

TOOTH ERUPTION IN THE EARLY CRETACEOUS BRITISH MAMMAL *TRICONODON* AND DESCRIPTION OF A NEW SPECIES

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Abstract: *Triconodon mordax*, from the lowest Cretaceous (Berriasian) part of the Purbeck Group, Dorset, is known by an ontogenetic series of specimens that document aspects of tooth eruption and replacement. Based on micro-computed tomography of four specimens we refer one mandible 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. *T. mordax* is variable in the number of mental foramina and posterior jaw morphology. Scans reveal an earlier developmental stage (p3 in early eruption) than previously recognized for *Triconodon*, and demonstrate sequential, anteroposterior replacement of premolars;

it remains unclear whether p1–2 were replaced. Scans also support an earlier hypothesis that m4 erupted late in life. Onset of m4 mineralization is likely to have 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. It remained in position and was subsequently accommodated in the active tooth row through unusually prolonged and localized growth of the posterior part of the mandible. This pattern is seen in some later triconodontids and appears to be unique to the family.

Key words: Eutriconodonta, eruption sequence, determinate growth, Cretaceous, *Triconodon*, tooth.

THE majority of extant mammals rely on the dentition to masticate the food in the mouth cavity for easier, more efficient, and complete digestion (Ungar 2010). Many different types of heterodont dentitions evolved independently in different clades, emphasizing various functional specializations (Thenius 1989). Despite the morphological and functional differences, a key character of most mammalian dentitions is a precise fit during occlusion (Ungar 2010). In turn, precise occlusion is related to other mammalian traits, notably multi-cusped teeth, reduction of tooth replacement (diphyodonty), and non-replacement of posterior teeth cheek (molars; e.g. Luo *et al.* 2004; Martin 2018).

The sequence of tooth replacement shows some degree of homoplasy during mammalian evolution. The ancestral mode of replacement in non-mammalian synapsids is an alternating one, where every second or every third tooth position was replaced (Luo *et al.* 2004). Most non-mammalian Mammaliaformes such as *Morganucodon* already 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 into molars, the more posteriorly situated teeth, which by definition are not replaced (see discussion in Jenkins & Schaff 1988). Additionally, the replacement pattern changed to a sequential pattern (e.g. p1 → p2 → p3 → p4 → p5) in Mammaliaformes. Sequential replacement is also considered as the plesiomorphic condition of crown Mammalia (Luo *et al.* 2004). 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 probably plesiomorphic for eutherians (Luo & Ji 2005). Extant

marsupials, and certain fossil metatherians (e.g. *Deltatheridium*), have limited their postnatal dental replacement to p3, which has been considered an adaptation to their elongated lactation period (Luckett 1993; Cifelli *et al.* 1996; Rougier *et al.* 1998). More recently, van Nievelt & 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 & Schaff 1988; Kielan-Jaworowska & 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 & Schaff 1988; Lopatin & Averianov 2014; Martin *et al.* 2015).

Eutriconodonta are a monophyletic taxon of non-trechnoterian crown Mammalia (Kielan-Jaworowska *et al.* 2004). They are of special interest due to their phylogenetic position and because they include early mammalian essays in carnivory (Simpson 1933; Jenkins & Crompton 1979). The core family, Triconodontidae, is best known from the Jurassic to the earliest Cretaceous but survived well into the Late Cretaceous (Fox 1969). Triconodontids have a diphyodont mode of tooth replacement and exhibit a modified version of the plesiomorphic triconodont pattern, wherein molars are dominated by a cusp A/a that extends well beyond the accessory cusps B/b and C/c (Fig. 1). 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 & Madsen 1998; Cifelli *et al.* 1998). However, the molar morphology within Triconodontidae is highly similar, which complicates their identification (Kielan-Jaworowska *et al.* 2004).

Taxonomy of *Triconodon*

To avoid imprecise terminology (such as ‘basal’ or ‘primitive’) when discussing the phylogenetic position of taxa, we use the term ‘stem lineage representative’ (e.g. Wägele

2005), when referring to a taxon that shows many plesiomorphic characters compared with a large sister taxon.

Owen (1859) first described *Triconodon mordax* in the chapter on palaeontology he provided for the eighth 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 an 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 listed the only specimen as ‘*Triconodon*, sp. ind.’, while in the following text he opined that it probably represents a distinct species. The only mention of *T. minor* by name is in the legend accompanying plate 4, 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.

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 group has turned out to be paraphyletic, with either *Trioracodon* or *Priacodon* being a sister taxon to all other Triconodontidae (Gaetano & Rougier 2011; Martin *et al.* 2015). However, the morphological distinction between these three genera (and most other 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

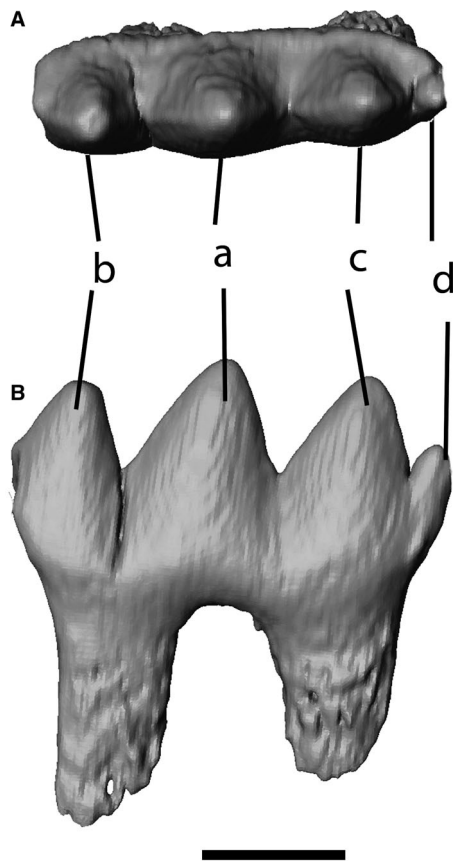


FIG. 1. Cusp terminology in Triconodontidae. The centre cusp, a, is the largest, followed by c and b. The height difference of these main cusps is minor in Triconodontidae compared with other taxa with triconodont molars such as Morganucodonta and Gobiconodonta, in which a is noticeably larger than b and c. The small cusp d interlocks with a tongue-and-groove system on the mesial side of the next posterior molar. Left m2 of *Triconodon mordax* (NHMUK PV OR 47764). A, occlusal view. B, buccal view. Mesial is to the left. Scale bar represents 1 mm.

four lower premolars and three molars (Simpson 1928). The latter can further be distinguished from *Triconodon* by the 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 used as a character to distinguish *Priacodon* from *Triconodon* and *Trioracodon* (Engelmann & 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 many Triconodontidae.

For this study, we follow the phylogenetic consensus that *Triconodon* is a stem lineage representative of most other members of Triconodontidae (e.g. Kielan-Jaworowska *et al.* 2004; Gaetano & Rougier 2011; Martin *et al.* 2015), with the exception of *Trioracodon* and possibly *Priacodon*. We use the paraphyletic name ‘Triconodontinae’ in a descriptive way, when referring to these genera that share many plesiomorphic characters, when compared with other members of Triconodontidae (Fig. 2).

Previous work on dental replacement and tooth eruption in Triconodon

Dental formula of *Triconodon mordax* ?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 NHMUK except for GSM 48746, referred to as the ‘Willett specimen’, which is in the collection of the British Geological Survey. This specimen, first described by Willett & 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 & 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, NHMUK PV OR 47763, 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 (Fig. 3). Because of the limited amount of wear on the other premolars, he concluded that p4 was the last premolar position to be replaced, occurring approximately at the time of replacement of the canine and before the eruption of the last molar. While there is evidence for an anterior → posterior replacement pattern, it remained unclear if the replacement pattern was

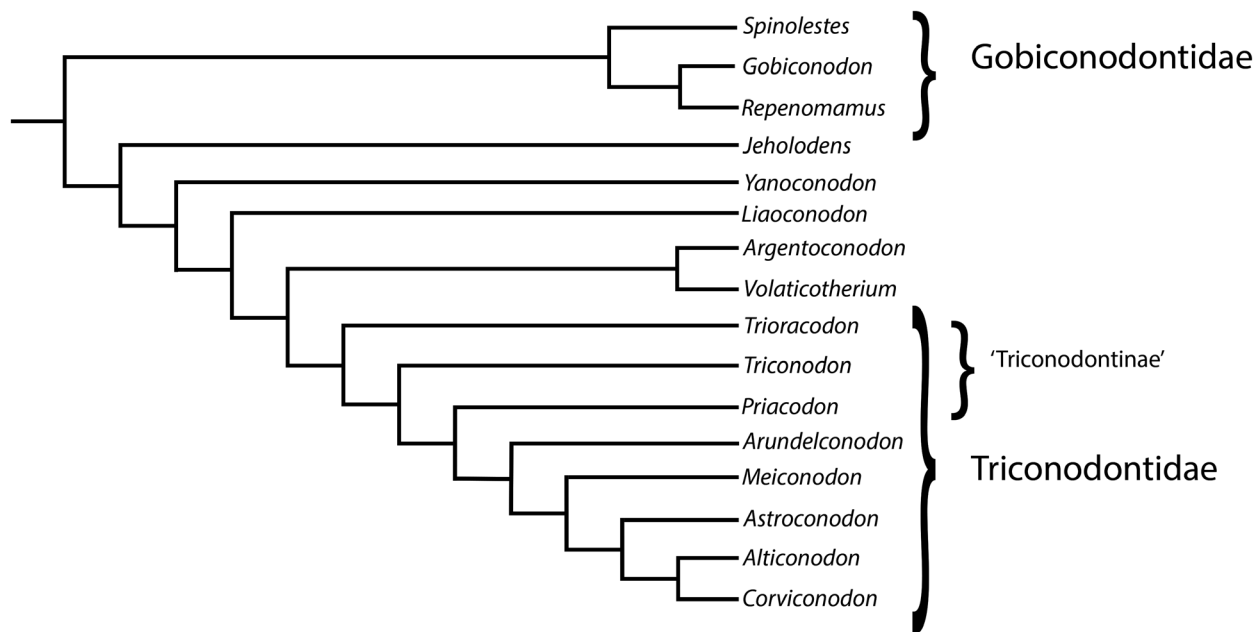


FIG. 2. Phylogeny of Eutriconodonta after Martin *et al.* (2015). While ‘Triconodontinae’ are probably a paraphyletic group (but see Cifelli & Madsen 1998), they do have highly similar molar morphologies. They also share a lot of (likely) plesiomorphic characters compared with other Triconodontidae, such as fewer molars (three and four) and small d cusps.

sequential or alternating. Although several new taxa of Triconodontidae have been described in recent years, major hypotheses on their tooth eruption and replacement date well back into the 20th century and have not been put to test since (e.g. Simpson 1928). We re-examined *Triconodon* using micro-computed tomography (μ CT) and address Simpson’s hypothesis on sequential premolar replacement and investigate tooth eruption, morphology, and taxonomy.

Institutional abbreviations. BM(NH), Natural History Museum, London, UK (specimens listed by earlier workers; Simpson 1928 and references therein); FMNH, Field Museum of Natural History, Chicago, Illinois, USA; GSM, British Geological Survey, Keyworth, UK; IVPP, Institute of Vertebrate Paleontology & Paleoanthropology, Beijing, China; NHMUK, Natural History Museum, London, UK. *Triconodon* specimens in the NHMUK bear two additional prefixes: PV (Palaeontology, Vertebrates) and OR (Old Register).

MATERIAL AND METHOD

The fossils were scanned using μ CT (Cifelli *et al.* 2020). The scans were performed with the Nikon Metrology HMX ST 225 scanner at the Natural History Museum, London. 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 (Fig. 4) is a left mandible with dentition, which is complete except for the incisors, p1, and p3. NHMUK PV OR 47763 (Fig. 3) 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 mandible in two pieces broken at the position of m3 (missing) and preserved on two slabs. The anterior part of the mandible 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 (Thomas 1887). 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 mandible, some associated cranial elements are preserved (Simpson 1928).

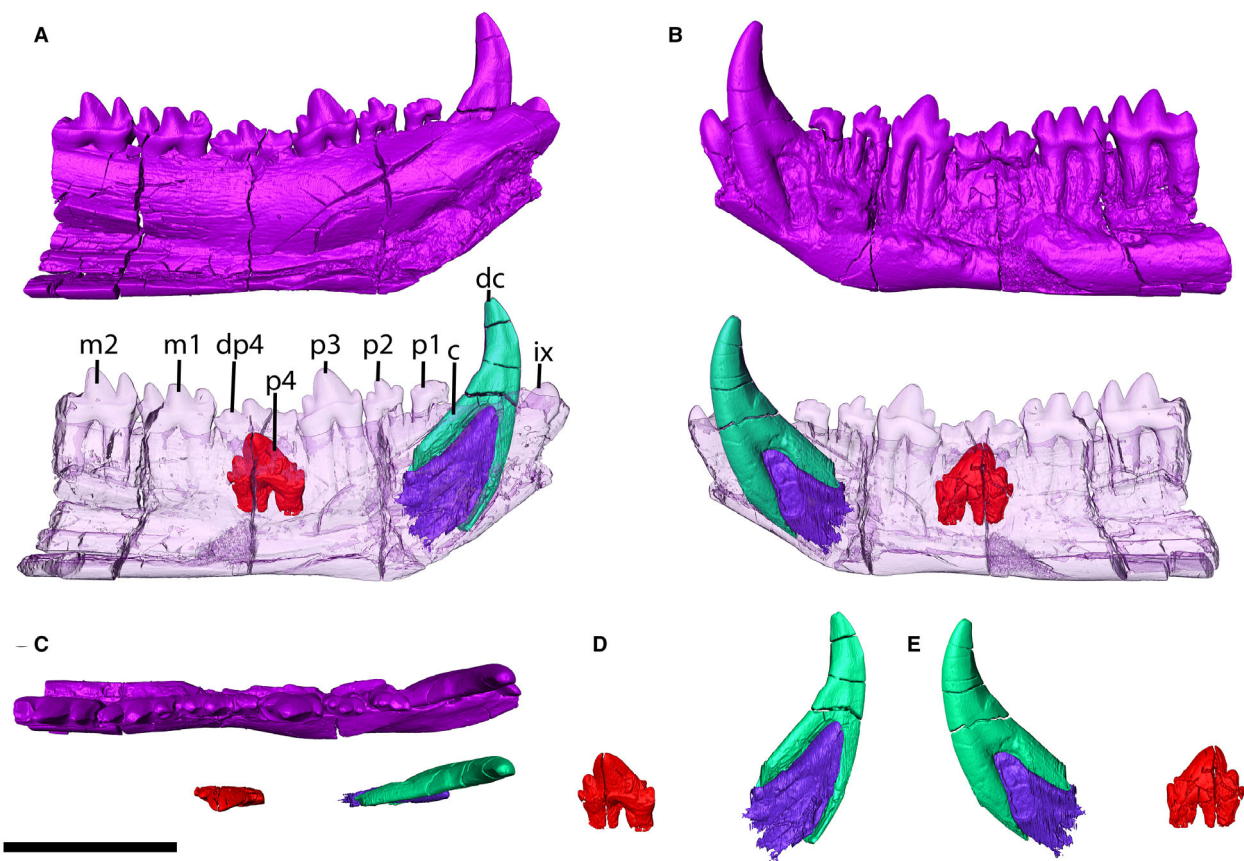


FIG. 3. Left anterior ramus of *Triconodon mordax* (NHMUK PV OR 47763). A, medial; B, lateral; C, occlusal view (anterior to the right). D–E, erupting p4 and canine in: D, lingual; E, buccal view. Scale bar represents 5 mm.

NHMUK PV OR 47768 (Fig. 5) is a fragmentary right mandible with three teeth visible: an erupting p3 and a molariform dp4, followed by the fragments of m1. Additionally, the roots of p1 and p2 and the dc(?) are present.

NHMUK PV OR 48395 (Fig. 6) was previously assigned to *Triconodon mordax* (Simpson 1928). It consists of a substantially complete left mandible and a fragmentary right mandible, as well as associated teeth

TABLE 1. Information on specimens scanned for this study.

Specimen number	Species	Elements	Locality	Scan resolution (mm)	Notes
PV OR 47763	<i>Triconodon mordax</i>	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 preserved only as an imprint of its buccal side. The a cusp of m4 is damaged.
PV OR 47764	<i>Triconodon mordax</i>	Left ramus:c, p2, p4, m1–4	Durlston Bay	0.0184	Holotype <i>T. mordax</i>
PV OR 47768	<i>Triconodon mordax</i>	Right ramus:p3, dp4, p4, m1	Durlston Bay	0.0147	
PV OR 48395	<i>Triconodon averianovi</i> sp. nov.	Left ramus:c, p1, p4, m1–4Right ramus: c, m1–3	Durlston Bay	0.0219	Holotype <i>T. averianovi</i> . An isolated premolar is probably the left p1 and an isolated canine belongs to the right ramus.

All specimens are in the NHMUK.

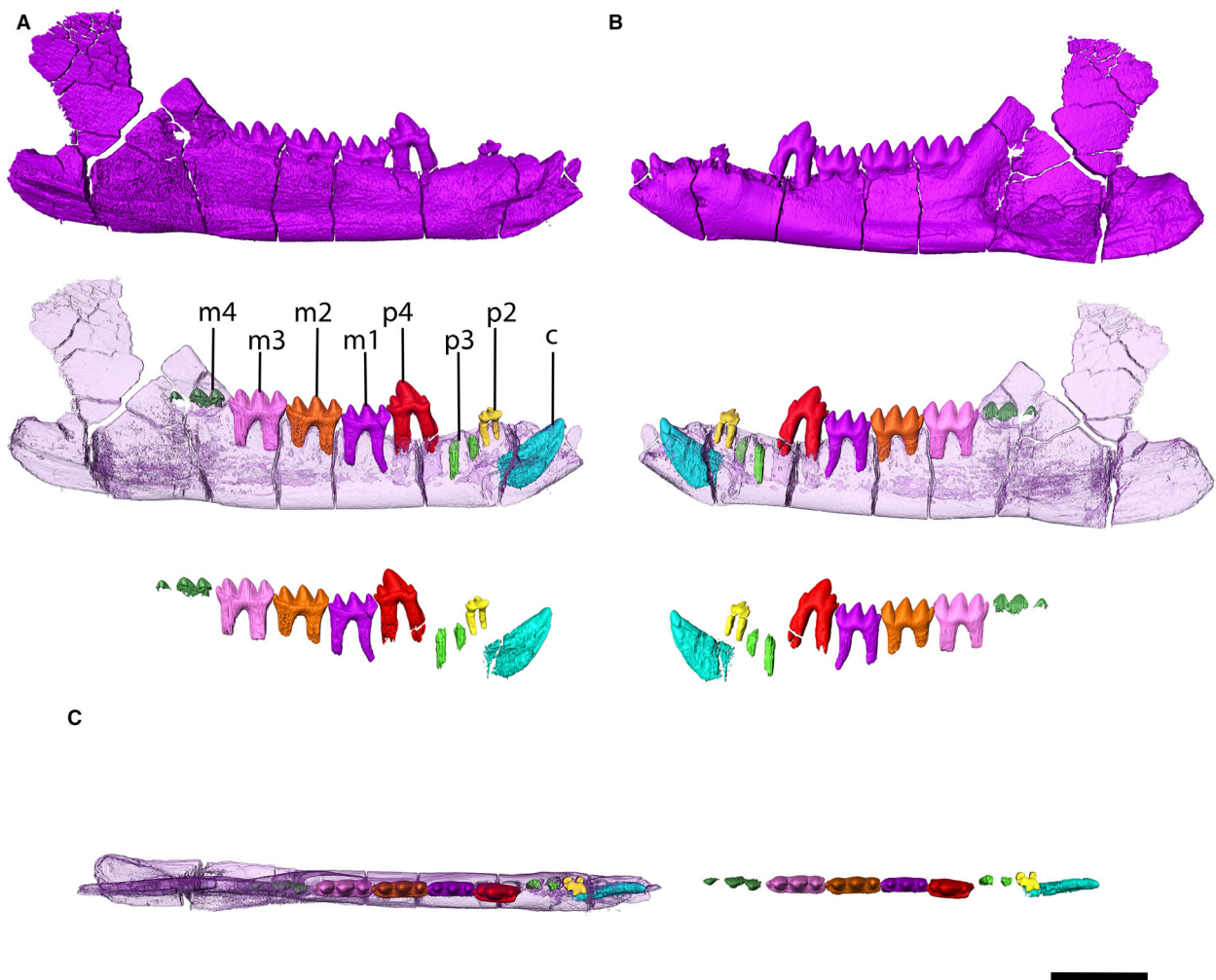


FIG. 4. Left ramus, holotype of *Triconodon mordax* (NHMUK PV OR 47764). A, medial; B, lateral; C, occlusal view (anterior to the right). Scale bar represents 5 mm.

(Figs 6, 7). For a detailed description of this specimen see below.

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

SYSTEMATIC PALAEOLOGY

Class MAMMALIA Linnaeus, 1758
 Order EUTRICONODONTA Kermack *et al.*, 1973
 Family TRICONODONTIDAE Marsh, 1887

Genus TRICONODON Owen, 1859
Triconodon averianovi sp. nov.
 Figures 6, 7, 8E–F

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

LSID. urn:lsid:zoobank.org:act:A73591DA-3D1F-4861-AEFF-6D58B95EEA01

Derivation of name. The species is named after Alexander O. Averianov, in recognition of his substantial contributions 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 (Table 2) with only

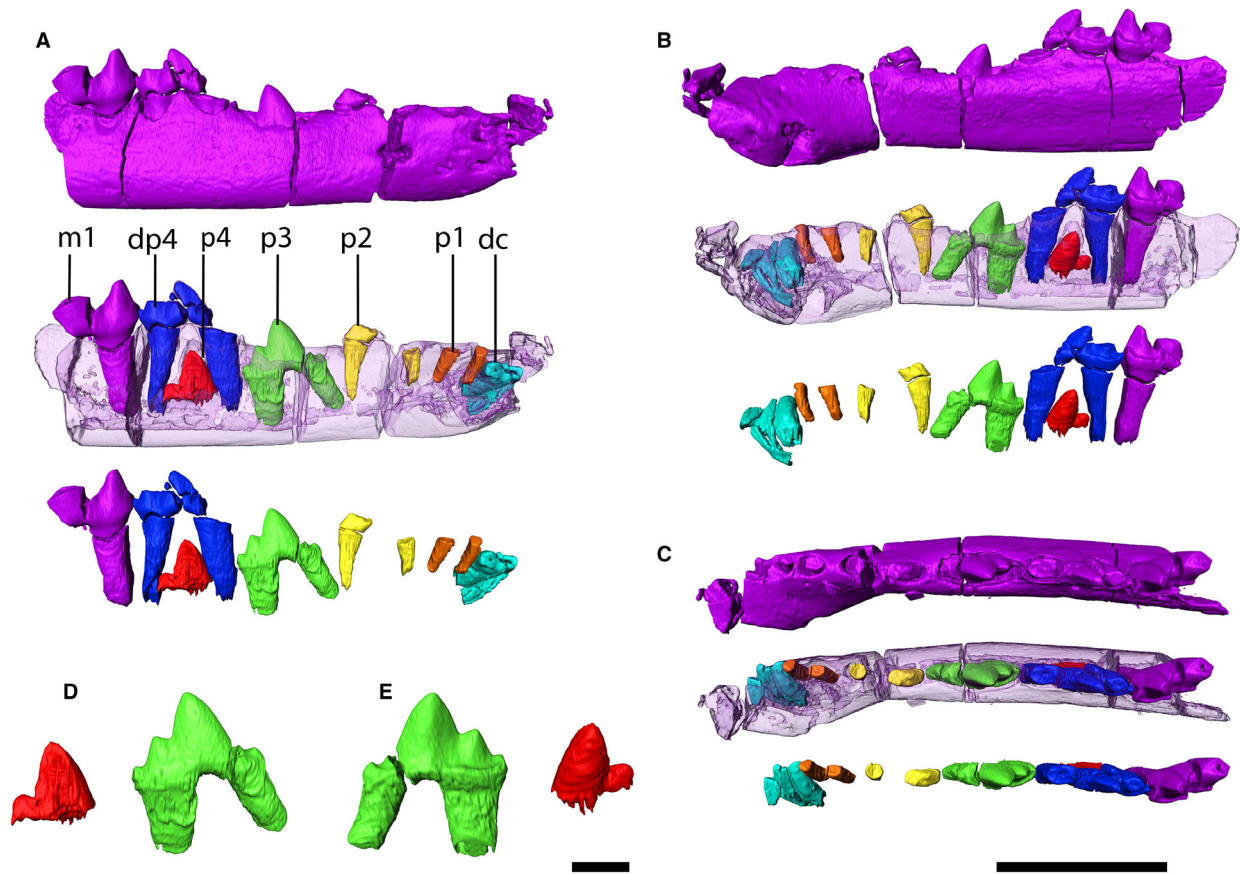


FIG. 5. Fragmentary right ramus of *Triconodon mordax*(?) (NHMUK PV OR 47768). A, lateral; B, medial; C, occlusal view (anterior to the left). D–E, enlarged erupting p3 and forming p4 in: D, buccal; E, lingual view. Scale bars represent: 5 mm (A–C); 1 mm (D, E).

cusps a and c are reduced. *T. averianovi* differs from *Arun-delconodon* 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 ‘Triconodontinae’. 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. NHMUK PV OR 48395 further differs from specimens referred to *T. mordax* by its shallower ramus. NHMUK 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.

Description

Material of NHMUK 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, pl. 5, fig. 3). The right ramus contains m1–m3 and the roots of p4 and of m4 (Fig. 7). 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 p2 and p3 are preserved (Fig. 6). 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. Judging by its crown morphology it is probably the missing p1. Its roots appear widely separated, a character usually associated with deciduous teeth. A deciduous tooth is unlikely to

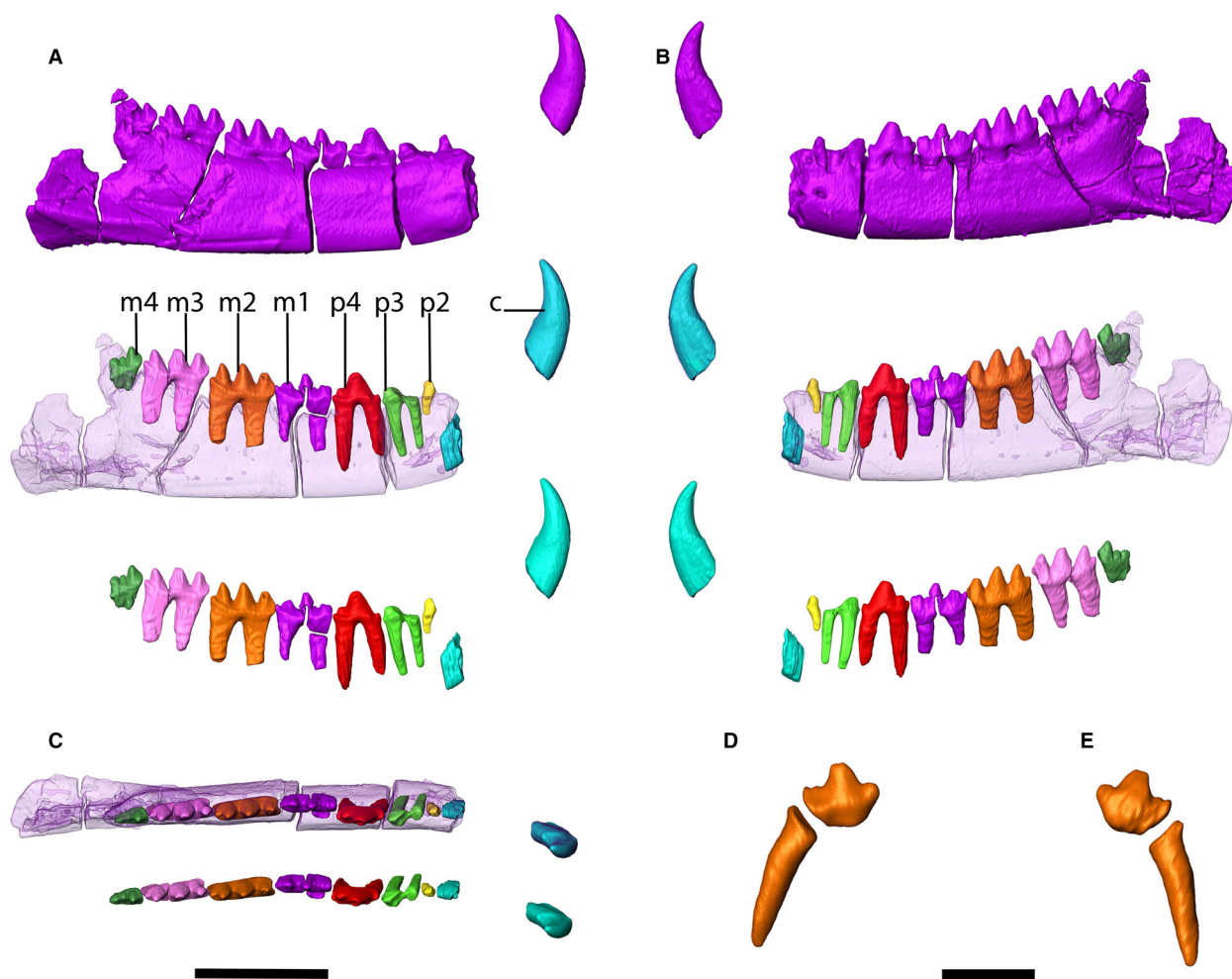


FIG. 6. Left ramus of *Triconodon averianovi* (NHMUK PV OR 48395). A, medial; B, lateral; C, occlusal view (anterior to the right). D, isolated p1 medial view. E, isolated p1 lateral view. Scale bars represent: 5 mm (A–C); 1 mm (D, E).

belong 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 consider it likely to be the permanent p1. No incisors are preserved.

Molars. Based on size (Table 2) and tooth count, NHMUK PV OR 48395 can be attributed to the genus *Triconodon*. *Triaracodon* 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 ‘Triconodontinae’, 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 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 & Madsen 1998; Cifelli *et al.* 1998); and similarly in *Priacodon frutaensis*, in which cusps a and c of m4 are reduced (Rasmussen & 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, given that NHMUK PV OR 48395 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. NHMUK PV OR

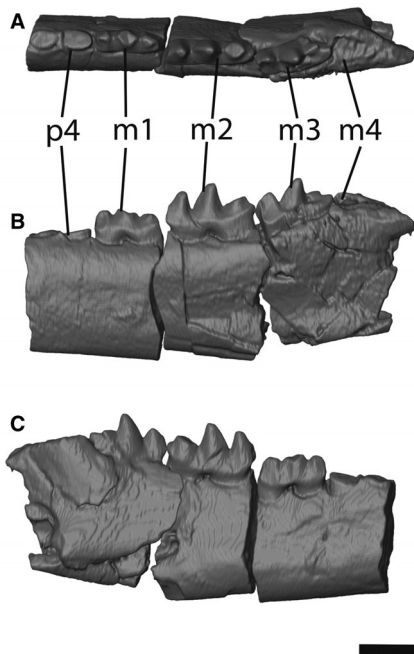


FIG. 7. Fragmentary right ramus of *Triconodon averianovi* (NHMUK PV OR 48395). A, occlusal view (anterior to the left); B, medial; C, lateral view. The crypt of m4 is preserved, providing information on its small size and its position within the ascending ramus. Scale bar represents 2.5 mm.

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 linguobuccally 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. 6D, E) but its crown is smaller and slenderer than that of NHMUK PV OR 47763 (*T. mordax*). It appears to have wear on most of its buccal side, while p1 of NHMUK PV OR 47763 (*T. mordax*) has one large mesial facet, most probably 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 NHMUK PV OR 48395 is only slightly taller than the adjacent m1, which differs from all other ‘Triconodontinae’, 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.

Canine. 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 probably single-rooted based on the incomplete erupting canines and comparison with *Trioracodon* (Fig. 9). The canine of *T. averianovi* is most likely to be 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 stage 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. 9).

Dentary. The jaw is gracile and shallower than that of *T. mordax*, although this difference is subtle (Figs 6, 8).

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).

LATE-STAGE ONTOGENY OF THE DENTITION IN *TRICONODON*

Tooth replacement pattern

The teeth of NHMUK PV OR 47768 have been interpreted as erupting p4, followed by the damaged m1 and m2 (Owen 1871; Simpson 1928). The μ Ct analysis revealed the cap of the main cusp of an erupting tooth below the supposed m1 (Fig. 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 NHMUK PV OR 47763 (Simpson 1928, fig. 24A), but it has more strongly diverging roots than the others. This probably is due to the ontogenetic stage of p4, because in NHMUK PV OR 47763 it is in the process of eruption, whereas in NHMUK 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. 5).

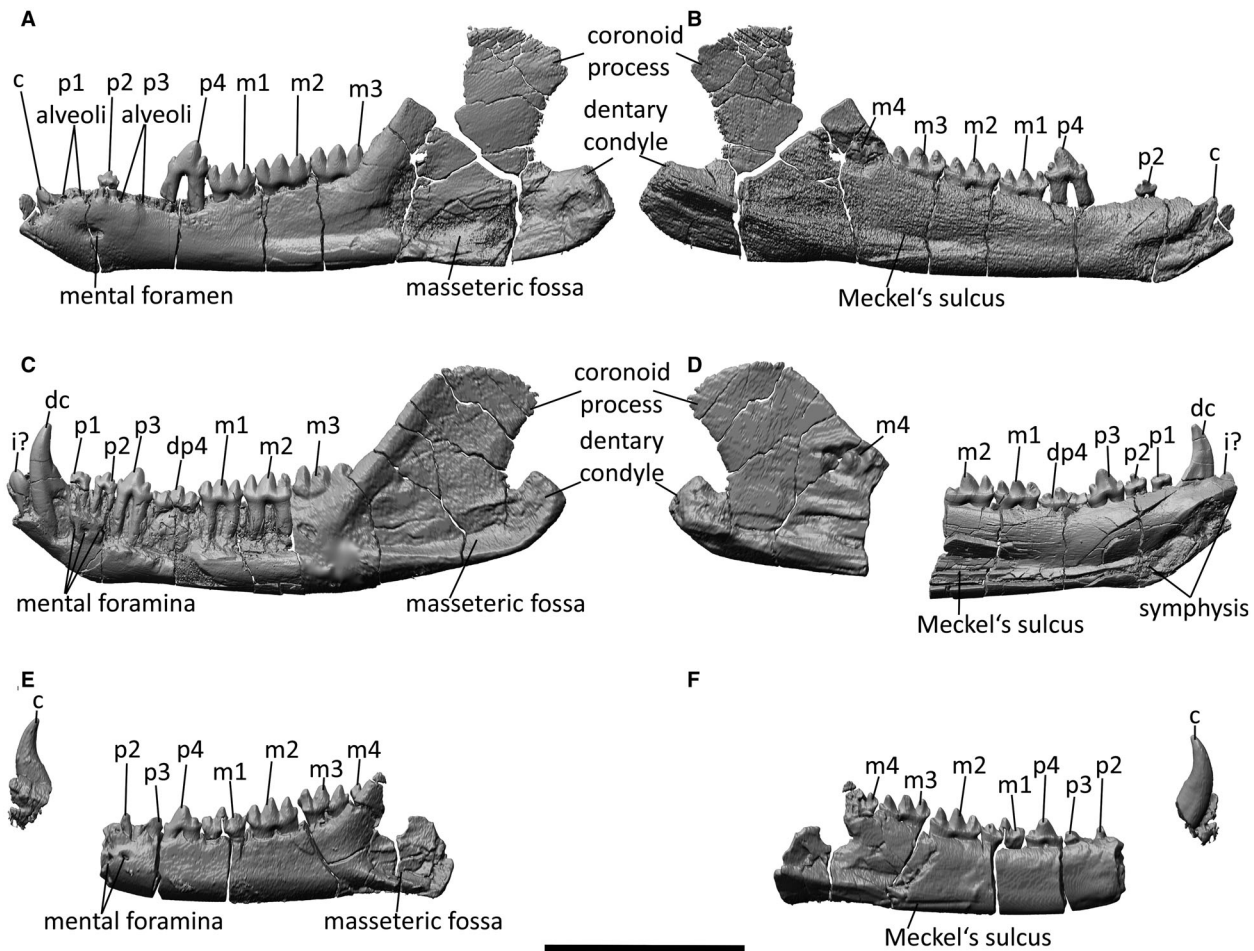


FIG. 8. Comparison of the dental rami of *Triconodon mordax* and *Triconodon averianovi*. A–B, holotype of *T. mordax* NHMUK PV OR 47764: A, lateral; B, medial view. C–D, *T. mordax* NHMUK PV OR 47763: C, lateral; D, medial view; this specimen was reconstructed based on the anterior part, which extends to 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* NHMUK PV OR 48395: E, lateral; D, medial view. Scale bar represents 10 mm.

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 Mammalia, which suggests that a sequential tooth replacement evolved within early Mammaliaformes (Luo *et al.* 2004). Within Eutriconodonta, sequential replacement is known for Gobiconodontidae (Jenkins & Schaff 1988). The new results and the phylogenetic position of *Triconodon* as a stem lineage representative of most other Triconodontidae except *Trioracodon* (and potentially *Priacodon*, depending on the phylogeny used) suggest that an anterior-to-posterior sequential premolar replacement condition is plesiomorphic for this family and probably 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 NHMUK PV OR 47763, that they might have been replaced before the eruption of p4. According to our re-examination of the specimen, this small amount of wear can be confirmed only for p2 and p3, while p1 shows a large anterior wear facet, probably caused by the upper canine. However, the presence or absence of wear on the small anterior premolars provides only limited evidence regarding the replacement. If there was no contact to the upper antagonists, the first premolar generation could have remained unworn for a long time. In contrast, a replaced premolar having a large antagonist (e.g. the canine) might show a large wear facet shortly after eruption. Given that

TABLE 2. Length measurements of the *Triconodon* dentition (mm).

Specimen number (NHMUK)	Species	p1	p2	p3	dp4	p4	m1	m2	m3	m4†
PV OR 47764	<i>T. mordax</i>	–	1.2	–	–	2.2	2.5	2.9	3	2.9†
PV OR 47763	<i>T. mordax</i>	1.0	1.2	1.8	2.3	2.3	2.2	–	3‡	3†
PV OR 47768	<i>T. mordax</i>	–	–	2.2	–	–	–	–	–	–
PV OR 48395	<i>T. averianovi</i> sp. nov.	0.9	–	–	–	1.8	2.2	2.4	2.5	1.2†

– Not present or too damaged to be measured.

†m4 is not fully formed in all specimens; length might be slightly underrepresented.

‡Tooth not preserved; measurements taken from the negative imprint.

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.

Ultimate molar locus

Simpson (1928) assumed that the fourth molar of *Triconodon* erupted late in life given that 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 μ CT data confirm this suggestion for the holotype of *T. mordax*, NHMUK PV OR 47764

(Figs 4, 8B). Based on the new data from NHMUK 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 (Fig. 8). The formation of the last molar in a crypt within the ascending ramus and above the active tooth row is apparently a common character found in various members of the Triconodontidae, some having multiple molars being formed in the ascending ramus, and unique for the family (for a similar, although different condition seen in various mammalian clades see below). A specimen of *Astroconodon* (FMNH PM 588) has been described with m4 partially and m5 completely hidden in the ascending ramus (Turnbull & 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

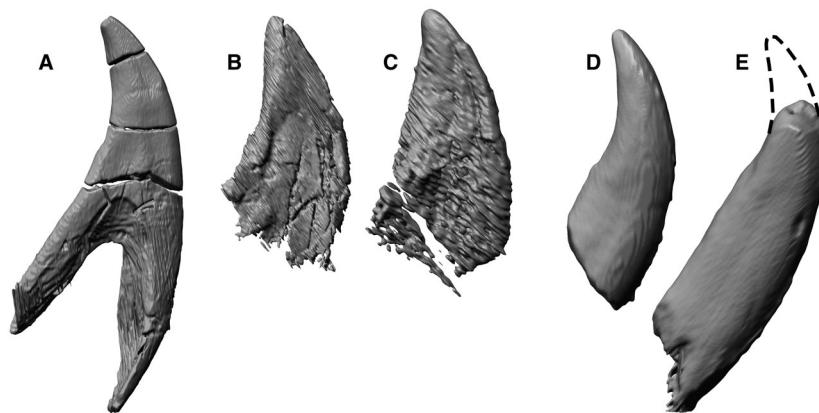


FIG. 9. Canine comparison of *Triconodon mordax* and *Triconodon averianovi*. A, left deciduous canine of NHMUK PV OR 47763. B, erupting left canine underneath the deciduous one of NHMUK PV OR 47763. C, erupting left canine of NHMUK PV OR 47764. D, left canine of NHMUK PV OR 48395 of *T. averianovi*. E, right canine of *T. averianovi*. The presence of a single root, the absence of a replacement and the ontogenetic stage are clear evidence for the canines of *T. averianovi* being permanent ones. However, their slender shape and curvature make them similar to 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. Given that no fully formed permanent canine of *T. mordax* is known, it remains unclear whether the canine was single or double rooted.

been described for *Meiconodon* (Kusuhashi *et al.* 2009). Similar to *Corviconodon* and *Astroconodon* the last lower molar (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.

The earliest representatives of Triconodontidae the ‘Triconodontinae’ (Fig. 2) 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 NHMUK 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 above the active tooth row 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 tumours 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.

A similar condition that differs in a key aspect from the formation of the posterior molars in Triconodontidae is found in multiple mammal clades (e.g. docodontans, multituberculates, artiodactyls, proboscideans, hyracoideans and sirenians; Beatty *et al.* 2012; Sallam *et al.* 2016; Asher *et al.* 2017; Sanders 2017; Schultz *et al.* 2017). In all of these taxa, molars are formed far posterior in the jaw and in some cases are partially hidden by the coronoid after eruption. However, as far as we are aware in no other taxon, except Triconodontidae, the molar formed within the coronoid above the active tooth row (Fig. 8B, D, F). Simpson (1928, p. 74) also noted one specimen of the non-eutriconodont mammal *Phascolotherium bucklandi* (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*, in which the most posterior molar formed underneath and erupted adjacent to the ascending ramus (Schultz *et al.* 2017), than to *Triconodon*. *Phascolotherium* has previously been placed in Eutriconodonta (Kielan-Jaworowska *et al.* 2004), but recent phylogenetic analyses place it outside of Eutriconodonta (Gaetano & Rougier 2011; Martin *et al.* 2015).

Ultimate molar eruption

Apart from the unusual placement in a crypt within the coronoid, the m4 develops regularly, with mineralization starting at the apices of the main cusps as described in Lockett (1993) for other mammals. At a later stage when the crown is formed, but the roots are not yet developed, most of the tooth is still hidden by the ascending ramus, but cusp b becomes visible in buccal view (Fig. 8E). 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 & Hayek 1984; Sanson 1989; Gomes Rodrigues *et al.* 2012;

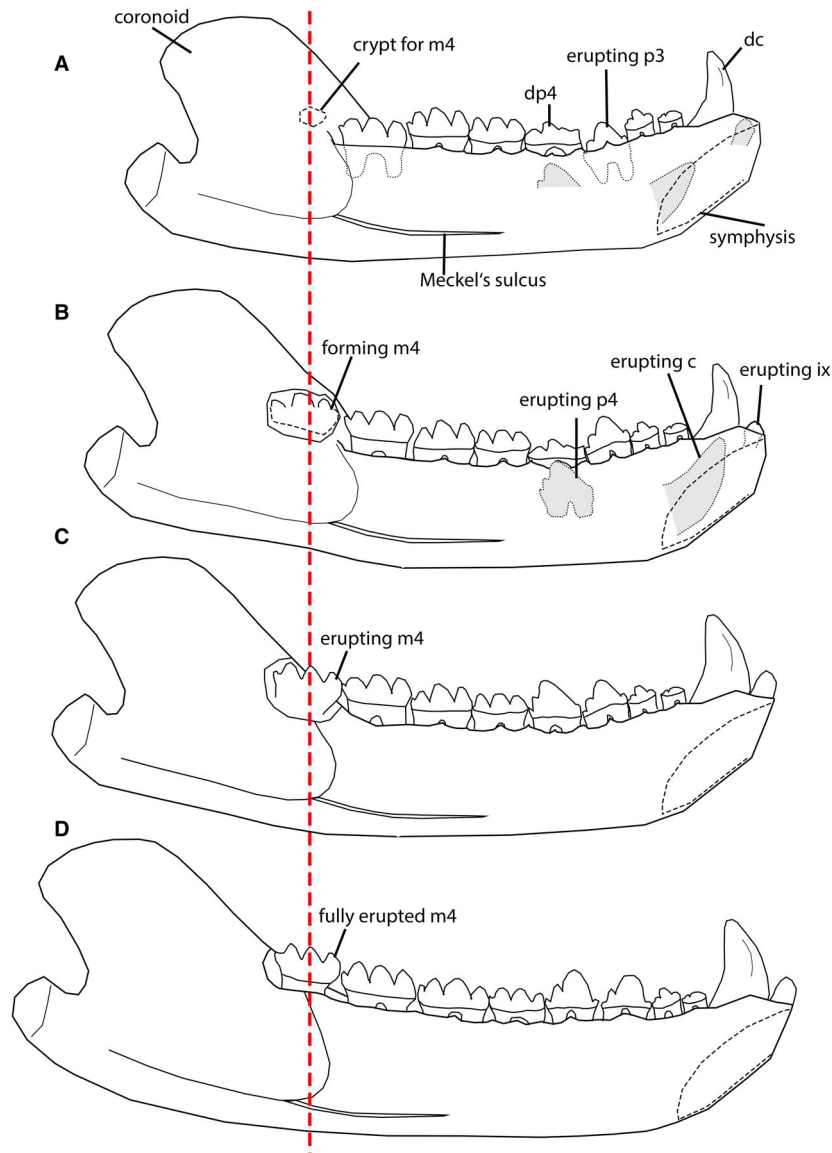


FIG. 10. Medial view of hypothetical late ontogenetic eruption stages of *Triconodon*, based on information obtained from NHMUK PV OR 47763, PV OR 47764, PV OR 47768, PV OR 48395, and the Willett specimen. The inclusion of the stage observed for NHMUK PV OR 48395 is based on the assumption that the condition observed for *T. averianovi* (NHMUK 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. Colour online.

Sanders 2017). However, this was probably not the case for *Triconodon*. Given that m4 is formed closely posterior to m3, all teeth would have to move mesially to create space. This would require a diastema that could be filled or shedding of anterior teeth in order to create the necessary space; neither is known 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 in addition to bone remodelling. Therefore, major active tooth movement, as seen for example in macropodoid kangaroos, is unlikely for *Triconodon* and we suggest that the change in position was primarily caused by mandibular growth. However, minor tooth movement to use the space created by localized mandibular growth, probably occurred. 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 several other clades with posterior erupting molars such as multituberculates, the docodontan *Docodon*, and some artiodactyls (Greenwald 1988; Sallam *et al.* 2016; Schultz *et al.* 2017). In multituberculates the distal end of the tooth row 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.* 2017). However, as stated above there is a key difference between these eruption patterns and that of *Triconodon*. In all of the other taxa, the molars are formed within the ramus and erupt upward. Therefore, the posterior molars can end up adjacent to the ascending coronoid (Greenwald 1988; Schultz *et al.* 2017, fig. 7d). In *Triconodon* m4 forms directly in the coronoid, within the ascending ramus and higher than the anterior molars. Therefore, the last molar of *Triconodon* does not erupt upwards, as in most mammals, but stays in place after it is fully formed. 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*).

In sum, restudy and 3D analysis of the relevant specimens provides a basis on which to reconstruct essential details for the antemolar replacement and molar eruption pattern of the later ontogenetic stages in *Triconodon* (Fig. 10). The formation of m4 probably 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 3, 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.

CONCLUSION

Taxonomy within Triconodontidae, especially at the species level, remains difficult. The holotype of *Triconodon mordax* (NHMUK PV OR 47764) and specimen NHMUK 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 NHMUK PV OR 48395 compared with specimens of *T. mordax* were considered sufficient to justify the assignment of a new species, *T. averianovi* sp. nov.

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 μ CT 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 non-trechnotherian Mammalia (Martin *et al.* 2015).

The formation of the posterior lower molars within the ascending ramus is unique in Triconodontidae. 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 growth aspect is analogous to other mammals, such as *Docodon* and some multituberculates, which exhibit molars that erupt lingual to the ascending ramus (Greenwald 1988; Schultz *et al.* 2017), however, in these taxa the tooth forms at the same height as its predecessor, while in Triconodontidae the molar forms above the active tooth row within the coronoid process. In *Triconodon* the ultimate lower molar (m4) is affected, while more derived Triconodontidae exhibit multiple posterior molars within the ascending ramus. Thus, the unusual locus could be linked to a secondary increase in molar count. This is supported by a phylogeny by Martin *et al.* (2015), in which *Trioracodon* (three lower molars) is considered to be a sister taxon to all other Triconodontidae. If three lower molars is the plesiomorphic condition for Triconodontidae, the unusual placement of the m4 in *Triconodon* would be linked to a secondary increase in molar count.

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DATA ARCHIVING STATEMENT

Models and associated scan data are archived on MorphoSource:
<https://doi.org/10.17602/m2/m115463> [NHMUK PV OR 47764; dentary]
<https://doi.org/10.17602/m2/m115464> [NHMUK PV OR 47768; dentary]
<https://doi.org/10.17602/m2/m114340> [NHMUK PV OR 47763; coronoid process]

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