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MICROWEAR ON CANINES AND KILLING BEHAVIOR IN LARGE CARNIVORES: SABER FUNCTION IN *SMILODON FATALIS*

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Canids and hyaenids display a high density of features of microwear on canine teeth that reflect their similarity in killing strategy. However, hyaenids tend to have a higher percentage of short and wide features (pits) because of the high percentage of bone in their diet. Canines of felids display relatively fewer features than canids and hyaenids, which suggest that felids apprehend prey by delivering deep, strong bites that result in less abrasion of the canines. I suggest that canids rely more heavily on their canines and incisors for feeding than do felids. *Smilodon fatalis*, a large saber-tooth cat from the Pleistocene of North America, is similar to living felids in having relatively few features of canines, but differs from cheetahs (*Acinonyx jubatus*) and African lions (*Panthera leo*) in having relatively more pits. *S. fatalis* showed no consistent similarity in features of microwear on canine teeth to six large carnivores (leopard, *Panthera pardus*; cheetah; African lion; spotted hyaena, *Crocuta crocuta*; African wild dog, *Lycaon pictus*; gray wolf, *Canis lupus*), which suggests that its killing behavior and possibly dietary preference differed from modern predators. *S. fatalis* may have avoided contact with bone during killing and feeding encounters, which caused fewer features to form on the upper canines.

Key words: *Smilodon*, saber-tooth cat, Plio-Pleistocene, canine, microwear

Upper canines with a saber-like shape are known to have evolved independently in flesh-eating mammals at least four times. A large species of creodont, *Apataelurus*, is recorded from Eocene localities in North America, whereas many nimravid cats are known to have been widespread during the Oligocene to Pliocene epochs. The Pliocene of South America is characterized by a saber-toothed marsupial, *Thylacosmilus*, which surpassed living tigers and lions in size. Many species of saber-toothed felids (subfamily Machairodontinae) also persisted in great numbers in the New and Old World until the end of the Pleistocene (Kurtén and Anderson, 1980; Simpson, 1941). The structural appearance of the elongate canines of saber-tooth cats has invited much speculation among carnivore biologists as to function and durability of canines (Akersten, 1985; Bohlin, 1940; Gonyea, 1976;

Martin, 1980; Simpson, 1941; Van Valkenburgh, 1988; Van Valkenburgh and Ruff, 1987). The absence of saber-like canines in extant carnivores has made inferences difficult. In the Pleistocene genus, *Smilodon*, the canines achieved extreme specialization and were surpassed in size by those of only two other genera, *Thylacosmilus* and *Barbourofelis*. *Smilodon* and its close relative *Megantereon* are regarded as members of the tribe Smilodontini (Kurtén and Anderson, 1980), a tribe characterized by extremely elongate upper canines that are slightly recurved. Many workers favor the hypothesis that *Smilodon* used its sabers primarily for stabbing and that slicing was a secondary effect as the sabers penetrated the prey (Matthew, 1901; Scott, 1936). A few studies not only question the stabbing hypothesis, but also suggest that *Smilodon* fed on carrion and was not an active pred-

ator, with its canines ill-adapted for stabbing and used mainly for slicing (Bohlin, 1940; Marinelli, 1938). The most recent hypothesis for function of canines in *Smilodon* is a canine-shear bite as the main action of the sabers (Akersten, 1985). This strategy involves the use of the sabers (upper canines) and upper and lower incisors to inflict a severe wound to the soft underbelly of the prey. The sabers made the first contact with the prey and created an initial fold of skin and flesh. With the help of the mandibular musculature, the short-lower canines and incisors were then used to anchor the fold. The head-depressing muscles completed the bite by forcing the sabers to shear through the lateral margins of the fold of flesh. The entire fold of flesh was then freed by a final pull of the head. This hypothesis has been questioned by some authors who argue that the relatively low curvature of the stomach of large ungulates would prevent the saber-tooth cat from getting the stomach into its mouth (Martin, 1989).

Analysis of microscopic wear patterns on teeth is an important avenue to infer use of teeth and diet in extant and extinct animals. For example, differences in dental microwear were linked to subtle differences in diet and behavior of several groups of primates. In addition, dietary preferences related to changes in availability of resources caused by shifting seasonal conditions (e.g., rain and temperature) were found to be correlated to seasonal differences in patterns of dental microwear of certain species (Bullington, 1988; Teaford, 1985, 1986; Teaford and Robinson, 1989). Questions that concern function of the jaw during mastication and ingestion of food also can be addressed by analysis of the orientation of features of microwear (Gordon, 1984; Grine, 1986; Hylander et al., 1987; Ryan, 1981; Teaford, 1991; Teaford and Byrd, 1989; Teaford and Walker, 1984; Young and Robson, 1987).

Previous work on dental microwear in carnivores has concentrated on post-canine teeth and generally has been limited to qualitative analyses (Taylor and Hannam,

1987; Walker, 1980). Few studies exist that deal with how carnivores use their anterior dentition during killing or feeding, although recent work by Van Valkenburgh et al. (1990) and Biknevicius and Van Valkenburgh (1996) has been instrumental in setting the foundation for more rigorous investigations. Van Valkenburgh et al. (1990) found that *S. fatalis* was most similar to the cheetah, *A. jubatus*, when microwear patterns on the lower carnassial (first molar) of *S. fatalis* were compared to eight extant species of carnivores. This similarity to cheetahs suggests a lack of bone in the diet of *S. fatalis*.

I investigated the relationship between patterns of microwear and function of canines (killing or biting behavior) in six extant carnivores (cheetah, *Acinonyx jubatus*; leopard, *Panthera pardus*; African lion, *Panthera leo*; African wild dog, *Lycaon pictus*; gray wolf, *Canis lupus*; spotted hyena, *Crocuta crocuta*) and the extinct saber-tooth cat, *S. fatalis*. I chose extant species that use two distinct modes of capturing prey of similar size (medium-large ungulates). Canids and hyaenids pursue potential prey for long distances and rely solely on their anterior teeth (canines and incisors) to disable prey. These predators use multiple bites to wound and dismember their prey during an attack. By contrast, felids pursue prey for short distances and then use their front limbs to hold onto the prey before delivering a single, strong, killing bite with the canines. In general, felids kill their prey by a bite to the nape, throat, or nose. Small prey are killed by a bite to the nape, whereas large prey are killed by holding the nose or by biting the throat, which occludes the trachea and results in suffocation (Ewer, 1973). This difference in killing behavior may result in different patterns of microwear on the canines. Furthermore, canines that come into contact with bone during an attack or during feeding are likely to exhibit relatively higher densities of features than those that do not (Van Valkenburgh et al., 1990). Thus, the quantification

and comparison of patterns of dental microwear among living and extinct carnivores can provide new information on the role of canines in apprehension of prey and use of carcasses.

MATERIALS AND METHODS

Each extant species was represented by 10 wild-shot adults from the National Museums of Kenya or the United States National Museum of Natural History, whereas fossil specimens of *S. fatalis* were housed at the Los Angeles County Museum of Natural History. I made impressions of the posterior portion of the mid-labial surface of each canine at a point about halfway along the length of the tooth. I prepared the impressions using vinyl-polysiloxane impression material (Express 3M, Dental Products Division, St. Paul, MN). I then made casts from these impressions using epoxy casting material (Epoxy-dent, Oxy Dental Products, Inc., Hillside, NJ). Each specimen was coated with ca. 200A of gold (SEM Coating Unit E 5100, Polaron Instruments, Inc., Baltimore, MD) and examined with an Omniscan scanning electron microscope (ETEC Instruments, Seattle, WA). For each individual, two micrographs were made magnifying the impression of 500 \times . This magnification was chosen over a lower magnification of 200 \times because it was much easier to distinguish the smallest features of microwear from artifacts of casting at the higher magnification (Teaford, 1991).

Maximum lengths, widths, angle of orientation, and density of features of microwear were computed for each micrograph using a digitizer pad (Summagraphics, Seymour, CN) linked to a personal computer. Data were stored using the software program, SIGMASCAN (Jandel Scientific, Inc., San Rafael, CA) and analyzed with the statistical package SYSTAT (Wilkinson, 1986). The orientation of features of microwear was measured relative to the baseline of each micrograph, which defined an anteroposterior horizontal line about at the middle of each canine. The two micrographs from each individual were treated as one sample and the total number and mean lengths and widths of features of microwear were computed. Each feature was categorized as either a pit or a scratch based on their length-to-width ratio. Pits were features with a length-to-width ratio less than 4:1, where-

as scratches were features with a ratio greater than 4:1 (Grine and Kay, 1988; Solounias et al., 1988; Teaford, 1988; Van Valkenburgh et al., 1990). I then calculated the percentages of pits and scratches for each species. Features truncated by the edge of a micrograph were used only in the categorization of features as pits or scratches.

I transformed linear measures to base 10 and obtained inverse sines for angles before statistical analysis. I analyzed deviations of patterns of microwear from the horizontal axis using the method of Batschelet (1965) for circular data. To test for differences among species, I performed a non-parametric analysis of variance (Kruskal-Wallis test, H) and multiple-comparison tests (Tukey) on the means or ranked data (Sokal and Rohlf, 1981; Zar, 1984).

RESULTS

The density of features differed significantly between species ($H = 21.07$, $d.f. = 6$, $P < 0.005$). The African wild dog had the greatest density of features and differed significantly from cheetahs and leopards, which exhibited the least number of features (Table 1). The spotted hyaena, gray wolf, and African lion were intermediate. *S. fatalis* had less features than any of the modern carnivores and differed significantly from the two canids.

Shape of feature differed significantly between species. The spotted hyaena and African wild dog had the shortest features, whereas the gray wolf had the longest. The three felids exhibited features of intermediate length ($H = 20.12$, $d.f. = 6$, $P < 0.05$; (Fig. 1). The African wild dog had narrower features than the felids, which exhibited features of intermediate width. The spotted hyaena exhibited the widest features ($H = 31.38$, $d.f. = 6$, $P < 0.005$). *S. fatalis* had relatively wide, but short, features and was closest to the spotted hyaena in shape of features. In all species, number of scratches exceeded that of pits. Among the living species, the percentage of features classified as scratches ranged from 65% in the spotted hyaena to 76% in the African wild dog. *S. fatalis* most closely resembled the spotted

TABLE 1.—Mean length and width, and number of features of microwear (per mm²) on upper canines of six extant carnivores and *Smilodon fatalis*. Pits are features with a length-to-width ratio of less than 4:1. Scratches are features with a length-to-width ratio of greater than 4:1. Angular deviation defines the mean orientation of features of microwear measured relative to a horizontal line about at the middle of each canine. Standard deviations are given in parentheses. Sample size is 10 for each species.

Species	Number of features	Length (μm)	Width (μm)	Percentage of scratches	Percentage of pits	Angular deviation
<i>Acinonyx jubatus</i>	71.1 (20.1)	89.5 (11.86)	2.63 (0.66)	72.34 (6.03)	27.66 (4.52)	53.6 (7.73)
<i>Panthera pardus</i>	71.3 (20.82)	87.2 (8.95)	2.62 (0.41)	74.67 (5.12)	25.31 (5.34)	56.9 (4.61)
<i>Panthera leo</i>	77.5 (29.57)	80.9 (20.93)	2.27 (0.55)	68.54 (4.13)	31.46 (4.46)	53.9 (6.06)
<i>Lycaon pictus</i>	111.4 (26.69)	70.4 (18.18)	1.70 (0.39)	75.81 (6.68)	24.19 (6.73)	48.4 (6.09)
<i>Canis lupus</i>	89.5 (32.03)	92.3 (14.69)	3.07 (0.31)	74.2 (6.39)	25.8 (6.18)	49.6 (6.14)
<i>Crocota crocuta</i>	84.4 (36.0)	65.7 (13.9)	2.88 (0.96)	64.83 (8.17)	35.17 (6.65)	54.3 (5.39)
<i>Smilodon fatalis</i>	49.0 (9.84)	74.5 (18.18)	3.4 (0.64)	64.67 (6.64)	35.33 (6.69)	50.2 (13.7)

hyaena in relative frequency of scratches and pits and differed significantly from the gray wolf, African wild dog, and leopard ($H = 19.92$, $d.f. = 6$, $P < 0.05$). No distinct patterns in orientation of features were revealed by visual examination of representative micrographs for each species (Fig. 2). This lack of distinct patterns was confirmed by examination of angular data ($H = 3.2$, $d.f. = 6$, $P = 0.78$).

DISCUSSION

Studies of microwear on molars suggested that shape of features was related to force of bite and position of the bite along the row of teeth (Gordon, 1982, 1984; Ryan, 1979). Killing and apprehending prey by carnivores involves stabbing and slicing by canines (Ewer, 1973). When jaws close, contact occurs between the anterior surface of the upper canine and the posterior edge of the lower canine, which results in the formation of a facet on each tooth close to the base of the crown. A second facet develops at the tips of the canine where high stresses are generated during penetration (Gorniak and Gans, 1980). In

this study, dental replicas were made near the facet-free posterior edges of the upper canines. The features of microwear in this area are likely formed during tooth-food-tooth contact. The action of pulling pieces of skin, meat, bone, and tendinous tissue from the carcass probably results in formation of features. The formation of scratches or pits may depend on the ratio of bone to meat in the diet (Van Valkenburgh et al., 1990), nature of the bite, and structure of enamel.

The African wild dog exhibited the narrowest features and had relatively low numbers of pits despite having the highest density of features. This canid is strictly a meat eater that avoids consumption of any significant amount of bone. Observations on wild dogs in the Serengeti revealed that dogs consumed 60% of a carcass leaving only contents of the rumen, bones, and skin (Van Lawick and Goodall, 1970). The high density of features probably was due to its style of killing, whereby potential prey was subjected to numerous bites before it was killed. This also was true of the gray wolf, which usually has to make many bites to

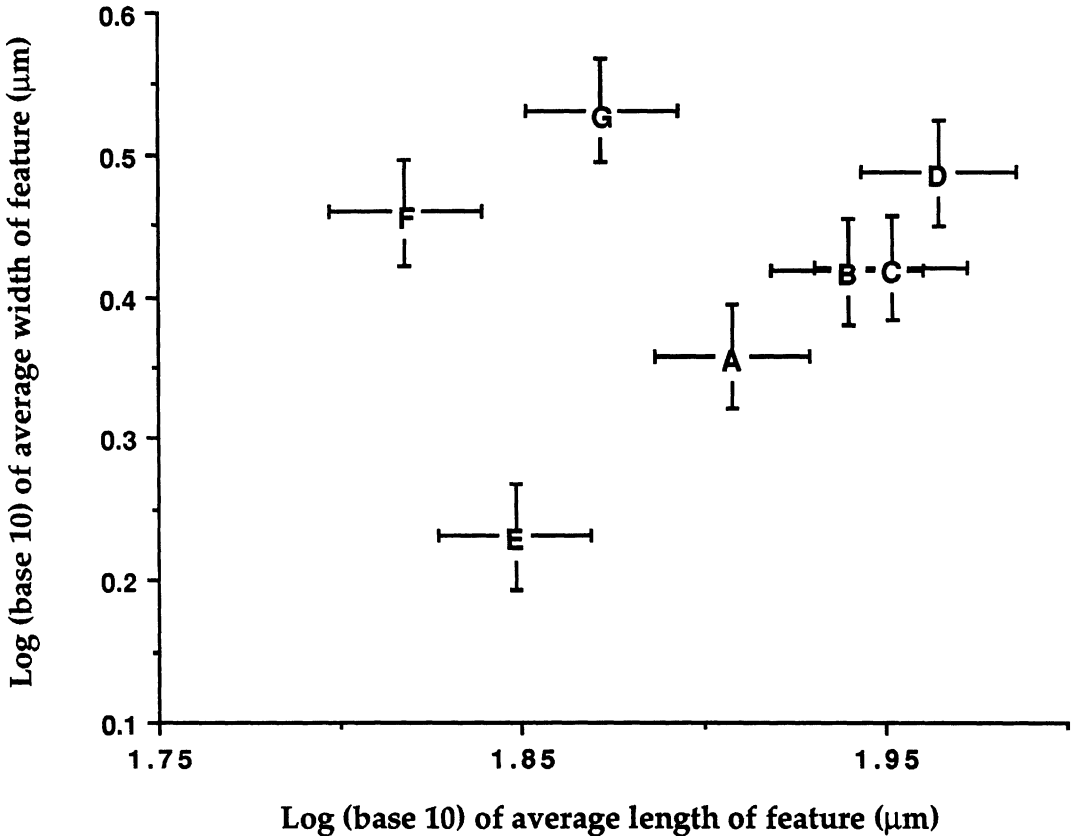


FIG. 1.—Relationship between log (base 10) of average width and log (base 10) of average length of features of microwear for *Panthera leo* (A), *P. pardus* (B), *Acinonyx jubatus* (C), *Canis lupus* (D), *Lycaon pictus* (E), *Crocuta crocuta* (F), and *Smilodon fatalis* (G). Error bars represent standard deviations.

get to inner parts of prey (Amman and Amman, 1989; Mech, 1970; Schaller, 1972; Van Lawick and Goodall, 1970). The spotted hyaena employs the same style of killing as many canids (Kruuk, 1972) and this behavior was reflected in similarity of a number of features. The spotted hyaena is a specialized bone crusher and showed a high percentage of pits, which suggested that canines were either impacted by the splintering bone from the premolars or that hyaenas occasionally use their anterior teeth to break bones (B. Van Valkenburgh, pers. comm.).

Unlike the canid-hyaena group, felids did not show any functional grouping in shape or frequency of features of microwear. The

cheetah and leopard had the least number of features, whereas the African lion was intermediate in shape and density of features. However, felids display relatively fewer features than do canids and hyaenids, which suggest that delivering deep, strong bites to apprehend prey result in less abrasion of the canines.

It also is possible that features of microwear on the canines are formed after prey has been killed and during ingestion. The sequence of dismembering a carcass is similar in large felids. Skin, fascia, and other tough parts are cut using carnassials and then meat is bolted down rapidly. African lions sometimes lick the hide and pluck out long hair from a carcass with their incisors

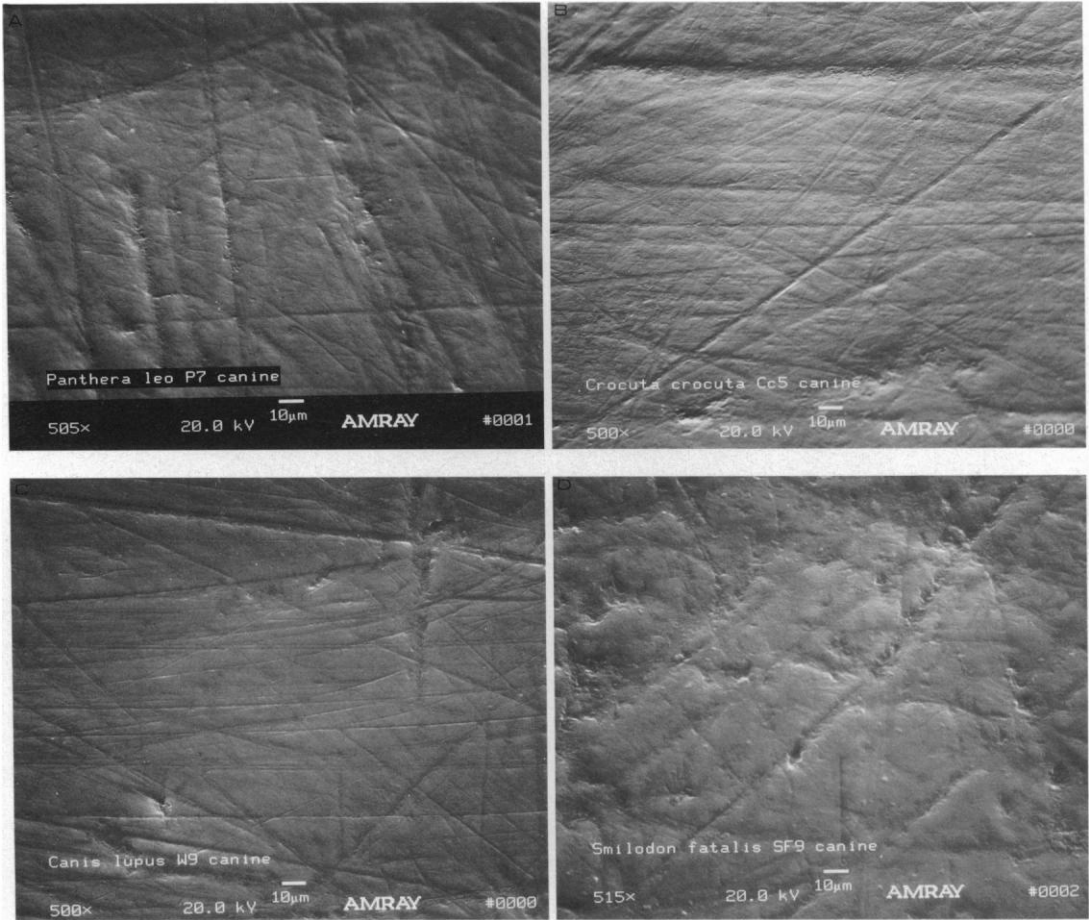


FIG. 2.—Micrographs of (a) *Panthera leo*, (b) *Crocuta crocuta*, (c) *Canis lupus*, and (d) *Smilodon fatalis*. Width of field for each micrograph is ca. 200 μm .

before starting to feed. Felids eat all parts of a carcass except the rumen contents, horns, teeth, and some bone splinters. Lions are peculiar in that they remove vegetation from the intestines by squeezing the intestines on their tongue past the incisors. Leopards and cheetahs discard the skeleton, skin, and digestive tract of large prey, but consume bones and skin of small prey (Schaller, 1972). Hyaenids and canids start feeding on their prey while it is still alive and the process of dismembering a carcass may take only a few minutes. In contrast to felids, these two groups ingest food rapidly and rely more heavily on their canines and incisors for feeding. Whereas wild dogs

concentrate on ingesting meat, hyaenas devour the entire carcass and occasionally swallow large pieces of bone in one gulp. Canids and hyaenids also consume small quantities of grass that may be laden with grit (Kruuk, 1972; Schaller, 1972). Perhaps canines are abraded by food and other extraneous material that is processed by incisors and premolars.

Smilodon fatalis tended to have few features of microwear that resembled the other felids; however, *S. fatalis* differed from cheetahs and African lions in having relatively more pits and wider features. *Smilodon* showed no consistent similarity in features of microwear on canine teeth to any

of the carnivores included in this study, which suggest that its style of killing and possibly dietary preference were different from that of modern predators. Perhaps *Smilodon* used its upper canines for killing, but not in feeding, which resulted in the formation of few features. This is in agreement with other studies of features of microwear on the molars of *Smilodon*, which suggested that *Smilodon* may have avoided contact with bone during encounters of killing and feeding (Biknevicius and Van Valkenburgh, 1996; Van Valkenburgh and Ruff, 1987; Van Valkenburgh et al., 1990). Emerson and Radinsky (1980) predicted that *Smilodon* may have had a force of bite that was comparable to, or even greater than that of many modern felids, which supports the idea that large force of bite produces wider features of microwear.

Upper canines of modern cats and, to a lesser extent, hyaenids are round in cross-section, recurved posteriorly and shaped like a cone. In contrast, upper canines of saber-toothed cats are more flattened (mediolaterally), which is similar to canids (Martin, 1980; Van Valkenburgh and Ruff, 1987). The sabers of *Smilodon* are long, recurved, blade-like teeth with an extremely thin veneer of enamel (Merriam and Stock, 1932). The enamel extends to the gum line along the posterior margin, but is more variable on the rest of the tooth. The posterior margin is more compressed than the anterior margin, especially toward the base of the exposed portion. The edges of the sabers have fine serrations that differ from the larger serrations of Scimitar cats (e.g., *Homotherium*). Functional significance of serrations on teeth in various groups of vertebrates such as crocodiles and dinosaurs suggests that serrations trap and cut sections of material to a depth determined by the height of the serrations. In addition to trapping and cutting action, serrations help to grip and rip when teeth are withdrawn (Abler, 1992). I hypothesize that sabers of *Homotherium* were likely more effective in ripping prey than those of *Smilodon*. As

further support for this hypothesis, fine serrations on sabers of *Smilodon* were more apparent in juveniles and wear smooth with age. Adults of *Smilodon* may have relied more on penetrating power of their smooth sabers with less emphasis on the ability to rip (B. Van Valkenburgh, pers. comm.).

The long canines of *Smilodon* remain an enigma for carnivore biologists. Some still favor the stabbing hypothesis, which postulates that *Smilodon* had the capacity to inflict deep wounds (Miller, 1969, 1980; Simpson, 1941). The majority favor saber bites that resulted in relatively shallower wounds. However, wounds were perhaps longer superficially than those inflicted by canines of living felids due to the great anteroposterior diameter of the sabers (Akersten, 1985; Biknevicius and Van Valkenburgh, 1996; Emerson and Radinsky, 1980; Kurtén, 1952; Van Valkenburgh and Ruff, 1987).

Little effort has been made to amass detailed qualitative and quantitative descriptions of extant carnivores feeding in the wild. Lack of this knowledge hinders us in formulating concrete hypotheses that explain the relationship between patterns of microwear and use of canines in killing, dismembering, and consuming prey. This study suggests that comparative analyses of microscopic patterns of wear can allow researchers to infer use of teeth in extinct saber-tooth cats. Similar analyses, coupled with experimental modeling, on other saber-tooth cats such as the Homotherini and nimravids will serve to expand our knowledge and improve our understanding of the complex paleoecology of these extinct predators.

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