

Crocodile Tooth Histology from a Pliocene Deposit in Chinchilla, Queensland

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Abstract

Chinchilla in the Western Downs Region of Queensland is home to the Chinchilla Rifle Range, a palaeontological site that has produced a significant well-preserved Pliocene vertebrate assemblage. Here, we describe and discuss the histology of a crocodile tooth recovered from the ca 3.5-million-year-old Chinchilla Sand deposit in the Rifle Range. The tooth is from the posterior jaw and likely belongs to a species of *Paludirex*. We discuss the tooth micro-morphology in relation to what is known about tooth histology in extant and extinct crocodylians with brevirostrine and platyrostral skull morphology. We hypothesised that there should be several similarities in the tooth micro-structures between related extinct and extant taxa. We found that the Chinchilla Sand fossil tooth is characterised by thin enamel that is likely prismless but shows incremental striations (also seen in dentine), similar to other crocodylians. This short study highlights the importance of microscopic techniques applied to fossil material. With further fossil evidence emerging from Chinchilla, and application of three-dimensional microscopy techniques to understand the nature of *Paludirex* enamel prisms, a better understanding of reptile palaeobiology can be developed for Queensland and Australia.

Keywords: dental microstructure, crocodile, enamel, *Paludirex*

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Introduction

Chinchilla Sand (previously ‘Chinchilla Formation’ Woods, 1956) is a collective of fluvialite deposits that extend for approximately 65 km between Nangram Lagoon and Warra, being predominately exposed along the Condamine River in Queensland (Price, 2012). Most, if not all known fossil deposits recovered from this region date to the

Pliocene (Bartholomai & Woods, 1976; Wilkinson et al., 2021). Palaeontological surveys and collection from the Chinchilla Sand have recovered at least 63 taxa of fauna spanning fish, reptiles, birds and mammals (Louys & Price, 2015). The reptiles include at least one (Crocodylidae) or possibly two families (Gavialidae) of crocodylians represented by cranial and/or dental material (Ristevski et al.,

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2020, 2021). No microstructural analyses have yet been conducted on any crocodylian specimens recovered from the Chinchilla Sand. The aim of this study is to use histology to gain preliminary insights into the fundamental structure of tooth micro-morphology in a Pliocene crocodile at Chinchilla, and test whether it might have been similar to that reported for extant and extinct crocodile taxa that exhibit brevirostine and platyrostral (Griff & Kirshner, 2015) skull morphologies. With suitable microscopic preservation, similar analyses could serve as a possible methodological future avenue to shed light on ancient crocodile dietary and predatory behaviours.

Today, Australia is home to two extant crocodile species, *Crocodylus porosus* (the saltwater crocodile) and *C. johnstoni* (the freshwater crocodile) – both found along the north of the country stretching from Western Australia to Queensland (Johnson, 1973). Prior to the arrival of *Crocodylus* in the Pliocene (Molnar, 1977), crocodylians of Cenozoic Australia comprised species within the Mekosuchinae (Crocodylidae), and possibly the Tomistominae (a clade of uncertain familial representation but possibly part of the Gavialidae; Ristevski et al. 2020; 2021). Nuclear and mtDNA suggest emergence of *Crocodylus* in the Miocene of the Indo-Pacific, 9 to 16 million years ago, a point from which the genus spread globally throughout the world, with most extant species occurring within the tropics (Srikulnath et al., 2015). The geologically oldest mekosuchine is *Kambara* from the early Eocene (Willis et al., 1993).

Mekosuchines comprise several genera, with species of *Paludirex* being the largest in body mass and most widely distributed through the Plio-Pleistocene. Based on proportions of their massive, broad snout and dorsally positioned eyes, species of *Paludirex* likely had a lifestyle similar to the mugger crocodile, with a diverse diet of fish, birds and mammals. Two species of *Paludirex* are recognised: *P. vincenti* occurring during the Plio-Pleistocene (with Chinchilla yielding the type specimen of the genus); and *P. gracilis* known only from the Pleistocene (Ristevski et al., 2020). An isolated posterior button tooth of the lower jaw, likely belonging to *Paludirex vincenti* and recovered from the Chinchilla Sand at the Chinchilla Rifle Range, is the focus of our study.

Crocodylian dentition has been of key interest in the study of reptilian biology because crocodiles are equipped with a highly specialised continuous tooth replacement (Poole, 1961; Finger et al., 2019; Whitlock & Richman, 2013). This process has resulted in large, empty pulp chambers comprising most of the tooth's internal structure, with a cap of dentine filling most of the small crown, and a relatively thin layer of enamel coating the entire tooth, including the root. Mesenchymal stem cells in the dental laminae of the root grow a tooth bud adjacent to the functional tooth, growing through the root and into the pulp chamber (Wu et al., 2013). As the bud continues to mature, the crown of the functional tooth, which is defined from the root by a distinctive 'hip', is dislodged and replaced by the bud as it finally erupts, reabsorbing the previous crown's root (Figure 1; Fruchard, 2012). As a result, crocodiles are notable polyphodonts able to replace their teeth up to 50 times in one lifetime (Poole, 1961). Understanding their tooth structure in the present and deep time is thus of great value to furthering knowledge of crocodile biology and tooth function.

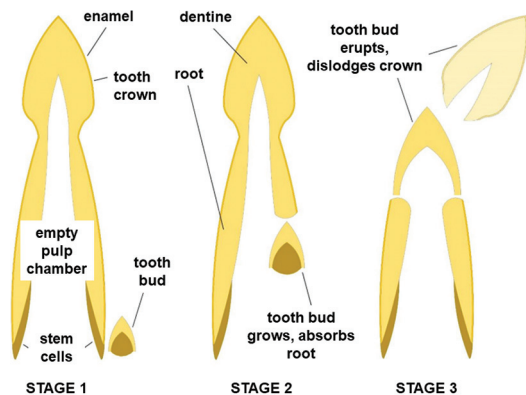


FIGURE 1. Schematic stages of crocodile tooth replacement. 'Functional' teeth are replaced by 'successor' teeth.

Generally, the morphology of teeth along the jaw of crocodylians does not vary as much as in mammals (Enax et al., 2013). Extant crocodylian teeth are thecodont, cone-shaped and unicuspid (Dauphin & Williams, 2008). They vary in shape and sharpness from the anterior to posterior in both the upper and lower jaws (Sellers et al., 2019). Tooth size and shape may also differ with sex

and age. Mekosuchines have the fifth premaxillary tooth larger than first maxillary tooth, and a high degree of disparity in tooth size (although not expressed in species of *Quinkana*) (Willis, 1997). Species of *Paludirex* had mostly conical-shaped teeth, a feature seen in other brevirostrine members of the family (e.g. *Crocodylus*) and thought to be associated with a feeding behaviour related to the suppression of struggling prey (Stein et al., 2017).

Histology applied to palaeontological specimens reveals the microstructure of enamel and dentine, which can be used to understand tooth growth and formation in relation to jaw and dietary biomechanics, evolution, and environmental factors in deep time (e.g. Cabreira & Cisneros, 2009; Zanolli et al., 2016; Heckeberg & Rauhut, 2020; Whitlock & Richman, 2013). Both modern and fossil crocodylian tooth structure and function have been studied, including experimental biomechanics of biting force, tooth replacement questions, and dentine incremental lines in alligatorids (e.g. Enax et al., 2013; Poole, 1961; Finger et al., 2019; Dauphin & Williams, 2008; Kieser et al., 1993; Szweczyk & Stachewicz, 2020; Kundanati et al., 2019; Sato et al., 1990; Mishima et al., 2003), but limited dental histology data exist in other members of the order. Crocodile dental enamel is particularly thin (relative to dentine in other reptiles), reportedly in the order of 100–200 μm in *C. porosus* (Enax et al., 2013). Using synchrotron X-ray microtomography methods, Enax and colleagues (2013) also reported that enamel in *C. porosus* does not show defined prisms and enamel crystallites, and as such their enamel is often referred to as ‘prismless’ or ‘aprismatic’. This is also one key feature that distinguishes reptile enamel from mammalian enamel (see Sander, 2000 for review in non-mammalian amniotes). The thin and aprismatic nature of crocodile tooth enamel may link to dental functionality in prey acquisition (Enax et al., 2013). Furthermore, the need for frequent tooth replacement could be justified by high frequencies of tooth damage resulting from grabbing prey (Enax et al., 2013). This study describes the histological features of enamel and dentine of the Chinchilla Sand tooth, and compares it to what is known for other crocodiles.

Materials and Methods

Chinchilla Sand, including its exposures in the Chinchilla Rifle Range, is located in the Western Downs Region of Queensland (Figure 2). The formation consists of fluvial deposits up to 30 m thick and includes interbedded gravels, sand, silts and clay (Louys & Price, 2015). The exposures in the Chinchilla Rifle Range preserve multiple episodes of deposition and typical fluvial structures such as cross-bedded sands. The Chinchilla Sand is thought to date to approximately 3.5 Ma based on biochronological correlation with other Pliocene vertebrate deposits in Australia (Bartholomai & Woods, 1976; Louys & Price, 2015).

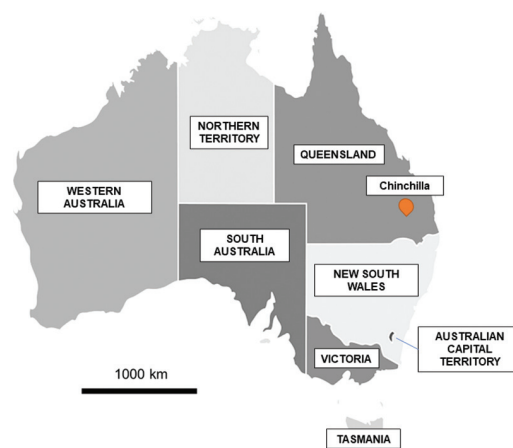


FIGURE 2. Schematic map of Australia showing (orange mark) Chinchilla in Queensland.

Several recent fieldtrips to the Rifle Range have yielded surface-collected fossils, including dental specimens, from which we selected a crocodile tooth for histology. The tooth likely belongs to *Paludirex vincenti*. Its gross morphology (Figure 3) closely resembles posterior or ‘button-shaped’ crocodile teeth (thecodont, cone-shaped, unicuspid, Dauphin & Williams, 2008; Sander, 1999). Further, species of *Paludirex* are similar in size to extant *C. porosus* and thus are relatively large-bodied crocodylids. On the basis of tooth morphology, we estimated the tooth to have come from the right side of the lower jaw. We acknowledge, however, that tooth shape may change throughout an individual crocodile’s lifespan (Fruchard, 2012). The size also depends on age and sex, which are unknown in the case of our isolated specimen.

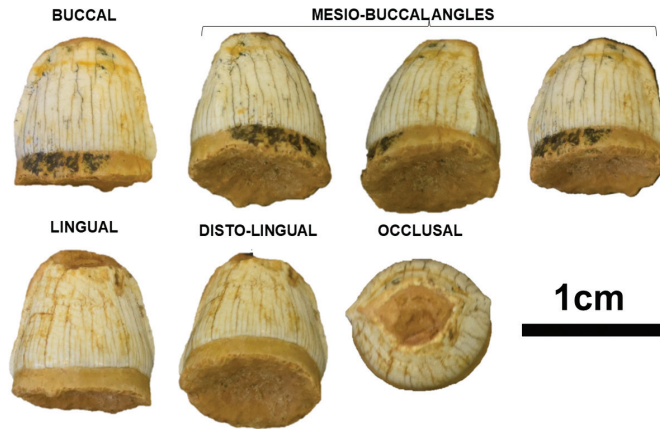


FIGURE 3. The crocodile tooth examined in the present study shown from different anatomical perspectives.

Poole (1961) termed crocodile teeth ‘functional’ and ‘successor’, with reference to their stage of formation and eruption. Based on Poole’s (1961) classification, our specimen appears to be a complete crown with a root cervix of a successor tooth. A functional tooth would include a hollow root extending from the crown. We are unable to provide an ontogenetic age estimate for this individual, though the size of the crown (see measurements below) implies it was an adult (Sellers et al., 2019).

Photographs of the tooth were taken from multiple angles. Using standard digital calipers we also took three repeated measurements of the specimen: maximum length, crown height, mid-crown length, mid-crown width, crown base (bordering with cervix) length, and crown base (bordering with cervix) width. We then followed standard methods for the preparation of fossil material for histological thin sectioning (e.g. Mahoney et al., 2017; Miskiewicz et al., 2019, 2020; Walker et al., 2020). The tooth was embedded in an epoxy resin solution and left to set overnight in 25 mm Buehler SamplKups® that had been coated with a release agent. This was followed by a section-cut made longitudinally (in a bucco-lingual plane) using a MICRACUT® 151 precision cutter equipped with a diamond cutting disc. The exposed surface was then smoothed with sandpaper, dried, coated with Araldite® glue, attached to glass microscope slides (46 × 27 mm) and left to dry. The glued sample was then trimmed on the Kemet MICRACUT® 151 precision cutter before being mechanically ground with a Buehler EcoMet 300® grinder-polisher until

optical clarity and an approximate 100 µm thickness were achieved. The sample was cleaned in an ultrasonic bath and immersed in a series of ethanol baths to sequentially dehydrate the sample. This was followed by a coating of xylene to eliminate all remaining water. Finally, the sample was cover-slipped with DPX glue. The sample was imaged using an Olympus BX53 high-powered microscope equipped with a DP74 camera. Regions of interest were photographed at objective magnifications of 20×, 40×, 60× and 100× where applicable. The reported microscopic measurements (e.g. the width of enamel band, distance between enamel increments) were measured using the ‘straight line’ tool of the open access ImageJ® software. We also estimated average (AET) and relative enamel thickness (RET) from a two-dimensional (2D) image of the full crown following Conroy and colleagues (1995) where $AET = c$ (area of enamel) / e (enamel–dentine junction, EDJ) and $RET = ((c/e)/b$ (dentine area) × 100) (Figure 4). We note the tip of the tooth crown is slightly worn, so RET and AET are not complete. We also acknowledge that defining prism morphology in reptilian enamel is best achieved using SEM methods (Sander, 1999) and, as such, ground histology has limited capabilities in clarifying whether enamel is aprismatic. Therefore, we provide only preliminary insights into enamel micro-morphology and focus more on a fundamental description of tooth micro-morphology, including enamel thickness, dentine–enamel proportions, and incremental nature of enamel and dentine (Kinaston et al., 2019).

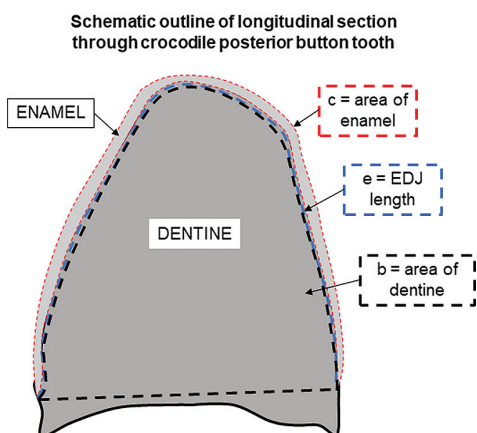


FIGURE 4. Schematic illustration of how tooth longitudinal section measurements used to calculate average enamel thickness = c (area of enamel) / e (enamel–dentine junction, EDJ), and relative enamel thickness = $((c/e)/\sqrt{b})$ (dentine area) $\times 100$, are derived. The measurements follow methods by Conroy et al. (1995).

Results

The gross anatomical dimensions of the tooth were: maximum length = 11.01 mm, mid-crown length = 9.60 mm, mid-crown with = 9.33 mm, crown base length = 9.81 mm, and crown base width = 8.76 mm. The preservation of histology was suitable for outlining its basic descriptions. The dentine proportion of the tooth was ~99.87%, showing the enamel to be relatively thin (~0.13%, area of cap = 6.91 mm², mid-crown average width taken from 15 measurements = 202.29 μ m, min = 167.77 μ m, max = 247.69 μ m). The estimated AET was 0.35 mm, whereas RET was 4.77 (unitless). Histologically, dentine showed increments (von Ebner's lines) and typical tubule structures that measure an average of 1.06 μ m peripherally (close to EDJ) (Figure 5). Enamel appeared possibly prismless, as is typical of reptiles, with no clear cross-striations detected in the 2D section and using light microscopy. Upon higher magnification examination and multiple re-focus attempts, small regions of cross-striation-like enamel were possibly seen (Figure 6), but it is inappropriate to evaluate this sufficiently using ground histology methods alone. Sander (1999) notes that prior ground histology attempts have found it difficult to examine enamel prisms in reptilian teeth. However, longer incremental striations running parallel to the EDJ were observed, although they were irregular in appearance, showing frequent curving (Figure 6). It was not possible to count the exact number of these striations per the entirety of the enamel thickness, but they appeared to occur every 3.4 μ m (Figure 6).

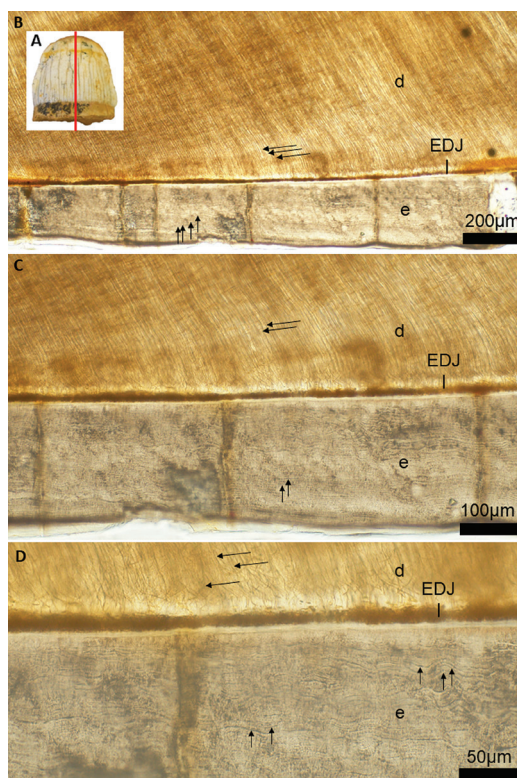


FIGURE 5. A series of histology images captured at the mid-crown of the crocodile tooth sample at an increasing magnification from B to D. The images are from an axial (longitudinal, A) cut of the tooth made into a thin section and viewed through light microscopy. d: dentine, e: enamel, EDJ: enamel–dentine junction. Vertical arrows point to incremental striations in the enamel, whereas the horizontal diagonal arrows point to dentine tubules.

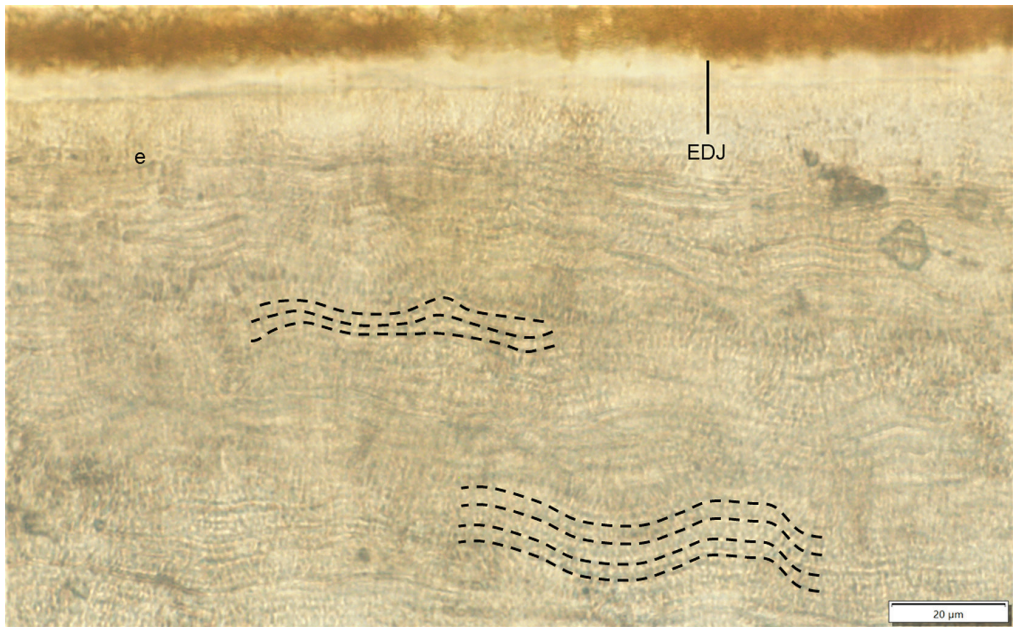


FIGURE 6. A close-up on a selected region of interest in regional enamel (e) from the mid-crown of the tooth. Enamel displays an irregular orientation of long incremental lines that run parallel to the enamel–dentine junction (EDJ). A series of localised successive lines can be identified – see dashed lines.

Discussion

The crocodile tooth from the Pliocene Chinchilla Sand shows microstructures that resemble features reported for other extant and extinct crocodylians – enamel is relatively thin, incremental and likely aprismatic, with incremental dentine consisting of numerous tubules (Enax et al., 2013; Sander, 2000; Sellers et al., 2019). The average width of enamel band in our specimen is in the range of measurements (100–200 μm) reported for *C. porosus* (Enax et al., 2013) and *Alligator mississippiensis* (Sato et al., 1990). Isolated posterior tooth specimens from fossil *Iharkutosuchus* and *Allognathosuchus* show AET (0.21 mm in *Allognathosuchus*) and RET (4.07 in *Iharkutosuchus*) measurements similar to that of our specimen (Sellers et al., 2019: 175). However, the Chinchilla Sand *Paludirex vincenti* RET value appears more similar to *Iharkutosuchus*. Sellers and colleagues (2019) reported AET and RET for a range of ontogenetic series of *A. mississippiensis* showing that enamel thickness increased with skull and body size. The AET and RET data for our specimen mirror closely those of the adult *A. mississippiensis*. We note that Sellers and

colleagues (2019) used micro-computed tomography (micro-CT) measurements rather than 2D histology methods. However, Olejniczak and colleagues (2008) had previously concluded that three-dimensional (3D)- and 2D-based measurements for AET/RET calculations remain highly agreeable. Because crocodylians possess the strongest bite-force of any extant animals (up to 16,414 N in *C. porosus*, Erickson et al., 2012), yet develop thin enamel, the extreme mechanical stresses which crocodylians place upon their teeth must be accommodated through their dental morphology. As such, root-dentine is far softer than crown dentine, resulting in a greater capacity for withstanding high impacts without deformation (Enax et al., 2013). The large roots maximise the amount of surface area in contact with the jawbone, dissipating the high energy loads from the individual's powerful bite (Enax et al., 2013). The use of crocodile teeth in grappling prey does also mean more frequent damage to a tooth that is coated with thin enamel, which can lead to higher rates of replacement. Indeed, it has been proposed that the specialised dental stem cell niche in crocodiles allows them to

generate new teeth rapidly and when necessary (Wu et al., 2013). We speculate that the Chinchilla crocodile would have exhibited similar prey-grappling behaviours to those known for modern crocodiles.

The lack of well-defined enamel rods found in the Chinchilla specimen agrees with the aprismatic nature of enamel reported for fossil and extant crocodiles, as well as other reptiles (e.g. *A. mississippiensis*, Sato et al., 1990). As prior studies using synchrotron X-ray microtomography or SEM have shown, the crystallites in crocodylian enamel are packed very tightly (Enax et al., 2013), oriented perpendicular to the surface of the tooth, forming a configuration known as parallel crystallite enamel (Sander, 2000). Enax and colleagues (2013) and Sato and colleagues (1990) reported findings very similar to ours, where longitudinal striations running parallel to the EDJ were seen with no shorter-period cross-striating incremental lines in *C. porosus* and *A. mississippiensis*, with Sato and colleagues (1990) naming those “lamella-like” (p. 167). Dentine tubule diameter in our specimen is also in the same range (1–2 µm) as a Thai *C. porosus* reported by Dauphin and Williams (2008). The existence of dentine incremental lines in our specimen, likely von Ebner lines, is also corroborated with those reported for *A. mississippiensis* and *Caiman crocodilus* (Erickson, 1996).

These comparisons imply that the Chinchilla crocodile showed tooth characteristics similar to those of extant crocodylians. However, we emphasise that these prior studies have used SEM, micro-CT and Synchrotron X-ray microtomography methods to examine enamel crystallites at 3D resolution and orientation. As our study is limited to histology, future analyses using complementary microscopy techniques will provide more insights into the comparison between samples from extinct and extant specimens, and will allow for a better integration of new with published data (Sander, 1999). This may be particularly useful for noting evolutionary differences in hydroxyapatite crystallite micro-morphology and texture. For example, a recent study by Vallcorba and colleagues (2021) noted postdepositional enamel differences between an Upper Cretaceous fossil crocodylomorph from Spain and *C. niloticus*, having applied Synchrotron X-ray microdiffraction techniques.

We acknowledge that the small sample size in our short study makes it difficult to make any more concrete conclusions for reptile palaeobiology in Queensland. Follow-up studies with larger sets of teeth and utilising multiple microscopy techniques will help build a more in-depth picture of Australian crocodylian dental structure and function.

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