Occlusion and Function of Triconodont Dentitions

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Summary

Over the last decades, many studies have focused on the tribosphenic molar and its functional aspects because it is considered to be a key innovation in mammalian evolution. Early triconodont dentitions have been examined to a lesser degree, despite being the plesiomorphic mammalian tooth morphology and, therefore, closely linked to the evolution of precise occlusion and food processing, which contributed to the evolution of endothermy. The majority of these studies were limited to descriptions and two-dimensional modeling. In this thesis, micro-computed tomography (µ-Ct) and 3D models were used to test existing occlusal models and to analyze the dental function of the different triconodont molar morphologies.
The triconodont molar is characterized by three linearly aligned main cusps a/A, b/B, and c/C. It is the characteristic molar pattern for the non-mammalian Mammaliaformes Morganucodonta and the early-diverging crown-group Mammalia Eutriconodonta, which were subjects of this study.

The early-diverging mammaliaforms *Morganucodon watsoni*, *Megazostrodon rudnerae*, and *Erythrotherium parringtoni* had a primarily orthal occlusal path. Differences in the occlusion of the main cusps of *Morganucodon* compared to the embrasure occlusion of *Megazostrodon* and *Erythrotherium* were confirmed with the Occlusal Fingerprint Analyser (OFA). The occlusion of *Morganucodon* further showed variation in trajectory and cusp placement.
The dentitions of Morganucodonta were well adapted to piercing and shear-cutting. 'Shearing flanks', which were the focus of previous studies, seemed to be rather a result of attrition, than functional areas in themselves.
Positioning of the upper molars within the maxilla of *Morganucodon* suggests a predetermined tooth placement to allow space for the lower dentition. These results are in contrast to previous hypotheses that stated that *Morganucodon* relied on extensive wear in order to form a precise occlusion.

While the molars of Morganucodonta emphasize the piercing capability with large, isolated cusps, the molars of Triconodontidae have a homogenous cusp-valley system that formed a continuous fore-aft crest that linked the entire molar series in a zig-zag pattern. It thus combines traits linked to both carnivorous diets (e.g. fore-aft cutting edges) and insectivorous diets (transverse crests and lobes). The molar series of triconodontids was highly uniform and

adapted to a precise fit; lower molar cusps were self-sharpening within the valleys between upper molar cusps. While the high degree of precision ensured good cutting capabilities, its uniformity likely put the dentition under greater evolutionary constraints than other molar types with more heterogeneous cusp morphologies. This explains the stereotyped nature of the triconodontid molar, which underwent little change during the 60–85 Ma range of the family. Contrary to previous studies, embrasure occlusion was confirmed for Triconodontidae based on the OFA analysis. Embrasure occlusion can be therefore considered the universal occlusal mode for all taxa with triconodont molars with the exception of few Morganucodonta. Additionally, sequential tooth replacement was confirmed for Triconodontidae, which is in accordance with their phylogenetic position as early-diverging crown Mammalia. A unique pattern, on the other hand, is the development of m4 within the lingual side of the coronoid process, well above the tooth row of *Triconodon*. It was subsequently accommodated in the active tooth row via unusually prolonged and localized growth of the posterior part of the mandible (and, by implication, the base of the skull rostrum), with the m4 remaining in position and not erupting upward. This pattern is also seen among some later triconodontids and appears to be unique to the family.
Over the course of this study, a new species of Triconodontidae *Triconodon averianovi* was described based on the partially reduced m4, its small p4, and gracile canine.

Gobiconodontidae, a clade of early crown-group Mammalia, are unique among Mesozoic mammals due to their large size, the replacement of their molariforms, and carnivorous diet. A type of embrasure occlusion was present that caused extensive wear and resulted in deep grooves between the upper molars. The occlusion is centered around mesiodistally oriented crests. They form in the course of increased wear that results in the loss of the smaller b/B and c/C cusps and extend from the tip of the large a/A cusps to the base of the molariforms. These crests provide the main cutting capability during the single-phased power stroke. Gobiconodontidae and Triconodontidae both share mesiodistally oriented crests, a faunivorous diet, as well as lingually inclined upper molars. However, the occlusion of Gobiconodontidae differs from the precise uniform system of Triconodontidae. Its primary focus is on the formation of long crests at the costs of tooth material. Given the large size of Gobiconodontidae, it seems likely that bite force was emphasized over precision. This interpretation is in agreement with the previous hypothesis that the replacement of the molariforms might have been necessary to compensate for the loss of tooth material.

The molars of all taxa, with a preserved maxilla, observed in this study were lingually inclined within the tooth row. This is interpreted as a mechanism to reduce the amount of roll required to keep the teeth in contact during occlusion.

Introduction

1.1 Phylogeny

The first Mesozoic mammal found (*Amphilestes broderipi*) and the first one to be described (*Phascolotherium bucklandi*) both have triconodont molars. Subsequently, several other taxa with triconodont dentitions were described (e.g. *Triconodon*, Owen 1859), which led to the erection of the family Triconodontidae (Marsh 1887) and, subsequently, the order "Triconodonta" (Osborn 1907). Multiple studies by Simpson (e.g. 1925a, b, 1928, 1929) greatly improved the knowledge on "Triconodonta". He excluded taxa with "symmetrodont" molar morphology and distinguished between taxa with equal cusp height, which are now the only members included in Triconodontidae (e.g. *Triconodon*) and "Amphilestidae" (e.g. *Phascolotherium*) that have larger a/A cusps. The latter were later raised to family status by Kühne (1958), but are considered paraphyletic by subsequent workers and more closely related to Zhangheotheriidae and Theria than Eutriconodonta according to some recent studies (e.g., Rougier et al. 2007b; Gaetano and Rougier 2011).

During the following decades, more specimens with a triconodont bauplan, most notably from the Late Triassic-Early Jurassic of England, South Africa, and China were described (e.g Parrington 1941; Kühne 1949; Crompton 1964). These taxa were included in "Triconodonta" based on their similar dental morphology (e.g. Mills 1971; Kermack et al. 1956; Jenkins and Crompton 1979). Their best-known representative is arguably *Morganucodon watsoni*, which was first described by Kühne (1949) based on isolated teeth from the Glamorgan fissure systems (UK). Later, Kühne (1958) established the family Morganucodontidae. Shortly before the description of *Morganucodon*, another species, *Eozostrodon parvus*, based on a premolar from the Holwell Quarry (UK) was described (Parrington 1941). Subsequently, the status of *Morganucodon* as a potential junior synonym of *Eozostrodon* was discussed. Some authors (e.g. Crompton and Jenkins 1968) considered *Eozostrodon* to be the only valid taxon (referring to the material as *Eozostrodon watsoni*), while others (e.g. Kermack et al. 1973) considered *Morganucodon* to be a valid species. However, after several years of uncertainty, Clemens (1979) concluded that *Eozostrodon* and *Morganucodon* were not synonymous, limiting the specimens assigned to *Eozostrodon* to those found in the Holwell Quarry and to one species *E. parvus*.

Kermack et al. (1973) recognized the differences between the mostly Late Triassic-Early Jurassic species compared and the mostly Late Jurassic-Early Cretaceous species and thus established Morganucodonta and Eutriconodonta (together with Docodonta) as suborders of “Triconodonta”. Subsequent studies highlighted further differences between these two taxa based on mandibular, basicranial and postcranial characters (e.g. Kemp 1983; Rowe 1988; Wible and Hopson 1993; Rougier et al. 1996; Ji et al. 1999). Most important for the interpretation of Eutriconodonta as crown Mammalia (unlike Morganucodonta) is the fact that there is no evidence for persisting attachment of the postdentary elements (articular, prearticular, angular, surangular) to the dentary (Kielan-Jaworowska et al. 2004). These elements are still integrated with the dentary in Morganucodonta and other non-mammalian Mammaliaformes (e.g. Allin and Hopson 1992; Crompton and Luo 1993; Lautenschlager et al. 2017, 2018).

Based on mandibular characters of *Megazostrodon*, Gow (1986) established Megazostrodontidae to separate *Megazsotrodon* from *Morganucodon*. Subsequently, Morganucodonta were elevated to ordinal rank (Stucky and McKenna 1993). For this study, Morganucodonta are considered the earliest diverging taxon within Mammaliaformes, while earlier diverging taxa with triconodont postcanine dentitions (e.g. *Sinocondon*) and *Barsilitherium* are considered non-mammaliaform Mammaliamorpha (Huttenlocker et al. 2018).

Trofimov (1978) first described *Gobiconodon*, based on isolated jaws and maxilla from the Aptian–Albian of Mongolia. Subsequently, Gobiconodontinae was considered a subfamily of “Amphilestinae” (Chow and Rich 1984) and later raised the former to family status by Jenkins and Schaff (1988). It differs from “Amphilestidae” by more robust teeth, specialized anterior dentition, curving upper tooth row, and molariform replacement (e.g. Jenkins and Schaff 1988; Kielan-Jaworowska and Dashzeveg 1998; Meng et al. 2005; Yuan *et al.* 2009; Butler and Sigogneau-Russell 2016).

Most recent studies consider Eutriconodonta (Gobiconodontidae, Triconodontidae, and their closest relatives) to be monophyletic and place them within crown-group Mammalia, while Morganucodonta are among the earliest diverging Mammaliaformes (Fig. 1.1) (e.g. Luo et al. 2002; Gaetano and Rougier 2011; Martin et al. 2015). While the phylogenetic position of the latter is well supported and mostly accepted, the placement and monophyly of Eutriconodonta are weakly supported given that their unifying dental character is the plesiomorph triconodont pattern (Kielan-Jaworowska et al. 2004). Some phylogenetic analyses result in a paraphyletic placement of their members (e.g. Hu et al. 1997; Ji et al. 1999; Huttenlocker et al. 2018). A phylogenetic analysis of Averianov and Lopatin (2011) removed Gobiconodontidae from Eutriconodonta and placed both taxa at the very base of Acrotheria, a proposed taxon that includes Monotremata, Theria, derived “Symmetrodonta”, and likely Dryolestida (the latter were excluded from the analysis). For this study, however, the interpretation of Eutriconodonta being a monophyletic taxon of early-diverging crown-group representatives is tentatively followed (Fig.1.1) (e.g. Martin et al. 2015).

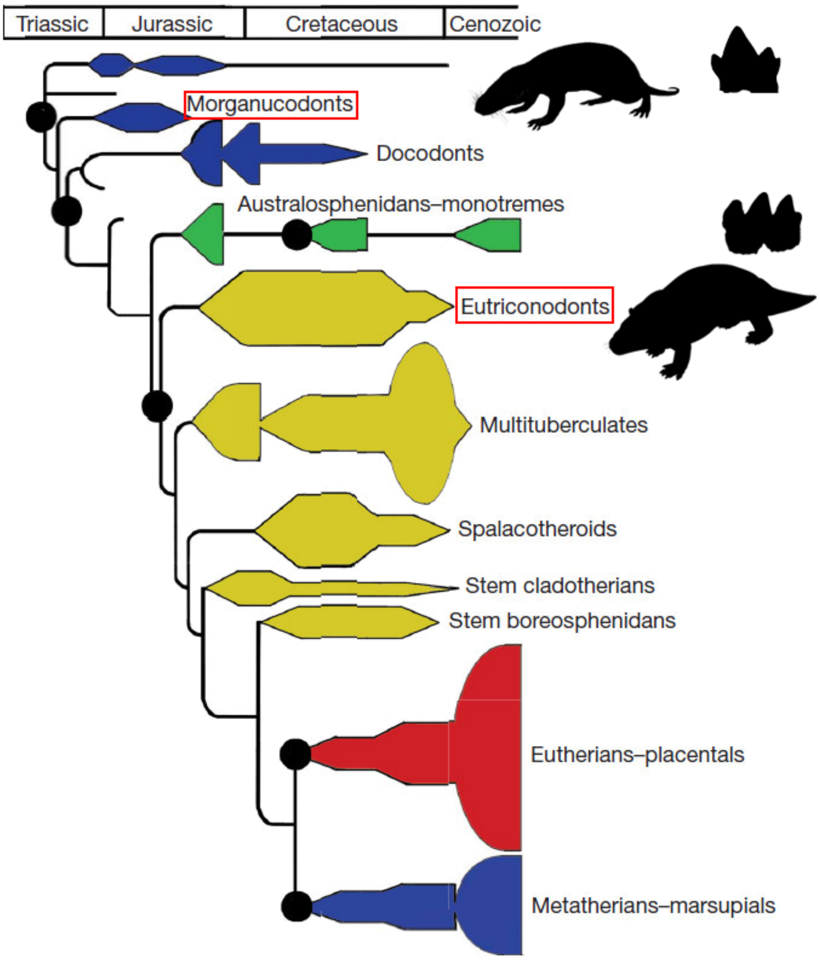

FIGURE 1.1. Phylogeny of Mesozoic mammals (*sensu lato*). Morganucodonta and Eutriconodonta were examined in this study, as they represent the two major clades among Mammaliaformes that retain a triconodont dentition. Modified after Luo (2007). Species silhouettes taken from phylopic.org.

1.2 The Evolution of the Triconodont Molar Pattern

A key innovation in mammalian evolution was the development of molars, complex teeth that are not replaced during the animal's lifetime. This, in addition to changes in the crani-mandibular region, allowed for a precise occlusion (Crompton and Jenkins 1968; Mills 1971). The latter greatly increased the ability to process food within the mouth cavity prior to its internal digestion, because the particle surface was increased and thus energy output by the ingested food maximized (Ungar 2010). The ability to pre-process food has been linked to the development of a high metabolic rate (Lucas 2004; Kemp 2005; Ungar 2010; Bhullar et al. 2019). As an adaptation to various dietary specializations, mammals exhibit a large variety of molar morphologies (Thenius 1989; Ungar 2010).

Triconodont teeth are characterized by a linear arrangement of the three main cusps A/a, B/b, and C/c, and the occasional presence of small posterior cusps D/d (Fig. 1.2, 1.3). This pattern represents the plesiomorphic mammaliaform condition, which originated in the non-mammalian synapsids such as *Thrinaxodon* and Probainognathidae (e.g. Butler and Clemens 2001; Kielan-Jaworowska et al. 2004; Martinelli et al. 2016). In these early triconodont dentitions, the A/a cusps were by far the largest, while the positioning and size of the smaller cusps were variable. Their function was also likely different from later triconodont teeth, since in *Thrinaxodon* no direct contact between the upper and lower molars was present in specimens with a fully closed jaw and wear facets were lacking (Crompton & Jenkins 1968; Crompton 1974).

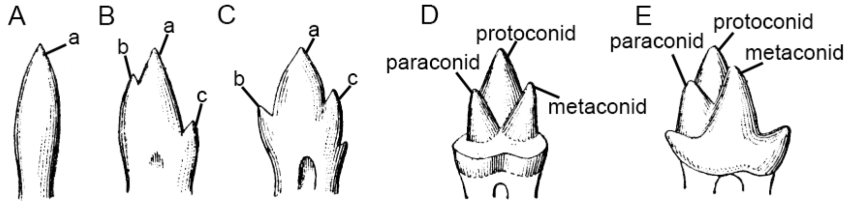

FIGURE 1.2. Evolution and cusp terminology of the triconodont molar. (A) Non-specified reptile, (B) *Dromatherium* a non-mammaliaform Cynodont, (C) *Microconodont* a non-mammaliaform Eucynodont that closely represents the ancestral molar condition of Morganucodonta, (D) *Spalacotherium* a Cretaceous mammal that represents the "symmetrodont" molar morphology, and (E) *Amphitherium* a pre-tribosphenic representative. The triconodont molar evolved from a single main cusp a with the addition of smaller adjacent cusps (A-C). The terminology of the crown-group Mammalia (D, E) differs, since homology of the cusps is unclear. Modified after Osborn (1897). Mesial to the left. Teeth not to scale.

Within Mammaliamorpha, early-diverging taxa such as *Brasilodon*, *Brasilitherium*, and *Sinocondon* developed molariforms similar to those of Morganucodonta (Bonnaparte et al. 2003, 2005; Zhang et al. 1998). They also differed from earlier triconodont dentitions in having a mobile symphysis and matching wear facets that indicate occluding teeth, although with little precision (Crompton 1985; Bonnaparte et al. 2005). Unlike Morganucodonta and most other Mammaliaformes, these early-diverging taxa also still replaced their molariforms (Zhang et al. 1998). In Morganucodonta, a more precise occlusion evolved with the combination of a fully functional dentary-squamosal joint and a diphyodont dentition without replacement of molariforms (Crompton and Jenkins 1968; Mills 1971). Note that Gow (1986) stated that replacement of m2 might have occurred in *Megazostrodon*, however, Kielan-Jaworowska et al. (2004) remarked that the evidence provided at this point is inconclusive. Concomitant with the development of diphyodonty, the evolution of the secondary jaw joint and changes in the jaw adductor muscles occurred, so that the teeth hold closely together during occlusion and prevent the teeth from being forced apart by the food (Kermack et al. 1973; Lautenschlager et al. 2018). Within Mammaliaformes, the pterygoid muscle-group was already inserting on the dentary in a mammalian fashion (Lautenschlager et al. 2017). These features, together with a mobile symphysis, allowed for a chewing path with a triangular trajectory that was crucial for mammalian mastication (Kielan-Jaworowska et al. 2004). This triangular trajectory consists of three separate strokes. A preparatory stroke with a small upward and buccal motion, a power stroke represented by a pronounced upward and lingual motion that results in occlusion, and afterward a downward and a buccal oriented recovery stroke (Hiiemäe and Kay 1972). During the power stroke, only one hemimandible is occluding, whereas the adductor musculature on both hemimandibles participates and, therefore, increases the potential bite force (Kemp 2005).

While Morganucodonta kept the triconodont bauplan, modifications and subsequently new molar types occurred in various lineages of early-diverging Mammaliaformes (e.g. Docodonta; Haramiyida). Most of the modifications utilized angulation of the molar cusps relative to one another, thus abandoning the linear arrangement. One of the oldest (first?) modifications of the molars within Mammaliaformes was the symmetrodont molar type present in some Late Triassic taxa (e.g. *Kuehneotherium*) (Davis 2011). It is characterized by angulation of the cusps, with cusp a being placed buccally and cusp A lingually relative to the adjacent b/B and c/C cusps (Fig. 1.3) (Crompton and Jenkins 1968, 1973).

“Symmetrodonts” are no monophyletic taxon. Similar to “Triconodonta”, some of their representatives are early-diverging Mammaliaformes while others (e.g. *Maotherium*) are crown-group mammals (Kielan-Jaworowska et al. 2004; Plogschties and Martin 2019). Even among the early-diverging Mammaliaformes, it is unlikely that taxa with “symmetrodont” molars form a monophyletic taxon comparable to Morganucodonta, given that most lineages of Mammaliaformes with complex molariforms likely evolved from a predecessor with angulated cusps. One example with “symmetrodont” molars is the Late Triassic *Woutersia* that is considered a stem-lineage representative of Docodonta (Luo and Martin 2005).

A later diverging non-mammalian mammaliaform is *Hadrocodium* (Huttenlocker et al. 2018). It retains a triconodont dentition similar to *Morganucodon* and *Megazostrodon* (Luo et al. 2001) and due to its phylogenetic position, it's molar morphology could represent the ancestral condition of crown-group Mammalia. If a triconodont molar morphology was indeed present at the base of the Mammalia, it was soon modified by most taxa (e.g. Australosphenida, Multituberculata, Dryolestida), with only the Eutriconodonta and “Amphilestidae” retaining the plesiomorphic molar morphology.
However, this interpretation is based on the assumption that the ancestral condition of Mammalia was a triconodont molar morphology. A phylogenetic analysis by Luo et al. (2002) placed the “symmetrodont” *Kuehneotherium* (a taxon not included by Huttenlocker et al. 2018) as closer related to crown-group Mammalia than *Hadrocodium*. This would support the interpretation that the “symmetrodont” molar morphology is the ancestral condition for Mammalia. The molars of Eutriconodonta would, therefore, be secondarily triconodont. This interpretation is supported by the slight angulation seen in molariforms of Gobiconodontidae (Fig. 1.3) and some other “triconodont” taxa (e.g. *Juchilestes*) (Kielan-Jaworowska et al. 2004; Gao et al. 2010).
Things are complicated by the incomplete nature of the fossil material of *Kuehneotherium*, which makes its phylogenetic position unstable (Luo et al. 2002). Currently, the phylogeny of early Mammaliaformes, as well as the placement of Eutriconodonta, is too volatile to resolve the ancestral condition for Mammalia with certainty.

Similar problems are faced when cusp homology is discussed. Cusp nomenclature for molars of extant therians, as well as most Mesozoic crown-group mammals, is based on the terminology of the tribosphenic molar. Cusps of non-mammalian Mammaliaformes on the other hand, are mostly labeled by assigned letters, with cusp a/A being the central main cusp

(Fig. 1.2) (Crompton and Jenkins 1968). Homologizing the cusps of non-mammalian Mammaliaformes and crown-group Mammalia was attempted (for an overview see Davis 2011). However, this is complicated due to the phylogenetic uncertainties described above, as well as the minor genetic and/or developmental changes required to change cusp expression during molar development (e.g. Jernvall 2000; Kavanagh et al. 2007; Salazar-Ciudad and Jernvall 2010; Harjunmaa et al. 2014). While it could be argued in favor of homologizing between the molar cusps of Tribosphenida and Eutriconodonta, given their position as crown-group Mammalia, most authors apply the morganucodontan nomenclature for Eutriconodonta (e.g. Kielan-Jaworowska et al. 2004). This study follows this convention for convenience and better comparability.

1.3 Morganucodonta Examined in this Study

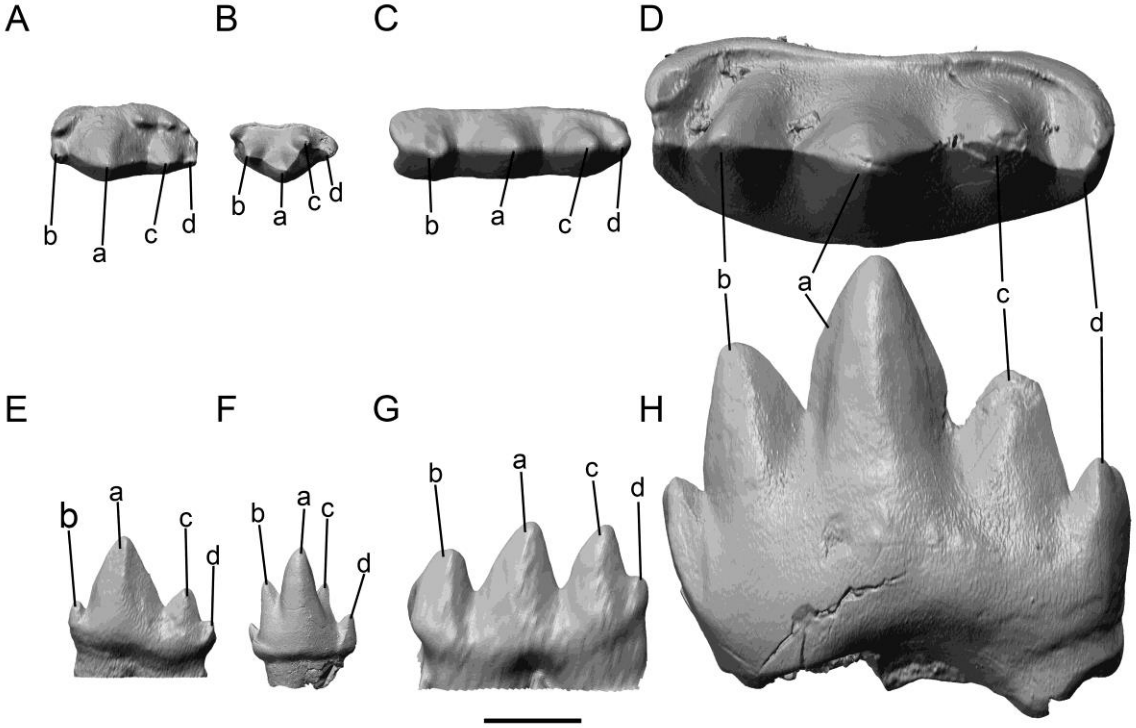

FIGURE 1.3. Comparision of lower triconodont and symmetrodont molariforms in (A-D) occlusal and (E-H) buccal view. (A, E) *Morganucodon*, (B, F) *Kuehneotherium*, (C, G) *Triconodon*, and (D, H) *Gobiconodon*. *Kuehneotherium* differs from the triconodont taxa in the lingual placement of its b and c cusps relative to cusp a. An incipient angulation is also present in *Gobiconodon*. The different terminology of *Kuehneotherium* compared to the one used for the symmetrodont *Spalacotherium* (Fig. 1.2) is based on the phylogenetic position of *Kuehneotherium* as a non-mammal mammaliaform. In part due to their size, *Triconodon* and *Gobiconodon* are considered carnivorous representatives of Mesozoic mammals. Mesial to the left. Model of *Kuehneotherium* courtesy of T. Plogschties. Scale bar equals 1 mm.

The primary representative of Morganucodonta in this study is *Morganucodon* (Chapter 2). Several skulls, postcranial material, as well as countless isolated teeth of *Morganucodon* have been found in sediments from the Late Triassic and Early Jurassic of Europe, China, and the United States, while most other members of Morganucodonta are primarily known by isolated teeth and jaw fragments (Kielan-Jaworowska et al. 2004). It therefore has become a crucial taxon for studies on the early evolution of mammalian traits (Kermack 1963; Crompton 1971, 1974; Mills 1971; Kermack et al. 1973, 1981; Parrington 1973, 1978; Jenkins and Parrington 1976; Crompton and Luo 1993; Luo 1994; Kielan-Jaworowska et al. 2004; Clemens 2011; Gill et al. 2014; Lautenschlager et al. 2018). Among species of *Morganucodon*, the species that is the primary subject of this study, *M. watsoni*, shows more plesiomorphic characters than the Asian species *M. heikuopengensis* and *M. oehleri* (Kielan-Jaworowska et al. 2004).

Within Morganucodonta, the dentition of *Morganucodon* has been compared to *Megazostrodon*, a mammaliaform known from the Early Jurassic of South Africa and Late Triassic of France (Crompton and Jenkins 1968; Crompton 1974; Debuysschere et al. 2015). Despite the relative similar molar morphology, two different occlusal patterns have been described (Crompton and Jenkins 1968). In *Megazostrodon*, cusps a/A occlude between two antagonistic molars (Fig. 1.4). This occlusal mode is usually referred to as ‘embrasure occlusion’ and is common in many non-triconodont taxa, e.g. *Kuehneotherium* (Crompton and Jenkins 1968; Crompton 1974). *Morganucodon* on the other hand has been described with cusp a occluding between cusps B and A and cusp A in between cusps a and c, resulting in one molar occluding primarily with a single antagonist (Crompton 1974; Mills 1971; Clemens 2011; Butler and Sigogneau-Russell 2016). However, it has also been noted that wear facets *Morganucodon* exhibit great variability (Crompton and Jenkins 1968).

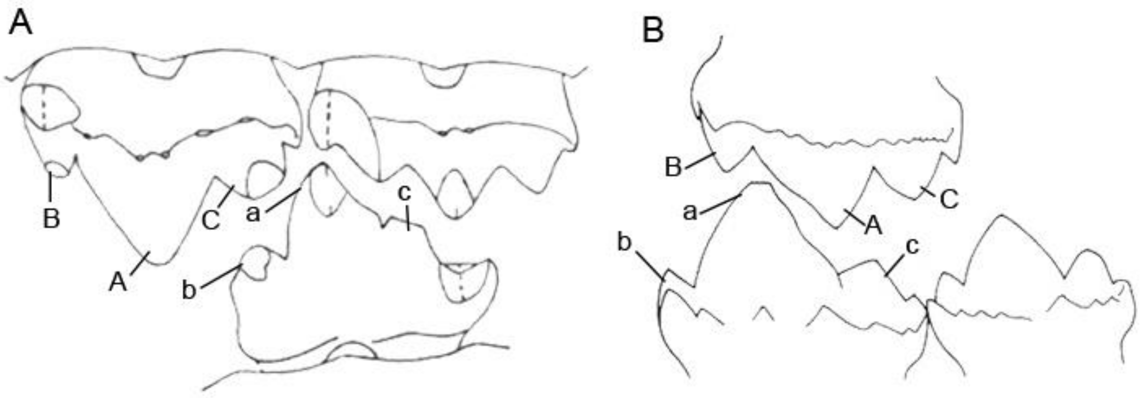

FIGURE 1.4. Comparison of the occlusion of (A) *Megazostrodon* and (B) *Morganucododon*. The a/A cusps of *Megazostrodon* enter the interdental space between two antagonistic molars during the power stroke. This type of occlusion is referred to as embrasure occlusion. It is defined by the positioning of the upper cusp A, therefore, any occlusion with the A cusp entering the interdental space is embrasure occlusion. In *Morganucodon*, cusp a has been described to enter the space between B and A and cusp A to utilize the space between cusps a and c. Embrasure occlusion has been described for some Morganucodonta, "Symmetrodonts", and Gobiconodontidae, while *Morganucodon*-like occlusion has been described for some other Morganucodonta and Triconodontidae. Mesial is to the left. Not to scale. (A) Modified after Crompton (1974), (B) modified after Crompton and Jenkins (1968).

The aim of this study (Chapter 2) is to test for occlusal differences between these otherwise similar taxa and to see whether occlusion in the earliest diphyodont mammaliaforms lacked precision and required extensive tooth wear in order to become effective (Crompton and Jenkins 1968; Mills 1971; Crompton 1974).

Additionally to *Morganucodon* and *Megazostrodon*, the morganucodontan *Erythrotherium parringtoni* was examined in this study (Chapter 3). This taxon is known by a single juvenile individual from the Early Jurassic of South Africa (Crompton 1964; Crompton and Jenkins 1968). Its morphology has been described as highly similar to *Morganucodon* and it was considered a junior synonym of the latter by some authors (Mills 1971; Kermack et al. 1973), but subsequently established as a valid taxon (Crompton 1974; Kielan-Jaworowska et al. 2004). Despite the mentioned morphological similarities, *Erythrotherium* has been described as having embrasure occlusion similar to that of *Megazostrodon* and unlike that of *Morganucodon*. Because this interpretation was based on a single wear facet (Crompton 1974), *Erythrotherium* was reexamined in this study and compared to *Megazostrodon* and *Morganucodon* (Chapter 3).

1.4 Triconodontidae Examined in this Study

Triconodontidae are the best-established family of Eutriconodonta from the Late Jurassic to the Late Cretaceous (Fox 1969; Kielan-Jaworowska 2004). Triconodontidae have been reported from North America, Europe, and Asia (e.g. Cifelli et al. 1998, Kusuhashi et al. 2009). Gliding taxa from the Early Jurassic of South America have been assigned to Triconodontidae as well (Rougier et al. 2007a; Rougier et al. 2007b; Montellano et al. 2008). However, for this study, the phylogeny on Triconodontidae provided by Martin et al. (2015) is used.

Their molars are buccolingually compressed and characterized by three main cusps b/B, a/A, and c/C and an accessory cusp d/D aligned in a row. A character that sets them apart from other “triconodont” taxa is their uniform cusp size and shape (Fig. 1.3.C). The molar row essentially represents one battery of an almost identical cusps-valley sequence with a continuous cutting edge (Simpson 1933). In more derived members, the d/D cusp can be enlarged and integrated into that series (e.g. *Astroconodon*) (Fox 1969; Cifelli and Madsen 1998). Most taxa have an interlocking system between adjacent molars with the d cusp fitting in an underhanging embayment anterior to cusp b of the succeeding molar (Patterson 1951; Fox 1969; 1976; Slaughter 1969; Cifelli and Madsen 1998; Cifelli et al. 1998, 1999; Kielan-Jaworowska et al. 2004; Rougier et al. 2007b).

Three early-diverging taxa of Triconodontidae, *Priacodon*, *Triconodon*, and *Trioracodon* (Gaetano and Rougier 2011; Martin 2015), are known from the Late Jurassic and Early Cretaceous of the United Kingdom and the United States (Simpson 1925a, b; 1928). Additionally, a fragmentary molar attributed to *Priacodon* has been described from Late Jurassic – Early Cretaceous of Portugal (Krusat 1989). Molar morphology of these early-diverging Triconodontidae is highly similar, which complicates their identification on species level (Kielan-Jaworowska et al. 2004).

Though several new taxa of Triconodontidae have been described in recent years, all major hypotheses on their dental function and occlusion date well back into the 20th century and have not been put to test since (e.g. Simpson 1925a, b, 1928; Mills 1971).

Simpson (1925b) discussed the occlusion of early-diverging Triconodontidae and summarized his reconstruction in an illustration depicting the relative positioning of upper and lower molars (Simpson 1925b, Fig. 21). Based on this interpretation, the main cusps (a/A) occluded between the interdental space of the antagonistic molars, similar to the embrasure occlusion that was later described for the morganucodontan *Megazostrodon* (Crompton and Jenkins

1968; Mills 1971). Subsequently, Mills (1971) replaced Simpson’s occlusal model for triconodontid occlusion. He argued that cusp a of the lower molars of *Triconodon* and *Trioracodon* must have occluded in between the upper cusps B and A, and that cusp A occluded between cusps a and c, an occlusion similar to that of *Morganucodon*. This was based on the assumption that the positioning proposed by Simpson (1925b, Fig. 21) would result in a mismatch of the ultimate premolars. Various authors (e.g. Kielan-Jaworowska et al. 2004, Martin et al. 2015) subsequently adopted Mills´ (1971) interpretation.

A study by Bhullar et al. (2019) argued that the roll of the active hemimandible during occlusion was an important step during the evolution of precise occlusion within mammals. Crompton and Luo (1993) described different inclinations of the upper and lower facets, with the lowers being more vertical and the uppers more horizontal on the molars of an unnamed triconodontid from the Cloverly Formation. Therefore, they concluded that the active hemimandible must have rotated medially during occlusion, in order to produce the observed facets. So far, this study represents the best evidence for roll during the power stroke for Mesozoic mammals. Given the proposed relevance of roll, its effect on the occlusion of Triconodontidae was examined in this study.

For this study, two early-diverging triconodontids were examined: *Triconodon mordax* (Chapter 4) and *Priacodon fruitaensis* (Chapter 5). The former is known by an ontogenetic series of 17 specimens from the Early Cretaceous (Berriasian) Purbeck Group at the Durlston Bay locality (Dorset, UK) (Simpson 1928). The latter represents the only case of a member of Triconodontidae of which a well-preserved matching upper and lower dentition has been described (Engelmann and Callison 1998).

Based on *T. mordax*, questions of tooth eruption, morphology, and taxonomy were addressed (Chapter 4). Based on *P. fruitaensis*, occlusal models were tested and dental function was examined to better understand the function and occlusion of Triconodontidae and to test the existing hypotheses on the occlusal mode (Simpson 1925b; Mills 1971), the roll of the hemimandible during the power stroke (Crompton and Luo 1993), and the diet (Osborn 1888; Simpson 1933) (Chapter 5).

The dental function of Triconodontidae was of particular interest, since they represent early-diverging crown Mammalia that retained a modified version of the plesiomorphic triconodont tooth pattern that is characterized by a high degree of uniformity and underwent only minor changes from the Late Jurassic till the Late Cretaceous.

1.5 Gobiconodontidae Examined in this Study

Gobiconodontidae are a family of large Eutriconodonta known from the Early Cretaceous of Asia, as well as North America and Western Europe (Fig. 1.3) (e.g. Trofimov 1978; Jenkins and Schaff 1988; Sweetman 2006; Martin et al 2015; Butler and Sigogneau-Russell 2016). They are known to be the best example for carnivory among Mesozoic mammals (Jenkins and Schaff 1988; Kielan-Jaworowska and Dashzeveg 1998; Kielan-Jaworowska et al. 2004).

The most abundant genus among Gobiconodontidae is *Gobiconodon*, for which multiple species have been described based on isolated teeth, several skulls, as well as postcranial material (Kielan-Jaworowska et al. 2004). Though, the morphological variation between the different species is large so that future studies might recognize addition genera (Kielan-Jaworowska et al. 2004).

Gobiconodontidae differ from most other mammals by replacing their molariforms, thus lacking true molars (*sensu stricto*) (Jenkins and Schaff 1988). However, both generations have molariform morphology and differ noticeably from the premolars (Kielan-Jaworowska et al. 2004). By contrast, molars in other mammals are not replaced and molariform premolars are usually replaced by less complex permanent premolars (Butler 1952, 1995). The extent of replacement is unclear. Jenkins and Schaff (1988) provided direct evidence for a single, sequential, front-to-back replacement of the anterior molariforms in *G. ostromi*. Lopatin and Averianov (2015) even argued for more than two generations of molariforms.

The lower molariforms have a triconodont bauplan with cusp a being the largest. They are similar to those of “Amphilestidae” with taller crowns and cusp c exceeding csup b in height. Upper molariforms are mediolaterally wide with labial and lingual cingula. The principal cusps of the upper molars are increasingly triangled towards posterior with cusp A being positioned more lingual than B and C (Kielan-Jaworowska et al. 2004, Butler and Sigogneau-Russell 2016).

So far, occlusal studies on Gobiconodontidae were limited to description and two-dimensional modeling and, with the exception of *G. ostromi*, were based on isolated teeth and fragments (Jenkins and Schaff 1988; Kielan-Jaworowska and Dashzeveg 1998; Butler and Sigogneau-Russell 2016). In this study, an undescribed gobiconodontid from the Early Cretaceous of China with matching upper and lower molariforms was examined to test the existing hypothesis on the occlusion of Gobiconodontidae and to compare the dental function to that of other Mesozoic mammals with triconodont dentitions.

1.6 Diet

For most Morganucodonta, an insectivorous diet has been assumed due to their size and molar morphology (e.g. Kielan-Jaworowska et al. 2004; Luo 2007). Microtexture analysis, finite element analysis, and physical testing have proposed that among Morganucodonta *Morganucodon* was capable of preying on relatively hard food such as coleopterans (Gill et al. 2014; Conith et al. 2016). Larger taxa might have had a more faunivorous diet that included small vertebrates (Martin et al. 2019).

Eutriconodonta are considered to have a faunivorous diet (Gaetano and Rougier 2011), with some representing early mammalian essays into carnivory (e.g. Simpson 1933, Jenkins and Crompton 1979; Hu et al. 2005). In the case of *Repenomamus*, stomach content of a small dinosaur is direct evidence for a carnivorous diet (Hu et al. 2005). Other Gobiconodontidae have been also been considered to be carnivorous, based on their large size (for Mesozoic mammals) and tooth and jaw morphology (Jenkins and Schaff 1988; Kielan-Jaworowska and Dashzeveg 1998; Kielan-Jaworowska et al. 2004). On average, Triconodontidae are smaller than Gobiconodontidae and direct evidence such as stomach content is missing. Nevertheless, based on their molar morphology they are often described as carnivorous, with Simpson (1933) going so far as describing the dentition as “one of the most ideally carnivorous ever evolved”. Their molar morphology has also been compared to the carnassials of extant Carnivora as well as pinking shears (Simpson 1933; Jenkins and Crompton 1979; Jenkins and Schaff 1988; Kielan-Jaworowska et al. 2004).

For some taxa, a piscivorous diet was hypothesized (e.g. *Astroconodon* and *Ichthyoconodon*) (Slaughter 1969; Sigogneau-Russell 1995). This assignment was based on the molar morphology that shows distally curved cusps and the presence of the fossils in lagoon sediments. However, Jenkins and Crompton (1979) challenged this and argued for an insectivorous diet of these taxa. The close morphological resemblance and phylogenetic position of *Ichthyoconodon* compared to gliding Eutriconodonta, such as *Volaticotherium*, (Gaetano and Rougier 2011) support this interpretation.

In this study tooth morphology and dental function of Morganucodonta (Chapter 2) and Eutriconodonta (Chapters 5 and 6) were examined to test these existing hypotheses.

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Occlusion and Dental Function of *Morganucodon* and *Megazostrodon*

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2.1 Abstract

The functional analysis of a well-preserved snout of the early-diverging mammaliaforms *Morganucodon watsoni*, with matching upper and lower dentitions, and of the holotype of *Megazostrodon rudnerae* showed that both taxa had a primarily orthal occlusal path. In *Morganucodon* the direction was individually variable and either strict orthal or slightly distally or mesially inclined. An analysis with the occlusal fingerprint analyser (OFA) software confirmed an earlier hypothesis that the main cusp A of the upper molars occluded between cusps b and a of the lower antagonists. According to the OFA analysis, there was more extensive contact between cusp a and the preceding anterior upper molar than previously assumed, showing some similarities to the two-on-one pattern described for *Megazostrodon*.

According to our analyses the molars of *Morganucodon* and *Megazostrodon* had an adaptation to piercing, as well as shear-cutting. ‘Shearing flanks’, which were the focus of previous studies, seemed to be rather a result of attrition, than functional areas in themselves. The posterior upper molars in *Morganucodon* were rotated along their longitudinal axis and lingually inclined within the tooth row, resulting in a triangle between M1 and M2 for the large m2 to occlude into. Together, this suggests a predetermined tooth placement, and that contrary to previous hypothesis *Morganucodon* did not rely on extensive wear in order to form a precise occlusion.

2.2 Introduction

Triconodont teeth are characterized by a linear arrangement of the three main cusps A/a, B/b, and C/c, and the occasional presence of a small posterior cusps D/d. This pattern represents the plesiomorphic mammaliaform condition, which originated in the non-mammalian synapsids such as *Thrinaxodon* (e.g. Butler and Clemens 2001; Kielan-Jaworowska et al. 2004). The Early Jurassic *Sinoconodon*, considered by Huttenlocker et al. (2018) as a non-mammaliaform mammaliamorph, replaced its triconodont molariforms and lacked precise mammalian occlusion (Crompton and Luo 1993). With the development of a fully functional dentary-squamosal joint and diphyodont dentition without replacement of molariforms, a more precise occlusion evolved (Crompton and Jenkins 1968; Mills 1971). This is exemplified in the early-diverging mammaliaform *Morganucodon*, that due to its early-diverging position and good representation in the fossil record of Europe and China, has become a crucial taxon for studies on the early evolution of mammalian traits (Kermack 1963; Crompton 1971, 1974; Mills 1971; Kermack et al. 1973, 1981; Parrington 1973, 1978; Jenkins and Parrington 1976; Crompton and Luo 1993; Luo 1994; Kielan-Jaworowska et al. 2004; Clemens 2011; Gill et al. 2014; Lautenschlager et al. 2018).

Concomitant with the evolution of the secondary jaw joint, changes in the jaw adductor muscles occurred, in order to hold the teeth closely together during occlusion and prevent the teeth from being forced apart by the food (Kermack et al. 1973; Lautenschlager et al. 2018). Within Mammaliaformes the pterygoid muscle-group was already inserting on the dentary in a mammalian fashion (Lautenschlager et al. 2017). Together with a mobile symphysis, these features allowed for a chewing path with a triangular trajectory, which was crucial for mammalian mastication (Kielan-Jaworowska et al. 2004). This triangular trajectory consists of three separate strokes. A small upward and buccal motion (preparatory stroke), a pronounced upward and lingual motion that results in occlusion (power stroke) and is followed by a downward and a buccal movement (recovery stroke) (Hiiemäe and Kay (1972) defined the movements of the triangular trajectory as the preparatory stroke, power stroke, and recovery stroke. During the power stroke, only one hemimandible is occluding, whereas the adductor musculature on both hemimandibles participates and therefore increases the potential bite force (Kemp 2005).

For the Morganucodonta an insectivorous diet has been assumed, due to their size and molar morphology (e.g. Kielan-Jaworowska et al. 2004; Luo 2007). This is corroborated by more recent work and according to micro-texture analysis, finite element analysis, and physical testing, *Morganucodon* was capable of preying on relatively hard food such as coleopterans (Gill et al. 2014; Conith et al. 2016).

In this study, we examine the dentitions of *Morganucodon* and *Megazostrodon*. The latter is a mammaliaform known from the Late Triassic of South Africa and France (Crompton and Jenkins 1968; Debuysschere et al. 2015). Although initially assigned to the Morganucodonta, Gow (1986) proposed the family Megazostrodontidae based on mandibular characters (Kielan-Jaworowska et al. 2004; Montellano et al. 2008; Close et al. 2015).

Both genera, *Morganucodon* and *Megazostrodon*, have overall similar molars with large a cusps in the lower molars and more similar cusp height in the uppers. However, different occlusal patterns for the two taxa have previously been proposed based on their wear patterns (Crompton and Jenkins 1968; Crompton 1974). Whereas in *Megazostrodon* cusps a/A occlude between two antagonistic molars in an ‘embrasure occlusion’, *Morganucodon* has been interpreted with cusp a occluding between cusps B and A and cusp A in between cusps a and c, which results in one molar occluding primarily with a single antagonist (Crompton 1974; Clemens 2011; Butler and Sigogneau-Russell 2016). Mills (1971) argued that both types of occlusion are so different that they must have been developed on two separate pathways from the ancestral condition.

Multiple studies with various methods over the last decades have focused on the tribosphenic molar and its functional aspects, since it is considered to be a key innovation in mammalian evolution (e.g. Crompton 1971; Evans and Sanson 1998; Kielan-Jaworowska et al. 2004; Spoutil et al. 2010; Schultz and Martin 2014; Schwermann 2014). Early triconodont dentitions have been studied to a lesser degree, despite the general assumption that the evolution of precise occlusion and food processing was closely linked to the evolution of endothermy (Lucas 2004; Kemp 2005). With a few exceptions, the majority of previous studies was limited to a description and two-dimensional modeling (e.g. Crompton and Jenkins 1968; Mills 1971; Crompton 1974). Here, we use micro-computed tomography (µ-Ct) and 3D models to re-examine the dentitions of *Morganucodon* and *Megazostrodon*. Additionally, we present a new application to test virtually the occlusal path with the occlusal fingerprint analyser (OFA) The aim of this study was to test for occlusal differences between these otherwise similar taxa and to see if occlusion in the earliest diphyodont mammaliaforms lacked precision and required extensive tooth wear in order to become effective (Crompton and Jenkins 1968; Mills 1971; Crompton 1974).

2.3 Material and Methods

Material from the following institutions and museums was used in this study: Natural History Museum, London (NHMUK PV M); University Museum of Zoology, Cambridge (UMZC); American Museum of Natural History, New York (AMNH), and Bernard Price Institute for Palaeontological Research, Johannesburg (BPI).

The examined specimen of *Morganucodon watsoni* Kühne 1949 is a fragmentary skull rostrum (UMZC Eo.CR.1) from the Glamorgan fissure systems. The fissures contain terrestrial deposits and are Hettangian in age (Whiteside et al. 2016). The specimen is from Pontalun (now known as Lithalun) quarry, fissure Pontalun 3. This fissure has yielded several thousand *Morganucodon* teeth and bones, together with material of *Kuehneotherium* and *Gephyrosaurus*. The abundance of *Morganucodon* is in stark contrast to the two described specimens of *Megazostrodon rudnerae* and the 19 isolated teeth of *Megazostrodon chenali* (Crompton 1974; Gow 1986; Debuysschere et al. 2015). UMZC Eo.CR.1 was first figured in Parrington (1978) and comprises both dentaries and the left maxilla. Almost the complete lower dentition is present with only the incisors damaged. The upper left dentition is present from P1 to M4, with cusp A broken on P4 and M3 and the crown broken on M4. The specimen is housed at the University Museum of Zoology, Cambridge (UK). As illustrated in Parrington (1978), the specimen was originally manually prepared and attached with wax to a wooden rod. One of the authors (PGG) had it remounted, in 2008, onto a custom made plastic SEM stub for scanning.

The dental striations of *M. watsoni* have been studied by Scanning Electron Microscopy (SEM) (Cambridge CamScan MV2300; Electron Optic Services, Inc.) on isolated teeth. A complete list of these specimens is added in the supplementary data (Supplementary Table 2.1). Based on their morphology the isolated teeth were assigned a tooth position. All molars are m2/M2, with the exception of UMZC Eo.M(Lr).32, which is an m1.

The holotype of *Megazostrodon rudnerae* (NHMUK PV M 26407) was found in a red bed series near Lesotho (South Africa) originally considered to be “probably of late Triassic age” (Crompton and Jenkins 1968: 429) but now regarded as Early Jurassic (Kielan-Jaworowska et al. 2004). It consists of a partial skeleton and a damaged skull with the upper and lower dentition mostly preserved. The left mandible was isolated during preparation and was coated for preservation. The specimen is in the collection of the Natural History Museum, London. Additional to new details that became evident by µCT-examination of the holotype we will point out some differences between the holotype and another well-preserved specimen of *Megazostrodon* BP/1/4983.

Length measurements were performed by determining the greatest mesio-distal extension of a tooth. Width (bucco-distal) measurements were performed on the middle of each tooth at the position of the cusps a/A.

2.3.1 Definitions

When discussing the function of teeth, multiple terms with varying definitions exist. Here we provide a definition of the relevant terms used in this study. We use the terms ‘attrition’ and ‘abrasion’ following the definition by Grippo et al. (2004), who defined attrition as wear caused by tooth-tooth contact and abrasion as wear caused by an outside source (e.g. food). ‘Crest’ defines an elongated morphological structure on the tooth surface. Crests mostly function as ‘blades’, which refers to a functional unit for the procession of food. ‘Blade’ is used following the definition provided by Lucas (2004), where he distinguishes between asymmetrical ‘blades’ as opposed to ‘wedges’. The former has an asymmetrical arrangement with one steeper side that passes another blade, whereas the latter is symmetrical. We use ‘shear-cutting’ following Schultz and Martin (2011), who define this process as two blades passing each other closely to break down food. This term is used instead of the term ‘cutting’, since the latter is often variably used with different definitions (e.g. Lucas 1979; Sibbing 1991). We distinguish between ‘shear-cutting’ and ‘shearing’. The latter is used here to describe a process when surfaces pass along each other and no cutting component is present. In these cases, shearing forces act on the food when the space between the antagonistic surfaces is decreased during the progressing movement.

2.3.2 Occlusal Fingerprint Analysis

The term ‘occlusal fingerprint’ was introduced by Kullmer et al. (2009) and describes the orientation and position of wear facets on the occlusal surface. Subsequently the Occlusal Fingerprint Analyser (OFA) software (ZiLoX IT GbR) was developed within the Research Unit 771 of the German research foundation (DFG) (a link to the OFA Software and the manual is available in the supplementary information) and has been used to analyze the chewing path of extinct and extant mammals (e.g. Benazzi et al. 2011, 2013; Koenigswald et al. 2013; Kullmer et al. 2009, 2013; Schultz and Martin 2014). Existing hypotheses on occlusion and tooth movement can be tested by collision detection of polygonal tooth models following a user-defined pathway. Thruought the manuscript the term “OFA” refers to the software, “OFA analysis” to an analysis performed with the software, and “OFA path” to a path that was calculated as part of an analysis. 3D data was acquired by micro-computed tomography (μCT). UMZC Eo.CR.1 was scanned with a custom-built μCT system Nanotom 180 NF (phoenix|X-ray Systems + Services GmbH) with a CMOS detector (Hamamatsu Photonics) and a high-power transmission-type X-ray nanofocus source with a tungsten anode in the Department of Physics, University of Helsinki (6.9 μm voxel size) and NHMUK PV M26407 with the Nikon Metrology HMX ST 225 scanner (Nikon Metrology GmbH) at the Natural History Museum London (13.2 μm voxel size). Polygonal models were created using Avizo (8.1, Visualization Sciences Group). Later data processing, e.g. measurements and the reduction of triangles, was performed with Polyworks (2014, InnovMetric Software Inc.); the file format used was .stl (little endian). Polyworks was also used to create topographic maps. Slope maps were created with the software Slopemapcreator (1.0) developed at the Institute of Geosciences of the University of Bonn.

2.3.3 OFA-Simulation of Striations

In this study, we present a new application for the OFA. The relative jaw movement for an OFA analysis is determined by the striations, as evident from SEM images. However, the striations taken from SEM micrographs are lines on two-dimensional images, whereas the occlusal path is in three dimensions. Therefore, it needs to be tested whether the inferred virtual OFA occlusal path matches the actual chewing stroke. Though an OFA path for complex molar morphologies can easily be tested by reproducing collisions that match all observed facets correctly, this might not work with more simple molars (e.g. *Morganucodon*), as their morphology allows for multiple differently oriented virtual paths to produce similar collisions. In *Morganucodon* for example, a lower molar had the freedom to move straight orthally, orthally with a mesial component, or orthally with a distal component, and with slight changes to the starting position still to end up in the same centric occlusion and very similar occlusal contact (see results below). In order to overcome this problem, we developed a method for testing whether the striations observed on the SEM images can be reproduced in the chosen OFA path. Small, tetrahedron shaped 3D models were uploaded in the OFA software and placed on the wear facets of the upper dentition virtual models. These tetrahedron shaped 3D models simulate grit particles that would result in striations on the lower dentition in vivo. Subsequently, collision parameters were changed to limit the contact of the lower teeth to the virtual grit particle and the display of collision was extended over multiple time steps. This results in collision lines where the lower dentition passed along the 'virtual grit particles'. If the virtual chewing direction corresponds to the original one, the virtual striations will have the same orientation as the ones observed under the SEM on original tooth surfaces.

2.3.4 Facet Nomenclature

The term 'facet' can be applied either to describe an enamel surface that was polished by attrition from an antagonist (e.g. Butler 1952) or, in a broader sense, as a wear surface caused by abrasion and/or attrition; the latter is not limited to enamel but is also observed on exposed dentine (Crompton and Jenkins 1968). This definition may also include apical wear (Crompton and Jenkins 1967). A detailed revision of the term 'facet' is given by Schwermann (2014). Unless stated otherwise, we use 'facet' in the broader sense that includes abrasion and the exposure of dentine. Apical wear that is solely caused by abrasion and completely lacks an antagonistic structure is referred to separately.

Different nomenclatures have been proposed for facets (e.g. Crompton and Hiimäe 1970; Crompton 1971; Butler 1973; Maier 1980). However, since the homology of facets is often difficult to address there is no universal system in place (Schultz et al. 2017). Crompton and Jenkins (1968) used numbers from 1- 4 for the facets of *Morganucodon watsoni* (=*Eozostrodon parvus*). During the course of this study, we recognized that this system is too simple to address all details of wear in *Morganucodon*. Therefore, we follow the modular system for facet nomenclature recently proposed by Schultz et al. (2017). The new system is morphology-based, not limited to specific taxa and indicates the location of each facet on the tooth (Fig. 2.1). Each facet label consists of two parts: The first part describes the location of the facet and the second part the orientation of the facet. For example, a facet on the mesio-lingual side of cusp a is labeled 'a-ml'. Another advantage of this system is its flexibility allowing modifications in order to include additional information. We modified this system by adding a third part to some facet labels. This was necessary since early wear stages in *Morganucodon* often have two separate facets on the same cusp with the same orientation. One of these two facets is usually located apically (mostly an enamel facet) and the other one closer to the base of the cusp (usually a dentine facet). To differentiate between these two separate facets, we added a notation referring to the location of the facet on the cusp, with ‘ap’ for apical and ‘cv’ for cervical. Therefore ‘a-ml-cv’ would refer to a mesio-lingually inclined facet that is only located on the base of the cusp, and ‘a-ml-ap’ to a facet only located near the apex of the cusp (Fig. 2.1); facet ‘a-ml’ would extend over the entire mesio-lingual side of cusp a.

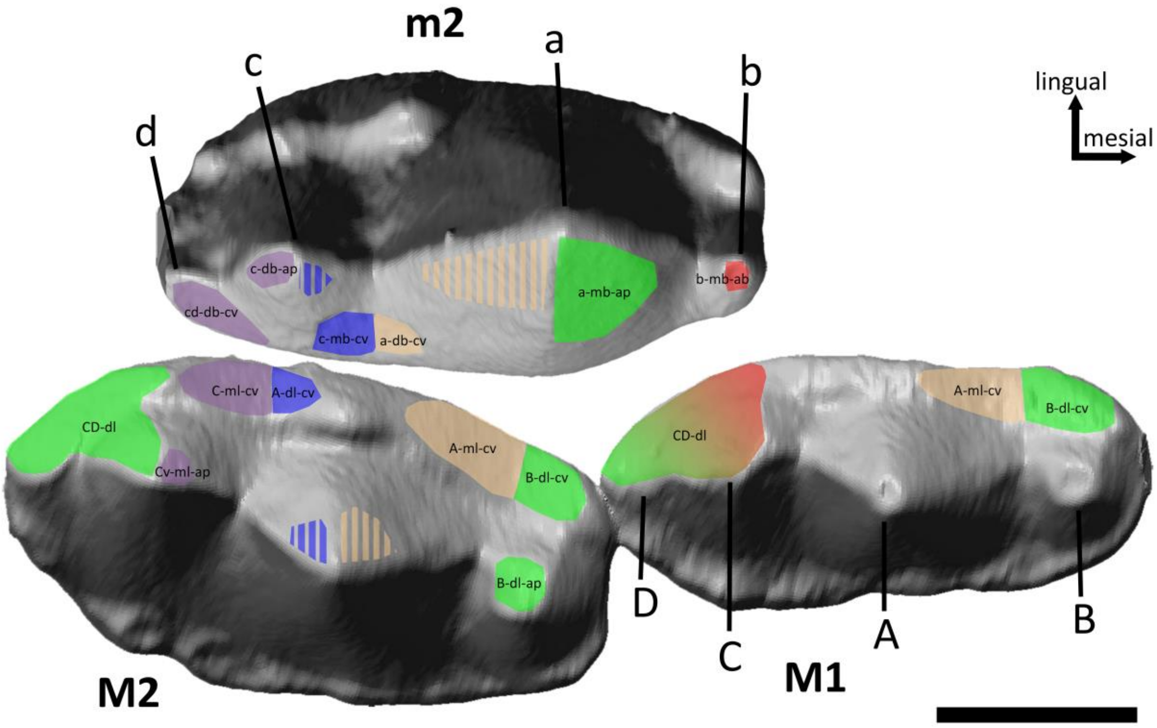

FIGURE 2.1. Facet terminology after Schultz et al. (2017). Left M1, M2, and m2 (the latter mirrored for better comparison) of *Morganucodon watsoni* (UMZC Eo.CR.1). The designation of facets is based on the morphological structure, the orientation, and optionally the information of facet position apically or cervically of the cusp (e.g. a-mb-ap is a facet at the apex of cusp a with mesio-buccal orientation). The color code represents corresponding facets. Note that the dashed areas on the cusp tips of a, c, and A represent contact areas for the corresponding facets, where facets are not yet visible due to thick enamel at the cusp tips. Scale bar equals 0.5 mm.

2.4 Results

2.4.1 Dental Morphology of *Morganucodon watsoni* UMZC Eo.CR.1

The tooth formula of UMZC Eo.CR.1 is ?I.?C.4P.4M/4i.1c.3p.4m (Fig. 2.2). Note that the lower premolars are p2-p4 and that p1 is either resorbed or not developed (for a detailed morphological description of the antemolar dentition and the root morphology see supplementary information).

Lower Molars—All lower molars show the triconodont pattern with three main cusps b, a and c in linear arrangement from mesial to distal, and a small distal cusp d. Additionally, a varying number of small cingulid cuspules is present on the lingual side. Among those, only cusps e and g (g=”kühnecone”) are constant in their position. All molars, except for the ultimates, are preserved in their natural position. The latter have moved partially out of their alveoli and are now inclined buccally in both dentaries.

The m2 is the largest and m4 the smallest molar, whereas m1 and m3 are similar in size, with m1 mesio-distally longer and higher than m3, and m3 linguo-buccally wider than m1. Cusp a is the dominant structure on every molar. This is most apparent for m2 where the difference in height between cusps a, b, and c is the largest. In relative cusp height, m1 and m3 are again more similar, with m1 having a slightly stronger cusp a. In m4 the height difference between the main cusps is the smallest. These proportions agree with the observation by Mills (1971) on *Morganucodon*.

The m1 differs from the other molars in having a pronounced furcation between the roots on the buccal and lingual side (Fig. 2.2D). The embrasure between cusps a and c is more acute in m1 and m2, compared to m3 where it is slightly more curved. This has also been observed on other specimens of *M. watsoni* and can be considered a general trait (pers. obs. PGG). The lingual cusps on m1 vary between the left and right dentary in the observed specimen. On the right m1, cusp e sits lingually to cusp b. This differs from the left m1 where cusp e is mesial to cusp b. A crest descends from cusp e in distal direction. On the right molar, this crest extends towards a small unnamed cuspule. The main difference occurs in cusp g, which is located in the valley between cusps a and c on the left m1. In the right m1, g is positioned slightly more mesially, closer to a than to c. Additionally, there is a second unnamed cusp of the same height, distally adjacent to cusp g. In both m1, cusp d is positioned low and almost underneath the mesial end of m2. Though there is a small space between p4 and m1, there is almost no space between m1 and m2.

The m2 is the largest lower molar. Though cusps b and c are similar in size to the corresponding cusps on m1 and m3, cusp a is higher, and mesio-distally as well as lingo-buccally much wider (Fig. 2.3). Cusp e is lingual to cusp b and slightly smaller. Cusp g is positioned on the disto-lingual side of cusp a and mesial of cusp c. Two additional small cuspules are present on the lingual cingulid between cusps a and c. On both sides, cusp d of m2 interlocks with cusps b and e of m3, whereas there is no similar contact between m1 and m2 possible, since the former is positioned considerably lower than the latter.

The m3 is shorter and wider than m2 and m1. The height difference between cusps a, b, and c is smaller and cusp c is more clearly separated from cusp a. The region between the bases of the cusps and the cervix is thicker, it also lacks the arch between the two roots that is visible on the lingual side of m1. There is no distal contact to m4; however, this might be due to post mortem movement of m4. A crest extends distally from cusp e on the lingual side. Cusp g is in the same position as in m2. It is smaller than in m2 but larger than in m1.

The m4 is smaller than its predecessors. Though reduced in size, it is not simplified in morphology, with all cusps present. Both roots are fused with a groove between. Similar to m3 the space between the cusp bases and the roots is prominent. The three main cusps are more similar in size than in the anterior molars, with approximately cusp a relatively doubled size of cusp c, and cusp b being slightly smaller than cusp c. Cusp e is very small. An additional cuspule is located mesio-lingually of cusp a. Cusp g is the largest of the cingular cusps and almost the size of cusp b, and sits disto-buccally to cusp a.

Upper Molars—There are four upper molars present. The M3 lacks its main cusp, and the crown of M4 was lost during preparation (Parrington 1978). Cusp A is the largest cusp followed by cusp C. On all upper molars, cusp C is slightly closer to A than cusp B. The upper molars differ from the lowers by having more similarly sized main cusps and a lingual cingulum, making them wider relative to their height (Fig. 2.2). Cusp D is small, only slightly larger than a cingular cuspule. Lingual to cusp B a cuspule E is present that contacts the preceding molar. The buccal cingula of the upper molars bears a number of small cuspules that are less pronounced than those of the lingual cingulids on the lower molars.

Posteriorly the upper molars become relatively wider, due to an increase in cingulum width (Table 2.1) (Mills 1971). M1 is the second longest upper molar, after M2. It is narrower than M2 and M3 because its lingual cingulum is less pronounced. The buccal cingulum is posteriorly more strongly developed and has more pronounced cuspules. Cusp D is barely

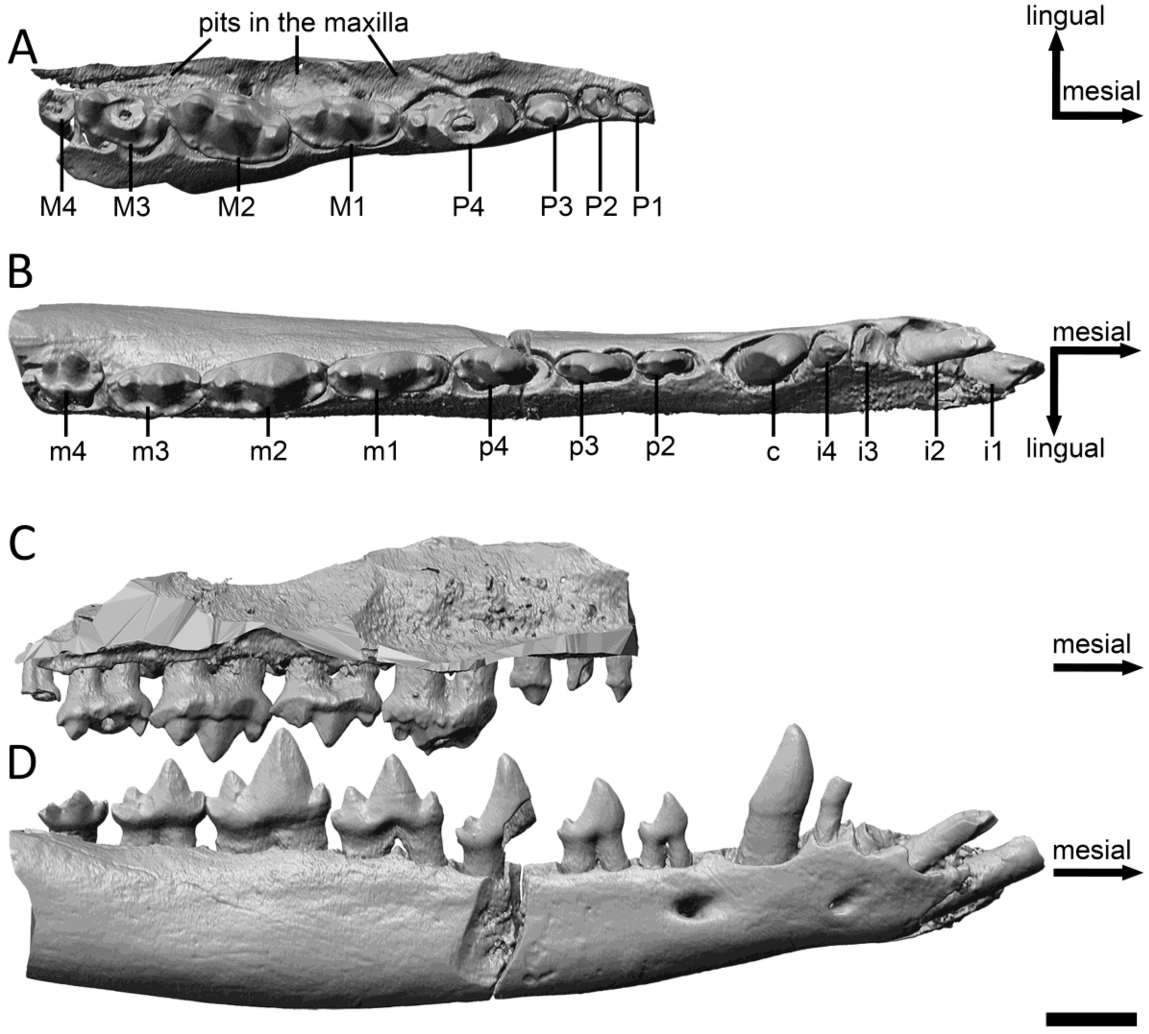

FIGURE 2.2. Left dentition of *Morganucodon* (UMZC Eo.CR.1). (A) upper tooth row in occlusal view, (B) lower tooth row in occlusal view (slightly tilted towards buccal for better visibility of the molar series), (C), upper tooth row in lingual view, and (D) lower tooth row in buccal view (mirrored for better comparison). Scale bar equals 1 mm.

recognizable due to wear. Compared to M2 and M3, M1 has the least pronounced cusps B and E. M2 and M3 are similar to M1 in morphology. However, both teeth have more pronounced, partially worn lingual cingula, which contribute considerably to their width, relative to M1. Another difference is the relative cusp height. Mills (1971) stated that the main cusps of the more posterior upper molars tend to be more equal in height. Although cusp A of M3 is damaged, the relative size of cusps B and C seem to support this observation.

Parrington (1971) and Kermack et al. (1981) noted pits in the maxilla of *Morganucodon* which accommodate cusp a of the lower molars. These are present in UMZC Eo.CR.1, and are located between the tooth loci of P5-M3. The pits for m1 and m3 are shallow, whereas the pit for m2 between M1 and M2 is deep (Fig. 2.2A, C).

Regarding the orientation of the upper molars, Mills (1971: 37) mentioned that within the maxilla “the long axis of the upper molars leans noticeably lingually”. This is also apparent in the posterior dentition of UMZC Eo.CR.1 (Fig. 2.4). Though the anterior teeth are oriented mesio-distally along the lateral margin of the maxilla, the molars do not follow this orientation. The alveoli of the posterior molars are shifted relative to the lateral margin of the maxilla. This is subtle in M1 with a change of 10° and more noticeable for M2-M4 with a change in orientation of 15° away from the lateral margin of the maxilla (Fig. 2.4A, angle α). Mills (1971) adds further that the individual teeth are at an angle to the line of the dentition. In UMZC Eo.Cr.1 this individual angle is in place only for M2-M4. It is caused by a lingual offset of the posterior roots relative to the tooth row, increasing the difference in orientation of M2 relative to the antemolar dentition to 28° (Fig. 2.4A angle β). With the slight angle of M1, the effective difference between M1 and M2 is 18°. This results in a wide triangular space between M1 and M2 into which cusp a of m2 can engage. This prominent shift in orientation beginning with M2 can be generalized for *M. watsoni*, since it was observed, additional to UMZC Eo.CR.1, in multiple maxillary fragments in the Cambridge collection.

An additional difference of the molars relative to the antemolar dentition, that has not been described so far, is the lingual inclination of the molars by 18° from the vertical (Fig. 2.4B angle γ). This is primarily expressed in the posterior positions and results in the roots pointing buccally and the apex of the cusps lingually.

TABLE 2.1. Width/Length measurements of P5-M3 of *Morganucodon* (UMZC Eo.CR.1) and *Megazostrodon* (NHMUK PV M 26407).

	P5		M1		M2		M3	
	Width/ Length		Width/ Length		Width/ Length		Width/ Length	
Morganucodon	0.57	1.32	0.57	1.28	0.77	1.44	0.6	1.1
Megazostrodon	0.63	1.4	0.54	1.55	0.67	1.29	0.61*	1.25

Note that the posterior molars of Megazostrodon are considerably wider if measured mesial or distal to the middle.

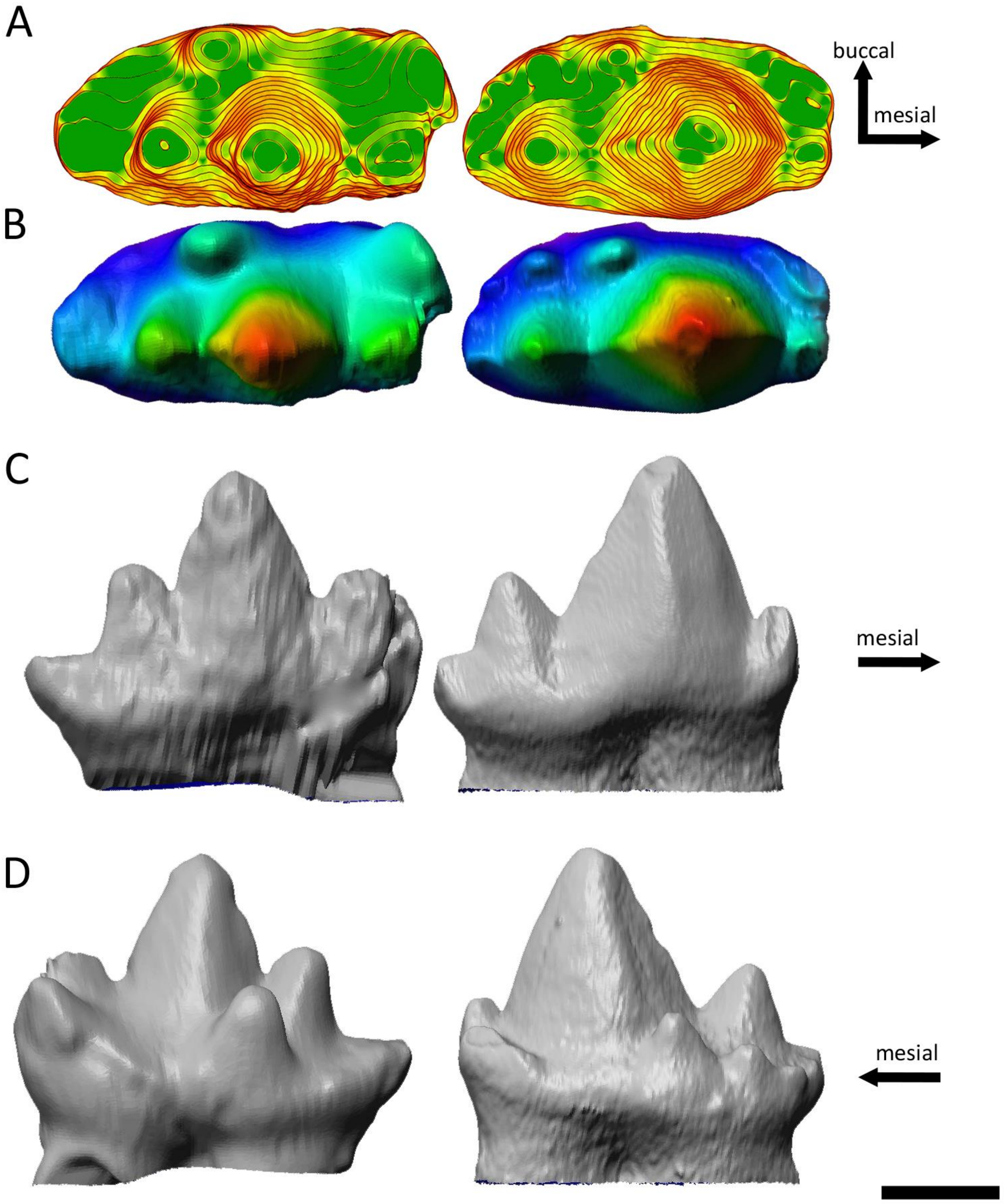

FIGURE 2.3. Comparison of the m2s of *Morganucodon* (UMZC Eo.CR.1) and *Megazostrodon* (NHMUK PV M 26407). The m2 of *Morganucodon* is dominated by cusp a, which covers almost the complete buccal-lingual extension of the tooth and its cusp tip located relatively mesially on the crown. *Megazostrodon* in comparison has a smaller cusp a, limited to the buccal side and more centered relative to the mesio-distal extension of the tooth. Cusp b of *Megazostrodon* is more isolated and larger than in *Morganucodon*, as are the buccal cingulum cusps E and G. Left: *Megazostrodon* Right: *Morganucodon*. (A) Slope map, steeper inclinations are dark red, less inclined areas green, (B) topographic map, high elevated regions are dark red, less elevated parts dark blue, (C) buccal view, and (D) lingual view. Scale bar equals 0.5 mm.

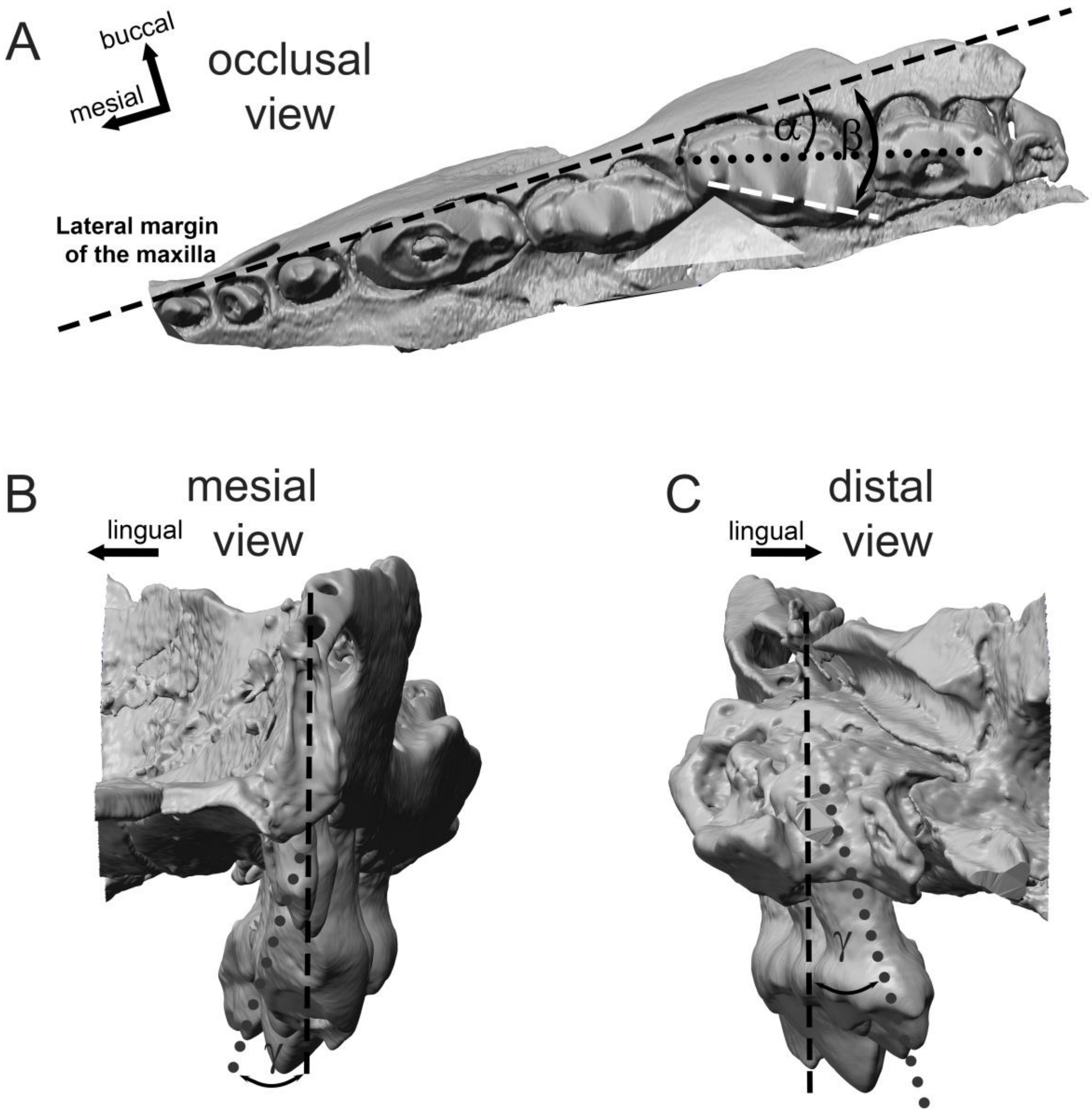

FIGURE 2.4. (A) Upper molar orientation in *Morganucodon* (UMZC Eo.CR.1). The antemolar teeth are oriented mesially parallel to the lateral margin of the maxilla (black dashed line), while the molars deviate from the lateral margin. While the deviation is subtle in M1 (10°), it is more evident in M2 and M3 by 15° (black dotted line, angle α). Additionally, M2 and M3 are further rotated so that their posterior roots are positioned slightly more lingually than their anterior roots, relative to the black dotted line, which causes additional lingual deviation to a total of 28° (white dashed line, angle β) for the cusps of these teeth. This results in an effective difference in orientation between M1 and M2 of 18°, generating a wide triangular space between M1 and M2. Its center hosts the pit in the maxilla, in which cusp a of m2 enters during occlusion. (B, C) The lingual inclination of the molars from mesial and distal view. The molars are inclined by 18° (grey dotted line, angle γ), which also affects the roots that are inclined buccally within the maxilla (the fragmentary M4 has been removed for better visibility).

2.4.2 Comparison of UMZC Eo.CR.1 to Other Species of *Morganucodon*

Four lower molars is the most common molar count in *M. watsoni*, although sometimes a fifth molar can be present. Based on the preparation of jaw fragments with four molars, Mills (1971) suggested that the presence of a fifth lower molar is due to variability rather than an ontogenetic phenomenon. Though the specimen in this study was most likely a young individual, all molars are erupted and were fully functional. Since there is no evidence for a tooth germ of a late erupting fifth molar visible in the CT-scan, we concur with Mills´ (1971) interpretation.

Luo et al. (1995) noted that the longest tooth (mesio-distal extension) in the Chinese species *Morganucodon oehleri* is M2, in *M. heikuopengensis* M1, and in *M. watsoni* the ultimate upper premolar. However, this is not the case in this specimen UMZC Eo.CR.1. P4 is 1.32 mm long, whereas M2 reaches 1.44 mm. Even if wear on P4 is taken into account, it is unlikely that it would have surpassed M2 in mesio-distal length. On the other hand, if height is considered instead of length, P4 is the largest tooth in this specimen of *M. watsoni*. This is considerably different from the P4 known for *M. oehleri*, which is less high than M1 and M2. It is an interesting difference that, when the upper dentition is considered, *M. oehleri* appears to have mostly relied on its three molars for food processing. *M. watsoni* on the other hand not only had one additional upper molar, but the wear on P4, which is similar to that seen on the molars (see below), suggests that it most likely shared some of their functions when it came to food processing.

The upper incisors of *M. oehleri* are small and peg-like, whereas the lowers are not preserved (Luo et al. 1995). The *M. watsoni* specimen described here has no upper incisors preserved. The lower i1 and i2 are relatively large and their shape and positioning suggest that they functioned like tweezers. Considering the small size of the upper incisors of *M. oehleri*, it appears as if this morphology would not make them suitable antagonists for the lowers of *M. watsoni*. Parrington (1971: 253) noted that the posterior upper incisors of *M. watsoni* have cuspules at the posterior base of the crown and that they therefore are “almost indistinguishable from the anterior premolar”. Based on the few existing drawings of upper incisors of both taxa, it is possible that both species might have differed in their incisor morphology and that that those of *M. watsoni* were relatively larger.

2.4.3 Wear Facets of UMZC Eo.CR.1

Premolars—There are traces of apical wear present on the premolars, which in some cases extends on the occlusal side of the main cusps towards the cervical margin. An absence of wear has formerly been reported for isolated anterior premolars of *Morganucodon* (Mills 1971). Wear on the molariform P4 is similar to that seen on molars. It shows a large mesio-lingual facet at the base of its main cusp A-ml-cv, and two small disto-lingual facets C-dl-ap and C-dl-cv. To A-ml-cv there is a corresponding disto-buccal oriented facet on the lower p4 a-db-ap.

m1—Among the first three lower molars m1 is the least worn, which has been reported also for other specimens of *Morganucodon* (Parrington 1978). Cusps a and c on the left and right m1 are unworn except for minor apical wear. Cusp b shows a facet on the mesio-buccal side of both m1 (b-mb), with the one on the right m1 being slightly larger. Two wear facets on the disto-buccal side of cusp a and the mesio-buccal side of c are present on the left m1 (a-db-cv, c-db-cv), but are absent on the right m1. Both molars have a wear facet on the disto-buccal side of cusp d (d-db).

m2—A large enamel facet (a-mb-ap) is present on the apical part of the mesio-buccal flank of cusp a on both m2. It extends from the apex almost down two thirds of the cusp height towards the base (Fig. 2.1). The wear in the embrasure between cusps a and c has been treated as one single facet by previous authors (Crompton and Jenkins 1968; Mills 1971). However, the worn area caused by the antagonistic cusp A has two different inclinations (mesial and distal) and therefore is divided into a mesial (c-mb-cv) and a distal (a-db-cv) facet (Fig. 2.1). Left and right m2 show similar wear facets. The only notable differences are a facet on the buccal side of cusp b (b-b) on the right m2, which is smaller and more mesially oriented on cusp b of the left m2 (b-mb-ap), and the absence of a disto-buccally oriented facet near the apex of cusp c (c-db-ap) which is present on the left m2. The posterior cusps c and d have a distally oriented facet at the base of cusp c that merges with cusp d (cd-db-cv).

Facets on the bucco-distal apex of a and bucco-mesial apex of c were expected due to wear on the upper antagonist but were not detected at this stage (see dashed areas in Fig. 2.1).

m3 and m4—The m3 is more strongly worn than the other molars. Although overall still similar in the expression of the facets, a comparison of both m3 shows greater differences between them relative to the left-right differences of the anterior molar positions. On the right m3, cusp b and the anterior flank of cusp a have two wear facets b-mb and a-mb-cv with slightly different orientations. The distally oriented facet a-db-cv is present on both molars.

The left m3 shows the adjacent facet c-mb-cv similar to m2 and m1. On the right m3, a substantial amount of cusp C is already worn, with a facet c-mb extending over the entire cusp. Cusp c on the left m3 has a large facet cd-db on its posterior flank that extends down to cusp d. Cusp d of the right m3 has an isolated facet d-db.

It appears as if the antagonist of the right m3 was positioned slightly more posteriorly resulting in stronger wear on the mesial side of c and less wear on the distal side of d. The left m4 is unworn, whereas the right m4 has apical wear on cusp b.

M1—The anterior part of the lingual cingulum is worn and two facets are present between A and B (B-dl-cv and A-ml-cv). Additionally, one large wear facet CD-dl extends over cusp C and D (Fig. 2.1). Wear on A and B of M1 is limited to apical wear only and was most likely not caused by contact with an antagonist but rather solely by attrition.

M2—The disto-lingually oriented facet CD-dl of M1 extends onto cusp B of M2 with the same orientation (B-dl-cv and B-dl-ap). B-dl-cv adjoins a mesio-lingually oriented facet A-ml-cv at the lingual cingulum. A similar situation occurs between cusps A and C where two facets A-dl-cv and C-ml-cv are situated next to each other on the cingulum. Above C-m-cv is a similarly oriented facet near the tip of C (C-ml-ap). Cusps C and D have a disto-lingual facet (CD-dl) similar to the one on M1 but slightly expressed, so that the outline of the cingulum is still visible (Fig. 2.1).

M3—Cusp B lacks a distally oriented facet, which is present on M1 and M2, but the cingulum on the anterior and posterior sides of A is worn (A-ml-cv and A-dl-cv). Though the mesial side of cusp C has a pronounced facet C-ml-ap, the presence of a small, similarly oriented facet C-ml-cv on the cingulum beneath remains ambiguous.

Since A is damaged it cannot be ruled out that there were facets on the sides of the cusp, but, given the pristine nature of cusp A of M1 and M2, this seems unlikely.

An overview of the wear facets present in UMZC Eo.CR.1 is available in the supplementary data (Supplementary Figs 2.1, 2.2).

2.4.4 The Influence of Enamel Thickness in Morganucodon and Megazostrodon on Observable Wear

In early ontogenetic stages of *Morganucodon* and *Megazostrodon*, wear on molars often occurs at the accessory cusps and near the base of the main cusps (Fig. 2.1). In *Morganucodon* this can be explained by the enamel thickness, which is thin at the base of the cusps so that dentine is easily exposed (pers. obs. PGG). Therefore, the dentine facets are more visible and might occur earlier than enamel facets close to the tips of the cusps. It is likely that this condition is also present in *Megazostrodon*.

2.4.5 Striations

Striations are microscopic scratches which occur on the facets during the chewing cycle (Gordon 1984). They are aligned parallel to the direction of tooth motion and therefore yield information on the relative movement. They have been used to determine different phases in the chewing cycle (e.g. Butler 1972; Schultz and Martin 2014). The tooth morphology can help to determine the exact direction along the striations (Butler 1972). Additionally, the direction of motion may be deduced from the wear of dentine on leading and trailing enamel edges on the occlusal surface (e.g. Greaves 1973; Rensberger 1973; Costa and Greaves 1981; Krause 1982; Kaiser and Fortelius 2003; Schultz et al. 2014).

In *Morganucodon* teeth, striations occur mostly on the enamel. On exposed dentine, only deep scratches are visible. Facets a-mb-ap and a-db-ap have the most pronounced striations. Due to the high crown relief and the necessity to incline the teeth in various directions in order to make the striations visible, it was not possible to make standardized measurements that refer to a reference plane. Therefore, given angles are mostly approximations (marked by '~') except when the angles between striae of the same specimen were measured. No striations were observed on UMZC Eo.CR.1. This is most likely because the specimen was only available for regular light microscopy, whereas striations on *Morganucodon* teeth usually require SEM to be visualized. We therefore observed isolated upper and lower molars to determine striation orientation in *Morganucodon*. In most of these isolated molars that were studied under SEM, the majority of striations had a similar orientation, which will be referred to as the predominant orientation (Fig. 2.5). Additionally, when a predominant orientation was present in some cases a small number of striae could deviate up to 40° from the predominant orientation. Some specimens did not exhibit any predominant orientation of striations. One of these (UMZC Eo.M(Lr).16) has posteriorly oriented striations on the anterior side of cusp a and anteriorly oriented striations on the posterior side of cusp a and the anterior side of cusp c. In *M. watsoni* a high degree of intra-specific variability is present, since the predominant orientations differ considerably between individuals. Three different predominant orientations have been observed: (1) vertical, (2) angled towards anterior, and (3) angled towards posterior. The posteriorly angled type appears to be the most common, but this should be validated with a larger sample size in the future. When oriented predominantly vertically, the striations are close to 90° from a lingual view relative to a hypothetical occlusal plane. The other orientations differ each by up to ~20° from the vertical one, which results in an overall intra-specific variability of the predominant orientation in *M. watsoni* of ~40°. This corresponds with the range of individual variability as mentioned above.

We do not think that tooth position was the deciding factor for the different orientations that have been observed. The isolated teeth, with the exception of UMZC Eo.M(Lr).32 are all likely to be second molars. UMZC Eo.M(Lr).32 is an m1 but shows the similar predominantly vertically inclined striations as AMNH 93800. Also, the first three molars are confined to a small region of the tooth row and, as stated above, individual teeth can show a wide range of orientations.

2.4.6 OFA-Reconstruction of the Masticatory Path of *Morganucodon watsoni*

For the OFA analysis, a path was chosen with a posterior movement of approximately 10°, since this striation direction was the predominant one on the isolated molars examined. However, it has to be noted that the other observed chewing directions resulted in similar collision patterns, when tested with the OFA. The similarity in collision pattern in multiple OFA analyses with differently oriented paths was achieved by slight variation of the starting position. A path with a ~10° mesial inclination initiated from a slightly posterior starting position resulted in a similar centric occlusion as a distally oriented one from a more anterior starting positon (Supplementary Fig. 2.3) The preferred chewing direction of specimen UMZC Eo.CR.1 remains unclear due to the absence of observable striations. With the variety of striae observed on the isolated molars it appears that the entire range of potential chewing directions was at least occasionally used. The OFA analysis was performed with m2, m3, M1, and M2.

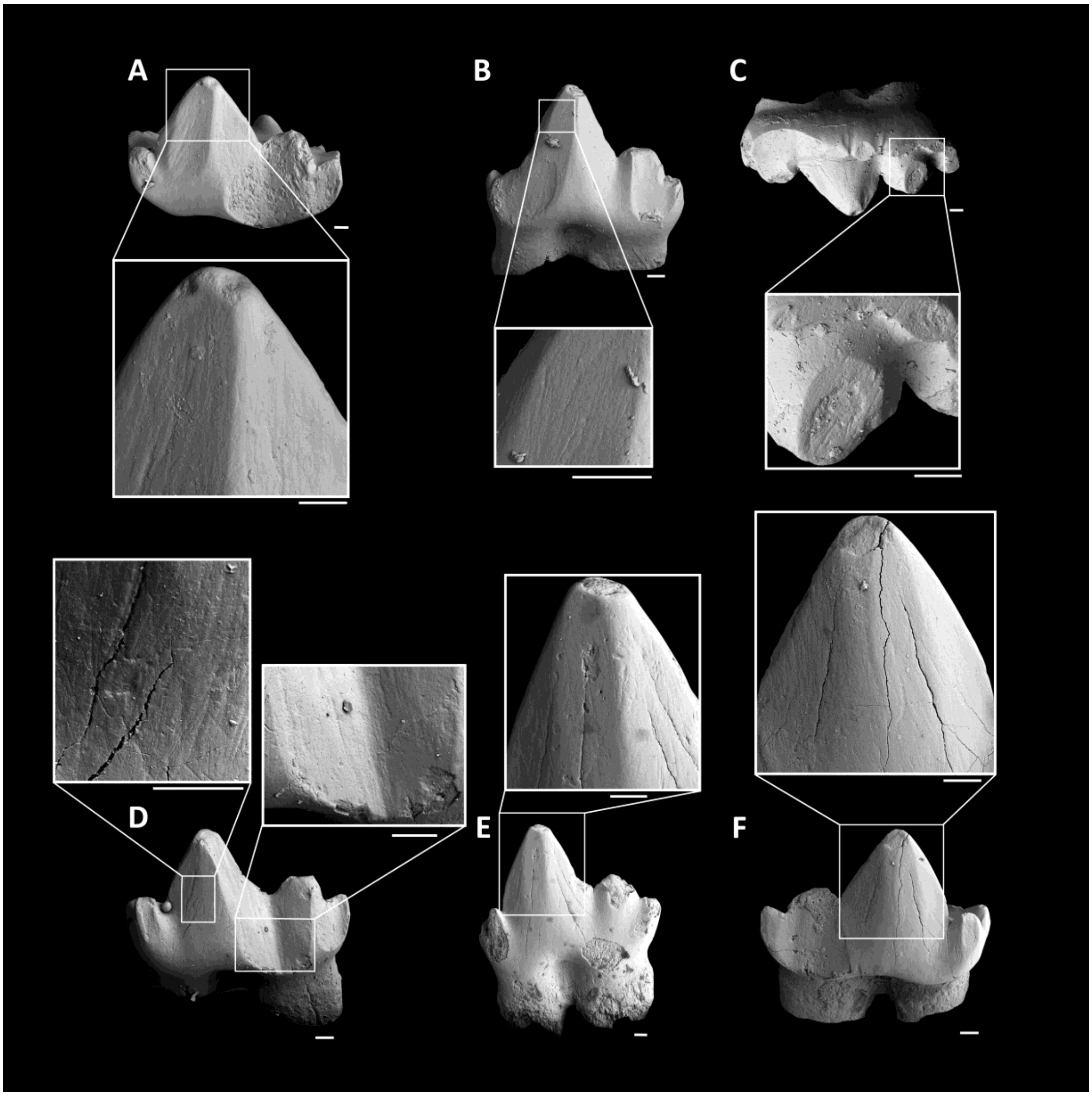

FIGURE 2.5. SEM images of isolated upper and lower molars of *Morganucodon watsoni* with different striation patterns. (A) Left lower molar with predominantly vertically inclined striations (AMNH 93800), (B) left lower molar with predominantly posteriorly inclined striations (UMZC Eo M(Lr).32), (C) right upper molar with predominantly posteriorly inclined striations (UMZC Eo.M(Ur).5); (D) left lower molar with no overall predominant inclination, but rather separate facets showing differently inclined striations (UMZC Eo.M(Lr).16), (E) left lower molar with predominantly anteriorly inclined striations (NHMUK PV M 100308), and (F) right lower molar with no predominant striation inclination, but striations overlapping with a range of inclination of 40° (NHMUK PV M 100304). Mesial is to the left (A-E) and to the right (F). All teeth are m2/M2 with the exception of UMZC Eo.M(Lr).32, which is an m1. Scale bars equal 100 µm.

During occlusion, the first contact is between the mesial apex of cusp a of m2 (facet a-mb) and cusp D of M1 (D-dl) and the distal part of cusp B of M2 (B-dl-cv) (Fig. 2.6A) (Appendix 2). This is followed by contact between cusp c of m2 (c-mb) with the distal apex of cusp A of M2 (A-dl-ap). When the lower dentition continues moving upwards and slightly posteriorly, cusp A of M2 enters between the embrasure of cusps a and c of m2. This results in the observed facets a-db-cv and c-mb-cv (Fig. 2.6B). At the same time the apex of cusp a of m3 enters between M2 and M3 in a similar fashion to the anterior molars. However, there is a notable difference in the arrangement of the upper molars. The vertex of the triangle formed between M1 and M2 is distal to cusp B of M2, whereas the vertex of the triangle between M2 and M3 is between both molars (Fig. 2.4A). Therefore, m2 and m3 occlude in different ways with their antagonists. Cusp a of m2 moves along the distal flank of cusp B of M2 (B-dl-ap and B-dl-cv) and attains full occlusion between A and B. Cusp a of m3 engages between M2 and M3.

In m2 the distal apex of cusp a does not make contact with the mesial side of cusp A of M2 (Fig. 2.6B yellow contact of *Morganucodon*) but only with the lingual cingulum beneath cusp A (A-ml-cv). This observation supports Mills´ (1971) hypothesis that the cingulum of the upper molars was used to prevent attrition between the main cusps.

The next collision occurs on the distal side of cusp C of M2, which contacts the mesially oriented side of cusp b of m3 and results in the corresponding facets C-dl and b-mb (Fig. 2.6B green contact area between M2 and m3 in *Morganucodon*). At M1 and m2 this contact of the posteriorly oriented facet of cusp C and the anterior facet of cusp b is also established (displayed as red contact area in Fig. 2.6B, since the facet on cusp b is still separated from cusp a in m2). Subsequently, the mesial side of cusp C of M2 reaches cusp d of m2 (C-ml and d-db). At the same time, cusp c of m2 contacts the upper lingual cingulum above A (A-dl-cv) and maximum intercuspation is attained. After this, no new contacts are established (Fig. 2.6C) and the cusps move further past each other until cusp a of m2 enters the pit in the maxilla and subsequently stops. There is no phase II of the power stroke present, unlike in tribosphenic molars (Hiimäe and Kay 1972; Schultz and Martin 2014).

The path is oriented towards lingual and distal (as noted above) with a direction of 101° (0° would represent an exact mesial movement and 90° a lingual translation without a mesial-distal component). It is predominantly orthal with a transverse component at a dip angle of 77° (Fig. 2.7). The direction of movement, which was reconstructed from the striations observed on SEM images, was tested by simulating striations using the OFA. The virtual striations and the striae observed on isolated molars are in accordance with this reconstruction (Fig. 2.8) (Appendix 2).

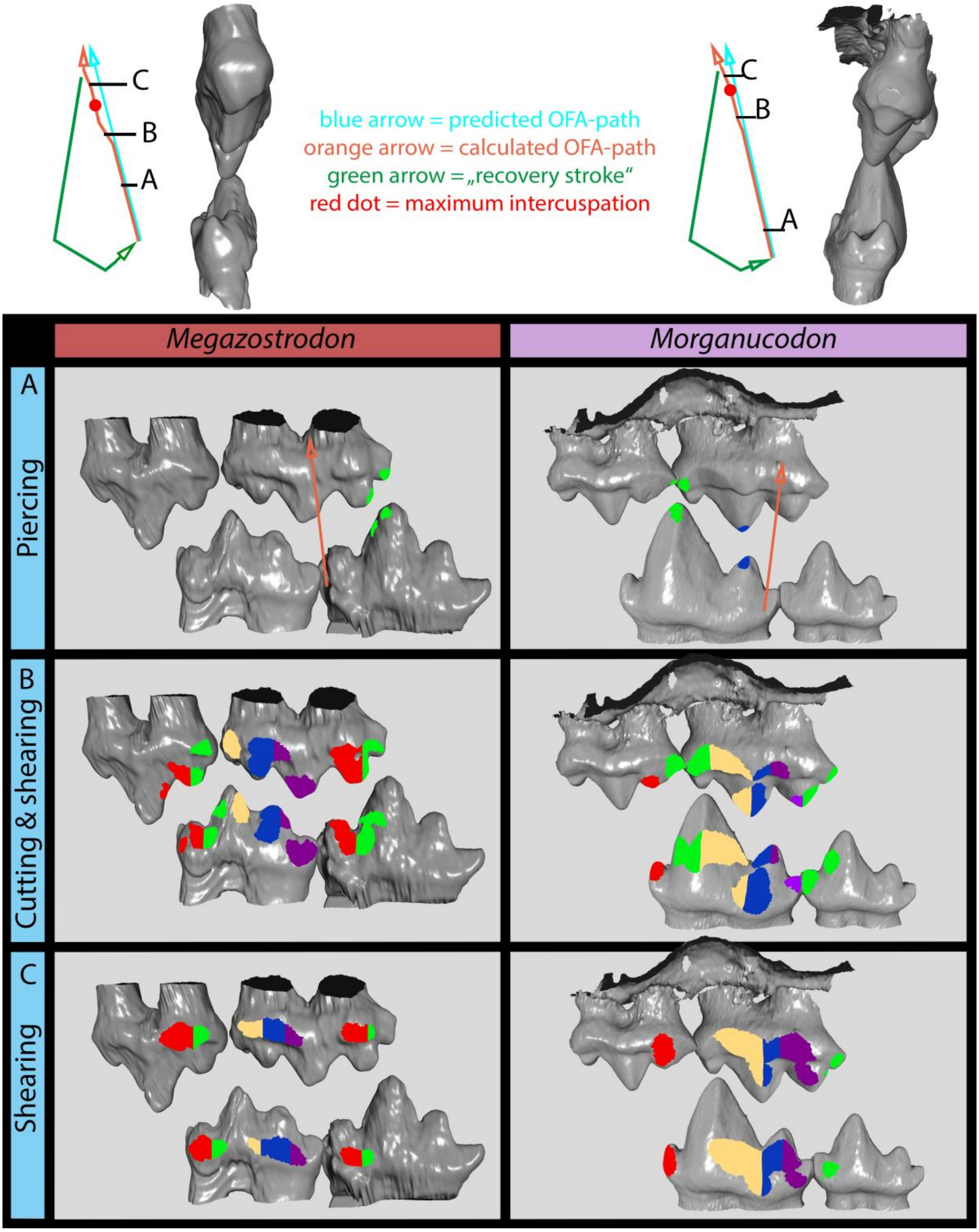

FIGURE 2.6. Collision detection on left upper and lower molars during the masticatory cycle of *Morganucodon* (M1, M2, m2, m3) and *Megazostrodon* (M1, M2, m1, m2). **Above**: The starting position with the tip of cusps a/A at the same height marks the beginning of the calculated chewing path; positions A, B, C refer to points in the chewing cycle depicted below. Blue arrow, predicted path; orange arrow, calculated path of the power stroke; green arrow, estimated recovery and preparatory stroke; red dot, maximum intercuspation. The models are seen from a mesial view, buccal to the right. **Below**: (A) initial contact, piercing of the food, (B) all cusps are in contact, shear-cutting along the crests and shearing along the flanks, while the amount of space for food in between the antagonists is reduced constantly, and (C) maximum intercuspation, with the apex of the main cusps past their antagonist, pure shearing with no space remaining between the antagonists. The upper images are in mesial view. Mesial is to the left. Note that the difference in position between (A) and (B) of the lower molars resembles the amount of mesial/distal movement of the analyzed path. The lower molars are placed underneath the uppers for better visibility, therefore there is no positional change to visualize the orthal movement. Mesial is to the left, upper molars are seen from lingual, lowers from buccal. Teeth at the same scale (lower molars mirrored).

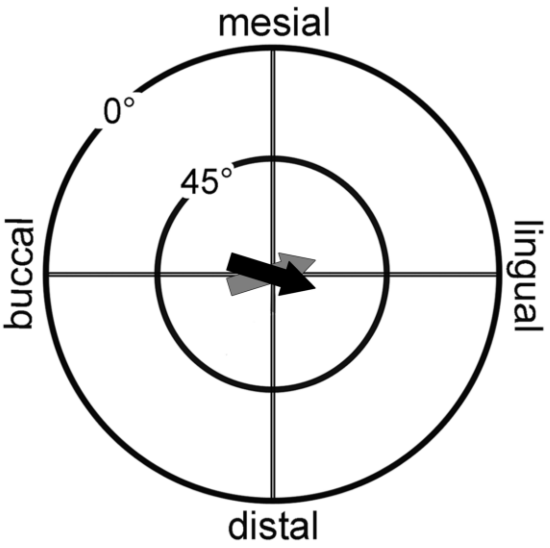

FIGURE 2.7. Mastication compass for *Morganucodon*. Arrow directions indicate the orientation of the power stroke. The black arrow marks the maximum distolingual and the light grey arrow the maximum mesiolingual range. The inclination of the power stroke is indicated by arrow length (70-80°). The single phased stroke has a point of maximum intercuspation, but subsequently the teeth continue to pass along each other without any change in direction or inclination, which is indicated by the arrow surpassing the central point.

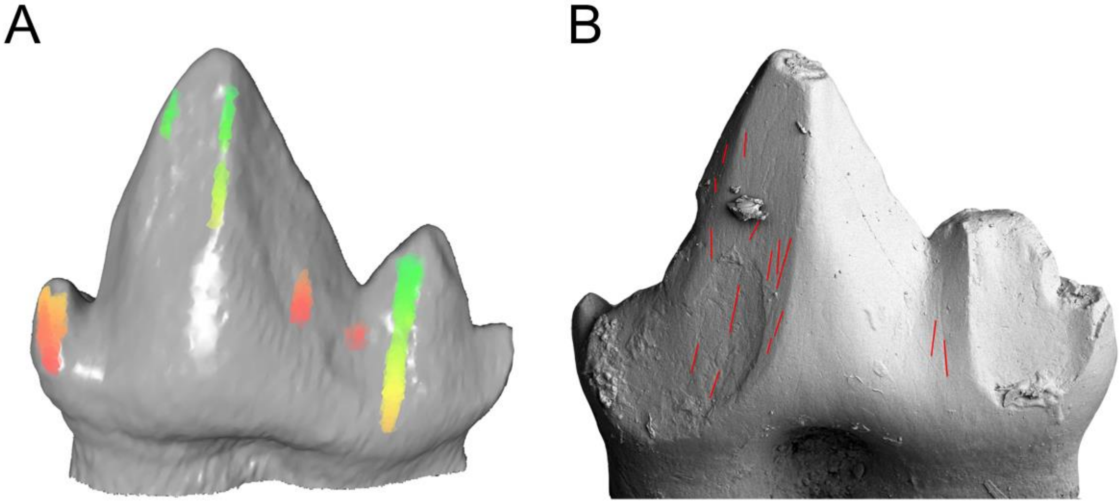

FIGURE 2.8. Striation simulation for testing the OFA path based on the direction derived from the striations observed in the SEM images. Small virtual grit particles were included in the OFA path used in this analysis. With a modification of the collision settings (collisions were reduced to contact with the particles and displayed for multiple time steps) we were able to create virtual striations. These virtual striations caused by the OFA path have the same orientation as those observed in the SEM images of isolated molars with predominantly posteriorly oriented striations. This demonstrates that the inclination of the OFA path accords with the inclination of the chewing path of these specimens. (A) Simulated striations based on the OFA path used in this study on the second lower left molar (UMZC Eo.CR.1) and (B) SEM images of a cast of an isolated m1 with striations highlighted by red lines (UMZC Eo.M(Lr).32).

2.4.7 *Megazostrodon* Tooth Positions

According to Crompton (1974), the tallest tooth in the upper tooth row of *M. rudnerae* is M1. Our interpretation of the tooth positions differs from Crompton´s (1974) original description. We consider the tooth described by Crompton (1974) as M1 to be the last upper premolar (P5), and the subsequent molars as M1-4. In Crompton´s (1974) original description some morphological aspects of the right upper and lower teeth were unclear because the teeth of the holotype specimen are partially preserved in occlusion.

From our µCT data it became evident that the lower dentition had been shifted postmortally and requires a reposition by almost one tooth position posteriorly in order to exactly fit with the uppers, see supplementary data (Supplementary Fig. 2.4). Apparently the lower jaw was slightly pushed forwards during decomposition and when the skull was crushed. Following our new interpretation, the lower teeth match the spaces between the corresponding upper teeth much better. This is most apparent in linguo-ventral view (Supplementary Fig. 2.4). According to Crompton (1974: 407, Fig. 5A) the tooth originally identified as p3 was positioned anterior to P1 , whereas in our interpretation p3 is positioned between P2 and P3. Our new interpretation is supported by the OFA analysis (Appendix 2) that demonstrated a better fit of upper and lower tooth rows and produced matching contact areas along the flanks of teeth involved. An OFA analysis using Crompton´s (1974) interpretation of tooth positions shows a poor fit of the tooth rows and gaps where teeth are not in contact, resulting in less and scattered contact areas

The tooth positions of specimen BP/1/4983 correspond with our new interpretation. In this older individual, the teeth are more worn, and the preserved ultimate upper premolar is higher than the first upper molar, which itself is elongated. This height and length difference between ultimate upper premolar and first upper molar also occurs in the holotype NHMUK PV M 26407 when our new interpretation is applied. In the upper tooth row more similarities between BP/1/4983 and NHMUK PV M 26407 are apparent: following our new interpretation, both specimens show a long M1 but shorter and wider M2.

Gow (1986) stated that the last three upper premolars are double-rooted. From the µCT scans, it is evident that the newly interpreted ultimate and penultimate upper premolars (P5 and P4) of the holotype NHMUK PV M 26407 have two roots, and the P3 has one wide single root which can be interpreted as two fused roots. This also appears to be the case for P3 of BP/1/4983. The tooth is rather small and its roots are not exposed. Possibly Gow (1986) interpreted the wide root of the P3 as being two separated roots. Although Crompton (1974) described P3-P5 as having two roots, the µCT data reveal that (based on his positional interpretation) only the ultimate upper premolar of NHMUK PV M 26407 has two clearly separated roots. Based on the new interpretation provided here, the ultimate and penultimate premolars are double rooted, whereas P3 has a single fused root, similar to BP/1/4983. Neither the more complete right maxilla nor the fragmentary left maxilla of NHMUK PV M 26407 have all upper premolars preserved (Crompton 1974: 406-407, Fig. 4A and 5A). The left anteriormost premolar preserved is large and has been interpreted as P2 by Crompton (1974). It is followed by fragments of two smaller premolars, a large double rooted premolar (interpreted by Crompton as P5) and a tooth fragment that was interpreted as the M1 by Crompton (1974) and which we consider as the ultimate premolar.

In the right maxilla, the condition is similar to a large single rooted anteriormost premolar which was interpreted as P1 by Crompton (1974). It is followed by a damaged area with no tooth preserved where presumably a smaller P2 had been (Crompton 1974: 407, Fig. 5A). Since BP/1/4983 has only five upper premolar positions, and P4 and P5 resemble the ultimate and penultimate of NHMUK PV M 26407, we think that the left maxilla holds a complete premolar series of P1-P5 (instead of P2-M1 as interpreted by Crompton 1974). In the right maxilla either all premolars are preserved and the most anterior tooth is P1 followed by a diastema and subsequent P2, or the most anterior tooth is a small canine and the empty space was occupied by the missing P1. The interpretation of the presence of P1-5 in the right maxilla is supported by the size ratios of the premolars that match those of the left maxilla, and no missing tooth was revealed by the µCT analysis.

2.4.8 Dental Characters of *Megazostrodon rudnerae*

The right M2 of NHMUK PV M 26407 has fused roots with only a groove on the buccal side and a slight separation at the distal end. The anterior part of the root is much wider and the root does not extend distally beyond cusp A (Fig. 2.9). The roots of M1 and M3 are fully separated, which is also the case for the roots of the M2 of specimen BP/1/4983. This suggests that the fusion of the M2-root of specimen NHMUK PV M 26407 represents individual variation.

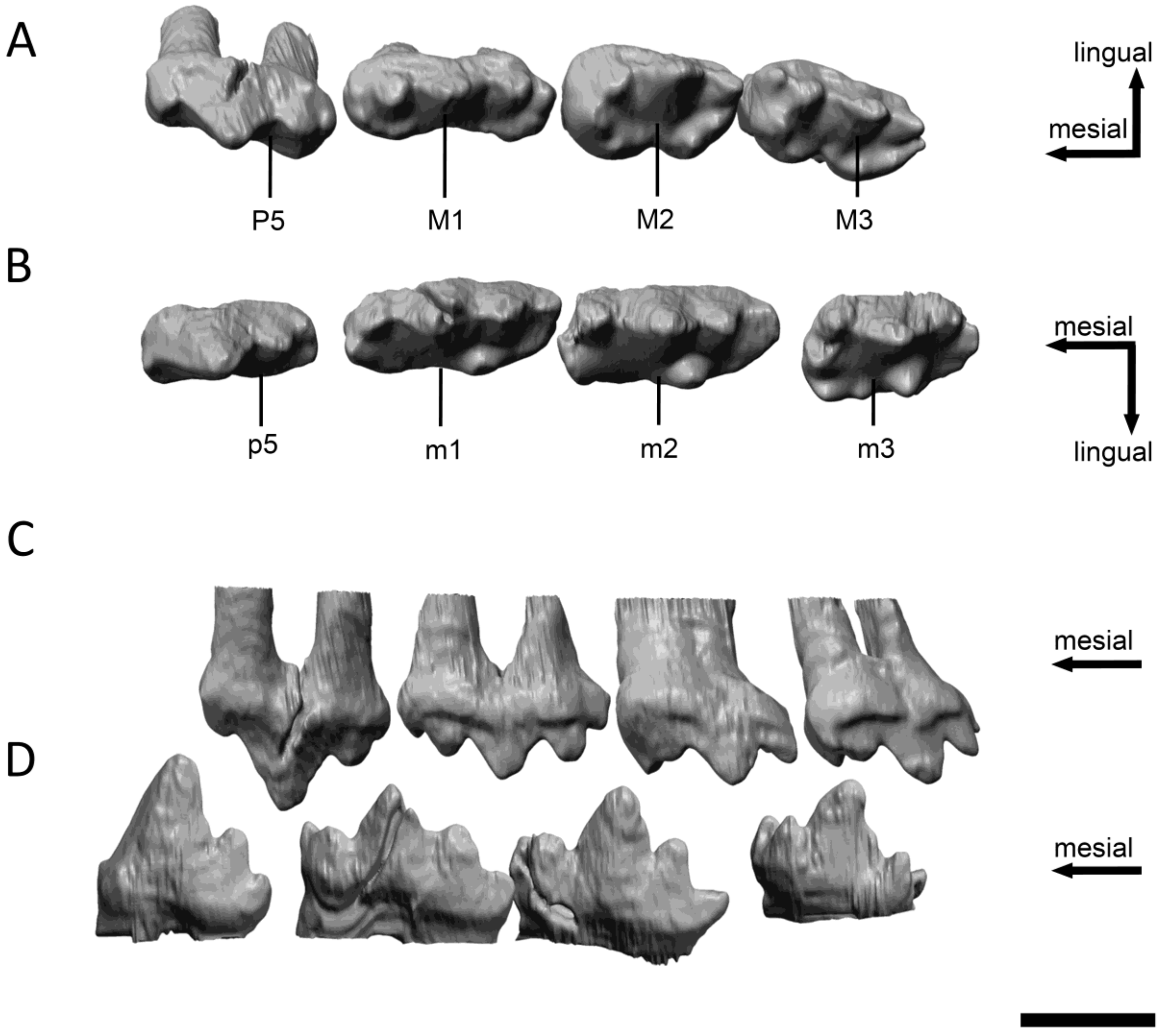

FIGURE 2.9. Right dentition of *Megazostrodon* (NHMUK PV M 26407). The M2 has a fused root that is positioned mesially underneath the tooth. It seems likely that this is individual variation, since M3 has separated roots. (A) Upper tooth row in occlusal view, (B) lower tooth row in occlusal view (slightly tilted towards buccal for better visibility of the molar series), (C) upper tooth row in lingual view, and (D) lower tooth row in buccal view (mirrored for better comparison). Scale bar equals 1 mm.

Gow (1986) assumed for BP/1/4983 a replacement of the left m2 based on inconsistencies in the amount of wear of adjacent molar positions and the antagonists. However, the scan of the ontogenetically younger specimen (based on the amount of wear) NHMUK PV M 26407 yielded no evidence for replacement of the m2.

Similar to *Morganucodon,* both specimens of *Megazostrodon* show a lingual inclination of their posterior upper molars, relative to the anterior dentition. Due to damage, no exact angle could be measured. The molars of both taxa show some morphological differences, which have been discussed in previous studies (e.g. Crompton 1974). Here we focus on the aspects that are relevant to understanding their occlusion. Compared to *Morganucodon*, all molars of *Megazostrodon* are more similar in cusp height for the three main cusps. This is primarily due to cusps a/A being less dominant in *Megazostrodon*. Furthermore, cusps a and c of the lower molars are closely together in *Megazostrodon* but stand wider apart in *Morganucodon* leaving space for the large upper cusp A to enter. The upper molars of *Megazostrodon* exhibit more morphological variation along the toothrow than those of *Morganucodon,* which are similar in shape and differ only in size and inclination (Fig. 2.2A, C). In *Megazostrodon* M1 differs from the posterior upper molars by being longer and narrower. Starting with M2, the upper molars are shorter and have very pronounced buccal cingula, which gives them a bulky appearance (Fig. 2.9). Both *Megazostrodon* specimens have pits in the maxilla, similar to those known for *Morganucodon* (Kermack et al 1981). However, they are generally less deep, and the deepest is between M1 and M2, instead of between M2 and M3 as in *M. watsoni*.

2.4.9 Facets of *Megazostrodon* NHMUK PV M 26407

The left dentary is isolated and shows an early stage of wear. The buccal side of the right dentary and the lingual side of the right maxilla are obscured by matrix (Crompton 1974) and only accessible via µCT scan. Therefore, the reconstruction of the wear facets on the right dentition is based on the µCT data, which implies that less pronounced facets may have been missed. However, similar to UMZC Eo.CR.1, the facets appear to be generally consistent on both dentaries (Table 2.2).

TABLE 2.2. Wear facets on the dentition of *Megazostrodon* (NHMUK PV M 26407).

	Wear on cusps			
Tooth position	b	a	c	d
p5 (left)				d-db
m1 (left)	b-mb		c-db-ap	d-b
m2 (left)	b-mb-ap	#		d-db-ap
m3 (left)	b-mb-ap			d-db-ap
p5 (right*)		a-mb-cv		d-db
m1 (right*)	b-mb		c-db-ap	d-b
m2 (right*)	b-mb-ap			d-b
m3 (right*)	-	-	-	-
P5 (right*)	B-ml		C-dl-ap (?)	
M1 (right)	B-ml	A-l	C-dl-ap (?)	
M2 (right)	B-ml		C-l-ap (?)	
M3 (right)	B-ml-ap (?)	A-ml-ap (?)		

2.4.10 OFA-Reconstruction of the Masticatory Path of *Megazostrodon*

For the analysis of *Megazostrodon,* m1 and m2 were put into occlusion with P5 and M1, whereas m2 and m3 together with M1 and M2 were used for *Morganucodon*. The configuration for *Morganucodon* was chosen because it best incorporated the most relevant aspects and also because m1 had little contact with its antagonist at this stage (see below). The different setting for *Megazostrodon* was caused by the damage and post mortal movement of m3, which made it unsuitable for the analysis. Nevertheless, given the similar nature of the dentition, the contact areas given by the OFA analyses can be compared between the two specimens to examine general similarities and differences.

Since no striations were detectable in *Megazostrodon* NHMUK PV M 26407 due to the protective coating covering the specimen, the OFA path is based on crown morphology and wear only. The analysis has been performed under the assumption that *Megazostrodon* had a primarily orthal chewing path. However, deviations similar to what has been described here for *Morganucodon* might have been possible.

Cusp a of m1 is damaged and therefore its mesio-distal extension at the apex is lessened, which results in a reduced contact area with its antagonist (Fig. 2.6B, C green and yellow contact area on m1 of *Megazostrodon*). The lack of observable striations and the damage of cusp a in m1 account for a certain imprecision of the OFA chewing-path reconstruction, which therefore should be considered an approximation.

Initial contact is made by the main cusps a/A of the upper and lower molars, which engage in the middle between their antagonists and first come in contact with cusps b/B, c/C, and d/D (Fig. 2.6 A-C yellow, green and purple contact area of *Megazostrodon*). Cusp A of M1 has one lingual oriented fact (A-l) which is represented by one lingual contact area (Fig. 2.6, purple area). However, it is likely that this will change with ontogenetic increase in wear. This is suggested by the facets of BP/1/4983, where the posterior less worn molars mostly show a single, lingually oriented facet on cusp A, whereas the most worn upper molar, M1, shows one large mesially and one large distally oriented facet. The early ontogenetic condition seen here in *Megazostrodon* differs from that of *Morganucodon*, where the lingual sides of cusp A of M1 and M2 get directly in contact with their mesial and distal flanks.

In *Morganucodon* the initial piercing segment (Fig. 2.6A) with only cusps a/A in contact takes up the majority of the power stroke. The accessory cusps in *Megazostrodon* on the other hand, come into contact soon after the initial contact of cusps a/A, resulting in a shorter piercing segment. Subsequently, cusp c occludes between cusps B and A, and cusp C enters in between cusps a and b. Similar to *Morganucodon*, maximum intercuspation is reached prior to the end of the power stroke (Fig. 2.6, red dot). Subsequently, the teeth continue to pass along each other, with potential for shearing along the flanks (Fig. 2.6 C).

The orthal chewing path is steep, with a dip angle of 73° and with a direction of 89° oriented lingually with no mesial or distal component.

2.5 Discussion

2.5.1 The Arrangement of the Upper Molar Series, Evidence for a Precise Occlusion

In *Morganucodon* the posterior upper molars are aligned differently than the teeth of the anterior dentition. This has considerable impact on the occlusion. The region of the tooth row including M2-M4 is rotated away from the maxillary rim. These molars are further individually rotated within the tooth row (Fig. 2.4 angles α, β). This leaves space for cusp a of m2 to engage between M1 and M2, coming simultaneously in contact with cusps C and D of M1 and cusps B, A , and C of M2. This extensive contact fully exploits the large crown of m2, which would not be possible with a linear molar arrangement. The relatively large pit in the maxilla between M1 and M2 further suggests that m2 engaged deeply between its antagonists (Fig. 2.2 A, C).

Additional to the rotation of the tooth row, the inward inclination of the posterior upper molars by 18° (Fig. 2.4, angle γ) functioned as a compensation for their wide profile relative to their antagonists. This inclination enabled the lower jaw to move orthally with minimal roll (sensu Grossnickle 2017) along the mobile symphysis, since the flanks of the upper lingual cusp are more vertically oriented to match the orientation of their lower antagonist (Fig. 2.10). This interpretation is supported by the fact that in *Morganucodon* the more posterior molars are relatively wider than the anterior ones (Mills 1971), and thus require more inclination than the anterior ones to match their antagonists. The inclination also creates a more asymmetrical blade type arrangement that can brush past each other instead of two opposing wedges, which would result in higher rates of tooth wear (Lucas 2004).

Though *Morganucodon* exhibits these shifts throughout the upper molar series, the situation is unclear for *Megazostrodon*. It appears as if the teeth are arranged more linearly than in *Morganucodon*, without a shift away from the lateral margin of the maxilla within the posterior part of the tooth row. The posterior molars in BP/1/4983 are further inclined than the anterior ones, similar to *Morganucodon*. However, both specimens of *Megazostrodon* are

damaged and the upper molars are slightly displaced. Therefore, no definitive statement regarding the arrangement of the upper dentition of *Megazostrodon* can be made at this point. Crompton and Jenkins (1968) suggested that the teeth of *Morganucodon* differed from that of modern mammals in requiring extensive wear to create matching surfaces.
However, the rotation and inclination of the posterior upper molars suggest a predetermined tooth placement and precise occlusion in *Morganucodon* before extensive wear was present. This supports Gill (2004), who argued that, when correctly oriented, molars of *Kuehneotherium* produced matching cutting blades, without the necessity of wearing away parts of the crown. She considered that this disagreement with the idea of remodeling of the crown by wear, before precise occlusion could occur, is also applicable to *Morganucodon*. This is further supported by the lack of replacement of molariforms in *Morganucodon,* unlike *Sinoconodon*, which has at least two generations of molariforms (Zhang et al. 1998). We therefore consider it more likely that the diphyodont dentition of *Morganucodon* was relatively precise after eruption and the teeth were fully functional, thus providing an advantage over non-diphyodont taxa. The results of the OFA analysis further supports the assumption that unworn or slightly worn teeth were fully functional, due to the presence of a piercing segment, as well as subsequent shear-cutting provided by the crests of the cusps. Another argument for a relatively precise occlusion was made by Mills (1971) who considered the variation in wear observed in *Morganucodon* similar to that of extant therians. So far, there has been no quantitative comparison of the variability of facet and occlusal patterns of *Morganucodon* compared to modern mammals, but Mills (1971) assignment appears reasonable after our observations.

2.5.2 Evidence Against a Precise Occlusion in *Morganucodon*

The discussed arrangement of the posterior upper molar series suggests a more precise tooth arrangement after eruption than previously thought. However, it appears as if the occlusion between m1 and M1 lost precision after the eruption of m2. This can be derived from wear facets on m1 and M1 in UMZC Eo.CR.1 that were not reproducible with the OFA. This supports the idea that *Morganucodon* lacked the precision of modern mammals.

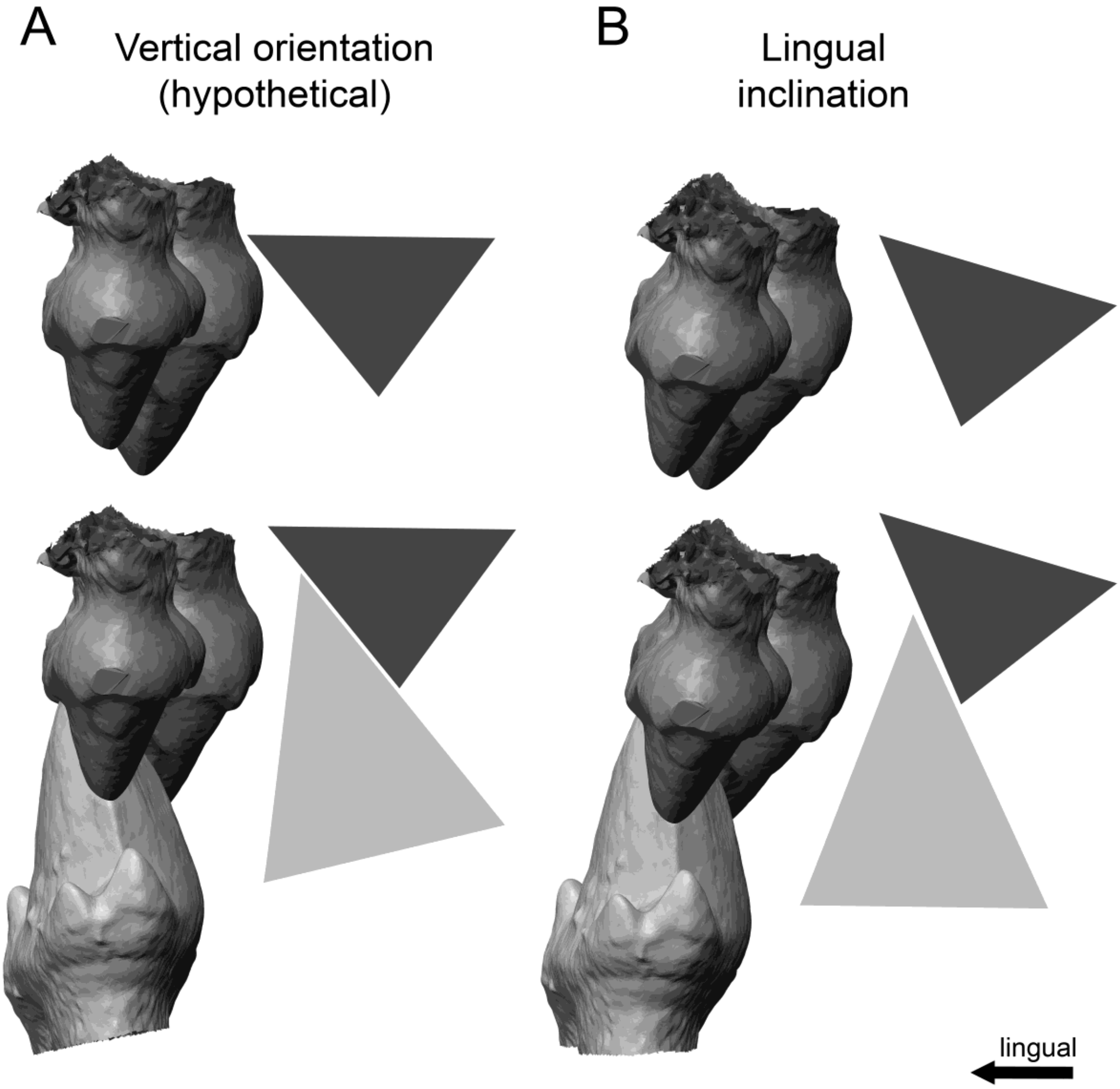

FIGURE 2.10. 3D models and schematic drawings of the influence of the lingual inclination of the posterior molars during mastication in *Morganucodon* (see also Fig. 4B, C). (A) M1, M2 and m1 in a hypothetical state without lingual inclination of the upper molars. The upper molars, due to their increased width and low height, would require a high degree of translation or roll from the lower jaw during occlusion. (B) the same molars with the uppers inclined at 18° as observed. The lowers molars are able to pass orthally along their antagonists with less translation/roll.

An OFA analysis of UMZC Eo.CR.1 where m1 was included, failed to simulate facet a-db-cv on m1, as well as facets B-dl-cv and A-ml-cv on M1, despite those facets being identical in shape and position to the ones seen on the more posterior molars. However, in order to let cusp A of M1 engage with the embrasure between cusps a and c and cusp a of m1 to engage with the embrasure of B and A, all posterior teeth needed to be removed from the analysis. When the entire tooth row was used for the analysis, the matching cusps of m1 and M1 could not be brought in occlusion (Fig. 2.11). There is no evidence for postmortem deformation of the tooth row and most of the molars still have an interlocking contact. On both dentaries, m2 is positioned higher than m1, with cusp d of m1 almost hidden below cusp b of m2. At an earlier ontogenetic stage, m1 probably was in much closer contact with M1, before the posterior teeth were fully erupted. At that point, the facets a-db-cv, B-dl-cv, and A-ml-cv on M1 were produced. After the eruption of m2 its posterior and higher position reduced the contact area of m1 to its antagonist, which would also explain the higher amount of wear of m2 and m3 relative to m1.

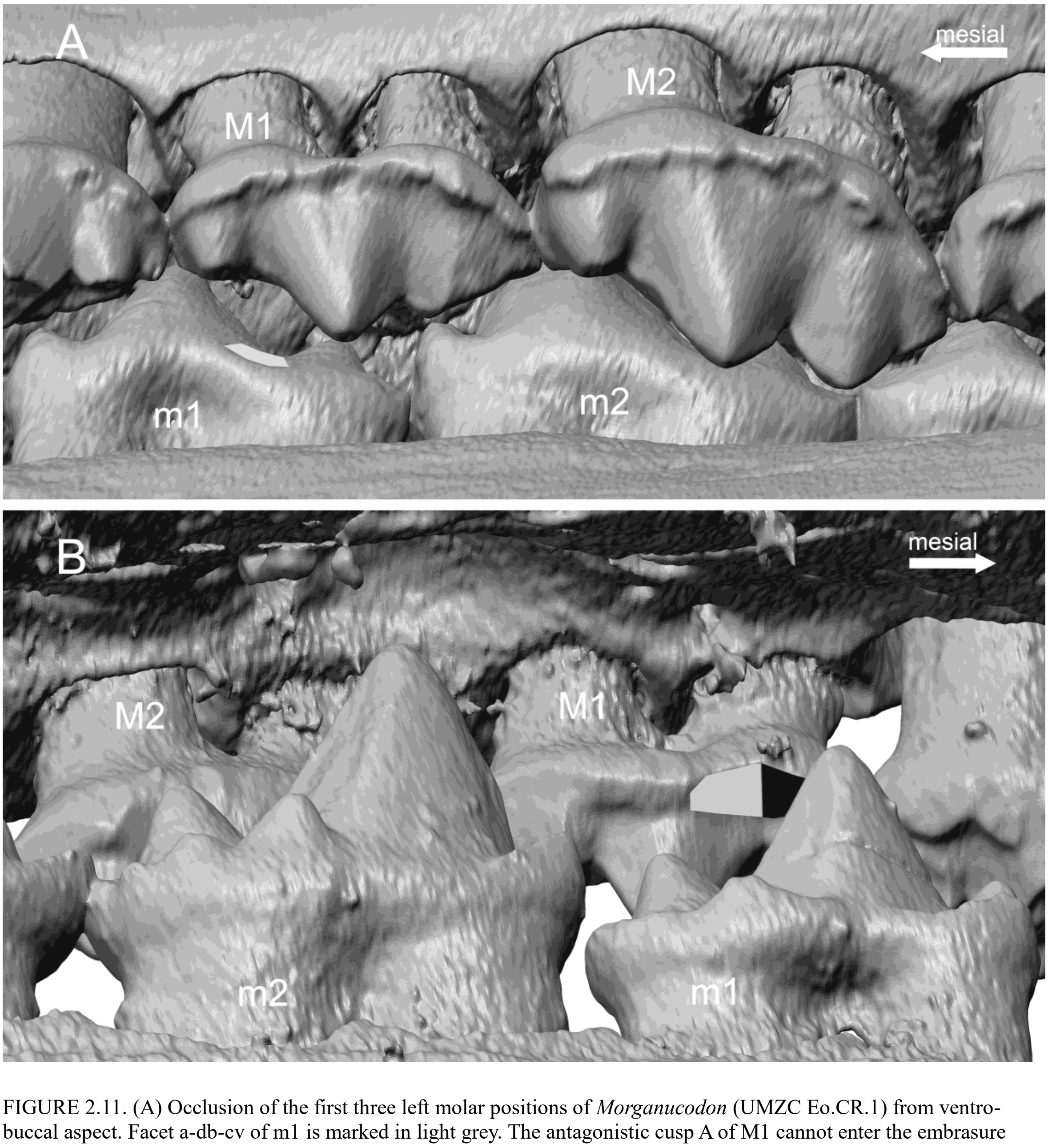

FIGURE 2.11. (A) Occlusion of the first three left molar positions of *Morganucodon* (UMZC Eo.CR.1) from ventro-buccal aspect. Facet a-db-cv of m1 is marked in light grey. The antagonistic cusp A of M1 cannot enter the embrasure between cusps a and c of m1 and does not reach the facet; any repositioning is blocked by cusp a of m2 where it enters the triangle created by the different orientations of M1 and M2 relative to the lateral margin of the maxilla. (B) The same position in ventro-lingual view. Facet A-ml-cv is marked in light grey and B-dl-cv in black. The apex of cusp a of m1 is located clearly anteriorly to its antagonistic facets, despite the rest of the tooth row being in full occlusion.

2.5.3 Chewing Direction in *Morganucodon*

Previously, the occlusal path in *Morganucodon* was reconstructed either as fully orthal or predominantly orthal with a slight movement towards anterior (Crompton and Jenkins 1968). However, the variety of striations on isolated *Morganucodon* teeth is evidence for a high degree of freedom during occlusion.

We observed five different types of striation pattern:

1. Orthal (Fig. 2.5A)
2. Posterior (Fig. 2.5B and C)
3. Anterior (Fig. 2.5E)
4. Irregular (Fig. 2.5F)
5. different orientations on different cusps within a single tooth (Fig. 2.5D)

The average striation orientation of specimens with predominantly anterior oriented striations differs from specimens with predominantly posterior striations by around 40°. This corresponds to the range of motions inferred from molars with irregular striation patterns. This variability of striations in *M. watsoni* molars was most likely permitted by its tooth morphology. Without a guiding structure, no autocclusion was present (Mellett 1985; Evans and Sanson 2006). Therefore, a certain freedom of movement was possible and orthal, as well as posteriorly or anteriorly oriented strokes were executed by *Morganucodon*. Most individuals appear to have developed a preferred chewing direction, which is then occasionally abandoned on single strokes. A few did not, and their molars exhibit the entire range of movements in an irregular pattern.

The ability to choose chewing directions and develop preferences required precise muscular control of the jaw movements, something that was also previously inferred based on the presence of matching wear facets (Crompton and Parker 1978).

There are other molar types that show striations with varying orientations on the same facet that are not caused by a freedom of movement, as we infer for *Morganucodon*. The two-phased chewing path of tribosphenic molars can result in differently oriented striations on the same facet (Hielscher et al. 2016). However, a multiphased chewing path can be ruled out for *Morganucodon* based on the crown morphology, the distribution of facets, and the results of the OFA analysis.

Striations with varying orientations can also be created during a single-phased chewing stroke, if the lower dentition is deflected during occlusion. This has been observed in the cladotherian *Dryolestes*, where the hypoflexid is redirected by contact with the paracone at around 10°. However, though the striations in *Dryolestes* are located on the same facet, they are still separated with the steeper ones being closer to the tip of the protoconid, whereas the less steep ones occur near the hypoflexid groove (Schultz and Martin 2014). In *Morganucodon,* the striations with varying inclinations are locally not separated (with the exception of Fig. 2.5D) and cross each other regularly (Fig. 2.5). Further, the angle between the striations in most *Morganucodon* molars is larger than the 10° reported for *Dryolestes*. The varying direction of the chewing movements had only minor impact on the centric occlusion (= the end of Phase I in tribosphenic occlusion, when teeth are in contact and fully occluded; since a Phase II is absent in the taxa described here centric occlusion reflects the end of the power stroke). An orthal power stroke was initiated with cusp a of the lower molar placed below two upper molars. Anteriorly oriented strokes started from a slightly more posterior occlusal position and posteriorly oriented strokes began with the lower molars shifted slightly forward. Accordingly, a similar position for each was attained at the end of the power stroke despite the minor initial differences.

2.5.4 Orientation and Angle of the Chewing Path in *Morganucodon* and *Megazostrodon*

Both taxa share a simple, single phased chewing path (Hiimäe and Kay 1972). Due to the lack of observable striations in NHMUK PV M 26407, it cannot be tested whether *Megazostrodon* had a similar freedom of chewing movement as *Morganucodon*. The predicted orthal OFA path for *Megazostrodon* indicated a slight anterior deviation. However, without a striation analysis no definite statement can be made as to whether this occurred in the original chewing path, or if it is an artifact caused by postmortem displacement of the teeth in NHMUK PV M 26407. For both taxa, an orthal movement with a dip angle of 77° (*Morganucodon*) and 73° (*Megazostrodon*) was reconstructed. All known morganucodontans had a mobile symphysis at the mandible (Kielan-Jaworowska et al. 2004). Therefore, the lingually orientated deviation can be attributed either to a transversal movement or to an inward roll of one hemimandible. Since the OFA path is based on a linear movement, the exact amount of both types of movement remains unclear. In modern mammals roll is relatively limited (Grossnickle 2017). However, Bhullar et al. (2019) described roll during occlusion for the extant marsupial *Monodelphis*. For *Morganucodon* they suggested a “considerable roll”, based on the presence of a “pseudoangular process” and previous interpretation of wear in that taxon. They considered that roll during occlusion was essential for the evolution of precise mammalian evolution. Although previous studies have forwarded roll during occlusion to explain wear facets in Mesozoic mammals, direct evidence for this is scarce. The most convincing evidence has been presented for an undescribed ‘triconodontid’ from the Early Cretaceous Cloverly Fromation, where the angles of the facets differs greatly between the upper and lower molars (Crompton and Luo 1993). This has also been described for the morganucodontan *Dinnetherium*, but with considerable less difference in facet orientation between upper and lower molars (Jenkins et al. 1983; Crompton and Luo 1993). Roll had also been linked to wear in *Sinoconodon*, though without further discussion (Crompton 1985). However, none of these studies has considered potential inclination of the upper molars, which could have had a major impact on the relative facet orientation and the required roll (Fig. 2.10). Based on the wear and striations of all specimens presented here, no distinction can be made between wear caused by transversal movement or roll. According to the OFA analysis, as stated above, it is not possible to say how much of the lateral movement of the power stroke was based on transversal movement and how much on roll. The OFA analysis was able to produce matching contact between upper and lower molars without the use of roll, due to the inclination of the upper molars (Fig. 2.10). It is important to note that this does not necessarily mean that roll was absent during the power stroke of *Morganucodon*. Nor does it exclude roll as an important factor in the evolution of precise mammalian occlusion. It does, however, highlight the difficulties of interpreting the amount of roll that was present during occlusion in extinct taxa, solely based on wear facets. At this point the exact amount of roll and its significance for *Morganucodon* can not be determined with certainty.

As stated above, it is possible that in *Megazostrodon* the posterior upper molars were inclined similarly to *Morganucodon*. In case that inclination was present in *Megazostrodon*, it is likely that it had the same function as in *Morganucodon*, since M3 and M4 of *Megazostrodon* are also wider than the anterior cheek teeth (Fig. 2.9B) and would otherwise require a high degree roll of the lower jaw. The inclination of the chewing path in *Morganucodon* is steeper than previously assumed by Butler (1972). He calculated an angle of 55° (if 90° is considered an orthally directed stroke) for *Morganucodon*, which differs from the considerably steeper 77° measured with the OFA. This difference can be explained by the inclination of the upper molars, this is supported by an earlier OFA analysis, which did not take the inclination into account and produced results matching those of Butler (1972).

Though the occlusal paths for both taxa were steep in a lingual direction, the striations observed for *Morganucodon* provide evidence for variability, which in some cases added anterior or posterior direction to the movement. Since no striations were observable in *Megazostrodon*, it remains unclear whether it had a similar range of motion.

2.5.5 Occlusion and Food Processing in *Morganucodon* and *Megazostrodon*

In relation to the term ‘grinding’ and the comparison of the teeth with a ‘mill’ (Mills 1971), Kermack et al. (1973: 161) assumed for the function of the *Morganucodon* dentition that “We very much doubt if anything but shearing is involved in the teeth during occlusion”. However, though grinding or crushing are definitely not present in the masticatory cycle of *Morganucodon,* due to the lack of a protocone and talonid basin or a functional equivalent, the function of the molars goes beyond shearing.

The beginning of the occlusal path for both taxa (Fig. 2.6A) was set with the tips of the main cusps positioned slightly past each other. The single phased power strokes of *Morganucodon* and *Megazostrodon* can be separated into three (partially overlapping) functional segments where different functions occur (Fig. 2.6). These three functions are piercing, shear-cutting and shearing. At the beginning piercing is the dominant function. Subsequently all cusps come into contact and shear-cutting occurs at crests that pass along each other. In UMZC Eo.CR.1 this is most apparent in the crest that runs from cusps C and D of M1, which is passed by the mesial crest of cusp a of m2. Meanwhile the cusps where the crests are not in close contact, or that have moved their crests already past each other, shear the food along their flanks. An example for the former is the distal crest of cusp a of m2, which is separated from cusp A of M2 by the lingual upper cingulum. The space between the two cusps initially leaves room for food, but gets smaller and smaller while the teeth move past each other. Here the food is stretched and sheared along the flanks of the cusps. An example of this is the facet along cusps C and D of M1 (CD-dl), where the mesial side of cusp a passes along, once the crests have moved past each other. Once the blades are past one another, the remaining food is moved and processed along the side of the facets. This is also the case during maximum intercuspation (Fig. 2.6C) where all crests have passed each other, and shearing is the only function still present. A similar situation occurs in *Megazostrodon*, where the crests of cusps a/A perform shear-cutting along the flanks of the supporting smaller mesial and distal cusps of their antagonists.

Piercing and shear-cutting apparently are the main functions during the masticatory cycle. In *Morganucodon* shearing is of secondary importance for food processing in the wide upper triangle between M1 and M2 along the upper lingual cingulum. In order to perform a shear-cutting function, the crests of two cusps need to pass along each other in close proximity, functioning as blades. Once the crests have moved past each other and the food is cut, there remains little to no space between the two cusps that now are in contact with their flanks. This can be compared with a pair of scissors where the material is cut along the blades, but the flanks of the blades do not participate in the actual process. Therefore, the extensive facets in later wear stages of *Morganucodon* are rather the result of attrition when the teeth move along each other than of the shear-cutting process (Crompton and Jenkins 1968), which occurs mostly along the enamel crests above the wear facets. This is evident in UMZC Eo.CR.1, where the most prominent facet is CD-dl of M1. Here shear-cutting along the crest by close contact with the antagonist is most pronounced. This contradicts previous assumptions that the molars of *Morganucodon* need extensive wear to become fully functional (Crompton and Jenkins 1968; Butler and Clemens 2001) and supports the hypothesis previously stated for *Kuehneotherium* that the teeth were fully functional at eruption (Gill 2004). A notable difference between both taxa is that in *Morganucodon* the first contact (piercing) occurs shortly after the starting position of the OFA analysis, whereas in *Megazostrodon* the first contact occurs much later (Fig. 2.6, upper part). This is caused by the higher and more massive cusp a of m2 in *Morganucodon* (Fig. 2.3), which contacts its antagonist before the other cusps get involved. For *Morganucodon* this also results in a long initial piercing segment during the power stroke, when only the main cusps are in contact (Fig. 2.6 A). This segment is longer than the combined later stages of the power stroke (Fig. 2.6B, C). In *Megazostrodon*, due to more similar cusp height, the piercing segment is considerably shorter than in *Morganucodon*. This emphasis on piercing in *Morganucodon* relative to *Megazostrodon* is also apparent in the morphology of the last upper premolar. In both taxa the ultimate upper premolar is molariform and the tallest tooth in the tooth row. This suggests that the ultimate premolar is at least partially functionally integrated into the molar series, especially in the initial piercing segment. However, the ultimate upper premolar of *Morganucodon* exhibits a considerably more massive cusp A than that of *Megazostrodon*. The assumption of a pronounced piercing segment supports Gill et al. (2014), who proposed that *Morganucodon* was capable of preying on harder prey, such as beetles, compared to the ‘symmetrodontan’ *Kuehneotherium*, which relied on softer prey. These results are also in agreement with Conith et al. (2016), who used physical models to demonstrate that in

Morganucodon the cusps occlude successively and therefore maximize force in hard food items.

In both *Morganucodon* and *Megazostrodon*, after maximum intercuspation is attained, the teeth continue a little further past along each other, until the end of the power stroke (Fig. 2.6). A difference between *Morganucodon* and *Megazostrodon* is the occlusion of the cusps. For *Megazostrodon,* an embrasure occlusion was hypothesized (Crompton and Jenkins 1968). This occlusal type is characterized by the placement of cusp a between two upper molars and cusp A between two lower molars. *Morganucodon* was described with cusp a moving between cusps B and A, and cusp A between cusps a and c. This results in one molar working primarily against a single antagonist (Crompton and Jenkins 1968; Crompton 1974). Though the embrasure occlusion hypothesis was confirmed for *Megazostrodon* by the OFA analysis, a more complex picture is suggested for *Morganucodon*. The initial contact of cusp a of m2 and m3 is not between cusps B and A, but rather between M1/M2 and M2/M3 respectively two upper molars. The tip of cusp a of m2 eventually ends up between cusps B and A when maximum intercuspation is attained; however, there is still substantial overlap of the bucco-mesial flank of cusp a with the linguo-distal side of M1, which is indicated by the prominent facet that extends from cusps C and D of M1 to cusp B of M2 (C/D-pl; B-pl). Furthermore, the situation for cusp a of m3 is different as it remains between two molars, creating a distally oriented facet CD-dl on M2 and a mesially oriented facet A-ml-cv on M3. However, it has to be noted that this difference in occlusion between m2 and m3 is the specific condition of UMZC Eo.CR.1 and that *Morganucodon* appears to be variable in this regard, based on facet variability observed on multiple fragmentary jaws at the UMZC.

2.5.6 Implications and Future Outlook

Mills (1971) suggested that there was no direct evolutionary connection between the *Morganucodon* pattern and the *Megazostrodon* pattern and that both must have derived from a common ancestor on different pathways. Though there are still notable differences between the two taxa, the similarities are more extensive than previously thought. The differences in occlusion between *Morganucodon* and *Megazostrodon* are driven by cusp size, cusp position, and molar orientation in the jaw, rather than solely by different relative position of the opposing teeth as assumed previously (Butler and Sigogneau-Russell 2016). Changes in cusp shape and size generally require only minor genetic and/or developmental changes (e.g. Jernvall 2000; Salazar-Ciudad and Jernvall 2010; Kavanagh et al. 2007; Harjunmaa et al. 2014). Therefore, a close evolutionary connection between the *Morganucodon* pattern and the *Megazostrodon* pattern cannot be categorically excluded just on the basis of molar occlusion. This becomes even more apparent if other taxa of Morganucodonta are considered, of which several were described as overlapping between the two patterns. For example, *Dinnetherium*, described as part of the Megazostrodontidae, but with ”*Morganucodon* like” occlusion (Crompton and Luo 1993). For *Brachyzostrodon,* a megazostrodontid, an occlusal pattern similar to that of *Morganucodon* has been inferred, although it differs by the presence of strong apical wear (Hahn 1991; Debuysschere 2015). For *Erythrotherium* as a member of Morganucodontidae, which has even been previously considered to be synonymous with *Morganucodon* (Kermack et al. 1973), an occlusal pattern similar to that of *Megazostrodon* has been described (Crompton 1974; Jenkins et al. 1983; Kielan-Jaworowska et al. 2004). *Bridetherium* (Clemens 2011) recently was described with very ‘*Morganucodon* like’ morphology but a unique wear pattern. These taxa and the results of this study demonstrate that the occlusal pattern of Morganucodonta was more complex and varied than previously thought and that the general dichotomy in occlusal pattern between *Morganucodon* and *Megazostrodon* does not exist.

2.6. Conclusions

The basal triconodont molar morphology of *Morganucodon* lacks guiding structures and therefore autocclusion, which results in a high degree of freedom of orientation during the masticatory cycle. For single strokes the deviation from a straight orthal inclination could amount up to 20° towards mesial or distal (resulting in a total degree of freedom of up to 40°). This is represented by the striations on the teeth, which show a high degree of individual freedom, as well as intraspecific variability (Fig. 2.5). Nevertheless, centric occlusion did not change, since power strokes with different orientations likely varied to a minor degree in their initial starting positions, with distally inclined strokes staring further mesial and vice versa, thus resulting in nearly identical centric occlusion at the end of the power stroke.

Previous studies have proposed the presence of roll during occlusion for the morganucodontans *Dinnetherium* and *Morganucodon* based on the orientation of wear facets (Jenkins et al. 1983; Crompton and Luo 1993; Bhullar et al. 2019). However, this interpretation based on wear is problematic due to the inclination of upper molars within the maxilla, which was not taken into account (Fig. 2.10). With our OFA analysis we were able to reconstruct observed wear without the assumption of roll during the power stroke. While this does not exclude the presence roll for *Morganucodon*, it provides evidence that roll was not necessary to create the wear facets described. Further studies are required to fully understand the presence and importance of roll in early Mammaliaformes.

The upper molar series of *Morganucodon* watsoni was rotated lingually away from the lateral margin of the maxilla, and M2-M4 further rotated individually, which resulted in a difference of orientation between M1 and M2 of 18° (Fig. 2.4). This angulation created a wide triangle that provided space for cusp a of m2 between M1 and M2. An inward inclination by 18° of the upper posterior molars (Fig. 2.4 angle γ), aligned the lingual side of the cusps in a favorable way and minimized the required roll of the corresponding hemimandible (Fig. 2.10). The observed arrangement of the upper molars around the second lower molar contradicts the assumption that *Morganucodon* lacked a precise occlusion during eruption (Crompton and Jenkins 1968).

However, an ontogenetic change in the occlusion of UMZC Eo.CR.1 occurred with the eruption of m2/M2 and their successors that left m1 with less contact than before and shifted the center of occlusion to m2 (Fig. 2.11). This suggests that *M. watsoni*, despite having a more precise occlusion than previously thought, still shows irregularities that usually do not occur in modern mammals, possibly as a result of the recent appearance of diphyodonty in this taxon.

The molars of *Morganucodon* show a high adaptation to piercing with tall elevated main cusps, as well as shear-cutting with crests that passed along each other in close proximity. Shearing was also present in the space between cusps a/A, provided by the upper lingual cingulum. During the upwards movement of the lower teeth, this space became smaller, while the flanks of the cusps moved along the trapped food. However, shearing was less emphasized than piercing and shear-cutting. Shearing surfaces, which have been considered as the primary functional regions on the molars of *Morganucodon* (Crompton and Jenkins 1968) seem to be a result of attrition, rather than important functional areas in themselves, when compared to cusp tips and crests. Compared to *Megazostrodon*, both taxa show a similar occlusal path, with the exception of a less pronounced piercing aspect in *Megazostrodon*, due to a relatively smaller cusp a (Fig. 2.6).

The previously proposed 'embrasure' occlusion holds up for *Megazostrodon*, whereas the occlusion of *Morganucodon* appears to be more complex than previously assumed (Crompton and Jenkins 1968; Crompton 1974), based on the facet analysis and the OFA reconstruction. In UMZC Eo.CR.1 the tip of cusp a initially comes into contact in between two antagonists and there is substantial overlap with the mesio-buccal side of cusp a and the disto-lingual side of the next upper anterior molar. The apex of cusp a of m2 eventually terminates its path between cusps B and A of M2. This is not the case in m3, where cusp a remains between two molars (Fig. 2.6). It has to be noted that this is based only on the OFA path of the specimen investigated and that this condition should not be generalized for *M. watsoni*, since facets on molars of fragmentary maxillae suggest that this pattern might be variable. Though *Morganucodon* shows more similarities to *Megazostrodon* in this aspect than previously assumed, the difference in occlusion of cusp A was confirmed. This seems to be mostly caused by molar size, since these are relatively shorter and wider in *Megazostrodon*, as well as cusp arrangement (in *Megazostrodon* cusps a and c are close together and would not yield enough space for cusp A) (Fig. 2.3). The difference between *Morganucodon* and *Megazostrodon* is, therefore, smaller than previously assumed and seems to be caused by slight differences in relative cusp size and arrangement rather than molar position. However, given the difference in placement of cusp A, the distinction in different occlusal modes can be confirmed. Though aspects of the dentition of *Morganucodon* (i.e. the occlusion of cusp a; inclination of the power stroke) were subject to a higher degree of individual variability than present in modern mammals, it was characterized by a relatively precise molar occlusion.

2.7 Acknowledgments

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2.9 Supplementary Information

2.9.1 Occlusal Fingerprint Analyser Software

The files are accessible via the DOI: 10.22000/374

To use the provided .ofa-project files, the OFA Software and the user manual can be downloaded at: https://www.ifgeo.uni-bonn.de/abteilungen/palaeontologie/arbeitsgruppen/vertebraten/ehemalige-forschergruppen/for-771/ofa/download

2.9.2 Dental Morphology of the Antemolar Dentition of UMZC Eo.CR.1

Incisors—Four lower incisors are present on each hemimandible. They are peg-like, inclined in a mesial direction and decrease in size from i1 to i4. Due to damage, the original dimensions for i1 and i2 can be only estimated, but i1 might have been similar in height to the canine. The upper incisors are not preserved.

Canine—The lower canine is inclined mesially as well, with slightly distally facing tip. It is single-rooted and the crown consists of a single large cusp with a convex mesial side.

Premolars—In both dentaries, p2, p3, and p4 are present, with p2 located above the second mental foramen. The latter seems to differ from most other specimens, where the second mental foramen is located between the canine and p1 (if present) (Kermack et al. 1973; pers. obs. PGG). There is more space between the canine and p2 than between any other teeth in the tooth row. This could be either attributed to a full reduction of the first premolar or its loss during ontogeny. The latter has been described for *M. watsoni* and *M. oehleri*, as well as for *Kuehneotherium* (Gill 1974; Kielan-Jaworowska et al. 2004). The premolars have a similar morphology and increase in size distally, with p4 being the second highest postcanine tooth in the dentary after m2. The mesial cusp is the largest one, and its tip is slightly curved backwards. The mesial flank is convex, the distal one concave. Distal to the main cusp a small cusp is present on the buccal side. Additionally, p4 has a cingulid with small cuspules on its lingo-distal side.

The upper premolars P1-P3 are small and peg-like. P4 differs in shape from the other premolars. P4 is the second longest (mesio-distally) upper tooth after M2. It is molariform, and even though cusp A is broken off, it is apparent that its main cusp was originally higher and more massive than that of the molars. Though cusp C and a very small cusp D are present, cusp B seems to be absent. However, it may have been small and now worn away, since there is a large wear facet mesial to cusp A. It lacks a pronounced lingual or labial cingulum and resembles in shape and cusp dimensions the lower molars. Only distally, next to cusps C and D, are a few small cuspules present that form a lingual and a mesial cingulid.

Tooth Root Morphology—The root of i1 is round and long. The other incisors (i2-i4) have slightly oval roots. They differ from the oval roots of the rest of the tooth row in that they extend mostly bucco-lingually and are shorter mesio-distally. The canine has a single large root with oval cross section (long axis mesio-distally oriented). In all lower premolars, the roots have a round cross-section, with the distal one being the larger one (Fig. 2D). The lower molars have two roots, which are completely separated in m1. At m2 and m3 the roots are partially fused close to the crown, but the alveoli remain separate. In m4 the roots are completely fused with a groove between. Though the cross-section of the mesial root of m1 is round, the distal root has an oval cross-section with mesio-distally oriented long axis. At m2 both roots are oval, with the distal root being larger. In m3 both roots are round, with the distal one being larger. In m4 both roots are of equal oval shape and size.

P1-P3 are single rooted, whereas P4 has two large, round, unfused roots, with the mesial one being slightly smaller. M1-M3 have separated roots as well. In cross section, M1 and M2 have oval roots (mesio-disally elongated), with the distal one being the larger, but both roots of M3 are of equal size and have round cross-sections. M4 appears to be either single-rooted or to have two fully fused round roots.

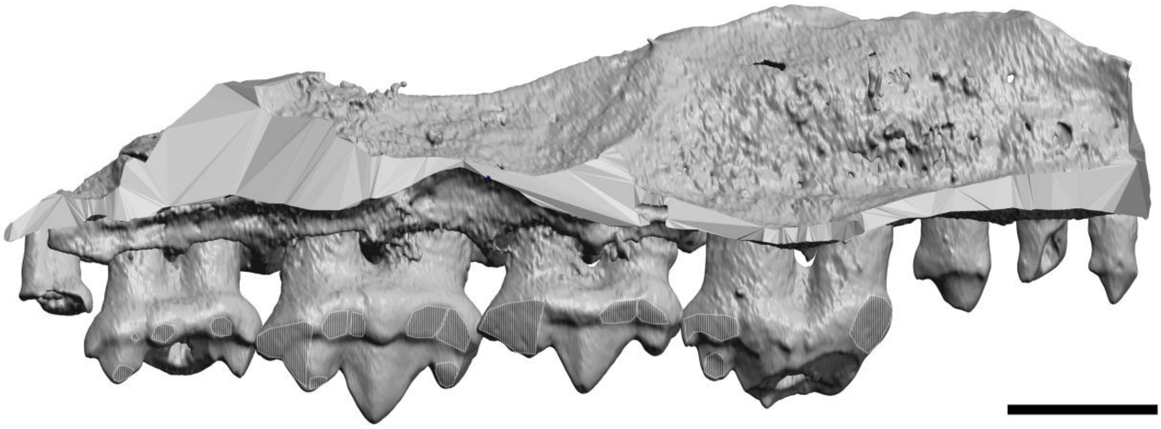

FIGURE 2.1S. Upper left dentition of *Morganucodon* (UMZC Eo.CR.1) in lingual view. Wear facets are highlighted. Scale bar equals 1 mm.

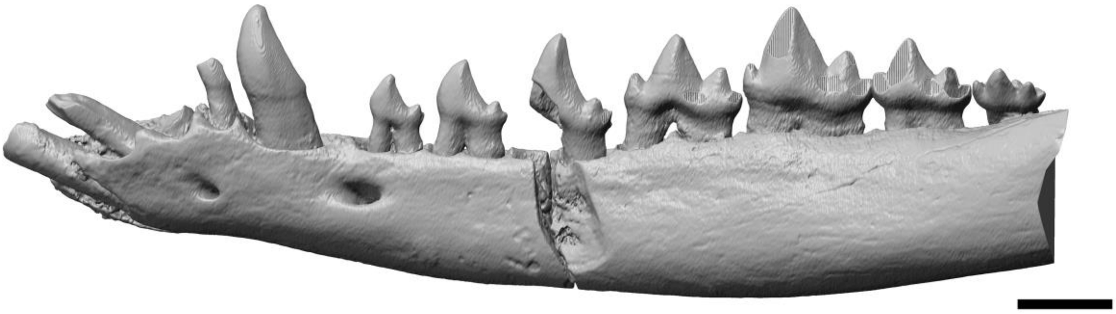

FIGURE 2.2S. Lower left dentition of *Morganucodon* (UMZC Eo.CR.1) in buccal view. Wear facets are highlighted. Scale bar equals 1 mm.

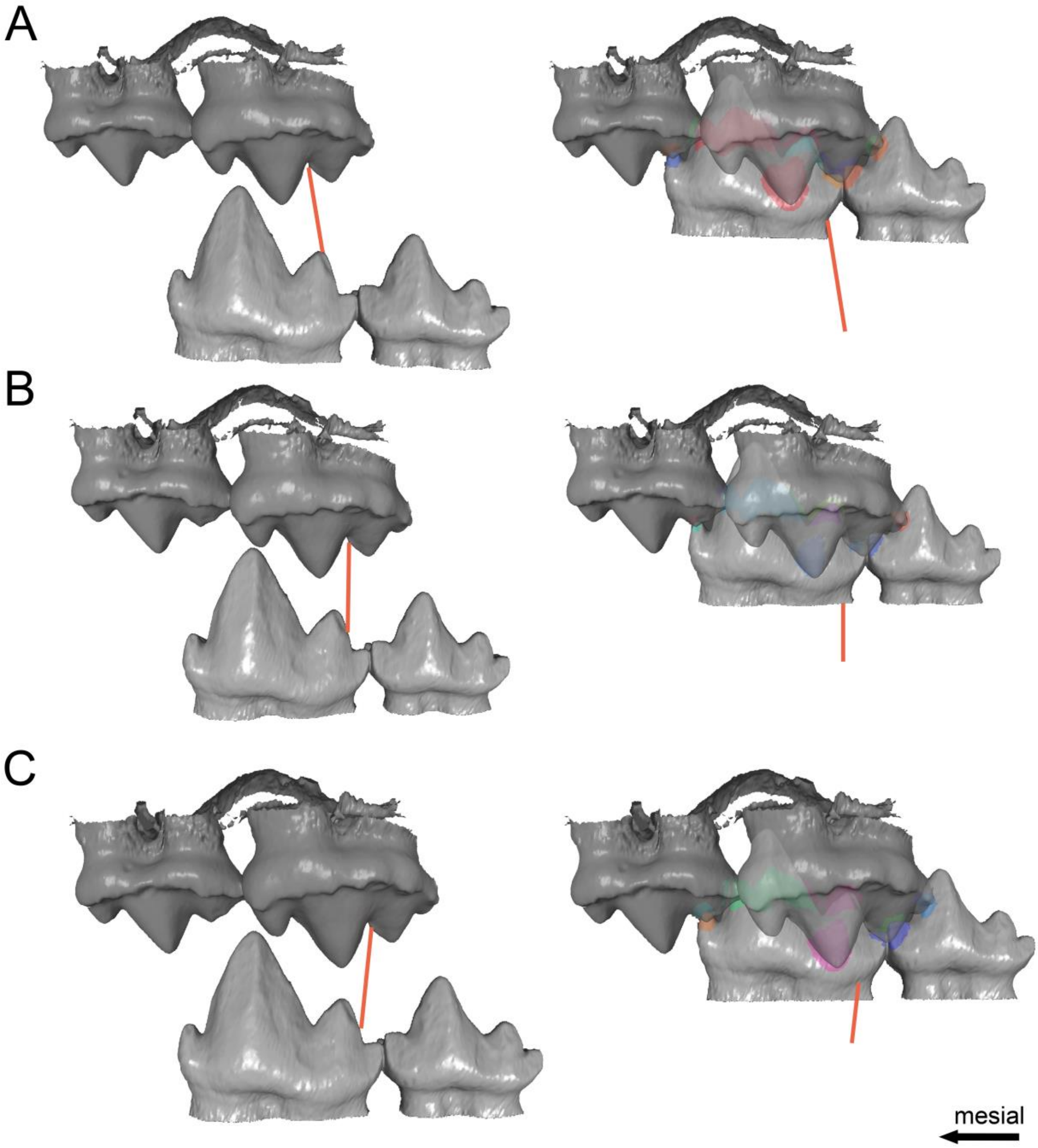

FIGURE 2.3S. Different OFA analysis with of UMZC Eo.CR.1 (m2, m3, M1, M2) with varying inclinations based on the striations observed on isolated teeth at the beginning (left) and later stages (right) of the power stroke. The orange lines indicate the orientation of the path. The colored areas represent virtual contact areas caused by the collision of the virtual models. (A) Mesial inclined path, (B) straight orthal path, and (C) distally inclined path. Note the similarities in the later stages of the power stroke. This is caused by slight differences of approximately 0,1 mm in the starting position, with the mesially inclined path starting further posterior and the distally inclined path further anterior. It is unclear if UMZC Eo.CR.1 had a preferred inclination as present on some of the isolated molars. However, every inclination was likely feasible and likely resulted in the same centric occlusion. For this study we focused on the distally inclined path (C).

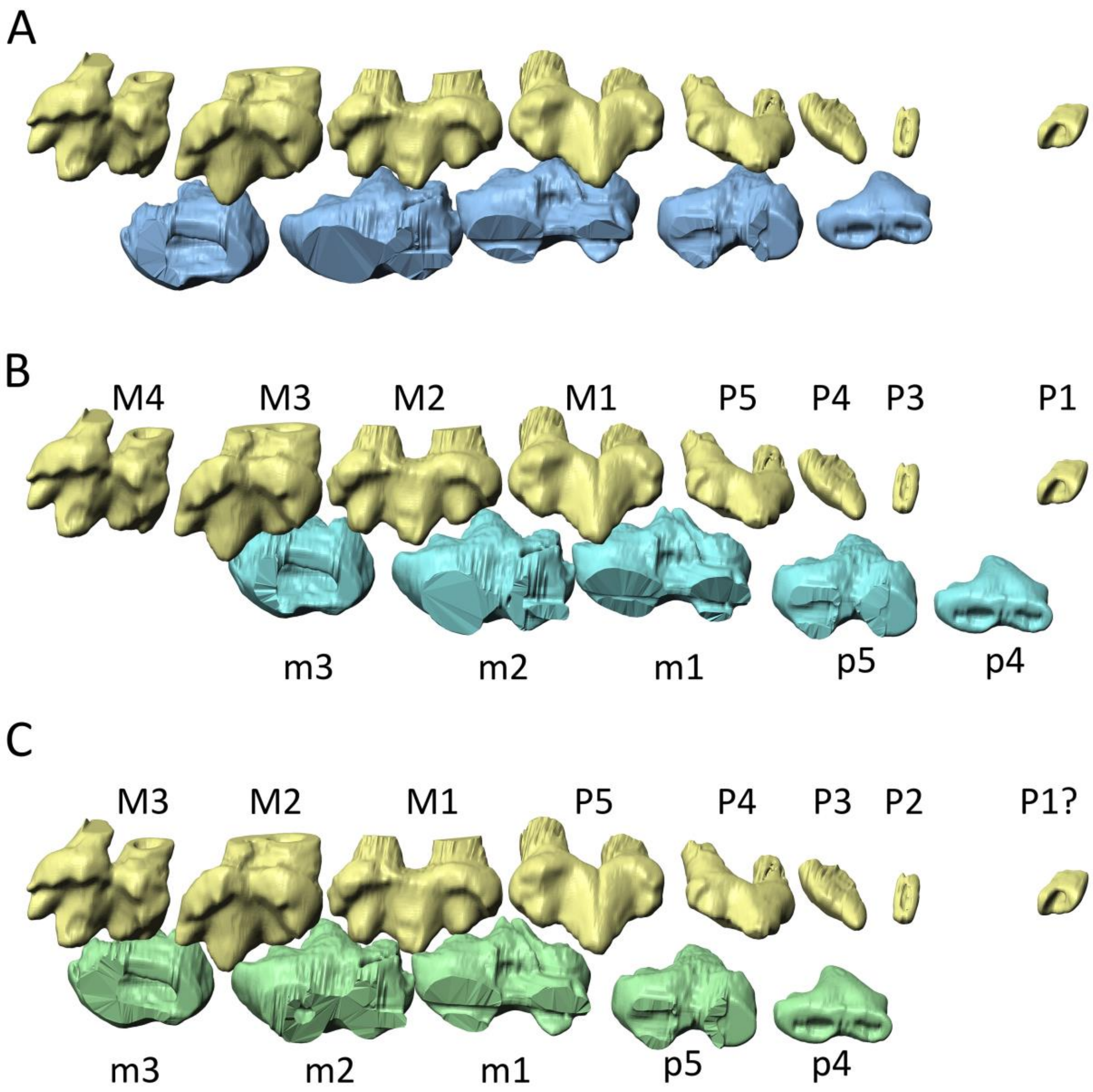

FIGURE 2.4S. Lower and upper right dentition of *Megazostrodon rudnerae* from a bucco-ventral view. (A) Teeth in their current position in the fossil, (B) teeth in occlusion based on the tooth positions assigned by Crompton (1974). Note, that Crompton (1974) interpreted the m4 to be missing, and (C) teeth in occlusion based on the interpretation of the tooth position provided here. The amount of repositioning required from the position in the fossil (A) is less and the premolar positions are aligned more convincingly, with the p4 occluding between P3 and P4.

TABLE S2.1. Specimen List

Number	Taxon	Fissure	Notes	Collection	Tooth position
NHMUK PV M 26407	*Megazostrodon rudnerae*	-	Holotype	NHM	m2
UMZC Eo.CR.1	*Morganucodon watsoni*	Pontalun 3		UMZC	
NHMUK PVM 100304	*Morganucodon watsoni*	Pontalun 3	Prepped without acid in Bristol by (PGG)	NHM	m2
NHMUK PVM 100308	*Morganucodon watsoni*	Pontalun 3	Prepped without acid in Bristol by (PGG)	NHM	m2
UMZC Eo.M(Lr).16	*Morganucodon watsoni*	Pontalun 3		UMZC	m2
UMZC Eo.M(Ur).5	*Morganucodon watsoni*	Pontalun 3		UMZC	M2 (?)
UMZC Eo.M(Lr).32	*Morganucodon watsoni*	Pontalun 3		UMZC	m1
AMNH 93800	*Morganucodon watsoni*	Pontalun 3 (?)		AMNH	m2

2.9.3 Supplementary References

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Molar Morphology and Occlusion of *Erythrotherium parringtoni*

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3.1 Abstract

The South African Early Jurassic morganucodontan *Erythrotherium parringtoni* is considered by some authors to be potentially synonymous with *Morganucodon* due to similar tooth morphology. However, despite their similar dental morphology, the occlusal pattern of *Erythrotherium* has been described as embrasure occlusion, close to the mode of *Megazostrodon rudnerae*, rather than that of *Morganucodon*. In this study the molars of *Erythrotherium* were re-examined and the two alternative occlusal hypotheses were tested using the Occlusal Fingerprint Analyser (OFA). Morphological comparison of the molars of *Erythrotherium* to those of *Morganucodon* showed similarities in cusp height and shape in lingual/buccal views, but the molars and individual cusps of *Erythrotherium* are considerably narrower and thus more gracile. With cusps a and c close together, cusp positioning differs from that of *Morganucodon* and shows similarities to the pattern of *Megazostrodon*. The upper molars are aligned in a straight row and lack the angle between M1 and M2 that is present in *Morganucodon*. This results in embrasure occlusion being the only viable occlusal mode for *Erythrotherium*, which was confirmed by the OFA analysis. A *Morganucodon*-like occlusion would allow only the main cusps a/A to make contact with their antagonists and thus major gaps would be present, causing considerable reduction of functionality of the dentition. Based on the morphological evidence and the differing occlusal mode the perpetuation of *Erythrotherium* as a separate genus is confirmed.

3.2 Introduction

The morganucodontan *Erythrotherium parringtoni* is known only from a single fragmentary juvenile skull with mandibles and some associated postcranial elements from the Early Jurassic of South Africa (Crompton 1964; Crompton and Jenkins 1968). Subsequent to its original description, Mills (1971) and Kermack (1973) considered *Erythrotherium* to be a junior synonym of *Morganucodon*, with the observed differences falling within the range of variability of *Morganucodon*. Crompton (1974) described the dentition in detail and corroborated the validity of *Erythrotherium* despite its overall similarity to *Morganucodon*, pointing out that the ultimate upper premolar is smaller than M1 and that m1 lacks cusp g (=Kühnecone), in contrast to *Morganucodon*. Postcranial elements were subsequently described by Jenkins and Parrington (1976), and Kielan-Jaworowska et al. (2004) considered *Erythrotherium* to be a valid taxon.

In Morganucodonta two types of occlusal modes are present. Embrasure occlusion, which is present in *Megazostrodon*, is characterized by cusps a and A of the lower resp. upper molars entering between two antagonistic molars during the power stroke (Crompton and Jenkins 1968). The other occlusal pattern is characterized by cusp a entering in between the valley of the upper cusps A and B and cusp A entering between lower cusps a and c (Crompton and Jenkins 1968). The best-known representative of this pattern is *Morganucodon*. However, wear facets in *Morganucodon* exhibit variability (Crompton and Jenkins 1968), and Jäger et al (2019b) showed that the occlusion of cusp a in *Morganucodon* was subject to variation and in some cases occluded anterior to B between two upper molars. Thus the most reliable difference between the two patterns is the occlusion of cusp A.

The occlusal pattern of *Erythrotherium* has been described as embrasure occlusion similar to that of *Megazostrodon* and unlike that of *Morganucodon*, despite the described similarities in molar morphology. This interpretation was based on a single wear facet on the mesial side of cusp B of M1, which would have required the lower cusp a to enter mesially to M1 (Crompton 1974). Therefore, additional evidence is required to address the occlusal relationships of *Erythrotherium*.

In this study micro-computed tomography (µ-Ct) and 3D models are used to re-examine the molars of *Erythrotherium* and to compare them to those of *Morganucodon watsoni* and *Megazostrodon rudnerae*. The hypothesis that *Erythrotherium* had embrasure type occlusion, similar to *Megazostrodon*, is tested with the Occlusal Fingerprint Analyser software (OFA).

3.3 Material and Methods

The holotype (SAM-PK-K00359) is housed in the Iziko South African Museum (ISAM). The specimen was scanned with (0.0067mm). Subsequently, the right lower m2 and m3 and upper M1 and M2 were segmented using Avizo (8.1, Visualization Sciences Group, France) and further processed using Polyworks (2014, InnovMetric Software Inc., Canada). Because the teeth are still in occlusion, and the difference in density between the occluding teeth and embedding matrix is low, the quality of the segmented 3D models is lower than the comparative digital models of *Morganucodon* and *Megazostrodon* first introduced in Jäger et al. (2019b), but still sufficient for confidence in the morphological and OFA results.

The molars discussed here were chosen for the OFA because they are bear little damage and because they previously have been accessible only in buccal view and thus have not been fully figured before. The most reliable OFA analyses are based on matching upper and lower dentitions, which is the case for the *Erythrotherium* specimen discussed here.

The term 'occlusal fingerprint' was introduced by Kullmer et al. (2009). It describes the orientation and position of wear facets on the occlusal surface. Within the Research Unit 771 of the German Research Foundation (DFG) the Occlusal Fingerprint Analyzer (OFA) software was developed and applied to analyze the chewing path of extinct and extant mammals (e.g. Benazzi et al. 2011, 2013; Koenigswald et al. 2013; Kullmer et al. 2009, 2013; Schultz and Martin 2014; Schultz et al. 2019; Jäger et al. 2019b). The polygonal tooth models follow a user-defined pathway based on occlusal hypotheses and the virtual collision of the teeth is simulated.

For comparison with *Erythrotherium*, the holotype of *Megazostrodon rudnerae* (NHMUK PV M 26407) and a well-preserved specimen of *Morganucodon watsoni* (UMZC Eo.CR.1) were examined. Both specimens were chosen because they have matching upper and lower dentitions, which were previously described in detail together with OFA analysis (Jäger et al. 2019b).

3.4 Results/Discussion

3.4.1 Morphology

The teeth of *Erythrotherium* were described in detail by Crompton (1964, 1974). Therefore, this study focuses on morphological comparison of 3D models of the molars of *Erythrotherium* with those of *Megazostrodon* and *Morganucodon*.

When m2 and m3 of *Erythrotherium* are compared to comparative molars of *Megazostrodon* and *Morganucodon,* several morphological differences are apparent (Figs 3.1, 3.2). In both the latter the m2 is noticeably larger than the m3. In *Erythrotherium* the m3 is slightly larger than the m2, which is not obvious at first glance since the m2 was shifted out of its alveoli and is now positioned slightly above the m3. Another noticeable difference is the width of the lower molars in occlusal view. The lower molars of *Erythrotherium* are much more slender, relative to their height, than those of *Morganucodon* and *Megazostrodon*, which appear more massive. This is partially due to a weaker cingulid in *Erythrotherium*, a difference already noted by Crompton (1964), but the difference in width is primarily driven by the slender main cusps of *Erythrotherium* (Fig. 3.1). This is most notable in the mesial region of cusp a. Despite being the tallest cusp it is almost as slender as cusps b and c. In *Morganucodon* on the other hand, cusp a has a wide base that noticeably surpasses that of cusps b and c and almost corresponds with the total tooth width. While cusp width differs between *Erythrotherium* and *Morganucodon*, the ratio of cusp height of a, b and c is almost equal. In *Megazostrodon*, cusp a is also the tallest cusp, but the height difference to the other cusps is less pronounced.

Cusp positioning of the lower molars of *Erythrotherium*, on the other hand, is more similar to that of *Megazostrodon* than to *Morganucodon*. In *Erythrotherium* and *Megazostrodon* a relatively large gap is present between cusps a and b, while cusps a and c are positioned more closely and are less separated. In contrast, in *Morganucodon* the space between cusps a and c is large enough to accommodate the upper molar cusp A during occlusion (Jäger et al. 2019b) and cusps a and b are positioned relatively close to each other. Cusp d is more distinct and upwards facing in *Erythrotherium* than in the other taxa where cusp d faces more posteriorly. Compared to *Morganucodon*, the small valley for interlocking with the next anterior molar formed by cusps b and e, is more prominent in *Erythrotherium* and thus similar to *Megazostrodon*.

In lingual and buccal views M1 and M2 of *Erythrotherium* and *Morganucodon* are highly similar. Relative cusp height and positioning of the main cusps are almost identical when seen from buccal or lingual. However, the morphological differences between these taxa become apparent in occlusal view. Similar to the lower molars, the upper molars of *Erythrotherium* are much more slender than those of the other taxa. Especially the upper molars of *Morganucodon* are more massive, due to wider cusps and cingula. In *Morganucodon* the more posterior upper molars, beginning with M2, are angled lingually relative to the anterior portion of the tooth row and therefore create space between M1 and M2 for the large central cusp a of m2. This enables the teeth to pass closely to each other despite the large size of the lower main cusp a (Jäger et al. 2019b). This change in orientation is absent in *Megazostrodon* and *Erythrotherium*.

The buccal cingulum of *Erythrotherium* is restricted to the distal and mesial regions and is absent next to cusp A. This division of the buccal cingulum similarly occurs in

Megazostrodon where it is more pronounced, whereas in *Morganucodon* it is continuous (Crompton 1974). Similar to the situation in the lower molars, upper molar cusp D is larger and more pronounced in *Erythrotherium* than in *Megazostrodon* and *Morganucodon*.

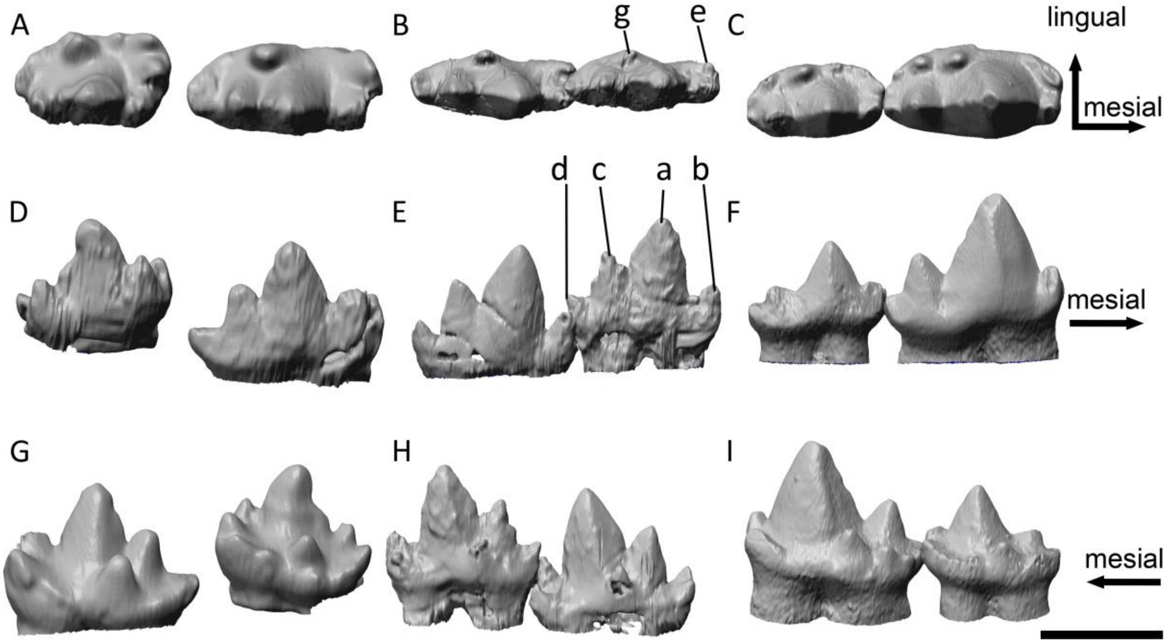

FIGURE 3.1. Comparison of m2 and m3 of (A, D, G) *Megazostrodon rudnerae* (NHMUK PV M 26407), (B, E, H) *Erythrotherium parringtoni*, and (C, F, I) *Morganucodon watsoni* (UMZC Eo.CR.1) in (A, B, C) occlusal view, (D, E, F) buccal view, and (G, H, I) lingual view. Scale bar equals 1 mm.

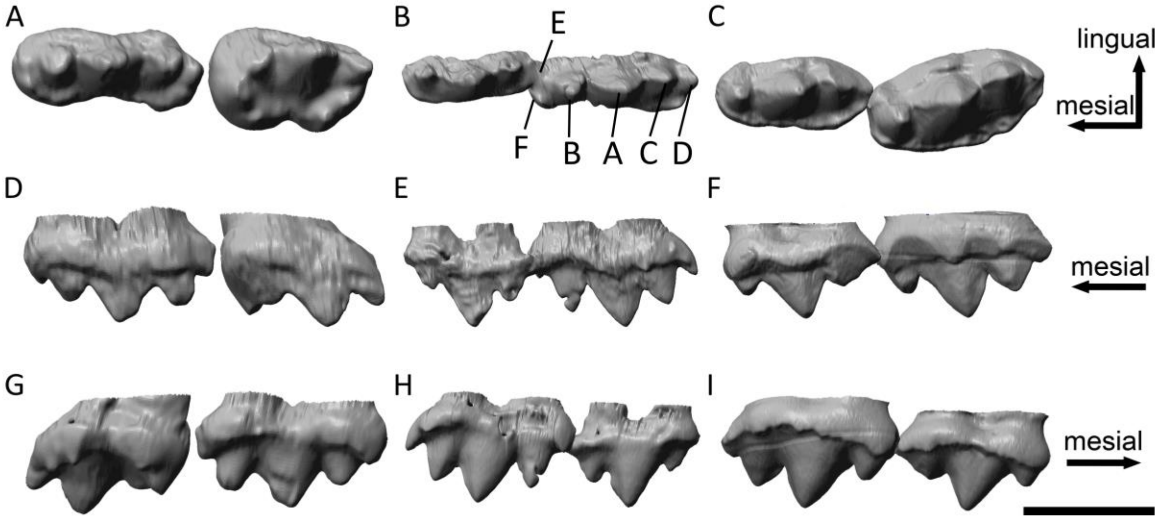

FIGURE 3.2. Comparison of M1 and M2 of (A, D, G) *Megazostrodon rudnerae* (NHMUK PV M 26407), (B, E, H) *Erythrotherium parringtoni*, and (C, F, I) *Morganucodon watsoni* (UMZC Eo.CR.1) in (A, B, C) occlusal view, (D, E, F), lingual view, and (G, H, I) buccal view. Scale bar equals 1 mm.

3.4.2 Wear

Because the teeth are preserved in occlusion and the 3D models therefore provide limited information, little can be said regarding wear on the molars. Based on the small degree of wear that he observed, Crompton (1974) concluded that the individual was most likely a juvenile. He described a mesially oriented facet on cusp B of the left upper M1 and this observation is confirmed by the µCt data. Clear wear facets are absent on the right m2, m3, M1, and M2 and the only additional regions on which wear facets can be identified are the buccal side of cusp b of m3 and the lingual side of cusp C of M2.

3.4.3 OFA Analysis

The OFA analysis was limited due to the lack of observable striations and wear facets, as well as the quality of the occlusal aspects of the 3D models (Appendix 2). Nevertheless, the results clearly support the hypothesis by Crompton (1974) that *Erythrotherium* had embrasure occlusion, rather than a *Morganucodon*-like occlusal mode. When the occlusal mode described for *Morganucodon* (Crompton and Jenkins, 1968) was applied, only the lower cusps a and c and upper cusps A and C were able to make contact (Fig. 3.3). While cusps a and A entered in the valleys between cusps B and A, and cusps a and c, their size, relative to the space between the antagonistic cusps, was too large, thus they prevented the rest of the molars from getting into close contact. Gaps are especially apparent for cusps b/B and d/D (Fig. 3.3H) with the *Morganucodon* occlusal mode, therefore, the few observed wear facets are located in areas that do not come into close contact with their antagonists. As stated above, in *Morganucodon* the more posterior upper molars, are angled to create space between M1 and M2 for the large central cusp a of m2 in order to provide space for the teeth to pass close to each other (Jäger et al. 2019b). Apart from this, cusps a and c are further spaced antero-posteriorly in the lower molars of *Morganucodon* (see above) which apparently is necessary for a functioning occlusion with a *Morganucodon*-like occlusal mode.

In contrast, when embrasure occlusion is applied for *Erythrotherium*, the teeth pass along each other in much closer proximity, resulting in more extensive collision surface detection on all cusps (Fig. 3.3). Cusp a occludes into the space between two molars, thus allowing cusp c to enter between cusps A and B, and cusp C to enter between cusps b and a. The limited space between cusps A and C is sufficient for the small cusp b to enter. Unlike for the simulation using a *Morganucodon*-like occlusal mode, with embrasure occlusion the observed wear facets on the lingual side of cusp C of M2 and the buccal side of cusp b of m3 come into contact over the course of the power stroke. The difference with a *Morganucodon*-like occlusion becomes most apparent when the two occlusal modes are compared during the later phase of the power stroke from a dorsal view (Fig. 3.3G-J). Embrasure occlusion results in a better fit along all teeth involved.

Bhullar et al. (2019) discussed the potential presence of roll during occlusion in early Mammaliaformes. For *Erythrotherium* the OFA was able to produce all observed wear facets without the application of roll. This does not exclude the presence of roll during the power stroke, however, it shows that if roll was present it was likely within a few degrees. This is in accordance with observations on *Morganucodon* (Jäger et al. 2019b).

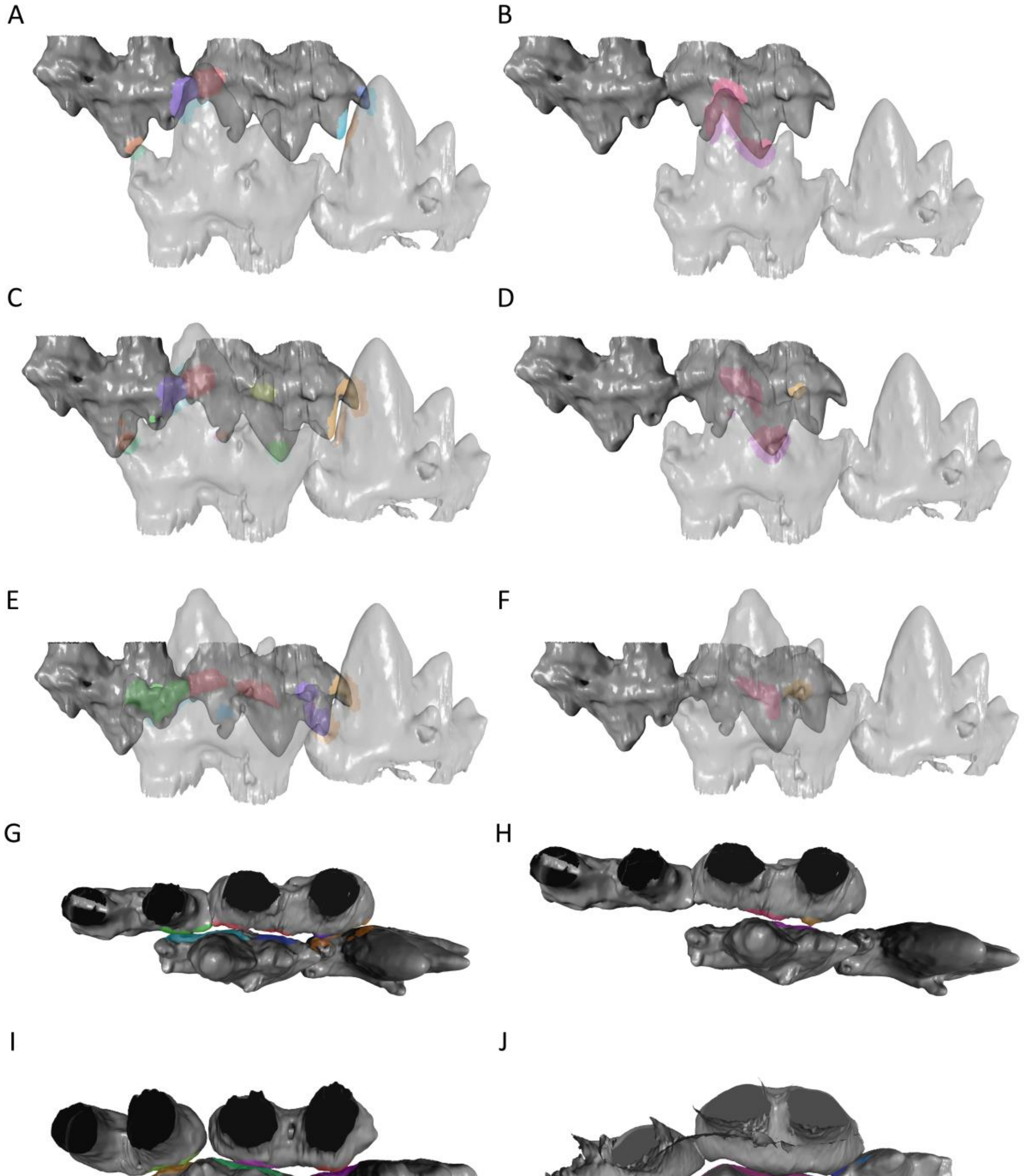

FIGURE 3.3. Comparison of the occlusal hypothesis for *Erythotherium parringtoni*, *Morganucodon*, and *Megazostrodon* with m2 and m3 as well as M1 and M2. Lingual view of *Erythrotherium* with (A, C, E) embrasure occlusion and (B, D, F) *Morganucodon*-like occlusion, compared in (A, B) early- , (C, D) middle- , and (E, F) late stages of the power stroke. Occlusal view of late wear stages of *Erythrotherium* with (G) embrasure occlusion, (H) *Morganucodon*-like occlusion, (I) *Megazostrodon* (NHMUK PV M 26407), and (J) *Morganucodon* (UMZC Eo.CR.1). *Morganucodon* has sufficient space between cusps a and c to accommodate cusp A. Additionally, the upper molars are angled to provide space for cusp a, especially the very large cusp a of m2. In comparison, the space between cusps a and c in *Erythrotherium* is much smaller and both lower and upper molars are aligned in a straight line, similar to *Megazostrodon*. Therefore, *Morganucodon*-like occlusion in *Erythrotherium* lacks contact for the b/B and d/D cusps. Embrasure occlusion on the other hand results in collision detection on all major cusps and correlates with observed wear facets. This becomes most apparent in the later stages of the power stroke, where embrasure occlusion results in well-aligned teeth with the a/A cusps utilizing the space between two antagonists. With *Morganucodon*-like occlusion the direct contact of the a/A cusps prevents close contact of the smaller cusps. Mesial is to the left. Teeth are not to scale.

3.5 Conclusion

We consider that the morphological differences between the molars of *Erythrotherium* and *Morganucodon* are sufficient to maintain *Erythrotherium* as a separate genus. While some aspects, such as cusp height and relative proportions are similar to *Morganucodon*, others, such as tooth width and the relative positions of the lower molar cusps, differ noticeably. While the dental morphology of *Erythrotherium* is more similar to that of *Morganucodon*, the occlusal mode (embrasure occlusion) resembles that of *Megazostrodon*, as previously observed by Crompton (1974). This supports the interpretation of Jäger et al. (2019b) that the difference in the occlusal mode of *Megazostrodon* and *Morganucodon* is primarily driven by relative cusp positioning and potentially by the angulation of the upper teeth within the maxillae, rather than by the exact position of the tooth along the longitudinal axis of the jaw (Crompton 1974).

Jäger et al. (2019a) argued that Triconodontidae, which previously were considered to have had a *Morganucodon*-like occlusion (Mills 1971), instead also had embrasure occlusion. With embrasure occlusion confirmed for *Erythortherium,* only *Morganucodon* and a few other members of Morganucodonta with a *Morganucodon*-like occlusal mode are remaining such as *Dinnetherium* and a new morganucodontan from Germany (Crompton and Luo 1993; Martin et al. 2019).

In non-mammaliaform synapsids such as *Thrinaxodon*, upper and lower molariforms did not come into contact during occlusion, thus the postcanines usually lack wear facets (Crompton and Jenkins 1968; Crompton 1974). In *Thrinaxodon* tooth positioning could vary considerably, with some specimens having the lower teeth positioned directly lingually to the uppers when the jaw is closed, while others have an alternating positioning of lower and upper teeth more similar to an embrasure pattern (Crompton 1974).

Mills (1971) argued that the mammaliamorph *Sinoconodon* had embrasure occlusion similar to *Megazostrodon*. A similar positioning was depicted by Crompton and Sun (1985, Fig. 1A) with cusps a/A positioned between two antagonists. However, molariforms in *Sinoconodon* were replaced and multiple studies pointed out that *Sinoconodon* lacked a constant occlusal pattern (Crompton 1974; Crompton and Sun 1985; Crompton and Luo 1993). For the Rhaetian ‘symmetrodontan’ *Woutersia* embrasure occlusion was suggested (Butler 1997).

While neither of the two occlusal modes can be confirmed as the ancestral condition of Mammaliaformes with certainty, embrasure occlusion appears to be the more likely, since *Morganucodon*-like occlusion appears to have been limited to *Morganucodon* and a few other taxa. Embrasure occlusion on the other hand was present in some other members of Morganucodonta, “symmetrodontans” and appears in non-mammaliaform cynodonts, although without occlusal contact.

We show here that *Morganucodon*-like occlusion required teeth with sufficient spacing between cusps a and c; the massive a cusps most likely also required the rearrangement of tooth position and inclination in the upper molar row (Jäger et al. 2019b). In that regard, it is noteworthy that *Morganucodon* apparently was abundant (Gill 2004) and arguably a highly successful mammaliaform and that this type of occlusal mode persisted at least till the Late Jurassic (Martin et al. 2019). One potential explanation is that *Morganucodon*-like occlusion was derived from embrasure occlusion and provided increased food processing capabilities relative to other early Mammaliaformes, contributing to the success of the genus.

3.6 Acknowledgements

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Tooth eruption in the Early Cretaceous British mammal *Triconodon* and description of a new species

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4.1 Abstract

Triconodon mordax, from the lowest Cretaceous (Berriasian) part of the Purbeck Group, Dorset, is one of the few Mesozoic mammals known by an ontogenetic series of specimens that document aspects of tooth eruption and replacement. Surface features of the 17 known specimens were fully described in the 1920s. Our re-study of these fossils includes micro-computed tomography of four specimens. We refer one specimen to a new species, *Triconodon averianovi*, which differs from *T. mordax* in having a more slender, curved c; p4 notably low crowned with slender main cusp and smaller accessory cusps; and molars with weak cingula, m4 being notably smaller with weak cusps a and c. The sample shows *T. mordax* to be variable in some features, notably the number of mental foramina and posterior jaw morphology. Scans reveal an earlier developmental stage (p3 in early eruption) than previously recognized for *T. mordax*, and demonstrate sequential, anteroposterior replacement of premolars, as seen in other non-trechnotherian mammals; it remains unclear whether p1–2 were replaced. Scans also support an earlier hypothesis that m4 erupted late in life; as in other mammals, mineralization began with tooth apices. Onset of m4 mineralization likely coincided with eruption of p3, followed by replacement of dp4 by p4 and eruption of c. The m4 developed within the lingual side of the coronoid process, well above the tooth row, and could not have functioned until it joined the molar series, anterior to the ascending ramus. This could not have been achieved through tooth movement, as in some living mammals (e.g. proboscideans); instead, the last molar was accommodated through unusually prolonged and localized growth of the posterior part of the mandible (and, by implication, the base of the skull rostrum), with the m4 remaining in position and not erupting upward. This pattern is seen among some later triconodontids and appears to be unique to the family.

Key words: Eutriconodonta, diphyodont replacement, eruption sequence, determinate growth

4.2 Introduction

The majority of extant mammals rely on the dentition to comminute the food in the mouth cavity for easier, more efficient, and complete digestion. Many different types of dentitions evolved independently in different clades, emphasizing various functional specializations. Despite the morphological and functional differences, a key character of most mammalian dentitions is a precise fit during occlusion. In turn, precise occlusion is related to other mammalian traits, notably reduction of tooth replacement (diphyodonty) and non-replacement of posterior teeth cheek (molars, e.g. Luo et al. 2004).

The sequence of tooth replacement shows some degree of homoplasy during mammalian evolution. The ancestral "reptilian" mode of replacement is an alternating one, where every other or every third tooth position was replaced (Luo et al. 2004). Early-diverging Mammaliaformes such as *Morganucodon* have a diphyodont mode of tooth replacement with two generations of antemolars. Parallel to this replacement pattern, postcanine teeth differentiated into premolars, which immediately succeed the canine and are replaced once; and the more posteriorly-situated molars, which by definition are not replaced (see discussion in Jenkins and Schaff 1988). Additionally, the replacement pattern changed to a sequential pattern (e.g. p1->p2->p3->p4->p5), which is the plesiomorphic condition for the crown Mammalia. The Trechnotheria secondarily developed alternating dental replacement, which is exceptionally well documented for the dryolestidan *Dryolestes* (Martin 1997, 1999). Based on a large sample size (including upper and lower dentitions of juveniles) from the Guimarota coal mine, it was demonstrated that tooth replacement occurred in two waves, with the first one consisting of i2-> i4 -> p1 -> p3 and the second wave of i1 -> i3 -> c -> p2 -> p4. A similar pattern, where p1 and p3 are replaced before p2, is also documented for the "symmetrodontan" *Zhangheotherium* and was likely present within basal eutherians (Luo and Ji 2005). Extant marsupials, and by extension certain fossil metatherians, have limited their postnatal dental replacement to p3, which has been considered an adaptation to their elongated lactation period (Cifelli et al. 1996; Luckett 1993; Rougier et al. 1998). More recently, van Nievelt and Smith (2005) showed that suppression of tooth replacement, which also occurs in diverse placental groups, cannot be explained by any single hypothesis. Among the various replacement patterns seen among Eutheria, the most common is a secondarily sequential replacement pattern (Luo et al. 2004).

Gobiconodontids, Mesozoic mammals that ranged up to badger size (Hu et al. 2005) and that are generally placed with triconodontids among Eutriconodonta (Martin et al. 2015), differ from other crown Mammalia because they replaced their molariform postcanine teeth with molariform successors that resemble in complexity their predecessors (Jenkins and Schaff 1988; Kielan-Jaworowska and Dashzeveg 1998; Luo et al. 2004; Martin et al. 2015). In other mammals, by contrast, molariform premolars are usually replaced by less complex permanent premolars (Butler 1952, 1995) and there is no replacement at more posterior loci. So far, there is no evidence for molariform replacement in putative relatives to Gobiconodontidae. The number of generations that have been reported for different gobiconodontids varies between two and three (Jenkins and Schaff 1988; Lopatin and Averianov 2014; Martin et al. 2015). Eutriconodonta are a monophyletic taxon of early crown Mammalia, which are characterized by a triconodont molar pattern (Kielan-Jaworowska et al. 2004). They are of special interest because of their phylogenetic position, as an early-diverging clade of Mammalia, and because they include early mammalian essays into carnivory (Simpson 1933; Jenkins and Crompton 1979). The core family, Triconodontidae, is best known from the Jurassic–earliest Cretaceous but survived well into the Late Cretaceous (Fox 1969). Triconodontids exhibit a modified version of the basal triconodont pattern, wherein molars are dominated by a cusp A/a that extends well beyond the accessory cusps B/b and C/c. In triconodontids, molars are characterized by equal or subequal height of all three main cusps; derived forms (e.g. *Corviconodon*) also have an enlarged accessory distal cusp d (Cifelli and Madsen 1998; Cifelli et al. 1998). However, the molar morphology within Triconodontidae is highly similar, which complicates their identification (Kielan-Jaworowska et al. 2004). Although several new taxa of Triconodontidae have been described in recent years, all major hypotheses on their dental function and occlusion date well back into the 20th century and have not been put to test since (e.g. Simpson 1928; Mills 1971). We reexamined the early-diverging triconodontid *Triconodon* with micro-computed tomography (µCT) and address questions of tooth eruption, morphology, and taxonomy.

4.2.1 Previous Work on Dental Replacement and Tooth Eruption in Triconodon

Dental formula of *Triconodon m*. ?I 1C ?P 4M; ?i 1c 4p 4m.

Simpson (1928) described an ontogenetic series of 17 specimens from the Early Cretaceous (Berriasian) Purbeck Group at the Durlston Bay (also known as Durdlestone Bay) locality (Dorset, UK) that he assigned to *Triconodon mordax* Owen, 1859. All specimens are housed in the NHM except for GSM 48746, referred to as "Willett specimen," which is in the collection of the British Geological Survey. (This specimen, first described by Willett and Willett 1881, is from the same locality, although called Swanage by them.) According to Simpson´s (1928) comparative analysis, four lower molars are present in *T. mordax*, contrary to its first description by Owen (1859, 1871), and confirming the views of Willett and Willett (1881), Lydekker (1887), and Osborn (1888). The fourth molar erupts late in life and can be observed on four specimens. Simpson (1928) further inferred that, in other ostensibly conspecific fossils with only three erupted molars, a fourth molar must be present, hidden in a crypt within the mandible.

Based on a specimen representing an immature individual, Simpson (1928) pointed out that the dp4 is molariform (as first suggested by Thomas 1887, who dissected the lingual side of the specimen in question) and that it was replaced by a premolariform successor. Because of the limited amount of wear on the other premolars, he concluded that p4 was the last premolar position to be replaced, approximately at the time of replacement of the canine and before the eruption of the last molar. While this is evidence for an anterior->posterior replacement pattern, it remained unclear if the replacement pattern was sequential or alternating.

4.2.2 Taxonomy of *Triconodon*

Owen (1859) first described *Triconodon mordax* in the in the chapter on paleontology section he provided for the 8th edition of the *Encyclopedia Britannica*. He later added the species *T. ferox*, *T. occisor*, and *T. major*, as well as the then-new genus *Triacanthodon* with one species, *T. serrula* (Owen 1871). As holotype for *Triacanthodon serrula* he suggested NHMUK PV OR 47763, with unerupted but clearly visible m4. Lydekker (1887) and Osborn (1888) challenged this interpretation and considered *Triacanthodon* to be synonymous with *Triconodon*. They suggested that *Triconodon* has four lower molars, of which the last erupted late in ontogeny. This was later acknowledged by Simpson (1928), who further considered the holotype of *T. minor* to be too similar to *Triconodon mordax* and not well enough preserved to justify a separate species. (Whether or not *T. minor* was formally established is debatable. Owen 1871, p. 63 lists the only specimen as "*Triconodon*, sp. ind.," while in the following text he opines it as likely representing a distinct species. The only mention of *T. minor* by name is in the legend accompanying Plate IV, which lists [*Triconodon*] "*minor* (?).") Simpson (1928) further noted that triconodontid fossils previously referred to *Triconodon ferox* Owen, 1871 represent adult individuals that both lack an m4 and are larger than those he referred to *T. mordax*. He placed these specimens in a then-new genus, as *Trioracodon ferox* (Owen, 1871), in which he also included the holotype of *Triconodon occisor* Owen, 1871.

4.2.3 Family-Group Classification of *Triconodon*

Previously the genera *Triconodon*, *Trioracodon*, and *Priacodon* were placed within the Subfamily "Triconodontinae" (Simpson 1928, 1929). In recent phylogenetic studies, this clade has turned out to be paraphyletic. Instead, these genera are placed at the base of the Triconodontidae (Gaetano and Rougier 2011; Martin et al. 2015). The distinction between these three genera (and most of the Triconodontidae) remains difficult, due to their similar molars. The main three criteria are molar cusp size and number of premolars and molars, as well as the presence or absence of a diastema. Cusp shape and relative cusp proportions appear to be variable (Kielan-Jaworowska et al. 2004). When the material is sufficiently complete, the numbers of premolars and molars are considered the primary characters to distinguish different genera. *Triconodon* has four lower premolars and four lower molars. *Priacodon* has a diastema posterior to the canine (which suggests that p1 might have been reduced at some point), three premolars and four lower molars. *Trioracodon* is characterized by four lower premolars and three molars. The latter can further be distinguished from *Triconodon* by size of its lower molars. According to the measurements provided by Simpson (1928), the largest molar of *Triconodon mordax* (an m3 of GSM 48746) has the same length (3.4 mm) as the shortest molar (m1) of two specimens of *Trioracodon ferox*.

Due to the fragmentary nature of the fossils in question, the numbers of premolars and molars are indeterminate for most specimens. Therefore, the presence versus absence of a diastema has been employed as an important character to distinguish *Priacodon* from *Triconodon* and *Trioracodon* (Engelmann and Callison 1998; Kielan-Jaworowska et al. 2004).

On the species level differentiation is even more problematic. In distinguishing between different *Priacodon* species, Simpson (1925) brought to occlusion upper and lower molars of different individuals, in order to see if the teeth match. Although he was himself critical of this method, he considered it as additional evidence to support his taxonomic assignments. Given that various factors such as wear stage, specimen size, and tooth position influence the occlusal fit, this method must be considered highly questionable, and it highlights the lack of diagnostic characters among basal Triconodontidae.

Institutional abbreviations. FMNH, Field Museum of Natural History, Chicago; GSM, British Geological Survey, Keyworth; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; NHMUK, the Natural History Museum, London (specimens listed by earlier workers (Simpson 1928 and references therein) with corresponding numbers and the acronym BM(NH)). *Triconodon* specimens in the NHMUK bear two additional prefixes: PV (Palaeontology, Vertebrates) and OR (Old Register). We use the full prefix at first citation and the last two alone (PV OR) thereafter.

4.3 Materials and Methods

Micro-computed tomography (μCT) was applied to scan the fossils. The scans were performed with the Nikon Metrology HMX ST 225 scanner at the NHM. Subsequently, polygonal models were created using Avizo (8.1, Visualization Sciences Group, France). Four specimens that had been assigned to *Triconodon mordax* by Simpson (1928) were examined in this study (Table 1). The holotype NHMUK PV OR 47764 is a left ramus with dentition, which is complete except for the incisors, p1, and p3. PV OR 47763 is a specimen that was originally named as *Triacanthodon serrula* by Owen (1871) and later considered to be synonymous with *Triconodon mordax* (Lydekker 1887; Osborn 1888; Simpson 1928). It consists of a left ramus in two pieces broken at the position of m3 (missing) and preserved on two slabs. The anterior part of the ramus is preserved on the main slab and the coronoid process and condyle are preserved on the counter slab. The anterior part was subsequently prepared and detached from the matrix. The buccal side of the bone had been removed to expose the roots and succeeding teeth (Thomas 1887). This part of the specimen shows the ultimate incisor, the deciduous canine, p1–3, dp4, and m1–2. The erupting c and p4 are visible, although their shapes remain unclear from the outside. The posterior part is still on the counter slab. The developing m4 is present in a small crypt on the lingual side of the ascending ramus. Due to the split of the specimen, m3 is not preserved, except for the imprint of its buccal side on the sediment. In addition to the ramus, some associated cranial elements are preserved (Simpson 1928).

PV OR 47768 is a fragmentary right ramus including three teeth or parts thereof, one in eruption. Simpson (1928) and Owen (1871) considered the erupting tooth to be p4, followed by the damaged m1 and m2. However, our study revealed that the erupting tooth is a p3; the tooth originally considered to be m1 is a molariform dp4, followed by the fragments of m1 (see results).

PV OR 48395 was previously assigned to *Triconodon mordax* (Simpson 1928). It consists of a substantially complete left ramus and a fragmentary right ramus, as well as associated teeth (Figs 4.1, 4.2). For a detailed description of this specimen see the results.

All specimens were found in the Early Cretaceous (Berriasian) beds of the Durlston Bay locality (Dorset, United Kingdom) (Simpson 1928).

TABLE 1. Specimens examined in this study

Specimen Number	Species	Elements	Locality	Scan Resolution (mm)	Notes
PV OR 47763	*Triconodon mordax*	Left ramus: i4(?),dc, c, p1, p2, p3, dp4, p4, m1-2, m4	Durlston Bay	0.0269 & 0.0087	Two pieces separately scanned m3 is only preserved by the imprint of its buccal side. The a cusp of m4 is damaged.
PV OR 47764	*Triconodon mordax*	Left ramus: c, p2, p4, m1-4	Durlston Bay	0.0184	Holotype *T. mordax*
PV OR 47768	*Triconodon mordax*	Right ramus: p3, dp4, p4, m1	Durlston Bay	0.0147	
PV OR 48395	*Triconodon averianovi* sp. nov.	Left ramus: c, p1, p4, m1-4 Right ramus: c, m1-3	Durlston Bay	0.0219	Holotype *T.* n. sp. An isolated premolar is likely the left p1 and an isolated canine belongs to the right ramus

All specimens are in the NHMUK.

4.4 Systematic Palaeontology

Class MAMMALIA Linnaeus, 1758
Order Eutriconodonta Kermack et al., 1973
Family TRICONODONTIDAE Marsh, 1887
Genus TRICONODON Owen, 1859
Triconodon averianovi sp. nov.
Figures 4.1, 4.2, 4.4E, F; Table 4.1

1928 *Triconodon mordax* Owen; Simpson, p. 78, plate 5, Fig. 3, p. 88 (unnumbered table).

Derivation of name—The species is named after Alexander Averianov, in recognition of his substantial contribution to the research of Mesozoic mammals.

Holotype and only known specimen—NHMUK PV OR 48395, left and right mandibular rami. Left ramus with canine, associated p1 (?), fragmentary p2 and p3, p4, m1–m3 and erupting m4. Right ramus with isolated canine, roots of p4, complete m1–m3, and roots of m4.

Diagnosis—*Triconodon averianovi* differs from *T. mordax* Owen, 1859 in having a small m4 with only cusp b being of regular size; cusps a and c are reduced. *T. averianovi* differs from *Arundelconodon* Cifelli et al., 1999, *Priacodon* Marsh, 1887, *Trioracodon* Simpson, 1928, and *T. mordax* in the morphology and size of its ultimate premolar (p4). It has a shorter and slenderer main cusp (a) and smaller accessory cusps (b, c) than the ultimate premolars of the other taxa. Its height barely surpasses that of m1, making it the smallest known ultimate premolar among early-diverging Triconodontidae. It further differs from *T. mordax* by its slenderer and more curved permanent canine, being more similar to the deciduous canine of the latter. The molars of *T. averianovi* differ from those of *T. mordax* in having more slender, better-separated cusps. PV OR 48395 further differs from specimens referred to *T. mordax* by its shallower ramus. PV OR 48395 differs from *Trioracodon* in having four molars instead of three significantly larger molars. On the lower molars it has less pronounced cingula than *Trioracodon* and *Triconodon mordax*. Differs from *Astroconodon* Patterson, 1951 and *Corviconodon* Cifelli et al., 1998 in having a Meckel's sulcus and from *Meiconodon* Kusuhashi et al., 2009 in having four instead of five lower molars.

4.4.1 Description

Material of NHM PV OR 48395—The holotype of *T. averianovi* consists of a left ramus and a fragmentary right ramus, both on a rock slab. Simpson (1928) erroneously listed two right rami on the slab, but considered both rami to belong to the same specimen in the following text. In his figure legend, he refers to the better-preserved ramus as the left ramus (Simpson 1928, plate 5, Fig. 3). The right ramus contains m1–m3 and the roots of p4 and of m4 (Fig. 4.2). The roots of the right m4 are hidden by the fragment of the ascending ramus. The right canine is embedded separately on the slab. It lacks the tip, which gives it a straighter appearance than its left counterpart. Of the left ramus the canine, p1, p4, m1–m4, as well as the roots of p2and p3 are preserved (Fig. 4.1). An artificial cut runs through the slab and the left ramus where p1 and the posterior part of the canine are to be expected. A small, originally two-rooted premolar (only one root is preserved) is embedded on the slab above the left canine. Judged by its crown morphology it could be the missing p1. However, its roots were apparently widely separated, a character usually associated with deciduous teeth. This would make it unlikely that the tooth belongs to the holotype specimen, because all other premolars, as well as the canines, appear to belong to the second tooth generation. However, given its close proximity to the specimen and matching size, we assign it tentatively to be the detached p1. No incisors are preserved.

Molars—Based on size and tooth count PV OR 48395 can be attributed to the genus *Tricondon*: *Trioracodon* is larger and has only three lower molars, while in similar-sized *Priacodon* the p1 is reduced and a diastema is present between the canine and the first premolar. There is no sign of premolar loss or alveolar plugging in *T. averianovi*.

The molars are similar to those of *T. mordax* and other early-diverging Triconodontidae, with three main cusps of almost equal height and an incipient cusp d, which interlocks in a tongue-and-groove system with two mesial crests (perhaps homologs of cusps e and f) on the following posterior molar. The interlocking is restricted to the tooth crown and does not affect the roots. A minor difference with respect to *T. mordax* is that in the latter, m3 is always the largest molar. In *T. averianovi* m2 and m3 are almost equal in length, with m2 being slightly longer. In *T. averianovi* m4 is short with only cusp b of regular size; by comparison, cusps a and c are reduced in size. Reduced last molars are also seen in *Corviconodon*, which has five molars: in *C. montanensis*, reduced cusps a and c are present, whereas cusp c is lacking in *C. utahensis* (Cifelli and Madsen 1998; Cifelli et al. 1998); and similarly in *Priacodon fruitaenensis*, in which cusps a and c of m4 are reduced (Rasmussen and Callison 1981). In *T.*

mordax the m4 is only slightly smaller than the m3, which is the largest of the lower molars, and its main cusps are of equal height (Simpson 1928). The small cusps a and c in m4 of *T. averianovi* suggest that they would not have occluded with the antagonist after the tooth was fully erupted. On all molars, the cusps of *T. averianovi* are slender and more pointed than those of *T. mordax,* which has already been noted by Simpson (1928). He pointed out that this shape difference could be attributed to wear, since the specimen represents one of the oldest individuals of the ontogenetic series. Wear, which is best visible on the molars of the right ramus, could indeed have influenced the cusp shape and their separation. However, other *T. mordax* specimens that are at a comparable ontogenetic stage judged by their dentition (e.g. NHM PV OR 47763, PV OR 47764, and GSM 48746) show wider cusps. Therefore, this character can be regarded as a difference between the two species. On m1, cusp d overhangs the posterior root, as is the case for m1 of *T. mordax*. However, on m2 and m3 cusp d does not overhang the posterior root, making them more similar to *Arundelconodon* in that regard. The molar roots are closely spaced and form cervically an acute angular arch while those of *T. mordax* are more widely spaced with a wider arch with flat top. In both species of *Triconodon,* the molar roots are liguobuccally compressed, relative to their mesiodistal length. This is more pronounced in *T. averianovi*.

Premolars—The premolars of *T. averianovi* are relatively small. The associated p1 has long roots (Fig. 4.1D, E) but its crown is smaller and slenderer than that of PV OR 47763 (*T. mordax*). It appears to have wear on most of its buccal side, while p1 of PV OR 47763 (*T. mordax*) has one large mesial facet, most likely caused by the upper canine. Of p2 and p3 only the roots are preserved. The roots of p3 and p4 are noticeably more robust than those of p1 and p2, although not much longer. The fourth premolar is damaged, with bits broken off the lingual side and the tip. Despite the damage, it is evident that it is smaller than that of *T. mordax*. All known p4s, as well as p3s of *T. mordax,* are larger than the p4 of *T. averianovi.* The p4 of PV OR 48395 is only slightly taller than the adjacent m1, which to our knowledge is different from all other early-diverging Triconodontidae, which all have p4s that are noticeably taller than m1. The main cusps a, b, and c are present on the p4, with cusp a being the largest. Cusp b is only slightly larger than the small uplift of the lingual cingulum on the distal end where cusp d would be expected. It is placed lower than the small cusp c, which bears a buccally-oriented wear facet on its tip.

In *T. mordax* the lower canine is replaced shortly after the p4 (Simpson 1928). The deciduous canines of *T. mordax* have two roots, while the permanent ones were most likely single-rooted based on the incomplete erupting canines (Fig. 4.3) and comparison with *Trioracodon*. The canine of *T. averianovi* is most likely a permanent one, based on the presence of a single root, the absence of a germ for a replacement at the canine locus, and the ontogenetic age of the specimen. The canine is less massive and more curved than those known for *T. mordax*, which are figured here for the first time. Its crown morphology is more similar to that of the deciduous canines known for *T. mordax* (Fig. 4.3).

Dentary—The jaw is gracile and shallower than that of *T. mordax*, although this difference is subtle (Figs 4.1, 4.4).

Occurrence—Durlston Bay locality, Swanage, Dorset, UK (given by Kermack 1988 as SZ 035772 039 786); probably bed DB 83 of Clements (1993), Lulworth Formation of the Purbeck Limestone Group, Berriasian, Lower Cretaceous (see Kielan-Jaworowska et al. 2004, p. 45).

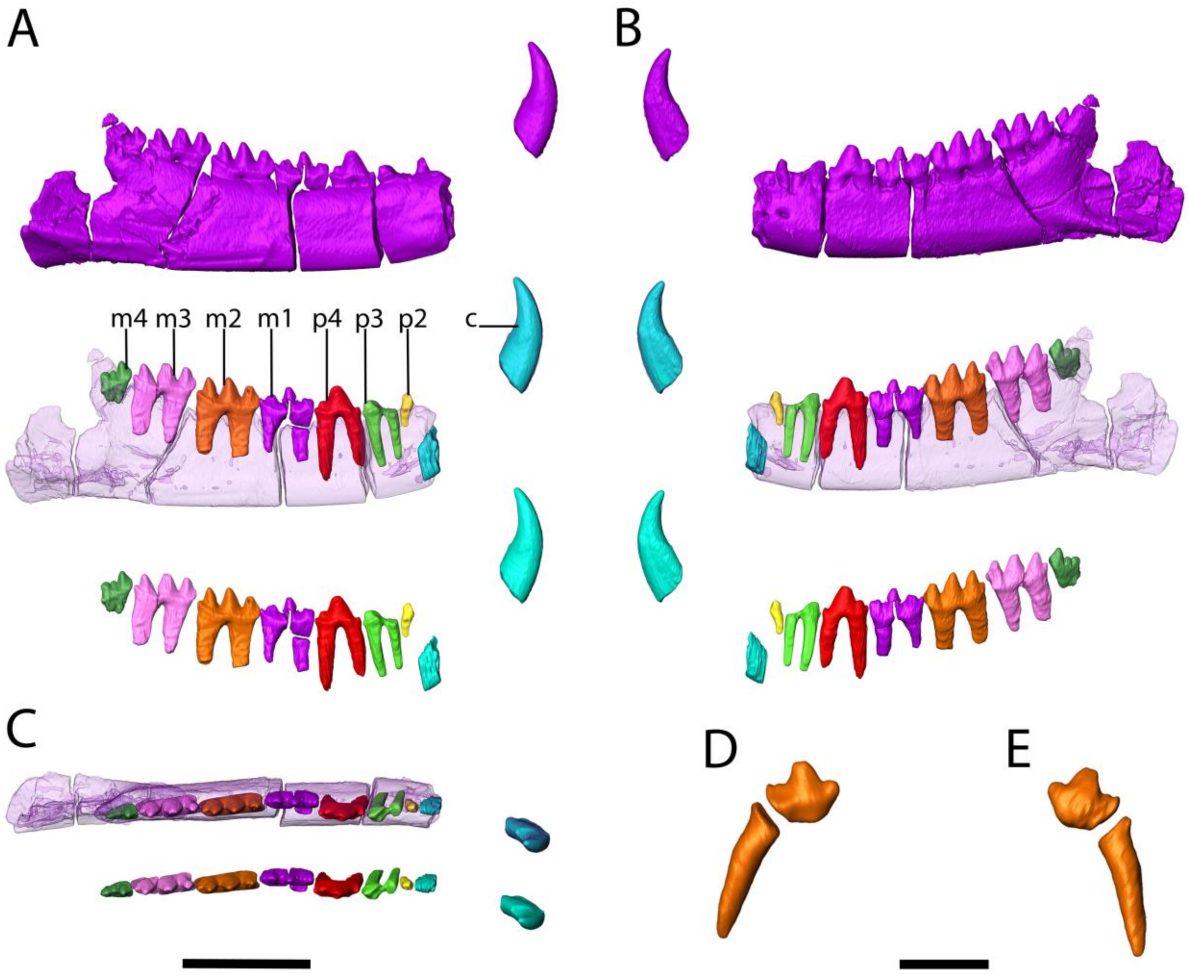

FIGURE 4.1. Left ramus of *Triconodon averianovi* (PV OR 48395). (A) Medial view, (B) lateral view, (C) occlusal view (anterior to the right), (D) isolated p1 medial view, and (E) isolated p1 lateral view.

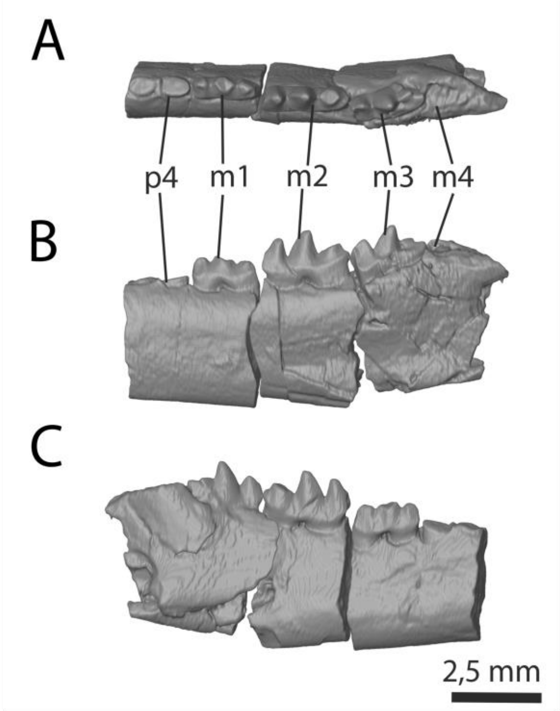

FIGURE 4.2. Fragmentary right ramus of *Triconodon averianovi* (PV OR 48395). (A) Occlusal view (anterior to the left), (B) medial view, and (C) lateral view. The crypt of m4 is preserved providing information on its small size and its position within the ascending ramus.

4.4.2 Late Stage Ontogeny of the Dentition in *Triconodon*

Tooth replacement pattern—The teeth of PV OR 47768 have been interpreted as erupting p4, followed by the damaged m1 and m2 (Owen 1871; Simpson 1928). The µCt analysis revealed the cap of the main cusp of an erupting tooth below the supposed m1 (Fig. 4.5). Accordingly, we propose the following reinterpretation of the tooth positions: The tooth previously considered as m2 is an m1, the former m1 is a molariform dp4, and the anterior erupting tooth is a p3. While the proof of a replacement is the strongest evidence for the new positional interpretation, it is further supported by morphology. The dp4 is mesiodistally elongated and buccolingually compressed. The dp4 is positioned lower than m1 and its cusp a is of similar size to cusp b of m1. These characters are also present in the dp4 of PV OR 47763 (Simpson 1928, Fig. 24A), but it has more strongly-diverging roots that the others. This probably is due to the ontogenetic age of p4, because in PV OR 47763 it is in the process of eruption, whereas in PV OR 47768 it is just about to form, and at this early stage the roots are not yet flared out. Additionally, the reconstruction of the roots within the alveoli further supports the new interpretation (Fig. 4.5).

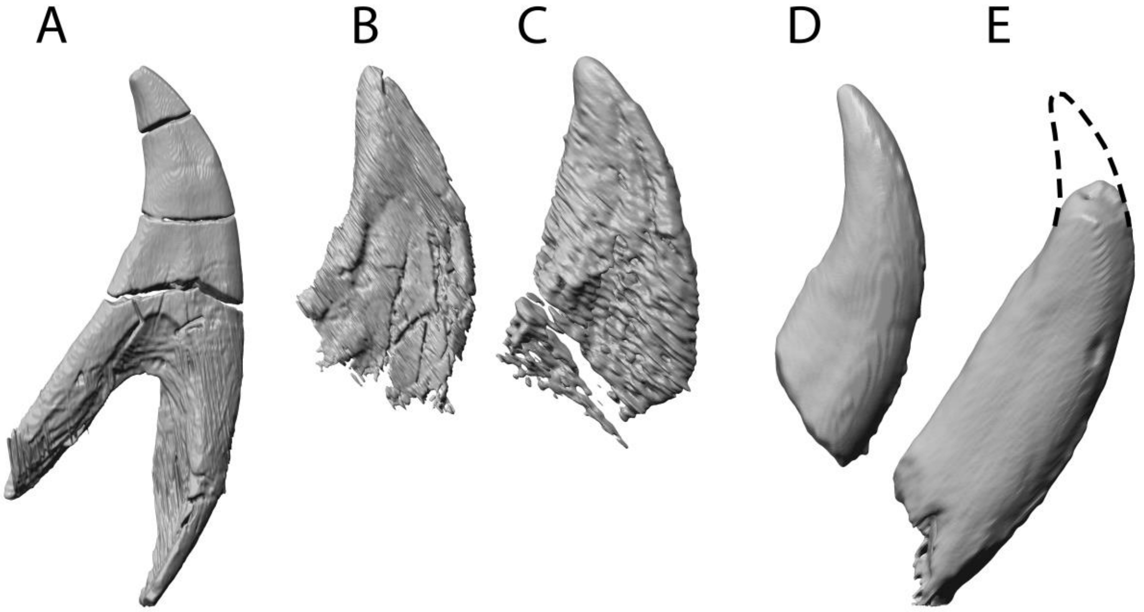

FIGURE 4.3. Canine comparison of (A, B, C) *Triconodon mordax* and (D, E) *T. averianovi*. (A) Left deciduous canine of PV OR 47763, (B) erupting left canine underneath the deciduous one of PV OR 47763, (C) erupting left canine of PV OR 47764, (D) left canine of PV OR 48395, and (E) right canine of PV OR 48395. The presence of a single root, the absence of a replacement, and the ontogenetic stage are clear evidence for the canines of *T. averianovi* to be permanent ones. However, their slender shape and curvature resemble the deciduous canines of *T. mordax*, especially when the roots are hidden in the dentary. The permanent canines of *T. mordax* meanwhile are considerably more massive and less curved. Based on the current reconstructions (B, C), it cannot be excluded that two roots would have formed. However, we consider it more likely that only a single root was present. Since no fully formed permanent canine of *T. mordax* is known, it remains unclear if the canine was single or double-rooted.

These observations support an anterior-to-posterior, sequential replacement of the premolars, with eruption of p3 preceding that of p4. This is in accordance with the pattern seen in other non-trechnotherian mammals, which suggest that a sequential tooth replacement evolved within early Mammaliaformes (Luo et al. 2004). Within Eutriconodonta, the Gobiconodontidae have a sequential replacement (Jenkins and Schaff 1988), which differ from other eutriconodontans by the multiple replacement of molariforms. The new results and the early-diverging position of *Triconodon* within the Triconodontidae suggest that an anterior-posterior sequential premolar replacement condition is plesiomorphic for this family and likely Eutriconodonta in general.

It remains unclear whether p1 and p2 were replaced in *Triconodon*. Simpson (1928) suggested, based on the little amount of wear on the anterior premolars in PV OR 47763, that they might have been replaced before the eruption of p4. According to our reexamination of the specimen, this holds up only for p2 and p3, while p1 shows a large anterior wear facet, likely caused by the upper canine. However, the presence or absence of wear on the small anterior premolars provides only limited evidence on the replacement. If there was no contact to the upper antagonists, the first premolar generation could have remained unworn for a long time. On the other hand, a replaced premolar having a large antagonist (e.g. the canine) might show a large wear facet shortly after eruption. Since the morphology of the upper anterior premolars is unknown, the interpretation of the presence of wear on p1 and the lack of it on p2 and its significance for replacement remain speculative. At this point it remains unclear if p1 and p2 were replaced.

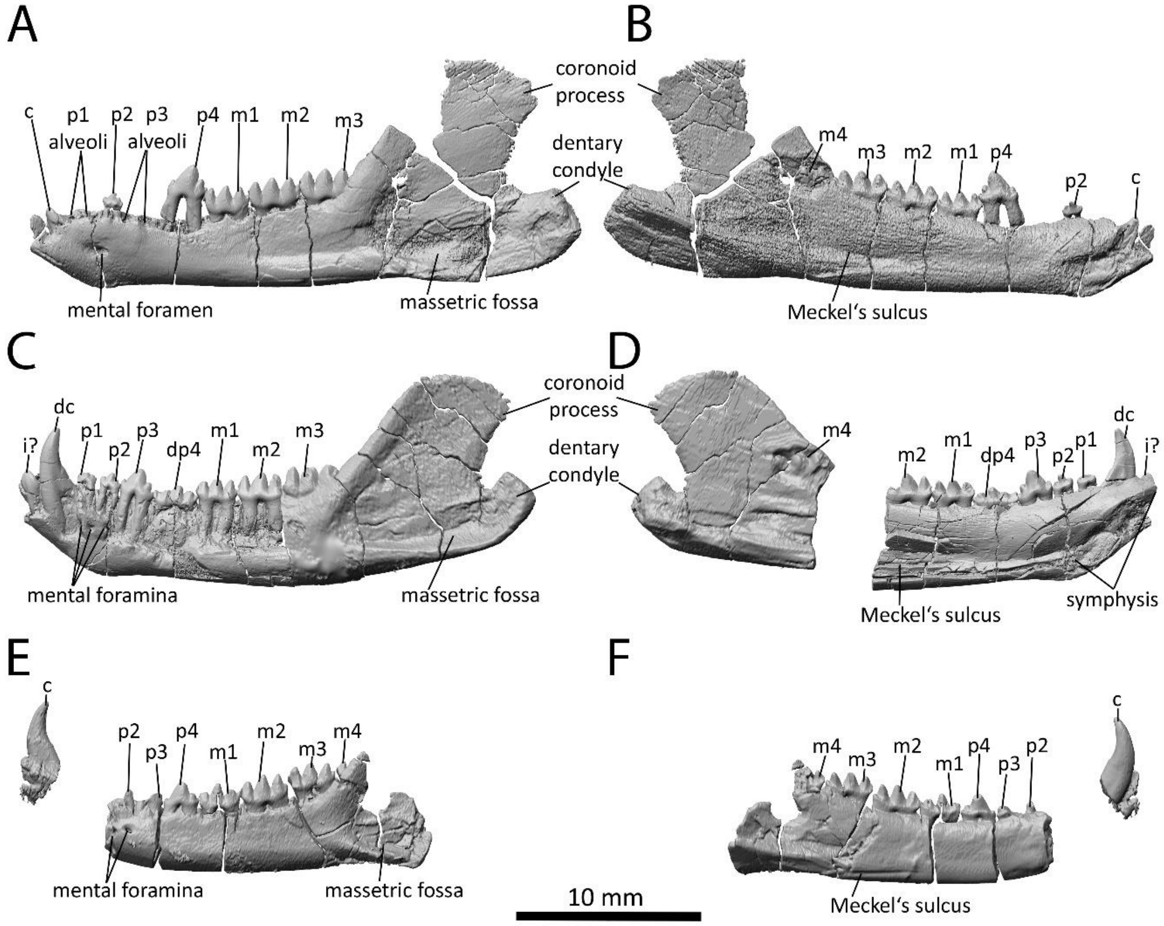

FIGURE 4.4. Comparison of the dental rami of *Triconodon mordax* and *T. averianovi*. (A, B) Holotype of *T. mordax* PV OR 47764 in (A) lateral and (B) medial view. (C, D) *T. mordax* PV OR 47763 in (C) lateral and (D) medial view. PV OR 47763 was reconstructed based on the anterior part, which extends till m2, the posterior ramus with the coronoid and the impression of the lingual side of the ramus in the sediment in between, including m3. The symphysis on the anterior medial side is large and extends below p3. The most notable difference to the holotype is the morphology of the posterior ramus and the presence of three mental foramina instead of one. (E, F) *T. averianovi* PV OR 48395 in (E) lateral and (F) medial view.

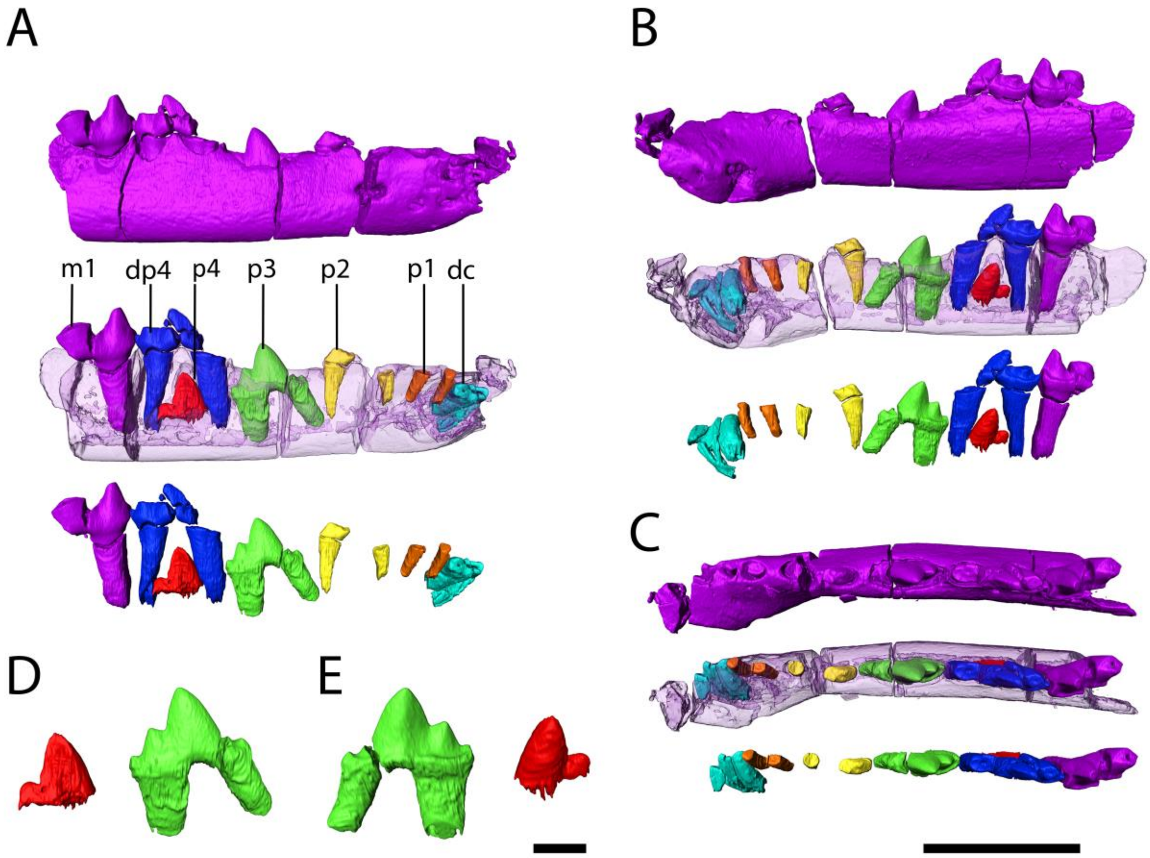

FIGURE 4.5. Fragmentary right ramus of *Triconodon mordax*(?) (PV OR 47768). (A) Lateral view, (B) medial view, (C) occlusal view (anterior to the left), (D, E) enlarged erupting p3 and forming p4 in (D) buccal and (E) lingual view.

Ultimate molar eruption—Simpson (1928) assumed that the fourth molar of *Triconodon* erupted late in life since only one specimen with a fully erupted m4 is known. He noticed in some specimens a germ of m4 in a formative capsule on the lingual side of the coronoid. He concluded that, in other specimens with only three erupted molars visible in buccal view, a fourth molar should be present, concealed by the coronoid. The µCT data confirm this suggestion for the holotype of *T. mordax*, NHMUK PV OR 47764 (Figs 4.4B, 4.6). Based on the new data from PV OR 47763, PV OR 47764, and PV OR 48395 it becomes apparent that the locus of the last molar is right behind m3 and that the capsule is embedded deep into the ascending ramus of the coronoid, slightly above the tooth row. The m4 develops regularly, with mineralization starting at the apices of the main cusps (Luckett 1993). At a later stage when the crown is formed, but the roots are not developed yet, most of the tooth is still hidden by the ascending ramus, but cusp b becomes visible in buccal view (Fig. 4.4E). When fully erupted, the tooth has passed beyond the ascending ramus and is visible in buccal view. It is worth emphasizing that the tooth remained non-functional up to this point, because it is the buccal surfaces of lower molar crowns that occlude with the lingual faces of their antagonists in the upper dentition. The mesial shift of m4 from the lingual side of the coronoid may have been achieved in two ways. One would be active tooth movement, in the form of horizontal tooth displacement, as has been documented for some rodents, macropodoid kangaroos, proboscideans, and sirenians (Domning and Hayek 1984; Sanson 1989; Sanders 2017). However, this was most likely not the case for *Triconodon*. Since m4 is formed closely posterior to m3, all teeth would have to move mesially to create space. This would either require a diastema that could be filled or shedding of anterior teeth in order to create the necessary space. Neither seems to have been the case in *Triconodon*. Further, the roots of the anterior molars are straight and show no sign of curvature, which is known for most of the recent taxa mentioned above. Therefore, an active tooth movement is highly unlikely for *Triconodon* and we suggest that the change in position was caused by mandibular growth. With the ramus growing in length, the coronoid shifts its position in a distal direction, exposing the previously-covered molar. This growth that occurred relatively late during ontogeny was substantial enough to fully expose the posterior molar (Simpson 1928 p. 79, Fig. 24D). Furthermore, because the preceding teeth remain in contact, it appears that growth might have been localized in the posterior part of the ramus.

This condition resembles that seen in multituberculates and the docodontan *Docodon*. In multituberculates the distal end of the toothrow laterally overlaps the anterior edge of the coronoid process (Greenwald 1988). In *Docodon victor*, starting with m5, upcoming molars erupt lingual to and partially hidden by the coronoid. With continuous growth of the mandible, the coronoid retracts and exposes the newly-erupted molar. Subsequently, the next molar erupts in a similar position as its predecessor (Schultz et al. 2019). However, it has to be noted that there is a key difference between these eruption patterns and that of *Triconodon*. In multituberculates and *Docodon victor*, the molars are formed within the ramus and erupt upward. Therefore, the posterior molars end up adjacent to the ascending coronoid (Greenwald 1988; Schultz et al. 2019, Fig. 7d). In *Triconodon* m4 forms directly below the coronoid process, within the ascending ramus and higher than the anterior molars Therefore, m4 of *Triconodon* never erupts upward, as in other mammals, but stays in place after it is fully formed.

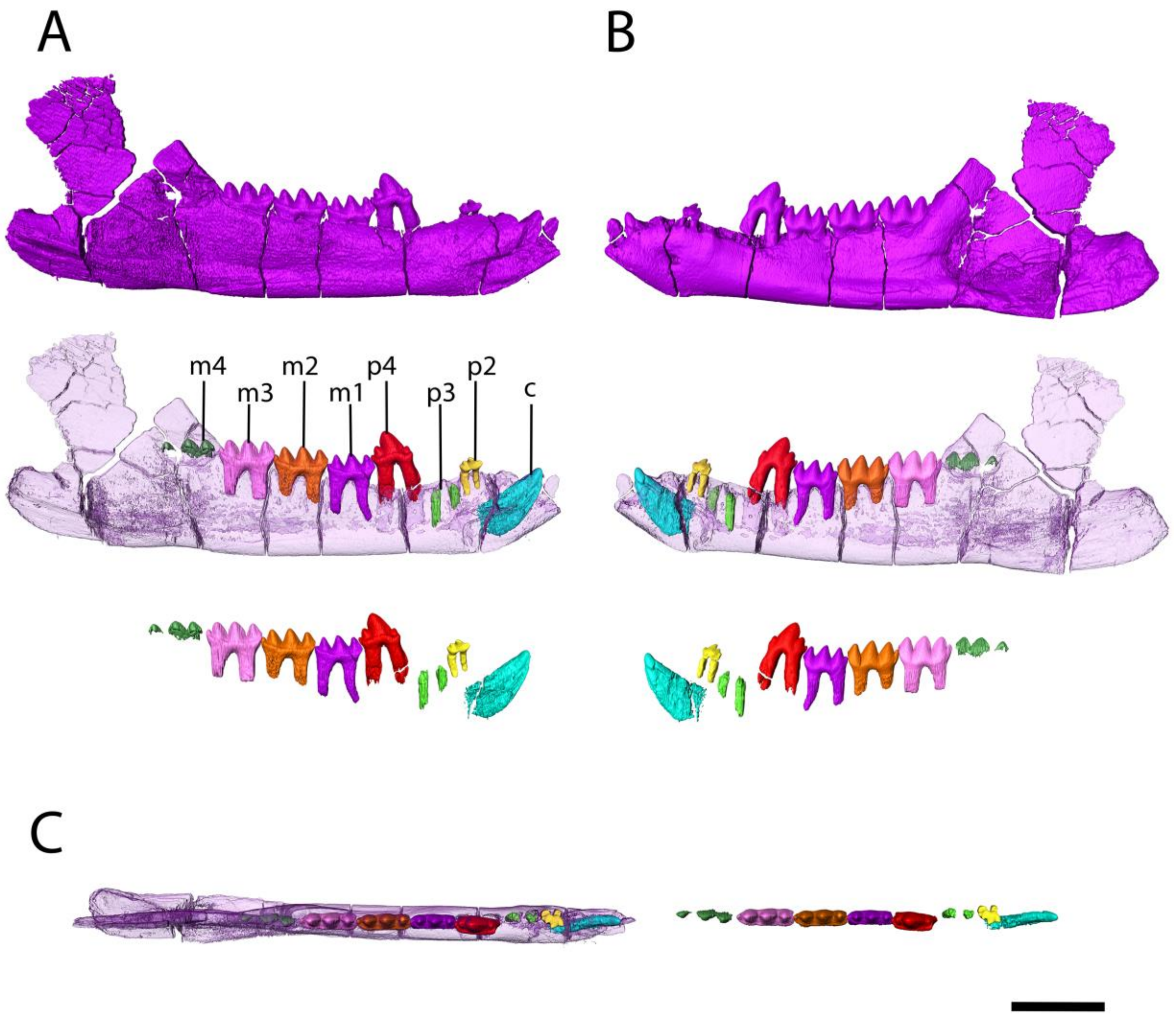

FIGURE 4.6. Left ramus, holotype of *Triconodon mordax* (PV OR 47764). (A) Medial view, (B) lateral view, and (C) occlusal view (anterior to the right).

The formation of the m4 in a crypt within the ascending ramus and above the active tooth row has so far only been observed in Triconodontidae. After formation, the tooth remains in position while the jaw grows. This is similar to other Mammaliaformes with a posterior eruption of molars further behind the ascending ramus (e.g. *Docodon*). The m4 of *Triconodon* came into use late in life, which is suggested by the fact that only one specimen is known with a fully-erupted m4. This is apparently a common character found in various members of the Triconodontidae, some having multiple molars being formed in the ascending ramus. A specimen of *Astrocondon* (FMNH PM 588) has been described with m4 partially and m5 completely hidden in the ascending ramus (Turnbull and Cifelli 1999). In *Corviconodon* (OMNH 33457) m5 is also fully covered by the ascending ramus and considerably higher placed than the active tooth row (Cifelli et al. 1998, Fig. 1).

This has also been described for *Meiconodon* (Kusuhashi et al. 2009). Similar to *Corviconodon* and *Astroconodon* the last lower molars (m5) erupts “from the coronoid process at a higher position than the other […] molariforms” (Kusuhashi et al. 2009 p. 774). Based on the images provided by Kusuhashi et al. (2009, Fig. 3) it appears as if the m5 has fully emerged from its crypt in referred specimen IVPP V14515 and is integrated into the active tooth row. Alternatively, the condition seen in *Meiconodon* could also occur with “regular” molar formation within the jaw and upward eruption; given the strong resemblance of the molar position to that of other Triconodontidae; however, we consider this less likely. Early-diverging representatives of the Triconodontidae have three (*Trioracodon*) or four molars (*Priacodon* and *Triconodon*). Most representatives with a higher molar count have their additional molars formed within the ascending ramus, which is possibly caused by a secondary increase in molar count. A potential challenge to this hypothesis is presented by *Trioracodon*, which is represented in the Purbeck fauna by *T. ferox* (Owen, 1871). *Trioracodon* closely resembles *Triconodon*, differing chiefly in its larger size and the presence of only three lower molars (as opposed to four in *Triconodon*). The m3 of PV OR 47782 (holotype of *Triconodon occisor* Owen, 1871; placed in *Trioracodon ferox* by Simpson 1928) shows some similarities to the m4 of *Triconodon*. Similar to the m4 of *Triconodon*, the m3 is partially hidden behind the ascending ramus, as is the case with m4 of *T. mordax*. Cusps c and d are covered by the ramus and embedded in a small crypt, which opens anteriorly. It is unclear if the m3 in *Trioracodon* was formed within the ascending ramus, which would challenge the hypothesis that the formation in a crypt was caused by an increase in molar count. Alternatively, the m3 of *Trioracodon* formed within the jaw and erupted upward, with the crypt resulting from upward movement of the tooth, and not a space in which the tooth formed. We tentatively consider the latter interpretation for *Trioracodon* to be more likely, but further study and perhaps additional specimens will be required to address the question adequately.

Although this type of molar placement has not been observed outside the Triconodontidae there are at least 15 cases of a human pathology named “ectopic third molar,” of which some bear resemblance to the condition observed in *Triconodon*. As potential reasons for the misplacement in humans, primarily aborted eruption, cysts and tumors have been discussed. However, the causes are not fully understood (Iglesias-Martin et al. 2012; see also Wang et al. 2008). In those pathological cases, the molars may be located in the mandibular ramus, the subcondylar region, the coronoid process, or directly in the condyle. It appears that, in most cases, the teeth tend to be not in an upright position. One noticeable exception is a case described in an abstract by Muller (1983), where the last molar is fully formed in an upright position within the coronoid process, bearing some resemblance to the condition described here for *Triconodon*. However, given that in *Triconodon* multiple specimens show the same position and a natural orientation of the last molar, there can be little doubt that the involved processes differ from the ones observed in humans and are not pathological in nature.

Simpson (1928 p. 74) further noted one specimen of *Phascolotherium bucklandi* (a taxon lying outside of the Triconodontidae; NHMUK M 7595), where the fifth lower molar is still in a "formative capsule beneath the anterior end of the coronoid." However, the condition described in this specimen is more similar to that of *Docodon*, where the most posterior molar formed underneath and erupted adjacent to the ascending ramus (Schultz et al. 2019), than to *Triconodon*. *Phascolotherium* has traditionally been referred to Amphilestidae (Amphilestinae of Simpson 1928), which are generally placed in Eutriconodonta (Kielan-Jaworowska et al. 2004 and references therein), but the analysis of Gaetano and Rougier (2011, Fig. 7) places amphilestids as successive sister taxa to symmetrodonts rather than to triconodontids and gobiconodontids (Eutriconodonta).

In sum, restudy and 3D analysis of the relevant specimens provides a basis to reconstruct essential details for the antemolar replacement and molar eruption pattern of the later ontogenetic stages in *Triconodon* (Fig. 4.7). The formation of m4 likely became sufficiently mineralized to be detectable when p3 was replaced. This was followed by the eruption of the last incisor (presumably) and the replacement of dp4 with its permanent successor. Subsequently, the eruption of the adult canine began before m4 was fully formed (Figs 4.4, 4.8). After the formation of the m4 crown was complete, it remained in its crypt until finally becoming fully functional when exposed by continuous growth of the jaw.

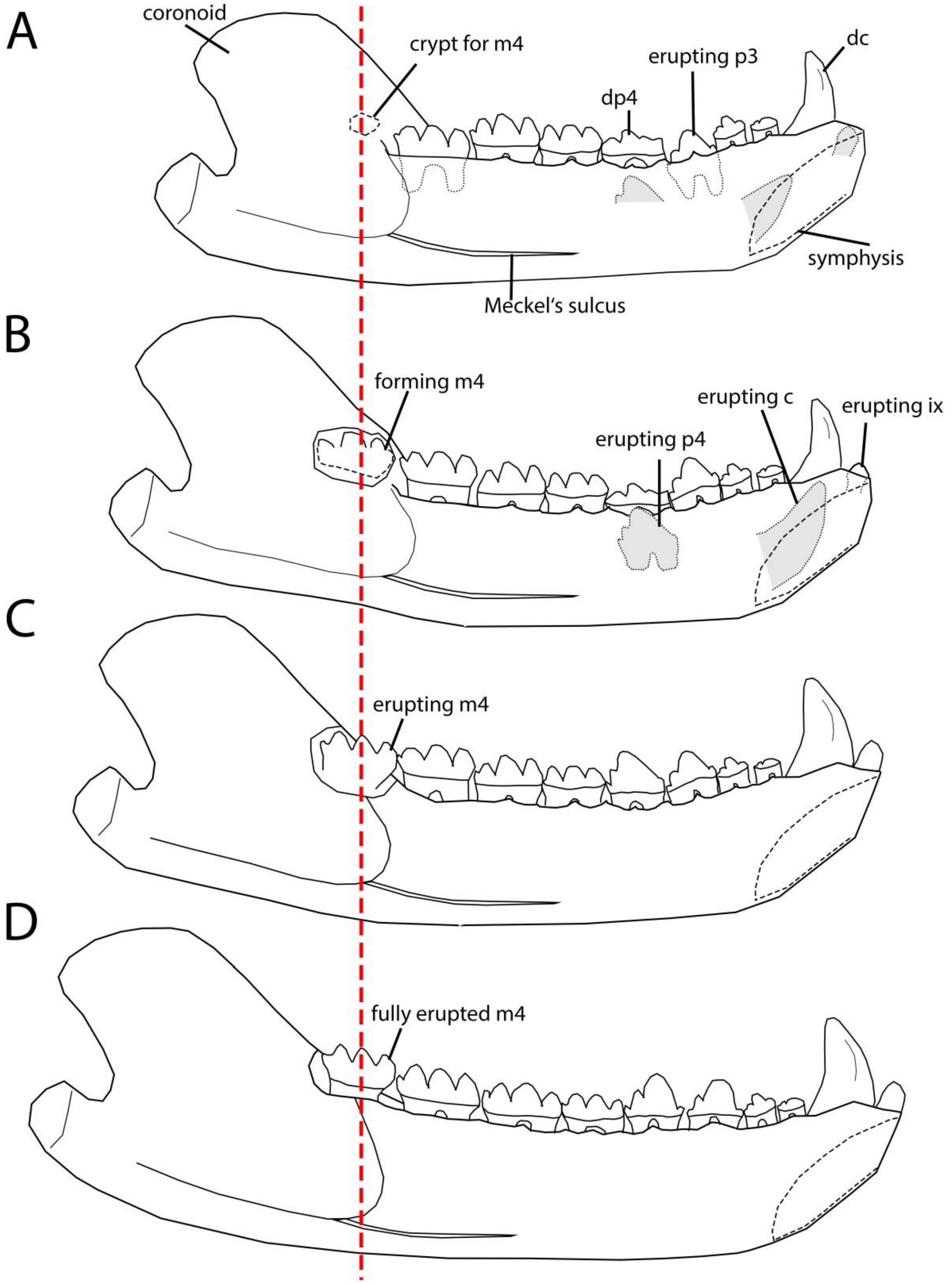

FIGURE 4.7. Medial view on hypothetical late ontogenetic eruption stages of *Triconodon mordax*, based on information obtained from PV OR 47763, PV OR 47764, PV OR 47768, PV OR 48395, and the "Willet specimen". The inclusion of the stage observed for PV OR 48395 is based on the assumption that the condition observed for *T. averianovi* (PV OR 48395) is likely to be highly similar to that of *T. mordax*. (A) With the eruption of p3 and m3(?) the crowns of p4 and c are partially formed, while the last incisor is about to erupt. It is likely that at this stage the crypt for m4 begins to form. (B) The eruption of the last incisor is followed by the p4. The enamel caps of m4 have formed. (C) The eruption of p4 is shortly followed by that of the canine. Subsequently, due to jaw growth, cusp b of m4 "moves" past the ascending ramus. (D) The posterior ramus has grown far enough for the m4 to become fully functional.

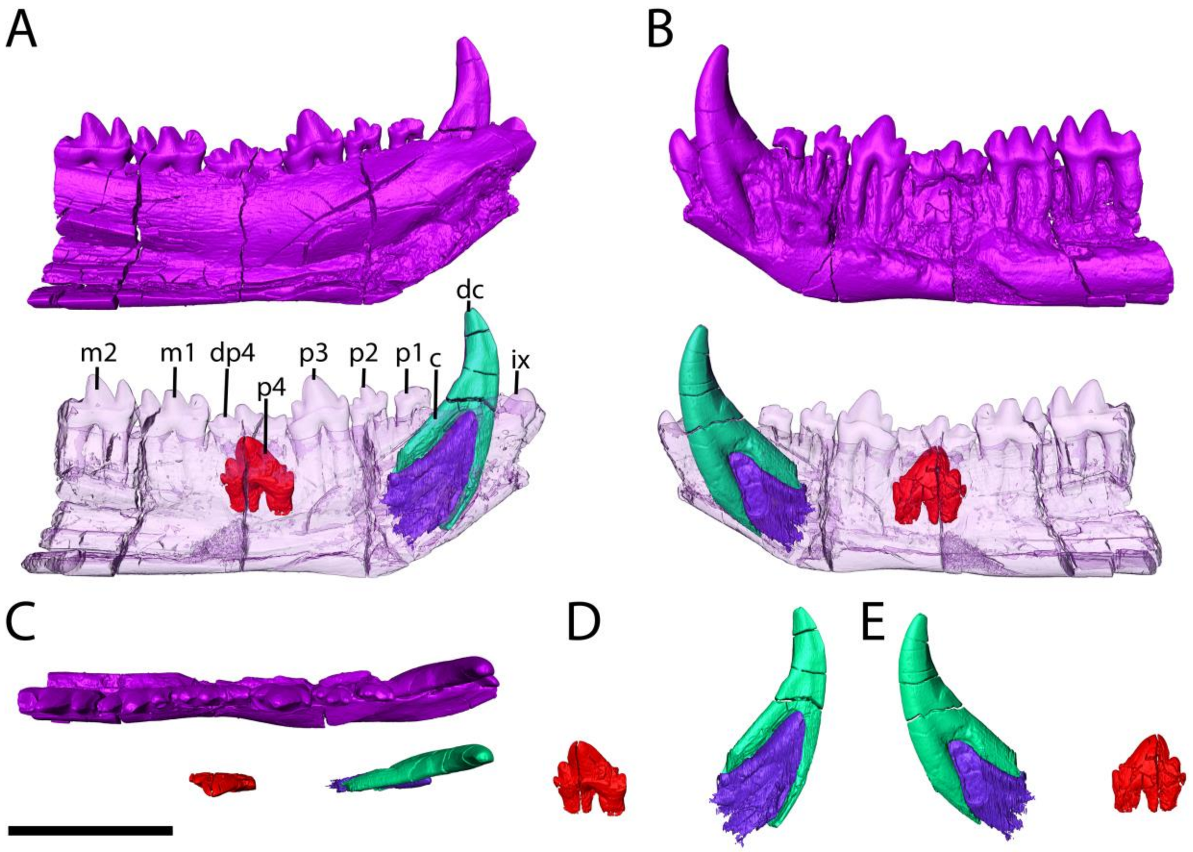

FIGURE 4.8. Left anterior ramus of *Triconodon mordax* (PV OR 47763). (A) Medial view, (B) lateral view, (C) occlusal view (anterior to the right), D, E) erupting p4, and canine in (D) lingual view and (E) buccal view.

4.4.3 Dentary: Intraspecific Variation and Adductor Insertions

Posterior mandibular ramus and muscle attachments—On the dorsolateral side of the coronoid process is a large area discernible that marks probable insertion of the *M. temporalis*. Below that, separated by a slight protuberance, is the region where the tendons of *M. masseter profundus* inserted (Fig. 4.9C, D). There is no clear morphological border that separates the attachment surfaces for the *M. masseter profundus* and *M. masseter superficialis*. However, since this division was already present in non-mammalian synapsids and more plesiomorphic mammaliaforms such as *Docodon* and *Morganucodon*, it is highly likely that this division was also present in *Triconodon* (Lautenschlager et al. 2017; Schultz et al. 2019). We consider the most likely attachment for the *M. masseter superficialis* to be on the ventral side of the wide masseteric fossa, extending toward the masseteric crest (sensu Simpson 1928). It is noteworthy that, in *Triconodon*, the masseteric crest demarcates the ventral boundary of the posterior mandibular ramus, while in *Trioracodon* a pterygoid crest extends ventral to the masseteric crest (Simpson 1928, Fig. 28). In this regard, the morphology of the posterior mandibular ramus of *Priacodon fruitaenensis* bears a closer resemblance to that of *Triconodon mordax* than to that of *Trioracodon* (Rasmussen and Callison 1981, Fig. 4A).

We interpret that most of the medial side of the coronoid process functioned as an attachment for the *M. temporalis,* which most likely also covered the crypt of the developing m4. The areas of attachment for the *M. pterygoideus lateralis* and *medialis* are tentatively assigned (Fig. 4.9A, B). The source of ambiguity lies in the morphological differences between the two specimens. While PV OR 47764 (Fig. 4.9A) has a slightly inclined, almost flat surface anterior to its condyle for the attachment of the M. pterygoideus lateralis, this area in PV OR 47763 is considerably steeper and less separated (Fig. 4.9B). Similarly, the attachment area for the *M. pterygoideus medialis* in PV OR 47764 is large and projects almost medially. In PV OR 47763, the same area projects almost ventrally due to the morphological differences (Figs 4.4, 4.9).

4.5 Conclusion

Taxonomy within early-diverging Triconodontidae, especially at the species level, remains difficult. The holotype of *Triconodon mordax* (PV OR 47764) and specimen PV OR 47763 exhibit a high degree of similarity in their dentitions but differ in the number of mental foramina and shape of the posterior jaw. The latter might also have affected the relative development of various adductor muscles. Differences in dental characters of PV OR 48395 compared to specimens of *T. mordax* were considered sufficient to justify the assignment of a new species *T. averianovi* n. sp. Further, a thorough revision of the Triconodontidae is necessary to address the differences (or lack thereof) between different genera and species. This study showed that µCT data are helpful to better compare specimens and to recognize differences that were previously overlooked or not accessible.

Sequential tooth replacement was hypothesized by Simpson (1928) for *Triconodon* and is confirmed in this study. This finding is concordant with the phylogenetic position of Eutriconodonta as early-diverging crown mammals (Martin et al. 2015)

The formation of the posterior lower molars in Triconodontidae within the ascending ramus is unique. After formation, the molar remains in place while the jaw grows until the tooth emerges in front of the ascending ramus, where the buccal crown face can meet its antagonist in the upper dentition, at which point it is fully integrated into the functional tooth row. The latter is analogous to other Mesozoic mammals, such as *Docodon* and some multituberculates, which exhibit molars that erupt lingual to the ascending ramus (Greenwald 1988; Schultz et al. 2019). In *Triconodon* the ultimate lower molar (m4) is affected, while more derived Triconodontidae exhibit multiple posterior molars within the ascending ramus. It is, therefore, possible that the unusual locus is linked to a secondary increase in molar count, if it is assumed that the plesiomorphic condition for Triconodontidae was three lower molars.

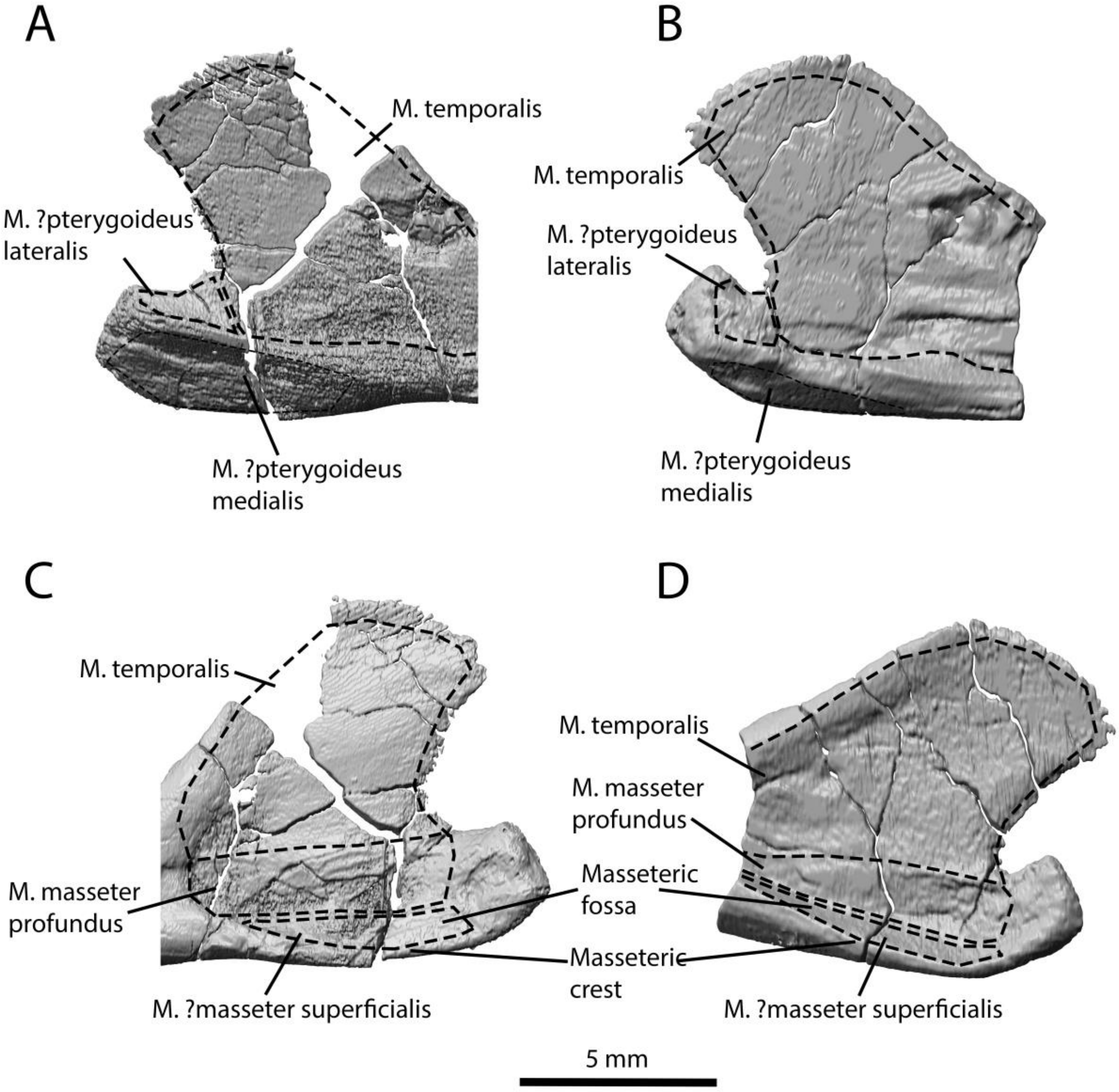

FIGURE 4.9. Interpretation of mandibular adductor muscle attachment in *Triconodon mordax* coronoids. PV OR 44764 in medial view (A) and lateral view (C). PV OR 47763 in medial view (B) and lateral view (D). While the surface area is nonindicative, morphological borders were used to estimate the muscle insertion areas by comparison to extant mammals (Barghusen 1968; Turnbull 1970; Lautenschlager et al. 2017).

4.6 Acknowledgements

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Molar occlusion and jaw roll in early crown mammals

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5.1 Abstract

Triconodontidae, Mesozoic mammals characterized by the primitive linear arrangement of three cusps on molars, are of particular interest because they represent early-diverging crown Mammalia and are hypothesized to have been carnivorous. We studied their chewing mechanism based on Occlusal Fingerprint Analysis (OFA) of the American Jurassic *Priacodon*, an early-diverging triconodontid known by associated upper and lower dentitions. The triconodontid molar series is unique among mammals and is not directly comparable to any extant counterpart. A highly homogenous cusp-valley system formed a continuous fore-aft crest that linked the entire molar series in a zig-zag pattern. OFA demonstrates that upper and lower molars of *P. fruitaensis* occluded in alternating fashion (embrasure occlusion), quite unlike the one-on-one pattern seen in the early mammaliaform *Morganucodon*, previously hypothesized for Triconodontidae. Embrasure occlusion for *P. fruitaensis* is supported by premolar positioning, wear facets, higher collision areas during the power stroke, and a better fit. Hence, embrasure occlusion is a general feature of Eutriconodonta; the *Morganucodon* pattern is limited to a few early mammaliaforms. OFA also confirmed that, unlike modern carnivores, significant rolling of the active hemimandible occurred during the power stroke. The roll rate was around 10° through the entire power stroke and therefore lower than previously assumed. This discrepancy is explained by a lingual inclination of the upper molars in the maxilla, similar to Gobiconodontidae and *Morganucodon*, which reduced the roll rate required for a matching occlusion. The fore-aft crests of the lower and upper molars passed along each other at the beginning of the power stroke; subsequently, lower cusps entered the valleys between upper cusps, with jaw roll maintaining close contact between the teeth. This is unlike the primitive pattern as represented by *Morganucodon*, wherein heavy reliance was placed on puncturing by enlarged principal cusps, rather than precise cutting on elongate shearing crests. The dentition of Triconodontidae combines traits linked to both carnivorous diets (e.g. fore-aft cutting edges) and insectivorous diets (transverse crests and lobes). This supports the interpretation of a varied faunivorous diet appropriate to the small body size of most triconodontids. A body mass of 127 g was calculated for *Priacodon ferox*. Total length of molar shear decreased with wear, suggesting the possibility of dietary shift during ontogeny.

The molar series of triconodontids was highly uniform and adapted to a precise fit; lower molar cusps were self-sharpening within the valleys between upper molar cusps. While this ensured good cutting capabilities, it likely put the dentition under greater evolutionary

constraints than other molar types with more heterogeneous cusp morphologies and is a likely explanation for the highly stereotyped nature of the triconodontid molar, which underwent little change during the 60–85 Ma range of the group.

5.2 Introduction

Triconodontidae is a family of Eutriconodonta that ranged from the Late Jurassic (possibly late Early Jurassic) through the Late Cretaceous (Fox 1969; Kielan-Jaworowska et al. 2004; Montellano et al. 2008; Gaetano and Rougier 2011; Butler and Sigogneau-Russell 2016; Martin 2018). Long-viewed as small but highly effective carnivores, their buccolingually compressed molars are characterized by three main, anteroposteriorly-aligned cusps (b/B, a/A, and c/C and an accessory cusp d/D). A common character that sets them apart from other "triconodont" taxa is their relatively uniform cusp size and shape. The molar row represents essentially one battery of an almost identical cusp-valley sequence with a continuous cutting edge (Simpson 1933). In more derived members, the d/D cusp can be enlarged and integrated into that series (e.g. *Alticonodon*) (Fox 1969; Cifelli and Madsen 1998). Most taxa have an interlocking system between adjacent molars, with cusp d fitting in an underhanging embayment anterior to cusp b of the succeeding molar (Patterson 1951; Slaughter 1969; Fox 1969, 1976; Cifelli et al. 1998, 1999; Kielan-Jaworowska et al. 2004; Rougier et al. 2007a). For this study, Triconodontidae is defined after Gaetano and Rougier (2011) as "the less inclusive group containing *Priacodon* and *Triconodon*, their common ancestor and all its descendents" [sic]. Triconodontidae have been reported from North America, Europe, Asia, and possibly South America (Cifelli et al. 1998; Rougier et al. 2007a, 2007b; Kusuhashi et al. 2009).

Most of the taxa that are with certainty placed within the Triconodontidae are of Late Jurassic age or younger. However, some fossils suggest an earlier diversification of the family. Montellano et al. (2008) described a potential early-diverging triconodontid from the late Early Jurassic of Mexico, *Victoriaconodon*, which shares some of the premolar characters found in Triconodontidae although the molars retain presumptively primitive cusp proportions (cusp a notably taller than b and c). Of similar age is the South American *Argentoconodon*, which shows similarities to *Volaticotherium* and *Ichthyoconodon*. These taxa may represent a clade of derived gliding Triconodontidae (Gaetano and Rougier 2011). If these three taxa indeed belong to Triconodontidae, one of the most derived representatives of the family

(*Argentoconodon*) would be the oldest known so far. However, according to a recent phylogeny by Martin et al. (2015), *Argentoconodon* and *Volaticotherium* split off prior to *Priacodon*, *Triconodon,* and *Trioracodon* and fall outside of the Triconodontidae. Another potential early representative is *Eotriconodon* from the Bathonian of the United Kingdom (Butler and Sigogneau-Russell 2016). Here we follow the phylogeny provided by Martin et al. (2015).

The three most basal taxa of Triconodontidae are *Priacodon*, *Triconodon*, and *Trioracodon* (Gaetano and Rougier 2011, Martin et al. 2015) from the Late Jurassic and Early Cretaceous of the United Kingdom and the United States (Simpson 1925a, 1925b, 1928, 1929). A fragmentary molar attributed to *Priacodon* has been described from Late Jurassic – Early Cretaceous of Portugal (Krusat 1989). Molar morphology of these early-diverging Triconodontidae is highly similar so that it is almost impossible to distinguish between the different genera based on molar morphology alone. Therefore, they are primarily distinguished by the number of postcanine teeth (Kielan-Jaworowska et al. 2004) . The differences in premolar and molar count are: *Triconodon* P?/4 M?/4, *Priacodon* P3/3 M4/4, and *Trioracodon* P4/4 M3/3. However, tooth count between the different genera is also problematic because upper and lower tooth counts can be different. In *P. fruitaensis*, for example, the postcanine formula is P4/3 and M3/4 (Engelmann and Callison 1998). This highlights the problem of systematics of these early-diverging Triconodontidae. On the other hand, and more to the point in the present context, the similarity of the dentitions among these three taxa in particular, and Triconodontidae in general, makes it easier to address occlusion and dental function for the entire family based on a single representative. In this study micro-computed tomography (µCT) and 3D models were applied to re-examine the dentition of the right ramus and maxilla of *P. fruitaensis*. The holotype, LACM 120451, is the only specimen known for an early-diverging triconodontid in which substantial, well-preserved upper and lower dentitions are positively associated. The aim of the study is to better understand the function and occlusion of Triconodontidae and to test existing hypotheses on the occlusal mode (Simpson 1925b; Mills 1971), the roll during the power stroke (Crompton and Luo 1993), and the diet (Osborn 1888, Simpson 1933). The dental function of Triconodontidae is of particular interest, as they represent early-diverging crown Mammalia that retained a modified version of the plesiomorphic triconodont tooth pattern, that is characterized by a high degree of uniformity and that underwent only minor changes from the Late Jurassic till the Late Cretaceous.

5.3 Material and Methods

The holotype of *P. fruitaensis*, LACM 120451 (Natural History Museum of Los Angeles, formerly Los Angeles County Museum) comprises right and left partial dentaries and maxillae, parts of the skull, and associated postcranial material. The left ramus served as the basis for initial description (Rasmussen and Callison 1981); subsequently, Rougier et al. (1996) provided an account of the petrosals, while Engelmann and Callison (1998) added important details to the dentary and lower dentition, also describing the maxillae and upper dentition, fragments of the skull, and some postcranial elements (humerus, radius, and partial femur). For this study, we re-examined the right ramus and maxilla (Fig. 5.1). The anterior part of the ramus is missing, p4, m1-4 are preserved but several cusps are damaged and p4 was shifted upwards and is not in its natural position. The condyle and the posterior part of the ramus are complete, with the exception of the uppermost region of the ascending ramus. The maxilla contains four premolars and three slightly damaged molars.

Existing hypotheses on the occlusion were virtually tested with the Occlusal Fingerprint Analyser (OFA) software. The term ‘occlusal fingerprint’, introduced by Kullmer et al. (2009), describes the orientation and position of wear facets on the occlusal surface. The OFA software was developed within the Research Unit 771 of the German Research Foundation (DFG) and enables the user to virtually analyze the chewing path and to test hypotheses on occlusal relationships (e.g. Kullmer et al. 2009, Benazzi et al. 2011, Kullmer et al. 2013, Koenigswald et al. 2013, Benazzi et al. 2013, Schultz and Martin 2014, Schultz et al. 2019). For the OFA analysis, the specimen was scanned with micro-computed tomography (µCT), using an NSI scanner at the University of Texas High-Resolution X-ray CT facility, with the following parameters: Fein Focus High Power source, 110 kV, 0.15 mA, no filter, Perkin Elmer detector, 0.25 pF gain, 1 fps, 1x1 binning, no flip, source to object 137.092 mm, source to detector 1316.876 mm, continuous CT scan, 2 frames averaged, 0 skip frames, 2400 projections, 5 gain calibrations, 0.762 mm calibration phantom, data range [-10.0, 500.0] (grayscale adjusted from NSI defaults), beam-hardening correction = 0.275, Voxel size = 10.4 µm, Total slices = 1934. Subsequently, the scan was segmented and a virtual 3D model was created using Avizo 8.1 (Visualization Sciences Group, France). Some data processing, e.g. virtual alignment and the reduction of triangles, was performed with Polyworks (2014, InnovMetric Software Inc., Canada); file format is .stl (little endian). For the OFA analysis, reduced models of m2–m4 and M2 and M3 were used. The anterior teeth were left out due to damage, which made them unsuitable for the analysis. Schultz et al. (2019) tested competing occlusal hypotheses by OFA analysis. Accordingly, the collision distance during the power stroke was used to detect the best-fit hypothetical path. Further, the OFA was used to simulate the roll (medial tilting of the dentary along its anterior-posterior axis) during the power stroke (Schultz et al. 2019) .

Values presented here for the roll rate refer to the degree of medial tilting during the power stroke. 0° is defined as the orientation in which the transverse axis of the condyle is in a horizontal position and the upper and lower premolars are oriented straight vertically.

The dental striations of *P. fruitaensis* were examined with scanning electron microscopy (SEM) (Cambridge CamScan MV2300) of a cast. The cast was made in polyurethane resin (BJB Enterprises, product TC-892).

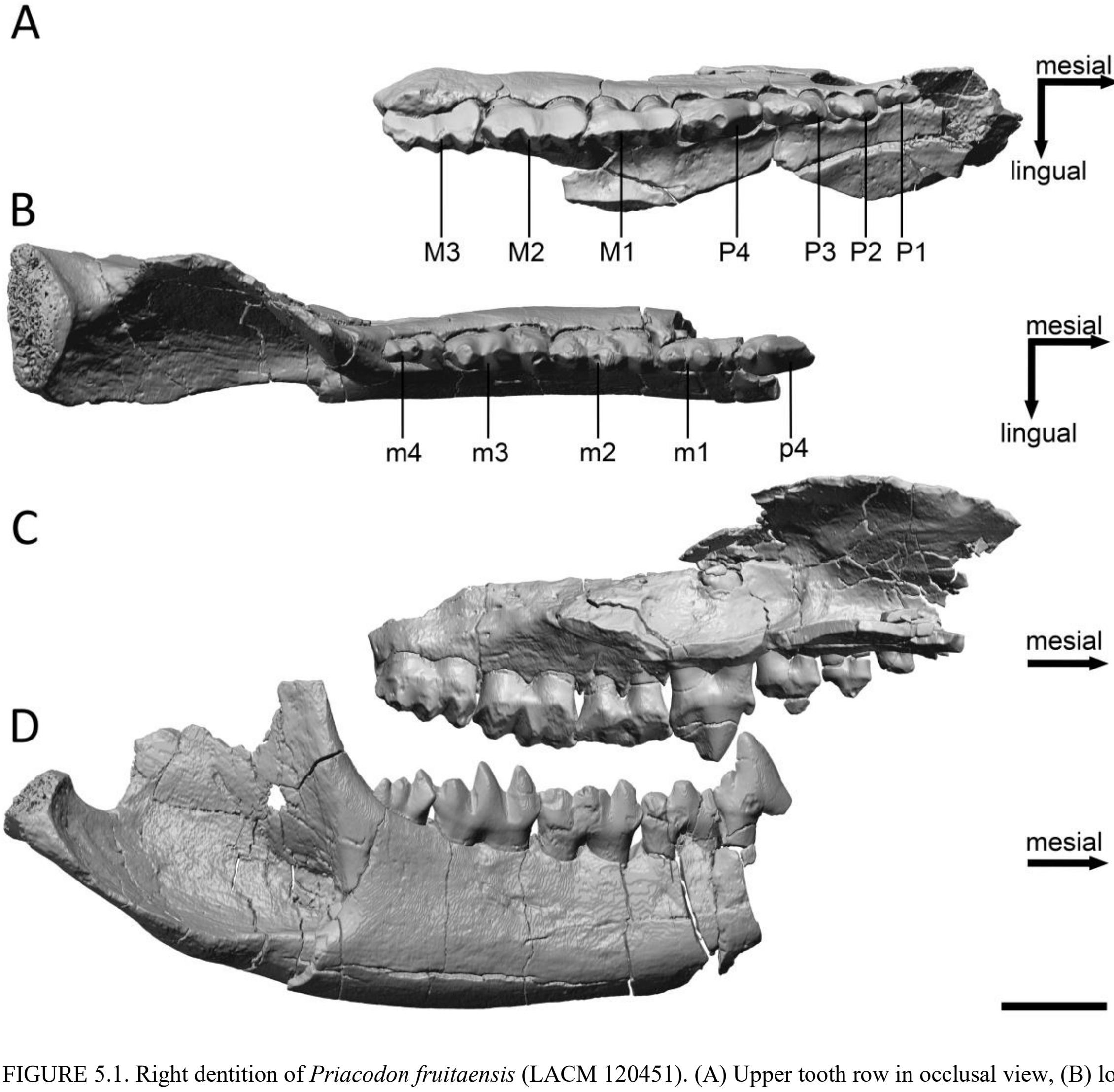

FIGURE 5.1. Right dentition of *Priacodon fruitaensis* (LACM 120451). (A) Upper tooth row in occlusal view, (B) lower tooth row in occlusal view, (C) upper tooth row in lingual view (mirrored for better comparison), and (D) lower tooth row in buccal view. Note that parts of the palatine have been digitally removed for better visibility and that p4 was repositioned in the virtual model to its natural position since it was post mortally damaged and shifted upwards. The posterior part of the jaw, beginning with the ascending ramus, was shifted laterally due to damage and the masseteric fossa, therefore, appears larger in occlusal view. Scale bar equals 2.5 mm.

5.4 Results

5.4.1 Morphology of the Ramus

The dentaries of *Priacodon fruitaensis* have previously been described in detail (Rasmussen and Callison 1981, Engelmann and Callison 1998). Here we confine observations to additional information from the µCT data and to characters that directly influence the occlusion. The most noticeable character of the sturdy ramus is the wide masseteric fossa on the distolateral side (Engelmann and Callison 1998), bordered ventrally by a prominent crest or flange. Its size is slightly exaggerated because the ventrodistal part of the ramus is broken and shifted medially. Simpson (1933) provided a schematic cross-section of the ramus of *Priacodon* (species not indicated) with a pronounced masseteric fossa, commenting that it is less strongly developed than in *Triconodon*. According to the µCT data, the masseteric fossa of *P. fruitaensis* is larger than that of both *Triconodon* and *Trioracodon*, with a more pronounced masseteric crest, despite *P. fruitaensis* being of similar size to *Triconodon* and smaller than *Trioracodon*.

This suggests that the M. masseter was stronger than in the other taxa. The importance of the masseter muscle for *P. fruitaensis* is also highlighted by an additional foramen in the anterior ventral wall of the masseteric fossa. This foramen is present on both rami and was originally referred to as blind ending “pocket” or “pit” (Rasmussen and Callison 1981, Engelmann and Callison 1998). The foramen is, however, connected to the mandibular canal (Fig. 5.2) and likely transmitted a blood vessel supplying the large masseter. Engelmann and Callison (1998) further note that this foramen (“pocket” or “pit”), despite lack of mention by previous authors, is present in all “triconodont specimens” from Como Bluff. If that is the case, it could be a relevant diagnostic character for future phylogenetic analyses, since it is absent in the Purbeck triconodontids.

The condyle is slightly damaged but noticeably wider than long and curved upwards. The damaged articular surface is oriented posterodorsally. It is oval (transversely elongated) and the anterior margin is convex anteriorly (Engelmann and Callison 1998) , being similar to that of other Triconodontidae such as *Trioracodon* (Simpson 1928).

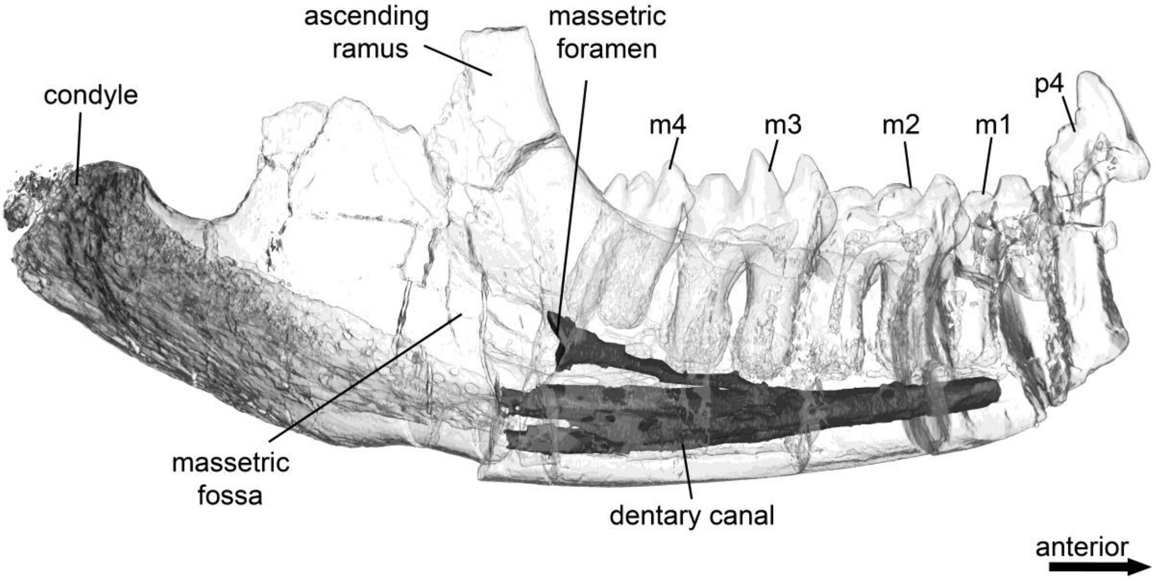

FIGURE 5.2. 3D model of the right mandible of the holotype of *Priacodon fruitaensis* in medial view. The anterior part of the dental canal and the masseteric foramen are highlighted. The masseteric foramen extends and narrows towards anterior until it projects ventrally and connects with the dental canal underneath the anterior root of m3. Other canals were not highlighted due to better visibility, most notably a branch that located underneath the masseteric foramen is also connected to the dental canal, but does not open in a foramen on the outer surface. The distal part extends towards posterior close to the condyle of the dental canal (not highlighted due to damage).

5.4.2 Wear Facets

p4—With the exception of apical wear, there are no distinct wear facets on p4. The anterior flank of cusp a is unclear, showing a slightly rugged surface. It might be a wear facet that was damaged post-mortem; however, given the lack of damage on the rest of the tooth, we provisionally consider this region as lacking a wear facet.

m1—The mesiobuccal sides of cusps b and c have clearly-defined, large wear facets. The only difference is that the facet on cusp c is oriented slightly more buccally than the facet on cusp b. Cusp a differs from b and c in having its enamel still preserved, except for the worn tip. A clearly separated facet cannot be distinguished but on the enamel surface many similarly-oriented striations are visible, and the enamel appears to be thinner on the buccal side than on the lingual side. This suggests that attrition (tooth-tooth contact) was present and equally distributed on cusp a.

m2—Most of the surface of m2 is damaged. The best-preserved cusp is b. The buccal and distal sides of cusp b show signs of wear with polished enamel. The most mesial part of cusp b has dentine exposed. Dentine probably was exposed on the tip as well, but this remains unclear due to damage. The valley between cusps a and b appears to have lost more of its enamel than the adjacent cusps. Due to damage little can be said regarding wear facets on cusps a and c, exception that polished enamel is present.

m3—The wear facets on m3 are well visible, due to the good preservation of the tooth (Fig. 5.3). The mesiobuccal region of cusp b has a wear facet with exposed dentine similar to cusp b of m1 and m2. Dentine is also exposed on the tip, which results in a prominent step to the enamel crest on the top of cusp b. The enamel on the buccal side is polished. On the distobuccal flank of cusp b the enamel is polished and partially worn away. This facet expands into a dentine depression near the base of the molar between cusps a and b. The exposure of dentine so low on the crown, while enamel is still present higher on the cusp flank, could have been caused by increased wear near the base of the tooth or thinner enamel in that region. The tip of cusp a is well preserved and exhibits a combination of polished enamel and exposed dentine that was likely also present on the damaged tip of cusp b, given the similarity to the preserved wear on cusp b. On the tip of cusp a, a sharp enamel edge borders deeply excavated dentine. Based on the excavated dentine it is evident that this edge was the leading edge where contact to the antagonist was first initiated (Greaves 1973; Rensberger 1973; Costa and Greaves 1981). The exposed dentine extends along the mesiobuccal flank into the valley between cusps a and b. From the tip in a buccal direction, the dentine is not exposed and enamel is still preserved, resulting in a second, smoother trailing edge. This enamel facet follows the same mesiobuccal inclination as the exposed dentine (Fig. 5.3). This suggests that, during the initial contact of the cusp tips at the beginning of the power stroke, most of the attrition forces were oriented mesially into the valley. Thus, the enamel on the buccal side of cusp a is still preserved while on the mesial side it is already worn away. This is evidence for a distal component in the orthal movement of the power stroke, which is further supported by the orientation of the striations and the OFA analysis (see below).

An enamel facet is present on the distal side of cusp a, which transitions into a dentine facet in the valley between cusps a and c. Although the tip of cusp c is damaged, dentine is exposed on its mesial flank and is bordered buccally by polished enamel, suggesting a similar condition to that observed on the mesiobuccal flank of cusp a. On the distobuccal flank of cusp c a wear facet is present with exposed dentine that extends into the valley between cusp c and cusp d. Compared to the other valleys, the dentine does not extend so far down before the facet ends in a shallow trailing edge to the enamel. Cusp d is enveloped by the mesial interlocking embayment of m4, and therefore fully incorporated in its mesial facet, with its dentine exposed as well.

m4—Similar to cusp a of m3, the mesial side of cusp b bears a large wear facet with exposed dentine that extends mesially. On its buccal side enamel is still present but is polished. The distobuccal side of cusp b bears a wear facet that differs from the homologous facets on the anterior molars because it does not extend deeply into the valley between cusps a and b but ends at the base of cusp b. Similarly, the mesial facet on cusp a appears to not extend into the valley, but due to damage this is ambiguous. The most posterior facet is a small, distally-oriented one on the upper distobuccal side of cusp a, with polished enamel. Cusp c is unworn.

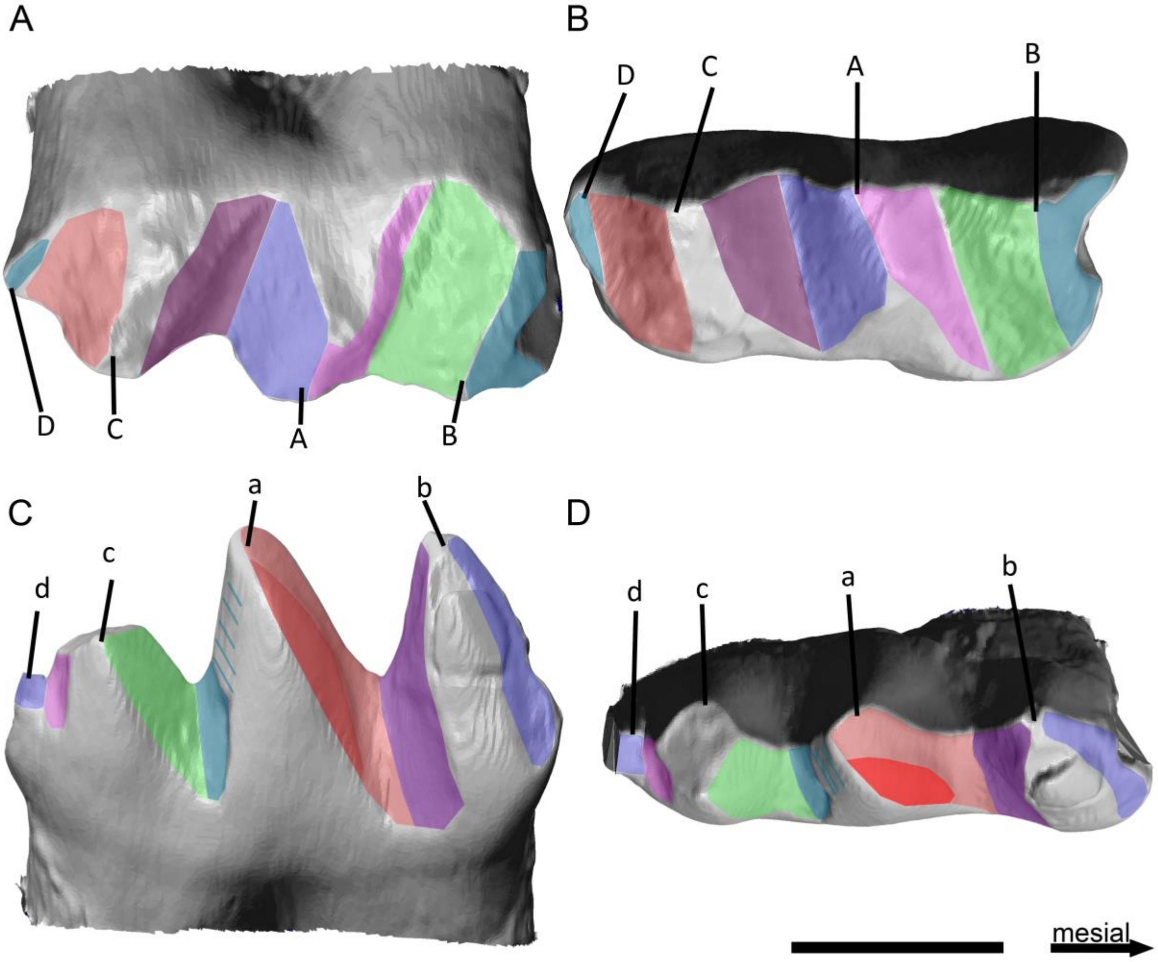

FIGURE 5.3. Corresponding wear facets of the right M3 and right m3 of the holotype of *Priacodon fruitaensis.* (A) Lingual view (tooth mirrored for better comparison), (B) occlusal view of M3, (C) buccal view, and (D) occlusal view of right m3. The dark red area represents the part of the anteriorly inclined wear facet on the mesial side of cusp a that still has enamel preserved, though the rest of the facet has dentine exposed. Scale bar equals 1 mm.

P4—The P4 shows few clearly developed wear facets. The most distinctive is a small facet at the cingulid on the lingual base of cusp C. The dentine is exposed, showing some faint striations, and the enamel edge is polished, which suggest that it was likely caused by attrition. Compared to the wear stage indicated by the molars, this facet is small. This may be explained by its position at the base of the premolar, which was barely reached by the lower antagonist at the end of the power stroke, or by a late replacement of P4. In *Triconodon* p4 is replaced before the eruption of the last lower molar (Jäger et al. 2019a). Given the ontogenetic stage of the specimen, with all molars fully functional, a recent replacement of P4, therefore, appears less likely. A faint wear facet extends from the posterior flank of cusp A to the tip of cusp C. It yields no clear picture in the SEM due to damage or coverage of some sort. We nevertheless consider this region to be affected by wear, since cusp A shows apical wear that widens distally and matches the ambiguous area. The enamel cap of A is worn. Dentine is exposed on the anterior and buccal sides and is surrounded by an enamel ring. From there, polished enamel extends slightly down on the distolingual side. While ambiguous, we think that the area in question has an incipient wear facet. The anterior side of P4 exhibits striations but lacks distinct wear facets.

M1—The wear on M1 mostly remains ambiguous since the tooth is damaged. It is unclear if dentine exposure in some regions was caused by wear or post-mortem damage. The valley between cusps A and C shows exposed dentine, as well as polished enamel. This is similar to M2 and M3 and characteristic for wear caused by the cusps of the antagonistic lower molars. The posterior side of cusp C exhibits polished dentine with faint striations, which is also the case in M2 and M3. The enamel appears to be less polished, probably owing to post-mortem damage. Between cusps B and A dentine is exposed and apparently most of cusp B was worn away, although this is not quite clear due to damage. Therefore, a wear facet is tentatively assigned to the distolingual flank of cusp B.

M2—M2 is well preserved and the facets are clearly recognizable. Most of the lingual side was affected by attrition, with four regions showing clear distinct features: The anterior flank of cusp B, the valley between cusps B and A, the valley between cusps A and C, and the posterior flank of cusp C. These regions have polished enamel and dentine with parallel striations. Unlike the valleys, the cusp tips are worn down to blunt ridges between the valleys and striations there tend to be less pronounced. The height differences between the leading edges of the crests and the trailing edges close to the base are less pronounced than in the lower molars.

M3—The anterior flank of cusp B, the valley between cusps B and A, the valley between cusps A and C, as well as the tip of cusps B and A show similar wear patterns as described for M2. The only difference in wear to M2 is in the posterior flank of cusp C. Unlike on the anterior molars, the flank lacks a facet since it does not come into contact with its antagonist, m4. The posterior part of the tip of cusp C, however, shows signs of wear. This region is somewhat affected by damage, which makes it difficult to identify the properties of the facet.

However, a circular exposure of dentine and enamel is recognizable. The latter becomes smoother towards the base (the direction an antagonist would have travelled) and shows remnants of striations. As the most posterior facet on the upper molars, it is likely that it was in contact with the most posterior facet on cusp a of m4. Given its size relative to the small cusp a of m4, the worn tip of cusp C must have almost encircled the smaller lower cusp. Therefore, the alternating pattern of cusp-valley occlusion was lost on the most posterior molars and replaced by direct cusp-cusp attrition.

5.4.3 Striation Analysis

SEM images of the wear facets of *P. fruitaensis* show a primarily orthal orientation of striations with a slight posterior component (Fig. 5.4). Striations are present on the enamel and, less clearly, on the dentine. On wear facets formed by attrition, the vast majority of striations are parallel.

Striations on areas without clearly defined wear facets tend to be less regular, with individual deep scratches showing a wider variety of orientations. Nevertheless, the majority of the striations are oriented orthally with a minial posterior deviation at around -5° (with 0° representing straight orthal movement). Similar parallel striations are present on the molars of the Cretaceous triconodontids *Astroconodon denisoni* and *Arundelconodon hottoni*, which are slightly more vertically oriented with orientations of approximately -2°. Striations described for *Corviconodon utahensis* are inclined further distally than those of *P. fruitaensis* and *Astroconodon denisoni* (Cifelli and Madsen 1998). This difference is independent of the molar position, and it is more likely that the inclination of the power stroke of *Corviconodon utahensis*, with approximately -15°, was more posteriorly directed than that of the other taxa described here. However, given the uniform striation pattern and little freedom provided by the molar morphology, it is safe to assume a very consistent power stroke with little variation for all Triconodontidae. This contrasts with striations on molars reported for *Morganucodon watsoni*. In this early mammaliaform striations can vary from -20° to +20°, sometimes within a single specimen (Jäger et al. 2019b).

Striations on LACM 120451 are better visible on the lower than on the upper molars. This is likely due to overall damage of the upper molars and the concentration of the upper molar striations in the valleys between the cusps, which yielded less potential for sharp SEM photographs.

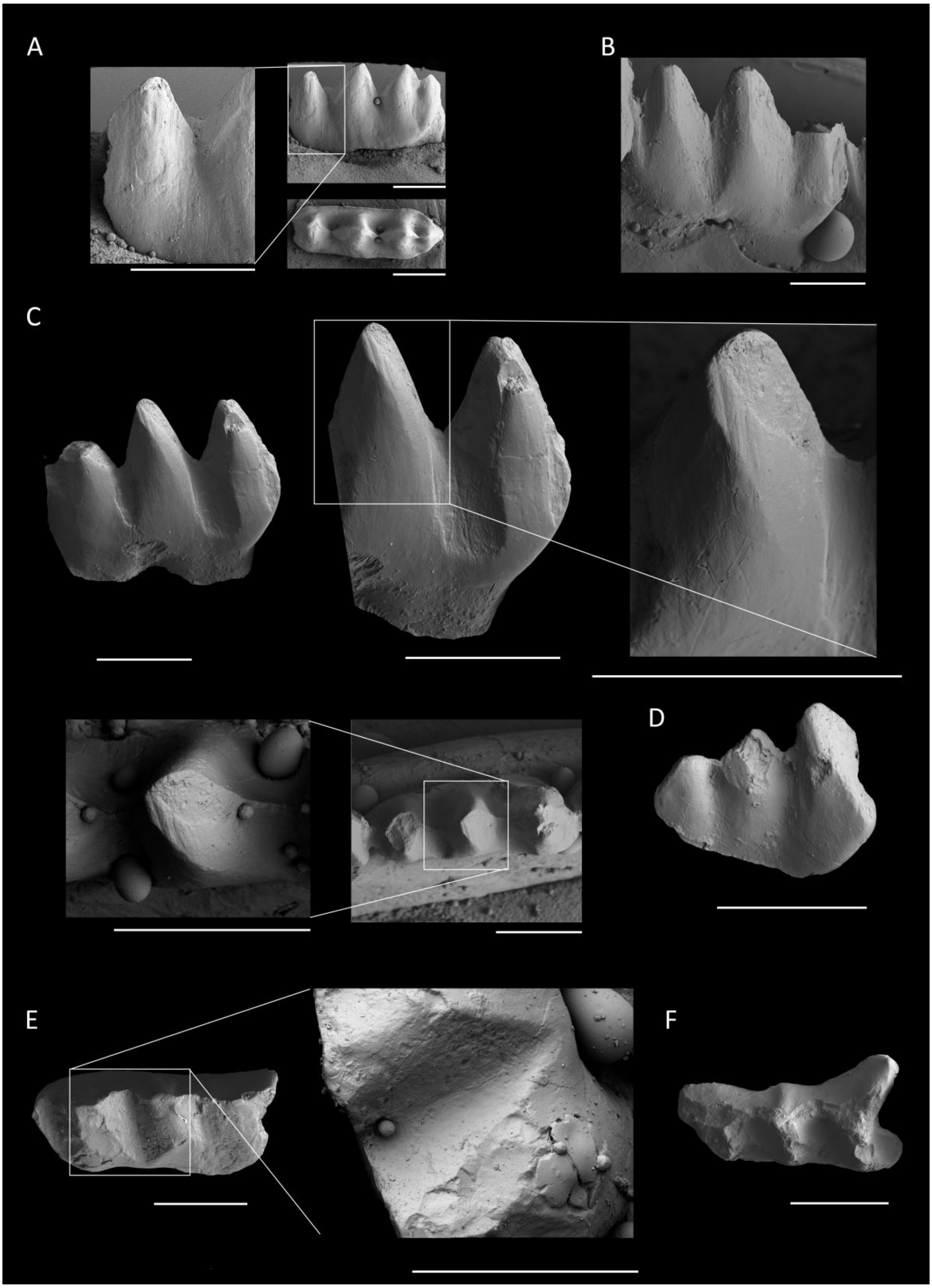

FIGURE 5.4. SEM images of molars of different Triconodontidae. (A) Isolated left lower molar of *Astroconodon denisoni* in lingual and occlusal view (SMP SMU 61759), (B) right m2 of *Arundelconodon hottoni* in lingual view (USNM 491129), (C) right m3 of *Priacodon fruitaensis* in lingual and occlusal view, (D) right of *P. fruitaensis* in lingual view, (E) M3 of *P. fruitaensis* in occlusal view, and (F) M4 of *P. fruitaensis* in occlusal view. Striations in all taxa indicate a steep, single phased power stroke. The posterior facet of m4 in *P. fruitaensis* (D) corresponds to the posterior facet of M4 (F). Mesial is to the left in A and to the right in B-F. Scale bar equals 1 mm.

5.5. Discussion

5.5.1 OFA and Occlusion

Simpson (1925b) discussed the occlusion of early-diverging Triconodontidae and summarized his reconstruction in an illustration depicting the relative positioning of upper and lower molars (Simpson 1925b, Fig. 21). This occlusal pattern was later also described for the early mammaliaform *Megazostrodon* and termed “embrasure occlusion”(Crompton and Jenkins 1968; Mills 1971). It is characterized by the main cusps (a/A) occluding in between the interdental space of the antagonistic molars. Simpson’s occlusal model for triconodontid occlusion was replaced by a different hypothesis by Mills (1971). He argued that, as in *Morganucodon*, cusp a of the lower molars of *Triconodon* and *Trioracodon* must have occluded in between the upper cusps B and A, and that cusp A occluded between cusps a and c. This model, known as one-on-one occlusion, assumed that the positioning proposed by Simpson (1925b, Fig. 21) would result in a mismatch of the ultimate premolars. Mills (1971) argued that the lower dentition had to be positioned further posterior relative to the upper, resulting in the different occlusal mode. His observations, however, were based on upper and lower dentitions of different individuals. So far, only one specimen of *Triacodon ferox* (NHMUK PV OR 47781) is known with preserved matching second lower and upper molars. Given that the m2 is only exposed in lingual aspect, (NHMUK PV OR 47781) could not have substantially contributed to his interpretation. In addition, he was likely influenced by the occlusion of *Morganucodon*, which was previously described by Crompton and Jenkins (1968) and which Mills (1971) analyzed in detail. In *Morganucodon* cusp a sometimes occludes between cusps B and A, and cusp A always occludes between cusps a and c (Jäger et al. 2019b). When Mills (1971) discussed *Morganucodon* and early-diverging Triconodontidae, both were considered to belong to “Triconodonta” (Osborn 1888), which later was recognized to be paraphyletic (Kermack et al. 1973) . Although not specifically stated by Mills (1971), it is very likely that his hypothesis on the occlusion of *Triconodon* and *Trioracodon* was influenced by the occlusion of *Morganucodon* and the supposed close phylogenetic relationship.

When the virtual models of the dentition of *P. fruitaensis* were placed in starting position of the power stroke, the ultimate premolars collided with each other under the one-on-one occlusal mode proposed by Mills (1971) was applied. In contrast, application of the occlusal mode after Simpson (1925b) resulted in a more natural positioning of the ultimate lower premolars (Fig. 5.5). This supports Simpson’s hypothesis on the occlusal mode and suggests that Mills´ (1971) argument on the premolar positioning is incorrect. Further evidence is provided by the analysis of wear on the ultimate lower molar (Figs 5.4D, 5.5). Cusp a of m4 has a clear wear facet on its distobuccal side. Following Mills´ (1971) occlusal mode, no antagonist would contact this facet (Figs 5.5, 5.6). In order to form a facet in this distal position with Mills´ (1971) occlusal mode, an additional upper molar is required. The Simpson (1925b) hypothesis, on the other hand, allows cusp A of M3 to contact this part of m4. This is further indicated by the circular shape of the facet on cusp A of M3, which suggests that the larger cusp A cusp circumvented small cusp a of m4.

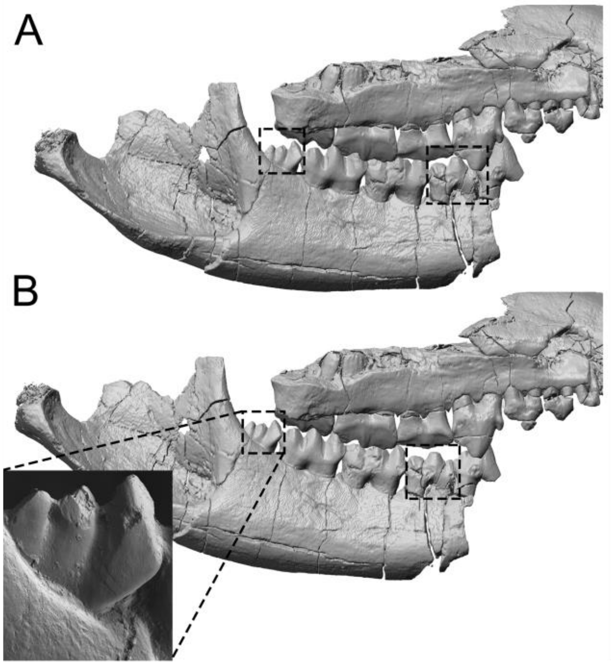

FIGURE 5.5. Right maxilla and right mandible of *Priacodon fruitaensis* in occlusal positions. (A) After Simpson (1925) and (B) after Mills (1971). Squares highlight differences in the anterior and posterior part of the tooth row. The occlusion after Mills (1971) results in the ultimate premolars not interlocking and the m4 left without an antagonist. The SEM images show wear facets on the m4 and m1 that require occlusion after Simpson (1925) to form. Note that p4 was repositioned in the virtual model to its natural position, since it was post mortally damaged and shifted upwards.

Schultz et al. (2019) first used the OFA to test competing hypotheses on the occlusion of *Docodon victor*. For the present study, we compared two OFA analyses, one based on the occlusion after Simpson (1925b) and one after Mills (1971) to provide quantitative assessment (Appendix 2). The Simpson model results in more contact over a longer period of time (Fig. 5.7). While more occlusal contact is not necessarily an argument for the validity of an occlusal hypothesis, in this case, the better fit of the occlusion after Simpson´s model is decisive.

At the beginning of the power stroke, both paths result in a similar amount of contacts. While the cusps of the lower molars progress deeper in the spaces between the upper cusps, the difference in fit in between the two occlusal hypotheses becomes apparent (Figs 5.6, 5.7). With a better fit, the cusps of the lower molars enter deeper into the valleys of the upper molars, resulting in more extensive contact (Fig. 5.7). Subsequently, the teeth are able to pass along each other smoothly and therefore stay in contact longer. Under the Mills model, the cusps enter the valleys to a much lesser degree and the teeth either get stuck or, in order to finish the path, must disengage before all cusps have managed to fully slide pass one another. This result is similar to what we have encountered when 3D printed models of the molar series were put manually into occlusion. While both occlusal models appear possible, in direct comparison the validity of Simpson's occlusal model is supported by a smoother passing, higher contact, and a better fit.

Mills´ (1971) hypothesis that Triconodontidae had a *Morganucodon*-type of occlusion was broadly accepted in following decades (Jenkins and Crompton 1979; Kielan-Jaworowska et al. 2004) and, in at least one case, a *Morganucodon*-type occlusal pattern has been uncritically ascribed to a Cretaceous (alticonodontine) triconodontid (Cifelli et al. 1998). As noted, Mills' (1971) hypothesis was likely influenced by the assumption of a close phylogenetic relationship between *Triconodon* and *Morganucodon*. Later studies demonstrated that Triconodontidae belong to the monophyletic Eutriconodonta within the mammalian crown-group, whereas *Morganucodon* is an early-diverging mammaliaform (Kermack et al. 1973; Rowe 1988; Kielan-Jaworowska et al. 2004). Within Eutriconodonta, clades such as Gobiconodontidae have embrasure occlusion and thus were believed to differ from Triconodontidae (Kielan-Jaworowska and Dashzeveg 1998; Kielan-Jaworowska et al. 2004). While never specifically addressed it must have been assumed that the latter either primitively retained or secondarily developed a *Morganucodon*-type of occlusion.

With embrasure occlusion confirmed for *P. fruitaensis*, it is highly likely that this type of occlusion was present in all Triconodontidae, given the overall similar molar morphology within the family. Accordingly, a uniform occlusal pattern can be assumed for Eutriconodonta, with all members likely to have had embrasure occlusion.

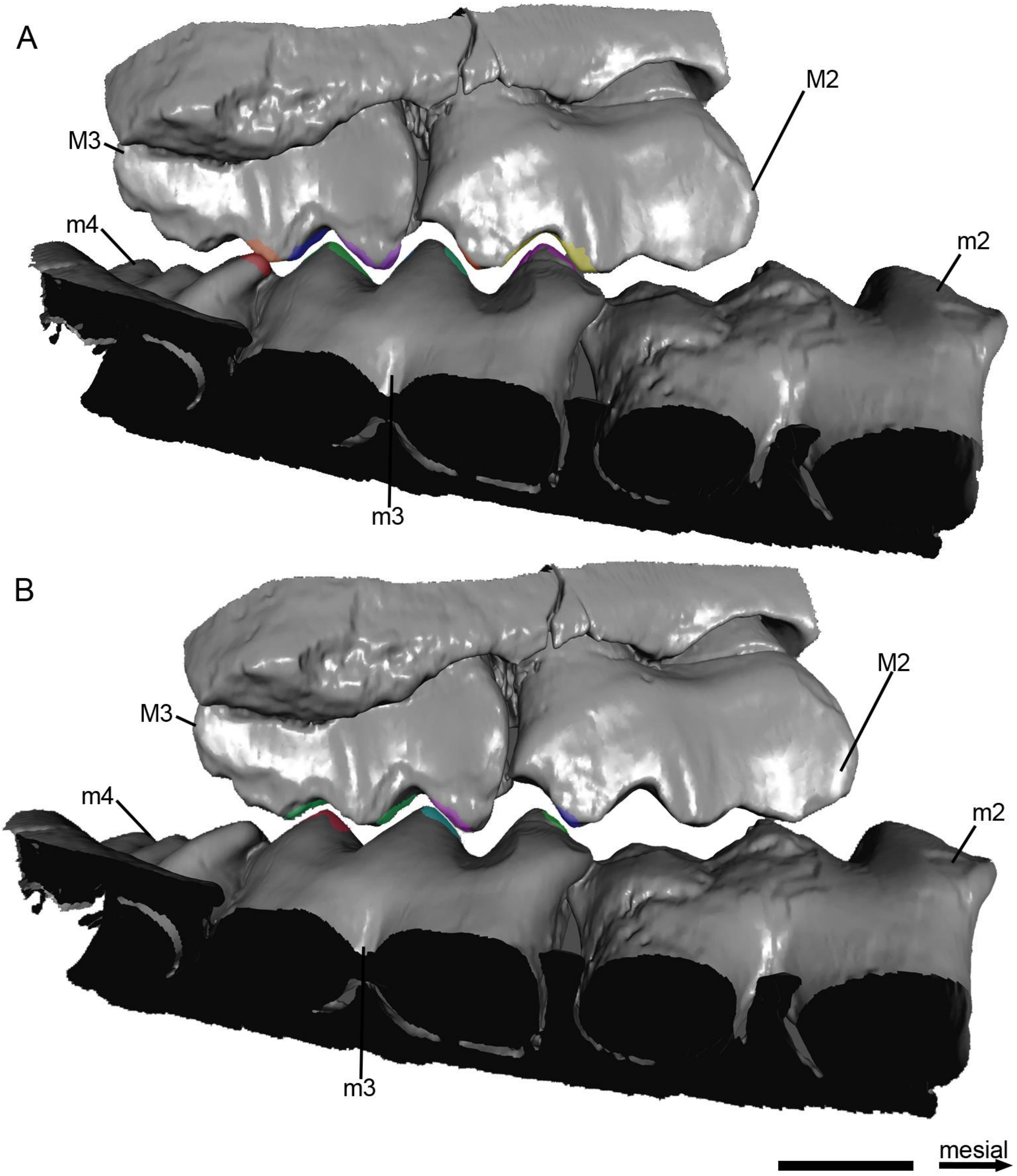

FIGURE 5.6. Ventral view of the OFA analysis of the right dentition of *Priacodon fruitaensis* in the middle of the power stroke for the discussed occlusal models. (A) After Simpson (1925) and (B) after Mills (1971). Although the cusp-valley system is homogenous, only minor differences in size of the individual cusps and valleys occur. These differences support the occlusion after Simpson (1925), since every cusp opposes a valley that matches its dimension. Colored areas represent the contact of the 3D models at this time stage of the analysis. Scale bar equals 1 mm.

This conclusion implies that the one-to-one type of occlusion was limited to *Morganucodon* and potentially a few other early mammaliaforms (e.g. *Dinnetherium*) (Crompton and Luo 1993). When molar morphology is compared among all taxa with triconodont (cusp-in-line) dentitions, a notable difference is that cusps B/b of *Morganucodon* are relatively small compared to the main cusps A/a. This might have been necessary for the transition from embrasure occlusion towards a *Morganucodon*-type, and could explain why it did not evolve within the Triconodontidae, which have cusps of more uniform height.

Hiiemae and Kay (1972) described two phases (I and II) in the power stroke of mammals with tribosphenic molars, which are characterized by a directional change and that cause different orientations in striations on different wear facets. Since all striations on wear facets in *P. fruitaensis* follow the same orientation and the molar morphology leaves little room for directional changes, it is safe to conclude that the power stroke was single phased (phase I), which is common for pretribosphenic dentitions (e.g. Schultz et al 2014; Schultz and Martin 2014).

At the beginning of the power stroke, most of the cusps come into contact in rapid succession (Fig. 5.8). In the OFA analysis, this is represented by an initial sharp increase in contact area during the beginning of the power stroke (Fig. 5.7). This rapid succession of cusp contact at the beginning of the power stroke is in marked contrast to what is seen among “triconodont” dentitions with large a/A cusps (e.g. *Morganucodon*) here, substantial contact is made on these principal cusps well before the smaller cusps (Jäger et al. 2019b). The absence of a

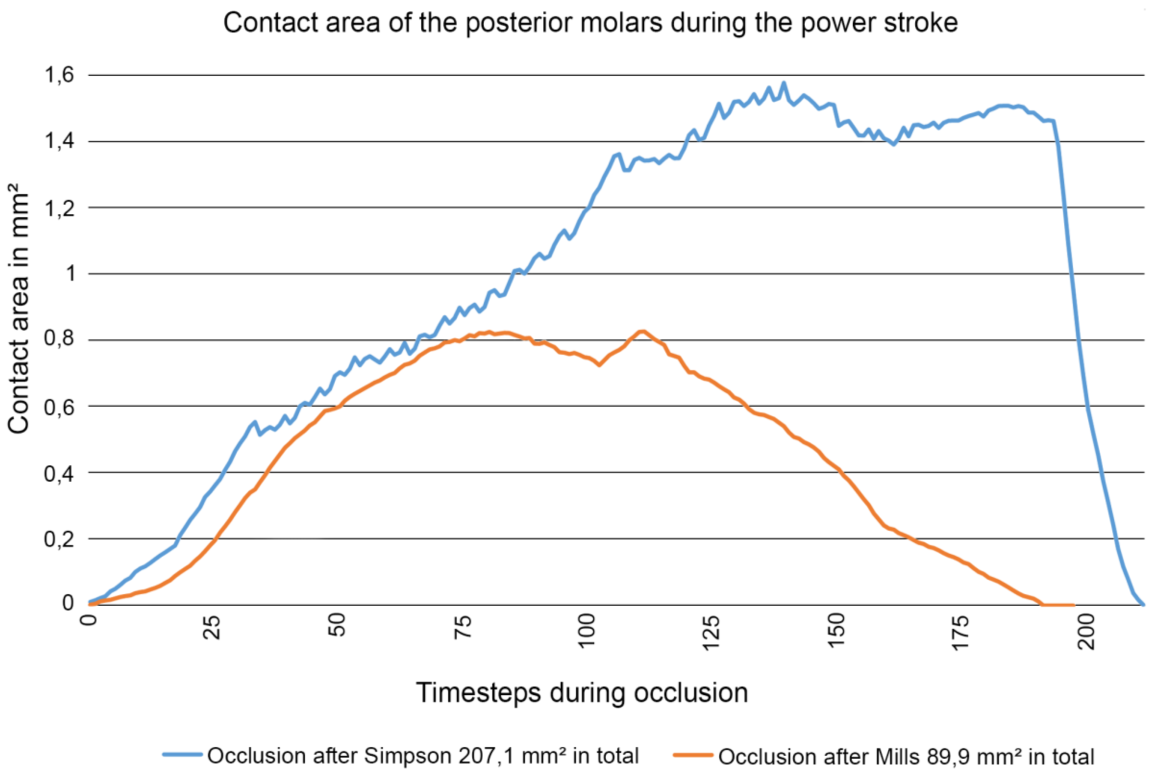

FIGURE 5.7. Quantitative comparison of upper and lower molar contact surfaces on the occlusal models of *Priacodon fruitaensis* after Simpson (1925) and Mills (1971) from the OFA analysis. Y-axis: contact surface area of M2-M3 with m2-m4 (in mm²) converted from the collision area detected by the OFA software (Kullmer et al. 2009, 2013). X-axis: time steps (1–211) of the occlusal movement of a single power stroke. Simpson´s (1925) embrasure occlusion (blue) can achieve larger total contact area and longer duration than Mills’ (1971) *Morganucodon*-like occlusion. While more contact does not validate the hypothesis by itself, it supports the interpretation of a better fit of the Simpson model.

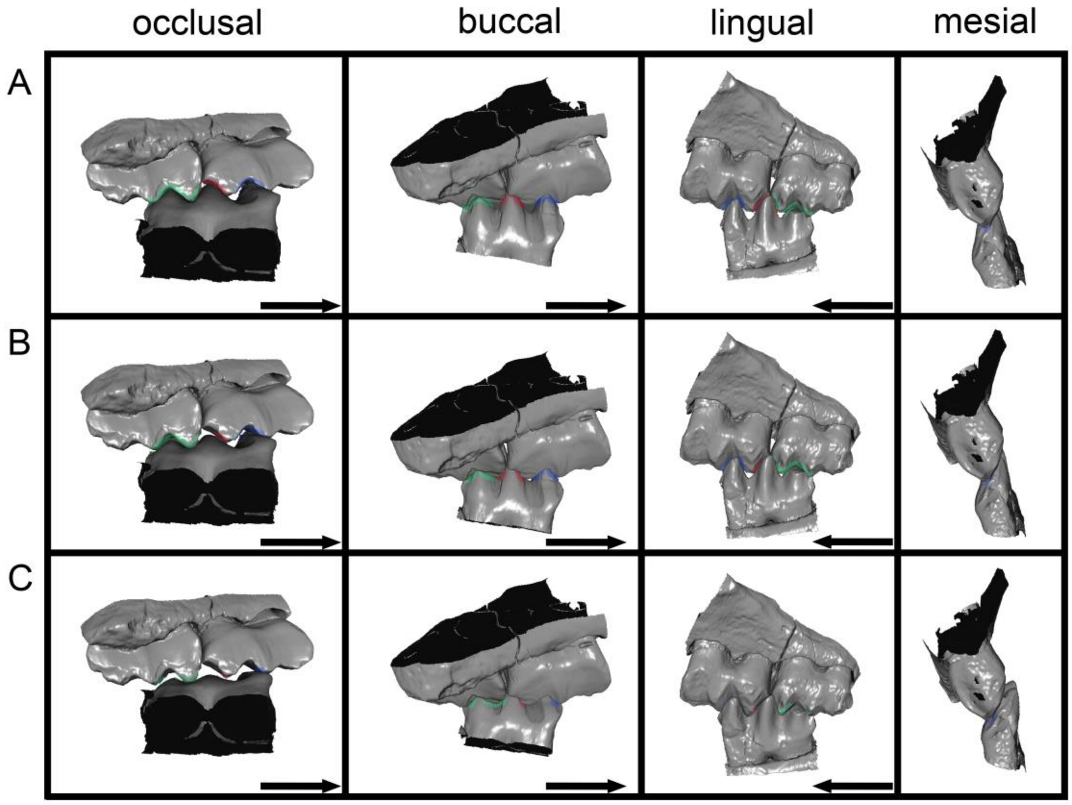

FIGURE 5.8. Collision detection on the right m3 with M3 and M4 during the masticatory cycle of *Priacodon fruitaensis*. Different stages of the power stroke. (A) Early, (B) middle, and (C) late; in occlusal, lingual, buccal and mesial view. Due to the small difference in cusp height, all cusps come into contact at the beginning of the power stroke. With the passing of the crests, most of the cutting function takes place in the first quarter of the power stroke. Food at this stage is either cut off (e.g. meat) or fragmented (e.g. insects). Subsequently, the food is compressed and sheared in the individual valleys between the teeth while the lower molar moves upwards. The movement is primarily orthal with a slight distal component following the valleys in the upper molars. Roll during the power stroke is approximately 10° as seen from mesial. Arrows indicate mesial direction. No scale.

height difference among triconodontid molar cusps, together with the fact that most cusps come in contact roughly at the same time, implies that precise alignment of the lower jaw, prior to the first contact, was required.

Simpson (1933, 1936) postulated that, during the initial orthal movement, the lower molar crests passed along the upper molar crests. Subsequently, during the later stage of the power stroke, when the lower molars move lingually and distally, their crests passed along the ridge-like cusps of the uppers. This hypothesis can be confirmed based on the OFA. The power stroke is oriented straight orthally, with a slight distal (backward) deviation, due to the orientation of the valleys in the upper molars. Simpson's model, confirmed herein, considers vertical and transverse jaw movement only. However, a third, rotational movement—roll of the active hemimandible about its longitudinal axis—is required in order to keep the teeth in close contact during the latter part of the power stroke (see below).

5.5.2 Roll

Roll (sensu Grossnickle 2017) of both the active and inactive hemimandible during the chewing cycle has been observed in several extant mammals (e.g. Crompton and Hiiemae 1970; Oron and Crompton 1985; Crompton et al. 2008; Bhullar et al. 2019). Roll requires a mobile symphysis and has been hypothesized to have been essential for the evolution of precise occlusion (Bhullar et al. 2019). Crompton and Luo (1993) described roll for an unnamed triconodontid from the Cloverly Formation. Wear facets on specimens of this species are similar to the ones described here for *Priacodon*, based on LACM 120451. Crompton and Luo (1993) noted different inclinations of the upper and lower facets, with the lowers being more vertical and the uppers more horizontal. Therefore, they concluded that the lower jaw must have rotated medially during occlusion, in order to produce the observed facets (Crompton and Luo 1993, Fig. 4.6). The OFA of LACM 120451 confirms the hypothesis that roll was present in the masticatory cycle of *Priacodon*. A comparison of paths with and without roll showed that the wear on the upper molars does not require roll to form, since most of it is caused by the tips of the lower molar cusps entering the valleys between the upper molar cusps. Wear on the lower molars, especially facets that extend far to the bases, as seen in m3 (Figs 5.3, 5.4), require a certain amount of roll in order to make contact with the upper molars. A notable difference from the hypothesis by Crompton and Luo (1993), however, is the amount of roll required (Fig. 5.8 mesial view). While no exact values were provided, based on their schematic drawing roll of roughly 20° can be assumed (Crompton and Luo 1993, Fig. 4.6). The OFA shows that roll of approximately 10° is sufficient to create the observed wear facets. The difference can be explained by the position of the upper molars in the maxilla and the lower molars in the ramus (Fig. 5.9). The hypothesis of Crompton and Luo (1993) assumed that the molars were positioned “straight,” with their cusps pointing straight ventrally and dorsally, respectively. When the maxilla and jaw are virtually aligned (based on a horizontal position of the palatine and the transverse axis of the condyle, as well as the straight orientation of the premolars) and put into occlusion it becomes evident that the upper molars in the maxilla are inclined lingually and the lower molars are inclined buccally, though to a much lesser degree. A similar inclination has been described for some Gobiconodontidae (Kielan-Jaworowska and Dashzeveg 1998, Fig. 5; Martin et al. 2015) and *Morganucodon watsoni* (Jäger et al. 2019b). While this inclination reduces the roll required to create matching occlusion, a roll of ~10° of the active hemimandible during the power stroke is still higher than the average observed roll for the extant marsupial *Monodelphis* (Bhullar et al. 2019).

Although roll of the active hemimandible was definitely present, it remains unclear at which point during the power stroke the roll was initiated. An extreme would have been deliberate rolling and active repositioning of the lower jaw prior to the power stroke, with lateral movement and inward rotation during the preparatory stroke. Subsequently, the jaw would have moved inward and upward during the power stroke. The advantage of early roll would have been that the cusps of the lower molars entered the valleys in the upper molars at a more favorable angle for passing the enamel crests of upper and lower molars.

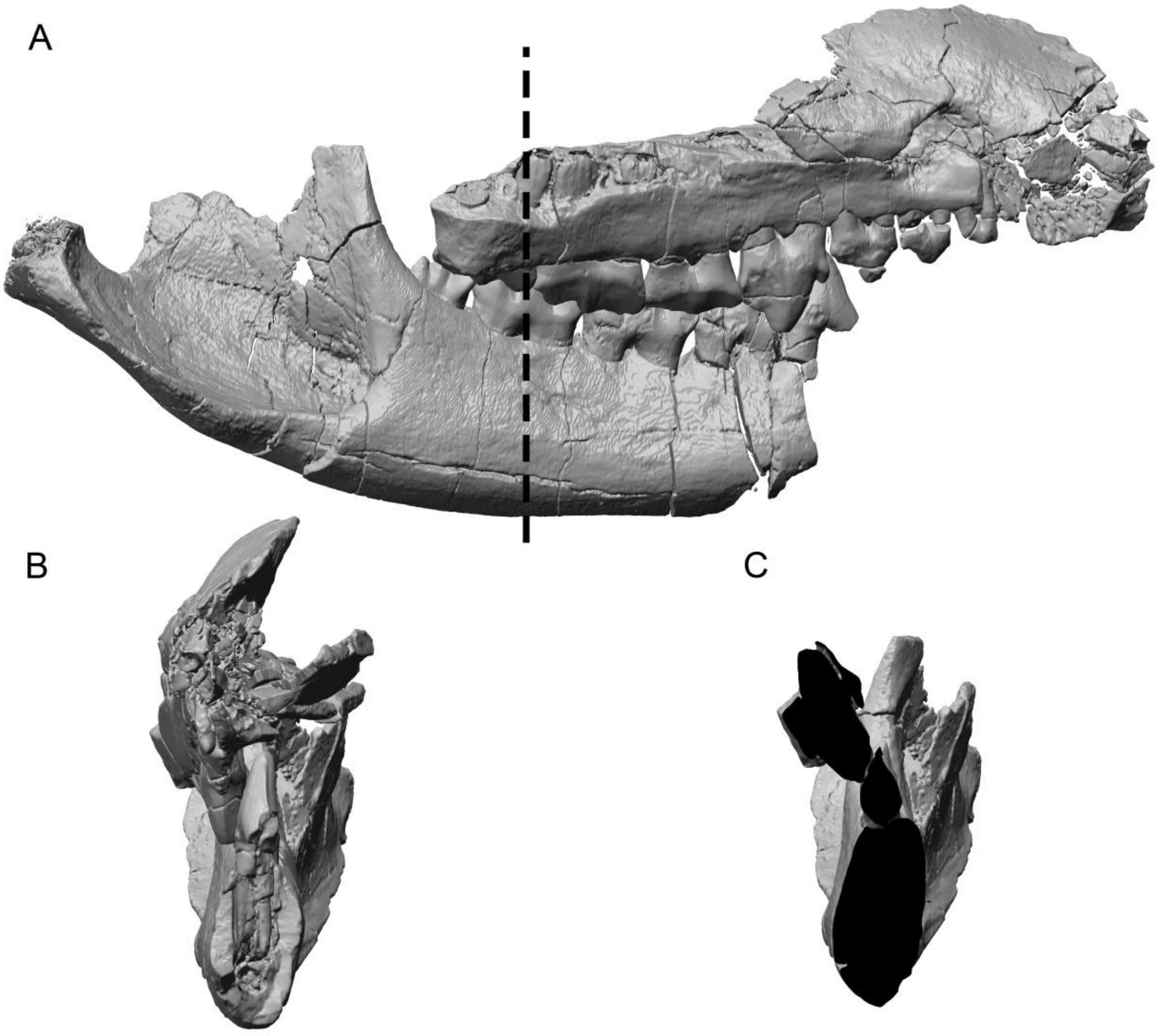

FIGURE 5.9. Right maxilla and mandible of *Priacodon fruitaensis* in (A) medial view, (B) anterior view, and (C) a section from anterior view. The dentitions are in contact but no roll was applied to the jaw (the ultimate premolars are facing each other vertically and the condyle is horizontal). The dotted line represents the plane for the section seen in (C). The anterior region and parts of the maxilla were removed to highlight the molar positioning within the maxilla and lower ramus. The posterior upper molars are inclined lingually and the lower molars buccally to a lesser degree. This inclination reduces the roll required to keep the teeth in contact during the power stroke and provides a better cutting edge alignment with the crests of the lower and upper molars passing each in a more efficient angle. No scale.

The other (more likely) possibility is that the lower molars rotated during the power stroke, after the initial contact of the teeth. In this scenario, the lower jaw might have been rotated actively, owing to contraction of the M. masseter superficialis; or passively, due to the redirection of an upward- directed pitch movement, caused by contact with the upper molars. In this case, the cusp tips of the lower molars would have entered the valleys at a steeper angle, thus the enamel crests would have been less ideal aligned initially. This scenario is supported by the wear of the lower molar cusp tips. The area of the cusp tip that is closest to the center shows exposed dentine while the buccal portion of the tip, although worn, has enamel still present. This suggests that the inner side of the lower cusp was subject to more attrition, as would occur during the first contact of the power stroke. This pattern is most noticeable on cusp a of m3 (Fig. 5.3C, D) and matches contact areas reproduced with the OFA (Fig. 5.8).

At this point, it remains unclear when the jaw rotated during occlusion. While it might have been biomechanically advantageous to incline the teeth prior to the power stroke this might not have been possible due to other factors such as limited active musculature control, stress on the jaw joint and the necessity of precise alignment prior to contact. We therefore consider a passive, semi-guided rotation, which relied on the upward force to redirect the lower jaw more likely. The OFA paths presented in this study are based on the latter assumption.

5.5.3 Dental Function and Diet

Several members of the Gobiconodontidae have been identified as carnivorous based on their size, dentition and stomach content (Jenkins and Schaff 1988; Hu et al. 2005). Triconodontidae have been similarly interpreted as carnivorous (Osborn 1888; Simpson 1933). Simpson (1933) went so far as to consider the dentition of Triconodontidae as “one of the most ideally carnivorous ever evolved.” However, for Triconodontidae, this has been solely based on dental and jaw morphology because direct evidence, such as stomach contents or coprolites, is missing. Triconodontidae are also noticeably smaller than gobiconodontids, which include some of the largest known Mesozoic mammals (Jenkins and Schaff 1988; Hu et al. 2005). Based on restored skull length (Kielan-Jaworowska et al. 2004) and using the equation of Luo et al. (2001), we estimate body mass of *Priacodon ferox* at 127 g, similar to other published estimates (111–115 g for *P. ferox*, Foster 2009). Scaling upward, based on average molar lengths (Simpson 1925a; Cifelli and Madsen 1998), yields estimates of 490–560 g for the largest member of the family, *Jugulator amplissimus*. By way of comparison, these estimates place triconodontids among the smallest of living carnivorans, such as the least weasel (*Mustela nivalis*, 25–250 g) and the dwarf mongooses (*Helogale* spp., 230–680 g; Nowak 1991).

This raises the question which dental characters support the interpretation of a carnivorous diet for triconodontids? Carnivora have evolved the carnassials, where P4 and m1 form mesiodistally elongated cutting edges that pass along each other in close proximity. Homoplastic structures evolved in the extinct creodonts, Hyaenodontidae (M2/m3) and Oxyaenidae (M1/m2) (Thenius 1989; Evans and Sanson 2006). Among carnivorous marsupials, *Thylacoleo carnifex* had enlarged carnassial-like premolars (Neidin 1991; Evans and Sanson 2006). Other marsupials such as *Thylacinus* lack specific carnassial teeth. However, all of their molars have long, primarily mesiodistally oriented crests (Thenius 1989), that enable the animal to slice portions of meat of larger prey.

Extant insectivorous taxa on the other hand, often (though not exclusively) have molars with buccolingually oriented crests or lobes (e.g. zalambdodont or dilambdodont dentitions) (Thenius 1989; Evans and Sanson 2006). These molars provide a high amount of cutting edge length in total and are well suited for fragmenting small insects and food that fits into the mouth (Kay et al. 1978; Evans 2005; Spoutil 2010), but due to their orientation lack the ability to cut off pieces from larger prey.

In Triconodontidae the cutting crests are oriented primarily mesiodistally (Fig. 5.6) (Kielan-Jaworowska et al. 2004). This supports the interpretation that Triconodontidae were carnivorous (Simpson 1933). However, the zigzag pattern of the upper molars elongates these crests and forms additional buccolingual lobes. This is a unique combination of both properties and provides the ability to fragment small prey (e.g. insects) into multiple small pieces with a single bite, which is not possible with a purely carnassial-like dentition. During later ontogeny, the upper molars tend to lose their buccolingually oriented elements and are reduced to a straight mesiodistal crest (Simpson 1933), as apparent in M1 of LACM 120451 (Fig. 5.1) (see below).

Summarizing, molar morphology of triconodontids is appropriate for carnivory but is also suggestive of reasonably good capacity for fragmenting arthropods. Small- and medium-bodied living predaceous mammals are notoriously opportunistic in their feeding predilections, although the smallest species rely predominantly on insects and other arthropods, while progressively larger taxa incorporate more vertebrate prey into their diets (e.g. Nowak 1991; Grossnickle and Polly 2013). Based on an estimated body mass range of ~100–550 g, a faunivorous diet combining insects and meat is appropriate for

Triconodontidae, with species at the larger end of that range relying more heavily on vertebrate prey. It is also possible that, within species, the loss of edge length and the reduction to straight mesiodistal crests on the upper molars was compensated by a shift to a more carnivorous diet during ontogeny.

Dental function of the dentition of Triconodontidae has been compared to that of pinking shears, due to the zig-zag pattern of the upper molars (Kielan-Jaworowska et al. 2004). Based on the OFA analysis, this comparison appears to be mostly correct. The lower molar crests pass along the upper molars crests in close proximity. However, if mostly passive roll is assumed (see above) and the jaw was not fully rotated prior to the power stroke, the angle of initial edge contact would not have been completely scissor-like (90°) but more obtuse, thus slightly limiting the cutting capabilities.

With a straight upwards movement at the beginning of the power stroke prior to edge contact, the cusps of the lower molars penetrated the food with most of the initial bite force. In that regard, the zig-zag patterns of the upper molars have helped to sharpen the lower molars. Each lower molar cusp passed along an upper molar crest and subsequently entered a valley encompassed by the wide upper molar cusps. Thus, the lower molars retained their pointed cusps and sharp crests. This could explain why most upper molars of Triconodontidae show clear signs of wear and loss of relief (Simpson 1933), while lower molars often exhibit wear facets but retain their relief well, even in older specimen (Simpson 1928: Fig. 24 D). Another potential explanation for the increased wear found on upper molars could be due to structural differences in the enamel between upper and lower molars relative to the attritional force vectors, which has been discussed for Gomphotheriidae to explain different rates of attrition for upper and lower molars (Fortelius 1985; Crompton et al. 1994).

While pinking shears obviously do not rely on pointed cusps, they appear to be an important aspect of the lower dentition of Triconodontidae, thus adding another element for food breakdown. This mechanism is also apparent in LACM 120451 although somewhat obscured by damage. Cusp a of m3 is pointed and sharp although the tip is worn and dentine exposed. Cusps C and D of M2 and cusp B of M3 on the other hand only retain a clear edge on the buccal side (the main crest), while the rest of the occlusal surface exhibits mostly exposed dentine and a worn surface. This is even more pronounced in the anterior molars since they have been in use longer. Despite having lost some of its tips by damage, it is apparent that cusp b of m2 still retains most of its original shape. On the corresponding distal part of M1, also badly damaged, most of the crown is worn down. The cusps are blunt and the valley's shallow due to crown loss and the zig-zag edge of the lingual crest is almost completely straight.

5.5.4 Comparison with Early Mammaliaform Triconodont Dentitions

Striations on the molars of the early mammaliaform *Morganucodon* show a high degree of variations, suggesting a considerable degree of freedom during occlusion (Jäger et al. 2019b). This is in contrast to the parallel, uniform striation pattern of *P. fruitaensis*, with the latter relying more on a precise uniform occlusion. While molar cusps of Triconodontidae tend to be of equal size, the early mammaliaform triconodont pattern is characterized by a large main cusp a/A. In *Morganucodon* this results in a pronounced piercing phase at the beginning of the power stroke in which only the main cusps are in contact (Jäger et al. 2019b). In contrast, in *P. fruitaensis* all cusps came into contact in rapid succession and the upper and lower crests passed along each other in close proximity along the entire tooth row. Though in *Morganucodon* crests also passed along each other in close proximity, the available functional edge length was lesser than in *P. fruitaensis*.

Based on jaw morphology and microtexture analysis Gill et al. (2014) concluded that *Morgnanucodon* was able to prey on brittle insects by applying relative large forces. This hypothesis is further supported by the robustness of cusp a, especially in the large m2 (Jäger et al. 2019b).

Though the large masseteric fossa and robust jaw suggest that *P. fruitaensis* and Triconodontidae in general was well adapted to high bite forces (Simpson 1933), the dental morphology exhibits less emphasis on high bite forces.

The differences in molar morphology between Triconodontidae and early triconodont mammaliaforms suggest a function change towards cutting rather than puncturing and shearing.

However, most taxa with *Morganucodon*-like dentitions were much smaller than the majority of Triconodontidae, with few exceptions such as *Paceyodon* or a new morganucodontan from Germany (Clemens 2011; Martin et al. 2019). This has to be taken into consideration when comparing both molar types since dental function is not only influenced by shape but also by scale (Evans and Sanson 1998; Fritz et al. 2009).

5.5.5 Uniformity of the Dentition

The molar pattern of Triconodontidae changed little for approximately 65-85 ma from the Late Jurassic till the Late Cretaceous. The changes that occur are general trends that affect few elements (Fig. 5.10). Cusp d becomes higher (Slaughter 1969), the tooth count increases, and the crown height increases, the latter being most apparent in the geologically youngest member *Alticonodon* (Fox 1969).

A potential explanation for the slow and gradual change could be the constraints presented by the highly precise occlusion of a uniform tooth battery. As demonstrated by the OFA, most molar cusps along the tooth row come into contact in rapid succession, with little freedom of movement provided by the close encompassment of the opposing valleys. This type of molar setting is not well suited for the development of new cusps or size changes in existing ones, since even small changes would likely reduce the precise fit in a system so centered on uniformity. For comparison a tribosphenic molar is more heterogeneous, thus changes in size and shape of single cusps can more easily be integrated into the existing morphology and be beneficial for the function of the teeth. This becomes apparent when both dentitions are compared (Fig. 5.11). The homogenous shape of the molars of Triconodontidae could have thus limited their potential for major modifications. The changes that occurred were within the constraints provided by the occlusion and seem to favor maximizing the total length of the cutting edges. Cusp d was already present in early-diverging Triconodontidae such as *Priacodon* and was involved in the occlusion together with cusp c. A gradual increase of its size increased the length of the cutting edge of each molar without impairing the precise occlusal fit. This is apparent from *Astroconodon* where cusp d is relatively large but still closely associated with cusp c (Slaughter 1969; Cifelli and Madsen 1998). The increase in crown height exemplified by the upper molars of *Alticonodon* represents a similar mechanism. Although not adding to the maximum edge length, it increased the amount of edge length over the lifespan, without interfering with the occlusal mode. This increase of crown height might have been driven by the difference in the amount of wear in the upper and lower dentition, discussed earlier. While crown height and the integration of cusps d/D appear to be the only morphological changes possible for the molars themselves, the addition of molars at the posterior end of the molar series was possible without interference with the constrained occlusal system. In *Triconodon* m4 is formed within the coronoid above the functional tooth row (Simpson 1928; Jäger et al. 2019a). This unusual placement could potentially be linked to an increase in tooth count, which increased the total length of cutting edge. The Early

Cretaceous *Meiconodon* and the Late Cretaceous *Corviconodon* have five lower molars, of which the last one is small and similar in shape to m4 of *P. fruitaensis* and the m4 of *T. averianovi* (Cifelli and Madsen 1998; Kusuashi 2009; Jäger et al. 2019a).

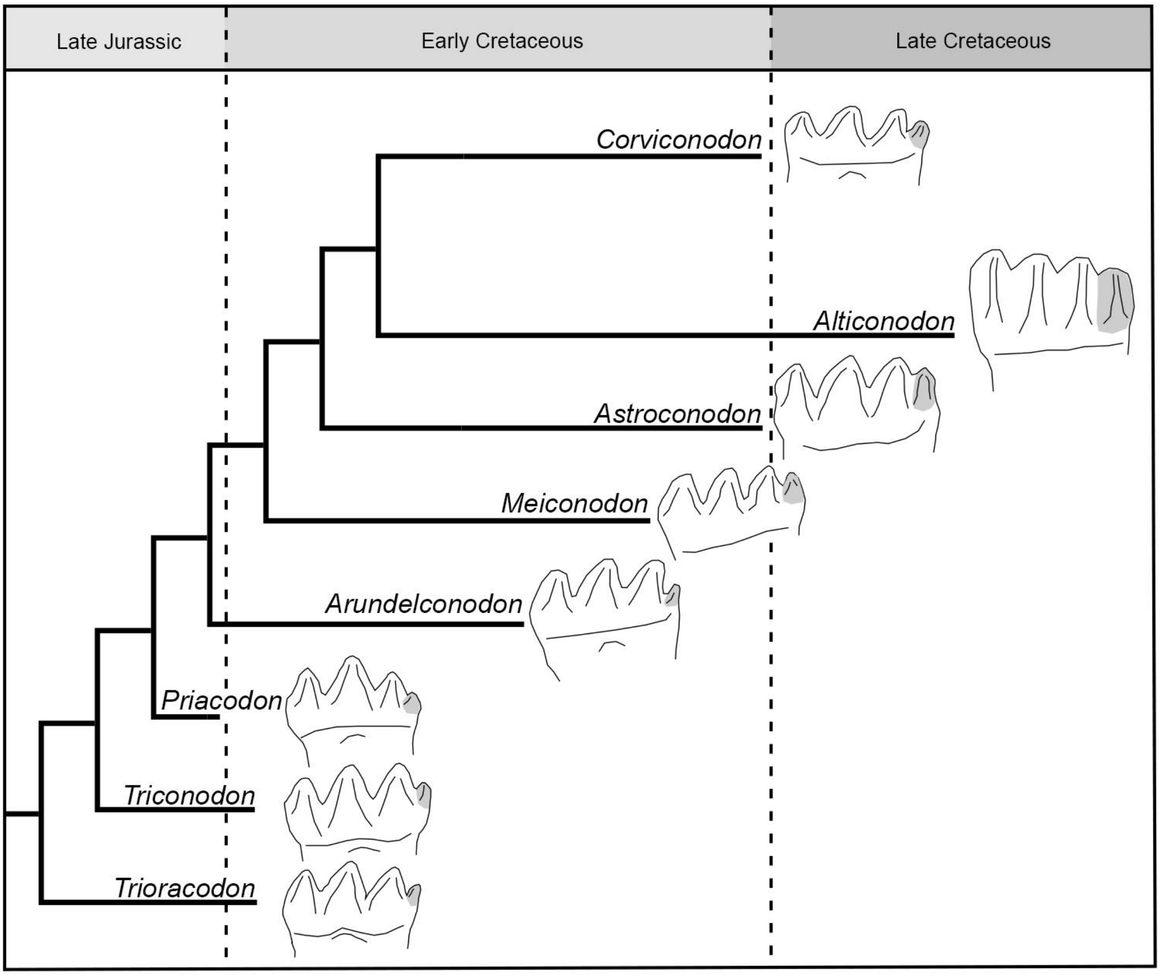

FIGURE 5.10. The development of molar cusp size in Triconodontidae. Cusp size of the three main cusps becomes more similar, while cusp d (light grey) increases in size. Its function changes from merely interlocking with the next posterior molar to an active unit during food processing. In this role it is initially still closely positioned next to cusp c (e.g. *Meiconodon*, *Astroconodon*). In the last lower molar of *Alticonodon,* it is a fully separated cusp that functions as a single unit in the tooth battery. *Astroconodon* and *Alticonodon* also show an increase in crown height. Tooth position varies, which can influence the relative size of the cusps to a small degree. The cusp dimensions of *Corviconodon* are approximations of the dimensions of unworn teeth based on the worn holotype of *C. uthaensis*. *Priacodon* is based on the holotype of *P. ferox* since no tooth is complete in the holotype of *P. fruitaensis*. The former has greater differences in cusp size than the latter. The phylogeny is based on Martin et al. (2015). Teeth not to scale.

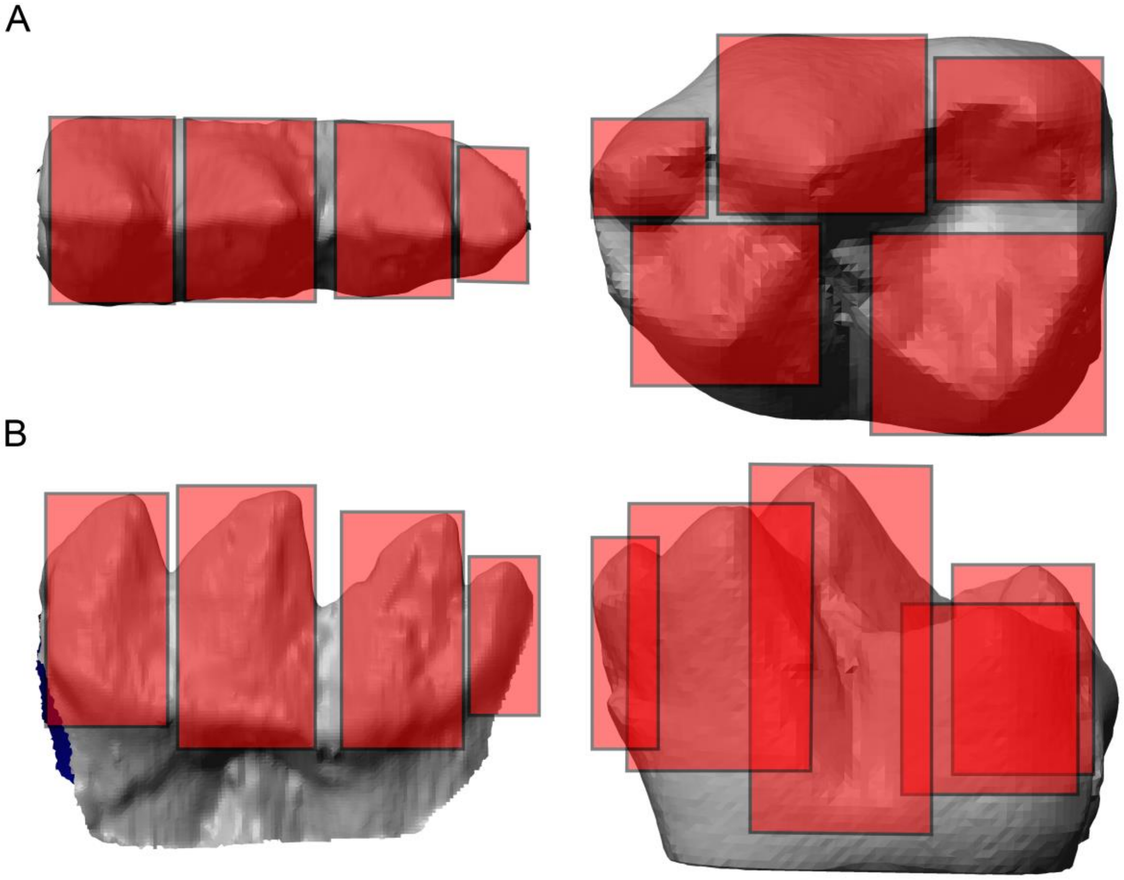

FIGURE 5.11. Comparison of a triconodontid (m3, undescribed specimen MCZ 19850) and a tribosphenic molar (m1, *Cantius* USGS 13634) in (A) occlusal and (B) lingual view. Squares are plotted over individual cusps to highlight them as functional units. It is apparent that the tribosphenic molar is more heterogeneous in its cusp dimensions, while the triconodontid molar is more uniform. In combination with its precise and enclosed occlusal pattern, this uniformity could have placed constraints on the evolutionary development of the molar morphology of Triconodontidae. Teeth not to scale.

5.6 Conclusion

Triconodontidae exhibit a molar series that is unique among mammals and is not directly comparable to any extant counterpart. A highly homogenous cusp-valley system formed a continuous system of mesiodistally oriented crests that linked the whole molar series (Simpson 1933). The occlusal mode of *P. fruitaensis* and therefore likely Triconodontidae in general was embrasure occlusion, as proposed by Simpson (1925b) and contrary to Mills (1971). This is supported by premolar positioning, wear facets, higher collision areas in OFA analysis during the power stroke, and a better fit. This unifies embrasure occlusion as a plesiomorphic character for all Eutriconodonta and limits the *Morganucodon*-pattern to a few taxa within the Morganucodonta. The upper molars were inclined lingually within the maxilla, similar to Gobiconodontidae (Martin et al. 2015) and *Morganucodon* (Mills 1971; Jäger et al. 2019b), which reduced the roll required for a matching occlusion. Roll of the active hemimandible during the power stroke was confirmed by the OFA. Roll was around 10° from the beginning until the end of the power stroke and therefore less than previously proposed (Crompton and Luo 1993). At the beginning of the power stroke, the mesiodistally oriented crests of the lower and upper molars passed along each other, subsequently, the lower cusps entered the valleys in between the upper cusps. This lead to translation of the lower teeth towards lingual, while the roll of the jaw kept the occlusal sides of the teeth in close contact. The function, therefore, differed from that of the early triconodont pattern of Morganucodonta, with the latter relying more on puncturing capabilities of large cusp a/A rather than precise cutting. The dentition of Triconodontidae combines traits linked to carnivorous diets (e.g. mesiodistally oriented cutting edges) and insectivorous diets (buccolingually oriented crests and lobes). This supports the interpretation of a faunivorous diet including insects and small vertebrates rather than a full carnivorous diet as proposed previously (Osborn 1888; Simpson 1933). The loss of blade length in the upper molars with increased wear is potential evidence for a change in diet during ontogeny. Based on the crest morphology, the pinking shear analogy (Kielan-Jaworowska 2004) holds up, but needs to be expanded to include the lower cusps, which are self-sharpening within the valleys of the upper cusps.

The molar series is highly uniform and adapted to a precise fit. While this ensured good cutting capabilities it likely put the dentition under greater evolutionary constraints as other molar types with more heterogeneous cusp morphologies.

5.7 Acknowledgments

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Occlusion and Dental Function of Gobiconodontidae

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6.1 Abstract

Gobiconodontidae are a clade of early crown-group Mammalia. They are unique among Mesozoic mammals due to their large size, the replacement of their molariforms and carnivorous diet. Here we analyse the molariform dentition and occlusion of an undescribed gobiconodontid from the Early Cretaceous of China. With the Occlusal Fingerprint Analyser (OFA) we confirmed a modified type of embrasure occlusion that causes extensive wear and results in deep grooves between the upper molars. Differences in the placement of the grooves suggests slight occlusal variations among Gobiconodontidae. The occlusion is centered around mesiodistally oriented crests. They form in the course of increased wear that results in the loss of the smaller b/B and c/C cusps and extends from the tip of the large a/A cusps to the base of the molariforms. These crests provide the main cutting capability during the single-phased power stroke.

The upper molariforms of the specimen examined in this study also exhibit small, lingually placed crests on the E cusps. These additional edges utilize the momentum of the power stroke after the main crests have passed and thus provide additional cutting capabilities. Gobiconodontidae and Triconodontidae both share mesiodistally oriented crests, a faunivorous diet, as well as lingually inclined upper molars, potentially to reduce the amount of required roll during the power stroke. However, while the occlusion of Triconodontidae is highly precise and based on a universally sized cusp-valley battery, the occlusion of Gobiconodontidae is primarily focused on the formation of long crests at the costs of tooth material. Given the large size of Gobiconodontidae it seems likely that bite force was emphasized over precision. This interpretation is in agreement with the previous hypothesis that the replacement of the molariforms might have been necessary to compensate for the loss of tooth material.

6.2 Introduction

Gobiconodontidae is a family of Eutriconodonta known from the Early Cretaceous of Asia, as well as North America and Western Europe (e.g. Trofimov, 1978; Jenkins and Schaff 1988; Sweetman 2006; Martin et al 2015; Butler and Sigogneau-Russell 2016). Other gobiconodontid-like taxa of Jurassic age have been described (e.g. *Huasteconodon*; Montellano et al. 2008), however, their classification as Gobiconodotidae has been questioned (Lopatin and Averianov 2015). For this study, we consider the genera *Gobiconodon*, *Repenomamus*, *Meemannodon, Hangjinia*, and *Spinolestes* as members of Gobiconodontidae (Trofimov 1978; Godefroit and Guo 1999; Li et al. 2001; Meng et al 2005; Martin et al. 2015).

The antemolar dentition of Gobiconodontidae is derived with a reduced number of large incisors and small canines (Kielan-Jaworowska et al. 2004). Gobiconodontidae further differ from most other mammals by replacing their molariforms, thus lacking true molars (*sensu stricto*) (Jenkins and Schaff 1988). Lopatin and Averianov (2015) even argued for more than two generations of molariforms. The lower molariforms have a triconodont bauplan with three main cusps a, b and c aligned in a row and the central a cusp being the largest. They are similar to those of “Amphilestidae” with taller crowns and cusp c exceeding cusp b in height. Upper molariforms are mediolaterally wide with labial and lingual cingula. The principal cusps of the upper molariforms are increasingly triangled towards posterior (Kielan-Jaworowska et al. 2004).

The most abundant genus within Gobiconodontidae is *Gobiconodon*, which is represented by multiple species based on several skulls as well as postcranial material. However, it has been noted that the morphological variation between the different species is substantial and that future studies might recognize additional genera (Kielan-Jaworowska et al. 2004).

For a *Repenomamus* specimen, stomach contents comprising a small dinosaur is direct evidence for a carnivorous diet (Hu et al. 2005). Other Gobiconodontidae have also been considered to be carnivorous, based on their large size (for Mesozoic mammals) and tooth and jaw morphology (Jenkins and Schaff 1988; Kielan-Jaworowska and Dashzeveg 1998; Kielan-Jaworowska et al. 2004).

Previous studies on the occlusion of Gobiconodontidae were limited to description, two-dimensional modeling, and, with the exception of *G. ostromi*, to isolated teeth and fragments (Jenkins and Schaff 1988; Kielan-Jaworowska and Dashzeveg 1998; Butler and Sigogneau-

Russell 2016). Here, we use micro-computed tomography (μ-Ct) and 3D models to examine the molariforms of an undescribed gobiconodontid. The aim of this study was to test the existing hypothesis on the occlusion of Gobiconodontidae and to compare the dental function to that of other Mesozoic mammals with triconodont dentitions.

6.3 Material and Methods

The specimen M130712C is an undescribed gobiconodontid from the Early Cretaceous of China. It consists of a skull with well-preserved left dentition, an almost complete right hemimandible, and a fragmentary left hemimandible. The specimen was scanned with the 180 kV x-ray tube of the v|tome|x s μCT device (GE Sensing & Inspection Technologies GmbH phoenix|x-ray) housed in the Institut of Geoscinences, University of Bonn, Germany. Scan settings for the upper dentition were set at 80 kV and 18 μA, a shutter speed of 40 ms per capture, and a voxel size of 72.15 μm. The lower left dentition was scanned with 60 kV, 18 μA, a shutter speed of 40 ms per capture, and a voxel size of 23.77 μm. The instrument produces isotropic voxels, and the single image size is 1024 x 1024 pixels. The data was subsequently processed and polygonal models were created with Avizo (8.1, Visualization Sciences Group, France). Further data processing, e.g. the reduction of triangles, was performed with Polyworks (2014, InnovMetric Software Inc., Canada); the file format used was .stl (little endian). Casts of the molariforms were examined with Scanning Electron Microscopy (SEM) (Cambridge CamScan MV2300to analyze wear facets and striations. An occlusal hypothesis based on the wear pattern was tested with the Occlusal Fingerprint Analyzer (OFA) software. Polygonal tooth models follow a user-defined pathway based on occlusal hypotheses and virtual collision of the teeth was simulated. The term ‘occlusal fingerprint’ describes the orientation and position of wear facets on an occlusal surface (Kullmer et al. 2009). The OFA software was developed and applied by the Research Unit 771 of the German research foundation (DFG) to analyze the chewing path of extinct and extant mammals (e.g. Benazzi et al. 2011, 2013; Koenigswald et al. 2013; Kullmer et al. 2009, 2013; Schultz and Martin 2014; Schultz et al. 2019).

A thorough morphological description of the specimen is currently in preparation. For this study, we follow the established cusp terminology of gobiconodontids (e.g. Kielan-Jaworowska and Dashzeveg 1998), with the addition of an additional cingular cusp on the distolingual side of the upper molars, lingual to cusp C, in this study preliminary named cusp X.

6.4 Results

6.4.1 Wear

Lower Molariforms—The left penultimate molariform is the most complete tooth and was therefore used for the OFA analysis and examined for the analysis of wear on the lower molariforms (Fig. 6.1). Differences to other molariforms that were observed are included, as well.

The anterior side of cusp b exhibits a large anteriorly oriented facet. A similarly inclined facet is also present on the most anterior part of the preserved part of cusp a. Given the similarities in inclination, it is likely that both facets were caused by the same antagonist.

The posterior side of cusps c and d show a posteriorly oriented facet. A corresponding facet is present on cusp d of the next anterior molariform. The facets on the lower molariforms are therefore oriented anteriorly on the anterior cusps and posteriorly on the posterior cusps, indicating that the space between two molariforms occupied the largest upper cusp A during occlusion.

The b cusp on the first left molariform is unworn, either because it does not make contact with its premolar antagonist (unfortunately the corresponding tooth is not well preserved) or because it had been recently replaced.

Wear on the ultimate right molariform differs from that on the other molariforms since it is only worn on its anterior side, displaying a large wear facet that extends from the base of cusp b to the tip of cusp a. A similar condition has been described for *G. haizhouensis* (Kusuhashi et al. 2016). The absence of posterior facets is due to the lack of an antagonist. The unusual size of the anterior facet could be either explained with long use of the molariform or a recent replacement that did not precisely match the position of the upper antagonist and thus resulted in a high amount of attrition. A depression on the buccal side of the jaw is present between the ultimate and penultimate molariforms, likely caused by the A cusp of the upper antagonist. A similar condition has been described for *G. hopsoni* (Rougier et al. 2001).

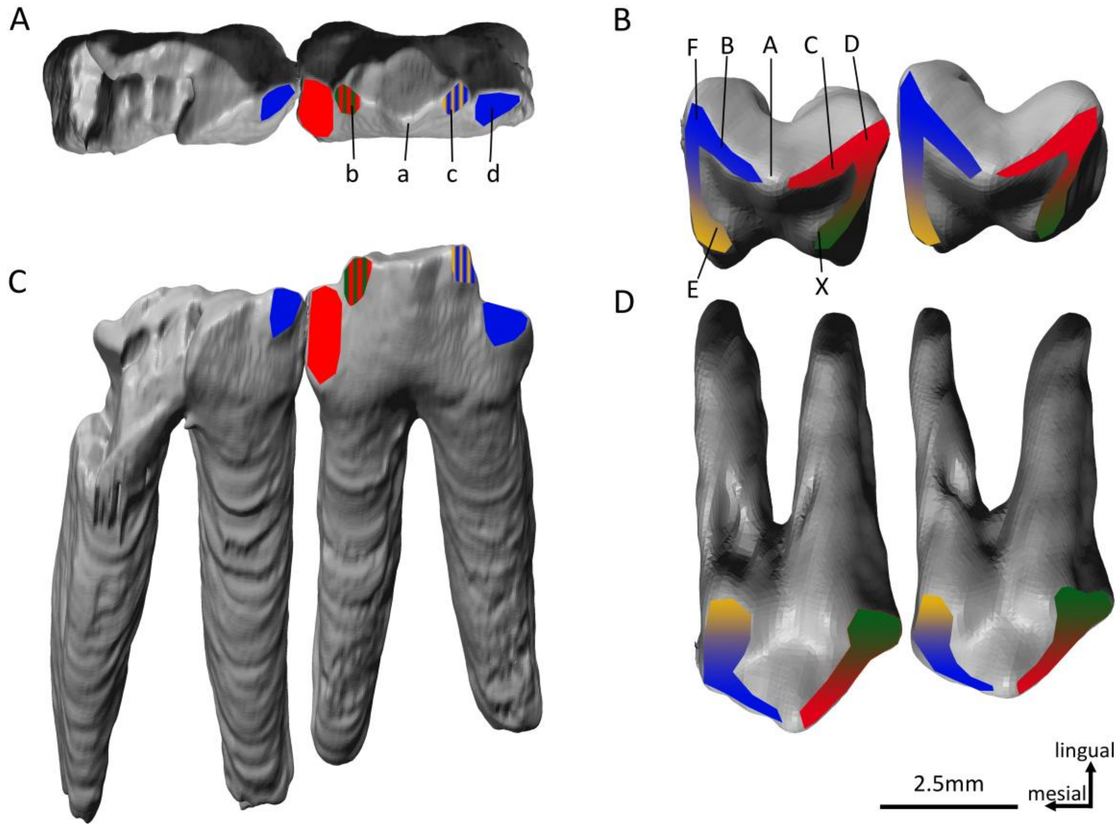

FIGURE 6.1. Wear facets of M130712C on the left second and third (A, C) lower and (B, D) upper molariforms in (A, B) occlusal, (C) buccal, and (D) lingual views. Facets on the crests of the lower molariforms make contact with the buccal crests on the upper molariforms, as well as the more lingually placed cusps E and X later during the power stroke when the teeth move further lingually. Upper molars in lingual view (D) were mirrored for better comparability.

Upper molariforms—All three upper molariforms show similar wear patterns. The wear pattern generally resembles that of the lower molariforms (Fig. 6.1). Large anteriorly oriented facets extend over the B and A cusps and the posteriorly oriented ones extend over A and C, both resulting in prominent crests. The relief of the B and C cusps is mostly worn away, with the exception of cusp B on the first molariform. A worn-out groove is present on the posterior side of each molariform (Fig. 6.2). These grooves were previously described for *G. borrisiaki* (although differing in their position in *G. borrisiaki*; see discussion) as well as *G. hoburensis* and interpreted as caused by cusp a of the corresponding lower molars (Kielan-Jaworowska and Dashzeveg 1998) and referred to as “interdental embrasures” by Butler and Sigogneau-Russell (2016). In all molariforms of M130712C, the anterior worn parts of the groove extend over the posterior side of cusp X and wrap around their lingual side. The posterior side of the groove is on the anterior side on the next posterior molariform. It extends from the buccal side lingually over cusp E, though appears to be less strong than the wear on the anterior side of the groove (Fig. 6.2). This results in the formation of sharp crests on the buccal side of cusps E, which will be referred to as secondary cutting edge and unlike to the wear on cusp X does not extend around the lingual side (Fig. 6.2).

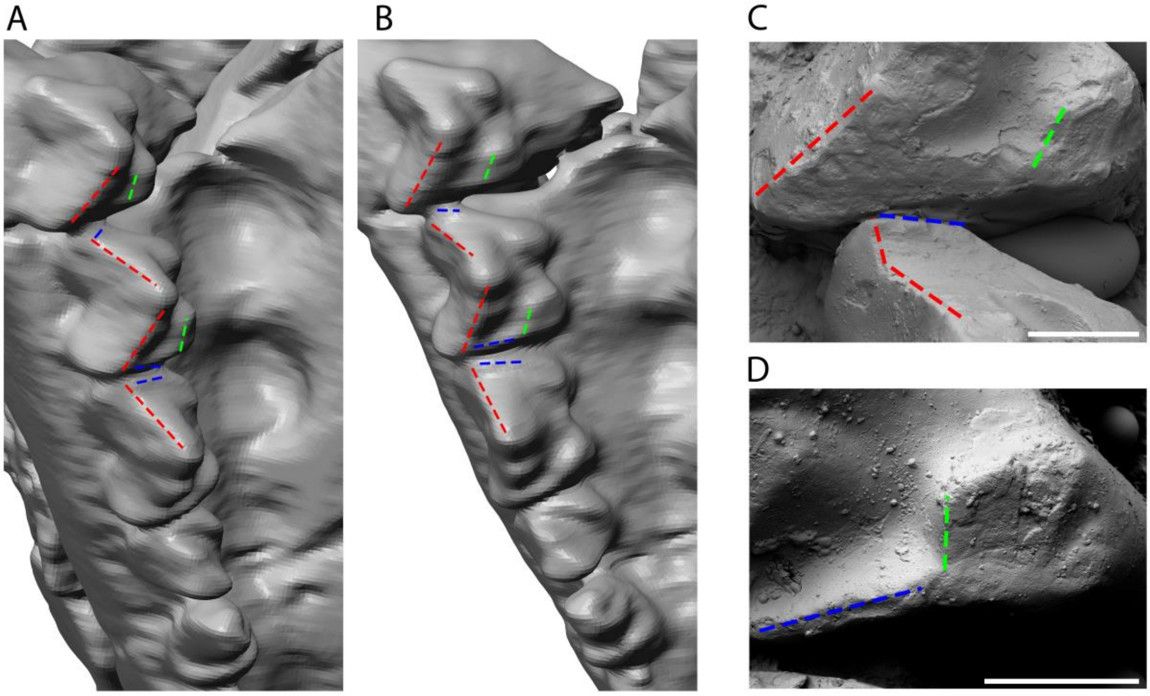

FIGURE 6.2. Upper molariforms of M130712C in (A) ventral and (B) occlusal view, and (C, D) SEM images of the groove between the ultimate and penultimate molariform and cusp E of the second (penultimate) molariform. Cusps B and C are worn and mesiodistally oriented crests are formed (dotted red lines). The tips of the lower a cusps have formed interdental grooves resulting in prominent edges (dotted blue lines) that are oriented buccolingually, parallel to the chewing direction. The buccal sides of the E cusps have short cutting edges (dotted green lines) that are parallel to the main crests and at a 90° angle to the trajectory of the lower molars during the power stroke. The difference between the ventral and occlusal views highlights the lingual inclination of the upper molariforms within the maxilla. Note that the occlusal view is tilted relative to the transversal plane, while the ventral view represents the natural position of the teeth during the power stroke relative to the lower dentition. Scale bar represents 1mm.

6.4.2 Palatal Fossae

Multiple palatal fossae are present in the palatal process of the maxilla. They are positioned roughly lingually to the C cusps of the upper molariforms and increase in depth towards posterior. Palatal fossae are found in multiple Mesozoic mammaliaforms such as *Morganucodon*, *Haldanodon*, *Maotherium*, *Priacodon,* and *Gobiconodon* and are sometimes also referred to as “pits” (e.g. Simpson 1933; Parrington 1971; Lillegraven and Krusat 1991; Jäger et al 2019b), or “embayment” (e.g. Plogschties and Martin 2019). They are entered by the lower main cusps at the end of the power stroke (Kielan-Jaworowska and Dashzeveg 1998; Rougier et al. 2001; Plogschties and Martin 2019; Jäger et al. 2019b). However, compared to *Morganucodon* the palatal fossae on M130712C are positioned anteriorly to and not between two molariforms (Fig. 6.2).

6.4.3 Inclination

The posterior upper molariforms are inclined lingually, similarly to those of *Priacodon fruitaenensis*, *Morganucodon watsoni,* and *Gobiconodon* (Kielan-Jaworowska and Dashzeveg 1998; Jäger et al. 2019a, b). It has been proposed that this inclination could have reduced roll required to pass the lower molariforms past the wider posterior uppers (Jäger et al. 2019b). Another potential reason is the improved alignment of upper and lower crests passing along each other (Jäger et al. 2019a). The latter reason seems to be likely the case for M130712C, given the worn crests of the main cusps.

6.5 Discussion

6.5.1 Occlusion in M130712C Compared to Other Gobiconodontids

Based on the wear facets and depressions in the lower jaw of M130712C, it is apparent that the main cusps A of the upper molariforms entered between two antagonists (Fig. 6.3). This type of embrasure occlusion is similar to that of other Gobiconodontidae, symmetrodontans and several morganucodontans (Crompton and Jenkins 1968; Crompton 1974; Kielan-Jaworowska et al. 2004; Butler and Sigogneau-Russell 2016). Additionally, cusp a of M130712C entered between two upper molariforms but it was positioned slightly anterior as indicated by the groove between the two upper antagonistic molariforms (Fig. 6.2), that is more pronounced on the posterior side of the anterior upper tooth. A similar condition appears to be present in *G. hoburensis* and possibly *G. ostromi*. In *G. borrisiaki* (PSS 10-15b), the grooves are also present but positioned further towards anterior and primarily formed by the posterior side of the anterior antagonist. The deepest part of the grooves is where cusps C would have been, which are worn away (Kielan-Jaworowska and Dashzevegh 1998). In M130712C, the deepest point of the grooves is in between two molariforms and wear extends similarly over both antagonists. A detailed interpretation of the occlusal difference between the two taxa is provided below. *G. hopsoni* also has a large wear facet on the anterior side of its last upper molariform (Rougier et al 2001); however, due to the high amount of wear and damage it is difficult to address, if the occlusion was similar to that of M130712C.

The mesial side of cusp a, as well as the worn cusp b, made contact with the posterior side of cusps A and C and later during the power stroke with the more lingually positioned cusp X (Fig. 6.3D). The posterior sides of cusps a and c made contact with the anterior sides of cusps

A and B. Given their small size and the close proximity of cusp b/B and c/C to the main cusps a/A, there is little freedom when it comes to the occlusal position of the smaller cusps.

After the initial contact during the power stroke, the lower molariforms of M130712C continued to move orthally as well as transversally towards lingual, as has been described for other Gobiconodontidae (Fig. 6.3) (Jenkins and Schaff 1988). While moving inwards the lower molar passed a crest formed by cusp E (Figs 6.2, 6.3). Subsequently the tips of cusps a entered the palatal fossae in the maxilla.

Jenkins and Schaff (1988) have argued for the presence of roll (*sensu* Grossnickle 2017) during the power stroke in *Gobiconodon*. This cannot be excluded for M130712C, and given the presence of a mobile symphysis, it is possible that the active hemimandible rolled a few degrees as a reaction to the involved forces.

However, it appears unlikely that roll was a major factor during the power stroke, given that all wear facets could be reconstructed with the OFA analysis (except those caused by the tip of cusp a that is missing) without the application of roll. One potential explanation might be the inclination of the upper molars of M130712C towards lingual within the maxilla (Figs 6.2, 3). This inclination can easily go unnoticed when only maxillary fragments are available. It enables close contact of the molars during the power stroke with minimal roll and has been noted for *Morganucodon* as well as for Triconodontidae (Mills 1971; Jäger et al. 2019a, b).

The occlusion of gobiconodontids still requires future studies. Occlusal models solely based on upper or lower teeth prove to be difficult. Butler and Sigogneau-Russell (2016) described an isolated lower molar (M46563) with a large facet on the distolingual side of cusp c and, based on the occlusion of *G. borrisiaki* concluded that the facet was caused by an antagonist with a large cusp B. Given the extension of the facet (Butler and Sigogneau-Russell 2016, Fig. 8) and the occlusion of M130712C as presented, it seems likely that a minor cusp B was present and that a large cusp A could have caused the facet instead. This example highlights the necessity of matching teeth and, if possible, 3D occlusal analysis, in order to test occlusal models.

Kielan-Jaworowska et al. (2004, Fig. 7.6 C) provided a figure that shows lower cusp a moving along upper cusp C. This drawing is likely based on *G. borrisiaki* and its more anterior positioned grooves. In M130712C, this occlusal relationship would result in large gaps and insufficient contact of cusp a to the next posterior upper molariform. Based on the OFA analysis, the only way to keep the teeth in close contact during occlusion is embrasure occlusion with the main cusps between two antagonists (Fig. 6.3). This is also indicated by the positioning of the grooves (Fig. 6.2) (Appendix 2).

Occlusion of cusps A appears to be universally in between two lower molariforms in all gobiconodontids. As stated above, the occlusal pattern of the lower cusps a seemed to differ between entering between two molariforms or over cusp C of the anterior upper antagonist. Currently, it appears likely that the determining factor between the two occlusal modes might be the separation of the cusps of both lower and upper molariforms as well as the prominence of cusps b and c cusps relative to cusp a. In M130712C, the a cusps are prominent and thus require a lot of space during occlusion. The other cusps, on the other hand, were considerably smaller and located close to the a cusps. Additionally, in PSS 10-15b (*G. borrisiaki*) the upper cusps A and C appear to be relatively well separated, while they are closer together in M130712C. Similar proportions as in M130712C appear to be present in *G. ostromi* (Jenkins and Schaff 1988), and possibly in *G. hoburensis*, which is described to differ from *G. borrisiaki* in having less prominent lower b and c cusps (Kielan-Jaworowska and Dashzevegh 1998). The lower molariforms of *G. haizhouensis* are also similar in their proportions to those of M130712C, but unfortunately no upper molariforms of the species are known (Kusuhashi et al. 2016).

If the difference is based on the required space for cusp a, taxa with more separated cusps like *G. borrisiaki* or isolated molariforms of *G.* sp. from the Early Cretaceous of West Siberia (Kielan-Jaworowska and Dashzevegh 1998; Averianov et al. 2005), would likely show an occlusal mode that results in more anterior positioned grooves.

This interpretation of differences in the occlusion of Gobiconodontidae should be considered as preliminary at this point. The observed differences could be the result of different wear stages. However, it appears as if increased wear in PSS 10-15b (*G. borrisiaki*)would deepen the groove till it eventually might reach the upper part of the posterior roots, while a later wear stage of M130712C would likely result in a deeper groove between both molars.

The interpretation is complicated by the replacement of molariforms which potentially could lead to different occlusal patterns within one individual. However, this appears to be not the case for the specimens discussed here, since an anterior groove is similarly shaped on the third and fourth upper molariforms of PSS 10-15b (*G. borrisiaki*) and absent on all molariforms of M130712C (Kielan-Jaworowska and Dashzevegh 1998).

To complicate things even further, it might not be possible to separate taxa with more prominent main cusps and less separation vs taxa with more separated cusps of equal height. Some specimens of *G. borrisiaki* appear to have less separation between the cusps (e.g. PDI M 3101-24 or PSS 10-15), while some specimens of *G. hoburensis* have less prominent a cusps (e.g. PSS 10-21) (Trofimov 1978; Kielan-Jaworowska and Dashzevegh 1998). These variations are also examplified by upper molars of *G. palaios* with SA 111 having cusps of almost equal height, while the holotype SA 107 exhibits a much larger A cusp relative to B and C (Sigogneau-Russell 2003).

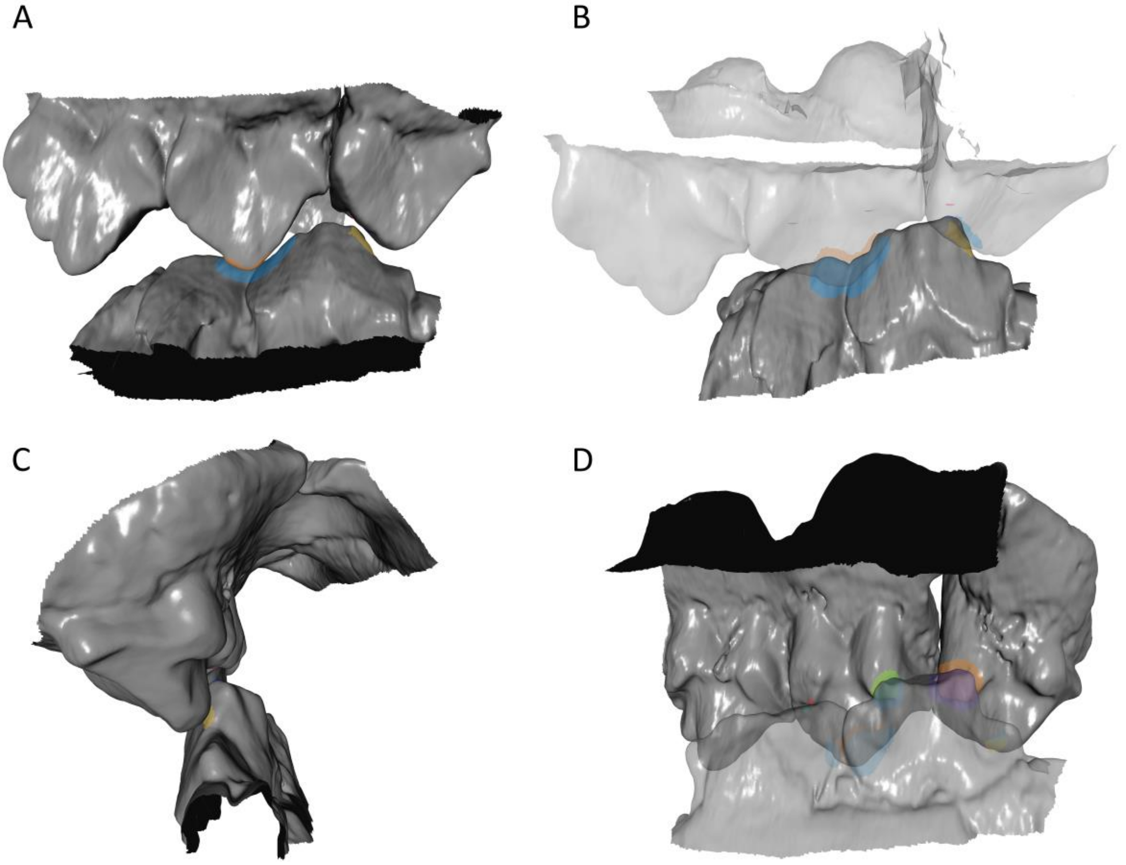

FIGURE 6.3. OFA analysis with m1, m2, and M1-M3 of M130712C in (A) buccoventral, (B) buccal, (C) distal, and (D) lingual view. (A-C) represent an early stage of the power stroke, while (D) represents a later stage when cusps E and X are in contact with cusp a. Embrasure occlusion is present, which is apparent by size of the a/A cusps that require the interdental space to occlude. Due to the missing tip of cusp a, no collisions could be reconstructed in the groove between the upper molariforms. The inclination of the upper molars in the maxilla enables the lower dentition to move orthally without the requirement of significant roll. Mesial is to the left. No scale.

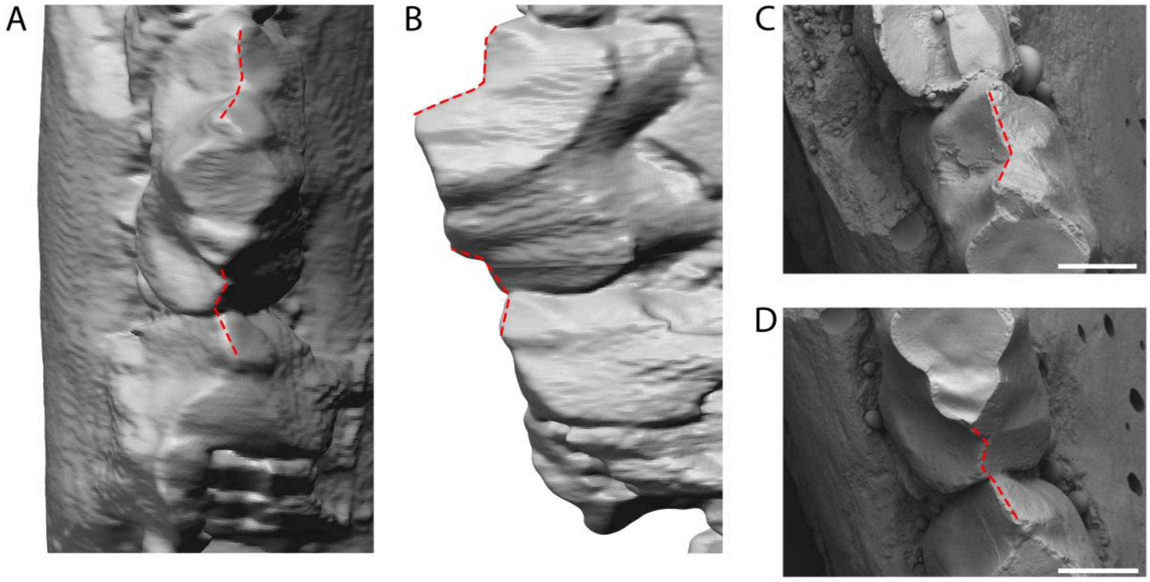

FIGURE 6.4. (A, B) 3D models and (C, D) SEM images of the third lower molariforms of M130712C in (A, C, D) occlusal and (B) lingual views. Cusps b and c are mostly worn and two crests (dotted red lines) extend from the tooth base to cusp a. Scale bar represents 1mm.

6.5.2 Dental Function of M130712C

It is apparent that the b/B and c/C cusps play a minor role and are worn quickly, resulting in long crests that cover the posterior and anterior crests of the a/A cusps (Figs 6.2, 6.4). With the tip of cusp a entering in the space between two molariforms, the crests of the main cusps pass along each other in close proximity. Thus, the primary function of the molariforms is to cut rather than to pierce as seen in early Mammaliaformes such as *Morganucodon* (Jäger et al. 2019b). The length of the crests and their roughly mesiodistal orientation suggest similarities to the carnassials of extant carnivorans (Fig. 6.4). However, as pointed out by Jenkins and Schaff (1988), the crests lack self-sharpening mechanics and are heavily affected by wear. Jenkins and Schaff (1988) further discuss the possibility that the replacement of the molariforms might have compensated the loss of tooth material and renewed the puncturing and shearing capabilities. It appears unlikely that puncturing was the primary function of the molariforms, due to the quick loss of the accessory cusps and the dominance of the crests as stated above. However, M130712C supports the assumption that the molariforms of gobiconodontids were replaced to compensate for increased wear. The presence of deep grooves, while a result of wear, at the same time provides a structure to guide the lower molariforms during the power stroke. Thus, they might also have played an important role after the replacement of a lower molariform in limiting the potential movement and ensuring that the replacement does not result in mismatching occlusion.

A trait that is not universal in Gobiconodontidae is the short edge found on cusp E of M130712C. While it is relatively small compared to the main crests, it still provides additional usage for the momentum of the lower molars while they pass lingually.

An interesting comparison to the molariforms of Gobiconodontidae are the molars of Triconodontidae. Both families are part of the Eutriconodonta, they share the triconodont molar pattern and are considered to be carnivorous, a rare adaptation among Mesozoic mammals. Additionally, both families extensively utilize mesiodistal oriented crests, likely as an adaptation to their diet. However, the strategies to provide and maintain these crests differ. In Triconodontidae a tendency towards equal cusp height is present. This creates a cusp-valley battery that extends over the molar series and requires a high degree of precision during occlusion. The latter is possible due to the uniformity of the molar series (Jäger et al. 2019a). This is in contrast to the dentition of Gobiconodontidae that appears to sacrifice precision for bite force. Precise occlusion of cutting crests is present as well, however, unlike in Triconodontidae, this is achieved by increased amounts of wear. Gobiconodontids, therefore, show no clear tendency towards equal cusp height. The focus on one large main cusp provides longevity of the main crests and the simplicity of the system, which is necessary due to the replacement of molariforms.

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Synthesis

Occlusion and Dental Function of Morganucodonta

The OFA analysis and SEM imaging provide evidence of a single phased power stroke in *Morganucodon watsoni* that was steep but subject to considerable variation of up to +-20° towards mesial or distal. While some specimens appeared to have developed a preferred chewing direction, others utilized the complete range of variability.

It was confirmed with the OFA that cusp A in *Morganucodon* occludes between cusps a and c. Therefore, the distinction between the occlusion of *M. watsoni* and embrasure occlusion present in *Megazostrodon rudnerae* is valid. The occlusion of cusp a in *Morganucodon* was more complex than previously described. Its initial contact at the beginning of the power stroke was between two molars. In some cases, it subsequently entered the space between cusps B and A, while in others it remained between two molars.

The upper molars of *Morganucodon* differ in their orientation within the maxilla, relative to the anterior dentition, to provide space for the large lower main cusps. They were further inclined with their tips pointing towards lingual. The latter likely reduced the required roll during occlusion. This indicates that the occlusion in *Morganucodon* was more precise than previously expected. It is also supported by the OFA analysis that the teeth precise occlusion was present directly after eruption and that *Morganucodon* did not depend on wear to become fully functional. Based on this unexpected level of precision in the occlusion and tooth positioning of Morganucodonta, it would be promising for future studies to investigate earlier diverging taxa such as *Sinocondon*, *Brasilodon*, and *Brasilitherium* to determine the pre-mammaliaform condition.

The main function of the molars of *Morganucodon*, and to a lesser degree *Megazostrodon*, was piercing, as emphasized by the massive a cusps. Later during the power stroke, when the crests of the cusps pass along each other, cutting and shearing took place.

Despite similar molar morphology of *Erythrotherium* and *Morganucodon*, previously unrecognized differences justify the separation in different genera. Embrasure occlusion for *Erythrotherium* was confirmed based on the OFA analysis. This difference to *Morganucodon* is caused by cusp positioning in *Erythrotherium*, which is more similar to *Megazostrodon* and thus prevents cusp A to enter between cusps a and c.

Occlusion and Dental Function of Triconodontidae

Priacodon fruitaensis had embrasure occlusion, which is in contrast to previous studies that proposed a *Morganucodon*-like occlusion for Triconodontidae. The new interpretation is based on wear facets and a comparative OFA analysis of both occlusal modes.

Thus, all Eutriconodonta, as well as most early Mammaliaformes had embrasure occlusion.

At the beginning of the power stroke in Triconodontidae, the mesiodistally oriented crests of the lower and upper molars passed along each other, and subsequently, the lower cusps entered the valleys in between the upper cusps, while the roll of the active hemimandible kept the occlusal sides of the teeth in close contact.

The dentition of Triconodonidae differed from that of Morganucodonta in having an emphasis on long, precisely occluding cutting edges rather than the piercing capabilities of high cusps. The cutting edges were oriented mesio-distally, similarly to modern Carnivora. However, the zig-zag pattern provided bucco-lingual extension, a trait found in extant insectivorous taxa. The cusps of the lower molars maintained pointy tips and sharp edges for most of their lifetime because they were able to sharpen themselves against the confined valleys of the upper molars.

Within Triconodontidae, molar morphology changed little from the Late Jurassic till Late Cretaceous, with the exception of a tendency to increase the amount of available cutting edges. The slow and gradual change could be due to constraints presented by the highly precise occlusion of the uniform tooth battery.

An inclination of the upper molar series towards lingual, similar to the one observed in *Morganucodon*, was present in Gobiconodontidae and Triconodontidae. Especially in case of the latter, this provided a better crest alignment and reduced the amount of roll required during the power stroke to approximately 10°, less than assumed in previous studies.

Tooth replacement in Triconodontidae was sequential, which is in accordance with its phylogenetic position as basal crown-group Mammalia.

A new species *Triconodon averianovi* has been assigned based on the partially reduced m4, its small p4, and gracile canine. This study once again highlights the problems of species and genera assignment in Triconodontidae that exist due to their uniform molar morphology.

Occlusion and Dental Function of Gobiconodontidae

Embrasure occlusion for Gobiconodontidae was confirmed based on the OFA analysis. Their dentition differs from that of Triconodontidae by emphasizing a large main cusp rather than equal cusp height. Wear resulted in a quick loss of the b/B and c/C cusps and in large bucco-lingually oriented crests.

During the power stroke, after the main crests passed another, the lower molars moved lingually, guided by grooves on the posterior parts of the upper molars. Subsequently, the crests of the lower molars passed along the lingually placed E and X cusps and a small crest formed by E.

Comparison of the Dental Function of Morganucodonta, Gobiconodontidae, and Triconodontidae

- Based on the results of the OFA analyses presented in this study, it is apparent that embrasure occlusion was present in Eutriconodonta and many Morganucodonta, while *Morganucodon*-like occlusion was limited to few taxa. It, therefore, appears likely, that this type of occlusion was a derived condition, modified from embrasure occlusion.
- The triconodont molar pattern further differed in morphology and function between Morganucodonta, Triconodontidae and Gobiconodontidae. In the insectivorous Morganucodonta, the primary molar function was piercing with an emphasis on large main cusps, while the alignment of cutting crests was less pronounced.
- Gobiconodontidae maintained the large a/A cusps but formed mesio-distally oriented cutting edges at the expense of the smaller cusps that were well adapted for a carnivorous diet, but relied heavily on tooth wear.
- The dentition of Gobiconodontidae and Morganucodonta is in contrast to that of Triconodontidae, which is characterized by highly precise uniform cusp batteries with elongated cutting edges that combine traits of carnivorous and insectivorous diets. However, the uniform triconodontid molar batteries likely were subject to greater constraints, thus limiting all members of the family to highly similar molar morphologies. For comparison, molariforms of Morganucodonta and Gobiconodontidae had a more heterogenous cusp morphology, with large main and small accessory cusps and were subject to greater morphological change.

- Despite these differences, all taxa with preserved maxillae observed in this study, showed an inclination of their upper molars towards lingual. This was likely to minimize the roll required to keep the teeth in close contact and improve crest alignment.

Appendix

7.1 Specimens figured in this study

Specimen number	Taxon	Order	Age
NHMUK PV M 26407	*Megazostrodon rudnerae*	Morganucodonta	Early Jurassic
UMZC Eo.CR.1	*Morganucodon watsoni*	Morganucodonta	Early Jurassic
NHMUK PVM 100304	*Morganucodon watsoni*	Morganucodonta	Early Jurassic
NHMUK PVM 100308	*Morganucodon watsoni*	Morganucodonta	Early Jurassic
UMZC Eo.M(Lr).16	*Morganucodon watsoni*	Morganucodonta	Early Jurassic
UMZC Eo.M(Ur).5	*Morganucodon watsoni*	Morganucodonta	Early Jurassic
UMZC Eo.M(Lr).32	*Morganucodon watsoni*	Morganucodonta	Early Jurassic
AMNH 93800	*Morganucodon watsoni*	Morganucodonta	Early Jurassic
SAM-PK-K00359	*Erythrotherium parringtoni*	Morganucodonta	Early Jurassic
NHMUK PV OR 47763	*Triconodon mordax*	Eutriconodonta	Early Cretaceous
NHMUK PV OR 47764	*Triconodon mordax*	Eutriconodonta	Early Cretaceous
NHMUK PV OR 47768	*Triconodon mordax*	Eutriconodonta	Early Cretaceous
NHMUK PV OR 48395	*Triconodon averianovi* sp. nov.	Eutriconodonta	Early Cretaceous
LACM 120451	*Priacodon fruitaensis*	Eutriconodonta	Late Jursassic
SMP SMU 61759	*Astroconodon denisoni*	Eutriconodonta	Early Cretaceous
USNM 491129	*Arundelconodon hottoni*	Eutriconodonta	Early Cretaceous
USGS 13634	*Cantius*	Primates	Early Eocene
MCZ 19850	Undescribed	Eutriconodonta Family: Triconodontidae	Early Cretaceous
M130712C	Undescribed	Eutriconodonta Family: Gobiconodontidae	Early Cretaceous
M 19143	*Kuehneotherium praecursoris*	Family: Kuehneotheriidae	Late Triassic- Early Jurassic
PM TGU 16/6-410	*Gobiconodon* sp.	Eutriconodonta	Early Cretaceous

7.2 OFA files used for this study are accessible via DOI: 10.22000/374. To use the .ofa-project files, the OFA Software and the user manual can be downloaded at: https://www.ifgeo.uni-bonn.de/abteilungen/palaeontologie/arbeitsgruppen/vertebraten/ehemalige-forschergruppen/for-771/ofa/download

File name	Specimen used	Taxon	Chapter	Figure
1 UMZC Eo CR 1	UMZC Eo.CR.1	*Morganucodon watsoni*	2	2.6
2 UMZC Eo Cr 1 striations	UMZC Eo.CR.1	*Morganucodon watsoni*	2	2.6
3 NHMUK PV M 26407	NHMUK PV M 26407	*Megazostrodon rudnerae*	2	2.7
4 SAM-PK-K00359 embrasure	SAM-PK-K00359	*Erythrotherium parringtoni*	3	3.3
5 SAM-PK-K00359 morganucodonlike	SAM-PK-K00359	*Erythrotherium parringtoni*	3	3.3
6 LACM_120451 m3	LACM 120451	*Priacodon fruitaensis*	5	5.8
7 LACM_120451 toothrow embrasure	LACM 120451	*Priacodon fruitaensis*	5	5.6 and 5.7
8 LACM_120451 toothrow morganucodonlike	LACM 120451	*Priacodon fruitaensis*	5	5.6 and 5.7
9 M 130712C	PM TGU 16/6-410	*Gobiconodon* sp.	6	6.3