

Evolutionary trends in the mastication patterns in some perissodactyls, cetartiodactyls, and proboscideans

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Introduction

Both tooth shape and mode of mastication gained an enormous variability during the evolution of large herbivorous mammals, which allowed them to exploit diverse ecological niches. The variability in mastication includes specific adaptations to diet and is linked to the evolutionary history of a group. In addition, teeth are composed of the hardest tissue of the vertebrate body and thus are the most abundant vertebrate remains in the fossil record. Because of that and the resistance of the enamel to the wear process, teeth are preferred objects in paleontology.

Teeth are worn and partly abraded by the continuous chewing processes and need to serve the entire lifespan of an animal. Wear creates facets typically appearing on the crown of molars forming light reflecting polished surfaces (Mills 1955, Butler 1973). These wear facets occur as matching pairs on upper and lower teeth; several numbering systems and nomenclatures were erected for descriptive and comparative purposes (see summary in Schultz et al. 2018, 2020, this volume). Attritional facets are generated during mastication by tooth-tooth contact between

antagonistic molars, abrasional facets occur during tooth-food interaction without a direct contact to the antagonistic tooth structure (Maier & Schneck 1981, Academy of Prosthodontics 2005, Grippo et al. 2004). Both types of facets generally occur on the same occlusal surface. Erupting teeth usually do not show the fully functional shape right from the beginning. Many teeth need at least some initial use to develop precise functioning surfaces. Despite the continuous abrasion of the surface over time, such functional surfaces need to function with the same precision for a relatively long period, at least for most of the animal's life.

In this chapter, we concentrate on the functional surfaces that last for a long period and which characterize various large herbivorous mammals. In the following we distinguish between functional surfaces being composed of primary and secondary surfaces. The two conditions were introduced by Fortelius (1985): (1) teeth with *primary functional crown shape* are shaped and functional as they erupt with full enamel cover, and (2) teeth with *secondary functional crown shape* are formed and maintained by wear. Follow-

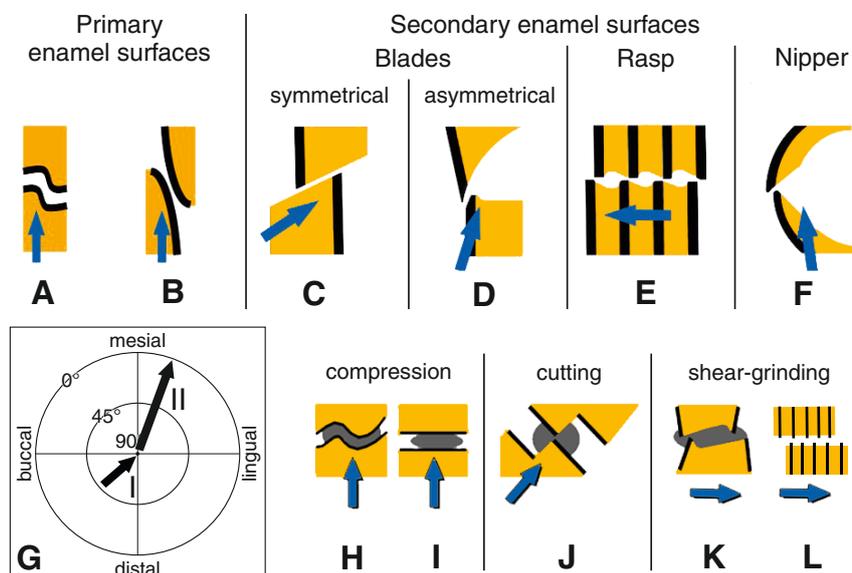


Fig. 11.1. Difference between primary and secondary functional enamel surfaces. **A,B**, all teeth that retain a primary functional surface mostly compress the food between the enamel coated (black layer) basins of the upper and lower teeth, or shear food along steep walls. **C–F**, secondary functional surfaces are characterized by enamel crests (black lines) and dentin basins (yellow), functional equivalent tools are blades (**C,D**), rasps (**E**) or nippers (**F**). **G**, the mastication compass is used to illustrate the direction of the lower jaw movements during the power stroke. The center of the circle depicts the maximal intercuspation between phase I and phase II. The arrows indicate the direction, the length of each arrow indicates the inclination during the jaw motion. In case phase II is descending the arrow is illustrated in gray. **H–L**, summary of tooth functions distinguished in this chapter: compression between primary occlusal surfaces (**H,I**), cutting along the enamel edges of a secondary occlusal surface (**J**), and shear-grinding along rasp-like secondary occlusal surfaces (**K,L**).

ing this definition, the closed enamel layer is the dominant functioning part in primary surfaces, which is also preserved for most of the individual's lifespan. Its morphology functions either as shearing surface or compressing chamber (Fig. 11.1). The enamel layer of primary functional surfaces is always impacted on the natural surface (outside), until heavy wear leads to the breakdown of the closed enamel layer. Secondary functional surfaces are characterized by widely exposed dentin in combination with enamel bands surrounding the dentin fields, enclosing either the whole occlusal surface or forming infolds and enamel islets (see Ruf et al. 2020, this volume). The difference in hardness of enamel and dentin creates protruding enamel crests during the wear process, which have functional significance for food breakdown. Once the initially closed enamel layer is opened, the cross section of the enamel becomes a functional surface. The protruding enamel crests can form sharp edges with blade-like functions or rounded crests with rasp-like functions (Fig. 11.1). Such protruding enamel bands of secondary surfaces can also be impacted on the natural inner side, when they form solid vertical walls and the dentin in front is scoured. Simple tooth forms with a primary functional surface can be compared to an anvil or a mortar (Lucas 1979), more complex enamel patterns of secondary functional surfaces function like a rasp. Symmetrical enamel blades are similar to scissors, whereas asymmetrical enamel blades are reminiscent of a paper cutter. Rodent incisors form nipper-facets along their incisors (secondary functional surfaces) functioning like pliers (Koenigswald 2016).

This chapter focuses on the evolutionary changes of the cheek tooth morphology of some mammal groups and the change in their function observed from reconstructed mastication processes. That includes the evolutionary transition from bunodont teeth with primary functional surfaces, to specialized teeth with blades or rasps formed by secondary functional surfaces.

The process of mastication is essential to herbivorous mammals, because plant material generally is nutrient-poor and has a high fiber content (Batzli & Hume 1994, Sanson 2006). Tough cellulose cell wall material is processed poorly in mammalian guts and needs to be broken down by tools first to make the nutritive cell content available and

to increase the surface area for digestive enzymes and bacteria (Crompton & Hiiemäe 1969, Lucas 1979, Wright et al. 2008). The evolutionary development of the cheek teeth of many large herbivores is dominated by opening the primary functional surface to form enamel bands and crests utilized to sufficiently break down plant-matter. In the mammalian dentition, premolars and molars are mainly involved in the mastication process (Crompton & Hiiemäe 1969, Lucas 1979). Due to natural selection, the complex crown morphology of cheek teeth in herbivorous mammals correlates with the type of diet, because the mechanical properties of the food strongly influence the shape of tooth crown elements after eruption (Maier 1980, Lucas 2004).

Most tools work only well when moved in a specific direction. Therefore most differentiated teeth follow a very distinct pathway during mastication. Of the different phases in the complex chewing cycle (Hiiemäe 1978, Hiiemäe & Kay 1972) only the power stroke is important for the function of teeth. It directly can be observed by watching the chewing animal or more accurately using cineradiography, or indirectly from muscle activity in living animals (Crompton et al. 2008, 2010), but in fossil mammals the movement needs to be reconstructed from the morphology of the occlusal surface, the wear facets, and striations. Describing the movements as vertical, horizontal, proal, palinal, or lateral is not sufficient, because most movements do not follow these traditionally used directions but are oblique in three dimensional space. The movements can be reconstructed with digital models of antagonistic teeth in the Occlusal Fingerprint Analyser software (OFA) (Kullmer et al. 2009, 2020, this volume) developed in the DFG Research Unit 771, and the directions of the movements can be visualized in two dimensions using the mastication compass (Koenigswald et al. 2012).

Institutional abbreviations

BSPG	Bayerische Staatssammlung für Paläontologie und Geologie, München
HLMD	Hessisches Landesmuseum Darmstadt
IGPB	Institute of Geosciences, Section Paleontology, Rheinische Friedrich-Wilhelms-Universität Bonn
TAMU	University of Texas at Austin, Texas Memorial Museum
UM	University of Michigan, Paleontological Museum

Perissodactyla

The earliest perissodactyls used the primary occlusal surface in combination with a two-phased power stroke (Janis 1990, Engels 2011, Mihlbachler et al. 2011). In the different groups of perissodactyls discussed here (Fig. 11.2), exposed dentin and the cross-section of enamel (i.e., the secondary functional surfaces) are increasingly utilized, and enamel bands are the dominant cutting devices for the mastication process. Despite the great diversity, the ectoloph remained the main element with shearing function in various groups, often combined with a shear-grinding function in the second phase of the mastication cycle. However, the ectoloph in modern horses is integrated in the almost flat occlusal surface of the hypsodont teeth,

and the alignment of the different chewing directions and inclinations of the two chewing phases to one horizontal movement of the power stroke led to the evolution of large rasp-like structures extended over the entire tooth surface. In rhinocerotoids the occurrence of modified enamel (i.e., vertical Hunter-Schreger bands) correlates with a higher degree of compression of the cusps and extreme lophodonty in this group (Rensberger & Koenigswald 1980). The absence of such modified enamel structure in the equoids, even in the ectoloph, correlates with the lesser importance of the ectoloph in equoids relative to brontotherians, chalicotherians, and rhinocerotoids.

Equoidea

Many studies investigated the evolution of equoid hypsodonty in particular, and the mammalian hypsodont dentition in general, which have been shown to be driven by the increasing grazing habit (e.g., MacFadden & Hulbert 1988, Fortelius et al. 2003, Strömberg 2006, Koenigswald 2011). The Equoidea comprise the two families Equidae and Palaeotheriidae. Both groups show a distinct evolutionary transformation of their molar morphology (Stirton 1941, Rensberger et al. 1984, MacFadden 1988, 2005, Joomun et al. 2008, Engels 2011, Evans & Janis 2014, Semprebon et al. 2016, Engels & Schultz 2018). The earliest forms have multi-cusped teeth that mainly compress the plant materials. Shearing and cutting along an enhanced ectoloph evolved in the Palaeotheriidae, whereas Equidae developed hypsodont teeth with a rasp like occlusal surface.

Early equoids (e.g., *Hyracotherium*, *Eurohippus*, *Propalaeotherium*) are mostly folivorous and frugivorous and show a mastication cycle consisting of two phases. In those forms the upper molars show larger contact surfaces and a cutting edge on the buccal side. These shearing surfaces are more strongly developed compared to more generalized functional precursory forms like the 'condylarth' *Phenacodus*. By developing a "mesostyle-like" structure the guidance of the power stroke is stronger in early equoids than in their bunodont ancestors with a simpler rounded cusp pattern (Fig. 11.3). The enhancement of the buccal cutting function leads to a rather effective reduction of leaves. In early equoids the buccal cusps of the upper premolars and molars show distinctly larger facet groups in combination with well-developed enamel crests compared to the 'condylarth' *Phenacodus*.

Eocene to Miocene Equidae (e.g., *Meshippus* and *Anchitherium*) and derived Palaeotheriidae (e.g., *Palaeotherium* and *Plagiolophus*) develop an elevated ectoloph with a higher occlusal relief and a distinct cutting function compared to the early forms, in combination with a stronger guidance of the lower molars sliding along the mesostyle. However, each family developed different adaptations to the vegetation of their changing environment. During evolution, the members of the more derived Equidae show a tendency to develop a one phase power stroke with emphasis of the cutting function on the buccal ectoloph (Fig. 11.4). In addition, enhancement of the shearing function was expressed by a double-blade on the buccal side of the upper molars and steep inclined shearing facets. The development of this functional complex enhancing cutting and shearing function exhibits similarities to the extant hypsodont members of the family with a flat occlusal rasp.

Derived Palaeotheriidae show different adaptations and maintain the two-phased power stroke. The occlusal surface of the molars clearly shows a separation of a buccal cutting/shearing function and a lingual crushing function constituted by a well-developed buccal facet group for processing leaves. Due to the more versatile teeth with distinct large shearing surfaces on the buccal side and a second phase in the power stroke, they are also able to process harder food items (e.g., twigs, hard fruits). The reduction of leaves appears not as efficient as in Paleogene-Neogene Equidae such as the Eocene-Oligocene *Meshippus* and Miocene *Anchitherium*. Those equids are in general special-

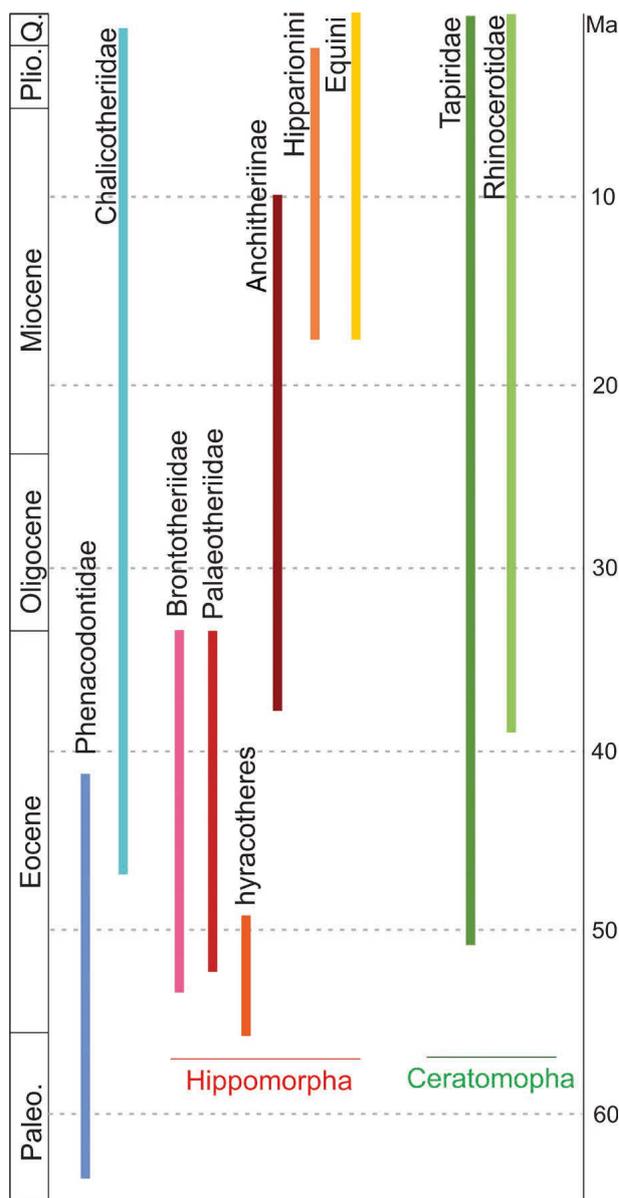


Fig. 11.2. Biostratigraphic ranges of perissodactyl groups discussed in this chapter. This diagram is based on data from MacFadden (2005), Strömberg (2006), Damuth & Janis (2011) and Muhlbachler et al. (2011). Abbreviations: Ma, megannums (million years); Paleo., Paleocene; Plio., Pliocene; Q., Quaternary.

ized leaf eaters, but are able to also comminute grasses. In comparison, modern hypsodont horses (genus *Equus*) with a flat occlusal surface and protruding enamel crests are adapted to a diet predominantly consisting of grass.

Equinae (i.e., Hipparionini and Equini) evolved hypsodont molars (MacFadden 2005, Strömberg 2006) in a heterochronic process of the tooth formation (Koenigswald 2011, Madden 2014). The direction of the power stroke of phase I and phase II becomes similarly adjusted during evolution. Thus, the lower molars cross the uppers from buccal to lingual horizontally in one stroke with no distinct separation of the two phases (e.g., centric occlusion) (Fig. 11.4). The occlusal surfaces function as rasps because softer materials cementum and dentin fill the gaps between the protruding harder enamel tooth elements. Such teeth

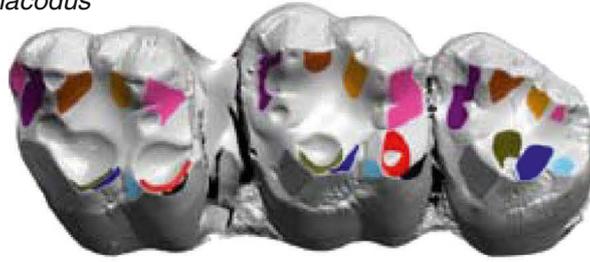
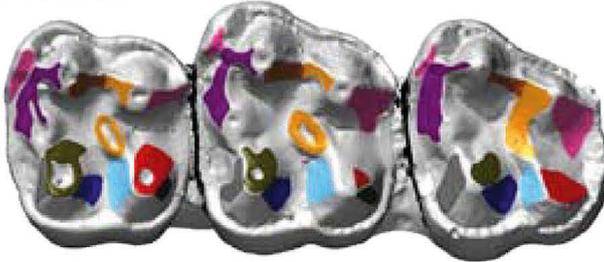
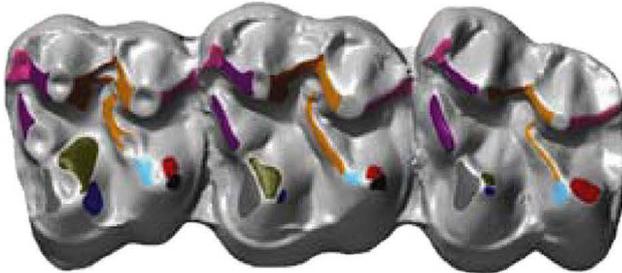
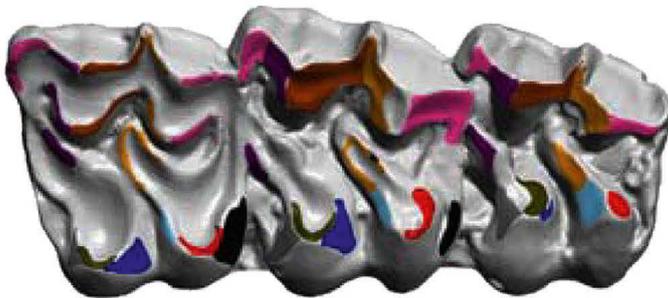
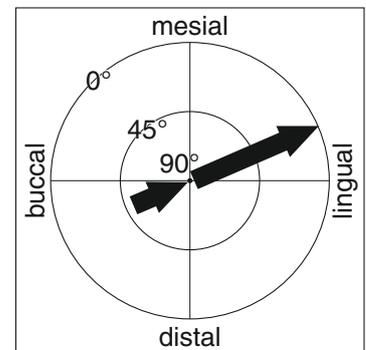
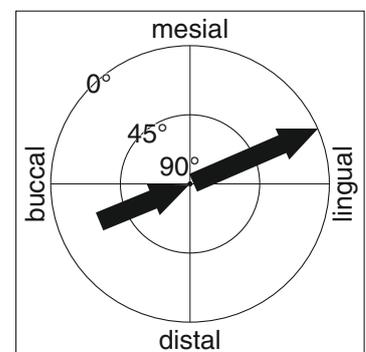
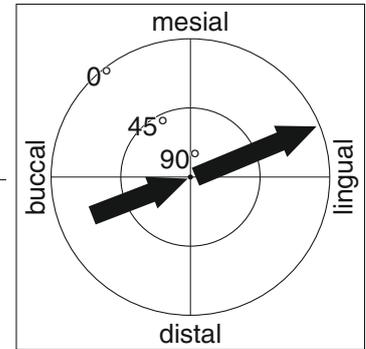
A *Phenacodus***B** *Hyracotherium***C** *Propalaeotherium***D** *Meshippus***E** *Palaeotherium*

Fig. 11.3. Molar series of *Phenacodus* and early Equoidea illustrating the enhancement of the ectoloph during the early equoid evolution. Molar facets colored after Butler (1951). **A**, *Phenacodus primaevus* (AMNH 15285); **B**, *Eohippus pernix* (USNM 522769); **C**, *Propalaeotherium hassiacum* (HLMD Me54a); **D**, *Meshippus bairdii* (BSPG 1959 XXIII 169); **E**, *Palaeotherium euzetense* (NHMB StH 2046). The mastication compasses show the stepwise steeper inclination of phase I reflecting the elevation of the ectoloph. Phase II is almost horizontal in all taxa. Not to scale. Virtual 3D surface models. Modified from Engels (2011) and combined with Koenigswald et al. (2013).

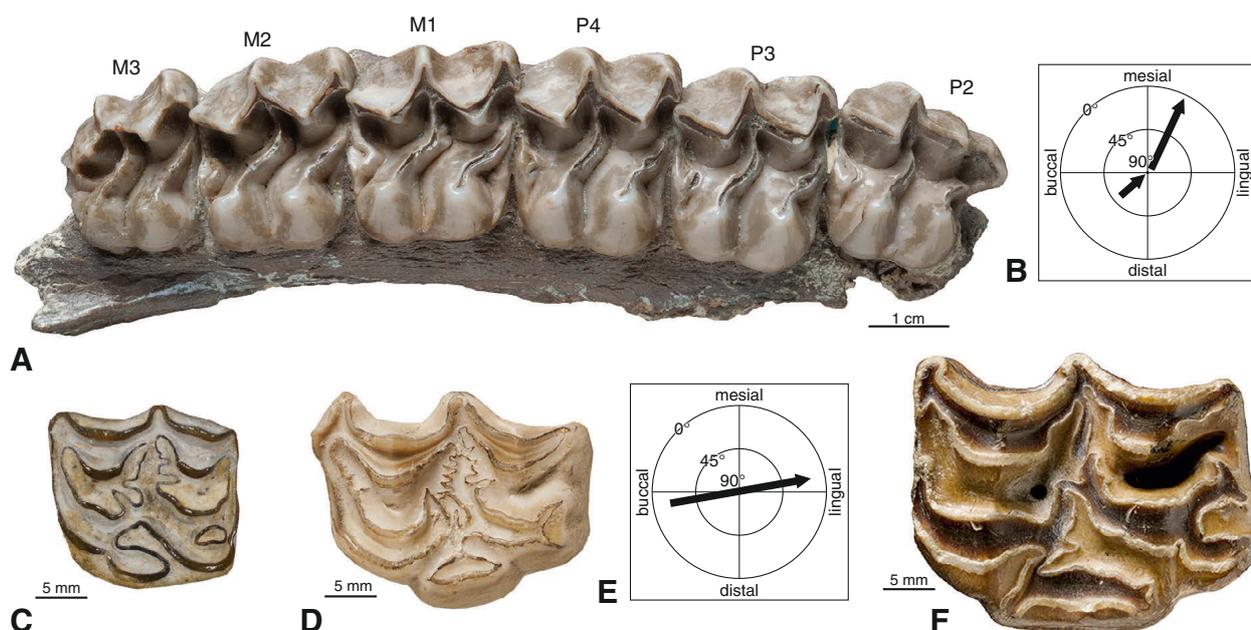


Fig. 11.4. Examples of the changing tooth morphology and mastication pattern in advanced Equoidea. **A**, *Anchitherium aurelianense steinheimense*, right maxilla with P2–M3, Miocene, Steinheim am Albuch, Germany (BSPG 1897 XIII4a); the premolars are molariform and the steep ectoloph is cutting during phase I. Abrasion along the crosslophs mark the beginning shear-grinding during phase II. **B**, mastication compass for *Anchitherium* illustrating the mesial shift of phase II. **C**, *Calippus (Merychippus) francisi*, left M1, Miocene, Noble Farm, New Mexico (TAMU 3016). **D**, *Hipparion* sp., right M3, Miocene, Samos (IGPB M7812). **E**, mastication compass for derived Equoidea with a flat occlusal surface. The power stroke is strictly directed bucco-lingually, phase I and phase II are continuous. **F**, *Equus caballus*, subfossil, right upper molar, Rhineland, Germany (IGPB M1850, mirrored); the two phases of the power stroke merged into a strict transverse movement, as indicated in the mastication compass (E). Photos: C, K. Bader; A, D, E, G. Oleschinski.

are regarded as highly specialized for grasses as diet (MacFadden 1988). The hypsodonty forms a reservoir of tooth material that compensates the high abrasion due to phytoliths and external abrasives such as grit or soil.

Tapiroidea and Rhinoceroidea

In the Eocene the molar morphology of early rhinocerotoids and tapiroids is very similar. The upper molars show the typical pattern with a strong and elevated buccal ectoloph and two linguo-buccally oriented crosslophs, the antero- and posteroloph (Rose 2006). The lower molars show two transverse lophids linked on the buccal side. Nevertheless, the mastication in these two groups develops in different directions as indicated by the facets on the lophs and lophids in the secondary occlusal surfaces. It has been shown that the heterogeneous occlusal surfaces may facilitate the comminution of heterogeneous browse, whereas uniform, broad grinding surfaces may enhance the comminution of physically more homogeneous grass (Taylor et al. 2013). In order to highlight the differences, the most primitive genera are not considered and the more derived ones of each group are discussed here.

The tapiroid mastication pattern was investigated in the Eocene *Lophiodon lautricense* from France, the Pliocene *Tapirus lundelius* from Florida, and the extant *Tapirus terrestris* from Brazil. *Lophiodon* is a rather large tapiroid (body size of a horse or a small rhino) with typical bilophodont lower molars and well-marked steeply inclined facets on the distal sides of the lophids (Koenigswald 2014). In the upper cheek teeth the facets are located on the mesial

sides of the crosslophs. In the functional facets the dentin is exposed and the shearing crests are formed by the sharpened cross-sections of the enamel. The posterior sides of the lophids cut like blades against the anterior sides of the crosslophs. Striations indicate a jaw movement in a mesio-lingual direction with a steep inclination. A facet on the buccal side of the paralophid fits to this direction. The crosslophs of the upper molars correspondingly have steep facets on their anterior sides (Fig. 11.5C). The ectoloph is not continuous, but it directs the movement of the lower jaw in mesiolingual direction, especially along the pronounced parastyle. Attrition sharpens the crests of the various facets indicating that the food items were primarily cut by symmetrical blades during phase I of the power stroke, whereas no facets represent a second phase (Fig. 11.5D).

In the molars of the upper Pliocene *Tapirus lundelius* a very similar set of facets was observed and a similar mastication pattern can be assumed. The transverse lophs and lophids are functioning like blades. The guiding function of the parastyle, however, is somewhat minor and the buccal facets on the paralophid are minimal.

In the extant *Tapirus terrestris* the cutting function of the symmetrical blades is the same, but the lateral aspect seems to be even more reduced than in *T. lundelius*. No lateral movement during the chewing process could be detected in an X-ray observation of a living tapir (personal comm. Marcus Clauss). Therefore, the tapiroid mastication pattern concentrates on the shearing function of the transverse symmetrical blades.

Rhinoceroidea share the basic pattern of the molars with tapirs (and several other perissodactyls) but during evolution the function developed in a different direction.

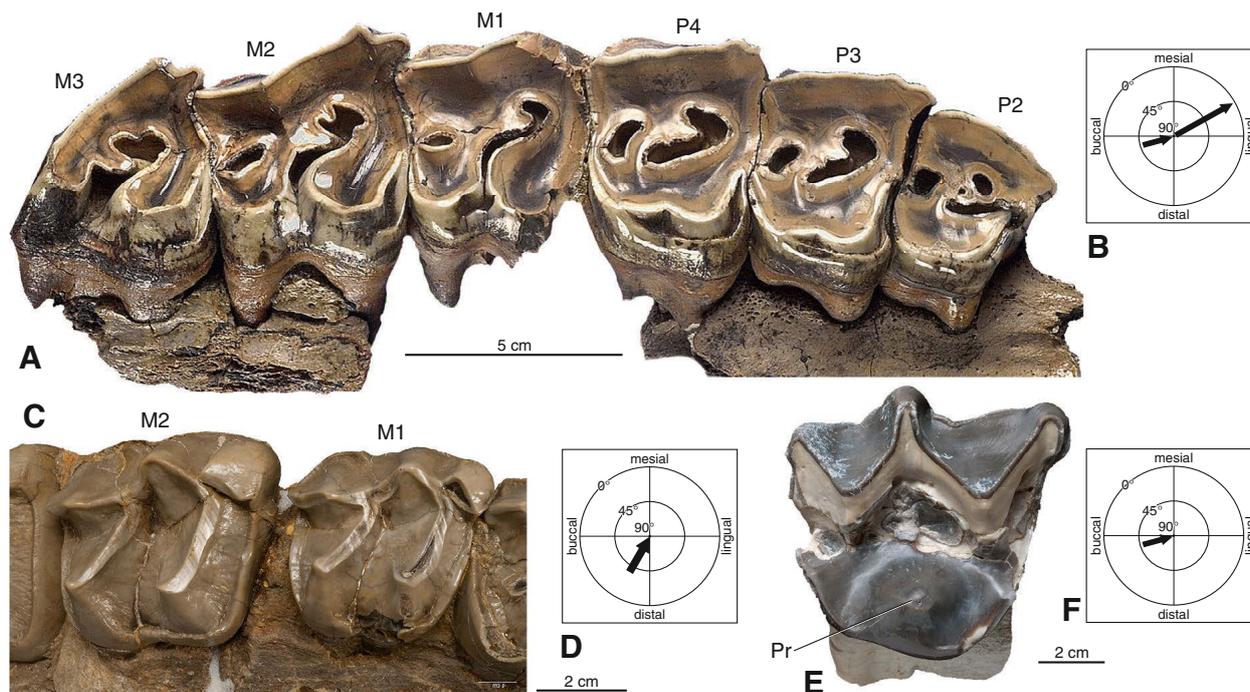


Fig. 11.5. In many perissodactyls the ectoloph has a shearing function. **A**, *Stephanorhinus etruscus* (Rhinocerotidae), right upper tooth row with P2–M3, Pleistocene, Brüggem, Germany (IGPB M4863); the ectolophs form the typical ectoloph-guillotine for phase I. During phase II the lower teeth shear across the crosslophs. The inclination between phase I and II is very distinct (**B**). **C**, *Lophiodon lautricense* (Tapiroidea), M1 and M2, Eocene, Robiac, France (HLMD-Ro 2, inverted); the ectoloph is of minor significance, but the crosslophs show blade facets of phase I of the power stroke. After cutting the food is compressed, but a phase II is lacking (**E**). **D**, *Megacerops* sp. (Brontotheriidae), right M2, Orellan, Badlands, South Dakota (HLMD WT735); the W-shaped ectoloph forms a cutting edge for phase I that ends at the massive protocone (Pr) functioning as a bumper. Thus, its mastication compass (**F**) shows no phase II. Photos: G. Oleschinski.

In the Late Eocene *Trigonias* from the White River Group the upper molars show a prominent ectoloph and two crosslophs. The dentin is exposed in an early stage of wear, but differently from tapirs. The buccal enamel of the ectoloph forms a continuous steep cutting edge supported by the dentin. In the two transverse lophs the dentin is exposed almost horizontally. The cutting ectoloph occurs in both premolars and molars (Fig. 11.5A). The antagonists for this device are shaped differently. Only a small facet is seen on the buccal sides of the lower molars and premolars. Thus, the ectoloph forms an asymmetrical blade with an abutment as antagonist, similar to a guillotine or paper cutter (Koenigswald 2016).

The cutting during phase I of the power stroke is followed by shear-grinding during phase II. The crosslophs in the upper molars as well as the lophids in the lower molars with the exposed dentin areas are well suited for shear-grinding with a low inclination. The direction of this grinding is oriented mesio-lingually (Fig. 11.5B).

The mastication process combining cutting and shear-grinding is very stable within tapiroids and rhinocerotoids, and occurs in the various genera of the Oligocene to the Pleistocene. This function is also found in the Eocene rhinocerotoid *Hyrachyus* and most of the later rhinoceroses, including the few extant species that are browsing: *Dicerorhinus sumatrensis*, *Rhinoceros sondaicus*, and the African *Diceros bicornis* (Hullot et al. 2019). Grazing and browsing extant rhino species are distinguished by tooth shape and microwear, and also by individual head posture (Schellhorn 2018), an additional indicator to identify grazing and browsing rhinos in the fossil record.

The extant white rhino *Ceratotherium simum* differs in its mastication pattern as does the Pleistocene *Coelodonta antiquitatis*. Their dentition is specialized for grazing and shear-grinding. The ectoloph is less prominently developed, allowing a shear-grinding movement across the entire occlusal surface which is rather flattened, and more complex transverse lophs increase the length of enamel crests in the rasp. Both genera show a trend towards hypsodonty to compensate for the increased wear. The Pleistocene *Elasmotherium* from Asia progressed in this trend for more intensive grinding even further (Kosintsev et al. 2018). The molars became euhypsodont and the crenulation of the enamel ridges in both crosslophs (and also the lower molar lophids) raised the effectiveness of the rasp.

Brontotheriidae and Chalicotheriidae

The upper molars of Brontotheriidae show a dominant ectoloph with a distinct W-shape and strongly folded prominent para- and metastyles, which resemble vertical pillars. The protocone forms an isolated large cone on the lingual side and the hypocone is somewhat smaller and often connects to the ectoloph via a minor crossloph (Fig. 11.5E, F).

The function of these teeth is mainly cutting along the W-shaped ectoloph (Fortelius 1985, Fahlke et al. 2013). The sharp edge is formed by enamel from the buccal side. It is so strongly inclined that the antagonist meets the enamel almost perpendicularly. The antagonist is formed by the continuous crest of the lower molar that forms a zig-zag line corresponding to the W-shaped ectoloph. In the lower

molars slight facets occur on the buccal side that form an abutment.

The asymmetrical blade in the upper molars and the matching abutment in the lower molars perform a guillotine-like (or paper-cutter-like) motion as in other perissodactyls with an enhanced ectoloph. Because the direction of movement is almost vertical, it functions more like a punching process. The cutting along the ectoloph blade represents phase I that is followed by compression of the cut food parts against the rounded protocone and hypocone. With

increasing wear the ectoloph facet shifts gradually to the buccal side and the space between the protocone and hypocone increases; however, both the cutting and compression functions are stable even in very old individuals.

Chalicotheres, although not closely related to brontotheres, possess a similar ectoloph morphology, but have lingual lophs instead of rounded cusps. A combination of punching, with a subsequent compression and shear along the lophs occurs in their dentition.

Cetartiodactyla

The complex mastication pattern of early terrestrial artiodactyls is characterized by the enhancement of a fourth cusp (i.e., the metaconule), from which the classical selenodont tooth pattern derived (Geisler et al. 2007). As in perissodactyls, the alignment of direction and inclination

of the two chewing phases of the power stroke allowed a continuous jaw movement in a transverse direction, with shearing across a secondary occlusal surface. A trend in modern groups of cetartiodactyls (e.g., camelids, bovids, cervids, antilocaprids) exists to increase the efficiency of

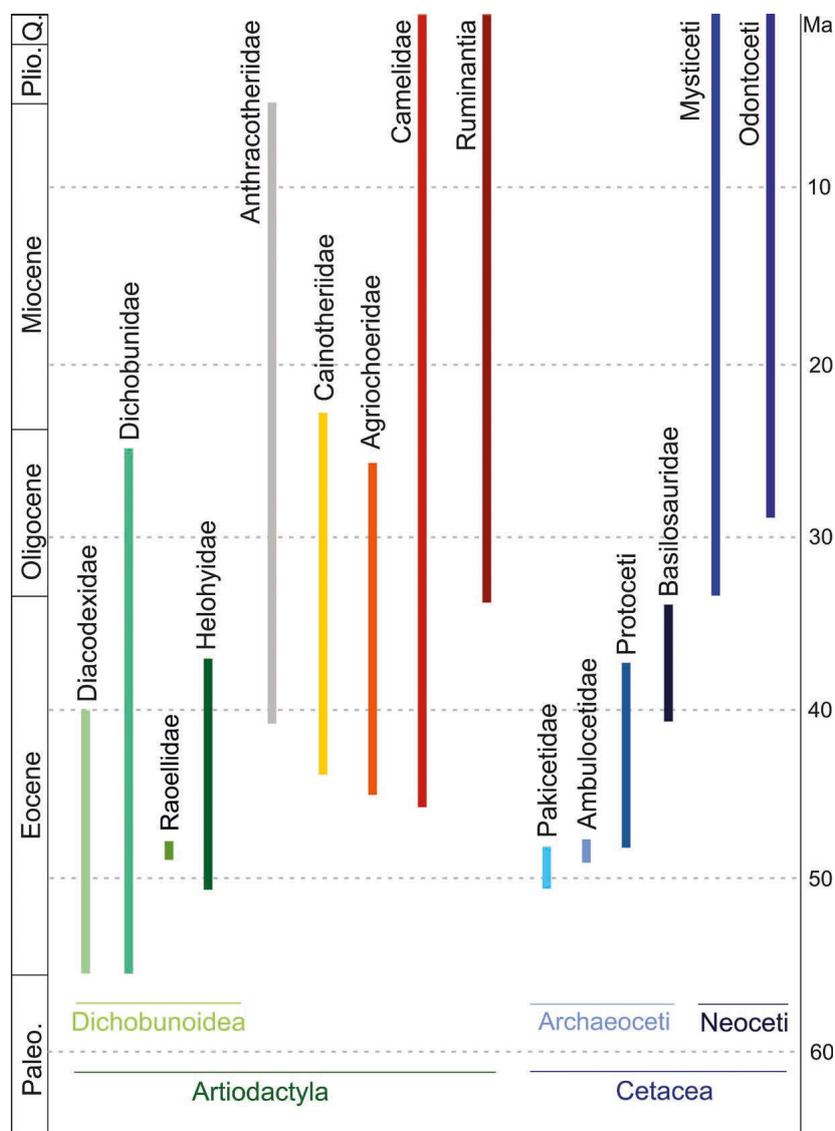


Fig. 11.6. Biostratigraphic ranges of cetartiodactyl groups discussed in this chapter. This diagram is based on data from Janis et al. (1998), Prothero & Foss (2007) and Houssaye et al. (2015). Abbreviations: Ma, mega-annums (million years); Paleo., Paleocene; Plio., Pliocene; Q., Quaternary.

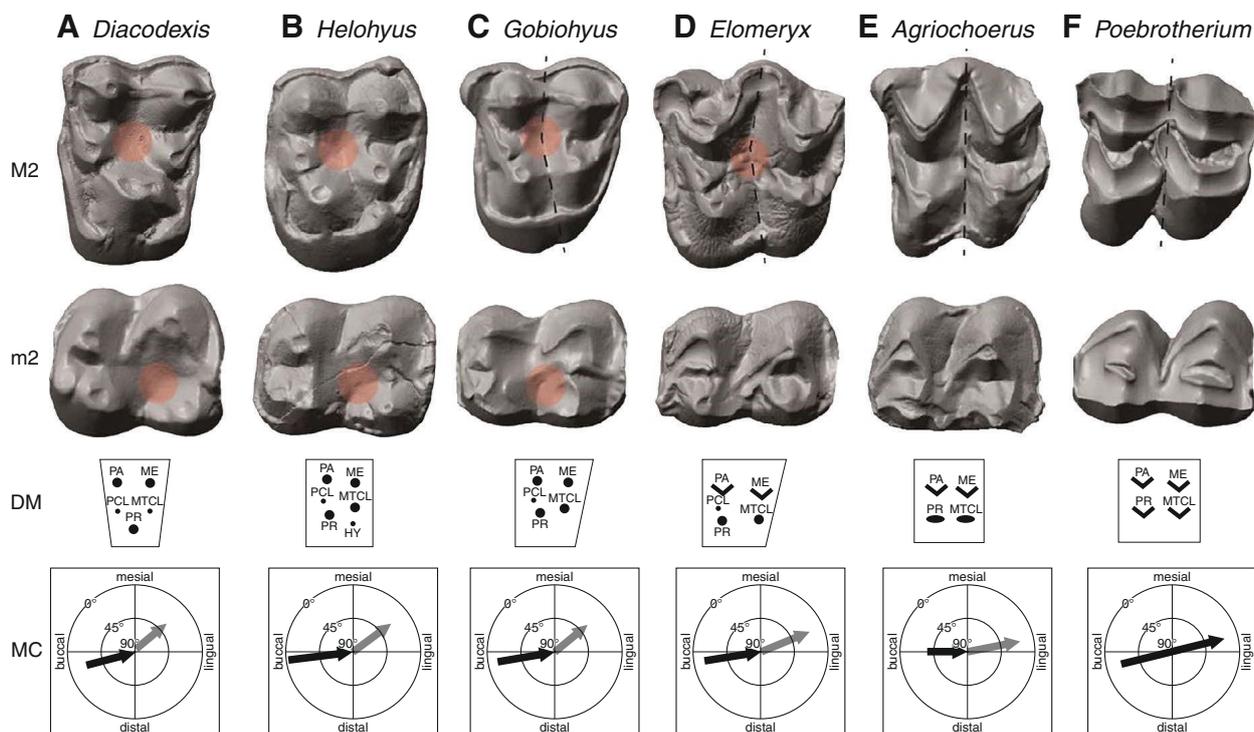


Fig. 11.7. Modification of trigon and trigonid basin (red dot) of the upper and lower molars during artiodactyl evolution to form the selenodont tooth type. In the derived types D to E the former basins form a trench (black dashed lines). **A**, *Diacodexis* sp. (M2, NMNH 5611; m2, CM 62046). **B**, *Helohyus plicodon* (M2, m2; AMNH 26279; m2, AMNH 16283). **D**, *Elomeryx borbonicus* (M2, m2; NMB Mar 550). **E**, *Agriochoerus* sp. (M2, m2; NMNH 215024). **F**, *Poebrotherium* sp. (M2, m2; AMNH 63821). In the first row upper second molars are illustrated, lower second molars follow in the second row below. Third row depicts simplified dental morphotypes (DM) of each taxon's upper molar. Last row, mastication compass (MC) for each taxon illustrating the shift from the ancestral two-phased power stroke to the one-phased power stroke of derived taxa. Not to scale. Virtual 3D surface models based on CT scans. Abbreviations: HY, hypocone; ME, metacone; MTCL, metaconulus; PA, paracone; PCL, paraconulus; PR, protocone.

the teeth processing fibrous diets for longer periods by the evolving hypsodont teeth. An exception are cetaceans. Marine cetaceans evolved from terrestrial artiodactyls with a two-phased mastication pattern and a primary functional occlusal surface (Gingerich et al. 2001, Thewissen & Bajpai 2001). During the adaptation to a piscivorous diet the tooth morphology was reduced to teeth with a single cusp that lost even their enamel cover in various species. The mastication pattern was simplified to a mainly orthal movement. Baleen whales, adapted to feed on very small crustaceans (krill), reduced their dentition completely.

Early terrestrial Cetartiodactyla

During the Paleogene radiation of cetartiodactyls numerous tooth shapes evolved. The selenodont dental pattern evolved convergently within several early terrestrial cetartiodactyl lineages (Fig. 11.6) (Janis & Fortelius 1988, Schwermann, 2016). The early cetartiodactyl *Diacodexis* exhibits a rather basic cheek dentition more similar to the tribosphenic tooth pattern of early therians with a typical two-phased power stroke. The two phases differ in inclination and direction but have equal significance for the power stroke: cutting (during phase I) and crushing (during phase II) the structural and reproductive plant parts of the dietary spectrum. A two-phased power stroke as reconstructed for *Diacodexis* is considered the ancestral pattern for North American and Eurasian terrestrial cetartiodactyls.

From this basal condition different evolutionary steps can be observed in other Eocene and later artiodactyls (Fig. 11.7), for example the enlargement of the occlusal surface by adding cusps or developing new functions by the conversion from bunodont to more selenodont cusps (Lihoreau & Ducrocq 2007). While the primary functional surface is of great significance with its complex morphology in the basal condition, the secondary surface is crucial for the functionality of selenodont cusps.

The dentitions of both *Dichobune* and *Helohyus* represent a stage of evolution, where the functional surface of the upper molars is enlarged by an additional cusp. The upper molars evolved a small hypocone and thus differ from the basic tribosphenic type (Fig. 11.7A,B). However, the power stroke is still similar to that of *Diacodexis*. In general the cusps are more rounded, and the crushing function is increased due to the presence of a hypocone.

The Asian *Gobiohyus* has an enlarged and lingually shifted metaconule (Fig. 11.7C). The buccal cusps of the upper molars show the beginning of a developing ectoloph and the enamel edge is extended by a large parastyle. The cusps are more pointed than the rounded cusps of *Dichobune* and *Helohyus* and wear produces doubled enamel edges on the distal and mesial crests of paracone and metacone. Despite the fact that the chewing motion is similar to that of *Diacodexis*, *Dichobune*, and *Helohyus*, structural plant elements probably constituted the greater part of the dietary spectrum. The teeth of *Gobiohyus* are the first in the fossil record of artiodactyls that indicate the

beginning significance of the secondary occlusal surface.

This preceding development can be observed in *Elomeryx*. The molars are intermediate between the bunodont and selenodont pattern. *Elomeryx* has selenodont buccal cusps on the upper molars on which wear produces doubled enamel edges (Fig. 11.7D). The lingual cusps in the upper molars are bunodont, and the trigon basin is partly reduced.

The similarities in the power strokes of *Elomeryx*, *Dichobune*, *Helohyus*, and *Gobiohyus* probably evolved convergently in their separate lineages (Schwermann 2016). The structural changes of the tooth surface with an improved shearing function indicate a greater portion of structural plant parts in the dietary spectrum. The reduction of the basins suggests a decreased importance of the crushing function.

Caenomeryx differs in its chewing function from the two-phased power stroke of the other taxa because of the parallel arrangement of cusps that allow a simple transverse movement. The molars of *Caenomeryx* function with the secondary surface. The cusps are selenodont and the basins are completely reduced. There is no distinct centric occlusion, but inclination changes after maximum intercuspatation. A second phase is characterized by tooth-tooth-contact and compression following maximum intercuspatation (Schwermann 2016). Overall, the dentition suggests a diet composed mainly of structural plant elements. In contrast, the small body size (around 2 kg, Tsubamoto 2014) indicates that fruits, seeds, sprouts and possibly insects were also part of the dietary spectrum.

The North American agriocherid *Agriocherus* and camelid *Poebrotherium* both have (buno-)selenodont dentitions with four-cusped molars and a uniform power stroke resulting from combining chewing phase I and II into one simple movement (Fig. 11.7E,F). There is no functional differentiation. In upper and lower molars the enamel crests are double-bladed which improves the shear-cutting function. Structural plant elements like leaves and grass were main parts of the diet of both genera.

The described taxa except *Caenomeryx* occur in the Eocene and thus represent an early evolutionary chapter of the very diverse group of artiodactyls. In modern artiodactyls the selenodont tooth morphology is dominant, and in many taxa within the Camelidae and Bovidae selenodonty is paired with hypsodonty.

The functional comparison of the basal bunodont teeth and the early selenodont teeth (and stages in between) shows that the masticatory movement changes from the basal two-phased condition to a unified, single chewing motion, which is performed in a stereotypic manner due to the complex selenodont cusp and crest morphology. As a result, the wear facets develop homogeneously and the ability to break down harder plant parts with each power stroke increases. The crushing function, which is performed by the protocone/talonid and hypoconid/trigon basin in tribosphenic and early artiodactyl bunodont teeth is reduced and shifted to the crests of the selenodont morphology. The combination of enamel bands and scoured dentin basins shears, crushes, and simultaneously cuts the food items, but in a different way than the mortar and pestle function of tribosphenic or bunodont artiodactyl molars (Schwermann 2016). The cutting and shearing function becomes increasingly important (Butler 1972). With the complete change to the selenodont tooth type the functionality of

the molars thus shifts from a primary occlusal surface of the bunodont dentition to a secondary occlusal surface of the selenodont dentition, using the exposed enamel ridges, enamel islets, and worn dentin basins in a rasp facet. The functional changes of the teeth go along with a shift in the dietary spectrum: While in early artiodactyls (e.g., *Diacodexis*) with blunt cusps reproductive plant elements (i.e., nuts, fruits, seeds, flowers) were the preferred diet, a shift to structural plant parts (i.e., leaves, nodes, internodes) as preferred diet occurred in artiodactyls with selenodont dentitions (Lucas & Luke 1984, Lucas 2004).

Aquatic Cetartiodactyla

The greatest evolutionary modification in tooth morphology and mastication occurred during the evolution of whales. Whales evolved from terrestrial Cetartiodactyla (Gingerich et al. 2001), possibly Raoellidae (Thewissen & Bajpai 2001), that had four-cusped molars like other early herbivorous terrestrial cetartiodactyls such as *Diacodexis*.

Eocene terrestrial Cetartiodactyla gave rise to the marine and carnivorous Odontoceti with single-cusped teeth, as well as to Mysticeti which reduced the teeth and use baleen for filter feeding (Fig. 11.6).

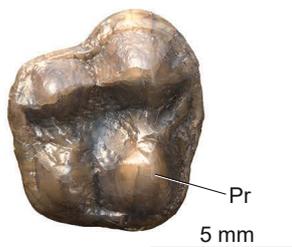
Modifications that happened during the evolution from terrestrial raoellids or raoellid-like cetartiodactyls to fully aquatic cetaceans included various changes, such as the simplification of the tooth morphology leading to single-cusped teeth that finally lost their enamel, modification in the dentition leading to homodonty, polyodonty, monophodonty, and a functional shift from mastication to filter feeding. The fossil record provides information on several intermediate stages.

Raoellidae from the Eocene of India (Fig. 11.8A) have molars with four distinct cusps that enable mastication (Koenigswald et al. 2012). The main function during phase I of the power stroke is compression of the plant material, and there is a slight mesial movement during phase II (Thewissen et al. 2011). The wear is limited and thus the primary surface persists. According to an analysis of stable isotopes the raoellid *Indohyus* was proven to be herbivorous (Thewissen et al. 2011).

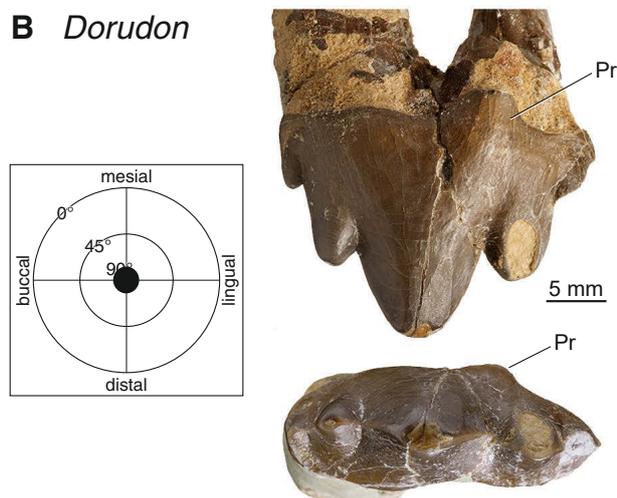
Pakicetidae, Ambulocetidae and Protocetidae were semiaquatic with fully functional hind limbs and – most probably – webbed feet. In the dentition, the premolars are enlarged and have a triangular shape, if viewed from the side, with shearing facets. Their size increases from front to back. The lowers intercalate with the upper ones, which is useful for catching fish. The molars are smaller than the premolars and the uppers have one cusp on the lingual side (i.e., the protocone) and no talonid basin in the lowers, reducing their function in mastication. Pakicetids have numerous adaptations for swimming and became piscivorous (Gingerich 1983, Thewissen et al. 2009). But they were not fully aquatic yet, at least for giving birth they came on land, which is also assumed for the protocetid *Maiacetus inuus* (Gingerich et al. 2009).

During the Middle Eocene, the next evolutionary level was reached by the fully aquatic Basilosauridae with reduced hind legs. They still had an almost complete dental formula lacking only M3, and replaced the deciduous premolars (Uhen 2004). The incisors and canines are pointed for grasping and catching slippery prey. The

A Raoellidae



B *Dorudon*



C *Bos*

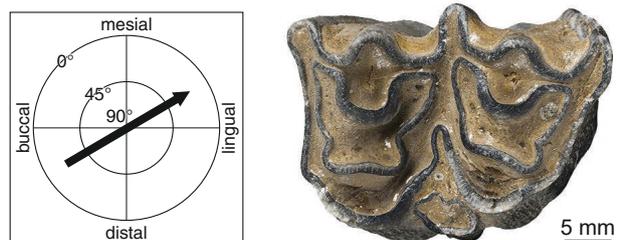


Fig. 11.8. Illustration of the drastic modification of tooth morphology and mastication pattern during the evolution of Cetartiodactyla, and in particular cetaceans. **A**, Raoellids (Middle Eocene, India, IGPB-KOE 2025) have square-shaped simple four-cusped molars with a primary functional surface. **B**, in the early whale *Dorudon atrox* (M2, Eocene, Wadi Hitan, Egypt, UM 101215) the premolars and molars are adapted to catching fish and molar morphology is reduced. The protocone (Pr) is a small swelling on the lingual side (lower picture occlusal view). The jaw movement is mainly orthal as shown in the mastication compass (central black circle). Terrestrial artiodactyls such as **(C)** *Bos primigenius* (upper molar, Pleistocene, Groß-Rohrheim, Germany, IGPB M 7824) evolved hypsodont teeth with functional flat secondary functional surfaces and one continuous power stroke. Photos: G. Oleschinski.

premolars are enlarged, laterally compressed, and have denticulate shearing crests. In the molars the lingual cusps (i.e., protocone and hypocone) were further reduced and the molars became premolariform. In upper molars the protocone is just a small bulge (Fig. 11.8B). The molars are distinctly smaller than the premolars and functionally only phase I of the chewing cycle is retained. In the Upper Eocene deposits from Egypt all teeth of *Basilosaurus* and *Dorudon* are fully covered with enamel (Fig. 11.8B). Larger prey was undoubtedly sectioned by the large denticulate premolars.

Coronodon havensteini, from the Oligocene of South Carolina (USA), which resembles basilosaurids in the dentition, was described as the first mysticete, although it does not have baleen (Geisler et al. 2017). The denticulate premolars of the lower jaw are of similar size and overlap with slots between them, through which water can pass. This indicates, together with other characters, that with slightly closed jaws water was pressed through and the small prey was kept in the mouth cavity like in a creel. The incisors show some tooth wear, probably resulting from sediment particles within the extruded water. Tooth function thus had totally changed because the process of chewing or catching and holding prey was no longer necessary. Modern Mysticeti reduced their teeth completely and replaced them with baleen, a novel integumentary structure (Peredo et al. 2018). They use ram feeding or suction feeding to get their food into the giant mouth (Marx et al. 2016).

From the basilosaurids another lineage led to the toothed whales. The dolphins are characterized by a large number of single-cusped teeth. In *Stenella attenuata* 44 teeth are present per quadrant. Homodonty replaced the traditional diversity seen in the mammalian dentition. The gene expression of BMP4 is regarded as a trigger for the single cusped teeth in the rear of the tooth row (Armfield et al. 2013). Thus, polydonta has replaced the tooth formula that in most lineages of terrestrial mammals is stable or shows reduction more often than augmentation. The pointed teeth are often covered by thin enamel. In addition, tooth replacement was suppressed, making toothed whales monophodont. These teeth have lost their chewing ability. The numerous teeth are suitable for catching and holding fish and other prey until they are swallowed.

In the large toothed whales, such as *Physeter microcephalus* or *Orcinus orca* the number of teeth is not exaggerated but each tooth is much larger. Their function for catching and holding the prey is recognizable from their intensive wear. The initial enamel cap is mostly worn off and the dentin tooth grows continuously. In the extant *Monodon* the continuously growing incisor is protruding from the mouth forwardly and used for various functions. A similar tooth, but turned backwards, was evolved by the Late Miocene *Odobenocetops* from Peru (Muizon 1993).

Proboscidea

Although proboscideans are fairly similar in their overall appearance and have many characteristic dental features in common (e.g., tusks, horizontal tooth replacement, and dominance of the last molars) the various lineages developed very different molar morphologies and mastication

patterns. Certainly the various tooth morphologies were adapted to different diets, but the enormous amount of plant material required daily by the large body size may prohibit the specialization into a very narrow food source.

The earliest proboscideans come from Africa but their fossil record is rather incomplete. *Eritherium* from the Paleocene of Morocco (Gheerbrant et al. 2012) has low-crowned molars. Lingual and buccal cusps oppose each other forming the prerequisite for transverse lophs that evolved in later taxa. In *Phosphatherium* (Gheerbrant et al. 2005) the molar cusps form transverse ridges that regularly have facets, in uppers on the anterior side and in lowers on the distal side. The transverse crests between the cusps are used for cutting. Thus the lower jaw is lifted with a slight anterior movement.

In the Early Miocene three proboscidean families expanded to Eurasia: Deinotheriidae, Mammutidae, and Gomphotheriidae. Their fossil record is more complete and the mastication process is better understood (Koenigswald 2016).

Deinotheriidae

Deinotheres retain their bilophodont molar structure throughout the Miocene without adding additional lophs at the posterior end of their molars (Harris 1975). Functionally, the deinothere pattern of mastication is a completion of the mastication pattern of the Phosphatheriidae. The lophs intercuscate deeply and create a broad facet in the lower molars on the distal side, and in the uppers on the anterior side. The sharp transverse crests are formed by the enamel of the leading side of each loph, where the food items are cut during phase I of the power stroke (Fig. 11.9A). Thus, deinothere molars form typical symmetrical blades. Phase I continues with progressing intercuscation. The cut food items are compressed between the enamel-covered sides of the following loph. No facets indicate a second phase of the power stroke in lateral direction. When lophs are worn down the remaining enamel ridges function as a rasp. Since the deinothere dentition has no horizontal shift, the entire battery of premolars and molars functions as a rasp in very old individuals.

Mammutidae

Mammutids are very conservative in their molar morphology and thus in their mastication pattern (Fig. 11.9B). The molars have up to three transverse lophs that intercuscate during mastication, but differently from those in deinotheres. Lophs are abraded by wear, but no development of facets on any specific side occurs. Therefore, during mastication the lophs meet the valley of the antagonist more or less vertically during phase I of the power stroke. Thus, the ingested plant material is strongly compressed. A slight lateral movement during phase II is indicated by striations and by the different abrasion in the pretrite and posttrite (the labial and lingual half-lophids) sides of the molars (Vacek 1877). During evolution only the M3/m3 are slightly elongated by an additional loph. Due to the horizontal tooth replacement, worn out premolars or molars are discarded, and in old individuals only the second and third molar are in function.

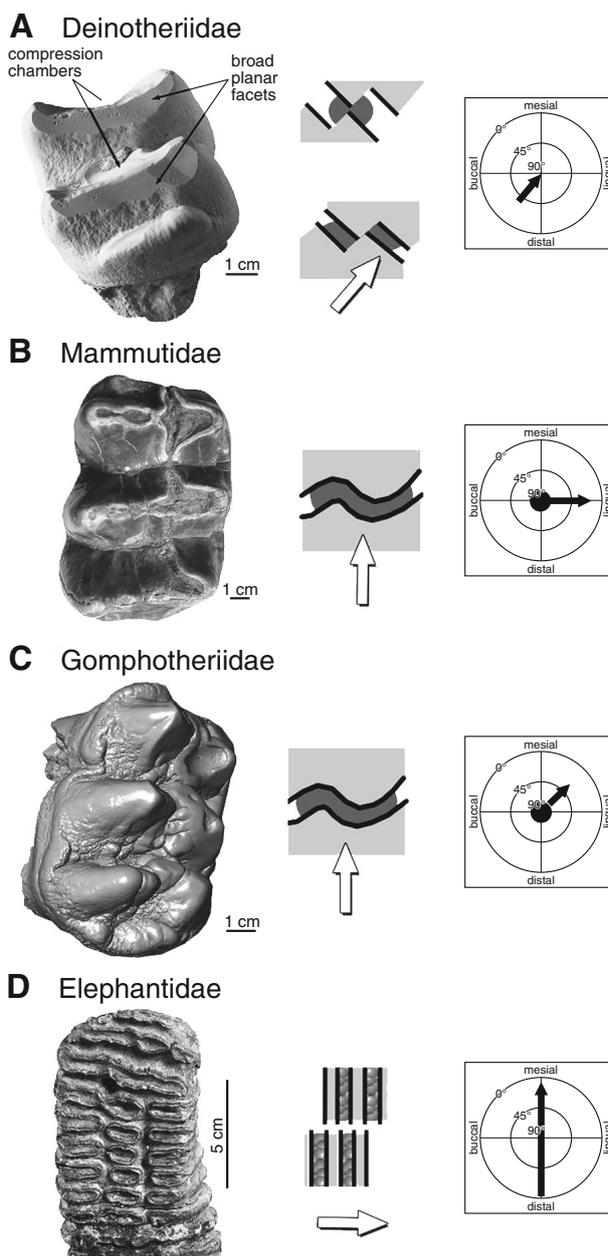


Fig. 11.9. Within proboscideans different tooth morphologies and mastication patterns evolved. **A**, in deinotheres during phase I, the food is cut along the lophs and consequently compressed between the primary functional surfaces. The power stroke ends with phase I, phase II does not exist. **B**, Mammutidae simply compress food without initial cutting during an orthal movement of the lower jaw. A slight lingual movement exists during phase II. **C**, gomphotheres compress food between the primary functional surfaces like mammutids by moving the lower jaw mesio-lingually. **D**, elephantids shear-grind the food along the typical rasp facets (secondary functional surface) performing a proal movement of the lower jaw. Modified from Koenigswald (2016).

Gomphotheriidae

Gomphothere molars have a rather bulbous structure. The main cusps form transverse lophs including additional conules (Tobien 1978). The valleys are filled with cusps that hinder a transverse movement (Fig. 11.9C). A thick enamel layer covers the cusps making the occlusal surface

more solid, and extending the use of the primary occlusal surface for mastication. The mastication pattern of Gomphotheriidae is not obvious because the wear facets are mostly rounded and do not indicate a distinct direction of the jaw movement. Manipulation of isolated antagonistic molars indicates a complex chewing motion composed of mesial and mesio-lingual movements. Virtual 3D models of the occlusal surfaces allow a much more detailed analysis in the OFA (Kullmer et al. 2009, 2020, this volume). According to the OFA analysis, the teeth occlude during phase I more or less in an orthal movement. This is followed by a movement in mesio-lingual direction with low inclination during phase II. In each chewing cycle, only one side of the tooth row is in occlusion. The main function of the molars is to reduce the size of food items by compression and squeezing. Due to the movement of the lower tooth row in mesio-lingual direction, the contact is more intense on the pretrite side than on the posttrite side (Koenigswald 2016). When the teeth are worn the thick enamel ridges function like a rasp. Due to the horizontal tooth replacement, the second and third molars are functionally very important and the M3/m3 are elongated by additional lophs.

Elephantidae

Elephantidae evolved during the Late Miocene. The molars of derived Elephantidae are characterized by hypsodonty and have an almost flat occlusal surface. The transverse ridges are formed by the enamel band enclosing the exposed dentin of the mesio-distally compressed lophs (Fig. 11.9D). The molar construction is characteristic for multicusped hypsodonty, because the individual lophs are elongated and fuse only at their very base (Koenigswald 2011). The space between the lamellae is filled with cementum. The primary surface is functionally unimportant, because the secondary one forms as soon as the lamellae are integrated into the chewing process and thus the occlusal surface. The sequence of lamellae forms an efficient rasp with ridges oriented almost perpendicularly to the jaw movement in mesial direction (Maglio 1972, Fortelius 1985).

The cheek teeth are replaced horizontally. The teeth are forming at the posterior end of the jaw and push forward. Because of the great length of the teeth, the anterior part may be worn down while lamellae are being added at the posterior end. The functional area in a jaw included either one full molar or two halves of adjacent molars. The functional area increases continuously with age corresponding to the increasing body size (Anders et al. 2011).

The occlusal surface functions like a rasp for breaking down the tough plant food. The power stroke is horizontal and mainly in a mesial direction perpendicular to the crests. Phases I and II cannot be distinguished.

Conclusion

The evolution of tooth function and adaptation of chewing movements is driven by different selective processes in the different groups of large-bodied herbivores, and it is difficult to find general rules in such diverse groups. However, the groups discussed above all have a brachydont four-cusped tooth morphology as ancestral pattern in common. Generally, three trends are apparent: (1) a simple ancestral state, using the primary tooth surface (closed enamel layer) and a two-phased chewing cycle with considerable crushing function, inherited from a most probably omnivorous origin (MacFadden 2000); (2) modification of the primary surface by restructuring the cusp arrangement of the cheek teeth integrating secondary tooth surfaces (enamel layer partly opened to form enamel crests and dentin basins) in combination with a simplified one-phased chewing cycle; (3) hypsodonty and euhipodonty (tooth crown higher than wide) integrating cementum, to add a third level of tooth tissue of different hardness and in order to fill the space between tall tooth lophs for stability.

Morphology-related aspects

In order to access the fibrous herbivorous diet the groups discussed above followed different evolutionary pathways, involving the modification of cusp numbers, arrangement of cusps, crown height, direction and length of the chewing path (among others). Hypsodonty (high crowned teeth) has evolved in several large herbivores as an adaptation to the

abrasive plant food, and the proportion of appearance of hypsodont teeth during mammal evolution increased over time (Janis & Fortelius 1988, Jernvall & Fortelius 2002, Damuth & Janis 2011, Samuels & Hopkins 2017). Looking at the extant species of grazers, the majority shows selenodont molars (utilizing the secondary functional surface) in combination with a transverse movement of the lower jaw, reflecting the advantage of selenodonty in connection with plant-based diet. Being able to access more nutrients benefits larger body sizes, and this in turn allows for increased tooth size (Janis & Fortelius 1988). A higher complexity level of the secondary occlusal surface is a relevant evolutionary process that was realized several times during evolution. While grazing species tend to have more elaborated and complex folded enamel ridges, browsers have less complex enamel ridges (Gailer & Kaiser 2014, Winkler & Kaiser 2015).

One main step in evolution was to achieve a larger occlusal surface, realized by the enlargement of the hypocone in early forms of Perissodactyla or the metaconule in most Cetartiodactyla (Hunter & Jernvall 1995). In early forms a primarily polished enamel surface (i.e., facets) works against an opposing enamel surface during chewing. The secondary functional surface is formed by opening the initially closed primary functional surface during the chewing process early in ontogeny. This wear process exposes enamel cross-sections across the occlusal surface forming continuous enamel bands and dentin basins, which act as shearing surfaces and compression chambers. The less

hard dentin is excavated during the lifetime of an animal and the enamel bands protrude and in some forms rasp-like structures are formed (e.g., molars of the proboscidean *Elephas*, the equid *Equus*, and some modern bovids). The structural difference between enamel and dentin is therefore an advantage for specialized occlusal surfaces, and tough plant food is sheared along enamel crests realized in most of the large herbivore groups discussed in this chapter. The proboscidean rasp with multiple transverse enamel crests is an extreme example for this utilization: however, in several perissodactyls only parts of the occlusal surface of a tooth form horizontal enamel bands (e.g., protoloph and metaloph in the upper molars of rhinoceroses) while the other parts are enhanced steep shearing surfaces (e.g., the ectoloph), and the combination of both is key to plant food reduction. The occurrence of a pronounced ectoloph in equids, tapiroids and rhinocerotoids reflects the fact that phylogeny limits the possibilities to modify the occlusal surface to adapt to a changing environment.

An exception of the evolutionary scenario from simple to complex enamel patterns is seen in the aquatic Cetartiodactyla. While also having dental origins in a simple cusped bunodont tooth pattern and a two-phased chewing cycle (e.g., Raoellidae), aquatic Cetartiodactyla developed an even more simple morphology of the teeth as an adaptation to the aquatic life style, where catching and swallowing prey supersedes mastication. In accordance with the process of adapting to a new habitat with a different environment, a change in feeding strategy occurred during the transition of terrestrial raoellids or raoellid-like cetartiodactyls to fully aquatic cetartiodactyls in the Middle Eocene. Toothed whales are active hunters, feeding on fish and octopus. Their derived archaeocete ancestors (e.g., Late Eocene *Dorudon*) retained only one phase of the chewing cycle and their cheek teeth are uniformly modified into cusp rows fully covered with enamel. Baleen whales modified their dentition into a filter feeding apparatus consisting of thin keratinized lamellae (baleen).

Diet related aspects

The rise of grasslands in the later Cenozoic triggered a number of dental adaptations in herbivorous mammals as described for the perissodactyls and cetartiodactyls discussed above. The groups of mammals discussed here are mainly herbivorous and can be broadly classified into two groups: browsers preferring leaves and grazers with a diet mostly consisting of grass. To differentiate between these two categories is important, because the mechanical properties, as well as the architecture and physical structure of grass and browse determine how the animals forage and masticate. In addition, the intake and procession rate of food is important for the maximization of energy production over shorter time scales (i.e., minutes, hours) which in turn is linked to different foraging strategies (Stephens & Krebs 1986). It is well known that grazers tend to have more robust mandibles and larger masseters compared to browsing species, because they have to comminute the relatively tough, highly fibrous plant food more thoroughly (Janis 1995, Fletcher et al. 2010). In general, plant food has low nutritive value until the cell contents of plant parts are released. Mastication is therefore an important process to break down the material to

make nutritives available. Chewing reduces the size of the particles, which in turn crucially reduces the digestive time in the intestines. It has been shown that Perissodactyla have stiffer mandibles than ruminant species (Zhou et al. 2019), which is linked to more heavy chewing of food in Perissodactyla before ingestion. This demands higher bite forces and greater stress resistance in perissodactyl mandibles, while ruminants shift comminution to a later state (rumination) with less mechanical effort. In fact, the smaller the particles are the larger is the surface area for the digestive enzymes to be effective. Digestion time is a significant constraint (Searle & Shipley 2008). Ruminants utilize regurgitation (i.e., re-exposure to saliva, chemical breakdown) and reprocessing (i.e., re-masticate) of food as an essential part of the digestion process, to regulate the rate of reduction of the particle size and hence the timing of the passage of the particles through the digestive system (Clauss et al. 2009, Fritz et al. 2009). Zhou et al. (2019) suggested that ruminants chew more “sloppily” regardless of the type of food, while hindgut fermenters chew more precisely. However, in modern ruminants feeding mainly on grasses, selenodonty (typical secondary occlusal surface) dominates with sharp enamel blades.

The large herbivore groups discussed in this chapter evolved their dentition from a simple cusped brachyodont tooth pattern by modifying cusp arrangements and facet patterns of the primary functional surface and, developing complex shear and rasp structures of the secondary functional surfaces over time. Those groups increased the ability to break down the fibrous plant food. In addition, large herbivores like equids and a large number of terrestrial cetartiodactyls adapted to the spreading of open range grasslands by developing hypsodont (high-crowned) teeth (MacFadden 2005). Hypsodont molars can tolerate intensive abrasion and their occlusal surfaces function constantly over a long period of time (Janis & Fortelius 1988, Damuth & Janis 2011, Koenigswald 2011). Two main factors that drive intensive wear and are known to trigger hypsodonty during evolution are phytoliths and grit (Williams & Kay 2001, Kaiser et al. 2013, Damuth & Janis 2014). Generally, grasses contain more phytoliths (hard opaline silicates) than browse (Hodson et al. 2005, Sanson et al. 2007). Because of a lower feeding height compared with browsing species, grazers tend to ingest more soil abrasives with plant matter, additionally increasing tooth wear (Janis & Fortelius 1988, Damuth & Janis 2011). It has been shown in rodents that continuously growing teeth require persistent stem cell presence at the base of the tooth (cervical loop) promoting tooth growth when the crown material is lost to wear by attrition (Jernvall & Thesleff 2012, Renvoisé & Michon 2014).

All ruminants with a diet mainly composed of grasses have high-crowned selenodont teeth (Williams & Kay 2001). During evolution, integration of the secondary functional surface (enamel crests and dentin basins) into the molar morphology for shearing tough fibrous plants in combination with a high molar crown to compensate for extensive tooth wear was crucial for herbivorous mammals to adapt to the changing environment with expanding grasslands. In correlation with the morphological change, a shift from a two-phased power stroke to a simple one-phased movement occurred several times in different groups independently. In all groups the tendency to increase the size of occlusal elements and functional surfaces is notable.

Acknowledgments

We thank Peter Göddertz, Georg Oleschinski, Olaf Dülfer, and Beate Mühlens for technical and organizational support (Bonn, Germany). We benefitted from the generosity of curators and colleagues around the world for providing material and discussion for this study: Elmar P. J. Heizmann, Reinhard Ziegler (Stuttgart, Germany), Gertrud Rößner (München, Germany), Ernest L. Lundelius (Austin, Texas, USA), Philipp D. Gingerich (Ann Arbor, Michigan, USA), Kenneth D. Rose, François Gould (Baltimore, Maryland, USA), David Bohaska (Washington D.C., USA), Marisa

Blume, Eric Milsom (Darmstadt, Germany), Elvira Brahm, Jörg Habersetzer, Michael Ackermann (Frankfurt, Germany), Loïc Costeur, Martin Schneider (Basel, Switzerland), Sally Shelton (Rapid City, South Dakota, USA), Judy Galkin (New York, USA), Rico Schellhorn (Bonn, Germany), Amy Henrici (Pittsburgh, USA). We are grateful to Philipp D. Gingerich for his advice and insights on the evolution of whales part of this chapter. We thank referees Christine M. Janis and Jessica M. Theodor for their input and advice that greatly improved the manuscript of the chapter.

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

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