INVESTIGATING THE TAXONOMIC UTILITY OF SERRATION DENSITY ON THE CANINES OF NORTH AMERICAN NIMRAVID FELIFORMS

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ABSTRACT

It has long been recognized that "dirk-tooth" and "scimitar-tooth" nimravids display relatively fine and coarse serrations on their canine teeth, respectively. However, little work has been done to determine if differences in canine serration density between nimravid taxa are taxonomically informative. If such differences are present, they would provide powerful tools for referring fragmentary, taxonomically ambiguous material to specific clades, enhancing our ability to assess the geographic and biostratigraphic ranges of these taxa. The present study focused on evaluating patterns of canine serration density among the nimravid taxa ***Nimravus*** (n=7), ***Dinictis*** (n=12), and the hoplophonins ***Hoplophoneus*** (n=19) and ***Nanosmilus*** (n=2). Serration density was measured on the upper and lower canines over a length of at least five millimeters and then averaged to obtain the serration count per millimeter (SPM). Significant differences (p-value > 0.001) were noted between the mean values obtained for the upper canines of ***Nimravus*** (2.14 SPM), Dinictis (3.39 SPM), and the clade **Hoplophonini** (4.48 SPM) and no overlap was observed in the values recorded for these three taxa, though the 95% confidence intervals for the latter two taxa do slightly overlap. Alternatively, values of SPM were found to be relatively consistent along the carinae of individual teeth, between left and right canines in individual specimens, and between deciduous and adult canines from the same taxon (the latter tested in ***Nimravus*** and ***Hoplophoneus***). Similar, taxonomically significant trends in SPM value are seen in the lower canines of the sampled taxa (though sample sizes were smaller) despite the fact that lower canines show less morphological variation within Nimravidae than upper canines. Preliminary examination of some specimens of other "saber-tooth" feliform carnivores (i.e., the barbourofelid *Barbourofelis* and the felids *Smilodon*, *Nimravides*, and *Pseudaelurus*) reveals that these "scimitar-tooth" and "dirk-tooth" taxa also display low and high SPM values, respectively. These preliminary results suggest that canine serration size in "saber-tooth" feliform carnivores is influenced by the morphology (but not overall size) of the upper canines. Though broader sampling of nimravid taxa is needed, these preliminary results suggest that SPM values are a useful tool for identifying fragmentary specimens to specific clades, though resolution to the genus or species level may not always be possible.

BACKGROUND & GOALS

The terms "scimitar-toothed" and "dirk-toothed" were first used to refer to the variable morphology of the upper canines of marchairodontid felids (Kurtén, 1968). These terms were later applied to other feliform clades (i.e., barbourofelids and nimravids) by various authors (e.g., Martin, 1980; Morlo et al., 2004). It is generally noted that "scimitar-toothed" and "dirk-toothed" ecomorphs in all these clades display relatively coarse and fine serrations, respectively (Martin, 1980, 1998; Bryant, 1991). However, no attempt to quantify these differences and define observed ranges for either these ecomorphs or for individual taxa has been attempted.

This research utilizes the general methodology developed by previous studies for assessing diversity in theropod tooth shape and serration density (e.g., Currie, 1990; Larson and Currie, 2013). Currie (1990) studied teeth in their original positions within the skull to determine the utility of identifying isolated or shed teeth with no such taxonomic anchor. That study established a satisfactory reference datum that was then utilized to evaluate taxonomic occurrences at similar localities that preserved only fragmentary material (Sankey et al., 2002; Longrich, 2008). However, these methods were not attempted on mammals because mammals only shed teeth once in their lifetime, resulting in significantly limited sample sizes. Nonetheless, nimravid and felid taxa demonstrate unique canine morphologies that could be useful in referring fragmentary material (e.g., isolated canines or very partial crania lacking other diagnostic features) to specific taxa if these differences can be confidently quantified.

THE GOALS OF THIS STUDY ARE:

1. **DETERMINE IF AVERAGE SERRATION DENSITY ON NIMRAVID CANINES DIFFERS SIGNIFICANTLY BETWEEN "SCIMITAR-TOOTHED" AND "DIRK-TOOTHED" TAXA**
2. **DETERMINE IF AVERAGE SERRATION DENSITY VALUES FOR NIMRAVID UPPER CANINES CAN BE USED TO REFER FRAGMENTARY SPECIMENS TO SPECIFIC TAXA**

METHODS & DATA

All specimens included in this study consist of at least partial crania and/or mandibles that preserve distinct apomorphic features that allow each specimen to be confidently referred to at least a specific genus, if not species. All canines measured were *in situ* in their respective alveoli. Measurements were collected as outlined in Figure 1 based on personal observation using digital calipers. In this study, the 'scimitar-toothed' ecomorph is represented by the taxon ***Nimravus*** and the 'dirk-toothed' ecomorph is represented by the clade **Hoplophonini**, here scored from the taxa ***Hoplophoneus*** and ***Nanosmilus***. The taxon ***Dinictis*** is traditionally regarded as a 'scimitar-toothed' taxon (e.g., Martin, 1998), but the morphometric analysis of 'sabertooth' cranial shape conducted by Slater and Van Valkenburgh (2009) placed ***Dinictis*** within the 'dirk-toothed' morphospace. Therefore, this study treats ***Dinictis*** as an intermediate taxon that was analyzed separately. A similar approach was followed for ***Pogonodon***, which is closely related to ***Dinicits*** (see Figure 2), though only lower canines were available from that taxon for this study (Table 2).

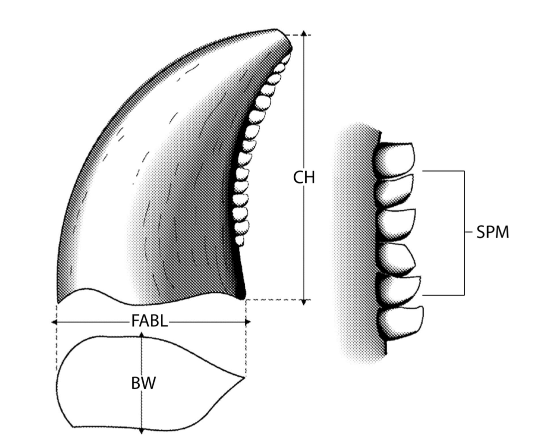

Figure 1: Diagram detailing the measurements of the upper and lower canines given in Tables 1 and 2 were obtained. **Abbreviations**: BW, basal width; CH, crown height; FABL, fore-aft basal length; SPM, serrations per millimeter. Modified from Sankey et al. (2002).

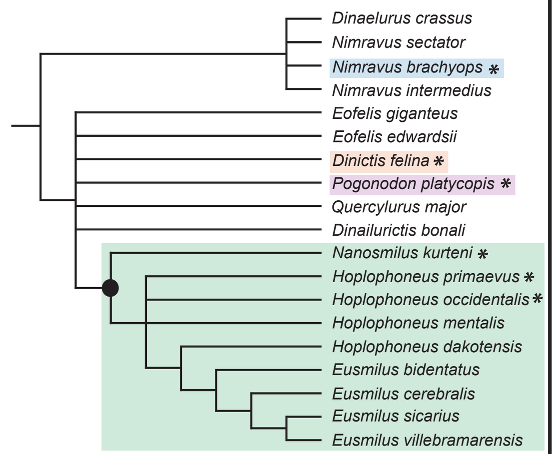

Figure 2: Systematic relationships within Nimravidae. Strict consensus of 90 MPTs resulting from a reanalysis of the Peigne (2003) dataset including additional, highly fragmentary terminal taxa. *Denotes taxa represented in this study. Black node marks the clade Hoplophonini.

Table 1: Measurements of nimravid upper canines organized by taxon. Only one canine was measured per specimen. See Figure 1 for explanation of measurements. See Figure 3 for examples of upper canine shape and serration density. **Abbreviations**: BW, basal width; CH, crown height; FABL, fore-aft basal length; SPM, serrations per millimeter. *Denotes holotype of ***Nanosmilus***. [#]Denotes the juvenile ***Dinictis*** specimen.

Nimravus	FABL	BW	CH	SPM
BADL 21658	20.9	11.8	-	2.0
BADL 42047	9.8	4.6	13.7	2.0
F:AM 99259	9.7	4.7	13.6	2.0
SDSM 348	14	7.9	34.3	2.0
SDSM 521	14.0	7.6	32.5	2.2
BADL 44450	11.9	6.6	28.6	2.4
SDSM 15012	-	-	-	2.4

Dinictis	FABL	BW	CH	SPM
SDSM 2564	-	-	-	3.0
UNSM 25752	-	-	-	3.0
BADL 30677	12.6	7.1	37.3	3.4
BADL 17188	13.1	-	-	3.4
SDSM 3670	16.6	-	45.1	3.4
SDSM 5311	-	-	-	3.4
SDSM 2663	-	-	-	3.5
SDSM 28145	-	-	-	3.5
SDSM 3145	-	-	-	3.5
UNSM 1028-38	-	-	-	3.5
UNSM 12-15-8-35SP	18.0	9.3	-	3.5
SDSM 2933	-	-	-	3.6
BADL 37844	10.0	5.6	18.5	4.3

Hoplophonini	FABL	BW	CH	SPM
UNSM 25506	-	-	-	3.8
CSC-41-42	17.2	-	60.8	3.9
UNSM 1-12-7-36SP	-	-	-	3.9
HC 450	14.3	-	-	4.0
UNSM 1070	15.6	-	-	4.1
UNSM 25748	-	-	50.4	4.1
UNSM 322-51	24.0	12.4	-	4.1
UNSM 1072	12.8	-	49.4	4.3
SDSM 28153	12.3	7.7	49.7	4.4
BADL 4893	-	-	-	4.4
BADL 59490	13.3	6.8	55.4	4.6
SDSM 2641	-	-	-	4.6
BADL 37540	-	-	-	4.7
SDSM 2544	15.4	8.3	58.1	4.7
BADL 37270	15.7	8.9	59.3	4.8
SDSM 5946	11.4		-	4.8
SDSM 536	13.7	7.8	51.6	4.0
SDSM 2544	15.7	8.2	56.3	4.9
SDSM 2662	13.0	5.8	40.7	4.9
SDSM 2643	16.9	8.4	-	5.0
UNSM 25505*	15.6	5.4	-	5.0
SDSM28139	12.8	5.8	-	5.2

Table 2: Measurements of nimravid lower canines organized by taxon. Only one canine was measured per specimen. See Figure 1 for explanation of measurements. **Abbreviations**: BW, basal width; CH, crown height; FABL, fore-aft basal length; SPM, serrations per millimeter. [#]Denotes juvenile ***Dinictis*** specimen.

Nimravus	FABL	BW	CH	SPM
BADL 21658	12.2	9.1	23.0	2.2
SDSM 348	10.2	7.4	18.5	2.3
BADL 42047	9.9	6.7	22.2	2.5
SDSM 521	10.9	6.7	-	2.5

Hoplophonini	FABL	BW	CH	SPM
HC 450	7.9	6.6	14.9	4.5
SDSM 28153	6.6	5.2	11.5	4.8
SDSM 2544	8.3	6.3	17.4	5.0

Dinictis	FABL	BW	CH	SPM
SDSM 2882	10.2	6.9	17.0	3.5
SDSM 3145	6.7	6.1	-	3.5
SDSM 2663	8.1	6.8	14.0	3.8
SDSM 2564	7.5	5.3	-	3.9
BADL 37844[#]	6.2	4.7	13.8	5.0

Pogonodon	FABL	BW	CH	SPM
SDSM 2865	11.9	8.4	18.4	2.9
SDSM 4081	10.8	8.9	17.5	2.9

SERRATION MORPHOLOGY

Nimravids and felids display distinct serration morphologies that can be used to easily distinguish between families. Nimravid serrations are somewhat 'hour-glass' shaped in lateral view, as elucidated by Bryant (1991), and are composed of very smooth enamel (Fig. 3). Felids display very tight and flat contacts between serrations and striations oriented parallel to serration junctions (Fig. 4B). In other saber-tooth feliforms, particularly *Barbourofelis* (Fig. 4A), the serration morphology is most similar to seen in nimravids (see also Bryant, 1991; Fig. 8).

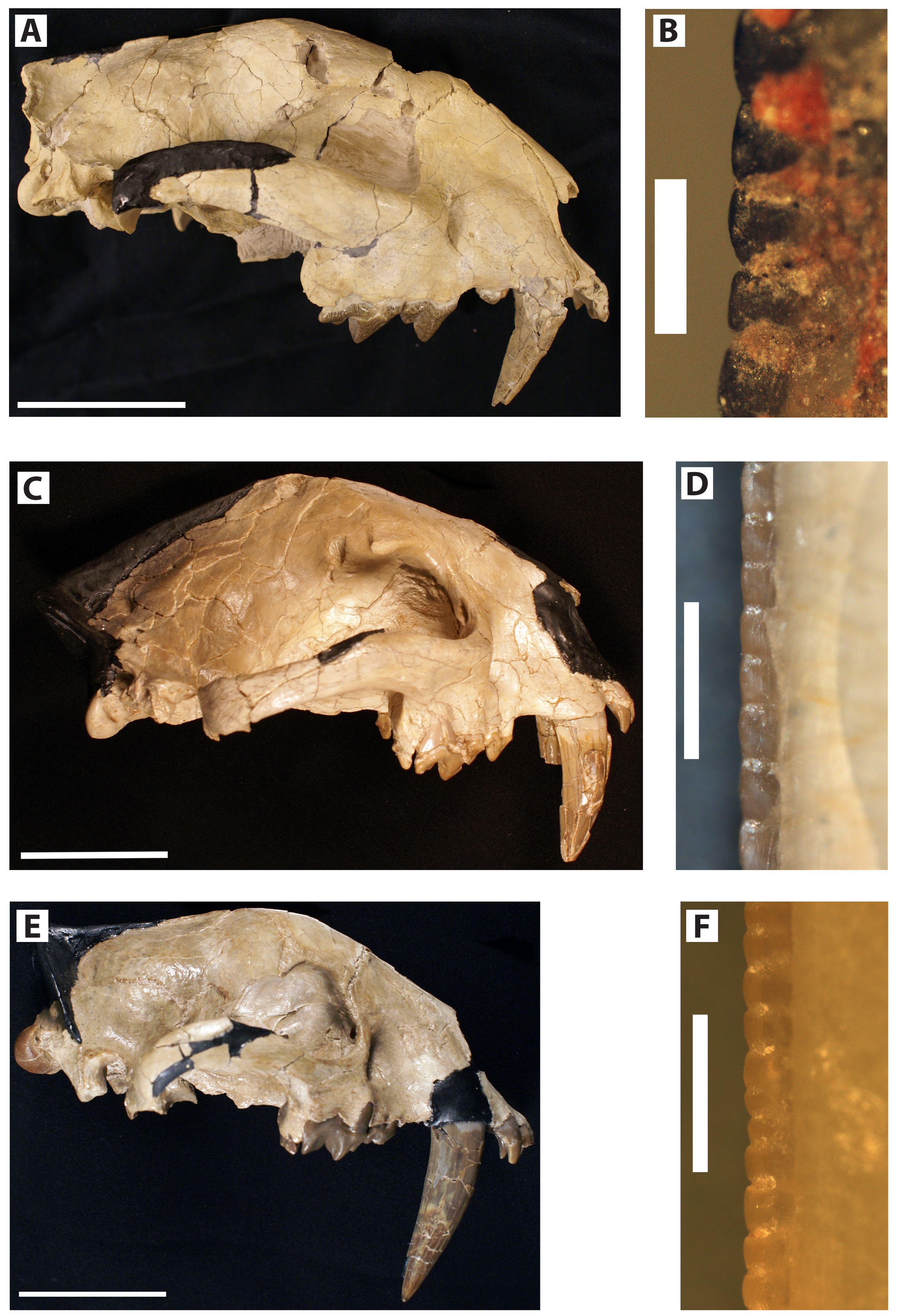

Figure 3: Upper canine serration size and morphology in the nimravid taxa: **A-B** ***Nimravus brachyops*** (SDSM 348: 2.0 SPM); **C-D** ***Dinictis felina*** (SDSM 2663: 3.5 SPM); and, **E-F** ***Hoplophoneus primaevus*** (SDSM 2544: 4.7 SPM). **B**, **D**, and **F** to scale with each other and with the serration images in Figure 4. Scale bar in **A**, **C**, and **E** = 5cm. Scale bar in **B**, **D**, and **F** = 1mm. All skulls photographed in right lateral view except **E**, which was reversed. All serration images are from the posterior carina.

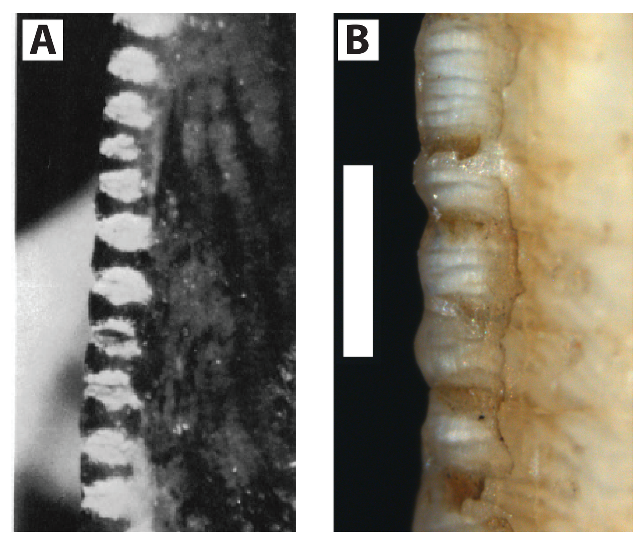

Figure 4: Serration size and morphology in: **A** the barbourofelid *Barbourofelis* (UF 36874); and, **B** the machairodontine felid *Smilodon* (SDSM 29100). Images to scale with each other and with the serration images in Figures 3b, d, and f. Scale bar in **B** = 1mm. Image in **A** modified from Bryant (1991:fig. 8b).

RESULTS

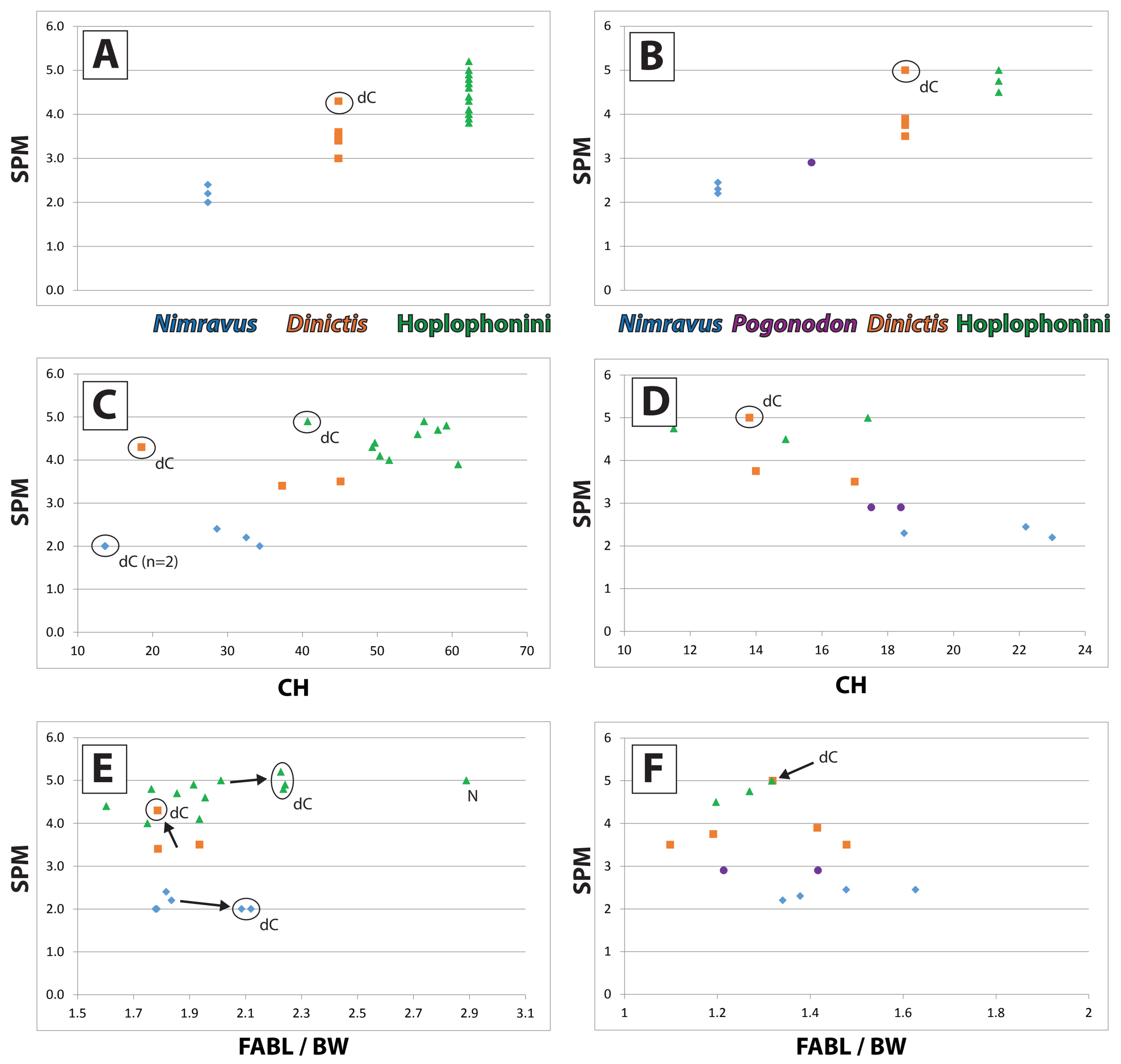

Figure 5: Graphs of measurements of nimravid upper (**A**, **C**, and **E**) and lower canines (**B**, **D**, and **F**). Measurements given in Tables 1 and 2. Colors correspond to those in Tables 1 and 2. See Figure 1 for explanation of measurements. **Abbreviations:** BW, basal width; CH, crown height; dC, deciduous canine; FABL, fore-aft basal length; N, ***Nanosmilus***; SPM, serrations per millimenter.

One-Way ANOVA

	Sum of Squares	Degrees of Freedom	Mean Square	F-Value	P-Value
Between Samples	30.82	2	15.41	131.99	**<0.0001**
Within Samples	4.43	38	0.12		
Total	35.26	40			

Table 3: Results of ANOVA test of mean values of SPM for ***Nimravus***, ***Dinicitis***, and **Hoplophonini**.

CONCLUSIONS

Overall, SPM values in the adult upper canines for the three taxa assessed in this study (***Nimravus***, ***Dinictis***, and **Hoplophonini**) are relatively consistent within each taxon (Fig. 4A) and the mean values of these groups are significantly different from each other (Table 3) with no observed overlapping values (Table 1). Thus, the previously qualified difference in serration density between 'scimitar-toothed' and 'dirk-toothed' taxa (low versus high values, respectively) can be accurately quantified in nimravids. As a result, the confident referral of isolated adult upper canines and fragmentary crania preserving adult upper canines to one of these three taxa based on SPM value is possible.

Nimravus and **Hoplophonini** show similar morphological trends between their deciduous and adult upper canines (Figs. 4C and E). Deciduous upper canines in these taxa are shorter (Fig. 4C) and the bases are relatively narrower than the adult upper canines (Fig. 4E); however, the SPM values remain constant between the deciduous and adult dentition.

Dinictis presents an unusual case. The deciduous upper canines have the same basal proportions as the adult canines, but they have a higher SPM value than the adult canines (Fig. 4E). In fact, they display SPM values typical of the **Hoplophonini** (Figs. 4A and E). This marked departure from the pattern observed in the other taxa in this study may indicate that juveniles of ***Dinictis*** were following a different life history strategy than other taxa.

INSTITUTIONAL ABBREVIATIONS:

BADL: Badlands National Park, Interior, South Dakota
HC: Harold Cook Collection [stored at SDSM], Rapid City, South Dakota
SDSM: South Dakota School of Mines and Technology, Rapid City, South Dakota
F:AM: Frick Collection, American Museum of Natural History, New York, New York
CSC: Chadron State College, Chadron, Nebraska
UNSM: University of Nebraska State Museum, Lincoln, Nebraska

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