- Alt, K. W. & Türp, J. C. (1997): Die Evolution der Z\u00e4hne, Phylogenie, Ontogenie, Variation. Quintessenz, Berlin.
- *Anders, U. & Koenigswald, W. v. (2013): Increasing and decreasing functional area of the dentition (FAD) during the life history of *Mammuthus primigenius* and other elephants. Paläontologische Zeitschrift 87: 515–527.
- *Anders, U., Koenigswald, W. v., Ruf, I. & Smith, B. H. (2011a): Generalized individual dental age stages for fossil and extant placental mammals. Paläontologische Zeitschrift 85: 321–339.
- *Anders, U., Koenigswald, W. v., Ruf, I. & Smith, B. H. (2011b): Erratum. Paläontologische Zeitschrift 85: 341.
- Asher, R. J. & Lehmann, T. (2008): Dental eruption in afrotherian mammals. BMC Biology 6: 14.

- Baumann, D. F. (1949): Die freilebenden Säugetiere der Schweiz. Hans Huber, Bern.
- Baskin, J. A. (1980): Evolutionary reversal in *Mylagaulus* (Mammalia, Rodentia) from the late Miocene of Florida. The American Midland Naturalist 104: 155–162.
- Bei, M., Stowell, S. & Maas, R. (2004): Msx2 controls ameloblast terminal differentiation. Developmental Dynamics 231: 758– 765.
- Berkovitz, B. K. B. (1972): Ontogeny of tooth replacement in the guinea pig (*Cavia cobaya*). Archives of Oral Biology 17: 711–718.
- Black, C. C. & Wood, A. E. (1956): Variation and tooth-replacement in a Miocene mylagaulid rodent. Journal of Paleontology 30: 672–684.
- Brandt, J. F. (1864): Observationes de Elasmotherii reliquiis. Mémoires de l'Académie Impériale des Sciences de St.-Pétersbourg, 7e série 8: 1–34.
- Cai, J., Cho, S. W., Kim, J. Y., Lee, M. J., Cha, Y. G. & Jung, H. S. (2007): Patterning the size and number of tooth and its cusps. Developmental Biology 304: 499–507.
- Calede, J. J. M. & Hopkins, S. S. B. (2012): Intraspecific versus interspecific variation in Miocene Great Basin mylagaulids: implications for systematics and evolutionary history. Zoological Journal of the Linnean Society 164: 427–450.
- Chen D., Zhao, M. & Mundy, G. R. (2004): Bone morphogenetic proteins. Growth Factors 22: 233–241.

- Dean, M. C., Beynon, A. D., Reid, D. J. & Whittaker, D. K. (1993): A longitudinal study of tooth growth in a single individual based on long- and short-period incremental markings in dentine and enamel. International Journal of Osteoarchaeology 3: 249–264.
- Domning, D. P. & Hayek, L.-A. C. (1984): Horizontal tooth replacement in the Amazonian manatee (*Trichechus inunguis*). Mammalia 48: 105–128.
- Dubost, G. & Henry, O. (2006): Comparison of diets of the acouchy, agouti and paca, the three largest terrestrial rodents of French Guianan forests. Journal of Tropical Ecology 22: 641–651.
- Ewer, R. F. (1969): Form and function in the grass cutter, *Thryonomys swinderianus* Temm. (Rodentia, Thryonomyidae). Ghana Journal of Science 9: 131–140.
- Fisher, D. C., Cherney, M. D., Newton, C. & Rountrey, A. N. (2014): Taxonomic overview and tusk growth analyses of Ziegler Reservoir proboscideans. Quaternary Research 82: 518–532.
- Fortelius, M. (1985): Ungulate cheek teeth: development, functional, and evolutionary interrelations. Acta Zoologica Fennica 180: 1–76.
- *Gailer, J. P., Calandra, I., Schulz-Kornas, E. & Kaiser, T. M. (2016): Morphology is not destiny: discrepancy between form, function and dietary adaptation in bovid cheek teeth. Journal of Mammalian Evolution 23: 369–383.
- Gaillard, J.-M., Pontier, D., Allaine, D., Loison, A., Herve, J. C. & Heizmann, A. (1997): Variation in growth form and precocity at birth in eutherian mammals. Proceedings of the Royal Society B 264: 859–868.
- Goddard, J. (1970): Age criteria and vital statistics of a black rhinoceros population. East African Wildlife Journal 8: 105–121.
- Gomes Rodrigues, H., Lihoreau, F., Orliac, M., Thewissen, J. G. M. & Boisserie, J.-R. (2019): Unexpected evolutionary patterns of dental ontogenetic traits in cetartiodactyl mammals. Proceedings of the Royal Society B 286: 20182417.
- Gomes Rodrigues, H., Marangoni, P., Šumbera, R., Tafforeau, P., Wendelen, W. & Viriot, L. (2011): Continuous dental replacement in a hyper-chisel tooth digging rodent. Proceedings of the National Academy of Sciences of the United States of America 108: 17355–17359.
- Gomes Rodrigues, H., Solé, F., Charles, C., Tafforeau, P., Vianey-Liaud, M. & Viriot, L. (2012): Evolutionary and biological implications of dental mesial drift in rodents: the case of the Ctenodactylidae (Rodentia, Mammalia). PLoS One 7:e50197.
- Graf, D. & Mitsiadis, T. A. (2013): Den Geheimnissen der Zahnentwicklung auf der Spur. Swiss Medical Forum 13: 168–170.
- Grau, G. A., Sanderson, G. C. & Rogers, J. P. (1970): Age determination of raccoons. Journal of Wildlife Management 34: 364–372.
- Greaves, W. S. (1973): The inference of jaw motion from tooth wear facets. Journal of Paleontology 47: 1000–1001.
- Habermehl, D. K.-H. (1975): Die Altersbestimmung bei Haus- und Labortieren. Paul Parey, Berlin.
- Habermehl, D. K.-H. (1985): Altersbestimmung bei Wild- und Pelztieren. Paul Parey, Berlin.
- Haeckel, E. (1866). Generelle Morphologie der Organismen. Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformirte Descendenz-Theorie (Vol. 2). Georg Reimer, Berlin.
- Hagmann, G. (1907): Über das Gebiß von *Coelogenys* und *Dasyprocta* in seinen verschiedenen Stadien der Abkauung. Zeitschrift für Morphologie und Anthropologie 10: 464–480.
- Harada, H. & Ohshima, H. (2004): New perspectives on tooth development and the dental stem cell niche. Achives of Histology and Cytology 67: 1–11.
- Harjunmaa, E., Seidel, K., Häkkinen, T., Renvoisé, E., Corfe, I. J., Kallonen, A., Zhang, Z.-Q., Evans, A. R., Mikkola, M. L., Salazar-Ciudad, I., Klein, O. D., Jernvall, J. (2014): Replaying evolutionary transitions from the dental fossil record. Nature 512: 44–48.
- Harman, M. T. & Smith, A. (1936): Some observations on the development of the teeth of *Cavia cobaya*. The Anatomical Record 66: 97–111.
- Heizmann, E. & Fahlbusch, V. (1983): Die mittelmiozäne Wirbeltierfauna vom Steinberg (Nördlinger Ries). Eine Übersicht. Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie 23: 83–93.

- Herrmann, N. (2002): Food-specialization and structural parameters of dental patterns of Arvicolinae (Rodentia, Mammalia). Senckenbergiana lethaea 82: 153–165.
- Hünermann, K. A. (1966): Der Bau des Biber-Prämolaren und seine Verwendbarkeit für die Systematik der Castoridae. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 125: 227–234.
- *Hummel, J., Findeisen, E., Südekum, K.-H., Ruf, I., Kaiser, T. M., Bucher, M., Clauss, M. & Codron, D. (2011): Another one bites the dust – faecal silica levels in large herbivores correlate with high-crowned teeth. Proceedings of the Royal Society B 278: 1742–1747.
- Janis, C. M. & Fortelius, M. (1988): On the means whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors. Biological Reviews 63: 197–230.
- Jekl, V., Hauptman, K., Jeklova, E. & Knotek, Z. (2011): Dental eruption chronology in degus (*Octodon degus*). Journal of Veterinary Dentistry 28: 16–20.
- Jernvall, J. (2000): Linking development with generation of novelty in mammalian teeth. Proceedings of the National Academy of Sciences of the United States of America 97: 2641–2645.
- Jernvall, J. & Thesleff, I. (2000): Reiterative signaling and patterning during mammalian tooth morphogenesis. Mechanisms of Development 92: 19–29.
- Jernvall, J., Keränen, S. V. E. & Thesleff, I. (2000): Evolutionary modification of development in mammalian teeth: quantifying gene expression patterns and topography. Proceedings of the National Academy of Sciences of the United States of America 97: 14444–14448.
- Kavanagh, K. D., Evans, A. R. & Jernvall, J. (2007): Predicting evolutionary patterns of mammalian teeth from development. Nature 449: 427–432.
- Kay, R. F. (1975): The functional adaptations of primate molar teeth. American Journal of Physical Anthropology 43: 195–216.
- Kelley, J. & Smith T. M. (2003): Age at first molar emergence in early Miocene Afropithecus turkanensis and life history evolution in the Hominoidea. Journal of Human Evolution 44: 307–329.
- Kitts, D. B. & Black, C. C. (1959): A Pliocene vertebrate local fauna from Roger Mills County, Oklahoma. Oklahoma Geological Survey 48: 27–47.
- Klein, R. & Cruz-Uribe, K. (1983): The computation of ungulate age (mortality) profiles from dental crown heights. Paleobiology 9: 70–78.
- Knußman, R. R. & Martin, R. (1988): Anthropologie: Handbuch der vergleichenden Biologie des Menschen, Bd. I/1. Gustav Fischer, Stuttgart.
- Koenigswald, W. v. (1980): Schmelzstruktur und Morphologie in den Molaren der Arvicolidae (Rodentia). Abhandlungen der senckenbergischen naturforschenden Gesellschaft 539: 1–129.
- Koenigswald, W. v. (1982): Zum Verständnis der Morphologie der Wühlmausmolaren (Arvicolidae, Rodentia, Mammalia). Zeitschrift für Geologische Wissenschaften 10: 951–962.
- *Koenigswald, W. v. (2011): Diversity of hypsodont teeth in mammalian dentitions – construction and classification. Palaeontographica A 294: 63–94.
- *Koenigswald, W. v. (2016): Specialized wear facets and late ontogeny in mammalian dentition. Historical Biology 30: 7–29.
- *Koenigswald, W. v. (2020): Construction and wear of mammalian teeth in terms of heterochrony. In: Martin, T. & Koenigswald, W. v. (eds.). Mammalian Teeth – Form and Function. Pfeil, Munich: 171–186.
- Koenigswald, W. v. & Kolfschoten, T. v. (1996): The *Mimomys-Arvicola* boundary and the enamel thickness quotient (SDQ) of *Arvicola* as stratigraphic markers in the Middle Pleistocene. In: Turner, C. (ed.). The Early Middle Pleistocene in Europe. Balkema, Rotterdam: 211–226.
- Koenigswald, W. v., Sander, P. M., Leite, M. B., Mörs, T. & Santel, W. (1994): Functional symmetries in the schmelzmuster and morphology of rootless rodent molars. Zoological Journal of the Linnean Society 110: 141–179.
- Koenigswald, W. v., Goin, F. & Pascual, R. (1999): Hypsodonty and enamel microstructure in the Paleocene gondwanatherian mammal *Sudamerica ameghinoi*. Acta Palaeontologica Polonica 44: 263–300.

- *Koenigswald, W. v., Anders, U., Engels, S., Schultz, J. & Ruf, I. (2010): Tooth morphology in fossil and extant Lagomorpha (Mammalia) reflects different mastication patterns. Journal of Mammalian Evolution 17: 275–299.
- Krause, D. W. (2014): Dental morphology of Vintana sertichi (Mammalia, Gondwanatheria) from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology 34, supplement to number 6: 137–165.
- Kroon, H. M. (1929): Die Lehre der Altersbestimmung der Haustiere, 3. Auflage. M. & H. Schaper, Hannover.
- Maglio, V. J. (1972): Evolution of mastication in the Elephantidae. Evolution 26: 638–658.
- Marks, Jr., S. C. & Schroeder, H. E. (1996): Tooth eruption: theories and facts. The Anatomical Record 245: 374–393.
- Martin, L. F., Winkler, D., Tütken, T., Codron D., De Cuyper, A., Hatt, J.-M. & Clauss, M. (2019): The way wear goes: phytolith-based wear on the dentine-enamel system in guinea pigs (*Cavia porcellus*). Proceedings of the Royal Society B 286: 20191921
- Mayhew, D. F. (1979): Evolution of a dental character in the beaver Castor fiber L. (Mammalia: Rodentia). Zoological Journal of the Linnean Society 65: 177–184.
- Merceron, G., Ramdarshan, A., Blondel, C., Boisserie, J.-R., Brunetiere, N., Francisco, A., Gautier, D., Milhet, X., Novello, A. & Pret, D. (2016): Untangling the environmental from the dietary: dust does not matter. Proceedings of the Royal Society B 283: 20161032.
- Mendoza, M. & Palmqvist, P. (2008): Hypsodonty in ungulates: an adaptation for grass consumption or for foraging in open habitat? Journal of Zoology 274: 134–142.
- Monson, T. A. & Hlusko, L. J. (2018): The evolution of dental eruption sequence in artiodactyls. Journal of Mammalian Evolution 25: 15–26
- Nagy, N. B. & Daniel, J. C. (1992): Development of the rabbit craniomandibular joint in association with tooth eruption. Archives of Oral Biology 37: 271–280.
- Nowak, R. M. (1991): Walker's Mammals of the World, 5th ed., Volume 1. Johns Hopkins, Baltimore and London.
- Osborn, J. W. (2008): A model of growth restraints to explain the development and evolution of tooth shapes in mammals. Journal of Theoretical Biology 225: 338–343.
- Piechocki, R. & Stiefel, A. (1977): Zahndurchbruch und Zahnwechsel beim Elbebiber, *Castor fiber albicus*. Anatomischer Anzeiger 142: 374–384.
- Popowics, T. E. & Fortelius, M. (1997): On the cutting edge: tooth blade sharpness in herbivorous and faunivorous mammals. Annales Zoologici Fennici 34: 73–88.
- Proffit, W. R., Prewitt, J. R., Baik, H. S. & Lee, C. F. (1991): Video microscope observations of human premolar eruption. Journal of Dental Research 70: 15–18.
- Rensberger, J. M. (1973): An occlusion model for mastication and dental wear in herbivorous mammals. Journal of Paleontology 47: 515–528.
- Renvoisé, E., Kavanagh, K. D., Lazzari, V., Häkkinen, T. J., Rice, R., Pantalacci, S., Salazar-Ciudad, I. & Jernvall, J. (2017): Mechanical constraint from growing jaw facilitates mammalian dental diversity. Proceedings of the National Academy of Sciences of the United States of America 114: 9403–9408.
- Rinderknecht, A., Bostelmann, T. E. & Ubilla, M. (2011): A new genus of giant Dinomyinae (Rodentia, Hystricognathi: Caviomorpha) from the late Miocene of Uruguay. Journal of Mammalogy 92: 169–178.
- Rountrey, A. N., Fisher, D. C., Vartanyan, S. & Fox, D. L. (2007): Carbon and nitrogen isotope analyses of a juvenile woolly mammoth tusk: evidence of weaning. Quaternary International 169/170: 166–173.
- Ruf, I. (2020). Ontogenetic transformations of the ethmoidal region in Muroidea (Rodentia, Mammalia): new insights from perinatal stages. Vertebrate Zoology 70: 383–415.
- Rusconi, C. (1930): Evolución cráneodental de la nutria (*Myocastor coypus bonariensis*) a través de su desarrollo postembrionario. Anales de la Sociedad Científica Argentina 110: 5–31.
- Rusconi, C. (1934): Apuntes sobre la evolución ontogenética de los molares del género Agouti (Rodentia). Revista Odontológica 22: 167–177.

- Sanson, G. D. (1989): Morphological adaptations of teeth to diets and feeding in the Macropodidea. In: Grigg, G., Jarman, P. & Hume, I. (eds.). Kangaroos, Wallabies and Rat-Kangaroos. Surrey Batty & Sons, Chipping Norton: 151–168.
- Schmidt-Kittler, N. (1984): Pattern analysis of occlusal surfaces in hypsodont herbivores and its bearing on morpho-functional studies. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen 87: 453–480.
- Schmidt-Kittler, N. (2002): Feeding specializations in rodents. Senckenbergiana lethaea 82: 141-152.
- *Schubert, A. M. (2019): Konstruktionsmorphologie hypsodonter Backenzähne bei rezenten und fossilen Rodentia (Mammalia). Dissertation, Rheinische Friedrich-Wilhelms-Universität Bonn. http://hss.ulb.uni-bonn.de/2019/5485/5485.htm
- Schultz, A.H. (1935): Eruption and decay of the permanent teeth in primates. American Journal of Physical Anthropology 14: 489–581.
- Schultz, A. H. (1960): Age changes in primates and their modification in man. In: Tanner, J. M. (ed.). Human Growth. Pergamon, Oxford: 1–20.
- Shigehara, N. (1980): Epiphyseal union, tooth eruption, and sexual maturation in the common tree shrew, with reference to its systematic problem. Primates 21: 1–19.
- Smith, B. H. (2000): 'Schultz's rule' and the evolution of tooth emergence and replacement patterns in primates and ungulates. In: Teaford, M., Smith, M. & Ferguson, M. (eds.). Development, Function and Evolution of Teeth. Cambridge University Press, Cambridge: 212–227.
- Smith, B. H., Crummett, T. L. & Brandt, K. L. (1994): Ages of eruption of primate teeth: a compendium for aging individuals and comparing life histories. Yearbook of Physical Anthropology 37: 177–231.
- Smith, T. M., Tafforeau, P., Le Cabec, A., Bonnin, A., Houssaye, A., Pouech, J., Moggi-Cecchi, J., Manthi, F., Ward, C., Makaremi, M. & Menter, C. G. (2015): Dental ontogeny in Pliocene and early Pleistocene hominins. PLoS One 10: e0118118.
- Soderwall, A. L., Kent, Jr., H. A., Turbyfill, C. L. & Britenbaker, A. L. (1960): Variation in gestation length and litter size of the golden hamster *Mesocricetus auratus*. Journal of Gerontology 15: 246–248.
- Sone, K., Koyasu, K., Kobayashi, S. & Oda, S.-i. (2008): Fetal growth and development of the coypu (*Myocastor coypus*): prenatal growth, tooth eruption, and cranial ossification. Mammalian Biology 73: 350–357.
- Strömberg, C. A. E. (2006): Evolution of hypsodonty in equids: testing a hypothesis of adaptation. Paleobiology 32: 236–258.
- Suraprasit, K., Chaimanee, Y., Martin, T. & Jaeger, J.-J. (2011): First castorid (Mammalia, Rodentia) from the Middle Miocene of Southeast Asia. Naturwissenschaften 98: 315–328.
- Teaford, M. F., Smith, M. M. & Ferguson, M. W. J. (2009): Development, Function and Evolution of Teeth. Cambridge University Press, New York.
- Thenius, E. (1989). Zähne und Gebiß der Säugetiere. De Gruyter, Berlin.
- Tobien, H. (1974): Zur Gebißstruktur, Systematik und Evolution der Genera Amphilagus und Titanomys (Lagomorpha, Mammalia) aus einigen Vorkommen im jüngeren Tertiär Mittel- und Westeuropas. Mainzer geowissenschaftliche Mitteilungen 3: 95–214.
- Tobien, H. (1975): Zur Gebißstruktur, Systematik und Evolution der Genera *Piezodus, Prolagus* und *Ptychoprolagus* (Lagomorpha, Mammalia) aus einigen Vorkommen des jüngeren Tertiär Mittel- und Westeuropas. Notizblatt des Hessischen Landesamtes für Bodenforschung zu Wiesbaden 103: 103–186.
- Townsend, K. E. B. & Croft, D. A. (2008): Enamel microwear in caviomorph rodents. Journal of Mammalogy 89: 730–743.
- Tummers, M. & Thesleff, I. (2003): Root or crown: a developmental choice orchestrated by the differential regulation of the epithelial stem cell niche in the tooth of two rodent species. Development 130: 1049–1057.
- Ubilla, M. & Rinderknecht, A. (2016): Lagostomus maximus (Desmarest) (Rodentia, Chinchillidae), the extant plains vizcacha in the Late Pleistocene of Uruguay. Alcheringa 40: 354–365.
- Ungar, P.S. (2010): Mammal Teeth: Origin, Evolution, and Diversity. The Johns Hopkins University Press, Baltimore.

- van Weers, D. J. (1990): Dimensions and occlusal patterns in molars of *Hystrix brachyura* Linnaeus, 1758 (Mammalia, Rodentia) in a system of wear categories. Bijdragen tot de Dierkunde 60: 121–134.
- van Weers, D. J. (1993): On the tooth morphology of the long-tailed porcupine *Trichys fasciculata* (Hystricidae: Rodentia), with notes on the genera *Atherurus* and *Hystrix*. Raffles Bulletin of Zoology 41: 251–261.
- van Weers, D. J. (2005): A taxonomic revision of the Pleistocene *Hystrix* (Hystricidae, Rodentia) from Eurasia with notes on the evolution of the family. Contributions to Zoology 74: 301–312.
- Williams, S. H. & Kay, R. F. (2001): A comparative test of adaptive explanations for hypsodonty in ungulates and rodents. Journal of Mammalian Evolution 8: 207–229.
- *Winkler, D. A. & Kaiser, T. M. (2015): Uneven distribution of enamel in the tooth crown of a Plains Zebra (*Equus quagga*). PeerJ 3: e1002.
- Yamada, F., Shiraishi, S., Taniguchi, A. & Uchida, T. A. (1990): Growth, development and age determination of the Japanese hare, *Lepus brachyurus brachyurus*. Journal of the Mammalogical Society of Japan 14: 65–77.
- Zouvelou, V., Luder, H. U., Mitsiadis, T. A. & Graf, D. (2009): Deletion of BMP7 affects the development of bones, teeth, and other ectodermal appendages of the orofacial complex. Journal of Experimental Zoology, Part B: Molecular and Developmental Evolution 312B: 361–374.