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The significance of enamel thickness in the teeth of *Alligator mississippiensis* and its diversity among crocodyliforms

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Abstract

Enamel is the hardest tissue in the vertebrate body. Although variation in enamel microstructure is often linked with diet, the gross proportions of the tissues that compose vertebrate teeth remain relatively unexplored in reptiles. To investigate the patterns of enamel thickness in crocodyliforms, we used micro-computed tomography scanning to evaluate enamel thickness in teeth of *Alligator mississippiensis* from rostral, intermediate and caudal locations in the tooth row from an ontogenetic range of animals. We also evaluated enamel thickness in the derived teeth of several extinct crocodyliforms with disparate craniodental morphologies. Our data show that enamel thickness scales isometrically with skull length. We also show that enamel is relatively thicker in caudal teeth than teeth in more rostral positions, concordant with the higher bite forces they experience during feeding. We compared our data with existing enamel thickness data reported from dinosaurs and mammalian taxa to find that archosaurs have markedly thinner enamel than most mammals. These findings serve as a basis for future investigations into the diversity and function of the proportions of dental tissues.

Introduction

Teeth are the structures many vertebrates employ to acquire and process food. Upon contact with food, muscle forces are transferred from the feeding animal into the food. Although these forces are integral to the function of the feeding apparatus, in excess they can lead to tooth wear or catastrophic tooth failure, compromising tooth function and thus feeding performance (King *et al.*, 2005). Thick enamel is thought to prolong the functional lifespan of a tooth by preventing fracture and resisting wear (Lucas *et al.*, 2008; Loch *et al.*, 2015). In animals with limited tooth replacement like mammals, traits like thick enamel presumably benefit the organism by prolonging the functional lifespan of teeth. However, polyphyodont vertebrates that replace their teeth continuously may not suffer comparable problems from losing a tooth, and thus it is unclear if and how polyphyodont vertebrates mediate enamel thickness over ontogeny and phylogeny.

Enamel is the hard, mineralized tissue on the outside of the typical tetrapod tooth that directly interacts with food (Fig. 1). Enamel structure has received a large share of attention in mammals including primates (Maas & Dumont, 1999), equids (Pfretzschner, 1993; Kilic *et al.*, 1997) and cetaceans (Loch *et al.*, 2015), as well as dinosaurs (Hwang, 2005) and reptiles in general (Sander, 1999). Only a few studies have reported gross proportions of dental tissues (Dumont, 1995; Martin, 2003; Loch *et al.*, 2015; Jones *et al.*, 2018), whereas most focus on micro- and ultrastructural details of enamel.

Thick enamel affords resistance to fractures that could affect teeth subject to high bite forces, such as those employed by durophagous taxa like bone-cracking hyenas and extinct molluscivorous placodonts (Kay, 1981; Dumont, 1995; Sander, 1999; Lucas *et al.*, 2008). Additionally, thick enamel provides more material to be worn away before a tooth loses function. This would be useful for taxa with abrasive diets, such as herbivores that consume phytoliths present in grasses or inadvertently consume dust or sand on vegetation in arid environments (Couzens, 2016).

An understanding of the variation of enamel thickness within a single taxon is necessary before we can attempt to study how enamel thickness varies with biomechanics and diet, and *Alligator mississippiensis* provides an opportunity with which to explore scaling relationships of dental tissues. *Alligator* ontogeny is characterized by a dramatic increase in body mass and bite force associated with shifting dietary niches (Erickson *et al.*, 2003). Further, *Alligator* teeth vary in morphology both among teeth from differing positions in the same individual and ontogenetically in the same tooth position (Fig. 2). Rostral teeth are slender and are used for apprehending prey whereas caudal teeth are blunt and used for crushing

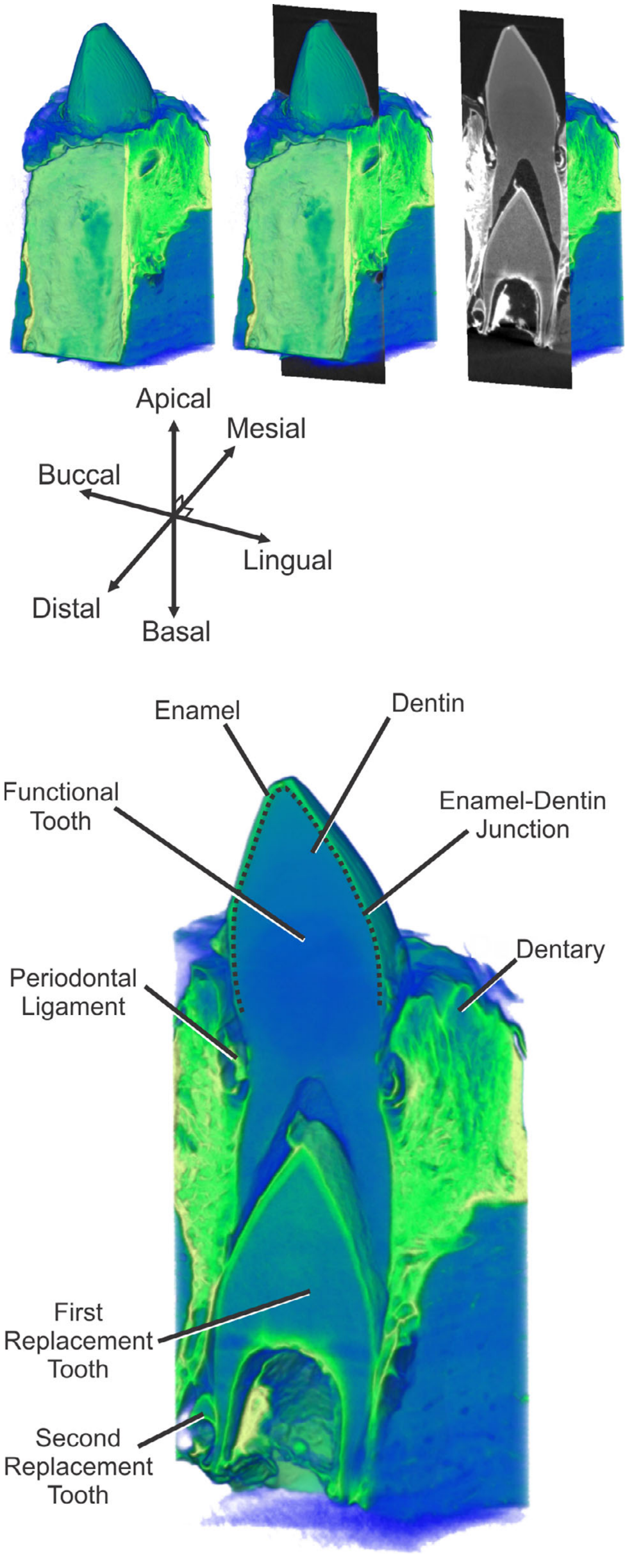

Figure 1 Caudal tooth of an individual of *Alligator* showing the studied dental tissues in situ. Green indicates high radiodensity, and blue indicates low radiodensity

with higher bite forces. Thus, the loading environment of a tooth substantially depends on both the location of the tooth along the tooth row and the size of the organism. However, it is unclear if this variation in loading is associated with differences in enamel thickness.

Here, we present the first whole-tooth measurements of absolute (or average) and size-standardized (or relative) enamel thickness (AET and RET, respectively) of crocodylian teeth. AET is an estimation of the average distance from the enamel–dentin junction to the outer enamel surface and is a linear measurement. RET is a dimensionless value that allows for comparisons of the relative thickness of enamel across disparate scales. We quantified AET and RET for a rostral, intermediate and caudal tooth in seven individuals of *Alligator mississippiensis*.

Alligators have relatively generalist diets among crocodylians (Brochu, 2001). Though there is some diversity in extant crocodylian feeding, the trophic diversity of extinct crocodyliforms is far greater (Case, 1925; Brochu, 2001; Turner & Sertich, 2010; Ősi, 2013). To begin to understand the relationship of enamel thickness and diet, we also measured enamel thickness in the caudal, relatively blunt molariforms of select extinct crocodyliforms with derived dental morphologies and presumed diets: an unnamed protosuchid (UCMP 97638), *Iharkutosuchus* (MTM VER 2018.837) and *Allognathosuchus* (YPM-PU 16989). UCMP 97638 is a protosuchian from the Jurassic of North America. Its bicuspid teeth had wear patterns that suggest active oral processing (Ősi, 2013). *Iharkutosuchus* is a stem eusuchian from the Cretaceous of Europe (Ősi *et al.*, 2007) and has complex, multi-cusped teeth reminiscent of mammalian dentition (Ősi & Weishampel, 2009) that are thought to engage in oral processing of plant matter. *Allognathosuchus* is an alligatoroid from the Eocene of North America with massive, globidontine teeth that have been interpreted as adaptations for durophagy (Simpson, 1930; Carpenter & Lindsey, 1980; Sander, 1999).

In order to compare dental proportions in crocodyliforms with those of others, we collected published enamel thickness data from select dinosaurs (Hwang, 2005), primates (Dumont, 1995; Olejniczak *et al.*, 2008), chiropterans (Dumont, 1995), odontocete cetartiodactyls (Loch *et al.*, 2015), terrestrial cetartiodactyls (Passey & Cerling, 2002), equids (Pfretzschner, 1993) and rodents (Wahlert, 1968; Moinichen *et al.*, 1996). In some cases, we collected measurements directly from scaled photographs. However, we could not control for planes of section and consistency in preparation.

Hypotheses

Because AET is a linear measure and should depend on size, we hypothesize that the variance in AET will be best explained by skull size (Hypothesis 1a). As RET is size-standardized, we hypothesize that the variance in RET will be best explained by tooth position (Hypothesis 1b). Because both AET and skull length are linear measures of size, they should scale with an isometric slope of one (Hypothesis 2a). Because caudal teeth experience the highest bite forces of the tooth

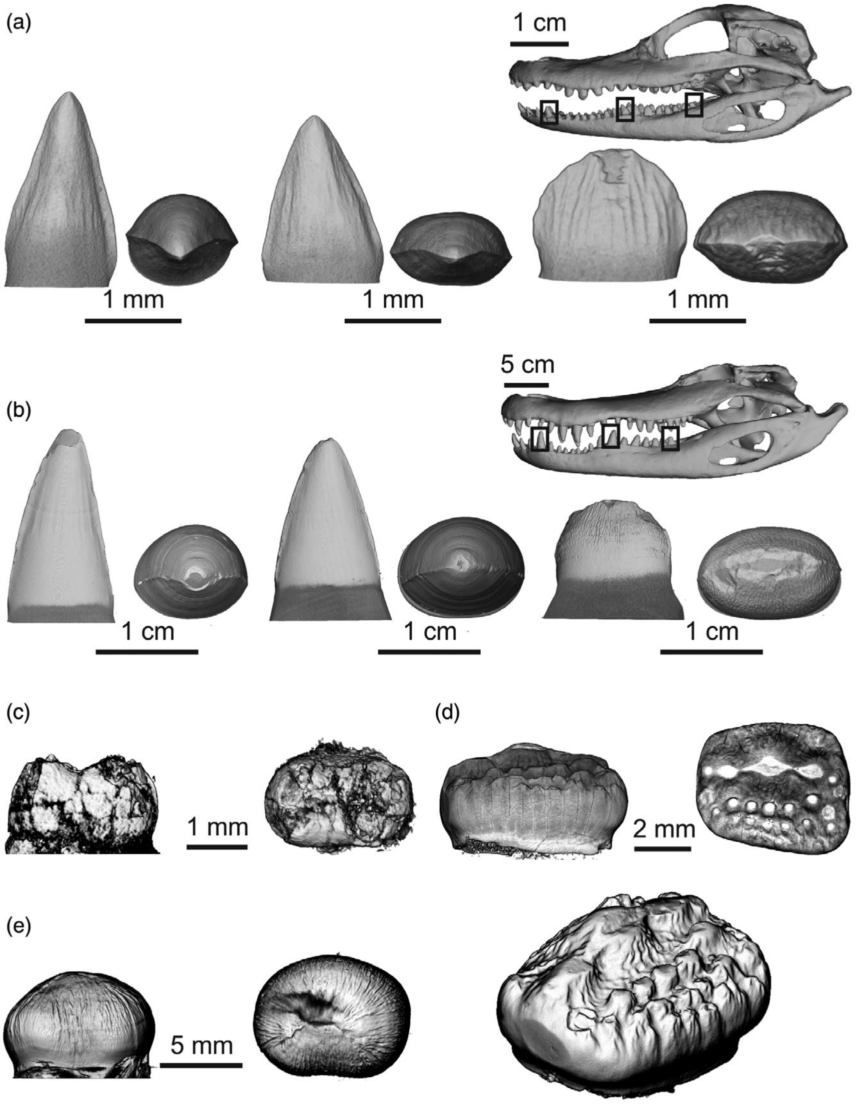

Figure 2 Sampled teeth in the present study. Each tooth is shown in a buccal view to the left and occlusal view to the right. (a) and (b) show changes in tooth shape between small and large individuals. (c–e) show studied fossil crocodyliform teeth. A, individual of Alligator; skull length ~5 cm. (b) individual of *Alligator*; skull length ~33 cm. Rectangles on skulls indicate the rostral, intermediate and caudal tooth positions, which are displayed left to right below each skull. (c) UCMP 97638. (d) *Iharkutosuchus*. (e) *Allognathosuchus*. (c and e) show mesial and occlusal views; (d) shows mesial, occlusal, and oblique views.

row, we hypothesize that RET will be higher in caudal teeth (Hypothesis 2b).

Materials and methods

Study specimens

Seven frozen individuals of *Alligator mississippiensis* were collected from Rockefeller Wildlife Refuge in Grand Chenier, Louisiana. The three most prominent mandibular teeth were removed from frozen individuals; these usually corresponded to the fourth (rostral), thirteenth (intermediate; caniform) and twentieth (caudal; molariform) mandibular teeth. A power analysis with a large effect size showed that seven individuals with three categories will yield a power of over 80%. The studied teeth span the range of *Alligator* tooth morphologies within an individual. Individuals ranged from 5 to 33.0 cm in skull length. Teeth were micro-computed tomography (microCT) scanned (Table 1), and enamel and dentin were manually segmented from the tooth crown in Avizo 9 (Visualization Sciences Group). To define the crown, the most apical slice containing a continuous ring of enamel and the most apical slice that contained no enamel were found; the basal border of the crown was defined as the plane halfway between these two slices. For the purposes of defining the crown, regions of discontinuous enamel resulting from fracture or wear were disregarded.

Table 1 Table of teeth scanned for this study. Individuals of *Alligator* had a rostral, intermediate and caudal tooth scanned at identical settings

Taxon	Specimen	Skull length (cm)	Scan location	Scan parameters	Voxel size (μm)
Alligator	MUVC AL_608	5.0	WUSTL	Scanco μCT 40; 70kV; 10W	8
Alligator	MUVC AL_122	7.30	UTCT	Xradia; 70kV; 10W	14.33
Alligator	MUVC AL_627	12.5	UMVA	Siemens Inveon; 80kv; 10W	21.044
Alligator	MUVC AL_607	16.5	WUSTL	Scanco μCT 40; 70kV; 10W	10
Alligator	MUVC AL_121	20.0	UTCT	Xradia; 70kV; 10W	88.53
Alligator	MUVC AL_152	27.0	UTCT	Xradia; 70kV; 10W	22.77
Alligator	MUVC AL_700	33.0	WUSTL	Scanco μCT 40; 70kV; 10W	15
Allognathosuchus	YPM-PU 16989		UTCT	Xradia; 60kV; 10W	14.69
Iharkutosuchus	MTM VER 2018.837		UTCT	Xradia; 70kV; 10W	9.51
UCMP 97638	UCMP 97638		UTCT	Xradia; 60kV; 10W	12.11

To compare the variation of enamel thickness among various groups, enamel thickness was measured in two molariform teeth of eusuchians: *Iharkutosuchus* and *Allognathosuchus*. The tooth from *Iharkutosuchus* was an isolated element that was most similar to the molariform teeth described by Ősi *et al.* (2007), Ősi (2008). The tooth from *Allognathosuchus* was isolated from the skull and based on its size, shaped and similarly to an articulated molariform tooth, we deduced this tooth was a loose molariform that fit in one of the empty alveoli. An additional *in situ* molariform was imaged from UCMP 97638, but the preservation status of this fossil precluded whole-tooth measures. To compare dental proportions in crocodyliforms with those of other toothed archosaurs, we compared our sample of crocodyliform teeth to measurements reported from linear measurements of sections of dinosaur teeth (Hwang, 2005). To compare enamel thickness between archosaurs and mammals, we surveyed the literature to find or measure enamel thickness data from several mammal clades. Authors have reported AET and RET in primates (Dumont, 1995; Olejniczak *et al.*, 2008) and chiropterans (Dumont, 1995). For odontocete cetartiodactyls (Loch *et al.*, 2015), terrestrial cetartiodactyls (Passey & Cerling, 2002) and equids (Pfretzschner, 1993), we collected various reports of linear measures of enamel thickness. For rodents (Wahlert, 1968; Moinichen *et al.*, 1996), we measured AET from three locations in published photographs of sections and report the average of these measures. As most of the data gathered from the literature lack information about tooth or skull size and are not collected in comparable manners, we cannot perform statistical analyses on these data. However, we present these comparisons as a baseline for further comparative research.

Table 2 Dental data measured from crocodyliform teeth

Specimen	Position	l_{Skull} (mm)	h_{Crown} (mm)	V_{E} (mm^3)	V_{D} (mm^3)	SA$_{\mathrm{EDJ}}$ (mm^2)	AET (mm)	RET
AL 608	Rostral	50	1.90	0.094	0.83	5.2	0.018	1.94
	Intermediate	50	1.90	0.15	0.90	5.4	0.027	2.97
	Caudal	50	0.925	0.11	0.32	2.5	0.044	6.50
AL 122	Rostral	73	1.90	0.090	0.85	3.2	0.029	3.01
	Intermediate	73	1.75	0.13	1.1	4.2	0.031	3.05
	Caudal	73	1.20	0.090	0.44	2.4	0.038	4.95
AL 627	Rostral	125	3.25	0.69	3.0	11.7	0.059	4.08
	Intermediate	125	3.50	0.88	4.9	16.8	0.052	3.08
	Caudal	125	1.70	0.44	1.4	6.5	0.067	6.09
AL 607	Rostral	165	6.00	2.2	21.13	46.5	0.046	1.68
	Intermediate	165	5.00	2.4	17.6	40.0	0.060	2.28
	Caudal	165	1.50	0.59	1.9	8.6	0.068	5.55
AL 121	Rostral	200	6.00	3.6	32.0	53.7	0.067	2.12
	Intermediate	200	5.25	4.9	31.3	46.5	0.106	3.37
	Caudal	200	2.60	1.7	9.3	18.6	0.091	4.31
AL 152	Rostral	270	10.5	10.6	129.6	70.8	0.145	2.96
	Intermediate	270	9.50	14.6	127.1	125.6	0.116	2.30
	Caudal	270	3.50	3.8	24.0	29.1	0.129	4.46
AL 700	Rostral	330	11.0	21.2	192.2	198.0	0.107	1.85
	Intermediate	330	13.8	36.3	368.6	290.4	0.125	1.74
	Caudal	330	4.5	10.3	51.7	73.4	0.140	3.7
Allog.	Caudal		4.75	25.984	143.02	122.107	0.21	4.07
Ihark.	Caudal		2.8	4.1867	36.7362	49.996	0.08	2.52

Allog., *Allognathus*; h_{crown}, crown height; *Ihark.*, *Iharkutosuchus*; l_{skull}, skull length; SA$_{\mathrm{EDJ}}$, surface area of enamel–dentin junction; V_{D}, dentin volume; V_{E}, enamel volume.

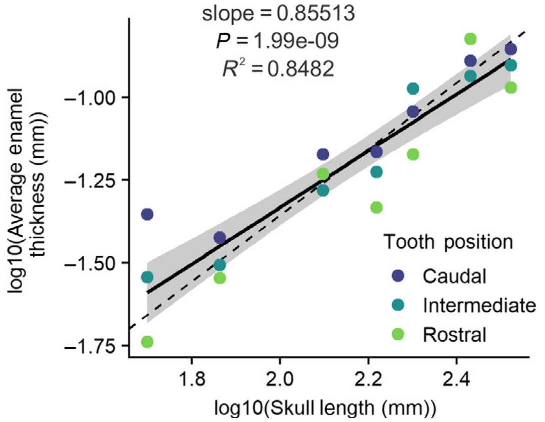

Figure 3 Average enamel thickness scales isometrically with skull length. The dashed line indicates the predicted isometric slope of 1, whereas the bold line indicates the slope of 0.85513 found in the present study. The 95% confidence intervals are shaded.

Dental metrics

Three-dimensional metrics of tissue were calculated following previously established methods (Olejniczak *et al.*, 2008). Average (or absolute) enamel thickness ($\mathrm{AET}_{3\mathrm{D}}$) measures the average linear distance from the enamel–dentin junction (EDJ) to the outer enamel surface. $\mathrm{AET}_{3\mathrm{D}}$ is defined in equation (1):

$$\mathrm{AET}_{3\mathrm{D}} = \frac{V_{\mathrm{E}}}{\mathrm{SA}_{\mathrm{EDJ}}}, \tag{1}$$

where $\mathrm{AET}_{3\mathrm{D}}$ is three-dimensional average enamel thickness, V_{E} is the volume of enamel and $\mathrm{SA}_{\mathrm{EDJ}}$ is the surface area of the enamel–dentin junction. Relative enamel thickness ($\mathrm{RET}_{3\mathrm{D}}$) is $\mathrm{AET}_{3\mathrm{D}}$ divided by the cube root of dentin volume and is a unitless, scale-free metric that permits meaningful interspecific comparisons. $\mathrm{RET}_{3\mathrm{D}}$ is described in equation (2):

$$\mathrm{RET}_{3\mathrm{D}} = \frac{\mathrm{AET}_{3\mathrm{D}}}{\sqrt[3]{V_{\mathrm{D}}}} = \frac{V_{\mathrm{E}}}{\mathrm{SA}_{\mathrm{EDJ}} \cdot \sqrt[3]{V_{\mathrm{D}}}}, \tag{2}$$

where V_{D} is the volume of dentin; all other variables are as in equation (1).

Statistical analyses

To test our hypotheses of relationships of enamel thickness and dental parameters, we determined best-fit linear models of absolute and relative enamel thickness against a combination of continuous (skull length) and discrete (tooth location) variables. To determine the most appropriate models of enamel thickness, we calculated the Akaike information criterion for each model, corrected for small sample size (AICc). The model with the lowest AICc score was considered to be the best model; models that differ by <4 in AICc were considered to be equivalently supported, in which case we selected the model with fewer parameters. Hypotheses 1a and 1b are hypotheses of model selection; a parameter best described by skull length would be best modeled

Table 3 Model summaries of average and relative enamel thickness against predictor variables

Resp. Var.	Pred. Var(s).	Part	β_0	β_1	β_2	β_3	AICc	R^2
AET	l_s	Upper	−2.6758	0.68548	N/A	N/A		
		Estimate	−3.0432	0.85510	N/A	N/A	**−31.04**	**0.8557**
		Lower	−3.4106	1.02372	N/A	N/A		
AET	p_{tooth}	Upper	−0.91504	0.23577	0.17181	N/A		
		Estimate	−1.1289	−0.06671	−0.13067	N/A	11.77	0.04377
		Lower	−1.3428	−0.36919	−0.43314	N/A		
AET	$l_{\mathrm{skull}} + p_{\mathrm{tooth}}$	Upper	−2.64547	1.00507	0.034612	−0.029347		
		Estimate	−2.97742	0.85513	−0.06671	−0.13067	−32.05	0.8995
		Lower	−3.30937	0.70519	−0.168035	−0.231994		
RET	l_s	Upper	11.59270	0.94314	N/A	N/A		
		Estimate	6.4720	−1.4070	N/A	N/A	79.61	0.07632
		Lower	1.135083	−3.75674	N/A	N/A		
RET	p_{tooth}	Upper	5.749797	−1.46287	−1.627887	N/A		
		Estimate	5.086	−2.401	−2.566	N/A	**59.30**	**0.6969**
		Lower	4.423074	−3.33914	−3.504158	N/A		
RET	$l_{\mathrm{skull}} + p_{\mathrm{tooth}}$	Upper	10.87463	−0.16587	−1.562462	−1.727483		
		Estimate	8.127	−1.407	−2.401	−2.566	56.71	0.7732
		Lower	5.380244	−2.64772	−3.239542	−3.404563		

Pred. Var(s)., Predictor variable(s); Resp. Var., Response variable; β_n, nth coefficient in linear model.
For models with one continuous predictor variable (l_s), β_0 is intercept and β_1 is slope. For models with one categorical predictor variable (p_{tooth}), β_0 is the estimate for caudal teeth and β_1 and β_2 are the offsets from caudal teeth estimate for intermediate and rostral teeth, respectively. For models with one continuous and one categorical predictor variable, β_0 is the estimate for caudal teeth (acting as intercept), β_1 is the slope, and β_1 and β_2 are the offsets from caudal teeth estimate for intermediate and rostral teeth, respectively. Upper, 97.5%, Lower, 2.5%. The AICc and R^2 values for the most-supported model are bolded.

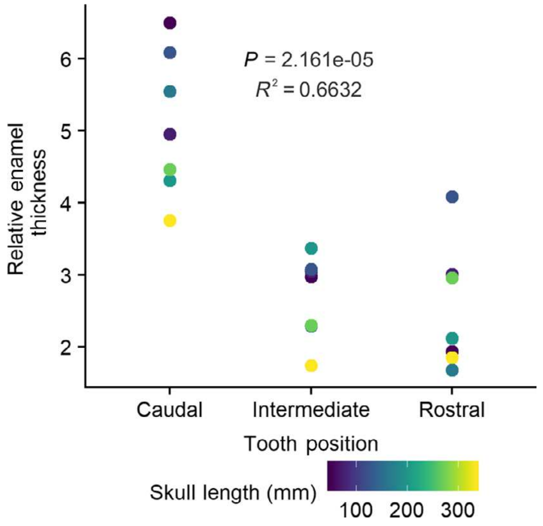

Figure 4 Relative enamel thickness is higher in caudal teeth than in teeth from other locations.

by a continuous variable (Hypothesis 1a), whereas a parameter best described by tooth position would be best modeled by a categorical variable (Hypothesis 1b). Hypotheses 2a and 2b are hypotheses of model content: a linear measure of absolute enamel thickness that scales isometrically with a linear measure of skull size will have a slope that is not significantly different from 0, whereas a linear measure of relative enamel thickness that varies categorically would result in a significant ANOVA.

Results

The results of dental measurements are shown in Table 2. Our results show that absolute enamel thickness scales isometrically with skull length independent of tooth position (Fig. 3; Table 3). By contrast, enamel is relatively thicker in caudal teeth but is independent of skull length (Fig. 4; Table 4).

Hypothesis testing

Hypothesis 1a: We hypothesized that AET would be best explained by skull length, and our data supported this hypothesis (Table 3). The model that best fits our AET data included skull length but not tooth position. *Hypothesis 1b*: We hypothesized that RET would be best explained by tooth position. This hypothesis is also supported by our data (Table 3). The best-fit model for our RET data included tooth position but not skull length.

Hypothesis 2a: We hypothesized that AET would scale isometrically with skull length. We found support for this hypothesis; the scaling coefficient of AET with skull length is not significantly different from 0 (AET slope 95% CI: 0.686548 to 1.023718; Fig. 3; Table 3). *Hypothesis 2b*: We hypothesized that RET would be lower in rostral teeth and higher in caudal. We found partial support for this hypothesis. The best-fit model for RET used tooth position as the covariate, but only the caudal tooth position has higher RET than the other two positions (Fig. 4; Table 4).

Table 4 Summary of average enamel thickness for amniotes

Clade	Mean AET (mm)
Crocodyliform	0.079946
Dinosaur	0.084856
Artiodactyl	1.098
Odontocete	0.251071
Perissodactyl	0.697128
Primate	0.760275
Rodent	0.107556

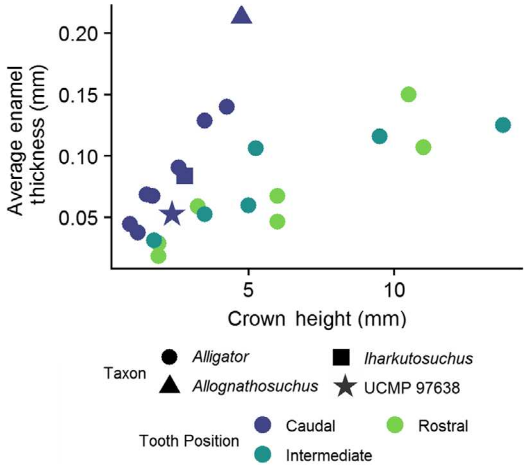

Figure 5 Comparison of average enamel thickness in *Alligator* and fossil crocodyliforms across a range of tooth crown heights.

Comparisons among taxa

Both relative and absolute enamel thickness in the crocodyliform fossils included in the present study were broadly comparable with enamel in extant *Alligator,* although the large globidont molariform of *Allognathosuchus* did have approximately 33% thicker enamel than an *Alligator* molariform of the same crown height (Fig. 5). In general, dinosaur enamel thickness is broadly comparable to dinosaur enamel thickness (Fig. 6) and archosaur enamel is considerably thinner than enamel from mammalian teeth (Fig. 7).

Discussion

This study investigated variation in dental tissue proportions in an ontogenetic series of *Alligator*. As a species with some heterodonty, considerable ontogenetic increases in size and bite force, and ontogenetic shifts in diets, the teeth of alligators are subject to widely variable loading throughout an individual's lifespan.

Relatively thick enamel is linked with crushing bites

We found thicker enamel in teeth involved in crushing feeding, lending support to the link between thick enamel and fracture

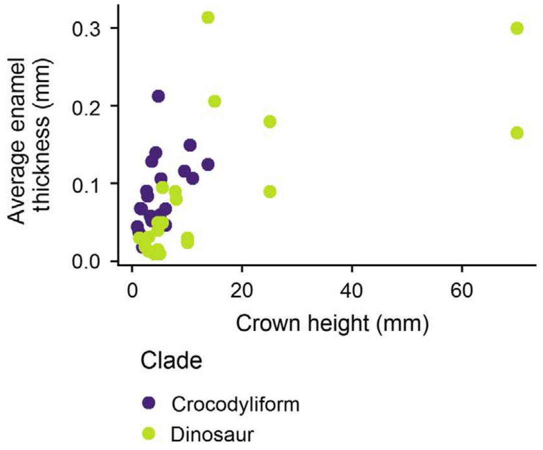

Figure 6 Comparison of average enamel thickness in dinosaurs and crocodyliforms.

resistance. Thick enamel has been suggested to lower the risk of tooth fracture resulting from high stress such those that result from hard-object feeding (Molnar & Gantt, 1977; Kay, 1981; Dumont, 1995; Maas & Dumont, 1999; Lucas *et al.*, 2008). A recent study investigated the relationship between body size and tooth pressure in Alligator (Gignac & Erickson, 2014). The authors found that tooth pressure (bite force divided by tooth contact area) in molariform (caudal) teeth is higher than pressure in caniform (rostral) teeth, and also note that higher pressure in caudal teeth facilitates the role these teeth play in crushing/ cracking hard prey. If thick enamel increases the fracture resistance of teeth (Molnar & Gantt, 1977; Kay, 1981; Dumont, 1995; Maas & Dumont, 1999; Lucas *et al.*, 2008), the relatively thick enamel in caudal teeth may serve to resist the higher stresses that these teeth. Despite the higher bite forces and stresses acting on caudal teeth (Gignac & Erickson, 2014; Sellers *et al.*, 2017), caudal teeth are less frequently broken (Erickson, 1996), suggesting that the thin-enameled rostral teeth are more susceptible to catastrophic failure.

Furthermore, we found *Allognathosuchus* teeth to have considerably thicker enamel than the rest of our studied crocodyliforms. Various workers have interpreted *Allognathosuchus* and similar fossil alligatoroids as durophagous, potentially specializing in eating turtles (Simpson, 1930; Carpenter & Lindsey, 1980). Thus, our data are consistent with the hypothesis that thicker enamel resists fracture formation and tooth failure that may result from high loading. Comparisons of teeth from durophagous, generalist and piscivorous crocodylians may yield additional insights into the interplay of enamel thickness in and feeding forces. Published sections of teeth in the giant Paleocene alligatoroid *Deinosuchus* show enamel that is several millimeters thick (Schwimmer, 2010); these teeth are considerably larger than teeth from any extant crocodylian and have correspondingly thicker enamel.

Crocodyliform and dinosaur enamel thickness

Although our analysis did not have the statistical power to detect subtle differences in enamel thickness between crocodyliforms and dinosaurs, enamel in crocodyliform teeth was thicker than that of dinosaur teeth of an equivalent size in most cases (Fig. 6). It is particularly noteworthy that enamel in two tyrannosaurid teeth was nearly the same thickness as the enamel of a much smaller *Allognathosuchus* tooth and several teeth from *Alligator*. The apparently thicker enamel in crocodyliforms may be related to the characteristic hard-biting feeding behavior. Extant crocodylians generate the highest bite forces measured among vertebrates (Erickson *et al.*, 2003).

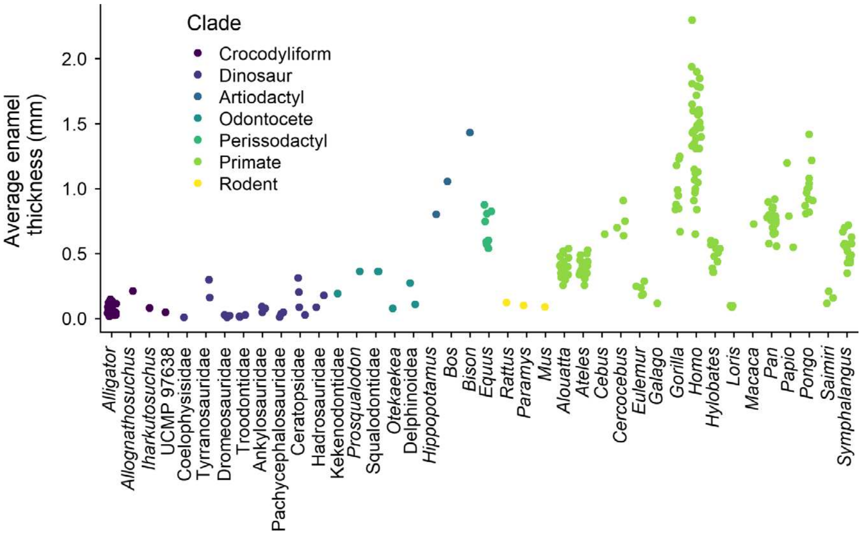

Figure 7 Average enamel thickness in various taxa. The mean AET of each mammalian clade was higher than that of both archosaurian clades.

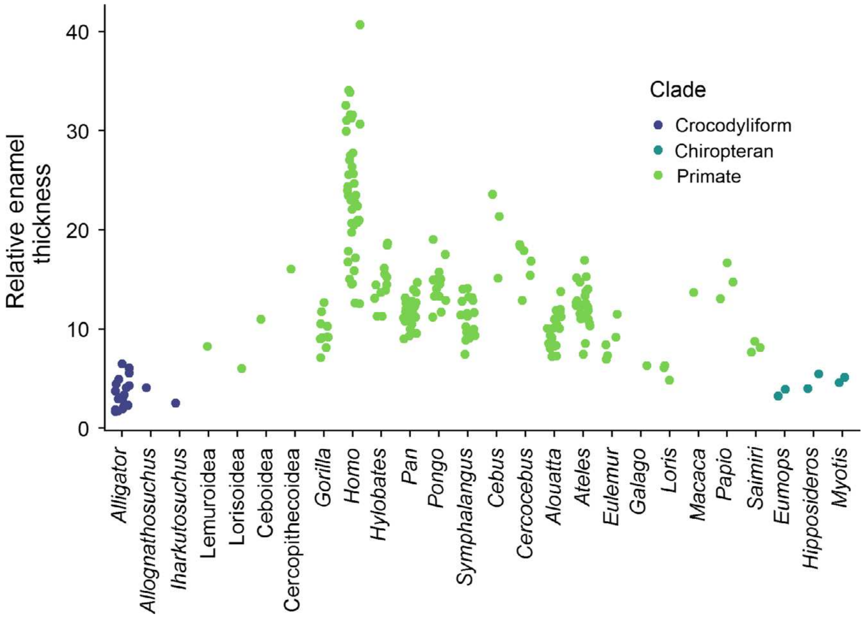

Figure 8 Relative enamel thickness in various taxa. The mean RET of both mammalian clades was higher than that of crocodyliforms.

Mammalian enamel is thicker than archosaurian enamel

Compared to most of our mammalian sample, archosaurs have both absolutely thinner (Fig. 7) and relatively thinner (Fig. 8) enamel. The range of AET in archosaur teeth (0.01–0.314 mm) only overlapped with the bottom of the range of AET from mammalian teeth (0.08–2.3 mm), and the means of each archosaurian AET were lower than the mean AET in each mammalian subclade (Table 4). Potential reasons for this difference include the permanent retention of the adult dentition in primates (and most mammals); that is, enamel may be thicker in mammals because the adult teeth must remain functional for the lifespan of the individual (Maas & Dumont, 1999; Lawn *et al.*, 2013), whereas crocodyliforms and other archosaurs continually replace their teeth. Thus, mammals may be under greater selective pressure to maintain the functional lifespan of a given tooth.

Rodents and odontocetes have thin enamel for mammals, but both taxa have potential reasons for having thin enamel. Rodent incisors are ever-growing (Goldberg *et al.*, 2014), and thus excessive wear does not pose a problem for rodents. Odontocetes are some of the only monophyodont mammals (Loch *et al.*, 2015), and so the evolutionary pressure to maintain functional teeth is likely still in place. However, odontocete evolution has been linked with a decrease in the biomechanical demands of feeding (Loch *et al.*, 2014; Loch *et al.*, 2015). Thus, most odontocetes may simply not need thick enamel. Investigation of the raptorial killer whale (*Orcinus orca*) and sperm whale (*Physeter macrocephalus*) and several extinct macroraptorial odontocetes known from fossils (Lambert *et al.*, 2010) may reveal alternative patterns.

Conclusions

Here, we present the first whole-tooth average and relative enamel thickness measured in an ontogenetic series of reptiles. Our results show that enamel thickness scales isometrically with skull length and that enamel is relatively thicker in caudal teeth. Our findings suggest that thick enamel in the caudal teeth of crocodylians may represent an adaptation to the high bite forces that these teeth experience.

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Author contributions

KCS, ABS and CMH all conceived of the study design, collected data, performed analyses and wrote the paper.

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