Molar diversity and functional adaptations in Mesozoic mammals

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Introduction

The vast diversity of molars seen in therian mammals is derived from the apomorphic tribosphenic respectively pretribosphenic molar pattern of the Mesozoic mammalian precursors (Fig. 10.1). The tribosphenic pattern appeared in the fossil record in two different lineages of mammals (Luo et al. 2001), the Middle Jurassic australosphenidans (e.g., Ambondro, Flynn et al. 1999; Asfaltomylos, Martin & Rauhut 2005) and Late Jurassic boreosphenidans (Juramaia, Luo et al. 2011). The Southern Hemisphere australosphenidans are considered stem monotremes that have completely reduced their permanent teeth in extant taxa, whereas boreosphenidans comprise all other mammals (metatherians and eutherians) with a striking diversity of dentitions (Luo 2007). Mammals with tribosphenic molars (boreosphenidans or tribosphenidans) are characterized by a two-phased masticatory power stroke with piercing and cutting function during phase I and subsequent grinding and crushing function during newly developed phase II, in contrast to the single-phased power stroke in pretribosphenidans (only phase I present) (Hiiemäe & Kay 1972, 1973, Kay & Hiiemäe 1974, Hiiemäe 1976, 1978). The two-phased power stroke with crushing and grinding function allowed the exploitation of more diverse food sources and likely fostered the great evolutionary success of therian mammals in the Cenozoic. But even before the appearance of tribosphenic molars in mammal evolution, other Mesozoic mammal lineages had already developed remarkably diverse dentitions and dietary specializations, and a second chewing phase seems to have evolved independently in several groups, including docodontans, multituberculates, and gondwanatherians. The selective pressure to enhance the ingestion and mastication of new food sources triggered a number of attempts in mammalian evolutionary history

to add a crushing function to the plesiomorphic piercing and cutting action of the molariforms among early mammaliaform lineages, independently from the evolution of the tribosphenic molar. Vivid examples are the Jurassic and Early Cretaceous docodontans that evolved complex molars with crushing functions (e.g., Kermack et al. 1987, Butler 1988, Pfretzschner et al. 2005), suitable for processing diverse diet, and also with disparate molar shapes and very divergent morphologies among docodontan taxa, such as some specialized teeth for piscivory of Castorocauda (Ji et al. 2006). Another example is the Late Cretaceous Malagasy gondwanatherian Vintana with the first known euhypsodont molars in mammalian evolutionary history with complex enamel folding and enamel islets, suitable for processing tough plant materials (Krause et al. 2014, Schultz et al. 2014).

Within the Deutsche Forschungsgemeinschaft (DFG) Research Unit FOR 771 "Function and performance enhancement in the mammalian dentition - phylogenetic and ontogenetic impact on the masticatory apparatus" several projects were devoted to the functional analysis of Mesozoic mammaliaform molariforms and molars for a better understanding of the evolutionary history of mammalian mastication. 3D investigation techniques such as µCT combined with the Occlusal Fingerprint Analyser (OFA) software (Kullmer et al. 2009, 2020, this volume) that was developed within the FOR 771 made a virtual reconstruction of the masticatory cycle and a guantitative analysis of dental function and occlusal relationships possible. The following chapter provides a review of the morphological diversity of Mesozoic mammalian molariforms and molars and their various functional and dietary adaptations.

Triconodont molariforms – three cusps in a row for piercing and cutting

The most plesiomorphic mammaliaform molariform teeth are of the triconodont type with three primary cusps aligned in a mesio-distal row. This molariform type characterizes stem mammalian Morganucodonta and has been retained as a symplesiomorphic character by crown mammalian Eutriconodonta.

Plesiomorphically, central cusp A/a is the highest, whereas mesial cusp B/b and distal cusp C/c are lower (Fig. 10.2). This molariform type characterizes morganucodontans and "amphilestids" (a paraphyletic assemblage of dentally plesiomorphic eutriconodontans) among Eutriconodonta. In more derived Eutriconodonta, the height difference between the central and mesial respectively distal cusps is much smaller, or they are of equal height, as in the eutriconodontan family Triconodontidae. In derived Eutriconodonta, an elongation of the cutting edges occurs compared to the plesiomorphic condition in Morganucodonta with relatively shorter cutting edges. The

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Fig. 10.1. Evolution of the tribosphenic lower molar. **A**, schematic diagram with functional transformation. Yellow, cutting edges of trigonid; green, hypoflexid groove (mainly shearing); red, crushing and grinding area within the (incipient) talonid basin. **B**, lower tribosphenic molar with wear facets (hatched areas); numbers of wear facets after Crompton (1971).

dental function of the triconodont molariform dentition is mainly piercing and cutting with a predominantly orthal jaw movement. Smaller taxa such as the morganucodontans *Morganucodon* and *Megazostrodon* were insectivorous. Based on a microtextural analysis of molariforms, Gill et al. (2014) concluded that *Morganucodon* mainly fed on hard-shelled insects such as coleopterans. Larger taxa such as the eutriconodontan *Gobiconodon* were faunivorous (Jenkins & Schaff 1988), and *Repenomamus*, the largest known Mesozoic mammal, was carnivorous, either scavenging or predatory, or both. Hu et al. (2005) reported on a *Repenomamus* specimen with remains of a juvenile psittacosaur in the stomach region. The morphological diversity of the cusps and the tooth size disparity of the triconodont molars suggest that, even with the same triconodont pattern, there occurred functional differences, leading to a dietary differentiation.

The chewing stroke of *Morganucodon* had been reconstructed as predominantly orthal with a slight movement in anterior or posterior direction (Crompton & Jenkins 1968). Jäger et al. (2019), however, found evidence for a relatively high degree of freedom during the masticatory cycle according to the varying orientations of striations on molars of *Morganucodon*. Due to the lack of guiding structures, the molars of *Morganucodon* have no auto-occlusion (*sensu* Mellet 1985, Evans & Sanson 2006, based on the teeth of



Fig. 10.2. Dentition of *Morganucodon*. A, left upper and B, left lower tooth row in occlusal view; C, left upper tooth row in lingual view and D, left lower tooth row in buccal view (mirrored). From Jäger et al. (2019).

Carnivora). Further, it is now demonstrated by OFA analysis that the occlusal movements in Morganucodon can have chewing strokes in orthal, distal and mesial orientations, and are more versatile than only the orthal movement as previously emphasized (Jäger et al. 2019). Most individuals apparently developed a preferred chewing direction, which suggests precise muscular control of the jaw movements which had been inferred previously based on the matching wear facets of Morganucodon (Crompton & Parker 1978). According to the crown morphology, distribution of wear facets, and the OFA analysis (Jäger et al. 2019), Morganucodon and Megazostrodon had a single-phased chewing stroke. This study supported the notion that piercing and shear-cutting were the main functions during the masticatory cycle of Morganucodon and Megazostrodon. According to Jäger et al. (2019), the teeth of Morganucodon were fully functional for piercing, shear-cutting, and (to a lesser extent) shearing upon tooth eruption. The extensive wear facets on the teeth in later ontogenetic stages, which were emphasized in earlier wear facet analyses (Crompton & Jenkins 1968, Mills 1971, Crompton 1974), were a

Chapter 10. T. Martin et al.: Molar diversity and functional adaptations in Mesozoic mammals

byproduct of attrition of tooth-to-tooth contact. The tooth action related to these extensive facets represents only a part of total masticatory functions. Further, the extent of wear facets is dependent on ageing. It takes time for individuals of *Morganucodon* to develop extensive and fully matched wear facets (Crompton & Jenkins 1968, Butler & Clemens 2001), but other dental occlusal functions may start earlier than the formation of extensive wear facets.

Morganucodon and Megazostrodon differ in pattern of cusps opposition between the upper and lower molars. *Megazostrodon* is characterized by an embrasure occlusion with lower molar cusp a entering between two upper molars, and upper molar cusp A between two lower molars (Crompton & Jenkins 1968). For *Morganucodon*, a differing occlusal mode was described, with lower molar cusp a occluding between upper molar cusps B and A, and upper molar cusp A occluding between lower molar cusps a and c (one-to-one occlusion) (Crompton & Jenkins 1968, Crompton 1974). Jäger et al. (2019) corroborated the embrasure occlusion for *Megazostrodon* by their OFA analysis. However, in *Morganucodon* the occlusal relationships are



Fig. 10.3. OFA collision contacts of *Megazostrodon* and *Morganucodon* during the masticatory cycle. M1, M2, m2, m3 of *Megazostrodon* and P5, M1, m1, m2 of *Morganucodon*. **A**, initial contact with piercing of food items; **B**, all cusps are in contact, shear cutting occurs along the crests and shearing along the flanks; **C**, maximum intercuspation with pure shearing; lower molars mirrored. Not to scale, mesial to the left. Modified from Jäger et al. (2019).

more variable, by cusp differences among tooth positions and also by stages of wear facet development on the same teeth in opposition (Fig. 10.3). The occlusal pattern is less distinctive between *Morganucodon* and *Megazostrodon* than suggested by Mills (1971), who argued that these two taxa followed two different evolutionary pathways. According to Jäger at al. (2019), the occlusal differences between *Morganucodon* and *Megazostrodon* are not solely



Fig. 10.4. Orientation of upper and lower molars of *Morganucodon* and implications for occlusion. Without inclination of upper molars (**A**) a considerable translation or roll of the mandible would be necessary. The observed inclination of 18° (**B**) enables the lower molars to pass orthally along their antagonists. Not to scale. Modified from Jäger et al. (2019).

caused by molar position as had been suggested earlier (Mills 1971, Butler & Sigogneau-Russell 2016), but also by variation of cusp size and cusp position. Because variations in cusp size and shape require only minor genetic changes (Jernvall 2000, Salazar-Ciudad & Jernvall 2010, Kavanagh et al. 2007, Harjunmaa et al. 2014), a difference of their patterns at this magnitude may not be sufficient to justify the separation of the Morganucodon and Megazostrodon lineages as suggested by Mills (1971). Other Morganucodonta overlap between the two occlusal modes, such as the megazostrodontids Dinnetherium (Crompton & Luo 1993) and Brachyzostrodon that have a "Morganucodon-like" occlusion, the latter differing by strong apical wear (Hahn et al. 1991, Debuysschere et al. 2015). The occlusion of the morganucodontid Erythrotherium closely resembles that of Megazostrodon (Crompton 1974, Jenkins et al. 1983, Kielan-Jaworowska et al. 2004), whereas Bridetherium has a unique wear pattern, although the molariforms are morphologically very close to those of Morganucodon (Clemens 2011). Bhullar et al. (2019) emphasized the importance of roll (rotation of the hemimandible around the long [horizontal] axis of the jaw) for the evolution of precise occlusion in mammals. They observed substantial roll of the hemimandible during the masticatory cycle of extant Monodelphis and suggested a "considerable roll" also for Morganucodon after the orientation of wear facets. However, the µCT observation of intact teeth in the maxilla demonstrates an inclination of the upper molars (Fig. 10.3), and the OFA analysis by Jäger et al. (2019) shows that the orientation angle of upper tooth wear facets is strongly influenced by this inclination. Therefore it may not be possible to infer a roll of the lower teeth based on the angle of wear facets on the upper molars (e.g., Crompton & Luo 1993). We interpret that it is not possible to differentiate between wear facets caused by transversal movements (Fig. 10.4)

or by roll; the role of the latter during the masticatory cycle of *Morganucodon* therefore remains ambiguous.

Within Eutriconodonta, the molars of Triconodontidae are characterized by cusps of equal size (Fig. 10.5). In earlier studies that investigated occlusal relationships in Trioracodon it was assumed that the main cusp a of the lower molars occluded in between cusps B and A of the upper antagonists, whereas the upper main cusp A occluded between cups a and c of the lower antagonists (Mills 1971, Crompton 1974) - an occlusal pattern that corresponds to that of Morganucodon. The OFA analysis of the holotype specimen of Priacodon fruitaensis revealed that the main cusps of upper and lower molars occlude better, if fitting in between two antagonists, thus that its occlusion is different from that of Morganucodon (Jäger et al. 2020). Because the dentition of Priacodon is very similar to that of other stem Triconodontidae, it can be assumed that this is the general occlusal pattern for all Eutriconodonta. It was previously proposed that there is a considerable rolling of the mandible during the masticatory cycle, on the basis of more obligue orientation of wear facets on the upper molars than the lower molars of triconodontids (Crompton & Luo 1993). We offer a different interpretation - we note that there is an in situ inclination of the upper molars within the maxilla in eutriconodontans as in Morganucodon (Fig. 10.4) which is hitherto unnoticed. Taking this inclination of the upper molars into account, the OFA analysis shows a roll rate of the active hemimandible of ~10° during the power stroke of Priacodon (Jäger et al. 2020), which is less than previously suggested for eutriconodontans, but already more than the roll rate of the extant marsupial Monodelphis (Bhullar et al. 2019). We hypothesize that the roll in Priacodon and eutriconodontans was a passive process caused by the inclination of the upper molars (Jäger et al. 2020). The equal height of the molar cusps requires a

Chapter 10. T. Martin et al.: Molar diversity and functional adaptations in Mesozoic mammals



Fig. 10.5. *Priacodon* upper and lower molars with corresponding wear facets. Right M3/m3 of *P. fruitaensis*. A, lingual aspect and (B) occlusal aspect of M3. C, buccal aspect and (D) occlusal aspect of m3. M3 is mirrored. Modified from Jäger et al. (2020).



Fig. 10.6. Occlusal pattern of *Priacodon*. Right dentition of *P. fruitaensis* with zig-zag pattern, in the middle of the power stroke. Contact areas indicated by colors. Modified from Jäger et al. (2020).



Fig. 10.7. Upper and lower molar of *Kuehneotherium*. Right upper M4 (mirrored) (A, B, C) and left lower m3 (D, E, F) of *K. praecursoris*. A, D, occlusal aspect; B, F, buccal aspect; C, E, lingual aspect. Modified from Plogschties (2020).

precise orientation of upper and lower teeth, because all cusps come into contact in short succession at the beginning of the power stroke. The function of the triconodontid molars can be compared to pinking shears. The molars form a mesio-distally oriented elongated cutting edge with linguo-buccal extensions (zig-zag pattern) (Fig. 10.6). This pattern of triconodontid molars combines the key characters of carnivorous extant mammals (mesio-distal cutting edges) and insectivorous mammals (prominent development of more linguo-buccally oriented cutting edges). From this we infer that triconodontid molars were capable of both carnivorous and insectivorous diets. The sharp cusps of the lower molars are self-sharpening when they occlude into the narrow valleys between the upper molar cusps. In comparison with the carnassials of carnivorans and creodontans, the molars of Triconodontidae are less specialized for cutting meat, and show instead a more generalized function for faunivorous diet (Jäger et al. 2020).

The general shape of the molars of Triconodontidae changed only little during evolution from the Late Jurassic to the Late Cretaceous. The number of molars was augmented, their crown height increased, and cusps D/d became larger which indicates a trend to maximize the cutting edges. The shape of the molars, however, is remarkably homogeneous and changed hardly through time. Apparently the homogenous *bauplan* and precise occlusion of the molars was subject to fitting constraints that prevented major changes such as the development of new cups (Jäger et al. 2020).

"Symmetrodontan" molars – reversed triangle pattern with increased shearing function

The symmetrodont molar pattern represents a more advanced evolutionary grade than the triconodont pattern, and is derived from the triconodont pattern. But Mesozoic mammals with symmetrodont molars do not designate a monophyletic clade. "Symmetrodontan" molars are characterized by angulation of the molar main cusps (A/a, B/b, C/c), and a very small cusp D/d, giving the teeth a symmetric appearance. Upper and lower molars are arranged as alternating reversed triangles, with cusp A in lingual position in the uppers and cusp a in buccal position in the lowers (Fig. 10.7). The "symmetrodontan" chewing cycle was characterized by embrasure occlusion, in which one upper molar occluded between two lowers (two-to-one occlusion, Fig. 10.8). Traditionally, two types



Fig. 10.8. Comparison of occlusal patterns of symmetrodont molars. A, *Kuehneotherium praecursoris*; B, *Maotherium sinense*; C, *Spalacolestes cretulablatta*. Stage 1: beginning of the power stroke; stage 2: closure of the intercuspid spaces; stage 3: end of power stoke, maximum intercuspation. Not to scale. Modified after Plogschties (2020).



Fig. 10.9. Total collision areas during the masticatory cycle of "symmetrodontans". A, Kuehneotherium praecursoris; B, Maotherium sinense; C, Spalacolestes cretulablatta after the OFA analysis with roll (wr; blue line) and without roll (wor; yellow line) of the mandible. Modified from Plogschties (2020).

of symmetrodont molars have been distinguished, the obtuse angled molars of kuehneotheriids and tinodontids and the acute angled molars of spalacotheriids. In obtuse angled "symmetrodontans", the trigonid angle of lower molars is above 90° (Li & Luo 2006) (80° according to Averianov et al. 2013), whereas it is less in "acute angled symmetrodontans". The best-studied obtuse angled "symmetrodontan" is the early Jurassic *Kuehneotherium*, of which thousands of isolated teeth have been recovered from Welsh fissure fillings (Kermack et al. 1968, Gill 2004, Gill

et al. 2014). Plogschties (2020) performed OFA analyses for *Kuehneotherium* with a roll of the hemimandible and without a roll; both chewing cycles are single-phased and differ only slightly (Fig. 10.9). Based on a finite element analysis of the mandible and microtexture analysis of the molars, Gill et al. (2014) concluded that *Kuehneotherium* fed on softer insects (such as lepidopterans) than *Morganucodon* which is also supported by its more slender jaw morphology. Conith et al. (2016) used simplified models of *Morganucodon* and *Kuehneotherium* molar tooth rows



Fig. 10.10. Cheek teeth of the tenrecid *Setifer setosus*. A, left P4-M3 (ZMB MAM 44292); B, right p4-m3 (ZMB MAM 44293) in occlusal view. Abbreviations: med, metaconid; MSS, mestostyl; PA, paracone; PAC, paracrista; pad, paraconid; PPAC, postparacrista; prd, protoconid; ST, stylocone. Modified from Schwermann (2014).

for physical biting experiments into soft and hard gels as proxies for soft- and hard-shelled insect prey. They found the triangulated molars of *Kuehneotherium* to be more suited to processing soft foods and the blade-like molars of *Morganucodon* to be more suited to processing hard foods, because the blade-like *Morganucodon* cusps penetrated through the hard food items and propagated cracks more easily. More importantly, the triangulated, more complex *Kuehneotherium* molars were found to inflict more damage to the prey. Accordingly, Conith et al. (2016) concluded that the changes from the triconodont to the symmetrodont molar pattern were driven primarily by selection for maximizing damage, and secondarily for maximizing biomechanical efficiency for food property.

Somewhat intermediate between kuehneotheriids and spalacotheriids regarding molar cusp angulation are the Early Cretaceous zhangheotheriids. Plogschties & Martin (2017) and Plogschties (2020) studied the occlusion and masticatory cycles of the zhangheotheriid Maotherium sinense and the spalacotheriid Spalacolestes cretulablatta by OFA. The chewing cycles of both taxa are single-phased, and the movement of the mandible is mainly orthal with a medial shift that allowed for a deep intercuspation. The orientation of the striations on the wear facets is more variable in *M. sinense* than in *S. cretulablatta*, indicating a less precise guidance of the molars in M. sinense. According to the OFA-analysis with one upper and two lower molars, the maximum contact area during the chewing cycle is almost two times larger for S. cretulablatta than for *M. sinense* (Fig. 10.9). At the beginning of the chewing cycle, the prey was fixed, pierced, and puncture-crushed by the main cusps of the upper and lower molars. Subsequently, M. sinense mainly stretched and sheared the food particles between the blunt crests and consecutively between the molar flanks. In S. cretulablatta (and spalacotheriids in general), the newly developed sharp crests that worked like a cigar cutter with two concave blades, allowed for an increased shear-cutting function. The prey was first cut with the molar crests and then sheared between the molar flanks (prevallid/postvallum and postvallid/prevallum). The second shearing process of zhangheotheriids, in which the indentation of the lower molar main cusps (protoconid-paraconid and protoconid-metaconid) and the lingual cingulum of the upper molars were involved, was replaced by a more efficient prevallum/prevallid and postvallum/postvallid crushing and shearing complex, a more extensive tooth-to-tooth contact and a more accurate guidance of the teeth in spalacotheriids. The development of circumferential cingulids provided additional guidance and crushing function against the paracone (Plogschties 2020).

In spalacotheriids ("acute angled symmetrodontans"), the angles of the upper molar primary trigon and of the lower molar trigonid are much smaller than in the other "symmetrodontans". Spalacotheriids have a higher molar count (five or more) than the other "symmetrodontans", and their molars are more strongly shortened mesiodistally and widened linguo-buccally (zalambdodonty). The increase in number of molars and the acute angulation of the primary trigon and trigonid are interpreted as a strong insectivorous specialization ("hyperinsectivory"), as seen in extant insectivorous tenrecids (Afrosoricida).

A functional analogue for spalacotheriid molars are the molars of certain extant tenrecs such as *Setifer* or *Tenrec* which have been studied by Schwermann (2014). Tenrecs are placental mammals (afrotherians) with zalambdodont molars that have secondarily lost the protocone and other cusps on the uppers, and reduced the talonid to a single cusp at the lowers (Fig. 10.10); this way the molars (especially the uppers) resemble the pretribosphenic morphology of cladotherians such as dryolestidans (Asher & Sánchez-Villagra 2005) but also of trechnotherian spalacotheriids (the term pretribosphenic is here used for molars with acute angulation of main cusps and lacking a protocone). In upper molars of *Setifer* the trigon comprises the lingually placed paracone and the buccally situated stylocone and meta-



Fig. 10.11. Pretribosphenic and tribosphenic molar structure terminology. Upper (left) and lower (right) molars of **A**, pretribosphenic *Nanolestes*, **B**, of a generalized tribosphenid, **C**, of *Setifer*. Not to scale. Modified from Schwermann (2014).

style, with the mesial paracrista and distal postparacrista as connecting shear-cutting edges (Fig. 10.11). Protocone and metacone are fully reduced, and the tooth crown is shortened mesio-lingually and widened linguo-buccally, closely resembling the shape of spalacotheriid upper molars. The lower molars are likewise mesio-distally short and linguobuccally wide and comprise the trigonid and a small talonid with a lingually placed single cusp (entoconid according to Thenius 1989). Schwermann (2014) analyzed the chewing stroke of *Setifer* by OFA and found a single-phased power stroke that ends when the paracone occludes with the talonid (centric occlusion) (Fig. 10.12). This is a general difference to pretribosphenic molars, which lack structures for a centric occlusion (*sensu* Schwermann 2014). The curved preparacrista and protocristid, respectively post-paracrista and paracristid glide past each other and the space between is narrowed like in a cigar cutter while the food items are shear-cut. The second phase of the power stroke which is characteristic for most boreosphenidans is not present in *Setifer* and other tenrecs.



Fig. 10.12. Contact areas during the masticatory cycles of pretribosphenic and tribosphenic molars. A, *Nanolestes* (pretribosphenic); B, *Setifer* (tribosphenic [zalambdodont]); C, *Didelphis* (tribosphenic). Modified from Schwermann (2014). Abbreviations: fac, facet; praecd, precingulid.



Fig. 10.13. Wear striation patterns on 3D surface model of lower molar of the dryolestid *Dryolestes leiriensis*. Wear in the hypoflexid groove and striations on facet 1 are caused by the paracrista of the upper antagonist. Molar main cusps with apical wear. The angle (\mathfrak{F}) between the hypoflexid groove (h) and occlusal plane (op) differs slightly from the angle (\mathfrak{F}) between the striations (s) and the occlusal plane (op). Directions of striations and inclination of the hypoflexid groove are traced by vectors (vect). Modified from Schultz & Martin (2011).

Pretribosphenic molars

The next functional step in mammalian molar evolution is represented by the pretribosphenic (sensu lato for acute angled molars without protocone and talonid basin) molars of dryolestidans (Cladotheria). The dryolestidan upper molar consists of the "primary trigon" which is not homologous to the trigon of tribosphenidans, because it lacks a protocone (Fig. 10.11A) which is a neomorphic cusp of tribosphenic molars. The "primary trigon" comprises paracone (cusp A), metacone (cusp C), and stylocone (cusp B) which are connected via the mesial paracrista and the distal metacrista. The parastyle (cusp E) is prominent and bulging, the metastyle (cusp D) generally less prominent, and on the buccal portion of the metacrista a cusp "C" of variable size is present which is a neomorph according to Davis (2011: 233). The lower molar trigonid consists of protoconid (cusp a), paraconid (cusp b), and metaconid (cusp c) and is homologous to that of boreosphenidans (Figs. 11A, 13). The mesial paracristid connects protoconid and metaconid, and the distal protocristid connects protoconid and metaconid (Martin 1999). At the mesial side, mesiolingual cuspule e and mesiobuccal cuspule f are variably present. Dryolestidans have a single-cusped talonid (cusp d, homologous either to hypoconulid or hypoconid, for discussion see Davis 2011) and a welldeveloped hypoflexid that is inclined in buccal direction. Like the dentition of "symmetrodontans", the dryolestidan dentition is characterized by an embrasure occlusion with the principal cusps of the upper and lower molars arranged in reversed triangles (Schultz & Martin 2011). The shearing function occurs on two almost vertically oriented shearing planes with sharp crests, on the mesial and distal sides of the triangles (Crompton 1971). This occlusal type has been described as embrasure shearing (Crompton et al. 1994). Dryolestidans developed new shearing surfaces which are

not present in "symmetrodontans". These occur along the hypoflexid groove of the unicuspid talonid in the lower molars, and in the upper molars on the mesial side of the paracone (Schultz & Martin 2011, 2014). During mastication, the paracone travels along the hypoflexid groove where the main shearing occurs; due to the low inclination of the guiding groove, there is also a certain crushing component. The power stroke ends when the paracone reaches the buccal end of the hypoflexid and thus, without a point of centric occlusion. According to Schultz & Martin (2011), the food particles are first cut at the crests of facets 1 and 2 and then sheared and transported in cervical direction into the hypoflexid guiding groove. The inclination of the shearing surface and the change of transport direction crush the particles when they touch the upper part of the hypoflexid groove (Fig. 10.13). Schultz & Martin (2011, 2014) stated that only shearing and no grinding occurs when the paracone travels along the hypoflexid groove, because the chewing forces do not change their direction during the downward movement in the groove. The chewing stroke in dryolestidans is single-phased (only phase I present). The OFA analysis of Dryolestes revealed that the power stroke starts with a fast increase of contact area between upper and lower molars reaching maximum size when the teeth occlude deepest into the interdental spaces of the lowers, ending soon after maximal intercuspation and without centric occlusion (Fig. 10.14). In the state of maximal intercuspation the steep shearing surfaces of primary trigon and trigonid are in full contact. After maximal intercuspation, the recovery stroke begins with lowering the lower jaw and all contact is lost at once (Schultz & Martin 2011, 2014).

In comparison, in the pretribosphenic stem zatherian Nanolestes with elongated single-cusped talonid (Martin



Fig. 10.14. Comparison of collisional molar contacts of Jurassic *Dryolestes* and extant *Monodelphis* after OFA detection. Pretribosphenic *Dryolestes* with single-phased power stroke ending with maximum intercuspation. Power stroke of tribosphenic *Monodelphis* is two-phased with phase II occurring after centric occlusion when the protocone moves out of the talonid basin. Abbreviations: A, entrance phase; B, maximum intercuspation; C, centric occlusion; D, phase II occlusion. Modified from Schultz & Martin (2014).



Fig. 10.15. Contact points and inferred bite forces during mastication of *Nanolestes*. Bite forces are identical in the (**A**) first and (**B**) second part of the occlusal movement. In the first part the protoconid and parastylar groove are in contact, in the second part the hypoflexid groove slides across the paracone. Abbreviations: F1, deflection force; F2, pressing force; FR, resulting bite force; hfd, hypoflexid; prd, protoconid; PA, paracone; PASg, parastylar groove. Not to scale. Modified from Schwermann (2014).

2002) (Fig. 10.11A), the parastylar groove of the upper molars is the guiding structure for the protoconid during the first part of phase I (Schwermann 2014, Schwermann et al. 2014) (Fig. 10.12A). In the second part of phase I the guiding of the chewing motion is performed by the hypoflexid groove in which the paracone travels along, just like in dryolestidans. This second part of phase I shows a considerable increase in contact area in the OFA simulation (Fig. 10.12A) which is reflected in extensive wear in the hypoflexid groove (Fig. 10.15B). The orthal bite force is differentiated into partial forces, which press the teeth vertically against each other and deflect the lower jaw. Due to the steep orientation of the parastylar and hypoflexid grooves, the deflection force is higher than the pressing force, resulting in a more powerful deflection of the lower jaw than occlusal biting force between the antagonistic molars (Fig. 10.15). Like in the other pretribosphenidans *sensu lato*, in *Nanolestes* phase I ends without a definitive point of centric occlusion, and a phase II is not present (Fig. 10.12A).

Due to their thin enamel, the dryolestidan molars exhibit a characteristic wear pattern with extensive exposure of dentin along the lower molar shearing edges, paracristid and protocristid (Schultz & Martin 2011, 2014). The striae on the facets are more steeply inclined near the protoconid tip and the protocristid edge (about 45°) than the more cervical striae (about 35°) (Fig. 10.13). The lower dentition is raised at about 45° at the beginning of the dryolestidan chewing cycle, and the first occlusal contact occurs between the v-shaped protocristid and crescent antagonistic paracrista (Schultz & Martin 2014). Protocristid and paracrista function like the blades of a cigar cutter when they pass each other and perform a shear-cutting function. According to Schultz & Martin (2014), the term "shear-cutting" is more appropriate than "cutting" for the function performed along the edges, because cutting is either defined by two blades that meet along their entire length or by a single blade that is pressed vertically against a horizontal surface (Lucas 1979, Sibbing 1991). The contact between paracristid and metacrista occurs slightly later.

Transition from pretribosphenic to tribosphenic pattern – towards crushing and grinding

During the transition from the pretribosphenic to the tribosphenic condition a fundamental morphological and functional transformation occurred (Crompton 1971, Davis 2011, Schultz & Martin 2014, Grossnickle 2020). In the upper molars, the neomorphic protocone developed in a lingual position, and the talonid basin formed at the distal side of the lower molars, surrounded by the three talonid cusps hypoconulid, hypoconid, and entoconid (Fig. 10.1). The hypoflexid groove lost its function as sole shearing surface and became part of the buccal rim of the talonid basin. The power stroke (and the contact phase) were prolonged by the addition of a second phase that occurred after occlusion of the protocone into the talonid basin (centric occlusion); Kay & Hiiemäe (1974) suggested that primitive tribosphenic taxa only had one phase, and that phase II convergently evolved in multiple therian lineages. Phase I is an upward, anterior, and medial movement of the lower molars, terminating in centric occlusion (here equivalent to maximum intercuspation) followed by phase II with an anterior, medial, and downward movement, followed by the recovery stroke (Hiiemäe & Crompton 1971, Hiiemäe 1976, 1978, Schultz & Martin 2014) (Fig. 10.14). Functionally, the development of a second phase to the chewing cycle added crushing and grinding function to the shear cutting function of phase I, enabling boreosphenidans to exploit a much wider range of food. An OFA study of the molars of extant Monodelphis documented phase II (Fig. 10.16) by detecting collisional contacts on the buccal wall within the talonid basin which occurred after a directional change in the chewing path, which is in accordance with the striations found on the surface (Schultz & Martin 2014; see also Hielscher et al. 2015 for bats). The additional collision contacts of the protocone and the talonid basin during phase II provide an increased potential for food reduction. Although it had been argued that the occlusal forces are much lower during phase II (Hiiemäe 1984, Hylander et al. 1987) compared to phase I (Wall et al. 2006), the observed small contact areas of phase II indicate a more versatile way of food comminution (Schultz & Martin 2014) which is dominated by food-to-tooth contacts and abrasive wear (Schwermann 2014). Although phase II added only a moderate increase of contact area to the chewing cycle in the tribosphenic pattern as exemplified by Monodelphis (Fig. 10.16), it was a crucial precondition for the modifications of transverse jaw movement in more derived boreosphenidans. According to Spoutil et al. (2010) the (functionally) basic pattern of tribosphenic molars is retained almost unmodified in many insectivorous mammals such as afrosoricidans, macroscelideans, and lipotyphlans. A number of studies demonstrated that the crushing function is important for the comminution of hard insect exoskeletons (Fraenkel & Rudall 1940; Freeman 1979, 1981; Moore & Sanson 1995; Evans & Sanson 1998, 2005a, b). The OFA analysis of the pretribosphenic dryolestidan molars shows mainly piercing and cutting function, with lesser ability to breakdown insect exoskeletons than found for tribosphenic molars (Schultz & Martin 2014). The tribosphenic molars with crushing function squeezed out the soft tissue of the insect prey in addition to sectioning the insect bodies into pieces, and thus allowed a more efficient extraction of the nutritious substances resulting in a higher energy gain in the digestive system. Schwermann (2014) conducted comparative feeding experiments with the didelphid Monodelphis and the scandentian Tupaia with molars resembling the tribosphenic groundplan on one side, and the tenrecid Setifer with zalambdodont molars (Fig. 10.10) resembling the dryolestidan dentition (reduced protocone and talonid basin) on the other. By analyzing feces Schwermann (2014) found some evidence that the taxa with tribosphenic molars broke the chitinous exoskeleton of mealworms into smaller pieces than Setifer. If corroborated, this would support the hypothesis that tribosphenic molars perform a better food breakup in comparison to zalambdodont or pretribosphenic molars. Throughout most of the Cretaceous, tribosphenids remained remarkably conservative in molar morphology and stayed mostly insectivorous (Kielan-Jaworowska et al. 2004, Martin 2018). In the latest Cretaceous, several lineages developed carnivorous dental adaptations such as some large stagodontids (body sizes up to 2000 g, Gordon 2003) and Nanocuris (Wilson & Riedel 2010) among metatherians, and the eutherian Altacreodus (Lillegraven 1969). The metatherian Didelphodon has large and bulbous third upper and lower premolars that indicate a durophagous specialization (Clemens 1968, Wilson et al.



Fig. 10.16. Collision areas during the power stroke of pretribosphenic (*Dryolestes*) and tribosphenic (*Monodelphis*) molars as detected by OFA analysis. Not to scale. From Schultz & Martin 2014.

2016, Cohen 2017). Others evolved adaptations towards omnivory/herbivory, such as the metatherian *Glasbius* (Wilson 2013) and the eutherian taeniodont *Schowalteria* (Fox & Naylor 2003), indicating parallel radiations and ecomorphological diversifications in metatherians and eutherians in the Late Cretaceous. This also probably occurred in parallel with ecological diversifications of other mammal groups (Grossnickle et al. 2019), like the meridiolestidan *Reigitherium* (Harper et al. 2018), cimolodontan multituberculates (Wilson et al. 2012; Grossnickle & Polly 2013), and gondwanatherians (Krause et al. 2014). Therians were likely diversifying ecologically prior to the K-Pg boundary (Grossnickle & Newham 2016), and their dietary flexibility was fostered by the phase II occlusion which allowed an increase of the crushing and grinding function.

"Pseudotribosphenic" molars – convergent evolution of crushing and grinding structures

Molars with protocone-like and talonid-like structures ("pseudotribosphenic" molars) developed several times independently in mammalian evolutionary history (see Martin 2018 and references therein). The most prominent example are the Australosphenida of the Southern Hemisphere. Discovery of the first australosphenidan teeth (Rich et al. 1997, 1999; Flynn et al. 1999) led to the hypothesis of a dual origin of tribosphenic molars in the Northern and Southern Hemispheres (Luo et al. 2001). Australosphenidans such as Asfaltomylos and Hesnoferus from the Middle to Late Jurassic Cañadon Asfalto Formation of Argentina possess a fully basined and distally situated talonid or "pseudotalonid" structure in the lower molars (Rauhut et al. 2002, Martin & Rauhut 2005, Rougier et al. 2007). However, talonid wear facets occur only on the top of the talonid rim (apical wear) and not within the basin as in tribosphenic molars of Northern Hemisphere boreosphenidans (Fig. 10.17). Upper molars of australosphenidans

have not been published yet, but an undescribed isolated upper molar of *Hesnoferus* possesses a linguo-buccally compressed and hook-like protocone or "pseudoprotocone" (G. W. Rougier, personal communication). Martin & Rauhut (2005) hypothesized that the tip of the protocone of *Asfaltomylos* occluded on the buccal side of the talonid and not into the talonid basin. If so, the crushing function occurred between the lingual flank of the protocone and the apices of the talonid cusps, respectively the talonid rim. According to Martin & Rauhut (2005), the same apical wear pattern is evident on the mandibular fragment of the australosphenidan *Ambondro* from the Middle Jurassic of Madagascar (Flynn et al. 1999).

Well-developed basined talonids are also present in the Australian australosphenidans *Ausktribosphenos* and *Bishops* (Rich et al. 1999, 2001a). Like in the South American australosphenidans and Malagasy *Ambondro*, the wear pattern of *Ausktribosphenos* is restricted to the



Fig. 10.17. Lower molars of *Asfaltomylos patagonicus*. SEM micrographs (A–C) and schematic drawing (D) of lower m2 and m3 with apical wear (white arrows) on the talonid rim in **A**, lingual, **B**, buccal, **C**,**D**, occlusal views. Abbreviations: hyd, hypoconid; hyld, hypoconulid; med, metaconid; pad, paraconid; prd, protoconid. Modified from Martin & Rauhut (2005).



Fig. 10.18. Terminology of docodontan (*Haldanodon*) molar morphology and occlusion of cusp Y into the "pseudotalonid basin". **A**, left upper molariform DP4; **B**, left lower molar; **C**,**D**, left upper molariform and left lower molar in centric occlusion with designation of cusps (**C**) and basins (**D**). Not to scale. Modified from Brinkkötter (2018).

talonid rim and no wear facets occur within the talonid basin (Martin & Rauhut 2005). Upper dentitions are not known for Ausktribosphenos and Bishops, but the lower molar wear pattern of Ausktribosphenos suggests a similar occlusal pattern like in Ambondro and the South American taxa. The Early Cretaceous monotreme Steropodon from Australia (Archer et al. 1985) is represented by a mandible fragment with three molars. The molars have a dilambdodont pattern, formed by trigonid and talonid. Like in the australosphenidans, the talonid of Steropodon exhibits wear only on the apices. A similar molar pattern occurs in the Early Cretaceous (Aptian) monotreme Teinolophos from Victoria (Rich et al. 1999, 2001b, 2016). Upper and lower dentitions are known for the late Early Cretaceous (Albian) Australian monotreme Kollikodon, the assumed sister taxon of Monotremata (Flannery et al. 1995, Pian et al. 2016). Kollikodon has polybunodont molars with strikingly thick enamel adapted to a durophagous diet with a crushing function of the molars.

Shuotherium and Pseudotribos from the Northern Hemisphere appear in cladistic analyses as members of Australosphenida (e.g., Luo et al. 2007). Both are characterized by talonid basins that sit at the mesial end of the lower molars (Chow & Rich 1982, Luo et al. 2007). Wang et al. (1998) reported an isolated upper molar of *Shuotherium* with a "pseudoprotocone" and wear facets 5' and 6' (analogous to Crompton's 1971 scheme) at the mesiolingual and distolingual flanks of the "pseudoprotocone". More recently, Luo et al. (2007) reported a partial skeleton of the shuotheriid *Pseudotribos* from the Middle Jurassic of China with mesially placed "pseudotalonids". The "pseudoprotocones" are preserved in occlusion with the "pseudotalonids" and demonstrate a pestle-to-mortar crushing function which differs from that of the Southern Hemisphere Australosphenida and is similar to that of Boreosphenida.

Docodonta form a major clade of stem mammals (mammaliaforms) that evolved molars with complex shearing, crushing and grinding function (Luo & Martin 2007) which have been studied in comparison to tribosphenic molars (Gingerich 1973, Butler 1988). The origin of the docodontan molar is still under dispute, and there is no consensus on the homologization of cusps (Luo & Martin 2007). The upper molars of docodontans are linguo-buccally widened with a mesiolingual cusp X and a mesiodistal cusp Y, of which the distolingual cusp Y has been homologized with the protocone and mesiolingual cusp X with the hypocone in the original description of *Simpsonodon* (Kermack et al.



Fig. 10.19. Contact areas during the two-phased power stroke of *Haldanodon* as detected by OFA analysis. Modified after Brinkkötter (2018).

1987: fig. 45) (Fig. 10.18). The lower docodontan molars have a mesial basin demarcated by cusps a-b-g that was named "pseudotalonid basin" by Kermack et al. (1987: 34). This term originally had been coined for the lower molars of Shuotherium (Chow and Rich 1982), and Kermack et al. (1987) were the first to apply it to docodontan molars (Simpsonodon). They designated distolingual cusp Y as "pseudoprotocone" by occlusal and functional reasons, because it bites into the "pseudotalonid basin" formed by cusps a-b-g in Simpsonodon. However, most subsequent authors (see Brinkkötter 2018 for discussion and references) considered larger mesiodistal cusp X to be the "pseudoprotocone" because it is in a similar mesiolingual position as the protocone of tribosphenic molars. Because cusp X does not occlude into the "pseudotalonid basin" formed by cusps a-b-g, it does not appear functionally equivalent to the protocone of tribosphenic molars. The different naming of the mesiolingual and mesiodistal cusps and varying morphology of molars in different docodontan taxa (e.g., presence or absence of crest b-g on lower molars, see Fig. 10.18B) caused confusion and major discussions on the identity of the docodontan "pseudoprotocone" and "pseudotalonid basin" (Luo & Martin 2007, Wang & Li 2016, Brinkkötter 2018). According to Brinkkötter's (2018) occlusal analysis of the Late Jurassic docodontan Haldanodon, smaller cusp Y is the cusp that actually occludes into the basin formed by cusps a-b-g ("pseudotalonid basin") of the lower molars; therefore cusp Y is considered the "pseudoprotocone" here. An OFA analysis and virtual reconstruction of the mastication cycle of Haldanodon (Brinkkötter et al. 2014, 2017, Brinkkötter 2018) basically show two phases in the power stroke (Fig. 10.19). In phase I the lower molars move upwards from buccal to lingual into centric occlusion and occlude in between the upper molars (Fig. 10.20). Phase II most probably is a downward movement in palinal (backward) direction, but a separate upward movement in proal (forward) direction cannot be excluded with certainty. During phase I the lingual flanks of the upper molar main cusps and the buccal flanks of the lower molar main cusps perform a shear-cutting function, and cusp b of the lower molar occludes into the "pseudotrigon basin" of the upper antagonistic molar performing a crushing function. Phase I ends when the lingual cusp Y of the upper molar slides into the "pseudotalonid basin" and grinding is performed. When the mesial border of the talonid basin is obliterated by wear, cusp Y glides over the basin rim, so that lower molar cusp b contacts the "pseudotrigon basin" performing additional grinding function. Most interestingly, according to Brinkkötter (2018) in Haldanodon the majority of crushing and grinding occurs within the large "pseudotrigon basin" of the upper molars and not in the "pseudotalonid basin" of the lowers. During the subsequent palinal downward movement of phase II, the lower molars perform a shear-grinding function when the distal crests move along the mesial flank of cusp X of the upper molars. Brinkkötter (2018) assumed a similar chewing stroke also for other docodontans, and she concluded that crushing and grinding were much more important in docodontan chewing than expected before.

Schultz et al. (2017) re-studied the mandible and dentition of *Docodon victor* and performed an OFA analysis of the chewing cycle which suggests that the trajectory of the lower molars has a continuous palinal (disto-lingual) component starting from the early contact during phase I and proceeding throughout phase II after centric occlusion. This slight difference from *Haldanodon*, in which phase I of the power stroke is described as an upward movement strictly from buccal to lingual with a palinal component only at the very end (Brinkkötter 2018), may be related to minor occlusal structural differences.

Differences in docodontan molar morphology (Luo & Martin 2007) suggest a possible diversification of dietary preferences apart from the insectivory that has been suggested for *Haldanodon* and *Docodon*. Pfretzschner et al. (2005) conducted an analogous chewing experiment based on epoxy casts of upper and lower molars and suggested a mainly omnivorous diet for the Late Jurassic docodontan *Dsungarodon* from China. The same dietary adaptation is assumed for *Simpsonodon*, which shows an extensive grinding area at the distal end of the lower molars. Although these docodontan molars performed in a similar efficient way as tribosphenic molars, their thin enamel made them



Fig. 10.20. Comparison of upper and lower molars of *Didelphis* and of *Haldanodon* in centric occlusion. **A**, M1, m1 and m2 of *Didelphis* and **B**, M2, m2 and m3 of *Haldanodon*. Not to scale. From Brinkkötter (2018).

much more prone to abrasion and therewith loss of efficiency; tribosphenic molars likely provided a longer-lasting functionality during lifetime (Brinkkötter et al. 2017, Brinkkötter 2018). The large Middle Jurassic docodontan *Itatodon* from Siberia (interpreted as a shuotheriid by Wang & Li 2016) has linguo-buccally compressed lower molars with well-developed cutting edges (Lopatin & Averianov 2005) that suggest a faunivorous or even carnivorous adaptation. The first and second lower molars (uppers are not preserved) of the semi-aquatic *Castorocauda lutrasimilis* from the Middle Jurassic of Liaoning Province (China) have linguo-buccally compressed tooth crowns, each with five cusps in straight alignment, three of which are slightly curved backwards. They are convergently similar to molars of Eocene whales or extant seals, and are interpreted as an adaptation for catching and holding slippery prey like fish and other aquatic animals (Ji et al. 2006).

Reduced peg-like molariforms without enamel

A peculiar, highly reduced dentition has been reported for the Late Jurassic *Fruitafossor*, a mammaliaform of uncertain systematic position from the Morrison Formation (Luo & Wible 2005). *Fruitafossor* has tubular and single-rooted molariforms with open-ended roots that completely lack enamel. The open root suggests that *Fruitafossor* probably had continuous tooth growth during life. These teeth are unique among Mesozoic mammaliaforms and convergently resemble the teeth of extant aardvarks and armadillos. Luo & Wible (2005) suggested that *Fruitafossor* possibly fed on colonial insects similar to modern insectivorous xenarthrans. It is important to note that according to the parsimony analysis by Luo & Wible (2005), *Fruitafossor* is not closely related to both eutherians or placental xenarthrans.

Multicusped teeth as early adaptation to omnivory-herbivory

The dentitions of Haramivida and Multituberculata differ from those of other Mesozoic stem mammals and crown mammals by their multicusped premolars and molars with a large number of cusps arranged in longitudinal rows (Fig. 10.21). The unique similarity of the molariforms of both groups led to the concept of Allotheria that unites haramiyidans and multituberculates in one clade (Hahn et al. 1989). Later it had been put forward that Haramiyida are stem mammals not closely related to Multituberculata which belong to crown Mammalia (Zhou et al. 2013, Luo et al. 2015, Puttick et al. 2017), but some authors keep up a multituberculate-haramiyidan clade (Meng et al. 2014, Bi et al. 2014, Krause et al. 2014). Recently, King & Beck (2019) proposed polyphyly of haramiyidans, with Haramiyavia and Thomasia being stem mammals (Luo et al. 2015) and euharamividans being crown mammals in a clade of their own separate from multituberculates which corroborates polyphyly of allotherians.

Haramividan molars show a central basin with a lingual and buccal bordering row of cups (in upper anterior molars a lingual offset with an additional cusp row can be present) (Zhou et al. 2013). The cusps are designated as buccal row A (upper)/a (lower) and lingual row B (upper)/b (lower), and are numbered consecutively from mesial to distal. The upper lingual row occludes into the basin of the lower molars. The jaw movements in haramiyidans were orthal (vertical) with a palinal (posterior) component as evident from striation analysis of the enamel surface (Butler 2000, Meng et al. 2014, Mao & Meng 2019) and from the kinematic animation study of tooth occlusion (Luo et al. 2015). Haramiyidans of the Late Triassic and Early Jurassic have brachyodont tooth crowns, but molars of Middle-Late Jurassic euharamiyidans show multiple hypsodont roots which are proximally fused, called dentin or root hypsodonty (Kermack et al. 1998, Zhou et al. 2013, Luo et al. 2017). Some Asian euharamiyidans such as the arboreal and gliding Vilevolodon have a unique dual mortarpestle occlusal pattern of the molars. The large anteriorly positioned cusp a1 of the lower molars occludes into the anteriorly positioned basin of the upper antagonists. At the same time the large posteriorly positioned cusp A1 of the upper molars occludes into the posteriorly positioned basin of the lower antagonists (Luo et al. 2017), as first recognized by Kermack et al. (1998). This molar morphology and occlusal pattern indicates crushing and grinding function and suggests a mainly herbivorous diet, with feeding on soft plant tissues and possible granivory (Luo et al. 2017).

Among multituberculates, Paulchoffatiidae have molars with cusps of differing heights and a basin-shaped m2 with only one cusp (Hahn & Hahn 2004, Yuan et al. 2013) which represents the most plesiomorphic tooth pattern among Multituberculata (Lazzari et al. 2010). Lazzari et al. (2010) studied the mastication of Paulchoffatiidae, and they reconstructed two different masticatory cycles, a puncture-crushing cycle and a grinding cycle that consists of two different phases. The first phase of the grinding cycle is obligue and can be seen as a precursor of the slicingcrushing cycle in ptilodontoid Cimolodonta (Krause 1982), whereas the second phase is fully palinal and homologous to the ptilodontoid grinding cycle. Paulchoffatiids exhibit fewer attrition facets than Cimolodonta and paulchoffatiid occlusion apparently was less precise than that of other multituberculates. Lazzari et al. (2010) noticed similarities to the occlusal pattern of Haramivida (Butler & McIntyre 1994) but pointed out that these are symplesiomorphic and do not imply a close relationship.

Gingerich (1977) and Krause (1982) analyzed the enamel microwear pattern, dentin wear pattern, and the cusp morphology of derived Cenozoic ptilodontoid Cimolodonta and reconstructed two chewing cycles: one that involves the ultimate premolars and a second one that involves the molars. During the first (slicing and crushing) cycle, the large arcuate and laterally compressed blade-like p4 cuts vertically deep into the food items that are held up against the upper premolar (P4). Subsequently, the sliced food items pass down on both sides of the p4 and cause vertical subparallel striations in the valleys between the almost vertical enamel ridges. The second (grinding) cycle is a palinal (backwards) movement of the mandible with the molars in occlusion (Gingerich 1977). This causes flat attrition facets with longitudinal striations inside the deep valleys between the cusp rows of upper and lower molars (Krause 1982). Multituberculates have enlarged lower incisors that are separated from the cheek teeth by a wide diastema. The incisors of derived multituberculates such as ptilodontoids and taeniolabidids are rootless and evergrowing and have the enamel restricted to the buccal side of the tooth. Due to the similarities of multituberculate and rodent dental form and function (Krause 1986), multituberculates have been dubbed "rodents of the Mesozoic" with similar dietary adaptations. However, in rodents with longitudinal chewing motion such as muroids, the power stroke is oriented proal (forward) and not palinal (backward) as in multituberculates.

Hypsodont molariforms with flat occlusal surface

The enigmatic Late Cretaceous-Paleocene Gondwanatheria from the southern landmasses evolved the first truly hypsodont molars in mammalian evolutionary history (Fig. 10.22). Monophyly of Gondwanatheria is generally accepted, but their phylogenetic relationship is under discussion. Cladistic analyses by Gurovich & Beck (2009) and Krause et al. (2014) support multituberculate affinities of Gondwanatheria, but the presence of four molariform positions in the mandible of the Paleocene gondwanatherian *Sudamerica* (Pascual et al. 1999) contradicts this assignment to multituberculates which have only two molars and no molariform lower premolars. A recent analysis using 84 cynodont taxa and 530 morphological characters recognized Gondwanatheria as sister taxon of Multituberculata



Fig. 10.21. Multicusped molars of multituberculata and Haramiyida. **A**, upper left tooth row of *Pseudobolodon oreas* with worn cusp showing the trailing edge (black arrow). From Lazzari et al. (2010), mirrored. **B**, buccal view of a lower p4 of a paulchoffatiid multituberculate with striations (close up) on the surface reflecting two directions of relative jaw movements (black double arrows). **C**, stereo-pair of the upper right tooth row of the haramiyidan *Megaconus*, modified from Zhou et al. (2013). **D**-**F**, occlusion pattern of multituberculates as represented by *Neoplagiaulax*. **D**, two rows of cusps of the lower molar (blue) interlock in the three rows of cusps of the upper molars (pink). **E**, close up of wear facets along the cusp rows of a lower molar. White arrows indicate striations. **F**, OFA simulation of the backward chewing movement typical for multituberculates, colored patches indicate occlusal contacts along the cusp rows.



Fig. 10.22. Hypsodont gondwanatherian molars. **A**, upper left tooth row of *Vintana sertichi* showing its unique flat occlusal surface with several enamel islets, modified from Krause et al. (2014). **B**,**C**, close ups of the last upper molariform (MF3) of *Vintana sertichi*, illustrating the uneven excavation of the enamel bands by wear, modified after Schultz et al. (2014). Black arrows indicate the leading edge, white arrows indicate the trailing edge. **D**,**E**, high crowned molariform of *Lavanify* sp. with long root (**D**) and flat occlusal surface (**E**), from Koenigswald & Krause (2014).

(Krause et al. 2020). Before the discovery of the skull of the sudamericid Vintana sertichi from the Late Cretaceous of Madagascar (Krause et al. 2014), Gondwanatheria were known only by fragmentary mandibles (Sudamerica) and isolated teeth. The skull of Vintana has three hypsodont molariforms preserved in both maxillae. The molariforms are characterized by enamel infoldings and enamel islets on the flat occlusal surfaces. Schultz et al. (2014) analyzed the occlusal relationships and reconstructed the chewing stroke of Vintana. The palinal (posteriorly directed) power stroke had a significant buccally directed component during the unilateral chewing. Parallel wear striations and flat occlusal surfaces without cusps suggest that the power stroke was almost horizontal, without a separation in different masticatory phases. The buccal component of the power stroke differentiates Vintana from other mammals and mammaliaforms with palinal chewing movements such as multituberculates (Krause 1982, Gambaryan & KielanJaworowska 1995, Lazzari et al. 2010), haramiyidans (Butler 2000, Butler & Hooker 2005, Zhou et al. 2013), and other gondwanatherians (Krause et al. 1992, Krause and Bonaparte 1993, Koenigswald et al. 1999). According to the hypsodont tooth morphology and striation analysis, Schultz et al. (2014) suggested a herbivorous diet for Vintana with a wide range of herbaceous material. Convergently to multituberculates and rodents, gondwanatherians evolved ever-growing incisors that are separated by wide diastemata from the hypsodont cheek teeth. Open-rooted upper and lower incisors and wide diastemata are also seen in the recently described gondwanatherian Adalatherium from the Maastrichtium of Madgascar (Krause et al. 2020). The presence of brachyodont postcanines with four cusps connected by prominent crests in Adalatherium, a dental pattern otherwise unknown from Mesozoic mammaliaforms, suggests that Gondwanatheria were dentally more diverse than hitherto believed.

Conclusion

Mesozoic mammals show a remarkable variety of dental morphologies and functional adaptations. Plesiomorphically, mammaliaforms had a single-phased (phase I) chewing stroke with a mainly piercing and cutting function. A second phase (phase II) that added a crushing and/or grinding function was evolved independently in several groups, including meta- and eutherians, "pseudotribosphenic" lineages, and multituberculates. The more complex chewing cycles with enhanced crushing and grinding in these lineages likely permitted greater dietary diversity and helped catalyze their ecological diversification.

Almost all morphological and functional types of teeth that are seen in Cenozoic therians were present in the Mesozoic, including peg-like dentin teeth, ever-growing incisors, and hypsodont molars. Not realized in Mesozoic mammals are dentitions with premolars and molars forming extensive crushing or grinding surfaces suited for processing large quantities of plant materials, as found in large herbivores such as perissodactyls, artiodactyls, and proboscideans. Mesozoic mammals were small, the majority had a body mass between 10 and 250 g, with the Early Cretaceous carnivorous *Repenomamus* being the largest known Mesozoic mammal weighting about 10 kg (see Martin 2018 and references therein). Large herbivores and subsequently large carnivorous mammals appeared only some million years after the extinction of the non-avian dinosaurs at the K/Pg-boundary. Among the earliest mega-herbivores is the Middle Eocene (Bridgerian, about 48 Myr) rhinoceros-sized Uintatherium with an estimated body mass of 1500 to 2000 kg (Turnbull 2002). The majority of Mesozoic mammaliaforms and mammals with non-tribosphenic mammalian tooth types became extinct before the K/Pg-boundary. A prominent exception are the multituberculates with multicusped cheek teeth that survived until the Late Eocene. The vast diversity of Cenozoic and extant therian molars is derived from the generalized tribosphenic molar with sensu lato insectivorous adaptation that remained almost unchanged from its first appearance in the Late Jurassic (Juramaia) until the K/Pg boundary when the hypothetical ancestor of crown placentals existed (O'Leary et al. 2013). Initial step towards a more complex molar pattern was the addition of a fourth main cusp, the hypocone, at the upper molars as seen. among others, in Paleocene stem macroscelideans such as Prolouisina, Adapisorex, and Walbeckodon. The guadritubercular pattern provided increased crushing area for more efficient processing of a wider array of food sources (Hunter & Jernvall 1995, Engler & Martin 2018). This modification marks the beginning of the success story of the tribosphenic molar in the Cenozoic which has its roots deep in the Mesozoic.

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