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Histological evidence of trauma in tusks of southern African dicynodonts

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Dicynodonts were a clade of globally-distributed therapsids known for their abundance in the fossil record and for surviving the Permo-Triassic mass extinction. The group had distinctive dental adaptations including a beak and, in many species, paired maxillary tusks. The function of these tusks has long been of interest, yet remains poorly understood. We report here on two instances of unusual morphology in tusk dentine from specimens of: 1) *Lystrosaurus* from the Karoo Basin of South Africa and, 2) an unidentified dicynodontoid from the Luangwa Basin of Zambia. In both, the cross-sectional shape of the tusk root is lobed and infolded, which histological features suggest is a result of abnormal dentine deposition. We infer that this abnormal morphology is likely the consequence of trauma given its reparative nature and structural similarities to trauma-related morphologies reported in the tusks of modern elephants. This study demonstrates that histological sampling of dicynodont tusks can shed light on the biology of this important clade of therapsids.

Keywords: Dicynodontia, Triassic, South Africa, Zambia, Permian, pathology, dentine.

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INTRODUCTION

Dicynodonts evolved one of the most specialized food processing systems within the synapsid lineage, characterized by a horn-covered beak and (oftentimes) maxillary tusks, along with a distinctive jaw hinge (Crompton & Hotton 1967; Angielczyk 2004). Enlarged, paired tusks, which are the namesake of the clade, have long intrigued palaeontologists with proposed functions including foraging for food, sexual dimorphism in some species and burrowing behaviours (Sullivan *et al*. 2002; Ray *et al*. 2005; Modesto & Botha-Brink 2010; Botha-Brink 2017). Despite this variety of proposed roles, gross morphological evidence has provided little insight into the function of dicynodont tusks.

Here we describe the histology of two tusks and their surrounding hard tissues in specimens of *Lystrosaurus* from the Karoo Basin of South Africa and an indeterminate dicynodontoid (possibly *Dicynodon*) from the Luangwa Basin of Zambia. Unusually, these specimens preserve anatomy consistent with a developmental anomaly or pathology, although non-pathological infolded dentine (i.e. plicidentine) is seen in some pelycosaur-grade synapsids (Brink *et al*. 2014). Based on comparisons with modern tusked animals, we conclude that trauma is the most likely explanation for this anomalous dentine anatomy, which can provide insight into the function of tusks in at least some dicynodonts.

MATERIALS AND METHODS

The tusk and surrounding alveolar jaw bone of the dicynodont specimens were prepared and thin-sectioned following standard methods (Lamm 2013). In both specimens, the tusks were broken where they emerge from the maxillae, but preserve most of the root portion of the tusks. Thin sections were made perpendicular to the long axis of the tusk, ground to a thickness of approximately 100 μm, and imaged with a Nikon Eclipse LV100POL microscope and NIS-Elements software.

SYSTEMATIC PALAEONTOLOGY

Synapsida Osborn, 1903
Therapsida Broom, 1905
Dicynodontia Owen, 1859
Dicynodontoidea Owen, 1859

Dicynodontoidea indet.

Referred specimen. NHCC LB836, tusk-bearing left and right maxillae from one individual.

Locality. This specimen was collected from locality L424, a medium-sized outcrop of the upper member of the Madumabisa Mudstone Formation near the southern border North Luangwa National Park (Northern Province, Zambia). Detailed locality information is available from NHCC or the authors.

Lystrosaurus Cope, 1870

Lystrosaurus indet.

Referred specimens. SAM-PK-K011603, tusk-bearing right maxilla; SAM-PK-K011604, partial skull, including orbits and snout.

Locality. SAM-PK-K011603 was collected near the bound-

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ary between the farms Weltrevreden and Ripplemead (Nieu Bethesda District, Eastern Cape Province) by Dr Roger Smith as field number RS 337, from rocks of the Triassic upper Palingkloof Member of the Balfour Formation (*Lystrosaurus* Assemblage Zone; Smith & Botha-Brink 2014). SAM-PK-K011604 was also collected by Dr Roger Smith from Lower Triassic rocks on the farm Donald 207 (Fairydale) in the Bethulie District, Eastern Cape Province, approximately 54 metres above the inferred Permo–Triassic boundary.

DESCRIPTION

Gross anatomy

SAM-PK-K011603 is an incomplete right maxilla preserving much of the lateral surface, including the palatal ramus, caniniform process, and a small section of the anterior process (Fig. 1a). Based on its size and anatomy, we refer it to *Lystrosaurus* sp., which accords well with its stratigraphic position, as there are no other dicynodont genera known from the Triassic portion of the Palingkloof Member of the Balfour Formation (Smith & Botha-Brink 2014).

Embedded within the maxilla is a section of tusk approximately 5 cm long, although it is only visible emerging from the dorsal and ventral surfaces of the bone. Approximately 5 mm of erupted crown is preserved with not enough material preserved to examine wear facets. Based on what is visible and the curve of the caniniform process, the root is slightly recurved and it tapers in diameter towards the occlusal surface. The root of SAM-PK-K011603 is damaged apically, but another, more complete *Lystrosaurus* specimen (SAM-PK-K011604) was sectioned longitudinally and reveals a wide open root with a distinct funnel-shaped pulp cavity (Fig. 1b), indicative of an ever-growing tusk (Steenkamp 2003).

NHCC LB836 includes associated left and right maxillae that contain incomplete tusks (Fig. 2). The caniniform processes of the maxillae are angled slightly perpendicular to the dorsoventral axis and more rugose than the surrounding maxillary bone (Fig. 2a). The left maxilla includes approximately 7.5 cm of tusk and the right is slightly more complete, preserving 8.4 cm of tusk including more of its dorsal portion. On both sides, the dorsal portion of the maxillae are broken to expose their interior anatomy as well as the roots of the tusks. On the right side, this broken surface exposes what appears to be regularly deposited dentine in a circular cross-sectional shape. The left side, however, reveals that the root of the tusk has deeply infolded dentine, which is visible macroscopically (Fig. 2b). Essentially none of the functional tusk is preserved on either side, including potential wear facets.

Histology

The tusk of SAM-PK-K011603 is composed of dentine with no outer capping tissue such as enamel or cementum preserved, although the lack of cementum in the preeruptive root could be preservational. From the root end (i.e. apex in standard dental terminology; Fehrenbach & Popowics 2016) towards the tip of the tusk, the cross-sectional shape of the tusk changes from having an unusual wavier border to a more expected circular one. The wavy margin is the surface expression of the infolding of the underlying dentine, which can extend deep to near the pulp cavity (Fig. 3a). Towards the tip end, the infoldings gradually become shallower and less exaggerated (Fig. 3b–d) until no irregularities are present (Fig. 3d). The most dramatic infolding is present on the anterior

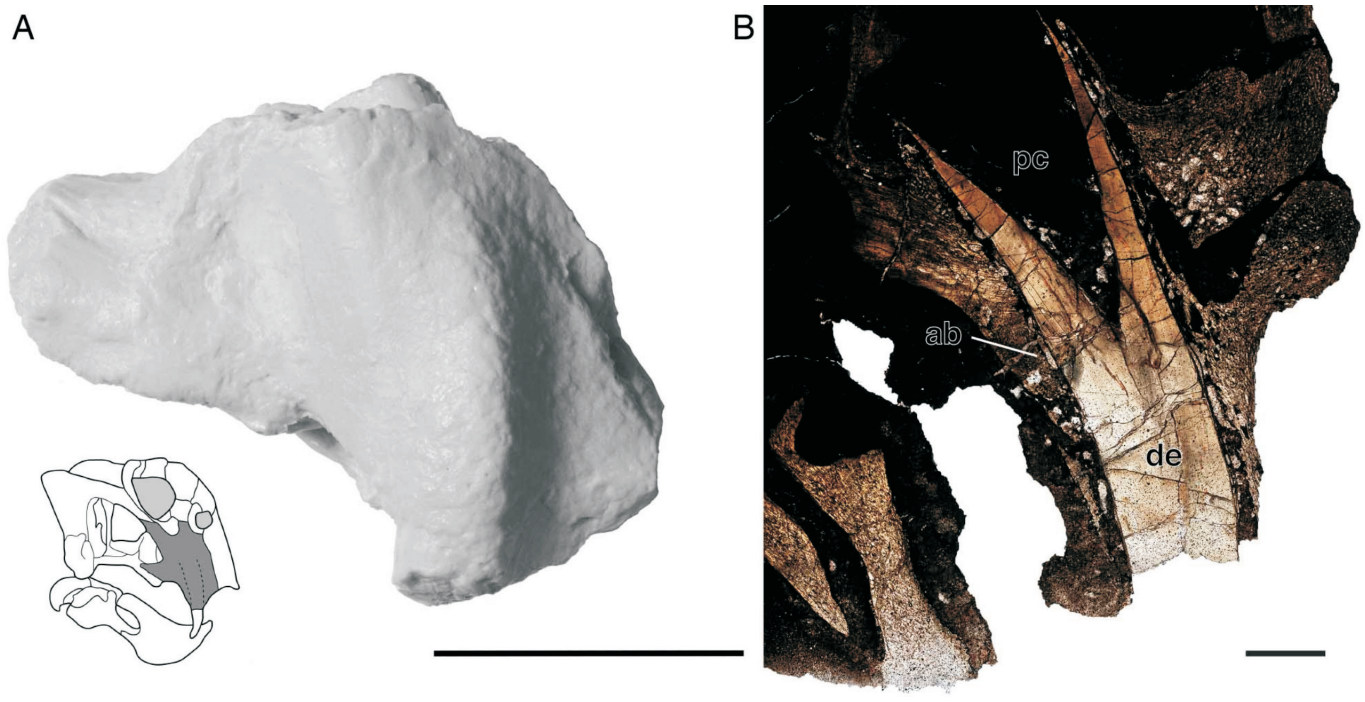


Figure 1. Gross anatomy and histology of *Lystrosaurus* tusks. **A**, Cast of SAM-PK-K011603 in right lateral view. **B**, Thin section of SAM-PK-K011604 with an open, funnel-shaped pulp cavity indicative of an ever-growing tusk. Scale bars equal: A, 3 cm; B, 5 mm. Abbreviations: ab, alveolar bone; de, dentine; pc, pulp cavity.

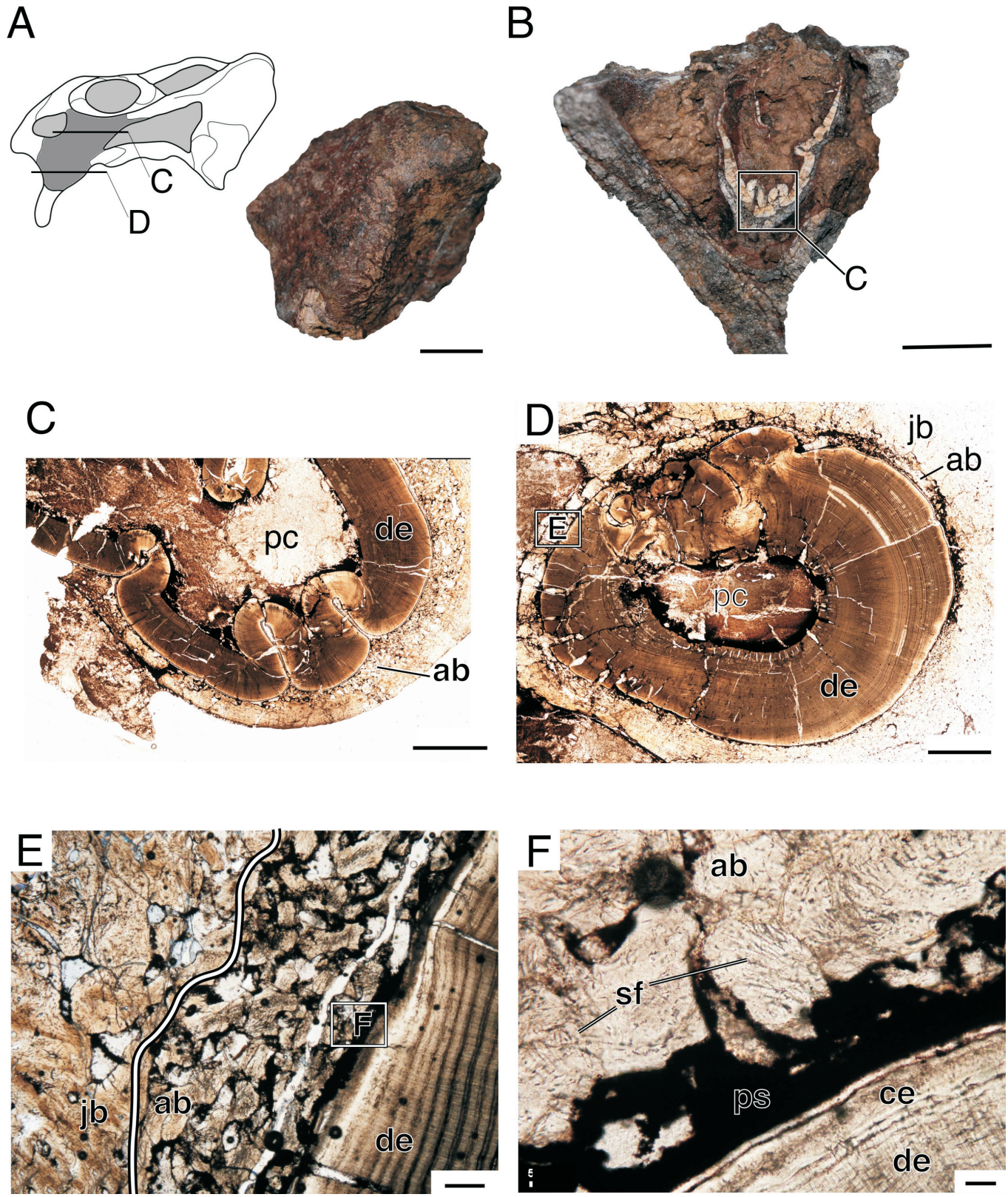


Figure 2. Gross anatomy and thin sections of dicynodontoid (NHCC LB836). **A**, Schematic representing where sections were taken from the pathological right tusk and the associated, normal left maxilla in left lateral view. **B**, Natural break showing the pathological right tusk root with anterior towards the top of the page. **C**, Thin section showing infolding near root end of tusk. **D**, Thin section taken near ventral end of maxilla showing less pronounced infolding. **E**, Boundary between more compact jaw bone and more vascularized alveolar bone. **F**, High magnification view of the periodontal space between the tusk root and alveolar bone. Scale bars equal: A–B, 1 cm; C–D, 5000 μm; E, 250 μm; F, 50 μm. Abbreviations: ab, alveolar bone; ce, cementum; de, dentine; jb, jaw bone; pc, pulp cavity; ps, periodontal space; sf, Sharpey's fibres.

margin of the root and continues with wavy margins on the medial and posterior edges (Fig. 3a–c).

The two predominant histological features of dentine, dentine tubules and incremental growth marks spaced approximately 20 μm apart, which correspond to the 5-day increments of lines of von Ebner in mammals (Simmer *et al*. 2008), are visible in this specimen (Fig. 3e–f). Both the dentine tubules and lines of von Ebner follow normal

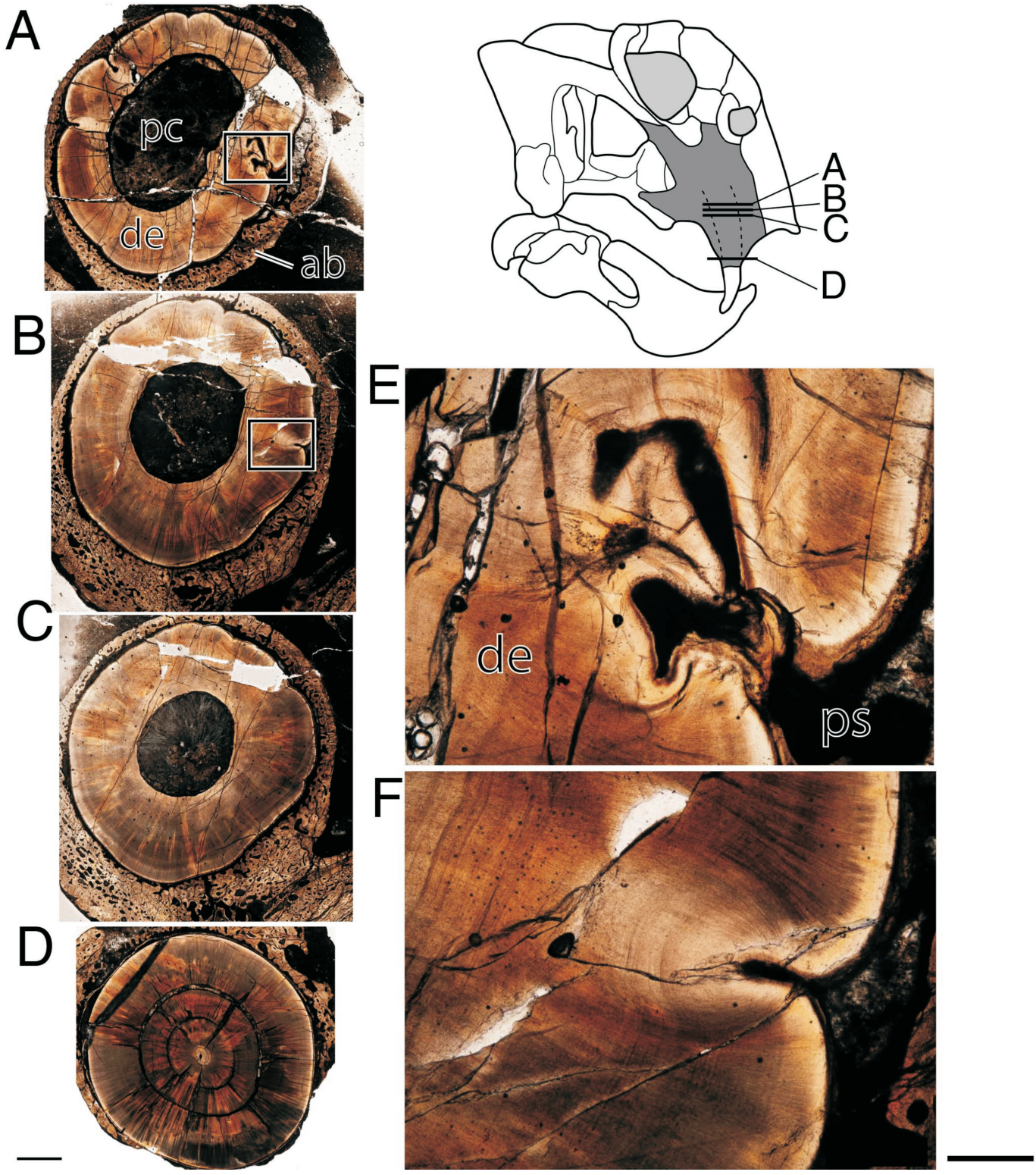


Figure 3. Thin sections of *Lystrosaurus* sp. (SAM-PK-K011603) taken at four locations along the apical-occlusal axis. **A**–**D**, Thin sections detailing the changes in unusual dentine morphology from the apical-most section with the most dramatic irregularities (A) to the occlusal-most section with regular morphology (D). **E**, Boxed portion of section (A) at high magnification detailing dentine infolding and periodontal space. **F**, Boxed portion of section (B) at high magnification detailing reduced but continued infolding. Scale bars equal: A–D, 2mm; E–F, 500 μm. Abbreviations: ab, alveolar bone; de, dentine; pc, pulp cavity; ps, periodontal space.

patterns in non-lobed portions of the tusk with the tubules radiating out from the pulp cavity and growth marks concentrically organized around the tusk. In the abnormal portions of the root, however, both features mirror the shape of its folded and irregular circumference.

The surrounding alveolar bone is composed of highly vascularized woven-fibred bone with primary osteons (i.e. fibrolamellar bone *sensu* Francillon-Viellot *et al*. 1990) with longitudinally oriented canals and evidence of extensive remodeling. A periodontal space is present between the tusk and the surrounding alveolar bone ranging in thickness from 90 μm to 500 μm. In sections taken both apically and towards the erupted end of the root, Sharpey's fibres running perpendicular to the

periodontal space are abundant and provide evidence of a soft-tissue periodontal ligamentous tooth attachment.

Unlike the left tusk of NHCC LB836, which appears to have regular dentine (Fig. 2a), the right side displays an irregular, infolding of dentine similar to that seen in SAM-PK-K011603. An open root and the abnormal dentine were apparent in the field when the specimen was collected due to breakage of the maxilla and its exposure of the apical portion of the tusk root (Fig. 2b). The tusk is composed of dentine (Fig. 2c–f) surrounded by alveolar bone with a thin layer of cementum preserved (Fig. 2f). A thin periodontal space is apparent around the tusk with Sharpey's fibres in the alveolar bone indicative of a gomphosis (Fig. 2f). The highly irregularly deposited dentine is more exaggerated in the apex of the root and the irregular patterning is consistent on both the labial and lingual margins (Fig. 2b). Towards the tip of the tusk, the irregular infolding is restricted to the posterolingual aspect of the tusk (Fig. 2d). Similar to the *Lystrosaurus* specimen, the unusual dentine shape in NHCC LB836 is reflected in the periodic depositional lines (also approximately 20 μm apart) as well as the dentine tubules (Fig. 2c).

DISCUSSION

Infolded dentine has been recognized in the roots of numerous groups of amniotes including Captorhinidae, Choristodera, Diadectomorpha, Ichthyosauria, Lepidosauria, Parareptilia and Sphenacodontidae (Brink *et al*. 2014; MacDougall *et al*. 2014; Maxwell *et al*. 2011; Meunier *et al*. 2013). Typically, the shape of the infolded dentine is regular and symmetrical, and has been termed plicidentine (Owen 1841; Tomes 1878). Although the dentine infoldings observed here are lobed like plicidentine, the distribution and depth of infoldings around the cross-sectional area is highly irregular. Additionally, lobed morphology has not been observed in the tusk roots of other dicynodont specimens that have been thin-sectioned (Thackeray 1991; Green 2012; Jaskinoski & Chinsamy-Turan 2012a; LeBlanc *et al*. 2018) nor are they visible in the contralateral maxilla of NHCC LB836, suggesting that the instances described here are anomalies. Although not examined under thin section, the long axis of the tusk of *Odontocyclops whaitsi* (AMNH 5566) does present some infolding (Angielczyk 2002), although it appears more regular than the infolding seen in SAM-PK-K011603 or NHCC LB836. The infolding observed in *Odontocyclops* could be a different abnormality or a different morphology formed from a similar etiology. However, without thin-sectioning, useful comparisons are limited.

The peculiar cross-sectional morphology of these specimens was formed by irregularities in the path of odontoblasts taken during their deposition of dentine, which is evidenced by the correspondence of dentine tubules and lines of von Ebner to the lobed morphology. Thus, there is good evidence that the lobed anatomy is a depositional anomaly, yet its etiology is difficult to determine definitively. It is interesting to note, however, that the lack of infoldings towards the emerging end of the tusks suggests that normal dentine deposition had occurred earlier in the individual's life. Thus, a congenital anomaly can be ruled out.

We suggest that trauma is the likely cause for the peculiar root morphology observed in these specimens. Mechanistically, the trauma could have resulted in either irregular original deposition (i.e. primary dentine) or reparative deposition (i.e. secondary dentine). In cross-section, the periphery of the tusks represents the earliest site of dentine deposition and thus, the abnormal and occasionally infolded margin could indicate that during the onset of tissue deposition trauma resulted in irregular odontoblast activity. Alternatively, secondary dentine could have been deposited to repair damaged primary dentine tissue giving rise to the unusual morphology, with either scenario depending on the timing of an injury. In either case, some external trauma to the tusk or maxilla would likely present itself as unusual alveolar bone with evidence of reparative bone. Surprisingly, we see no evidence of malformations or trauma to the maxilla, but given the rapid turnover rate of alveolar bone, it is possible that such evidence has been remodelled away (e.g. Vignery & Baron 1980).

The folded morphology seen in these specimens is remarkably similar to what has been described in modern elephant tusks that have experienced trauma (Miles & Grigson 1990) and in many ways, dicynodont tusks are comparable to elephant tusks. The tusks of the *Lystrosaurus* and the dicynodontoid described here were ever-growing and anchored to the maxilla by a periodontal ligament (i.e. gomphosis). Among therapsids, LeBlanc *et al*. (2018) reported evidence for a ligamentous tooth attachment in the cynodonts *Diademodon*, *Cynognathus*, *Galesaurus*, the therocephalian *Bauria*, gorgonopsians and tapinocephalids, and Jasinoski & Chinsamy (2012b) made a similar report for *Tritylodon*. The tusks of elephants are ever-growing and in cases of trauma, 'the portion of the tooth developing at the time of an injury usually has a crinkled appearance with irregular formation increasing towards the growing end and the tissues showing signs of defective mineralization' (Miles & Grigson 1990: 404). In elephants, the most common reported sources of trauma are falling or fighting. In addition, tusk abrasion and wear are frequent causes of damage in digging animals like walruses (Steenkamp 2003). Digging and foraging have been proposed as potential uses for dicynodonts tusks (e.g. King 1990; King & Cluver 1991) and thus, it is unsurprising that they would occasionally accrue damage.

Despite being distinct species separated by millions of years, SAM-PK-K011603 and NHCC LB836 share remarkably similar, albeit unusual, dental histology, which in turn suggests the potential for similar behaviour and utilization of their tusks. The limited sample here does not preclude alternative functions in different species; however, it does lend support that many – if not most dicynodonts – used their tusks to forage and dig, and that occasionally these activities resulted in trauma to their developing dental tissues. Continued analysis of the internal anatomy of dicynodont tusks will elucidate more about their evolution and development as well as shed

light on their functional significance. This study demonstrates how given the lack of external, gross anatomical indications of the abnormality noted here, histological sampling is an important tool in garnering more information about the biology of these animals.

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INSTITUTIONAL ABBREVIATIONS

SAM Iziko South African Museum, Cape Town.
NHCC National Heritage Conservation Commission, Lusaka.

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