

SPLIT CARINAE ON A SPECIMEN OF FALSE SABER-TOOTHED CAT (CARNIVORA: NIMRAVIDAE) AND THE IMPLICATIONS FOR ANALOGOUS TOOTH ABNORMALITY FORMATION IN MAMMALS AND THEROPOD DINOSAURS

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ABSTRACT

An anomalous specimen of *Dinictis felina* (Carnivora: Nimravidae) from the Scenic Member of the Brule Formation in South Dakota was recently identified possessing bilaterally symmetrically split carinae on the anterior surfaces of the upper canines. The anterior carinae display normal serration patterns from the apex until they bifurcate towards the base. The primary carinae maintain their normal positions while the accessory carinae diverge laterally before curving dorsally towards the tooth base. Though other types of mammalian, particularly human, tooth abnormalities are thoroughly documented, split carinae are previously unreported in mammalian taxa. However, these anomalies are well documented in disparate families of theropod dinosaurs (Tyrannosauridae, Dromaeosauridae, and Carcharodontosauridae). The aforementioned morphology of the carinae of the *D. felina* specimen is similar to that previously noted in theropods (e.g., split carinae on the anterior face of the tooth), suggesting a possibly homologous underlying cause. Three hypotheses for the split carinae abnormality documented in theropods were previously proposed: trauma, aberrant tooth replacement, and genetic expression. The continuous cycle of tooth replacement in theropods and lack of genetic information in fossil material made it difficult to confidently identify a preferred hypothesis, though genetic expression was more rigorously supported. We propose that these hypotheses are not mutually exclusive, and that genetic expression, influenced by other factors initiating epigenetic modification, is the most parsimonious interpretation for the presence of split carinae in both mammals and theropods given the constrained pattern of mammalian tooth replacement, clear bilateral symmetry of the split carinae, and serration morphology of the accessory carinae in this specimen of *D. felina*.

INTRODUCTION

Cuvier's principle of the correlation of parts is one of key principles within the foundations of paleontology and comparative anatomy. Cuvier argued that the skeletal anatomy of living and fossil organisms could be reliably utilized for "evidence-based reconstruction" (Benton, 2010). The form and function of skeletal anatomy is expected to reflect the physiological, behavioral characteristics, and developmental constraints of an organism and its evolutionary heritage, and if properly evaluated, can consistently determine scientific interpretations and reconstructions. The form and function of teeth can fulfill numerous purposes, aside from feeding, such as protection, grooming, digging, etc. Teeth primarily reflect the dietary needs of an organism, along with evolutionary heritage, and remain somewhat consistent or repetitive throughout the evolution of vertebrate groups. We can observe morphologic analogy in animals that infer similar herbivorous, omnivorous, or carnivorous feeding adaptations for dietary needs. Carnivorous vertebrates are a common example used to demonstrate Cuvier's founding principles and are easily recognizable (e.g., the serrations on saber-toothed feliform carnivore canines in correlation with the denticles in theropod dinosaur teeth). Significant analogous structures demonstrate morphologic repetition throughout biogeographically restricted niches as well as temporal reemergence of feeding functionality in the fossil record, inferring potential environmental influence into the evolution of form and function. Bakker (1998) suggested allosaurid theropods could serve as an adequate saber-toothed cat analogue for Jurassic ecosystems. Though Bakker's (1998) correlation may be somewhat imprecise, there are distinct parallels of form and function of the teeth belonging to the aforementioned taxa.

Three families of saber-toothed Feliformia demonstrate distinct and temporally repetitive dental analogies: Nimravidae in the Late Eocene to Late Oligocene; Barbourofelidae in the Late Miocene; and machairodontine Felidae in the Late Miocene to Pleistocene (Martin 1998a, 1998b). The saber-toothed condition is not unique to Feliformia and has also been exemplified in South American sprassodont marsupials (i.e., *Thylacosmilus*) from the Miocene, the creodont *Machairoides* from the Middle Eocene of North America and therapsids (i.e., *Gorgonopsidae*) from the Permian (see Antón 2013). However, the presence of analogous but not homologous structures in closely related taxonomic groups can create difficulty in using dental characters to resolve alpha level taxonomy and systematic relationships of taxa (see Currie et al. 1990). Analogous morphology and life habits could be expected to correlate with pathologies and abnormalities. These can either be involved with the form and function of the animal directly, or as an indirect result of activity. Examples of bacterial bone infection osteomyelitis, commonly occurring from cat bites (e.g., Chodakewitz and Bia 1988), have been documented in correlation with predator-associated trauma in several extinct groups. Osteomyelitis has been identified or suggested to occur in a dorsal spine injury in *Dimetrodon* from the Permian of Texas (Moodie 1921), multiple injuries in the allosaurid theropod *Allosaurus fragilis* from the Late Jurassic Cleveland-Lloyd Quarry in Utah (Hanna 2002), multiple injuries in the abelisaurid

theropod *Majungasaurus crenatissimus* from the Late Cretaceous of Madagascar (Farke and O'Connor 2007), pathology in the tyrannosaurid theropod *Tyrannosaurus rex* from the Late Cretaceous of South Dakota (Brochu 2003), and a femur injury in the titanosuchid therapsid *Jonkeria parva* from the Permian of South Africa (Shelton et al. 2017), to list just a few examples.

Morphologically similar tooth deformations are also known to occur in closely related taxonomic groups and have been especially well-documented in theropod dinosaurs (Currie et al. 1990; Erickson 1995). A diverse array of theropod dinosaurs share macro- and micro-anatomical features within their teeth, spanning the entirety of their evolution and geographic occurrences and have warranted detailed study to provide insight into systematics and paleoecology, while briefly noting dental abnormalities (e.g., Currie et al. 1990). One of the more intriguing tooth abnormalities found in theropod dinosaurs is the bifurcation of the anterior carinae. Split carinae in theropod dinosaurs typically occur basal to the apex of the tooth, with the paired carinae orienting parallel towards the tooth base. The split carinae abnormality is also observed in several other vertebrate clades with serrated or non-serrated carinae. Itano (2013) has documented this abnormality in sharks, specifically the Neogene *Otodus megalodon* and Carboniferous *Edestus minor*. Itano (2013) inferred that the abnormality of supernumerary carinae were the result of potential trauma during various stages of tooth development. Beatty and Heckert (2009) cited the abnormality in a phytosaur, but did not elaborate on the abnormality beyond its presence in the specimen. Hungerbühler (2000) observed the same condition in the Triassic phytosaur *Nicosaurus kapfii* but referred to Erickson (1995) for explanation of origins. Outside of these previous examples, the split carinae abnormality is more thoroughly documented in theropod dinosaurs (e.g., Currie et al. 1990; Erickson 1995). Erickson (1995) was the first to provide a thorough study of the abnormality within the Tyrannosauridae throughout the Late Cretaceous. Tyrannosaurids that exhibit the pathology include *Tyrannosaurus*, *Daspletosaurus*, *Albertosaurus*, and *Alectrosaurus*. The frequency of split carinae varied anywhere between 6-27% through stratigraphic locations. Erickson (1995) also observed the same feature in the more distantly related theropod *Allosaurus*. After Erickson's (1995) work, split carinae were observed and documented in an unidentified charcarodontosaurid (Candiero and Tanke 2008), in *Dromaeosaurus albertensis* (Fiorillo and Gangloff 2008), and in unidentified dromaeosaurid and troodontid taxa (Han et al. 2011). Though various factors have been linked to tooth deformities (see Hillson 1986), Erickson (1995) narrowed his examinations into three more plausible and testable hypotheses that could explain this abnormality: trauma, aberrant tooth replacement, and genetic expression. Of the three, Erickson (1995) concluded that genetic polymorphism had the most support, especially when compared to secondary tooth traits expressed and thoroughly studied in fossil rodents (Barnosky 1986, 1993) and humans (e.g., Hrdlicka 1920). Erickson (1995) based his conclusion on multiple similarities between abnormalities in extant and extinct taxa, including graded degrees of expression, secondary tooth traits being found at the same location on affected teeth, phenotypically neutral traits with no apparent selective or functional significance, and secondary tooth traits being locally expressed

within dentitions. However, later studies in genetic expression demonstrated that epigenetic factors (i.e., nutrition, disease, etc.) influence and modify genetic expression in tooth formation, and that the multiple hypotheses provided by Erickson (1995) are not mutually exclusive (Brook 2009; Seo et al. 2015). The complex and dynamic interactions between genetic expression with environmental influences of epigenetic factors is a more plausible cause of supernumerary tooth features, where the fossils provide examples of such expression.

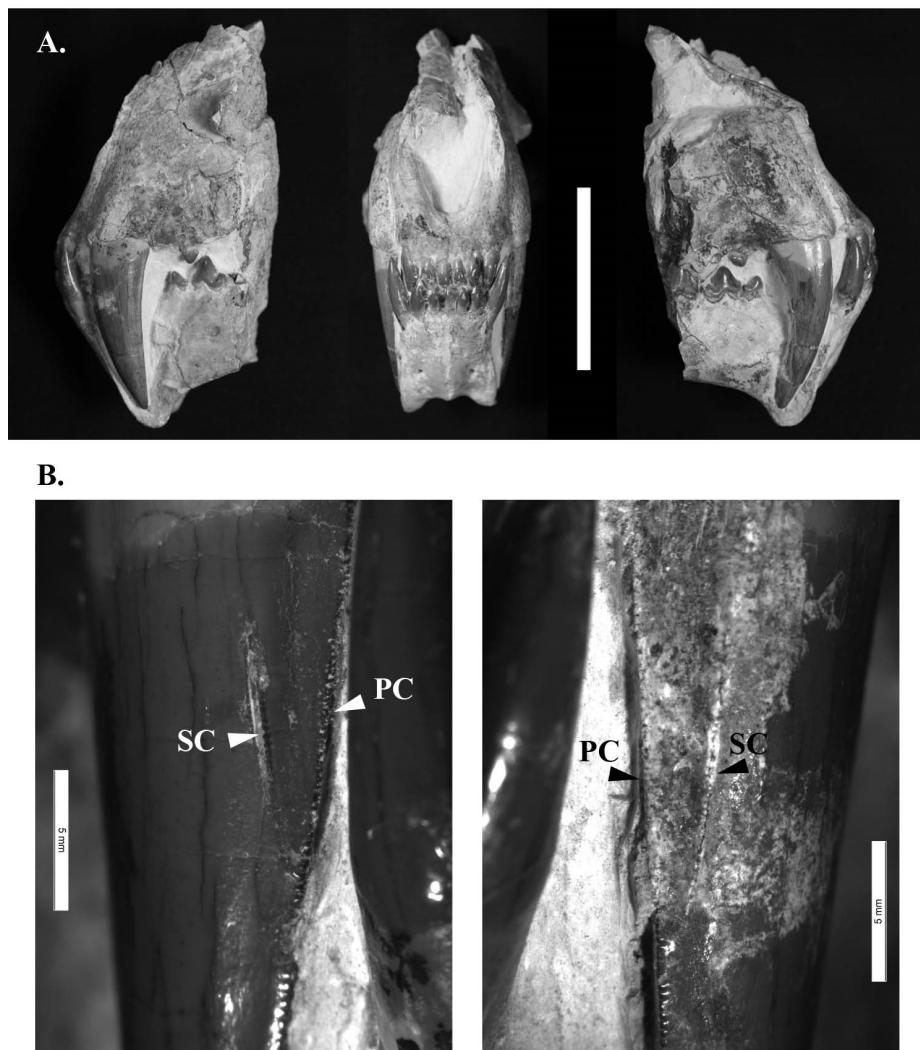


Figure 1. SDSM 3670, *Dinctis felina* in (A.) left, anterior, and right views (scale bar = 5 cm). (B.) Right and left canines with split carinae with arrows marking the (PC) primary carina and (SC) secondary carina (scale bar = 5 mm).

In this study we report the first mammalian occurrence of the split carinae abnormality discovered in the upper canines of the nimravid *Dinictis felina* (SDSM 3670; Figure 1 and Figure 2). Nimravid canines typically possess serrated carinae on the anterior and posterior sides of the canines. However, SDSM 3670 displays a bifurcation of the anterior carinae on the upper left and right canines (Figure 1). This abnormality has not been reported previously in any mammalian taxon, making it difficult to correlate the cause of this abnormality. In this study we describe the morphology of the split carinae in SDSM 3670 and review previously proposed hypotheses for the development of split carinae in light of this discovery.

Museum Abbreviations—BADL, Badlands National Park, Interior, South Dakota; SDSM, South Dakota School of Mines and Technology, Rapid City, South Dakota.

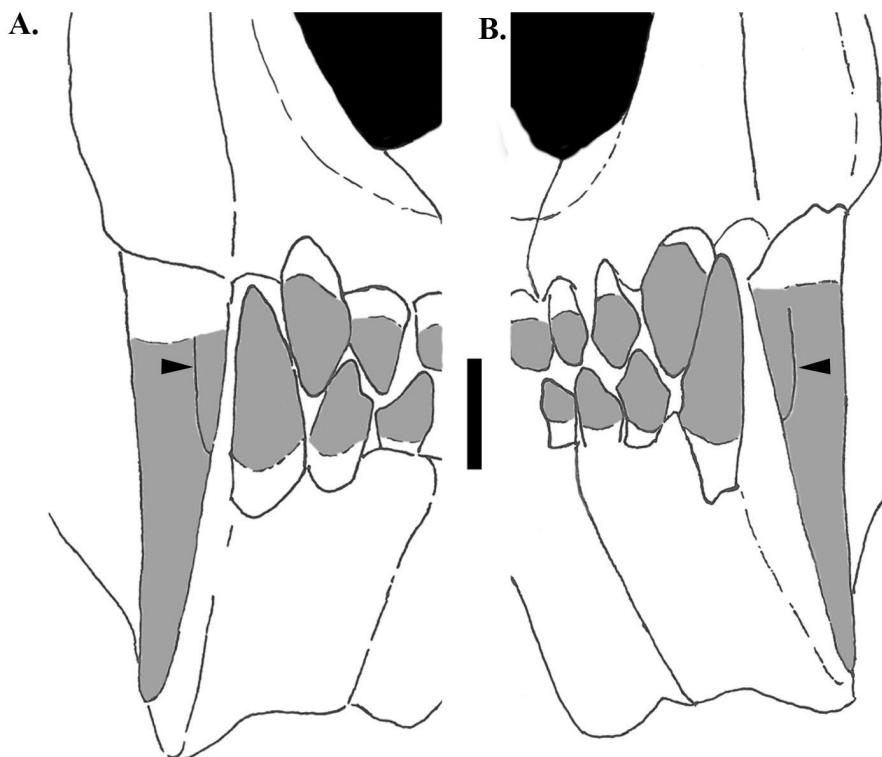


Figure 2. A line drawing of SDSM 3670, *Dinictis felina* in oblique, anterior views of the (A.) right and (B.) left canines with arrows indicating the position of the accessory carinae (scale bar = 1 cm).

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758

CARNIVORA Bowdich, 1821

NIMRAVIDAE Cope, 1880

Dinictis felina Leidy, 1854

Dinictis felina Leidy, 1854

Daptophilus squalidens Cope, 1873

Dinictis squalidens Cope, 1879

Dinictis cyclops Cope, 1879

Dinictis fortis Adams, 1895

Dinictis bombifrons Adams, 1895

Dinictis paucidens Riggs, 1896

Dinictis felina Bryant, 1996

Dinictis cyclops Bryant, 1996

Dinictis felina Barrett, 2016

Referred Specimen—SDSM 3670; Anterior portion of skull and dentaries with right I1-3, C, P2-3, i1-3, c, P2-3, left I1-3, C, P2, i1-3, c, p2-3. Figure 1 and Figure 2.

Locality and Horizon—3 miles Northeast Slide, North Cuny Table. Lower Oreodon Beds, Scenic Member, Brule Formation. Early Orellan North American Land Mammal Age.

Description—Refer to Barrett (2016) for the contemporary genus and species description. *Dinictis felina* represents a monotypic genus (Barrett 2016). Since most of the skull is absent, there are a few characters that distinguish SDSM 3670 as *D. felina*, which includes a short glenial flange, the caniniform I3, serration density within 2.8-4.8 serrations per millimeter (mean 3.6) (see Barrett 2016). Also, the lower canine is almost twice the height of the lower incisors, whereas the lower canine and incisors are of near equal height in *Hoplophoneus*. Abnormalities are found with the anterior carinae of the left and right upper canines. The primary carinae remain in their natural position, with slight mesial orientation near the base. The secondary carinae bifurcate laterally at 1.8 cm from the base and become oriented parallel to the primary carinae as they extend dorsally. Serration density on the primary carinae maintain consistent, uniform morphology (~3 serrations per mm). The laterally bifurcated carinae display irregular serrations, similar to what has been observed in *Hoplophoneus* canines (~4-6 serrations per mm; see Figure 3; Boyd and Welsh 2013).

DISCUSSION

As previously discussed, saber-toothed nimravids share analogous serrated dental anatomy with other carnivorous vertebrates based on their characteristic needs in catching and processing prey. Other carnivorous vertebrates with serrated tooth anatomy (e.g., sharks and dinosaurs) provide some clues to the potential

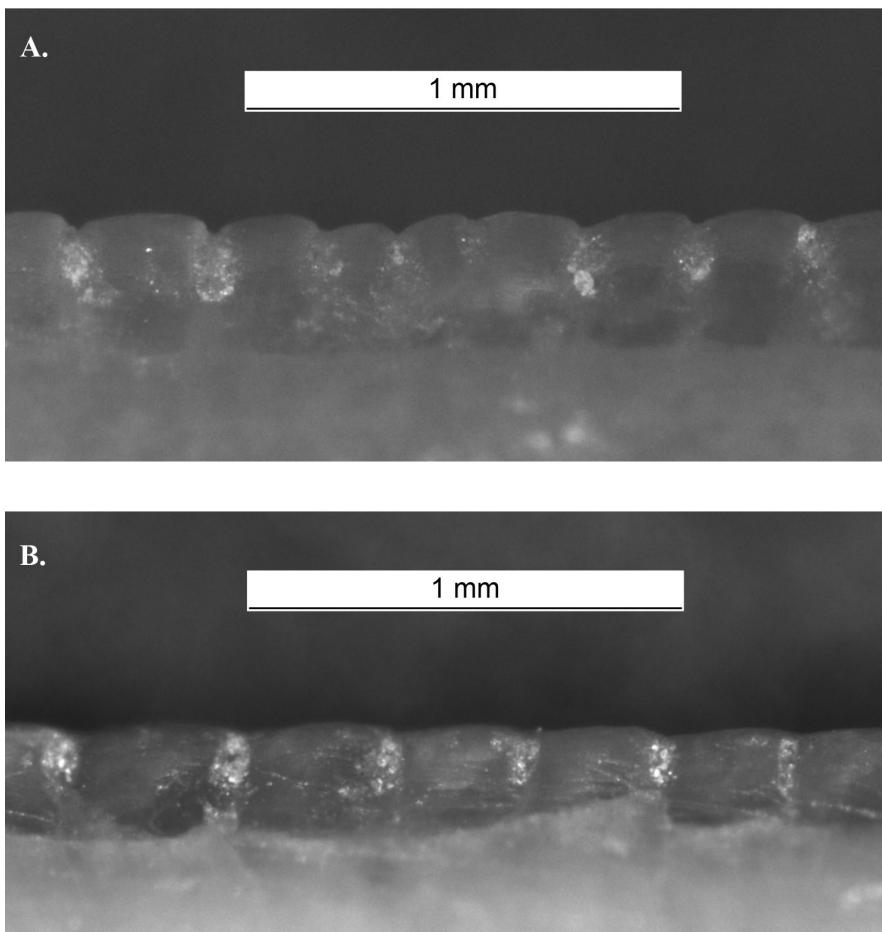


Figure 3. Examples of nimravid canine serration density and morphology with (A.) *Hoplophoneus* sp. (BADL 37340) and (B.) *Dinictis* sp. (SDSM 2663).

origins of these anomalous secondary tooth features. However, a distinct single-most parsimonious conclusion was difficult to ascertain in previous studies given that these other vertebrate clades consistently shed and replace teeth during their lifetimes. The identification of split carinae in a mammalian taxon, which utilizes only two sets of teeth during its lifetime, allows for the three previously proposed hypotheses for the cause of this abnormality to be revisited and helps elucidate the cause of the split carinae abnormality.

Trauma—Impact or injury to the tooth while it is still developing might be responsible for the irregular location of split carinae along the anterior surface of teeth, as suggested by Itano (2013). However, it is perplexing that trauma would only affect the anterior margin of the tooth as observed within theropod dinosaurs. Additionally, if split carinae were the result of injury then wound calluses or other diagnostic bone pathologies would be expected to be associated with

split carinae, yet *in situ* teeth bearing these abnormalities are not associated with any pathological bone texture (Erickson 1995). Tooth impact resulting in enamel spalling is also observed in tyrannosaurid theropods (see Brochu 2003; Schubert and Ungar 2005), but no split carinae have been observed in direct correlation to tooth damage. While we have observed enamel spalling and tooth trauma in some nimravids (e.g., SDSM 28153, BADL 53913; Figure 4), we have observed no pathologic bone associated with this damage. There is no alteration to the position or morphology of carinae or serrations in nimravid specimens we have examined that display tooth damage. SDSM 3670 does not show any evidence of pathologic bone or damaged canines that would infer trauma being a cause of split carinae (Figure 1). It is possible that trauma to deciduous canines may have affected the development of the adult canines because adult canines in nimravids erupt late in their ontogenetic development (Bryant 1988); however, this would suggest any potential trauma must have been simultaneous and symmetrical to the left and right deciduous teeth. Therefore, we conclude that trauma is not a fully satisfactory cause for the split carinae observed in SDSM 3670, as Erickson (1995) also concluded for tyrannosaurid theropods.

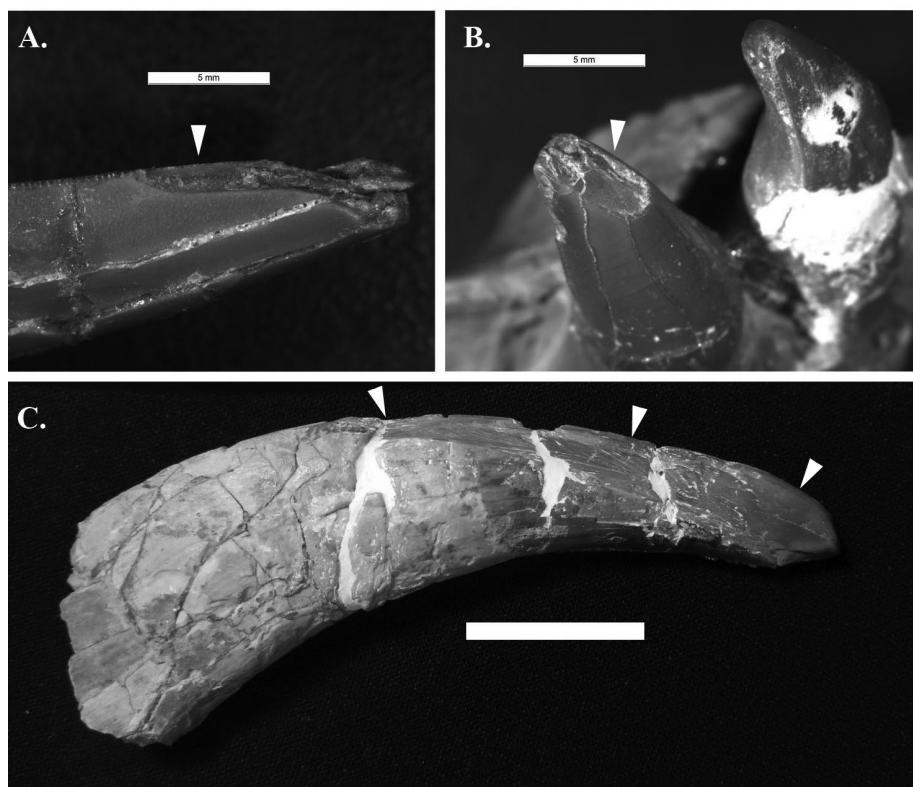


Figure 4. Enamel spalling (marked with arrows) and wear observed in Hoplophoneus specimens. SDSM 28153 (A.) upper and (B.) lower canines Scale = 5 mm. View of BADL 53913, (C.) canine with extreme spalling Scale = 2 cm.

Aberrant tooth development—Tooth development which has been prolonged in the alveolar cavity is a plausible cause for the development of tooth abnormalities. For example, the former theropod dinosaur taxon *Paronychodon*, which was based solely on isolated teeth, was distinguished in part by the presence of longitudinal ridges on the teeth (Cope 1876). These ridges were abnormal and irregular crenulations, as opposed to carinae. It was later demonstrated that *Paronychodon*-like ridges were irregular aberrant tooth deformations found in multiple Late Cretaceous theropods (*Dromaeosaurus*, *Richardoestesia*, *Saurornitholestes*, *Troodon*, and possibly tyrannosaurids: Currie et al. 1990; Longrich 2008). Currie et al. (1990) explained that the *Paronychodon* tooth form observed in multiple theropod dinosaur taxa was likely an abnormality that resulted from prolonged contact with the medial alveolar socket during tooth development. Based upon these observations, aberrant tooth replacement has proven to be sufficient in explaining the *Paronychodon* condition among theropods, but has not been correlated to split carinae in either theropod dinosaurs or nimravid mammals. The consistent placement of split carinae on the anterior face of the teeth does not seem to demonstrate the same irregular development observed in specimens with the *Paronychodon* condition. Additionally, this hypothesis alone does not satisfactorily account for the bilateral symmetry of the split carinae observed in SDSM 3670.

Genetic expression—A genetic cause could be implied by the mirrored morphology combined with the bilateral symmetry of the split carinae observed in SDSM 3670. The splits in the carinae occur at the same position between the left and right upper canines, and the accessory carinae each extend laterally from the main carinae. Also, the serration size and morphology along the accessory carinae closely resemble that observed in *Hoplophoneus* (higher serration density and less uniform morphology) as opposed to the main carinae that display a lower serration density and a more uniform morphology as observed in *Dinictis* (Figure 3; Boyd and Welsh 2013). *Hoplophoneus* has been considered to be phylogenetically derived in comparison to *Dinictis* (Bryant 1996; Peigné 2003; Barrett 2016), and the serration morphology could reflect this relationship but needs further study. These features demonstrate that the formation of the split carinae in SDSM 3670 is likely the result of strict factors of genetic control rather than coincidental trauma or aberrant tooth replacement. There is precedent for genetic factors controlling dental variation in extant animals. Perhaps the most well documented would be the relationship between the development of shovel-shaped (sinodont) incisors in humans, where a variety of accessory lingual ridges or basal tubercles are formed (see Hrdlicka 1920), and variations in the *ectodysplasin A receptor* (*EDAR*) gene (e.g., Kimura et al. 2009; Park et al. 2012). No extant mammalian taxon exhibits serrated carinae, and genetic analysis cannot be conducted on extinct organisms, preventing direct study of the potential for variations in genes such as the *EDAR* gene to produce split carinae; however, the correlation between the development of the sinodont incisor in humans and specific variations in the *EDAR* gene show that these types of genetic expression are plausible (Kimura et al. 2009; Park et al. 2012). Further studies into epigenetic factors influencing genetic expression in tooth development demonstrated that environmental factors

(i.e., nutrition, pollution, disease) can instigate complex molecular interactions resulting in epigenetic modifications, which influence gene expression, altering phenotypic variation (Brook 2009; Seo et al. 2015). Brook (2009) further elaborates that the inhibition of apoptosis during tooth development results in stimulating cell proliferation, leading to folding of inner enamel epithelium, resulting in dental anomalies. Given the evidence outlined above, we conclude that the hypothesis of genetic expression, with epigenetic factors, provides the most parsimonious explanation for the presence of split carinae in SDSM 3670. However, the specific cause initiating epigenetic-genetic modification has yet to be determined.

CONCLUSIONS

Of the three most testable hypotheses proposed by Erikson (1995), we conclude that no singular hypothesis is adequate, but that complex interactions between environment, animal health, and other factors inducing epigenetic modification and subsequent genetic expression can provide the most parsimonious explanation regarding the development of split carinae in theropod dinosaurs and nimravid mammals. The morphology described in SDSM 3670 best supports genetic expression as the most parsimonious cause of the abnormality, but this is likely due to an undetermined environmental influence initiating epigenetic modification. Aside from the strict characterization of the abnormality in an extinct organism, the development of accessory carinae appears to adhere well with the constraints of secondary tooth features resulting from variability in the *EDAR* gene, as demonstrated by Kimura et al. (2009) and Park et al. (2012), along with environmental factors influencing epigenetic modification of gene expression (Brook 2009; Seo et al. 2015). Based on this conclusion, one could also infer that the development of split carinae across multiple vertebrate clades results from an abnormality that is genetically widespread within Vertebrata. This particular form of secondary tooth feature is difficult to trace more broadly across vertebrate groups because the presence of carinae, serrated or non-serrated, are infrequent within vertebrate clades. Also, serrated carinae are typically found in phylogenetically disparate carnivorous vertebrates, compounding the rarity of such features as well as confounding the determination of causes. However, genetic controls of tooth formation should be expected to be more universal within vertebrate clades, with abnormalities being expressed within the fossil record only when particular macro-anatomical features are present (e.g., tooth count, the arrangement of cusps, orientation of ridges, etc.). The relatively high rate of continuous tooth replacement present in theropod dinosaurs (e.g., D'Emic et al. 2019) may explain why split carinae are better documented within that clade than among mammalian taxa that bear only two sets of teeth in their lifetime. Alternatively, if the development of split carinae does have a genetic cause, the low rate of occurrence in mammalian taxa could result from negative selection pressure for this trait in those taxa. While we cannot identify a clear detrimental

effect of the presence of split carinae, variations in the *EDAR* gene are known to have pleiotropic effects on dental morphology (Park et al. 2012).

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