Connecting Hunter-Schreger Band Microstructure to Enamel Microwear Features: New Insights from Durophagous Carnivores

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Several recent studies have clarified the link between microwear features and diet among living carnivorans, but it is still unclear whether previously interpreted evolutionary trends for dietary specialization, based on examination of enamel microstructure, are consistent with such insights from microwear analysis. This study examined the relationship between microwear and microstructure features using a sample of fossil hyaenids and canids. Hunter-Schreger Bands (HSB) and microwear features were examined at the same magnification level using optical stereomicroscopy. Multiple trials conducted on each specimen showed higher variance of smaller (<0.03 mm) microwear features compared to large (>0.03 mm) features. The number of pits was positively correlated with more derived HSB in both p4 and m1; fossil teeth with derived HSB possessed microwear features similar to patterns found in modern spotted hyenas. Microscopic scratches were not as closely associated with HSB patterns, but large scratches were more tightly linked to HSB than smaller ones on p4. An examination of evolutionary trends in HSB specialization in the two carnivoran lineages showed that derived HSB patterns evolved prior to the highly robust craniodental characteristics typical of later bone-cracking ecomorphologies. Therefore, the increase of hard food in the diet of less specialized hyaenids and canids was accompanied by a mosaic mode of evolution, with microstructural changes preceding key macrostructural morphological adaptations.

Key words: Mammalia, Borophagine, Canidae, Hyaenidae, durophagy, bone-cracking, Miocene, Cenozoic.

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Introduction

Carnivoran enamel microstructure is arranged into Hunter-Schreger Bands (HSB), specializations of which have evolved convergently across the order (Stefen 1997). Increased folding of HSB into sharp-angled, "zig-zag" patterns is thought to provide structural support and biomechanical advantages in the teeth of species that also possess craniodental specializations for durophagy (Ferretti 1999, 2007; Stefen 1999; Stefen and Rensberger 1999). In those durophagous ecomorphologies, enamel microstructural changes are accompanied by macrostructural changes in morphology, such as more robust premolars, deeper skulls, and relatively shorter rostra (Werdelin 1989; Van Valkenburgh 2007; Tseng and Wang 2011). Inferences of paleoecology from morphological features in durophagous species, however, have seldom been linked with more direct indicators of paleodiet.

Dental microwear features, the patterns of abrasion on teeth from food and other ingested particles, have been studied as direct indicators revealing the diets of extinct animals (Walker et al. 1978; Peters 1982). In a paleoecological context, microwear analyses have been applied to a number of vertebrate groups, including dinosaurs (Williams et al. 2009), crocodilians (Osi and Weishampel 2009), fishes (Purnell et al. 2006), and a wide range of mammals: marsupials (e.g., Robson and Young 1990), primates (e.g., Daegling and Grine 1994; Scott et al. 2005), rodents (e.g., Rodrigues et al. 2009), sirenians (Domning and Beatty 2007), carnivorans (Hagura and Onodera 1987; Van Valkenburgh et al. 1990; Anyonge 1996; Goillot et al. 2009; Peigne et al. 2009; Schubert et al. 2010), xenarthrans (Green 2009), and, most commonly, ungulate mammals (e.g., Merceron et al. 2004; Kaiser and Brinkmann 2006; Sanson et al. 2007; Semprebon and Rivals 2007; Joomun et al. 2008; Merceron et al. 2010, among others). Compared to the large number of studies that interpret paleodiets using microwear analysis, the link between enamel microstructure and microwear patterns has been less commonly explored (Maas 1991; Teaford et al. 1996). This study focuses on the correlation between enamel microstructure and enamel microwear patterns among durophagous mammalian carnivores, using fossil canids and hyaenids as a case study.

Canidae and Hyaenidae are two carnivoran families that have convergently evolved bone-cracking ecomorphologies (Werdelin 1996). Specialized enamel microstructure in mod-

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ern spotted hyenas is linked with their bone-rich diet (Kruuk 1972; Rensberger and Wang 2005; Rensberger and Stefen 2006). Similar microstructural specializations are observed in fossil hyaenids (Ferretti 2007) and borophagine canids (Stefen 1999). However, it is not known whether microstructural adaptations for increased structural strength are actually associated with microwear indicators of more hard food in the diet. Previous microwear studies on durophagous carnivores found that spotted hyenas possess a larger number of microscopic pits relative to scratches on their teeth, and also fewer narrow microwear features when compared to non-durophagous species (Van Valkenburgh et al. 1990). Therefore, I test the hypothesis that HSB specialization is linked to increasing numbers of large microwear features and also more pits relative to scratches.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; F:AM, Frick Collection, American Museum of Natural History; HMV, Hezheng Paleozoology Museum, Gansu, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; LACM, Natural History Museum of Los Angeles County, California, USA; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley, California, USA; PPHM, Panhandle-Plains Historical Museum, Texas, USA; UAMZ, University of Alberta Museum of Zoology, Alberta, Canada; UCMP, University of California Museum of Paleontology, Berkeley, California, USA; USNM, National Museum of Natural History (also NMNH), Smithsonian Institution, Washington D.C., USA.

Other abbreviations.—HSB, Hunter-Schreger Bands.

Material and methods

Microwear analysis.—Both microwear and microstructure methods used in this study were non-invasive, and therefore could be applied across both fossil and extant specimens without destructive sampling. 64 p4 specimens and 75 m1 specimens were examined in the study (Appendices 1, 2). The lower fourth premolar (p4) is used to crack bones, and the lower first molar (m1; carnassial) is used to both cut flesh and crack bones in the durophagous spotted hyena (Kruuk 1972). Specimens included fossil hyaenids and canids, as well as the extant spotted hyena *Crocuta crocuta* and the African hunting dog *Lycaon pictus* (Appendices 1, 2). All specimens were cleaned with cotton swabs and either acetone or ethanol solutions. Specimens were then examined under an optical stereomicroscope to make sure the enamel surface was free of adhesives or sediment matrix. Molds were made with a vinyl polysiloxane material (3M ESPE Dental Products, St. Paul, MN, USA) through a dispensing gun as described in Solounias and Semprebon (2002). All specimens were molded twice, with the first mold used as a cleaning layer, which was discarded. Second molds were then cast using high-resolution, spectrally clear, optical grade epoxy resin (EPO-TEK 301, Epoxy Technology Inc., Billerica, MA, USA). The casts were evacuated in a vacuum chamber for 20 minutes, and then left to set at room temperature for five days.

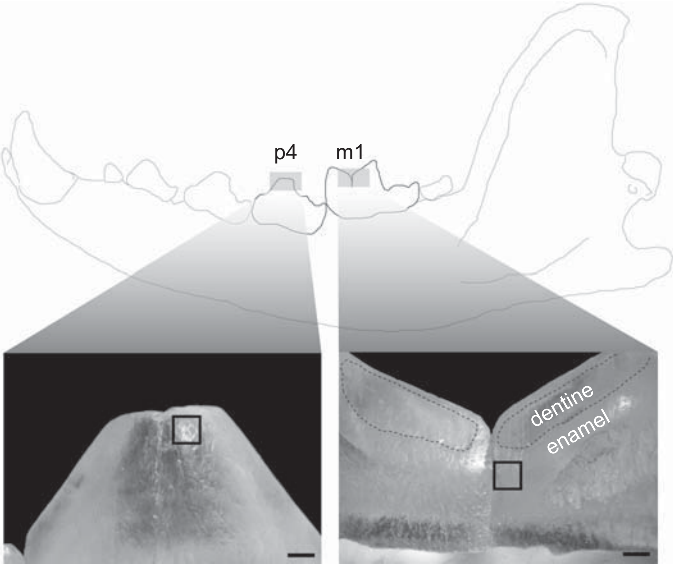

Fig. 1. Tooth positions examined in the study, shown on a spotted hyena dentary. Black squares indicate the approximate size of the area examined during each trial. Note the exposed areas of dentine on the shear facet of m1; all trials were done on the enamel portion of the teeth only.

Examination for microwear features was done using an optical stereomicroscope at 30× magnification (compared to 35× in Solounias and Semprebon 2002). Microwear features were recorded inside a 1 × 1 mm^2 area, which was delineated on the labial edge of the p4 and m1 wear facet using a crossed stage micrometer scale fitted inside the eyepiece of the microscope (Fig. 1). Care was taken to examine only areas on the enamel portion of the tooth crown, as opposed to the dentine area present on the shear facet of the lower molar (Fig. 1); weathering and laboratory preparation can easily create artificial features on the dentine, which is a softer material than enamel. Features were either scored as scratches (i.e., length:width ratio > 4:1) or pits (i.e., length:width ratio < 4:1). At 30×, all features with widths smaller than the width between two micrometer ticks (<0.03 mm) were scored as small, while those larger than 0.03 mm were scored as large. As such, four categories of features were analyzed: small versus large scratches, and small versus large pits (Fig. 2).

All specimens were examined three times by the author, with the interval between any two trials on the same specimen ranging from four days to six months apart. Analyses were done in ~4 hour sittings, with random sampling of specimens in no particular order of examination. No attempts were made to analyze identical 1 × 1 mm^2 areas on the tooth during each trial, as the trials were intended to include a sample of different areas on the labial face of the wear facets. It should be noted that the methods employed in this study were aimed to address the specific question of the connection between microwear signals and enamel microstructure in durophagous hyaenids

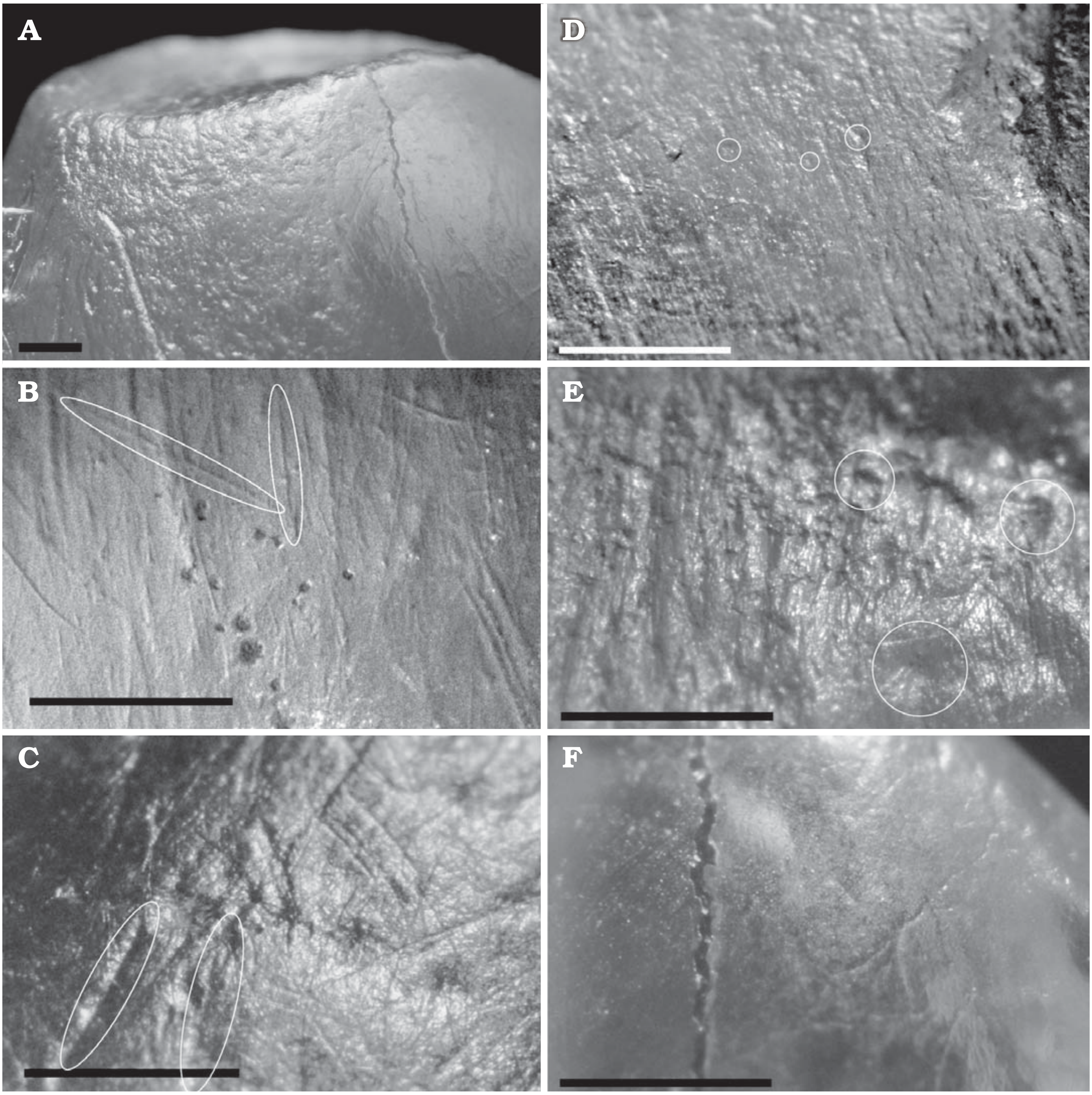

Fig. 2. Examples of microwear features examined. **A**. Labial (buccal) wear facet on p4 of the extant spotted hyena *Crocuta crocuta* Erxleben, 1777 (cast of MVZ173771), showing a typical specimen with moderate tooth crown attrition. **B**. Examples of small (thin) scratches (MVZ173771). **C**. Examples of large (thick) scratches (*C. crocuta*, MVZ165179). **D**. Examples of small pits (*Borophagus secundus* VanderHoof, 1931, UCMP30479). **E**. Examples of large pits (*C. crocuta*, MVZ165160). **F**. p4 crown surface of the African hunting dog *Lycaon pictus* Temminck, 1820 (MVZ4842); note paucity of microwear features. Scale bars 1 mm.

and canids; results from other microwear studies should not be compared directly to the data in this study. Furthermore, results obtained from replication of the methods used here in studies of other taxa also should not be directly compared to the results of the present study, as such comparisons are potentially affected by other taxon-specific factors with yet unknown influence on microwear patterns (see Discussion).

Microstructure analysis.—All of the fossil specimens examined in the microwear analysis were also analyzed for HSB specialization (Stefen 1997). Specimens with lighter-colored enamel preservation and clean surfaces can be examined directly with an oblique light source, illuminating HSB patterns without the necessity of sectioning the specimens (Koenigswald 1980; Stefen and Rensberger 1999). Only

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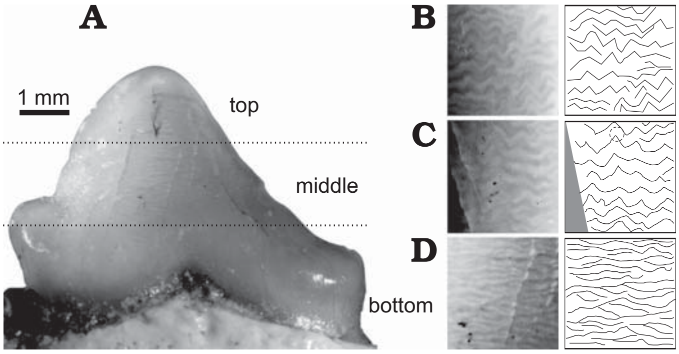

Fig. 3. Method of enamel microstructure analysis. **A**. Three regions of the tooth crown were examined for Hunter-Schreger Bands (HSB), representing top, middle, and bottom thirds of the crown. One of three types of HSB was recorded for each region. **B**. Examples of a region with mostly (> 50%) zig-zag HSB. **C**. Region with acute-angled undulating HSB (note that some zig-zag HSB is also present, e.g., indicated by a dotted circle). **D**. Undulating HSB.

specimens that fit such criteria were chosen for both microwear and microstructure analyses. At the time of cleaning and molding, the original specimens were analyzed with an optical stereomicroscope at 30× magnification. HSB patterns were recorded at three levels on the tooth crown: the top, middle, and bottom 33% of the crown (Fig. 3). The most commonly found (> 50% of the region) HSB was recorded as representative of that region; if two HSB categories were equally common in a given region, the more derived HSB pattern was recorded. As previously categorized by Stefen (1997), the most derived HSB pattern in carnivorans is zig-zag HSB, followed by acute-angled undulating HSB, and then undulating HSB (Fig. 3B–D).

To obtain a context for evolutionary changes in HSB patterns across different tooth positions in fossil hyaenids and canids, additional specimens were examined for HSB only (Appendix 3). Samples were taken from those used by Tseng (2011). The entire lower dentition, in addition to p4 and m1, was subject to HSB analysis as described above. Where possible, complete dentaries were used, supplemented by isolated specimens as appropriate (Appendix 3). An abbreviation system was created to refer to different degrees of HSB specialization: a single letter representing HSB pattern at each of the three levels of the crown, with "z" for zig-zag, "a" for acute-angled undulating, and "u" for undulating HSB (e.g., "zau" for a tooth with zig-zag HSB at the top 33% of the crown, acute-undulating HSB at the middle, and undulating HSB at the bottom of the crown).

Results

Microwear features exhibited different degrees of intra-tooth variation across the three trials conducted on each specimen; large microwear features (>0.03 mm) tended to have lower variance than smaller (<0.03 mm) features. In addition, m1 tended to have more variable counts in microwear features compared to p4 (Fig. 4). For all subsequent comparisons of microwear feature counts, mean values of the trials were used to represent each specimen.

Specimens containing at least 33% zig-zag HSB had a larger range of small and large pit counts compared to teeth with less specialized HSB; however, this is true only for p4, but not m1 (Fig. 5A, B, E, F). The number of small scratches showed no trend across different HSB categories, either in p4 or m1 (Fig. 5C, G). Large scratches in p4 specimens with all zig-zag HSB were more numerous than in all less derived teeth, with the former approaching the count in *Crocuta*; no such pattern was present in m1 specimens (Fig. 5D, H).

In order to achieve comparable sample sizes for statistical analysis, HSB categories were combined into three bins, and analyses of variance (ANOVA) were conducted on the categories along with the modern *Crocuta* sample (Table 1, Fig. 6). The number of pits (both large and small) was significantly different across HSB categories on p4, and the increase was incremental (Fig. 6A, B). The number of pits was also significantly different on m1, but the number of large pits among fossil specimens did not approach the range observed in modern *Crocuta* (Fig. 6F). Among scratches, only large scratches on p4 were significantly different across categories, with the increase being incremental as observed for large pits on p4 (Fig. 6D).

Table 1. ANOVA of microwear features according to categories of HSB specialization. Statistical testing was done on binned category data (as in Fig. 6).

	p4 vs. HSB		m1 vs. HSB	
	$F_{3,59}$	p	$F_{3,70}$	p
Small pits	8.33	<0.001*	8.13	<0.001*
Large pits	5.42	0.002*	11.46	<0.001*
Small scratches	0.99	0.405	0.47	0.702
Large scratches	4.72	0.005*	0.57	0.637

In an evolutionary context, derived zig-zag HSB (zau to zzz) were not observed among the hesperocyonine canids examined; in borophagine canids, zig-zag HSB were observed in the m1 of *Microtomarctus* and all subsequent genera (Fig. 7A). Zig-zag HSB spread throughout the premolar dentition in more derived borophagines, and in *Epicyon*, specimens with all zig-zag HSB across p1–m2 were observed. Zig-zag HSB were present in the premolars and first molar of the hyaenid *Ictitherium*, and in most of the subsequent hyaenid genera (Fig. 7B). Cheek tooth dentitions in hyaenids became reduced in the derived, larger-bodied genera, in which p1 and m2 were lost. The remaining cheek teeth in those genera retained full zig-zag HSB patterns.

Discussion

Microwear analysis of the p4 and m1 teeth of fossil hyaenids and canids showed a general increase in both the number and

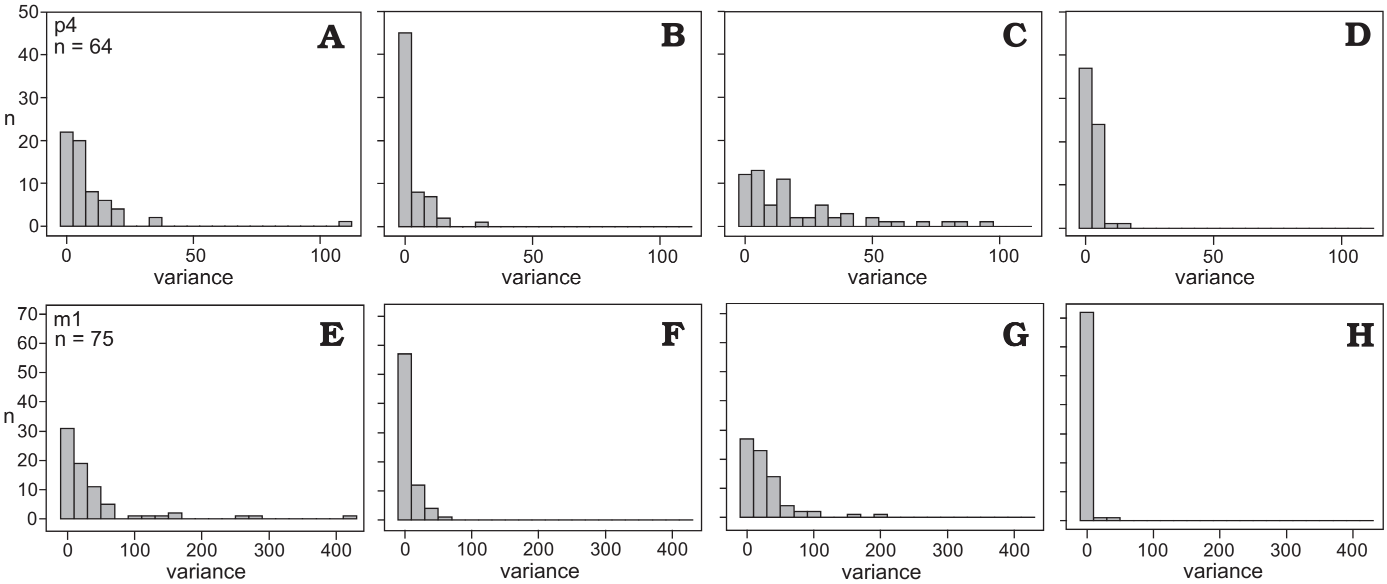

Fig. 4. Histograms of variance among specimen microwear trials in p4 (**A**–**D**) and m1 (**E**–**H**). **A**, **E**. Small scratches. **B**, **F**. Large scratches. **C**, **G**. Small pits. **D**, **H**. Large pits. Plot ranges for p4 and m1 were adjusted to show maximum spread of data, respectively.

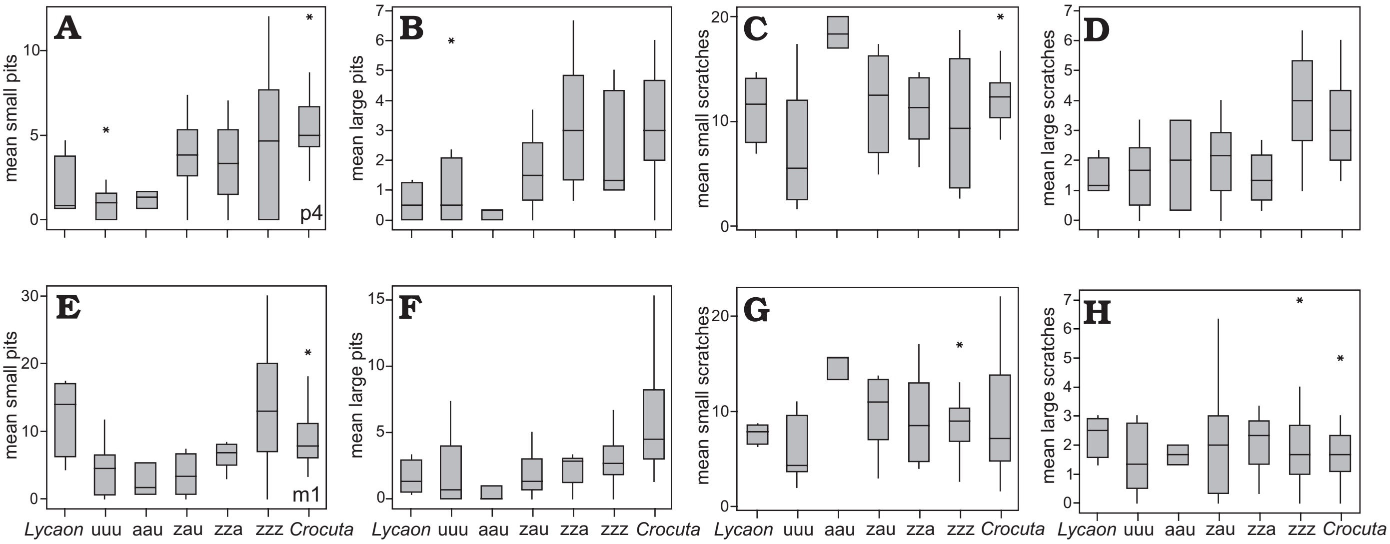

Fig. 5. Box plots of microwear features across HSB categories in p4 (**A**–**D**) and m1 (**E**–**H**) specimens. Boxes represent inter-quartile ranges, horizontal lines within boxes are medians; vertical lines show upper and lower limits, and asterisks represent outliers. Abbreviations: a, acute-angled undulating HSB; u, undulating HSB; z, zig-zag HSB.

variability of large and small pits with more derived HSB (Figs. 5A, B, E, F, 6A, B, E, F). These findings are consistent with those of Van Valkenburgh et al. (1990), who found a relatively higher number of pits and a higher variability of microwear features in carnivorans with more hard food in their diets. These trends have been shown to be correlated to increasing HSB specialization in this study, supporting the initial hypothesis that derived HSB is associated with an increase in both the number of pits and the variability of features.

These results are also consistent with previous functional interpretations of the derived zig-zag HSB in allowing a more durophagous diet (Stefen and Rensberger 1999). The intensely folded layers of enamel prisms of zig-zag HSB is thought to function in resisting the large stresses incurred from consumption of hard foods, such as bone. In addition, the layered structure of HSB can also shorten or halt crack propagation in instances of local enamel failure (Chai et al. 2009). Accordingly, zig-zag HSB evolved convergently not only in fossil canids and hyaenids, but also in other carnivoran lineages with tendencies to consume hard food items (Stefen 2001).

On the other hand, the number and variability of scratches showed no clear trend with increasing HSB specialization (Figs. 5C, D, G, H, 6C, D, G, H). The only results that supported the hypothesis of an increase in larger features with HSB specialization are the number of large scratches on p4 specimens (Fig. 6D). Feature orientation, which was not ana-

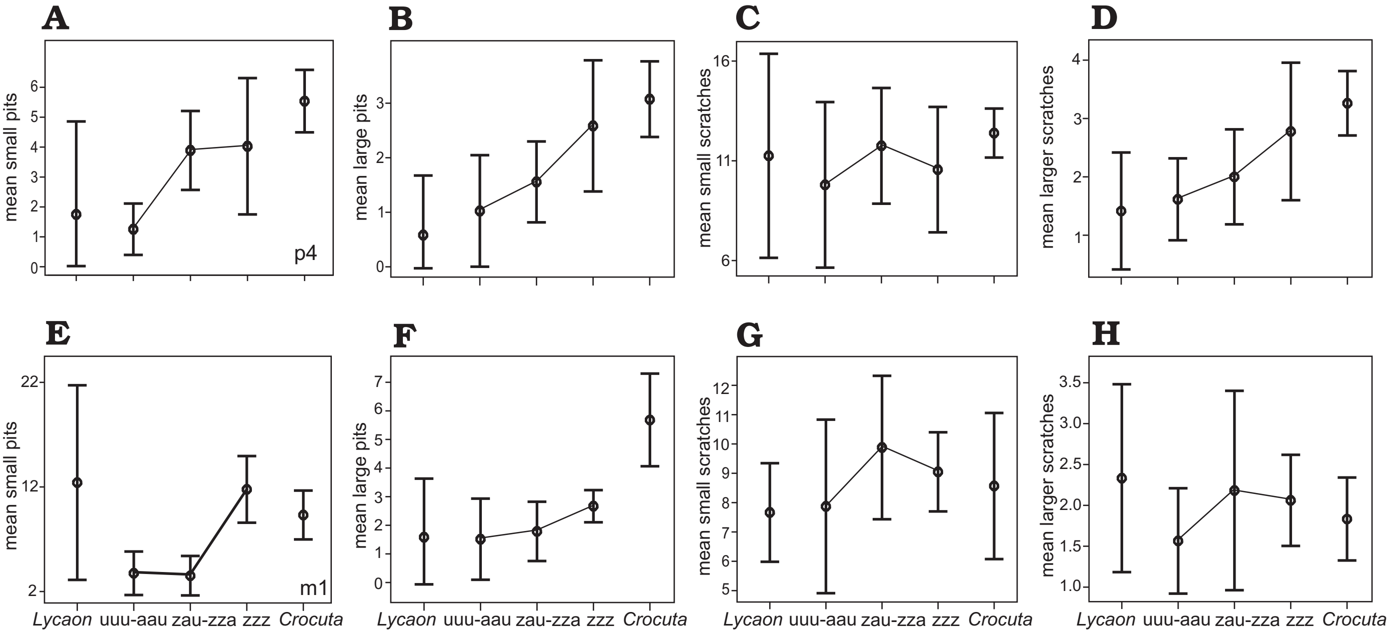

Fig. 6. Plots of mean values and 95% confidence intervals for binned HSB categories in p4 (**A**–**D**) and m1 (**E**–**H**) specimens. Mean values are connected in fossil samples to show trend. Abbreviations: a, acute-angled undulating HSB; u, undulating HSB; z, zig-zag HSB.

lyzed in this study, could distinguish HSB patterns on the basis of scratch distribution. Differences in the proportion of parallel scratches are expected not only in teeth that occlude more precisely (e.g., carnassial teeth) versus teeth that occlude in between other teeth (e.g., carnivoran second to fourth premolars), but also in the teeth of durophagous species on which scratches are more randomly distributed (Van Valkenburgh et al. 1990). Nevertheless, the overlap in the number of large and small scratches of extant *Crocuta* and *Lycaon* specimens indicates that such counts do not differentiate between modern bone-cracking and soft-meat hypercarnivores in the context of this study (Fig. 5C, D, G, H). Therefore, the trends that are present across different categories of HSB specialization are more in line with microwear features (i.e., large pits) clearly associated with durophagy, supporting the interpretation of evolutionary specialization of HSB as being in close association with an increase of hard foods in the diet (Stefen 1999; Ferretti 2007; Goillot et al. 2009).

If we apply this close association between a hard-food rich diet and increasingly derived HSB to the examination of evolutionary patterns of HSB change in fossil hyaenids and canids, the resulting trend shows that zig-zag HSB in both lineages appeared prior to the large-bodied bone-cracking ecomorphologies typically recognized from craniodental morphology (Fig. 7). The borophagine genera *Aelurodon, Epicyon*, and *Borophagus*, and the hyaenid genera *Pachycrocuta, Adcrocuta,* and *Crocuta* are commonly categorized as bone-crackers (Werdelin 1989; Van Valkenburgh and Koepfli 1993; Wang et al. 1999). However, zig-zag HSB evolved no later than in the canid *Microtomarctus* and the hyaenid *Ictitherium* (Fig. 7). This difference in the timing of the appearance of robust craniodental morphology, and the more continuous increase of hard foods in the diet implied by HSB specialization, indicate a mosaic mode of character evolution. In other words, the suite of morphological features present in the derived bone-cracking canids and hyaenids, including both microstructural and macrostructural characteristics, evolved in stages. Microstructural changes occurred prior to macrostructural ones, as a response to increasingly durophagous diets as inferred from microwear patterns (Figs. 6, 7). Such a mode of adaptive change may be pervasive especially in the gradual evolution of the hyaenids, as evidence of mosaic morphological evolution has also been found in overall craniodental morphology, exemplified by the intermediate biomechanical adaptations of the transitional bone cracker *Ikelohyaena abronia* (Tseng and Stynder 2011).

Interestingly, while p4 and m1 shared similar numbers of microscopic scratch features, m1 tended to have a much larger number of both large and small pits (Fig. 5A, B, E, F). Larger numbers of microwear features on m1 may reflect the important function of the tooth as a main flesh-shearing tool, which is also used by the extant *Crocuta crocuta* in cracking hard food items (Van Valkenburgh 1996). It is also likely that at least some of the microscopic pits resulted from corrosion by stomach acids, as regurgitation is relatively common in *Crocuta crocuta* (Kruuk 1972; Van Valkenburgh 1996). Nevertheless, microwear patterns from both p4 and m1 support a close relationship with HSB specialization, and evolutionary trends show that the entire cheek dentition was eventually specialized for increased durophagy in both borophagine canids and hyaenids (Fig. 7). Tooth crown attrition in modern hyaenids, derived fossil hyaenids and borophagine canids shows that all cheek teeth can be heavily worn, indicating their use in durophagy (personal observation).

There have been few published studies exploring the relationship between microstructure and microwear patterns.

Maas (1991) conducted experiments to examine the relationship between prism structure, shear force, and abrasive particle size, and found that the size and number of microscopic scratches can be confounded by the type of prism arrangement present in the enamel of a given species. Teaford et al. (1996) found that enamel crystallite and prism microstructure and microwear data provided complementary information that allowed a more nuanced reconstruction of the paleodiets of Oligocene anthropoids. However, no study has specifically looked at microwear and microstructure across types of Hunter Schreger Bands. The findings from the current study, even though narrow in scope, provide evidence that such microstructure-microwear comparisons at the HSB level are also informative. Even so, care should still be taken in interpreting or extrapolating the results of this study to other durophagous taxa. Dental wear patterns observed on the enamel likely resulted from complex interactions among body size, masticatory musculature, behavior, etc., in addition to morphology and microstructure. The interactions among these physical and physiological factors still need to be clarified with carefully designed studies.

Multiple trials of microwear analysis conducted in this study showed that larger features tend to be less variable within each tooth across examinations than smaller features (Fig. 4). Smaller features may be more variable simply because a larger number of them can occur within the defined areas sampled on each tooth. Such a trend may also reflect an inherent source of error based on the inability of the observer to discern increasingly miniscule features (Palmeirim 1998), and software-based microwear analytical methods have been proposed in order to make counting of features more objective (Ungar 1995; Scott et al. 2005). Application of a software-based approach may clarify the high variability and lack of correlation of microscopic scratches to HSB patterns found by the current study, but the general agreement of results with previous microwear studies of carnivorans indicates that a consistent trend in microwear features is present, regardless of the type of method employed (see below). Along the same lines, agreement of results based on different levels of magnification (SEM, confocal microscopy, high-magnification stereomicroscopy, low-magnification stereomicroscopy) shows that dietary signals for durophagy are present across multiple levels of scale, at least in carnivorans (Van Valkenburgh 1990; Goillot et al. 2009; Schubert et al. 2010; this study).

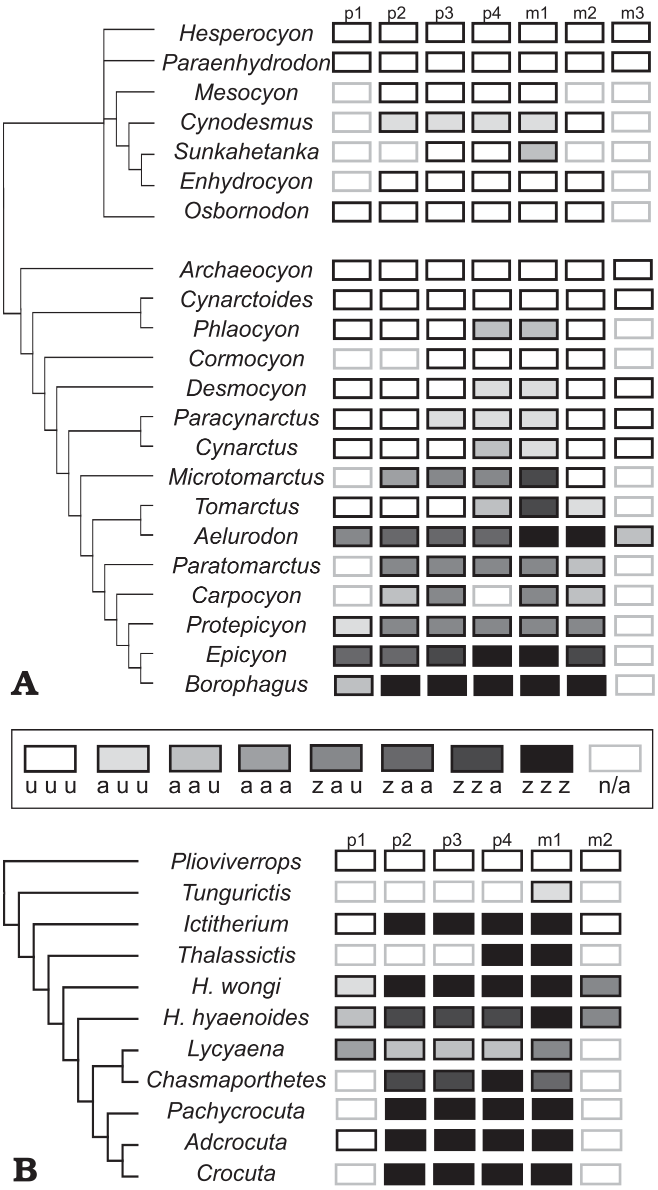

Fig. 7. Intra-dentition evolution of HSB microstructure in fossil Canidae (**A**) and Hyaenidae (**B**). Phylogenies for fossil canids based on Wang (1994) and Wang et al. (1999), and for hyaenids based on Werdelin and Solounias (1991). Progressively more derived HSB patterns are indicated by darker shades of grey. Abbreviations: a, acute-angled undulating HSB; u, undulating HSB; z, zig-zag HSB.

More recently, the application of microwear texture analysis to the carnassial teeth of *Crocuta crocuta* has provided promising results for correlating bone consumption with enamel surface complexity (Schubert et al. 2010). Results from texture analysis supported the main findings of Van Valkenburgh et al. (1990), which were based on Scanning Electron Microscope images. Taken together, the durophagous *C. crocuta* tends to show a larger number of pits and the wider range of feature sizes, as well as more variable scratch directions relative to the main occlusal axis (Van Valkenburgh et al. 1990; Schubert et al. 2010). Results from the current study are consistent with these findings, and indicate that HSB microstructure specialization is likely to be positively correlated to additional characteristic features of durophagous taxa found using SEM and texture analysis as well. One caveat to be noted here is that this and other studies cited above were all conducted on carnivoran mammals, and therefore caution should be taken when discussing durophagy in other taxa. Microwear patterns for similar diets may differ in unrelated taxa, and such differences need to be quantified before any direct comparisons are made.

In conclusion, a sample of fossil hyaenid and canid specimens were examined for HSB microstructure and microwear features, and a connection between the number of pits and the degree of HSB specialization was found. By contrast, the correlation between HSB and microscopic scratches was not as strong. In general, patterns on p4 are more pronounced than those on m1. The first appearance of zig-zag HSB in borophagine canids and hyaenids occurred prior to the evolution of robust craniodental morphology. The association between increasing HSB specialization and more microwear features is indicative of a durophagous diet, and both indicate that hard foods were already being incorporated in the diet of less specialized hyaenids and borophagines. Therefore, the present adaptations for durophagy seen in spotted hyenas have evolved in a mosaic manner, with microstructural adaptations appearing before macrostructural modifications.

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Appendix 1

Premolar specimens used in the study. Abbreviations: HSB, Hunter-Schreger Bands; a, acute-angled undulating HSB; u, undulating HSB; z, zig-zag HSB; SL, large scratches; SS, small scratches; PL, large pits; PS, small pits.

Species	Specimen number	HSB	SL mean	SS mean	PL mean	PS mean
Lycaon pictus	MVZ117806	–	1.00	14.67	1.00	1.00
	MVZ124258	–	1.00	7.00	1.33	4.67
	MVZ184089	–	1.33	12.33	0.00	0.67
	MVZ4842	–	2.33	11.00	0.00	0.67
Cynarctus sp.	F:AM27543	uuu	2.67	6.67	0.33	1.33
	F:AM49405	uuu	2.00	2.67	0.00	0.00
Phlaocyon sp.	F:AM49006	uuu	0.00	6.33	0.00	0.00
Phlaocyon leucosteus	F:AM8768	uuu	1.00	4.67	1.33	1.33
Phlaocyon minor	F:AM27578	uuu	0.00	4.67	0.00	0.00
Tomarctus brevirostris	F:AM61121	uuu	2.00	1.67	2.00	0.67
	F:AM61127	uuu	1.33	11.00	6.00	5.33
Tomarctus hippophagus	F:AM27232	uuu	0.67	2.00	0.67	0.33
	F:AM27505	uuu	2.33	15.00	0.00	1.33
	F:AM61213	uuu	3.33	17.33	2.33	2.33
Hyaenictitherium wongi	F:AM4-L34	aau	0.33	17.00	0.00	0.67
Ictitherium sp.	F:AM10-L26	aau	2.00	20.00	0.33	1.67
	F:AM11-L131	aau	3.33	18.33	0.33	1.33

Species	Specimen number	HSB	SL mean	SS mean	PL mean	PS mean
Aelurodon ferox	F:AM61746	zau	3.67	16.00	2.00	5.33
	F:AM61749	zau	1.33	5.00	2.33	3.33
	F:AM61768	zau	0.00	5.67	3.67	3.67
	F:AM67372	zau	2.67	8.00	2.67	2.33
Aelurodon taxoides	UCMP33478	zau	2.33	10.00	1.00	5.33
Chasmaporthetes lunensis	F:AM99786	zau	2.00	16.33	1.00	4.00
Lycyaena chaeretis	F:AM26-B47	zau	2.67	17.33	2.00	7.33
	F:AM56-L560	zau	0.33	6.67	0.00	0.00
Hyaenictitherium wongi	F:AM11-L114	zau	1.00	14.33	0.67	3.67
	F:AM42-L357	zau	4.00	16.67	0.67	1.00
	F:AM93-B1000	zau	3.00	11.67	2.67	4.67
	F:AMB-L15	zau	1.00	13.33	0.00	6.00
Adcrocuta eximia	F:AM26372	zza	0.33	13.67	2.00	3.00
Aelurodon ferox	F:AM70624	zza	1.67	5.67	6.67	3.67
Chasmaporthetes lunensis	F:AM99788	zza	1.00	14.67	0.67	0.00
Epicyon haydeni	F:AM61524	zza	2.67	11.00	3.00	3.33
	F:AM61531	zza	1.33	11.33	3.00	7.00
Adcrocuta eximia	F:AM57-L533	zzz	1.00	12.33	1.33	0.00
Epicyon haydeni	F:AM61494A	zzz	4.00	7.67	2.00	7.67
	F:AM61532	zzz	3.00	9.33	5.00	5.00
	F:AM61540	zzz	5.33	2.67	4.33	4.67
	USNM127	zzz	4.00	16.00	1.00	12.00
Pachycrocuta brevirostris	F:AM107781	zzz	6.33	3.67	1.00	0.00
Pliocrocuta perrieri	F:AM107767	zzz	2.67	18.67	1.00	2.00
Crocuta crocuta	MVZ165160	–	3.67	13.67	4.67	7.67
	MVZ165163	–	4.67	16.67	2.67	4.33
	MVZ165165	–	6.00	14.33	5.00	2.67
	MVZ165166	–	4.33	10.33	2.00	2.67
	MVZ165169	–	4.67	9.33	4.00	6.00
	MVZ165170	–	1.33	16.00	1.33	2.33
	MVZ165175	–	2.33	12.33	3.67	4.67
	MVZ165176	–	3.00	12.67	4.00	5.00
	MVZ165179	–	4.67	16.33	2.00	3.00
	MVZ165181	–	3.67	12.33	2.00	8.67
	MVZ165182	–	1.33	8.67	2.00	4.33
	MVZ173733	–	4.00	13.00	4.67	8.67
	MVZ173734	–	1.67	20.00	4.67	4.67
	MVZ173743	–	2.00	11.33	5.00	6.33
	MVZ173744	–	2.00	8.33	0.00	4.33
	MVZ173746	–	5.00	11.67	3.00	4.33
	MVZ173747	–	3.00	12.67	6.00	12.00
	MVZ173756	–	4.00	10.00	4.00	8.67
	MVZ173761	–	2.00	10.33	0.00	2.67
	MVZ173768	–	3.00	11.00	3.33	5.33
	MVZ173770	–	3.33	11.33	1.67	6.67
	MVZ173771	–	2.33	9.67	2.00	5.67
	MVZ184551	–	3.00	13.00	3.00	6.67

Appendix 2

Molar specimens used in the study. *Borophagus* specimens are corresponding upper fourth premolars. Abbreviations: HSB, Hunter-Schreger Bands; a, acute-angled undulating HSB; u, undulating HSB; z, zig-zag HSB; SL, large scratches; SS, small scratches; PL, large pits; PS, small pits.

Species	Specimen number	HSB	SL mean	SS mean	PL mean	PS mean
Lycaon pictus	MVZ117806	–	1.33	8.67	3.33	12.00
	MVZ124258	–	2.33	7.33	0.33	17.33
	MVZ184089	–	3.00	8.33	1.67	16.00
	MVZ4842	–	2.67	6.33	1.00	4.33
Cynarctus sp.	F:AM27543	uuu	3.00	3.67	1.33	0.00
	F:AM49405	uuu	0.00	2.00	0.00	0.67
Phlaocyon sp.	F:AM49006	uuu	0.00	5.00	0.00	6.33
Phlaocyon leucosteus	F:AM8768	uuu	2.67	10.33	0.00	7.00
Phlaocyon minor	F:AM27578	uuu	0.67	9.33	0.00	5.00
Tomarctus brevirostris	F:AM61121	uuu	3.00	3.67	5.00	0.33
	F:AM61127	uuu	1.67	4.00	7.33	1.00
Tomarctus hippophagus	F:AM27232	uuu	0.67	4.00	0.67	4.00
	F:AM27505	uuu	2.67	4.67	0.67	5.00
	F:AM61213	uuu	1.00	11.00	3.67	11.67
Hyaenictitherium wongi	F:AM4-L34	auu	1.33	15.67	0.00	1.67
Ictitherium sp.	F:AM10-L26	aau	1.67	15.67	0.00	0.67
	F:AM11-L131	aau	2.00	13.33	1.00	5.33
Aelurodon ferox	F:AM61746	zau	2.67	9.00	2.33	5.33
	F:AM61749	zau	0.00	5.33	1.33	0.00
	F:AM61768	zau	2.67	3.00	3.00	7.33
	F:AM67372	zau	3.33	7.00	5.00	3.33
Aelurodon taxoides	UCMP33478	zau	2.00	12.67	3.33	0.00
Chasmaporthetes lunensis	F:AM99786	zau	6.33	11.00	0.67	1.67
Lycyaena chaeretis	F:AM56-L560	zau	0.00	13.67	0.00	7.33
Hyaenictitherium wongi	F:AM11-L114	zau	1.67	11.67	0.67	0.67
	F:AM42-L357	zau	3.00	13.33	2.00	6.67
	F:AM93-B1000	zau	2.00	13.67	1.33	3.33
	F:AMB-L15	zau	0.33	8.33	0.00	3.00
Adcrocuta eximia	F:AM26372	zza	2.00	17.00	0.00	8.33
Aelurodon ferox	F:AM70624	zza	2.67	5.00	3.00	5.67
Chasmaporthetes lunensis	F:AM99788	zza	1.67	11.67	1.67	3.00
Lycyaena chaeretis	F:AM26-B47	zza	0.33	4.00	3.33	6.33
Epicyon haydeni	F:AM61524	zza	3.33	9.67	3.00	8.00
	F:AM61531	zza	2.67	7.33	2.67	7.33
Adcrocuta eximia	F:AM57-L533	zzz	1.33	12.33	0.00	0.00
Borophagus secundus	UCMP30102	zzz	0.00	13.00	1.67	18.67
	UCMP30103	zzz	3.00	17.00	2.00	17.67
	UCMP30116	zzz	3.00	8.33	2.00	22.00
	UCMP30129	zzz	2.33	10.00	4.33	21.33
	UCMP30130	zzz	2.33	9.33	4.00	13.33
	UCMP30131	zzz	1.67	8.33	3.00	9.00
	UCMP30132	zzz	1.67	6.67	1.67	16.67
	UCMP30136	zzz	1.33	9.33	2.67	14.33
	UCMP30478	zzz	1.00	10.67	1.00	7.67
	UCMP30479	zzz	2.33	7.00	4.33	13.00
	UCMP30482	zzz	0.33	6.00	4.33	30.00
	UCMP30484	zzz	0.33	9.00	2.67	27.00
	UCMP30486	zzz	1.00	10.00	2.67	24.33
	UCMP30668	zzz	1.67	6.00	4.00	11.00

Species	Specimen number	HSB	SL mean	SS mean	PL mean	PS mean
Epicyon haydeni	F:AM61494A	zzz	2.67	9.67	2.67	3.00
	F:AM61532	zzz	2.67	8.00	6.67	10.00
	F:AM61540	zzz	4.00	8.00	3.33	5.67
	USNM127	zzz	7.00	6.00	2.00	8.00
Pachycrocuta brevirostris	F:AM107781	zzz	2.33	2.67	1.33	0.00
Pliocrocuta perrieri	F:AM107767	zzz	1.00	12.33	2.00	6.33
Crocuta crocuta	MVZ165160	–	2.33	22.00	1.33	4.67
	MVZ165163	–	1.33	1.67	9.00	18.00
	MVZ165165	–	1.33	6.33	5.00	10.67
	MVZ165166	–	1.33	7.67	2.33	6.00
	MVZ165169	–	1.00	5.33	6.67	6.67
	MVZ165175	–	0.67	7.33	7.33	7.33
	MVZ165176	–	2.67	7.00	3.67	8.00
	MVZ165179	–	1.67	15.33	9.67	17.67
	MVZ165181	–	1.00	15.00	4.00	21.67
	MVZ165182	–	0.00	15.00	3.00	6.33
	MVZ173733	–	1.67	9.33	2.67	7.67
	MVZ173743	–	3.00	15.33	3.00	5.33
	MVZ173744	–	2.33	10.33	2.00	3.33
	MVZ173746	–	2.00	5.00	15.33	11.33
	MVZ173747	–	1.67	4.67	5.33	6.33
	MVZ173756	–	0.67	5.00	8.33	8.33
	MVZ173761	–	2.00	4.00	4.00	4.67
	MVZ173770	–	5.00	7.67	4.00	8.67
	MVZ173771	–	2.00	2.67	8.00	14.67
	MVZ184551	–	3.00	4.67	9.00	9.00

Appendix 3

Specimens examined for evolution of Hunter-Schreger Band enamel microstructure.

Hesperocyoninae: *Hesperocyon gregarius*: LACM-CIT100 (left and right), 94 (left and right), 621, 1400 (left and right), 1444, 1526, 4917 (left and right), LACM4932 (left and right), 4933 (left and right), USNM15937 (left and right), 450576, 450577; *Paraenhydrocyon josephi*: AMNH6910, F:AM27753; *P. robustus*: F:AM12884; *Mesocyon brachyops*: LACM-CIT1242, 1346, 1819 (left and right), LACM 5265; *M. coryphaeus*: UCMP1383 (left and right), 1307 (left and right), 1165 (left and right); "*Mesocyon*" *temnodon*: F:AM 102381; *Sunkahetanka geringensis*: LACM9406, 15910 (left and right); *Osbornodon iamonensis*: USNM8836; *O. renjiei*: F:AM63316

Borophaginae: *Archaeocyon pavidus*: F:AM63970, 50338, LACM-CIT1338, UCMP76652 (left and right); *Otarocyon macdonaldi*: F:AM38986; *Rhizocyon oregonensis*: UCMP79365; *Phlaocyon annectens*: F:AM49006, 50299; *P. leucosteus*: AMNH8768; *P. latidens*: UCMP76296; *Cormocyon* sp.: LACM2739, 5424 (left and right), 2743; *Paracynarctus kelloggi*: UCMP11474; ?*Cynarctus marylandica*: USNM15561; *Metatomarctus* sp.: UCMP12604; *Metatomarctus* sp. A: UCMP38290; *Microtomarctus conferta*: LACM-CIT1232 (left and right); *Protomarctus optatus*: F:AM 61270; *Tephrocyon* sp.: UCMP19460, 19461; *Tomarctus hippophaga*: F:AM24270, 61156, LACM-CIT774; *Tomarctus sp.*: LACM 34061, UCMP24291, 24292 (left and right); *Aelurodon mcgrewi*: F:AM27153, 8307; *A. asthenostylus*: F:AM28355; *A. ferox*: USNM 352360 (left and right), V523, UCMP32241; *Paratomarctus temerarius*: F:AM50146; *P. euthos*: F:AM61101, 67121, *Paratomarctus sp.*: LACM1377 (left and right); *Carpocyon webbi*: F:AM27366B, 61335, 61336; *Protepicyon raki*: F:AM61738; *Epicyon saevus*: LACM59697 (left and right), 59813 (left and right), 127794, F:AM 61418, 67396, USNM128; *E. haydeni*: LACM143519, 127790 (left and right), PPHM1100, F:AM61498, 61476, 61552, USNM127; *Borophagus sp.*: LACM34060, 62702, 62703, UCMP30626; *B. pugnator*: F:AM61662; *B. parvus*: F:AM108396, LACM62698; *B. secundus*: 61690-5, three isolated AMNH specimens, UCMP30492, 30476; *B. littoralis*: LACM16734 (left and right)

Hyaenidae: *Plioviverrops* sp.: F:AM96607; *Tungurictis spocki*: F:AM26600; *Thalassictis* sp.: IVPP 65001; *Ictitherium* sp.: F:AM China 4-L94; HMV 0163 (left and right), 0432 (left and right); *Hyaenictitherium hyaenoides*: AMNH26371, HMV 0550 (left and right), 0552 (left and right), 0553, 0556, 0560, 0573 (left and right), 0169 (left and right), IVPP V14737 (left and right), V14738; *H. wongi*: F:AM China 11-L112, HMV 0751 (left and right), IVPP Baode Ex. 2, 30; *Lycyaena* sp.: F:AM China 38-B296, 45-L400, 26-B47, IVPP V2923; *Chasmaporthetes lunensis*: IVPP V15162; *C. ossifragus*: USNM10223; *C.* sp.: AMNH26369, LACM74046, LACM-CIT164 (left and right); *Palinhyaena reperta*: AMNH26370; *Pachycrocuta brevirostris*: AMNH27756, 27757, HMV C0066 (left and right), C0193 (left and right), IVPP 193013, V13932 (left and right); *Adcrocuta eximia*: AMNH26373, 26374, F:AM China 10-L4, HMV 0543, 0577 (left and right), 1435 (left and right); *Crocuta crocuta honanensis*: IVPP L.21625; *C. c. ultima*: IVPP V2003, V15160, V15163, V15164 (left and right).