

POSTCANINE MICROSTRUCTURE IN *CRICODON METABOLUS*, A MIDDLE TRIASSIC GOMPHODONT CYNODONT FROM SOUTH-EASTERN AFRICA

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Abstract: *Cricodon metabolus* is a trirachodontid cynodont from the Anisian (Middle Triassic) of eastern and southern Africa. It has labiolingually expanded (gomphodont) postcanines but also a sectorial tooth in the last postcanine locus. In this paper, we examine the crown microstructure of isolated sectorial and gomphodont postcanines belonging to the holotype specimen of this taxon using scanning electron microscopy. The enamel of both teeth is prismless and composed of discontinuous columnar divergence units, supporting the consistent presence of synapsid columnar enamel in cynognathians. Abundant tubules and numerous irregularly spaced incremental lines are also visible in the enamel and

dentine layers in each tooth. This study reveals that the enamel thickness varies along the tooth row in *Cricodon* as the enamel layer of the gomphodont postcanines is 11.5 times thicker than that of the sectorial crown. It is likely that this difference reflects occlusal stresses and fewer replacements in gomphodont postcanines relative to sectorial teeth. Approximately 100 incremental growth lines of von Ebner are present in the dentine layer, indicating that the deposition of the dentine by odontoblasts occurred for three months before the animal's death.

Key words: Trirachodontidae, Gomphodontia, postcanine, enamel, dentine, microstructure.

GOMPHODONTS were one of the most diverse groups of cynodonts and one of the dominant Middle to Late Triassic vertebrates in South America and southern Africa. They appeared in the Olenekian and radiated into three main clades: Diademodontidae, Trirachodontidae and Traversodontidae (e.g. Battail 1983; Abdala & Ribeiro 2003; Hopson 2005, 2014). Gomphodonts are distinctly heterodont and bear conical anterior incisors, large pointed canines, and molariform teeth that sometimes include sectorial postcanines (Reisz & Sues 2000; Abdala *et al.* 2006). The postcanines of members of the clade Gomphodontia are morphologically diverse but share a gomphodont morphology, that is they are labiolingually enlarged and show tooth-on-tooth occlusion (e.g. Seeley 1895, 1908; Crompton 1972; Reisz & Sues 2000; Abdala *et al.* 2006; Hopson 2014). Differentiation of the three main gomphodont clades is based mainly on postcanine heterodonty and morphology. Diademodontids have conical, ovoid gomphodont and sectorial postcanine teeth, whereas trirachodontids typically have ellipsoid gomphodont teeth and sectorial teeth, and traversodontids possess rectangular to trapezoidal uppers and quadrangular lower teeth, with sectorial postcanines in some juveniles (Abdala *et al.* 2006; Liu & Abdala 2014).

The external morphology of gomphodont postcanines is relatively well known from investigations of tooth morphology, occlusion, replacement, wear, function and ontogeny (e.g. Seeley 1894, 1895, 1908; Ziegler 1969; Hopson 1971, 2005, 2014; Crompton 1972; Osborn 1974; Grine 1976, 1977, 1978; Goñi & Goin 1987, 1988, 1991; Abdala *et al.* 2002, 2006; Liu & Sues 2010; Martinelli 2010; Sues & Hopson 2010). The tooth crown microstructure of gomphodonts, on the other hand, has only been cursorily studied in *Diademodon*, *Massetognathus*, *Exaeretodon* and *Boreogomphodon* (Moss 1969; Grine 1978; Grine *et al.* 1979; Osborn & Hillman 1979; Stern & Crompton 1995; Sander 1997; Abdala & Malabarba 2007). In addition, the internal tooth structure has never been investigated in a definitive trirachodontid taxon, and all previous studies on crown microstructure in gomphodonts are restricted to a single crown type of the tooth row (i.e. they do not compare enamel of different tooth morphologies).

Cricodon metabolus is a trirachodontid represented by incomplete cranial and postcranial material from the Anisian (Middle Triassic) Manda Formation of Njalila, Ruhuhu Basin, Tanzania (Crompton 1955). Specimens referred to this taxon are also known from the latest

Anisian Subzone C of the *Cynognathus* Assemblage Zone of the Burgersdorp Formation, Karoo Basin, South Africa (Abdala *et al.* 2005) and from the contemporaneous Ntawere Formation of the Luangwa Basin of north-eastern Zambia (Peacock *et al.* 2013; Hopson & Sidor 2015). This study aims to explore the microstructure of a sectorial tooth and a gomphodont postcanine in the same specimen of the trirachodontid *Cricodon metabolus* (Crompton 1955), and to use these data to investigate the evolution of the dentition in gomphodont cynodonts. We also investigate the distribution of enamel microstructure in non-mammaliaform cynodonts and enamel thickness along the trirachodontid tooth row. Finally, incremental lines of von Ebner in the dentine of the gomphodont tooth are analysed to determine the temporal interval of dentine deposition.

Institutional abbreviation. UMZC, University Museum of Zoology, Cambridge, UK.

MATERIAL AND METHOD

Terminology

Dental positional nomenclature follows Smith & Dodson (2003) and Hendrickx *et al.* (2015). The anatomical nomenclature used to describe and annotate external tooth sub-units follows the terminology and abbreviations of Hopson (2005) for gomphodont teeth, and Abdala *et al.* (2006) for the sectorial postcanine. Descriptions of the internal microstructure of the crown, especially enamel microstructure, use the terminology provided by Sander (1999, 2000). For the planes of sectioning we follow the terminology given by Wood & Stern (1997) and Sander (1999, 2000), that is, transverse, sagittal (rather than longitudinal or vertical), horizontal (rather than cross) and tangential.

Material

Material used for this study includes a gomphodont and a sectorial postcanine of the holotype specimen of *Cricodon metabolus* UMZC T905 (Figs 1, 2). The teeth were found isolated but in close proximity to the rest of the skeleton, and belong to a single individual (Crompton 1955). The sectorial postcanine is a complete tooth from the distalmost end of the tooth row (either of the right maxilla or the left dentary). This crown measures 6.77 mm apicobasally from cervix to apex on its mesial side (Fig. 1) and 5.91 mm in its distal side, with a length and a width of 5.11 mm and 3.61 mm at the cervical line, respectively (Hendrickx *et al.* 2016). It also measures 2.9 mm labiolingually and 5.2 mm mesiodistally in the basal horizontal section (section 2; Fig. 1A), and 1.5 mm

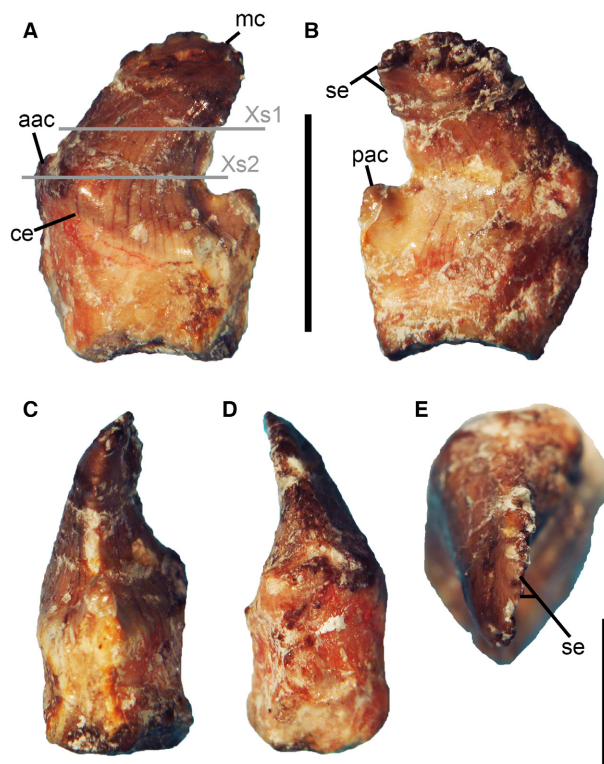


FIG. 1. Sectorial postcanine of the holotype specimen of *Cricodon metabolus* (UMZC T905); right distal maxilla or left distal dentary tooth. A, labial; B, lingual; C, distal; D, mesial; and E, apical views. *Abbreviations:* aac, anterior accessory cusp; ce, cervix; mc, main cusp; pac, posterior accessory cusp; se, serration; Xs1, apicalmost horizontal section; Xs2, basalmost horizontal section. Scale bars represent: 5 mm (A–D); 3 mm (E). Colour online.

labiolingually and 2.4 mm mesiodistally in the apical horizontal section (section 1; Fig. 1A). The gomphodont tooth is a left maxillary postcanine, of which a part of the lingual crown is broken (Fig. 2). Portions of the upper central cusp and the upper external cusp are also missing. The crown measures 10.31 mm labiolingually, 5.74 mm mesiodistally in its longest part at the cervix, and 4.34 mm apicobasally on its mesial side, in the highest point of the central crest (Hendrickx *et al.* 2016). At the level of the external cusp, the crown measures 4.16 mm apicobasally and 3.71 mm mesiodistally at the cervix.

Histological method

Both teeth were embedded in epoxy resin and sectioned with a diamond saw. The two postcanines were each sectioned twice in horizontal section: through the complete crown for the sectorial tooth, and through the upper external cusp for the gomphodont postcanine. The gomphodont tooth was also sagittally sectioned twice: immediately

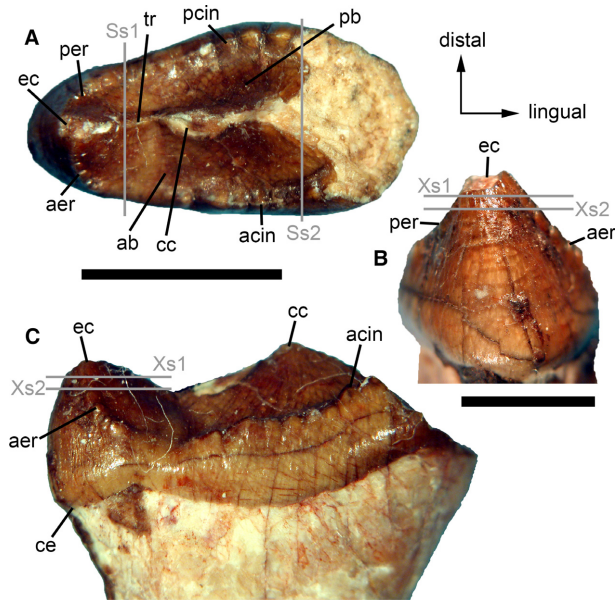


FIG. 2. Upper gomphodont postcanine of the holotype specimen of *Cricodon metabolus* (UMZC T905); left maxillary tooth. A, apical; B, labial; and C, mesial views. *Abbreviations:* ab, anterior basin; acin, anterior cingulum; aer, anteroexternal ridge; cc, central cusp; ce, cervix; ec, external cusp; pb, posterior basin; pcin, posterior cingulum; per, posteroexternal ridge; Ss1, labialmost sagittal section; Ss2, lingualmost sagittal section; tr, transverse ridge; Xs1, apicalmost horizontal section; Xs2, basalmost horizontal section. Scale bars represent: 5 mm (A, C); 3 mm (B). Colour online.

lingual to the upper external cusp, and lingual to the central cusp. The cut surfaces were polished and etched with 1 N HCl for 60 s, then washed in water. Sections were examined with a scanning electron microscope (SEM; Figs 3–5) Philips XL 30, and with a binocular incident light microscope (Fig. 5D). For the SEM, the specimens were mounted on stubs and sputter-coated with gold.

RESULTS

Sectorial postcanine

The sectorial tooth shows an enamel layer of variable thickness in horizontal section, varying from 9 to 10 μm in the labial portion of the crown in the apical section (Hendrickx *et al.* 2016), and from 11 to 12 and 26 μm in the labiodistal part of the postcanine in the apical and basal sections, respectively (Fig. 3B, C; Hendrickx *et al.* 2016). The enamel thickness is 5 μm in the labiomesial margin of the crown in the apical section, and gets thinner apically and mesially. The thickest enamel layer measured was in the distal part of the basal section of the crown

where it reaches 33 μm . The enamel microstructure can be seen in tangential section of the mesial portion of the crown (Fig. 3D, E), and in horizontal section of the rest of the tooth (Fig. 3B, C). The enamel microstructure closely matches the typical synapsid columnar enamel (SCE sensu Sander 1997) composed of short and discontinuous columnar divergence units whose crystallites are here tilted at an angle of 60–70° from the enamel–dentine junction (EDJ) in horizontal section (Fig. 3C). Planes of crystallite divergence are clearly observed in some parts of the enamel layer (black arrow in Fig. 3C). The enamel layer of the sectorial tooth does not show any evidence of incremental lines in horizontal section. Odontoblast tubules are abundant in the dentine layer where they can easily be seen as pits or sinuous casts projecting from the horizontal section surface (Fig. 3D–F). The tubular density is homogeneous throughout the dentine surface, with 7–8 tubules per 10 μm^2 .

Gomphodont postcanine

The enamel layer thickness of the gomphodont tooth is also variable in the apical horizontal section of the upper external cusp, ranging from 130 to 150 μm in the mesiolingual part, and from 175 to 225 μm in the labial and labiodistal portions of the cusp (Fig. 4A, B; Hendrickx *et al.* 2016). The enamel layer is thicker at the level of the posterior–external ridges where it reaches 280 μm . It is thinner in the more basal horizontal section, where it varies from 90 to 110 μm in the lingual part, 130 to 170 μm in the mesial portion, and 180 to 190 μm in the labial margin of the cusp. Based on both horizontal sections, the enamel reaches its greatest thickness in the labial portion of the crown, and is thinner lingually. The thickness of the enamel layer of the postcanine also increases apically in sagittal section, being the thickest (200 μm) at the transverse ridge and the thinnest (40 μm) in the basalmost portions of the mesial and distal margins of the tooth (Fig. 5A). The enamel layer also thickens at the level of the external ridges in the apical section (130 μm) and decreases towards the anterior and posterior basins (80–90 μm ; Fig. 5A).

The enamel microstructure of the gomphodont postcanine can be observed in horizontal and sagittal sections (Figs 4, 5). Similar to the sectorial tooth, the enamel microstructure of the gomphodont tooth has an SCE made of a multitude of short, discontinuous columnar divergence units forming a uniform schmelzmuster (Fig. 4B, C). These columns are poorly defined and measure 7–8 μm wide and 5–15 μm in length in sagittal section. The crystallites are tilted at an angle of 60–70° from the enamel–dentine junction in sagittal section (Fig. 5B). The columnar units form poorly delimited triangles or polygons in horizontal section (Fig. 4E). Irregularly

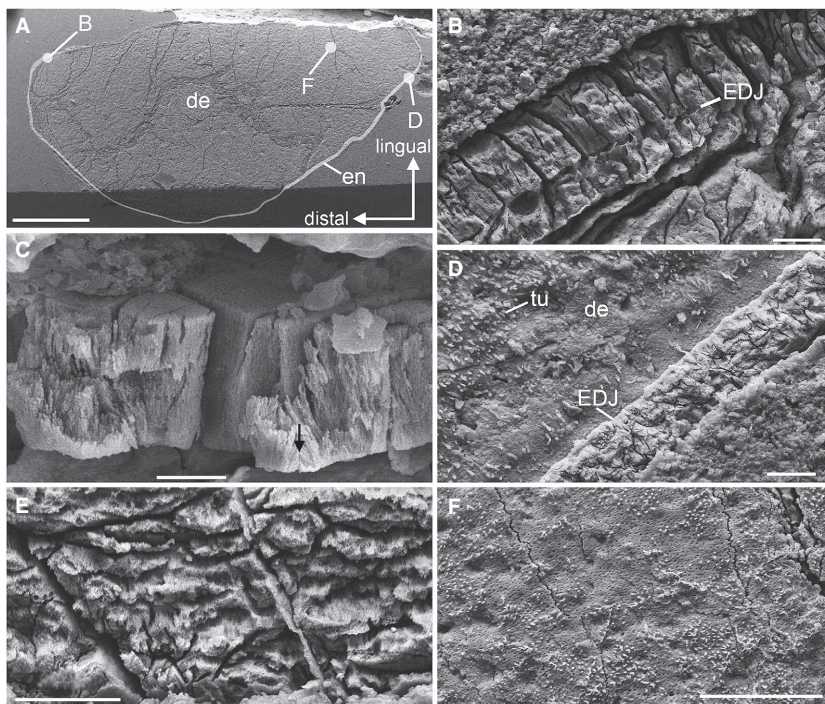


FIG. 3. Crown microstructure of a sectorial postcanine of *Cricodon metabolus* (UMZC T905); horizontal section of the crown. A, basalmost section with enamel layer in lighter grey; positions of images in B, F and D are indicated (close-ups in C and E are from another, more apical section). B, close-up of the linguodistal portion of enamel in horizontal section (basalmost section). C, labiodistal portion of enamel (apicalmost section); black arrow highlights the plane of crystallite divergence. D, labiomésial part of crown in oblique tangential section (basalmost section). E, enamel in oblique tangential section (apicalmost section). F, linguomesial portion of dentine in horizontal section (basalmost section). *Abbreviations:* de, dentine; EDJ, enamel–dentine junction; en, enamel; tu, tubule. Scale bars represent: 1 mm (A); 100 μm (F); 20 μm (B, D, E); 5 μm (C).

spaced incremental lines are visible in the enamel in the basalmost portions of the crown in sagittal section (Fig. 5C). These lines are absent in the rest of the crown, for example, the external ridges and basins (Fig. 5B). In the distobasal part of the postcanine, 19 incremental lines were counted (short white lines in Fig. 5C), yet marginal lines are barely discernible and more incremental lines may have been present. A large number of incremental lines are also clearly seen in some portions of the dentine in sagittal section, from the pulp cavity limit (Fig. 5F) to the EDJ. Similar to the enamel, these dentine lines are not regularly spaced, yet they are numerous and greatly exceed the 19 lines observed in the enamel. We counted 6 lines per 100 μm (mean increment width of 16.66 μm ; width fluctuating from 10 to 35 μm) in the portion of the dentine bordering the pulp cavity, 4 (almost 5) lines per 100 μm (mean increment width of 25 μm in average; width fluctuating from 20 to 25 μm) in the middle part of the dentine close to the pulp cavity, and 3 lines (mean increment width of 33.33 μm in average; width fluctuating from 27 to 35 μm) in the central portion of the dentine layer (Fig. 5D). Given the absence of incremental lines in some portions of the dentine, the actual number of dentine lines cannot be known. However, given a dentine layer thickness of around 2 mm in sagittal section of the mesial portion of the dentine and 4–5 dentine lines per 100 μm on average, around 80–100 dentine lines are present in the whole layer. Odontoblast tubules are also abundant in the dentine layer of the gomphodont tooth, both in the centre part of the

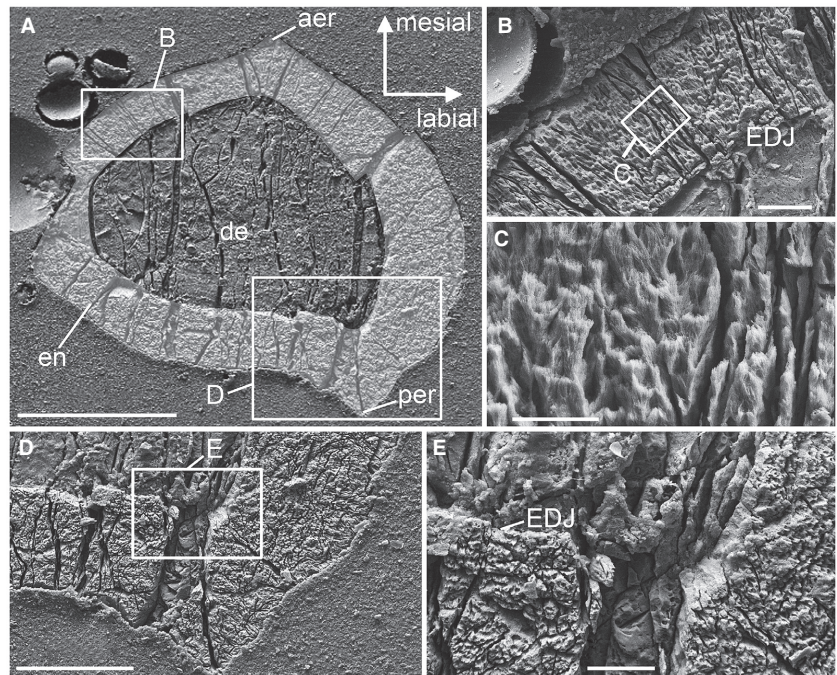
crown and in the external cusp, where there are around 10 dentine tubules per 10 μm^2 (Fig. 5E).

DISCUSSION

Distribution of enamel microstructure in non-mammaliaform cynodonts

Our investigation of postcanine microstructure in *Cricodon metabolus* reveals for the first time the presence of columnar divergence units in both sectorial and gomphodont teeth of a trirachodontid, and the consistent presence of SCE in cynognathians (Fig. 6). Using polarized light microscopy, Moss (1969) described the presence of bands ('tubules' *sensu* Moss 1969) in the enamel of an unpublished traversodontid tooth from the Luangwa Valley of Tanzania (and three other synapsids), lying 6–8 μm apart. These bands were recently interpreted as probable columnar enamel units by Abdala & Malabarba (2007). Grine (1978) and Grine *et al.* (1979) also identified prismless enamel as well as incremental lines in the basalmost gomphodont *Diademodon* using SEM. However, Osborn & Hillman (1979) highlighted the probable presence of enamel tubules and prismatic enamel without interprismatic regions in the basalmost gomphodont *Diademodon* and the traversodontid *Massetognathus* using polarized light microscopy. A prismatic enamel microstructure with putative prisms being inconspicuous

FIG. 4. Crown microstructure of an upper gomphodont postcanine of *Cricodon metabolus* (UMZC T905). A, horizontal section of the upper external cusp (apicalmost section) with enamel layer in lighter grey. B, C, close-ups of the linguomesial portion of cusp in horizontal section. D, E, close-ups of the labiodistal portion of cusp and posteroexternal ridge in horizontal section. Abbreviations: aer, anteroexternal ridge; de, dentine; EDJ, enamel–dentine junction; en, enamel; per, posteroexternal ridge. Scale bars represent: 500 μm (A); 200 μm (D); 50 μm (B, E); 20 μm (C).



and discontinuous, combined with well-defined incremental lines and tubules, was also observed in isolated traversodontid teeth from the Middle Triassic Yerrapalli Formation of Pranhita–Godavari Basin, India, using SEM (Sahni 1985, 1987; Sahni & Lester 1988). The prismatic and poorly organized enamel microstructure illustrated by Sahni & Lester (1988, fig. 10) in the traversodontid was, however, interpreted as columnar by Abdala & Malabarba (2007). Given that only isolated trirachodontid teeth were documented in these deposits (Chatterjee *et al.* 1969), Abdala & Malabarba (2007) also interpreted the traversodontid teeth analysed by Sahni & Lester (1988) as belonging to Trirachodontidae. The enamel microstructure was re-explored in *Massetognathus*, this time using SEM, by Stern & Crompton (1995) who observed faint incremental lines and a columnar enamel type with pinched portions of columns, an interpretation disputed by Sander (1997). The latter noted that the enamel of the cynognathians *Cynognathus*, *Diademodon* and *Boreogomphodon* was thick, and that its microstructure was prismless and columnar. More recently, Abdala & Malabarba (2007) described prismless enamel with parallel and discontinuous columns and well-defined incremental lines (especially in the Brazilian species *Exaeretodon riograndensis*) as well as tubular structures in the dentine of the derived traversodontid *Exaeretodon*.

Although SCE seems to be consistently present in cynognathians, two other types of enamel microstructure have been described in non-mammaliaform cynodonts. Thin enamel composed of parallel and non-columnar

crystallites was observed in the basal cynodont *Procynosuchus* by Sander (1997). Likewise, the enamel microstructure of the extensively sampled tritheledontid *Pachygenelus* was reported to be made of plesiomorphic prisms (Sander 1997; Wood & Stern 1997; Wood & Rougier 2005). Prismatic enamel was also reported in the tritylodontid *Oligokyphus* by Dauphin & Jaeger (1987), but their ‘prisms’ were interpreted instead as columnar units (Lester & Koenigswald 1989; Sander 1997, 1999).

Prismatic enamel was also observed in the tritylodontid *Montirictus kuwajimaensis* from the Lower Cretaceous of Japan (Kamiya *et al.* 2006; Matsuoka *et al.* 2016). Several aspects of Kamiya *et al.*’s (2006) results are surprising. These authors only illustrated a single prism in their figure 3, and did not present observations showing that this structure was repeated. The prism structure shown in this figure 3 was observed in a part of the enamel of a single specimen, a distal cusp of a lower left postcanine (N. Kusuhashi, pers. comm. 2016). The 10 μm diameter of this prism is much larger than the 2.5–5.5 μm reported for plesiomorphic prisms (i.e. Wood & Stern 1997). It is, however, within the range of values reported for the diameter of prisms forming the gigantoprismatic enamel reported in multituberculates (Fosse *et al.* 1978; Carlson & Krause 1985; Mao *et al.* 2015), a group also present in the Japanese fauna (Matsuoka *et al.* 2002). Kamiya *et al.* (2006) also reported the presence of structureless wavy enamel in the same tritylodontid. Although it is possible that prismatic enamel was present in a tritylodontid, clearer evidence is necessary to validate Kamiya *et al.*’s

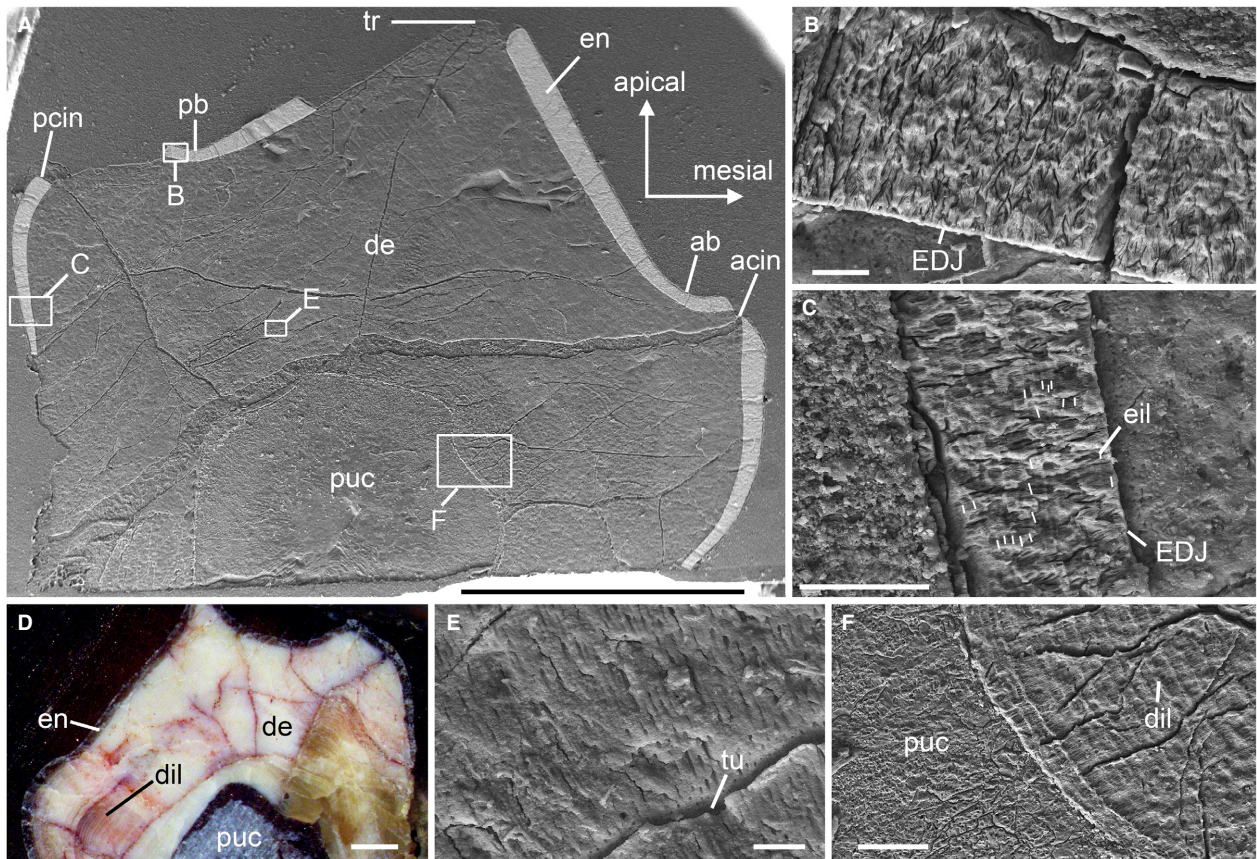


FIG. 5. Crown microstructure of an upper gomphodont postcanine of *Criconodon metabolus* (UMZC T905). A, sagittal section of the tooth with enamel layer in lighter grey. B, close-up of the posterior basin. C, distobasal portion of enamel (lingualmost section); short white lines highlight the incremental lines of the enamel. D, sagittal section of the crown (labialmost non-SEM section). E, close-up of the mesioapical portion of dentine. F, mesiobasal portions of dentine and pulp cavity (lingualmost section). *Abbreviations:* ab, anterior basin; acin, anterior cingulum; de, dentine; dil, dentine incremental lines; EDJ, enamel–dentine junction; eil, enamel incremental line; en, enamel; pb, posterior basin; pcin, posterior cingulum; puc, pulp cavity; tr, transversal ridge; tu, tubule. Scale bars represent: 2 mm (A); 500 μm (D); 100 μm (F); 50 μm (C); 20 μm (B, E). Colour online.

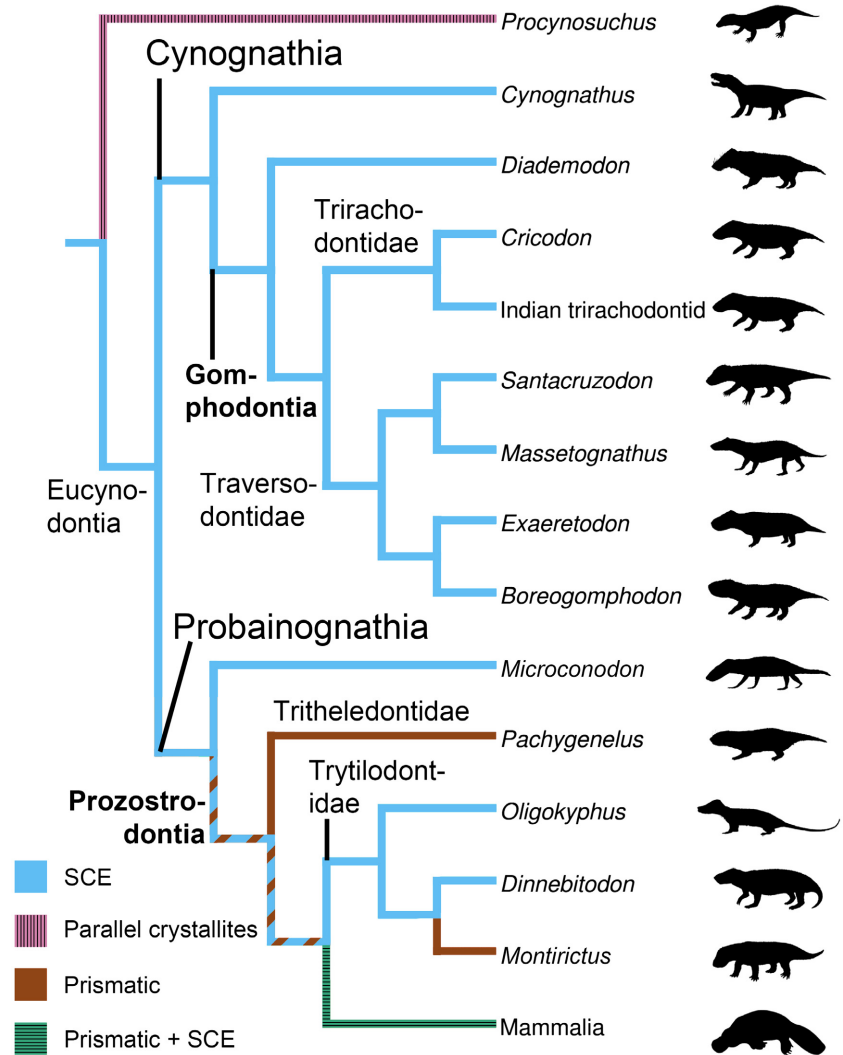
(2006) interpretation. Besides these two basal prozostroodontians (*sensu* Liu & Olsen 2010), all other non-mammaliaform probainognathians sampled (i.e. *Microconodon*, *Dinnebitodon* and *Oligokyphus*), as well as some basal Mammaliaformes (e.g. *Morganucodon* and *Sinoconodon*) show SCE (Sander 1997; Wood & Stern 1997). This suggests that prismatic enamel evolved in probainognathians, and either appeared in basal prozostroodontians and then was lost in some tritylodontids and basal Mammaliaformes, or was independently acquired in Mammaliaformes, tritheledontids and possibly in some tritylodontids (Fig. 6).

Ecological implications

Enamel thickness. This study highlights variation of enamel thickness in different types of crowns along the

tooth row in a cynognathian. In *Criconodon*, the enamel layer of the gomphodont postcanine is approximately 11.5 times thicker than that of the sectorial tooth (the average enamel thickness of the two cross-sections is 15.42 μm for the sectorial tooth and 176.5 μm for the gomphodont postcanine; Hendrickx *et al.* 2016). Thick enamel on the gomphodont postcanine most likely reflects several independent factors. First, these labiolingually expanded teeth with large occlusal surfaces were used to chew, crush and grind hard and fibrous plant material (Grine 1977; Hillson 2005; Ungar 2010). They were therefore exposed to higher loads and apically-oriented stresses. A study of the marsupial *Didelphis virginiana* shows that thicker enamel is represented in basin rims where there is tooth-on-tooth occlusion (Stern *et al.* 1989). We hypothesize here that thicker enamel was an evolutionary response to the increased stresses resulting from tooth-on-tooth occlusion necessary for efficient

FIG. 6. Distribution of the different types of enamel microstructure in basal cynodont taxa based on this study and Stern & Crompton (1995), Sander (1997), Wood & Stern (1997), Weiss *et al.* (2005), Kamiya *et al.* (2006) and Abdala & Malabarba (2007). Tree topology based on Watabe *et al.* (2007) and Liu & Olsen (2010). The placement of *Microconodon* in the phylogeny is tentative (see Sues 2001). *Abbreviation:* SCE, synapsid columnar enamel. Cynodont silhouettes by Sarah Werning (*Ornithorhynchus*), Nobu Tamura (*Cynognathus*, *Procynosuchus*), and José Eduardo Camargo Martínez (all others; modified). Colour online.



grinding. The labio-lingually compressed, serrated and distally recurved sectorial postcanines were, on the other hand, used to shear plant material (Crompton 1955). Enamel is a metabolically costly material and, because these teeth were not subjected to the same occlusal stresses, it is likely that its thickness was not maintained. Sectorial teeth of cynodonts are morphologically similar to ziphodont teeth of reptiles (Hendrickx *et al.* 2015), which generally show thin enamel as well (Sander 1999, 2000). Indeed, because enamel is a brittle material, thin teeth with higher bending loads might crack if they had thicker enamel walls (P. M. Sander, pers. comm. 2016). Therefore, a biomechanical factor might also explain the thin enamel observed in the sectorial postcanine of *Cricodon*.

Another potential factor influencing enamel thickness in *Cricodon* is the pattern and timing of tooth replacement. The sectorial teeth in the posterior locus of the postcanine series of *Cricodon metabolus* are sequentially replaced by gomphodont teeth (Crompton 1955), a

pattern also represented in the trirachodontid *Langbergia* (Abdala *et al.* 2006). Replacement of distal sectorial postcanines with gomphodont teeth has also been observed in some traversodontids, including *Scalenodon*, *Boreogomphodon*, *Massetognathus* and *Andescynodon* (Crompton 1955; Goñi & Goin 1991; Abdala *et al.* 2002, 2013; Liu & Sues 2010). In such a rapidly replaced tooth, there may have been relaxed selection for thick enamel layers or perhaps even active selection for thin enamel due to the high cost of production of this material. The gomphodont teeth of *Cricodon metabolus* and other gomphodont taxa were, on the other hand, kept for a much longer time before being replaced, and thicker enamel would have provided superior wear resistance. Interestingly, there are gomphodont cynodonts that completely lack replacement of gomphodont postcanines (e.g. in the traversodontid *Exaeretodon*; Abdala *et al.* 2013). In these cases, old gomphodont crowns are lost anteriorly in the postcanine series and new gomphodont crowns are added in posterior

loci. Therefore there is a progression in the degree of wear of the teeth of the postcanine series, with anterior teeth being completely eroded, central ones showing only part of their original morphology, and posterior crowns with freshly erupting occlusal surfaces.

Enamel and dentine incremental lines. Incremental lines are clearly visible in both the enamel and dentine layers of the gomphodont tooth of *Cricodon metabolus* (Fig. 5). In the enamel, these lines represent the striae of Retzius (Retzius 1837), which record the changes in morphology of the secretory surface during amelogenesis (Sander 1999) and 'represent a temporary but profound periodic slowing of enamel formation in various multiples of whole days' (Bromage *et al.* 2009, p. 389; see Sander (1999) for more details on the nature of these incremental lines). As observed in *Massetognathus* (Stern & Crompton 1995), the striae of Retzius are parallel to the EDJ and do not intersect the outer surface of the tooth (Fig. 5C) so that there are probably no perikymata. A total of 19 irregularly spaced striae of Retzius, with a spacing between 3 and 5 μm , were counted in the gomphodont postcanine of *Cricodon*, which is well above the range of what has been recorded in living mammals (Fukuhara 1959; Dean *et al.* 2001; Fitzgerald & Rose 2008). Little information on the number of striae of Retzius in basal cynodonts is available in the literature. Well-defined incremental lines are present in the enamel of an Indian traversodontid (Sahni & Lester 1988; here interpreted as a trirachodontid), *Massetognathus* (Stern & Crompton 1995) and *Exaeretodon riograndensis* (Abdala & Malabarba 2007). Although no information is provided in those publications on the number of striae of Retzius for these taxa, we obtained an approximate estimate of 90 striae in the enamel layer of the traversodontid *E. riograndensis* (Abdala & Malabarba 2007, fig. 4E). This number is well above that observed in the *Cricodon* gomphodont tooth and could result from the much larger size of the crown of *Exaeretodon*. However, we estimate 11 to 12 striae of Retzius in the enamel layer of *Massetognathus* (Stern & Crompton 1995, fig. 13), more similar to what was observed in *Cricodon*.

Given their average spacing of no less than 30 μm , the incremental lines in the dentine are probably incremental lines of von Ebner rather than contour lines of Owen (Erickson 1996a, b; Ten Cate 1998). Incremental lines of von Ebner form 'when dentine is sporadically deposited and/or mineralized due to the influence of short term (<5 days) endogenous biorhythms' (Erickson 1996a, p. 189), and are produced on a daily basis in most mammalian taxa and archosaurs (Erickson 1996a, b; Dean 2000 and references therein). The 80–100 incremental lines in the dentine of the gomphodont tooth of *Cricodon* suggest that the deposition of the dentine odontoblast

had been ongoing for approximately three months before the animal died. The average width of the von Ebner incremental lines (c. 22.22 μm , or an average of 4.5 von Ebner incremental lines per 100 μm) is close to upper and lower values of the range reported for dicynodont tusks: 16–22 μm in *Diictodon* (Thackeray 1991), 17.4 μm in *Lystrosaurus* (Jasinowski & Chinsamy-Turan 2012), and 18.8–31.5 μm in two American dicynodont tusks (Green 2012). The average width of these lines in *Cricodon* is higher than that reported for the incisors of the tritylodontid *Tritylodon* (average of 13.6–13.7 μm ; Jasinowski & Chinsamy 2012). Values for incremental line spacing known in reptiles include: some crocodylians (average of 13 μm in *Alligator mississippiensis* and *Caiman crocodylus*; Erickson 1996a, b), theropods (average of 13.51 μm in *Deinonychus*, *Troodon*, *Albertosaurus* and *Tyrannosaurus*; Erickson 1996b), hadrosaurids (average of 14.18 μm in *Prosaurolophus*, *Maiasaura* and *Edmontosaurus*; Erickson 1996b) and mosasaurs (average of 10.9 μm in *Mosasaurus hoffmanni*; Chinsamy *et al.* 2012). It is unknown whether the number of striae of Retzius in the enamel and the average width of the von Ebner incremental lines in the dentine bear any phylogenetic signal.

CONCLUSIONS

Investigation of the postcanine microstructure in the trirachodontid cynodont *Cricodon metabolus* reveals the presence of irregularly spaced incremental lines in the enamel and dentine layers, odontoblast tubules in the dentine, and short and discontinuous columnar divergence units in the enamel. These observations support the consistent presence of synapsid columnar enamel in Cynognathia. Tritheledontidae (and possibly some Tritylodontidae) are the only clades of non-mammaliaform cynodonts with prismatic enamel. This suggests that prisms either evolved in basal prozostrodontians and were lost in some tritylodontids and basal Mammaliaformes, or were independently acquired in tritheledontids, tritylodontids and mammals. *Cricodon* gomphodont postcanines display an approximately 1100% thicker enamel layer than the sectorial postcanines. This difference is more likely due to the fact that gomphodont postcanines are optimized for the higher loads and stresses of occlusion with few replacements, whereas sectorial postcanines lack tooth-on-tooth occlusion and were rapidly replaced by gomphodont teeth during the animal's lifetime. The average width of the von Ebner incremental lines in the dentine of the *Cricodon* gomphodont postcanine is close to lower values of the range represented in some dicynodonts but higher than that of *Tritylodon* incisors. Given the presence of around 80–100 incremental growth lines in the whole dentine layer, deposition of the dentine by

odontoblasts and the maturation of the tooth crown took approximately three months before the animal's death.

Enamel microstructure has so far been explored using SEM techniques in seven gomphodont taxa: *Diademodon tetragonus*, *Cricodon metabolus*, trirachodontid teeth from India, *Massetognathus pascuali*, *Exaeretodon frenguelli*, *Exaeretodon riograndensis* and *Boreogomphodon jeffersoni* (Stern & Crompton 1995; Sander 1997; Abdala & Malabarba 2007), which accounts for less than 20% of the current diversity of the clade. In future investigations of enamel properties in trirachodontid and traversodontid taxa, it is crucial to examine variation of enamel thickness as well as number and spacing of striae of Retzius and incremental lines of von Ebner for each tooth type. This will allow for a more accurate assessment of the taxonomic potential of the tooth microstructures in Gomphodontia, as well as the morphological variation of these dental features along the tooth row.

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DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.8d1t2>. Archived data include measurements taken on the crown and enamel and dentine layers of the gomphodont and sectorial postcanines of *Cricodon metabolus* UMZC T905.

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