Tooth enamel microstructure of *Revueltosaurus* and *Krzyzanowskisaurus* (Reptilia:Archosauria) from the Upper Triassic Chinle Group, USA: Implications for function, growth, and phylogeny

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ABSTRACT

Tooth enamel microstructure can carry significant phylogenetic, ontogenetic, and functional information within amniotes. Here we provide the first descriptions of the tooth enamel microstructure of two Late Triassic taxa, the crurotarsan *Revueltosaurus callenderi* Hunt and the putative ornithischian *Krzyzanowskisaurus hunti* (Heckert), which some consider closely related. To test the hypotheses that enamel thickness corresponds to function and/or phylogeny we analyzed the enamel of each at various scales, measuring enamel thickness and examining microstructural features throughout both longitudinal and cross-sectional thickness using previously established techniques to facilitate comparisons. Both taxa possess thick (up to ~150 µm) enamel for their size (< 20 mm crown height). Enamel in *R. callenderi* ranged from ~5-152 µm across a premaxillary tooth in longitudinal section, and ~42-92 µm in a maxillary/dentary tooth transverse section. *K. hunti* enamel thickness was ~18-155 µm longitudinally and ~29-75 µm transversely. Both also had well-developed basal unit layers (BUL) and weakly developed columnar microstructure. Well-developed lines of incremental growth (LIG) are present in both taxa, through which the columnar enamel grades into parallel crystallite enamel. Their enamel microstructure is therefore grossly similar to that of several ornithischian taxa, especially ankylosaurs, with which they are strongly convergent, and also compares well to rauisuchids and tyrannosaurids. The relatively unique combination of microstructural characteristics in the schmelzmuster of *R. callenderi* and *K. hunti* supports the hypothesis that they are closely related, but does not conclusively preclude a different taxonomic placement for *K. hunti* so we retain its separate generic designation.

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INTRODUCTION

Studies of diapsid tooth enamel microstructure are in their infancy relative to those of synapsids, yet have already yielded insight into amniote evolution ranging from functional interpretations to documenting convergent evolution at multiple levels (Sander, 1999; Hwang, 2005). Within this framework, we examined the enamel microstructure of two teeth each of the unusual crurotarsan *Revueltosaurus callenderi* Hunt, 1989 and the putative ornithischian *Krzyzanowskisaurus hunti* (Heckert, 2002); both archosaurs are known from Upper Triassic strata in the American Southwest (Figure 1). *Revueltosaurus* is a classic example of how much, or how little, fossil teeth can reveal regarding a reptile (non-synapsid amniote). When it was known solely from its teeth, *Revueltosaurus callenderi* was variously considered a prosauropod (Hunt, 1988), an ?ornithischian (Hunt, 1989), an ornithischian "form genus" (Padian, 1990), Ornithischia *incertae sedis* and/or a *nomen dubium* (Sereno, 1991; Norman et al., 2004) and a valid ornithischian taxon (Hunt and Lucas, 1994; Hunt et al., 1998; Heckert, 2002). Upon the discovery of more complete material, including skulls and postcrania, Parker et al. (2005) demonstrated that, although the teeth are diagnostic, *R. callenderi* is actually a crurotarsan archosaur. The present study on the microstructure of *R. callenderi* was first undertaken when *Revueltosaurus* was considered a basal ornithischian, as all of the ornithischian taxa sampled in the definitive treatment of reptilian enamel microstructure (Sander, 1999) were both young (Early Cretaceous or younger) and relatively derived (e.g., *Iguanodon*). Thus, this study was originally designed to help fill in that gap. Now that *Revueltosaurus* has been found to occupy a very different branch of the archosaurian tree, we feel that there is still something to learn from documenting these structures, both to complement and expand upon Sander's (1999) work and to provide basic morphological information on this unusual taxon. Similarly, *Krzyzanowskisaurus* was originally described as *Revueltosaurus hunti* (Heckert, 2002). Heckert (2005) assigned it to its own genus and considered it an ornithischian (Heckert, 2002) but Parker et al. (2005) considered it to likely represent a *Revueltosaurus*-like crurotarsan (Figure 2).

Anatomical abbreviations: BUL = basal unit layer; EDJ = enamel-dentine junction; LIG = lines of incremental growth (incremental lines of some authors); OES = outer enamel surface.

Institutional abbreviations: NMMNH = New Mexico Museum of Natural History and Science, Albuquerque; UCMP = University of California Museum of Paleontology, Berkeley.

MATERIALS AND METHODS

We sectioned two teeth of *Revueltosaurus callenderi* from its type locality (NMMNH locality 1) in the Bull Canyon Formation of eastern New Mexico. These teeth include both a premaxillary (NMMNH P-33799) and a maxillary/dentary (NMMNH P-33798) tooth, as first hypothesized by Hunt (1989) and confirmed by Parker et al. (2005) with more complete materials. The teeth were embedded in epoxy and sectioned at the Steinmann-Institut für Geologie, Mineralogie und Paläontologie, Bereich Paläontologie, then called the Institut für Paläontologie, Universität Bonn, using techniques similar to that utilized by Sander (1999) in his previous studies (Sander, personal commun. 2005). The premaxillary tooth was sectioned longitudinally and the maxillary tooth was sectioned transversely. We also sectioned two teeth of *Krzyzanowskisaurus hunti* from the Petrified Forest Formation of eastern Arizona using similar protocols as described by Hwang (2005). We sectioned UCMP 165213 in longitudinal section and UCMP 165211 in transverse section. All teeth were etched for 30 seconds in 5% HCl. They were then cleaned in an ultrasonic bath for 30 seconds before being coated with gold in a sputter coater. The scanning electron microscope (SEM) images here were taken using a Quanta 200 ESEM utilizing XT microscope server imaging software housed at the College of Arts and Sciences microscopy facility at Appalachian State University.

We note that tooth position is harder to establish in *Krzyzanowskisaurus* than *Revueltosaurus*, as most *Krzyzanowskisaurus* teeth resemble more complex versions of *Revueltosaurus* premaxillary teeth. Heckert (2002, 2005) hypothesized that the taller, less symmetrical tooth crowns of *Krzyzanowskisaurus* lacking additional cingula are probably premaxillary teeth, and that the more complex teeth with labial and lingual cingula likely represent maxillary/dentary teeth. However, it is also possible that these doubly cingulated teeth wore against an outer, rhamphotheca-like (beak) structure. Regardless, according to this hypothesis UCMP 165213 may represent a premaxillary tooth, and UCMP 165211 may represent a maxillary/dentary tooth. Accordingly, we sectioned them longitudinally and transversely, respectively, to facilitate comparisons with *Revueltosaurus*. These teeth
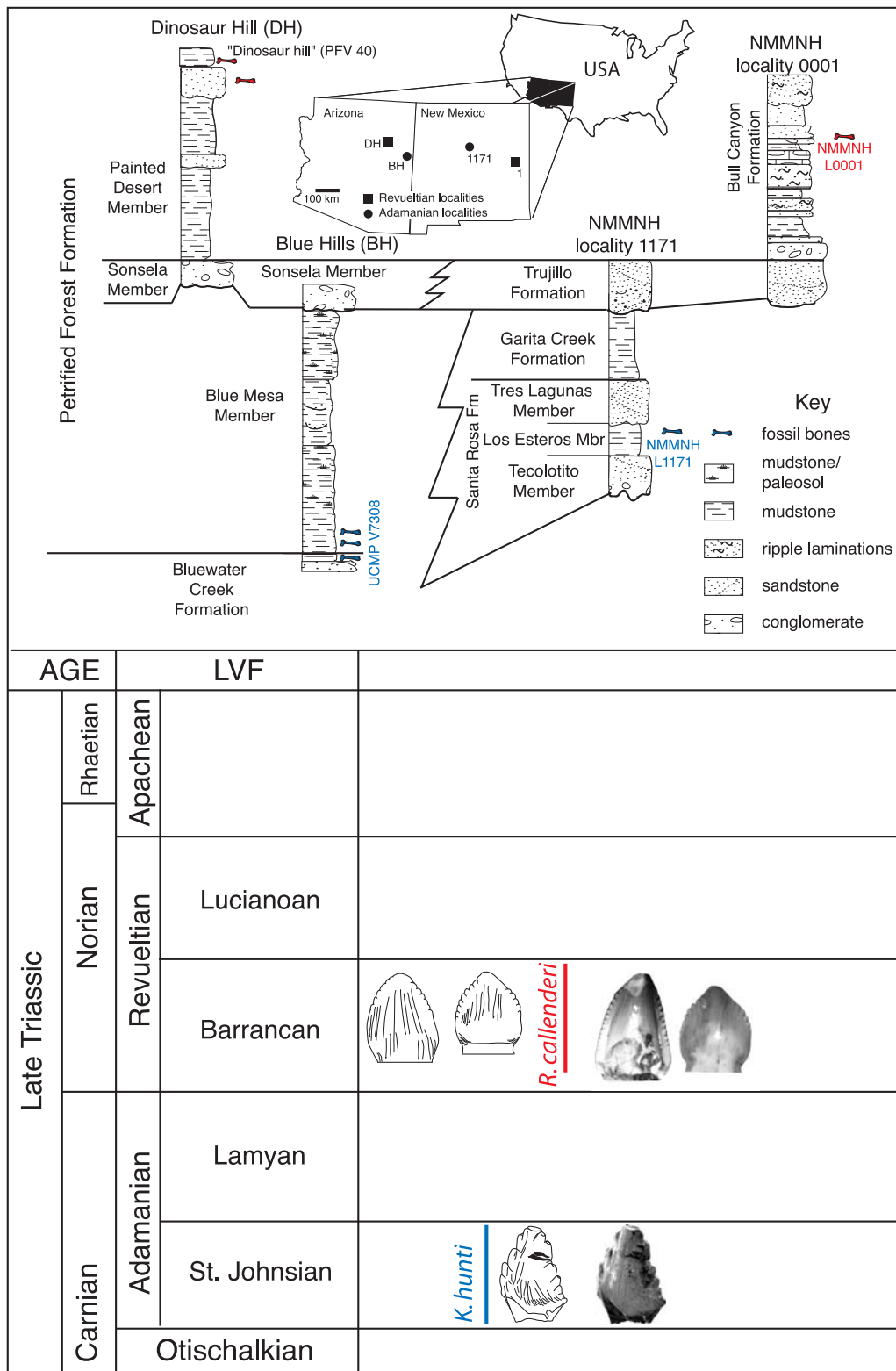
FIGURE 1. Location map and stratigraphic section showing the geographic and stratigraphic distribution of *Revuelto-saurus* and *Krzyzanowskisaurus*. This includes the localites of the *Revueltosaurus* (NMMNH locality 1) and *Krzyzanowskisaurus* (UCMP locality 7307) teeth described here. Tooth illustrations after Heckert (2002, 2005). LVF = land vertebrate faunachron (following Lucas et al., 2007); L-1171 = type location of *Krzyzanowskisaurus hunti*; PFV = locality yielding abundant *Revueltosaurus* fossils in the Petrified Forest National Park.
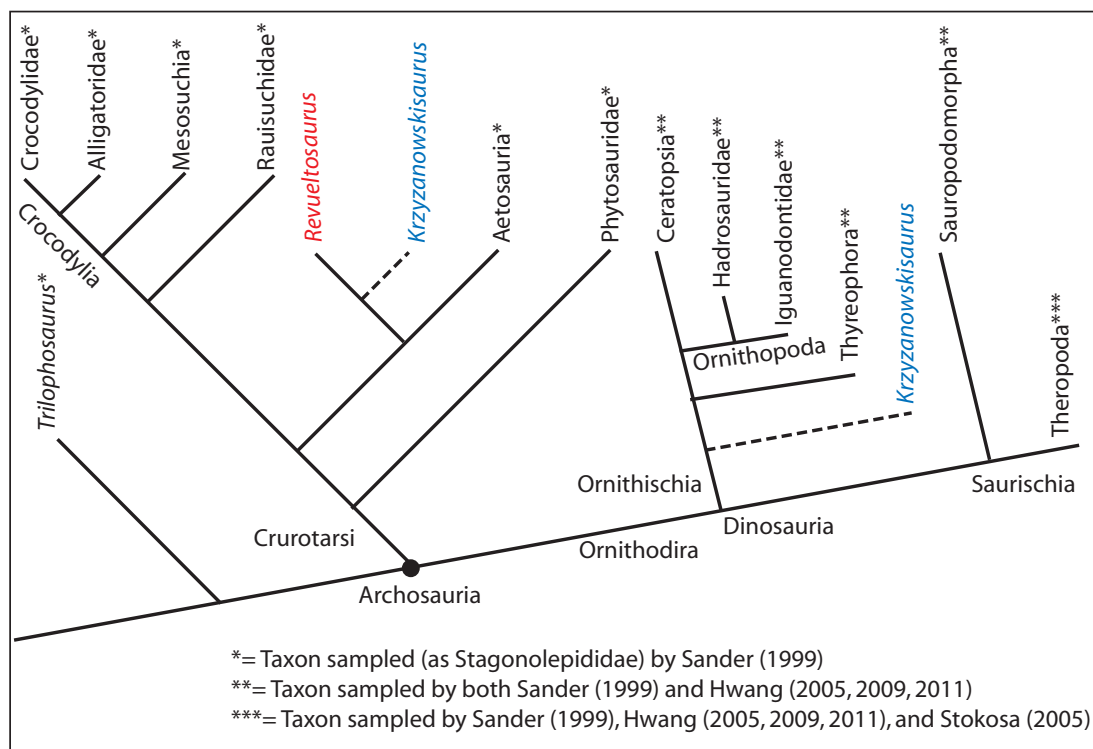
FIGURE 2. Generalized archosaurian phylogeny showing the relationships of taxa sampled by Sander (1999) and Hwang (2005) (in black) as well as *Revueltosaurus* (blue) and *Krzyzanowskisaurus* (red). Dashed lines demonstrate the two hypothesized positions of *Krzyzanowskisaurus*, either as a crurotarsan closely allied to *Revueltosaurus* (e.g., Parker et al., 2005; Irmis et al., 2007) or a basal ornithischian (Heckert, 2002, 2005).

were not as well preserved, and thus were less amenable to sectioning and SEM examination, resulting in fewer images and measurements, although we note that there is no reason not to consider the available images and measurements representative.

The tooth enamel microstructure terminology we utilize reflects that developed in previous studies, principally Sander (1999, 2000) and Hwang (2005), and the macroscopic tooth descriptions follow Smith and Dodson (2003) generally and previous descriptions of *Revueltosaurus* teeth (e.g., Hunt, 1989; Hunt and Lucas, 1994; Heckert, 2002) in particular. We note that this means that we use mesial/distal, labial/lingual, and basal/apical (or occlusal) to describe and orient isolated teeth and features of the tooth crown. Descriptions of microstructural features follow the standardized format of Hwang (2005, 2011), with enamel described from the enamel-dentine junction (EDJ) outward to the outer enamel surface (OES). Enamel thickness and distribution is described first, followed by type and schmelzmuster, followed by discussion of any special features. Particular features we describe are the basal unit layer (BUL) and lines of incre-

mental growth (LIG). We use the term "lines of incremental growth" (LIG) here, as used by Hwang (2005) to describe interruptions in the microstructural texture. These are the "incremental lines" of Sander (1999) and Stokosa (2005) and are also known as "striae of Retzius" in mammalian/human anatomical terminology. Presently it is unclear what governs the growth cycles of LIGs in reptiles, although Appenzeller et al. (2005) recently argued that they are developed daily and represent the activity of the autonomous nervous system.

We calculated the enamel thicknesses reported here by measuring their thickness perpendicular to the enamel-dentine junction in the images used here, using the program tpsDig 2.0 (Rohlf, 2010). Although tpsDig provided up to five significant figures (to hundredth of a micron), for a variety of reasons we suggest using no more than three. We recognize the difficulty of replicating measurements, especially if the section images are not perfectly perpendicular to the electron gun, and so made 10 measurements (close together) on one image to assess the precision of the tpsDig measurement protocol. After accepting the mean of these measurements as the "true value" (and the

number reported in the tables), we calculated the absolute value of the difference between measured and "true" values, and divided the mean of that difference by the "true value." We used a similar procedure for the median value, and both the mean and median values provide a relative error of 0.5% (0.005), so we consider these measurements the most precise estimates of sauropsid enamel thickness in the literature. Obviously, slightly oblique sections will inflate thickness measurements, so the measurements we provide, although more precise than any previously reported for archosaurian tooth enamel microstructure, should be considered as maximum estimates.

HISTORY OF STUDY

There are two distinct aspects of the history of this study, one regarding the study of *Revueltosaurus* and *Krzyzanowskisaurus* and another related to the study of reptilian tooth enamel microstructure.

Regarding the first aspect, Hunt (1989) named *Revueltosaurus callenderi* as an ?ornithischian dinosaur. Various authors reported additional occurrences and noted its biostratigraphic utility (e.g., Padian, 1990; Hunt and Lucas, 1994; Long and Murry, 1995; Heckert and Lucas, 1997; Hunt et al., 1998). Although there was some debate regarding the validity of the taxon, most workers accepted it as a likely basal ornithischian albeit a *nomen dubium* (e.g., Sereno, 1991; Norman et al., 2004). Heckert (2002) reviewed *Revueltosaurus* occurrences and recognized a second species, *Revueltosaurus hunti* for older, more complex teeth originally assigned to *Revueltosaurus callenderi* by Long and Murry (1995). Parker et al. (2005; see also Hunt et al., 2005) reported postcrania associated with tooth-bearing elements demonstrating that *R. callenderi* was a crurotarsan, not a dinosaur, and Heckert (2005) coined the new generic name *Krzyzanowskisaurus* for "*R.*" *hunti*. The affinities of the latter remain enigmatic, with Parker et al. (2005) positing that it likely represents a crurotarsan allied to *R. callenderi*, and Heckert (2005) hypothesizing that the more derived dentition of *Krzyzanowskisaurus* really is that of an ornithischian. Irmis et al. (2007; see also Nesbitt et al., 2007) interpreted the "cingulum" of *Krzyzanowskisaurus hunti* to represent an autapomorphic state, but otherwise considered the tooth morphology similar enough to justify retention of "*K.*" *hunti* in *Revueltosaurus* as *R. hunti* To date, unambiguous *Krzyzanowskisaurus* remains are known only from

teeth, so we chose to investigate the tooth enamel microstructure of *Revueltosaurus* and *Krzyzanowskisaurus* as an additional means of assessing the degree of similarity between the two taxa.

"Reptilian" (sauropsid) tooth enamel microstructure studies were not truly feasible until the advent of SEM microscopy (see Sander, 1999 for a more complete review). Accordingly, the study of archosaurian tooth enamel has a history of study nearly as brief as the taxonomic history of *Revueltosaurus* and *Krzyzanowskisaurus*. Buffetaut et al. (1986) were the first to publish SEM images of dinosaurian tooth enamel microstructure, and additional studies led by Dauphin (Dauphin, 1988, Dauphin et al., 1988a,b) were published shortly thereafter. These later studies sampled a variety of dinosaurian and non-dinosaurian archosaurs, among others, and in these taxa the enamel microstructure was described in general terms. Following the monumental work on synapsid enamel microstructure edited by Koenigswald and Sander (1997), Sander (1999, 2000) published the first reasonably systematic survey of sauropsid tooth enamel microstructure. His work, especially the 1999 monograph, remains the standard reference for microstructural features in non-synapsid amniotes. More recently Stokosa (2001, 2005) examined the microstructure of a variety of tyrannosaurid and dromaeosaurid taxa from the Upper Cretaceous of western North America, and Hwang (2005, 2006, 2007, 2009, 2011) sampled an array of dinosaurian teeth from the Mesozoic of North America as well as the Cretaceous of Asia *en route* to completing a dissertation (Hwang, 2007) and related abstracts and papers (Hwang, 2005, 2006, 2009, 2011). Unlike Sander (1999), who saw little phylogenetic signal in enamel microstructure, especially at lower (family-level) taxonomic rank, Hwang (2005, 2009) identified some similarity in tooth enamel microstructures related to phylogenetic position, although she concurs with Sander (1999) that relatively few unambiguous synapomorphies are evident in the enamel microstructure at lower taxonomic levels. In Table 1 we summarize many of the observations of Sander (1999), Hwang (2005, 2009), and Stokosa (2005) as well as our interpretations of the results of earlier workers based on their descriptions and published illustrations. This study supersedes an extended abstract we published previously that focused solely on *Revueltosaurus* (Heckert and Camp, 2006).

TABLE 1. Comparison of tooth enamel thickness and enamel microstructural features in different archosauromorphs compiled from the literature.

Tooth Enamel Microstructure

Higher Taxon	Taxon	Sampler	minimum thickness	maximum thickness	Parallel	Columnar	BUL	LIG	Wavy	Tubules	Comments
Archosauromorpha	*Trilophosaurus*	Sander (1999)	20	20			x	x			
Crurotarsi	*Phytosauridae* (Dockum)	Sander (1999)	20	20	x			x			I and III
	Phytosauridae (Dockum)	Sander (1999)		150	x	x	x	x			II
	Phytosauridae (Hallau)	Sander (1999)		60		x					
	Rauisuchidae	Sander (1999)	60	100	x	x	x	x			95% columnar; outer is parallel; rare LIG
Mesosuchia	*Machimosaurus hugi*	Sander (1999)		350	x	x	x				LIG rare
Crocodylia: Alligatoridae	*Allognathosuchus* sp.	Sander (1999)		300	x	x		x			up to 50/50 columnar/parallel; sometimes 95/5; LIG only in parallel
	Alligator mississippiensis	Sander (1999)		1000	x	x	x	x			Mostly columnar; LIG in columnar enamel
Crocodylia: Crocodylidae	*Deinosuchus riograndensis*	Sander (1999)	<150	525		x	x				40% columnar; 55% microunit; only specimen w/ described microunits
	Asiatosuchus	Sander (1999)		500		x	x				compound unit enamel/weakly columnar
	Pristichampsa	Sander (1999)	20	50	x	x		x			LIG best in the carinae
	Eusuchia indet	Sander (1999)	50	125	x	x		x			Columnar yields to parallel
Dinosauria:Saurischia: Theropoda											
	Basal Theropoda indet.	Hwang (2009)			x	x	x			x	100 µm average thickness; Kayenta Fm "carnosaur" in UCMP collections
D:S:T:Ceratosauria	*Coelophysis bauri*	Hwang (2005, 2011)	10	10	x			x			*C. bauri* of Hwang (2005) a distinct taxon (Hwang, 2011, p. 192)
	Ceratosaurus nasicornis	Hwang (2011)	20	70	x	x	x	x		x	120 µm average thickness; varies wildly
	Majungasaurus sp.	Hwang (2011)	<50	>90	x	x	x	x		x	
D:S:T:Allosauroidea	*Allosaurus fragilis*	Hwang (2011)	20	>85	x	x	x	x			
	cf. *Allosaurus*	Sander (1999)	10	15	x						Not even LIG
	Charcharodontosaurus	Buffetaut et al. (1986)				x					called "prisms" in published description

TABLE 1 (continued).

Higher Taxon	Taxon	Sampler	minimum thickness	maximum thickness	Parallel	Columnar	BUL	LIG	Wavy	Tubules	Comments
	Spinosaurus	Buffetaut et al. (1986)				x					called "prisms" in published description
	"Carnosaur"	Buffetaut et al. (1986)			x	?	x				
D:S:T: Coelurosauria						x					
D:S:T:C: Tyrannosauridae	*Tyrannosauridae* indet. (TX)	Sander (1999)	150	200	x	x					Thickest at base of carina; parallel only at the outer edge, great columnar
	Tyrannosauridae indet. (MT)	Sander (1999)		120	x	x	x				
	Tyrannosauridae indet.	Hwang (2005, 2009)			x	x	x			x	115 µm average thickness
	Tyrannosauridae indet. (="*Nanotyrannus*")	Hwang (2009)			x	x				x	60µm average thickness; juvenile tyrannosaurid assigned to "*Nanotyrannus*" in UWGM collections
	Daspletosaurus torosus	Hwang (2011)				x		x		x	80 µm average thickness
	cf. *Gorgosaurus* sp.	Hwang (2009)			x	x	x			x	80 µm average thickness
	Gorgosaurus libratus	Hwang (2011)			x	x	x	x		x	
	Albertosaurus sarcophagus	Hwang (2005)	60	180	x	x					
	Albertosaurus sp.	Stokosa (2005)	100	120	x	x				x	
	?Albertosaurus gen. A. indet.	Stokosa (2005)	40	55	x	x		x			SDSM 12737; tip of tooth
	?Albertosaurus gen. A. indet.	Stokosa (2005)	180	200	x	x		x			SDSM 15143
	?Albertosaurus gen. A. indet.	Stokosa (2005)	95	100	x	x		x			SDSM 64351
	Tyrannosaurus sp.	Hwang (2011)				x				x	200 µm average thickness
	cf. *Tyrannosaurus rex*	Stokosa (2005)	45	50	x	x		x		x	SDSM 15135; Poorly developed columnar
	cf. *Tyrannosaurus rex*	Stokosa (2005)	60	75							SDSM 64287
	cf. *Tyrannosaurus rex*	Stokosa (2005)	80	90							SDSM 15115
	Tarbosaurus	Dauphin et al. (1989)				x					intrepreted from pl. 2, fig. 4
	Tarbosaurus	Hwang (2005)		300	x	x					
D:S:T:C: *incertae sedis*	*Richardoestesia* cf. *R. gilmorei*	Stokosa (2005)	10	10	x						

TABLE 1 (continued).

Higher Taxon	Taxon	Sampler	minimum thickness	maximum thickness	Parallel	Columnar	BUL	LIG	Wavy	Tubules	Comments
	Richardoestesia gilmorei	Hwang (2011)	~10	~10	x		x	x		x	10 µm average thickness
	Richardoestesia isosceles	Hwang (2011)	~13	~13	x		x			x	13 µm average thickness
	Richardoestesia sp.	Stokosa (2005)	10	15	x						
D:S:T:C:Maniraptora	Troodontid indet. A	Hwang (2005)		60	x						
	Troodontid indet. B	Hwang (2005)			x	x					
	Troodontid n. gen. et. Sp.	Hwang (2005)		30	x			x			
	Troodon sp.	Sander (1999)		20	x	x	x				Columnar units small (2µm) and weak, seem to arise from BUL (Sander, p. 65)
	Troodon sp.	Hwang (2009, 2011)			x		x				20µm average thickness; parallel crystallites
	Troodon sp. cf. *T. formosus*	Stokosa (2005)	10	15	x						
	Paronychodon cf. *P. lacustris*	Stokosa (2005)	0	15	x						
	Paronychodon lacustris	Sander (1999)		20	x			x			LIG are few and weak
	Paronychodon (Troodontid)	Hwang (2005)			x			x			
	Byronosaurus jaffei	Hwang (2005)		13	x			x			
	Paronychodon (Dromaeosaurid)	Hwang (2005)									
	Velociraptor	Dauphin et al. (1989)			x						interpreted from pl. 1, figs. 4-5
	Velociraptor mongoliensis	Hwang (2005)		24	x		x				
	Bambiraptor feinbergi	Hwang (2005)			x			x?			No LIG in Hwang (2005), but faint in Hwang (writ. Comm.)
	Dromaeosauridae indet.	Hwang (2005)		55	x		x				
	Deinonychus antirrhopus	Hwang (2011)	17	30+	x		x	x		x	BUL poorly developed; LIG faint
	Saurornitholestes sp.	Hwang (2011)	7	20+	x		x			x	BUL half of enamel thickness
	Dromaemosaurus sp.	Hwang (2011)	25	35	x		x	x		x	BUL half of enamel thickness, but not well-developed
	Dromaeosaurus sp. cf. *D. albertensis*	Stokosa (2005)	40	45	x	x		x			Columnar at EDJ, divergent parallel more at OES

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TABLE 1 (continued).

Higher Taxon	Taxon	Sampler	minimum thickness	maximum thickness	Parallel	Columnar	BUL	LIG	Wavy	Tubules	Comments
D:S:T:Avialae	Indeterminate Avialan A	Hwang (2011)			x		x			x	20 µm average thickness
	Indeterminate Avialan B	Hwang (2011)			x		x			x	16 µm average thickness
Sauropodomorpha											
	Plateosaurus engelhardti	Sander (1999)	10	40	x	?			x		Columnar is very poorly developed; probably more divergent parallel
	cf. *Diplodocus*	Sander (1999)		150			x				Pseudo-wavy (Sander, p. 68)
	Diplodocus longus	Hwang (2011)	440	490		x	x	x		x	465 µm average thickness
	Camarasaurus sp.	Hwang (2011)	700	1000+	x	x	x	x			850 µm average thickness
	Titanosauridae indet.	Hwang (2011)			x	x	x	x		x	170 µm average thickness
Dinosauria:Ornithischia											
D:O:Stegosauria	*Stegosaurus* sp.	Hwang (2011)			x		x	x			30-40 µm average thickness
D:O:Ankylosauria	*Ankylosauria* indet.	Sander (1999)		60		x	x				
	Ankylosaurus magniventris	Hwang (2005)		60	x	x	x	x			
	Edmontonia rugosidens	Hwang (2005)		100+	x	x	x	x			
	Sauropelta edwardsi	Hwang (2005)		105	x	x	x	x			
	Euplocephalus	Hwang (2009, 2011)	35	65	x	x	x	x		x	55 µm average thickness; originally identified as a pachycephalosaurid
Dinosauria:Ornithischia:Euornithopoda											
D:O:E: Hypsilophodontidae	*Thescelosaurus* sp.	Sander (1999)	14	140	x		x				BUL thin
	Thescelosaurus sp.	Hwang (2011)	20	90	x	x	x			x	Hwang (2011) suspects Sander's (1999) specimen is not Thescelosaurus
D:O:E:Dryomorpha	*Dryosaurus altus*	Hwang (2011)					x	x	x	x	55-65 µm average thickness
	Camptosaurus dispar	Hwang (2011)					x		x	x	
D:O:E: Iguanodontidae	*Iguanodon* sp.	Sander (1999)	100	150			x		x		Inner and outer wavy enamel
	Tenontosaurus tilleti	Hwang (2005)		100+	x	x	x			x	
D:O:E: Hadrosauridae	*Hadrosauridae* indet.	Sander (1999)	160	210			x		x		
	Hadrosaurinae indet.	Hwang (2009)				x				x	

TABLE 1 (continued).

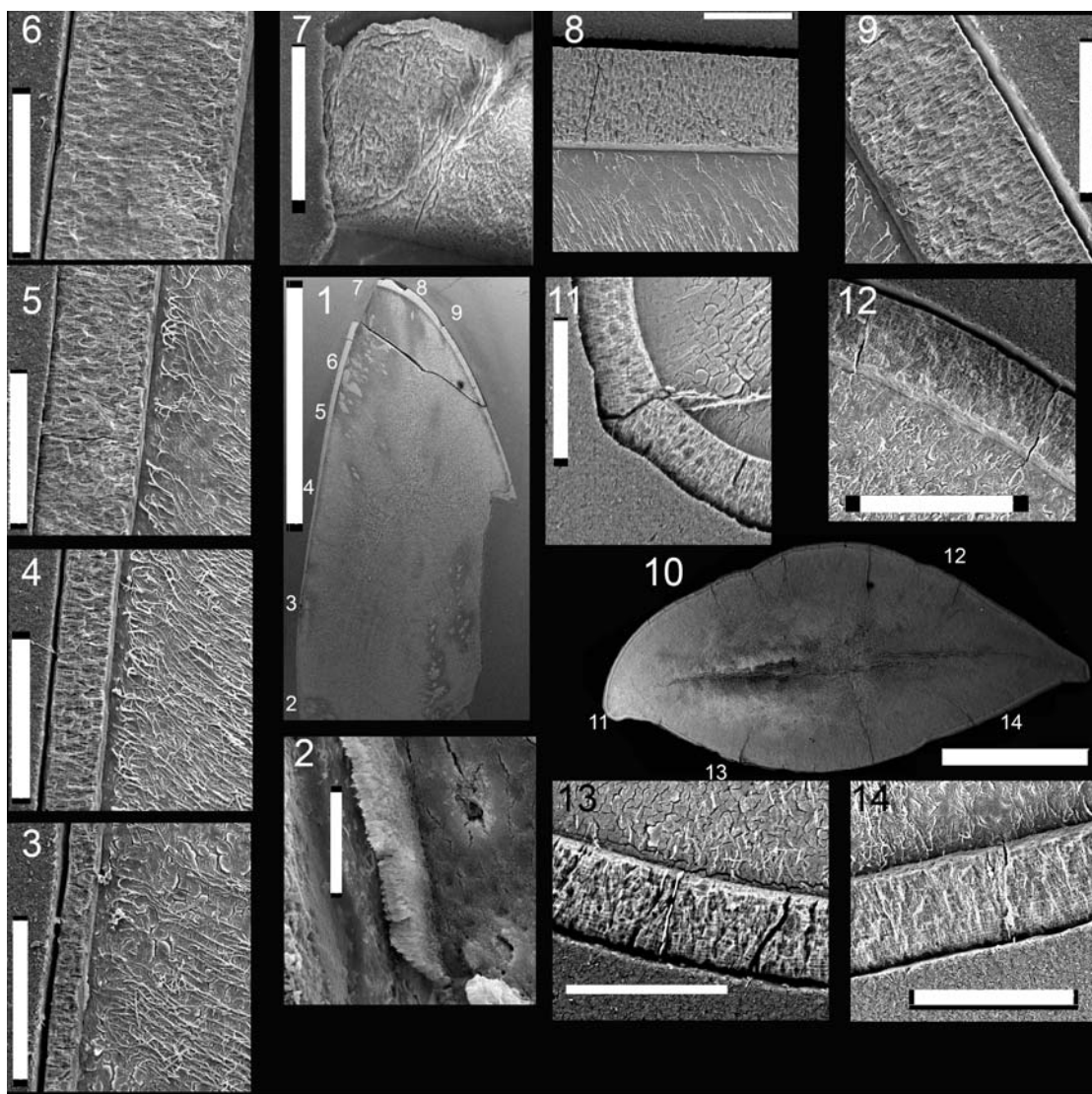| Higher Taxon	Taxon	Sampler	minimum thickness	maximum thickness	Parallel	Columnar	BUL	LIG	Wavy	Tubules	Comments
	Anatosaurus sp.	Sander (1999)	100	100+			x		x	x	BUL inverted
	Saurolophus sp.	Hwang (2011)		165+			x		x		115 µm average thickness
	Gilmoreosaurus mongoliensis	Hwang (2005)					x		x		
	Bactrosaurus johnsoni	Hwang (2005)					x		x		
	Kritosaurus navajovius	Hwang (2005)					x		x		
	Hypacrosaurus altispinus	Hwang (2005)					x		x		
	Corythosaurus casuaris	Hwang (2005)					x		x		
	Prosaurolophus maximus	Hwang (2011)		~200			x		x		135 µm average thickness
Dinosauria:Ornithischia: Ceratopsia											
	Neoceratopsia indet.	Hwang (2009)				x					Average 285 µm; originally assigned to *Thescelosaurus* sp.
	Psittacosaurus sp.	Hwang (2005)				x	x			?	enamel voids
	Protoceratops	Dauphin et al. (1988)			x	x	x				interpreted from pl. 1, figs. 7-8 (maxilla) and 12 (premaxilla)
	Leptoceratops gracilis	Hwang (2005)		420		x	x			x	
	Protoceratops sp.	Hwang (2005)		120+		x	x			x	
D:O:C:Ceratopsidae	Ceratopsidae indet. (Can)	Sander (1999)	150			x	x	x		x	
	Ceratopsidae indet. (WY)	Sander (1999)									
	Triceratops sp.	Hwang (2005)		325		x	x			x	
	Centrosaurus apertus	Hwang (2011)				x	x	x		x	170-270 µm average thickness depending on position
	Pachyrhinosaurus canadensis	Hwang (2011)				x	x	x		x	170-270 µm average thickness depending on position
Dinosauria:Ornithischia:Pachycephalosauridae											
	Pachycephalosauridae indet. A	Hwang (2005)		20	x						anterior tooth, diverging parallel
	Pachycephalosauridae indet. B	Hwang (2005)		40	x	x	x				posterior tooth, incipient columnar
	Pachycephalosauridae indet. C	Hwang (2005)		50	x	x	x				posterior tooth, incipient columnar

FIGURE 3. Variation in enamel thickness in the teeth of *Revueltosaurus callenderi.* 1-9, premaxillary tooth (P-33799); 10-14, maxillary tooth (P-33798). 1, overview of premaxillary tooth indicating approximate place where measurements and micrographs shown in this figure and Figure 4 were taken; 2-9, close-up views showing enamel thickness variation, with enamel-dentine junction (EDJ) oriented relative to overview in (1); and 10, overview of maxillary tooth section, indicating approximate place where measurements and micrographs shown in this figure and Figure 5 were taken; 11-14, close-up views showing enamel thickness variation, with enamel-dentine junction (EDJ) oriented relative to overview in (10). Scale bars equal 100 µm except for 1 (5 mm), 2 (10 µm), and 10 (2 mm).

DESCRIPTION

Revueltosaurus

Here we provide details of the enamel microstructural features observed in the topotype premaxillary tooth (NMMNH P-33799; Figures 3.1–9, 4) and maxillary-dentary tooth (NMMNH P-33798; Figures 3.10–14, 5) of *Revueltosaurus callenderi* following the format of Hwang (2005, 2011).

Enamel distribution and thickness. Enamel thickness varied considerably throughout the longitudinal section of the premaxillary tooth of *Revueltosaurus* and very little across the transverse section of the maxillary/dentary tooth (Figures 4, 5). In the premaxillary tooth, the enamel was thinnest basally (~4.9 µm) and thickest apically (as much as 152 µm), with average enamel thickness approximately 66 µm (Table 2), although excluding more basal portions of the tooth (enamel < 40 µm thick) results in an average enamel thicknesses of approximately 83 µm in the more functional portion of the tooth crown. The enamel in the maxillary-
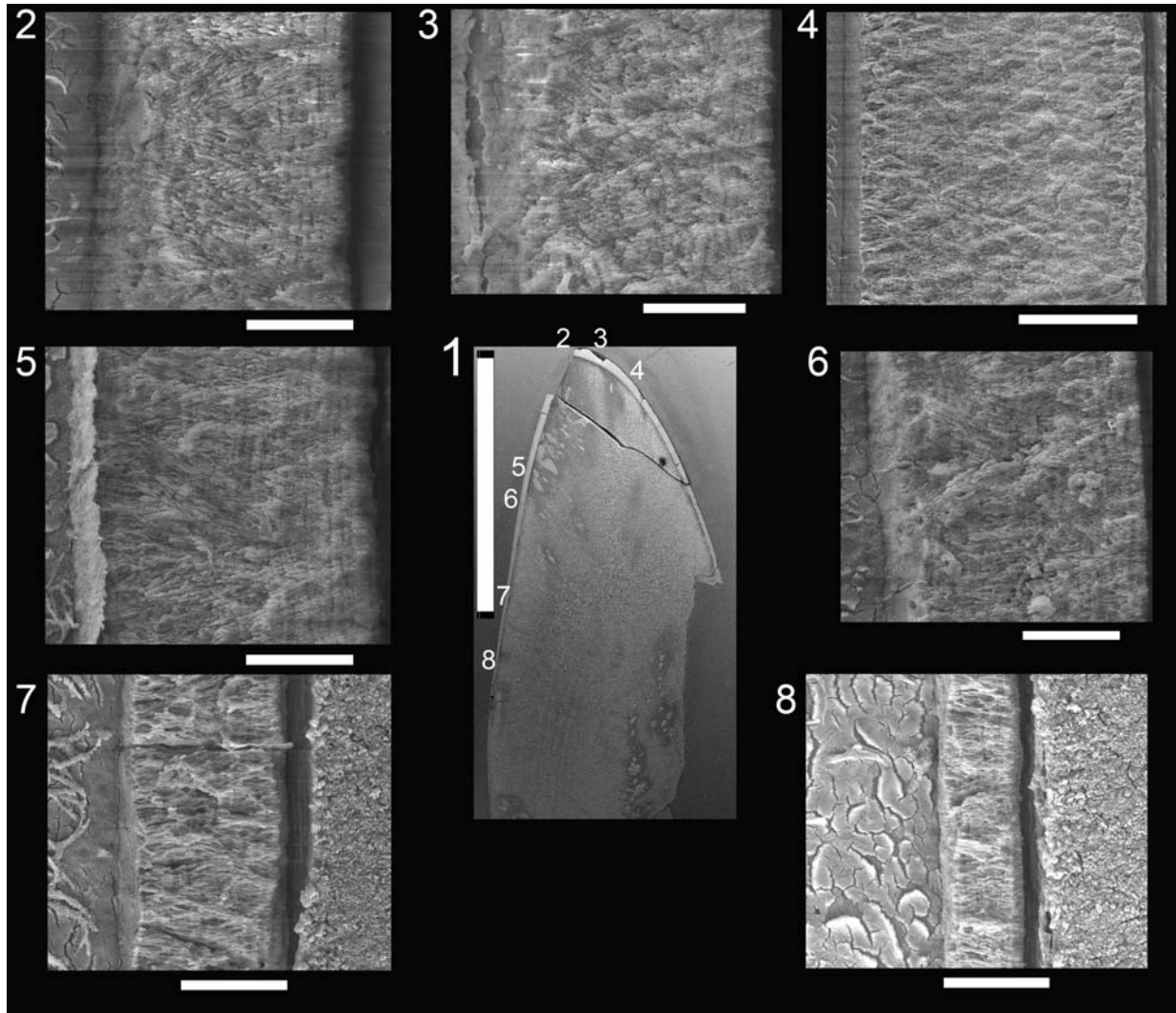
FIGURE 4. Scanning electron microscope images of NMMNH P-33799, *Revueltosaurus callenderi* premaxillary tooth showing variation in enamel microstructure in longitudinal section. 1, overview of tooth indicating approximate place where measurements and micrographs shown in this figure were taken; 2-8, close-up views showing enamel thickness variation, with enamel-dentine junction (EDJ) oriented relative to overview in (1) and outer enamel surface (OES) away from the same overview. White scale bars equal 20 µm except for 1 (5 mm) and 4 (50 µm).

dentary tooth was almost uniformly 50-55 µm thick except across the denticles, where it thickened to as much as 92.0 µm but was more typically ~60-63 µm. Average transverse thickness was approximately 55.5 µm (discounting the one 92.0 µm measurement) and 58.5 µm counting all measurements, including one thin (42 µm) measurement.

Enamel types and schmelzmuster. Typically *Revueltosaurus* teeth have a thin (< 5 µm) but well-developed BUL from which weakly developed columnar enamel emanates (Figures 4, 5). Individual columnar units are difficult to discern but are ~10µm across basally and expand to ~15-20 µm

across closer to the OES. Generally these are better seen in transverse sections in the maxillary-dentary tooth (Figure 5.2, 5.4–5) than in the premaxillary tooth (Figure 4.2). The outer quarter to half of the enamel thickness bears numerous well-developed LIGs. Again, these are more distinct in the transversely sectioned maxillary tooth (Figure 5.2–8) than in the longitudinal section of the premaxillary tooth (Figure 4.2, 5, 8). Rarely LIGs are evident for more than half of the tooth's enamel thickness. LIGs are less than 2 µm apart and, in transverse section, approximately 15 can be traced across a micrograph (Figure 5.5–8). They are fainter and difficult to trace, but much more numer-
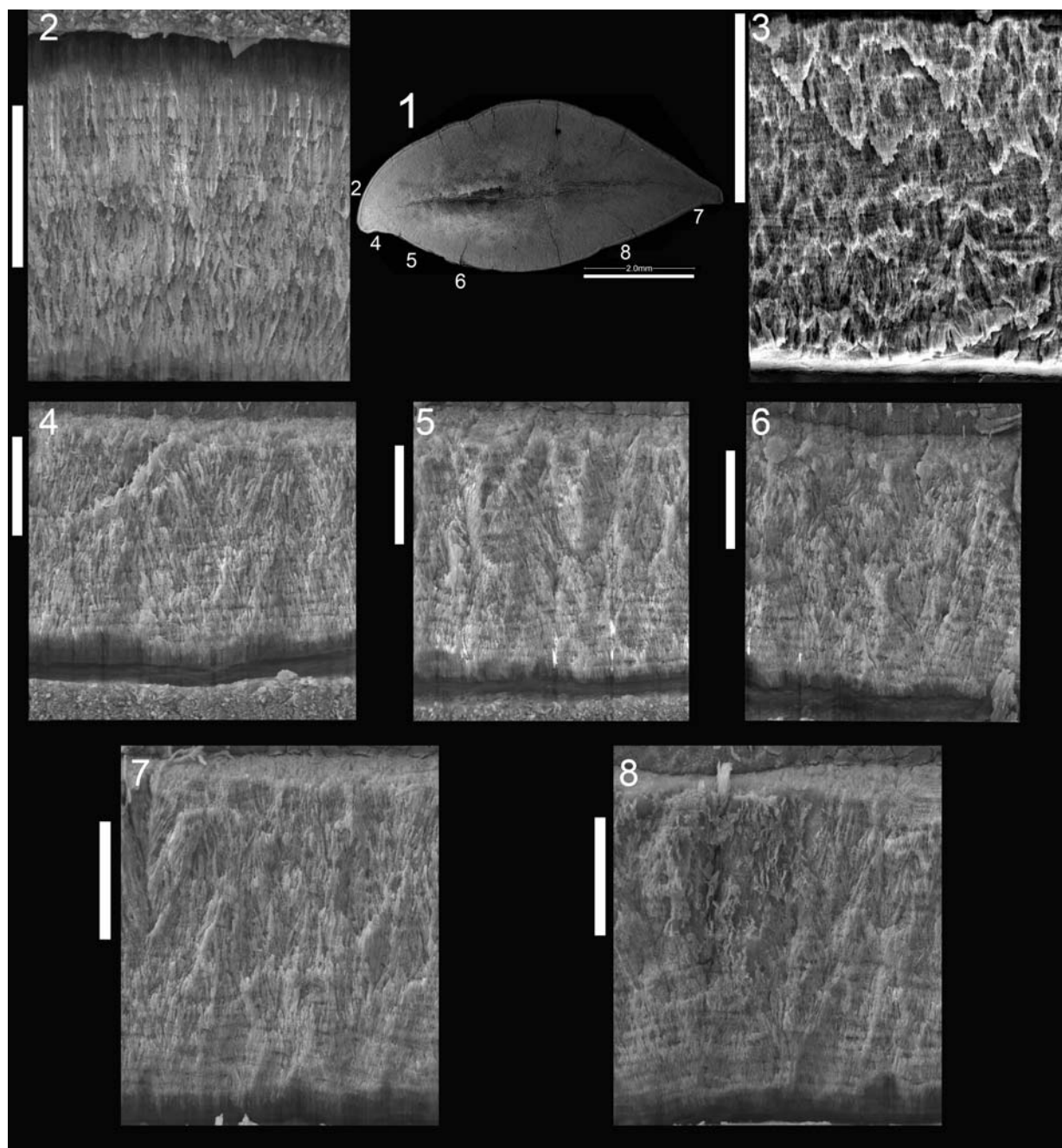
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FIGURE 5. Scanning electron microscope images of NMMNH P-33798, *Revueltosaurus callenderi* maxillary tooth enamel microstructure in transverse section. 1, overview of tooth indicating approximate place where measurements and micrographs shown in this figure were taken; 2-8, close-up views showing enamel thickness variation, with EDJ oriented relative to overview in (1) and OES away from the same overview. Scale bars equal 20 μm except 1 (2 mm), 3 (50 μm).

ous in the tip of the premaxillary tooth (Figure 4.4). Near the OES, in the region with the most LIGS, the enamel reverts to a stacked series of parallel crystallites that accounts for approximately 10 μm of the total enamel thickness.

Special types and features. The densely packed LIGs are probably the most distinctive feature of the schmelzmuster in *Revueltosaurus callenderi*. The fact that they are both prominent and densely packed may reflect particularly slow ontogenetic

TABLE 2. Measurements of enamel thickness in the teeth of *Revueltosaurus* and *Krzyzanowskisaurus* sampled here.

***Revueltosaurus callenderi* enamel measurements from longitudinal section of NMMNH P-33798**

Figure	Section	Enamel thickness (µm)	Measured at:
3.2	Longitudinal	4.87	end of [full width of] enamel (thinnest enamel)
3.3	Longitudinal	20.42	middle of frame
3.4	Longitudinal	36.23	middle of frame
3.5	Longitudinal	68.48	middle of frame
3.6	Longitudinal	115.56	top of frame (thickest enamel)
3.7	Longitudinal	114.88	left of frame (thickest enamel)
3.8	Longitudinal	152.13	bottom of frame (thickest enamel)
3.9	Longitudinal	103.34	middle of frame
4.2	Longitudinal	46.88	middle of frame
4.3	Longitudinal	50.08	middle of frame
4.4	Longitudinal	52.43	middle of frame
4.5	Longitudinal	53.93	middle of frame
4.6	Longitudinal	15.47	middle of frame
4.7	Longitudinal	31.36	middle of frame
4.8	Longitudinal	127.6	middle of frame

"Tooth has total crown height (TCH) of 13.1 mm, total crown length (TCL) 8.1 mm"

***Revueltosaurus callenderi* enamel measurements from transverse section of NMMNH P-33797**

Figure	Section	Enamel thickness (µm)	Measured at:
3.11	Transverse	51.5	on denticle
3.12	Transverse	53.41	middle of frame
3.13	Transverse	55.15	middle of frame
3.14	Transverse	59.66	middle of frame
5.1	Transverse	42.8	left of frame (EDJ visible)
5.3	Transverse	92.47	middle of frame
5.4	Transverse	50.77	middle of frame
5.5	Transverse	54.48	middle of frame
5.6	Transverse	53.32	middle of frame
5.7	Transverse	62.79	middle of frame
5.8	Transverse	60.04	middle of frame
TCH: 6 mm+ (broken)		TCL: ~6 mm	

development of each tooth (see text in comparisons and discussion that follows).

Krzyzanowskisaurus

Here we provide details of the enamel microstructural features observed in the hypothesized premaxillary tooth (UCMP 165213; Figure 6) and the hypothesized maxillary-dentary tooth (UCMP 165211; Figure 7) of *Krzyzanowskisaurus hunti* following the format of Hwang (2005, 2011).

Enamel distribution and thickness. As in *Revueltosaurus*, the greatest variation in enamel thickness is through the longitudinal section, which ranged from 18-151 µm thick (Table 2), although only the thicker, more apical sections were preserved well and thus are illustrated in Figure 6. As in *Revueltosaurus*, *Krzyzanowskisaurus* had very

TABLE 2 (continued).

***Revueltosaurus callenderi* enamel measurements from longitudinal section of NMMNH P-33798**

***Krzyzanowskisaurus hunti* enamel measurements from longitudinal section of UCMP 165213**

Figure	Section	Enamel thickness (µm)	Measured at:
6.2	Longitudinal	112.8	middle of frame
6.3	Longitudinal	138.89	left of frame (EDJ visible)
6.4	Longitudinal	151.25	right of frame (unbroken outer edge of enamel)
TCH: ~6 mm (incomplete)		TCL: 6 mm	

***Krzyzanowskisaurus hunti* enamel measurements from transverse sectionof UCMP 165211**

Figure	Section	Enamel thickness (µm)	Measured at:
7.1	Transverse	55.38	middle of bend
7.2	Transverse	64.34	middle of frame
7.3	Transverse	50.49	middle of frame
7.4	Transverse	65.54	middle of frame
7.5	Transverse	63.38	middle of frame
7.6	Transverse	43.47	middle of frame
7.7	Transverse	61.82	middle of frame
TCH: ~10.4 mm	TCL: ~7.4 mm		

thin enamel basally and the thickest enamel apically. All of the reasonably well-preserved, more apical sections illustrated in Figure 6 have enamel more than 100 µm thick. The complex shape of the transverse section (see Figure 7) led to samples of very thin enamel between the denticles and main body of the tooth, and much thicker enamel across the denticles more mesially and distally and thus ranged from 43.5 to 65.5 µm thick. Typical thicknesses were ~50-65 µm with an average thickness of approximately 58 µm.

Enamel types and schmelzmuster. The EDJ is clearly demarcated in both the longitudinal and transverse section and marked with a distinct BUL of small, diffuse columns. This BUL is also less than 5 µm thick. In both longitudinal and transverse sections the individual columns are relatively small and defined by packages of crystallites ~ 5 µm across and 10 µm long. In some views (e.g., Figure 6.3–5, 7.3, 7.5, 7.7) it appears that the enamel is comprised of at least two, and sometimes three or four, "stacks" of such columns. LIGs are particularly visible in transverse section but much less than 2 µm apart, so as many as 25 are evident in some teeth (Figure 7.3, 7.6). As in *Revueltosaurus*, there

is a transtion within the LIGS from the more basal poorly developed columnar units to parallel crystallite enamel, which dominates the outermost ~10 µm of the tooth (Figures 6.2, 7.3–7).

Special types and features. In many ways the schmelzmuster of *Krzyzanowskisaurus hunti* is extremely similar to that of *Revueltosaurus callenderi*, from its thickness to the presence of numerous LIGs. The teeth sampled for this study were approximately the same size, and the enamel thickness in each taxon is essentially the same. Similarly, the schmelzmuster of *K. hunti*, as in *R. callenderi*, consists of a BUL from which columnar enamel emanates, bears numerous closely spaced LIGs that are much more prominent near the OES than near the enamel-dentine junction, and grades into parallel crystallite enamel near the OES. The significance of these features and their similarities are discussed in the following sections.

COMPARISONS

Both *Revueltosaurus* and *Krzyzanowskisaurus* have relatively thick enamel for teeth of their size—enamel thickness varies from a low of ~5 µm
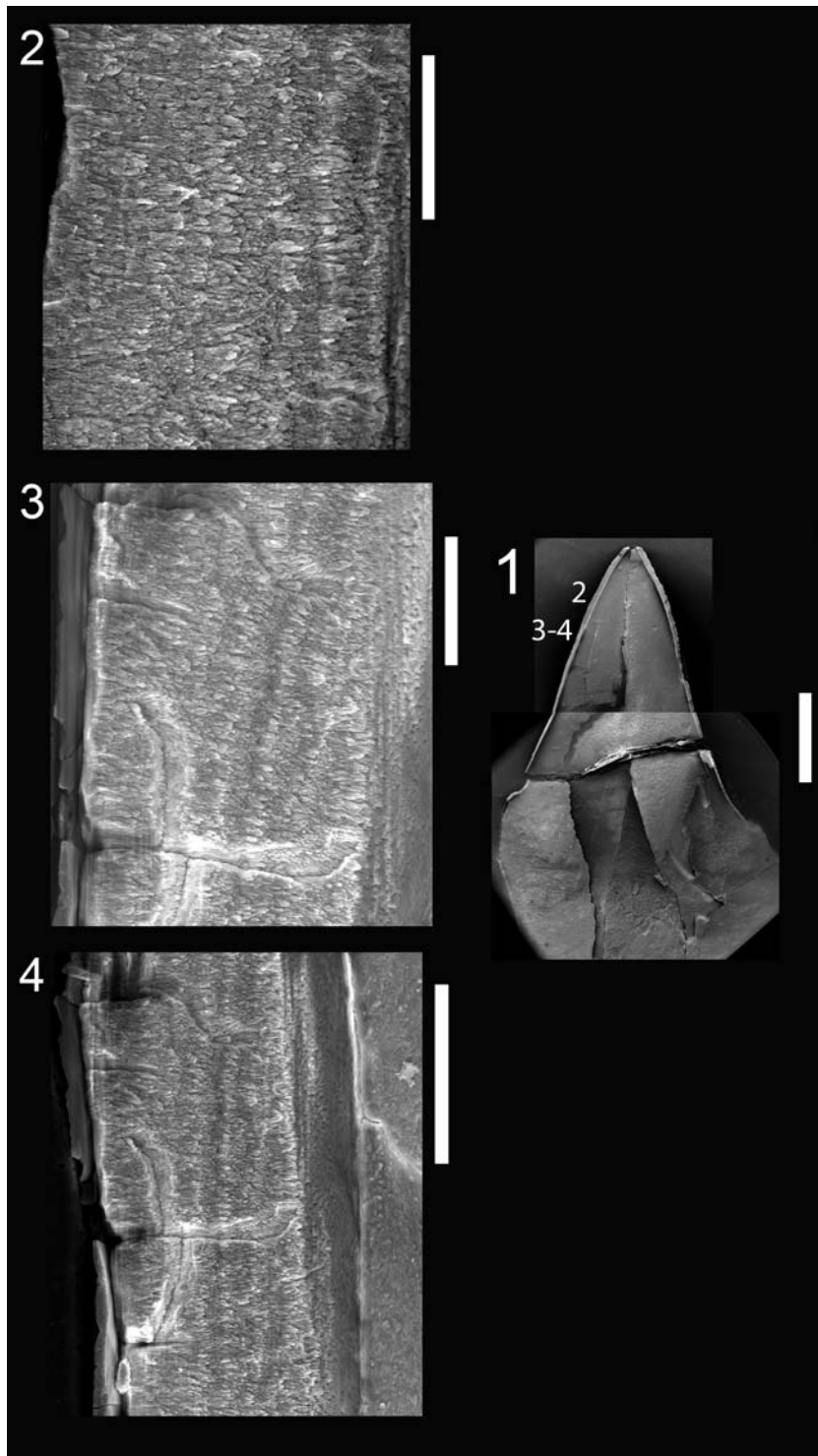
FIGURE 6. Scanning electron microscope images of UCMP 165213, *Krzyzanowskisaurus hunti* tooth enamel microstructure in longitudinal section. 1, overview of tooth indicating approximate place where measurements and micrographs shown in this figure were taken; 2-4, close-up views showing enamel thickness variation, with EDJ oriented relative to overview in (1) and OES away from the same overview. Scale bars equal 2 mm (1), 50 μm (2-3), and 100 μm (4).
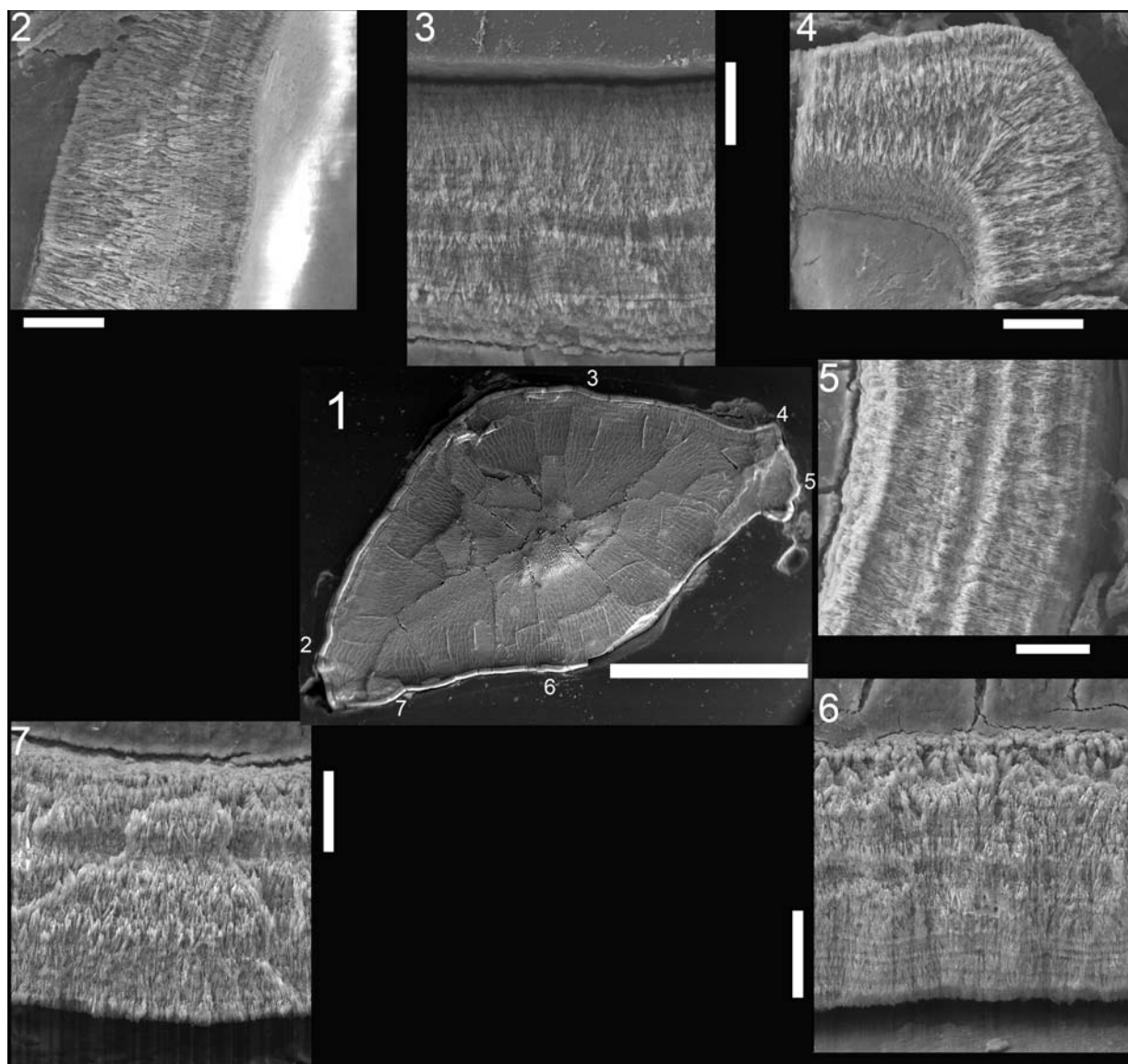
FIGURE 7. Scanning electron microscope images of UCMP 165211, *Krzyzanowskisaurus hunti* premaxillary tooth enamel microstructure in transverse section. 1, overview of tooth indicating approximate place where measurements and micrographs shown in this figure were taken; 2-7, close-up views showing enamel thickness variation, with EDJ oriented relative to overview in (1) and OES away from the same overview. Scale bar equals 20 μm except 1 (2 mm).

to as much as 152 μm. Even though the "premaxillary" tooth of *Krzyzanowskisaurus* is approximately 25% shorter, the enamel is comparable in thickness. The longitudinal sections of the premaxillary teeth capture the entire range of variation from more basal enamel (~5 μm) to apical enamel (~152 μm). In the maxillary/dentary teeth, the range was not as pronounced (generally 50-65 μm, with one measurement each above and below this range), which probably reflects relatively uniform thickness in cross-section, although the enamel is thicker along the denticles. At the microstructural level, both taxa exhibit columnar microstructure that emanates from a BUL. The columnar enamel is then interrupted by numerous LIGS before transitioning into a region ~10 μm thick dominated by parallel (crystallite) enamel that extends to the OES. In amniotes, parallel (crystallite) enamel is generally considered primitive and columnar enamel derived, with the assumption that columnar enamel is perhaps associated with a diet requiring greater tooth strength (resistance to fracture) (Sander, 1999). Existing theories suggest that columnar enamel in these taxa reflects a diet with

less emphasis on grinding and more on biting (Sander, 1999), something we explore in greater detail later.

Of the many taxa Sander (1999) sampled, *Revueltosaurus* teeth are most similar in enamel thickness and microstructure to rauisuchids (Sander, 1999, plate 9f) among contemporaneous taxa, and tyrannosaurs (Sander, 1999, plate 13b–c) among more derived, younger taxa. The similarities with the rauisuchid tooth include the presence of a BUL, weakly developed columnar enamel, and numerous LIGs. The similarities with the rauisuchids taxa include the presence of a BUL, weakly developed columnar enamel, and numerous LIGs, although the enamel of the rauisuchid illustrated by Sander (1999, plate 9f) appears to average almost 100 μm thick. Certainly, some phytosaurs (e.g., Sander, 1999; Figure 6a) exhibit better-developed columns, something we have seen in our own preliminary work (Camp and Heckert, 2007). Interestingly, the enamel of both *Revueltosaurus* and *Krzyzanowskisaurus* is substantially thicker than that of *Trilophosaurus buettneri* (e.g., Sander, 1999, plate 9d–e), one of the few other possibly herbivorous tetrapods known from the Upper Triassic of the American Southwest. The columns we illustrate here are better developed than those of *Plateosaurus* (Sander, 1999, plate 13h) but not as well developed as in the tyrannosaurid illustrated by Sander (1999, plate 13b–c). As in *Diplodocus* (Sander, 1999, plate 14a–b), the columnar units are more readily discerned in cross-section than longitudinal section. The enamel microstructure of *Revueltosaurus callenderi* is also similar to that of the ankylosaurid "*Palaeoscincus*" (Sander, 1999, plate 14f). Sander (1999) documented several sauropsid taxa that possessed both parallel crystallite and columnar enamel, including some ichthyosaurs and mosasaurs, but the schmelzmuster we document here is more homogenous than Sander found in those taxa.

Stokosa (2005; see also Stokosa, 2001) made extensive comparisons of small (*Troodon*, *Paronychodon*, *Richardoestesia*, *Dromaeosaurus*) and large (tyrannosaurid) latest Cretaceous theropods. Generally speaking, she found that the smaller taxa, particularly *Troodon* and *Richardoestesia*, lack columnar enamel and other more complex structural features, and thus are very different from the schmelzmuster we document in *Revueltosaurus* and *Krzyzanowskisaurus.* Although Stokosa's (2005) analysis was restricted to Late Cretaceous coelurosaurian theropods, we note that she also reported columnar enamel similar to what we report here in several dromaeosaurid and tyrannosaurid theropods (but note that Hwang [2011] considered Stokosa's [2005] "columnar" enamel as a BUL). The columns we document here are not as well developed as those illustrated by Stokosa (2005, figure 9.6c–d) for *Tyrannosaurus rex.* Conversely, the LIGs we report here are more pronounced than those Stokosa (2005, figure 9.3c) found in *Dromaeosaurus.*

Hwang's (2005, 2009, 2011) work was restricted to the Dinosauria but is the most comprehensive sampling of dinosaurs to date. Again, enamel thickness in *Revueltosaurus* and *Krzyzanowskisaurus* is comparable to that found in much larger teeth (e.g., the tyrannosaurid theropods, Table 1). Other key features we observed in the schmelzmuster of *Revueltosaurus* and *Krzyzanowskisaurus* include a BUL, columnar enamel consisting of relatively small (< 15μm diameter) columns, and numerous LIGs that mark a transition from columnar to parallel crystallite enamel. Hwang (2011, figure 18) reported an identical combination of features in the four genera of ankylosaurs she sampled. Indeed, the schmelzmuster of the Triassic taxa we sampled is extremely similar to that *Ankylosaurus magniventris* as illustrated by Hwang (2005, figure 10a–c; Hwang, 2011, figure 13a). Points of detailed similarity include the comparable enamel thickness, thin but well-defined BUL, and poorly developed columns basally that grade into a zone with pronounced LIGS before transitioning into a zone of parallel crystallite enamel (see especially Hwang, 2005, figure 10a, c). A single unidentified pachycephalosaurid also possessed similar enamel, although it has what Hwang (2011) identified as "incipient columnar enamel" rather than the true columnar enamel identified here. The hypsilophodont ornithischian *Thescelosaurus* possesses similar schmelzmuster, including a BUL, columns, and at least some LIGs (accidentally omitted from Hwang, 2011, figure 18), but also possesses a parallel crystallite enamel cap forming the outer enamel surface similar to that of the thyreophorans. The presence of a BUL and relatively narrow columns is probably synapomorphic for ornithischians (Hwang, 2011), but no ornithischian exactly matches the schmelzmuster characteristics of either *Revueltosaurus* or *Krzyzanowskisaurus.* We therefore consider these similarities to be the result of convergence and find it intriguing that this convergence appears strongest with ankylosaurs, whose teeth are also superficially similar to the Tri-

assic taxa, especially those of *Krzyzanowskisaurus.*

Several theropods and a few of the sauropodomorphs Hwang (2005, 2011) sampled share one or two features (BUL, narrow columnar enamel, LIGs) with *Revueltosaurus* and *Krzyzanowskisaurus*, but none share all three, and in general the schmelzmuster of saurischians is distinct from these taxa. Interestingly, Triassic saurischians, including both *Coelophysis* and the "prosauropods" (basal sauropodomorphs) *Plateosaurus* and "*Gyposaurus*" have less sophisticated tooth enamel microstructure than do the taxa examined here (Sander, 1999; Hwang, 2005, 2011).

DISCUSSION

These results demonstrate that (1) enamel thickness is variable within a tooth; therefore, enamel thickness reports must either be standardized to a specific location on a tooth (which we consider unlikely to be repeatable in archosaurs) or else reported as a range tied to morphological landmarks (which we think more likely and have practiced here); (2) *Revueltosaurus* and *Krzyzanowskisaurus* both had columnar enamel microstructure through most of the enamel, but grading into an outer portion composed of parallel crystallite enamel, suggesting selection for more durable tooth enamel; (3) the numerous LIGS in these teeth suggest that they may have had a lengthy developmental stage and were retained in the jaw for long periods of time; and (4) the overall similarity of microstructural features (schmelzmuster) in *Krzyzanowskisaurus* and *Revueltosaurus* lends credence to the hypothesis that the two taxa are in fact closely related.

Regarding the first point, most, if not all, workers have acknowledged the variable thickness of reptilian tooth enamel. However, what is lacking in most reports, even the relatively comprehensive approaches of Sander (1999) and Hwang (2005), is any standardized assessment of this variation (note the many "holes" in Table 1, especially with regard to minimal enamel thickness). This has been addressed somewhat in more recent papers (Hwang, 2009, 2011), but there is still a need for standardization, especially given the relative ease of image acquisition and digital measurement now compared to the first tooth enamel microstucture workers. Sources of variation evident in this study include tooth position, location on the tooth, and, potentially, taxonomic position. Future studies need to better document tooth size, shape, and when

possible, position *prior* to embedding and sectioning, so that sources of thickness variation are better constrained and therefore understood. We feel that there is real need to compare actual tooth size to enamel thickness, but with the exception of Hwang's most recent (2011) paper, whole tooth measurements are lacking in the literature. As an example of how these comparisons might be significant, consider that the maximum enamel thickness we report here for *Revueltosaurus* is similar to that reported in many tyrannosaurs (Sander, 1999; Hwang, 2005; Stokosa, 2005). However, the teeth we sectioned are more than an order of magnitude smaller in total crown height and significantly smaller in crown width and length than tyrannosaur teeth, and thus are probably, volumetrically, nearly two orders of magnitude smaller than tyrannosaur teeth. Almost surely there is some biological significance to the fact that, in spite of this volumetric difference, *Revueltosaurus* and *Krzyzanowskisaurus* had enamel nearly as thick as that of *Tyrannosaurus*, but without more rigorous, standardized reporting protocols, this fact is easily lost. There is, as Sander (1999) and Hwang (2005, 2011) admitted, certainly much homoplasy among tooth enamel microstructure across sauropsids. One fact to consider in this analysis is that *Revueltosaurus* and *Krzyzanowskisaurus* teeth are similar in size to those of theropods much smaller than *T. rex*, and that tyrannosaurs doubtless possessed some of the largest teeth of any reptile, although Hwang (2005) noted that tyrannosaurid teeth possess proportionately thin enamel relative to their size. The underlying biological reasons for this variation can only be investigated if the variation itself is documented, as we strive do to here.

The relatively thick enamel of *Revueltosaurus* and *Krzyzanowskisaurus*, especially given the small size of the teeth, suggests selection for teeth particularly resistant to abrasion. Although much thinner than the enamel of some of the durophagous taxa examined by Sander (1999), *Revueltosaurus* and *Krzyzanowskisaurus* teeth have enamel that is thicker than that of most relatively closely related taxa, especially when controlled for size. With their phyllodont (leaf-like) to spatulate shape and relatively coarse, non-perpendicular denticles, the teeth of both taxa fit within the broadly defined "non-oral processing herbivore" adaptive complex of Sander (1999), and possess many characteristics considered "putatively herbivorous traits" by Zanno and Mackovicky (2011), who focused on dinosaurs but still produced hypotheses relevant to more basal archosauriformes. How-

ever, tooth enamel microstructure provides few additional clues to the diet of either taxon. Sander (1999) noted that columnar enamel appears less-well adapted to true grinding surfaces than does parallel crystallite enamel, based in part on the widespread occurrence of thin caps of parallel crystallite enamel atop the thick columnar enamel of many undoubtedly durophagous reptiles. On the other hand, Sander (1999) and Hwang (2005, 2007, 2011) have documented schmelzmuster of almost entirely columnar enamel in many taxa whose teeth were clearly involved in grinding, such as ceratopsian dinosaurs. However, these taxa actively abrade the tooth through the outer enamel surface, so this may be different than the parallel crystallite enamel "cap" of durophagous taxa. Columnar enamel is thought to better resist bending forces, especially in reptiles where the enamel tends to be thin relative to the dentine, and must therefore accommodate not only external stresses, but also the resulting strain on the dentine (e.g., Koenigswald and Pfretzschner, 1992; Rensberger, 1997; Sander, 1999). Sander (1999) thus considered parallel crystallite enamel superior to columnar in terms of resisting wear and abrasion, but columnar enamel superior to parallel crystallite enamel in resisting cracking and bending. The presence of parallel crystallite enamel in the outer portions of the teeth in *Revueltosaurus* and *Krzyzanowskisaurus* is thus somewhat similar to durophagous taxa documented by Sander (1999), although the Triassic enamel is much thinner (< 100 μm) than some of the mosasaur, crocodilian, and ichthyosaur specimens examined by Sander (1999). It thus appears likely that both *Revueltosaurus* and *Krzyzanowskisaurus* ate items that placed a greater emphasis on biting than on true grinding, even though Heckert (2002, 2005) demonstrated relatively precise abrasion of the denticles in both taxa. At present it is not possible to accurately discern the shape of the skull of *Revueltosaurus* (e.g., Parker et al., 2005), so it is unclear whether this wear might be the result of feeding habits, such as ingesting or stripping twigs and branches or other roughage while browsing or eating Triassic ground cover or roots and other subterranean plant matter mixed with soil while "grazing."

Both *Revueltosaurus* and *Krzyzanowskisaurus* possess numerous LIGs. These are especially apparent in the outer layers of the *Revueltosaurus* maxillary-dentary tooth in transverse section, but remain apparent even in the thin enamel near the base of the premaxillary tooth. *Revueltosaurus*

LIGs are both well developed and numerous (20+ bands apparent in Figure 4.4), suggesting a lengthy growth period for each tooth. Indeed, these LIGs are similar in terms of both frequency and dominance of the enamel microstructure to that of a rauisuchian illustrated by Sander (1999, plate 9f). Generally speaking, LIGs are more prevalent in taxa with parallel crystallite than columnar enamel, but do occur in many of the taxa that bracket both *Revueltosaurus* and *Krzyzanowskisaurus* phylogenetically. However, the frequency of LIGs seen in the teeth here far outstrips that of any comparably sized taxon in Sander (1999) or Hwang (2011), suggesting that these teeth were slower-developing and/or retained longer than in, for example, ornithischian dinosaurs. Ornithischians with relatively similar patterns of LIGs include an indeterminate ankylosaur and *Thescelosaurus* (Sander, 1999, plate 14g–h, respectively), although we note that Hwang (2011, figure 16a–c) reported a different schmelzmuster in *Thescelosaurus*, casting some doubt on the affinities of the *Thescelosaurus* tooth illustrated by Sander (plate 14h). There are examples of presumably fast-growing taxa, such as troodontid theropods, with numerous LIGS (Hwang, 2005, 2011), and the relatively slow-growing extant *Uromastyx* is the only reptile known to have "mammalian-like" prismatic enamel (Sander, 2000). Appenzeller et al. (2005) posited that LIGS (striae of Retzius) are actually tied to diurnal rhythms of the autonomous nervous system. If this is correct, then the developed ment of these teeth was probably on the order of two weeks to a month, assuming no remodeling. What is intriguing about the Appenzeller et al. (2005) study is that these striae are found across a wide range of taxa, yet are absent from an equally wide assortment of taxa as well.

Teeth assigned to *Krzyzanowskisaurus hunti* by Heckert (2005) had variously been considered conspecific (Long and Murry, 1995) or congeneric (Heckert, 2002) with *Revueltosaurus callenderi* based on overall similarity. Parker et al. (2005) and later Irmis et al. (2007; see also Nesbitt et al., 2007) argued that, while distinct at the specific level, *K. hunti* teeth should be assigned to *Revueltosaurus*. Heckert's (2005) designation of a new species was in part an effort to demonstrate the more ornithischian-like characteristics of *K. hunti*. Parker et al. (2005) and Irmis et al. (2007) in turn argued, in part, that *Revueltosaurus* osteoderms and an isolated squamosal from the same locality (UCMP 7308) in the UCMP collections supported their taxonomic argument. As Heckert (2005)

noted, this argument is weakened by the disarticulated nature of material from UCMP 7308, which yields an extensive, and largely undescribed, fauna ranging from osteichthyans to phytosaurs and aetosaurs (see also Long and Murry, 1995; Heckert et al., 2005).

One point of this study was to see if tooth enamel microstructure could provide additional insight into the relatedness of *Revueltosaurus* and *Krzyzanowskisaurus*. Although Sander (1999) reported relatively little phylogenetic signal in tooth enamel microstructural features, Hwang (2005, 2011) has reported a variety of synapomorphies that unite at least some dinosaurian taxa and has argued (Hwang, 2009) that enamel microstructure can even be used to help identify isolated and/or fragmentary teeth.

It is clear from this study that numerous features of the enamel microstructure of *R. callenderi* and *K. hunti* are quite similar. Although only a few other Triassic archosaurs have been sampled, the schmelzmuster of these taxa, with a thin BUL, relatively thick, columnar enamel, and numerous fine LIG are unlike any other taxon reported by Sander (1999) or Hwang (2005, 2011). As part of another project we have begun examining the microstructure of phytosaur teeth, greatly expanding upon Sander's (1999) sample of three teeth, and have not found any teeth with this same combination of features (e.g., Camp and Heckert, 2007). Thus, we are inclined to tentatively accept the hypothesis of Parker et al. (2005; Irmis et al., 2007) that *Krzyzanowskisaurus hunti* is in fact closely allied to *R. callenderi*. However, we prefer to keep the separate generic name of *K. hunti*, noting that it remains likely that, when more complete *Krzyzanowskisaurus* fossils are found, they will likely be considered distinct at the generic level. Indeed, throughout the Upper Triassic, archosauriform taxa with distinctive dentitions are almost always assigned to different genera, including both shuvosaurids (*Shuvosaurus, Effigia,* Nesbitt, 2007) and silesaurids (*Silesaurus, Asilisaurus*, and *Diodorus*, Nesbitt et al., 2010; Kammerer et al., 2012). Thus, until more diagnostic skeletal material unambiguously associated with *Krzyzanowskisaurus* is found, we advocate retaining the two taxa as separate, but closely related genera. Because *Revueltosaurus* is now widely considered the sister taxon to aetosaurs (e.g., Nesbitt, 2011; Butler et al., 2011), obtaining enamel microstructural details of aetosaurs is highly desirable to see if these complex features (thick, complex enamel with many LIGs, for example) are present in aetosaurs, which have comparatively simple dentitions, albeit with some taxonomic variation (e.g., Walker, 1961; Heckert and Lucas, 2000).

CONCLUSIONS

Tooth enamel microstructure in *Revueltosaurus callenderi* and *Krzyzanowskisaurus hunti* is relatively unique among archosaurs, and the enamel itself is particularly thick for teeth of their size. Neither result is terribly surprising, as Hwang (2011) notes that, in dinosaurs, schmelzmuster complexity correlates with tooth complexity, and these teeth have long been recognized as among the most complex of Triassic archosauriforms. The thickness of the enamel in these teeth appears impressive for their size, although comparisons across taxa using the literature are hampered by a dearth of data reporting original tooth size. The numerous LIGs may hint at teeth with an exceptionally long life in the jaw. Whether this is a reflection of functional utility (teeth well adapted for their function and only rarely shed) or simply an indication of slow growth cannot be determined. The details of the tooth enamel microstructure of both taxa most closely resembles that of ankylosaurs, indicating convergent evolution between the Triassic taxa and the much later ornithischians.

Future studies of archosauriform tooth enamel microstructure should address several problems: (1) Standardization of thickness measurements to landmarks if possible; (2) consideration of enamel thickness and complexity relative to overall tooth size; (3) wider taxonomic sampling, especially among Triassic archosauriforms to determine the extent that these features reveal aspects of the diversification of archosaurs during the Triassic. This is especially important as revueltosaurs, silesaurids, and shuvosaurids, among others, represent early "experiments" in herbivory, or at least are not obviously carnivorous forms, within Archosauria. With more complex methodologies now being employed to analyze dietary preferences in similar taxa, such as Jurassic-Cretaceous theropods (Zanno and Mackovicky, 2011), it is important to establish repeatable, if not quantifiable, descriptions of enamel microstructure characteristics, as these are clearly of great adaptive significance.

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