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Relationships between dental microwear and diet in Carnivora (Mammalia) — Implications for the reconstruction of the diet of extinct taxa

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ABSTRACT

Food consumption causes distinct microwear patterns on teeth, especially in mammals that actively masticate food. Here we perform a microwear analysis to assess the relationships between diet and microwear features of diverse Carnivora. Our database includes approximately 230 individuals of 17 extant species having different diets. We analyse both slicing and grinding facets of M1 and m1. The proposed method is reproducible and allows the differentiation, especially on slicing facets, of microwear poles that are significantly distinct from one another. In carnivorans, the microwear features mainly result from their foraging behavior and the proportion of certain food items consumed. We applied our method to extinct taxa such as the amphicyonid *Amphicyon major*. The results on the m1 slicing facet indicate dietary similarities between this large Miocene predator and the extant red fox; results from the m1 grinding facet do not have equivalent in extant taxa, however.

1. Introduction

Carnivora are among the most diverse mammalian orders (McKenna and Bell, 1997; Nowak, 1999; Flynn et al., 2005). Such a great diversity includes a remarkable variety of diets and dental morphologies, from hypercarnivory in meat-eating felids to hypocarnivory such as in the kinkajou (*Potos flavus*), which is a frugivore, or the great panda (*Ailuropoda melanoleuca*), which is an herbivore. A family like the Ursidae documents this dietary diversity well, by including an omnivore (the brown bear *Ursus arctos*), a meat eater (the polar bear *Ursus maritimus*), an insectivore (the sloth bear *Melursus ursinus*), an herbivore (the giant panda *Ailuropoda melanoleuca*), and a foli-frugivore (the spectacled bear *Tremarctos ornatus*) (Sacco and Van Valkenburgh, 2004 and references in Table 1). Past communities of carnivorans (defined thereafter as members of the order Carnivora) also displayed considerable morphological (dentition, locomotor apparatus) and ecological diversity (*e.g.*, Van Valkenburgh, 1988, 1994), which undoubtedly demonstrates that dietary diversity was also great in the past. Many previous studies have used correlations between dental and/or cranio-mandibular features of carnivorans and their dietary specialisation (*e.g.*, Emerson and Radinsky, 1980; Van Valkenburgh and Ruff, 1987; Biknevicius and Ruff, 1992; Biknevicius et al., 1996; Binder and Van Valkenburgh, 2000; Holliday and Steppan, 2004; Therrien, 2005; Anyonge and Baker, 2006; Evans et al., 2007). However, cranial and dental morphological features partly result from ancestry or systematic affinities (Popowics, 2003; Sacco and Van Valkenburgh, 2004), and therefore, may bias inferences about the diet of some extinct species.

Alternative methods exist. Based on isotope analysis, Feranec (2004) suggested that the sabertoothed cat, *Smilodon fatalis*, from the tar pits of Rancho La Brea, California consumed animals that fed on C_3 vegetation. However, because isotopic ratios depend on the length of the trophic chain, isotopic analysis on extinct mammalian predators are indirect and difficult to interpret (Roth and Hobson, 2000; Bocherens and Drucker, 2003; Sponheimer et al., 2003; Codron et al., 2005). Trace element ratios (Sr/Ca and Ba/Ca) have also been used to infer predator–prey relationships (*e.g.*, Sillen and Lee-Thorp, 1994; Balter et al., 2001), but diagenetic processes often obscure the signal. Analysis of dental micro-abrasion or microwear is an additional method to infer the diet of fossil taxa. Dental microwear analysis consists of a quantification and a comparison of different types of microwear resulting from the abrasion of dental surface caused by consumption and mastication of food during the last days of life of an animal (Rensberger, 1978; Teaford and Oyen, 1989). Until now, such analyses were generally applied to extant primates and ungulates to reconstruct the diet, then the environment of their fossil relatives (Walker et al., 1978; Janis, 1990; Teaford, 1991; Solounias and Semprebon, 2002; Merceron et al., 2004, 2005a,b,c; Merceron and Ungar, 2005; Merceron et al., 2006; Merceron and Madelaine, 2006). Microwear analyses were also applied to extant and/or extinct carnivorans in a couple of studies, with promising, though heterogeneous, results. Taylor and Hannam (1986) used 32 specimens belonging to 12 different species

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Table 1
Diets and references of recent taxa studied here (sorted by diet)

Diet	Vernacular name	Species	References
Meat eater	Malagasy civet	*Fossa fossana*	Nowak (1999), Muñoz Garcia and Williams (2005)
	Polar bear	*Ursus maritimus*	De Master and Stirling (1981), Nowak (1999)
	Serval	*Leptailurus serval*	Estes (1991), Nowak (1999), Muñoz Garcia and Williams (2005)
Bone eater	Spotted hyena	*Crocuta crocuta*	Estes (1991), Nowak (1999)
	Stripped hyena	*Hyaena hyaena*	Rieger (1981), Estes (1991), Nowak (1999), Muñoz Garcia and Williams (2005)
Piscivore	European river otter	*Lutra lutra*	Herfst (1984), Hainard (1989), Nowak (1999), Muñoz Garcia and Williams (2005), Tüzün and Albayrak (2005)
Herbivore	Great panda	*Ailuropoda melanoleuca*	Chorn and Hoffman (1978), Schaller et al. (1989), Nowak (1999)
	Lesser panda	*Ailurus fulgens*	Roberts and Gittleman (1984), Nowak (1999), Muñoz Garcia and Williams (2005)
Larva and worm eater	Falanouc	*Eupleres goudotii*	Garbutt (1999), Nowak (1999)
Insectivore	Sloth bear	*Melursus ursinus*	Nowak (1999), Muñoz Garcia and Williams (2005)
	Stripped mongoose	*Mungos mungo*	Estes (1991), Nowak (1999)
	Slender mongoose	*Galerella sanguinea*	Estes (1991), Nowak (1999), Muñoz Garcia and Williams (2005)
Frugivore	Spectacled bear	*Tremarctos ornatus*	Nowak (1999)
	Kinkajou	*Potos flavus*	Ford and Hoffman (1988), Nowak (1999), Muñoz Garcia and Williams (2005)
Malacophage	Sea otter	*Enhydra lutris*	Estes (1980), Hainard (1989), Nowak (1999)
Omnivore	European badger	*Meles meles*	Hainard (1989), Nowak (1999), Boesi and Biancardi (2002), Lanszki (2004), Virgós et al. (2004), Muñoz Garcia and Williams (2005)
	Red fox	*Vulpes vulpes*	Hainard (1989), Nowak (1999), Muñoz Garcia and Williams (2005)

of Viverridae. They showed the presence of two types of wear, pits and furrows. Their observations on the whole tooth row, without reference to facets and based on a low number of specimens, are difficult to interpret. Van Valkenburgh et al. (1990) analysed the microwear of 90 specimens of large carnivorans belonging to nine extant species. They showed possible relationships between microwear patterns on the labial facet of the lower carnassial paraconid and bone consumption. Moreover, they demonstrate that the sabertoothed cat *S. fatalis* avoided bones during killing and feeding. Anyonge (1996) confirmed the results of Van Valkenburgh et al. (1990), based on an analysis of the canine teeth in six extant species and *S. fatalis*. In his study of early Paleocene mammals of Colorado, Dewar (2003a) dealt more with the surface and the wear level of dental facets than with the relationships between diet and microwear. In his subsequent analysis on microwear types in carnivorans (Dewar, 2003b), this author used the paracone of the first upper molar (M1) and included only six extant species, which provides limited useful information to infer the diet of fossil taxa.

It is not currently possible to compare the results of these previous studies because they used different dental facets generally from small samples (in terms of extant species and/or number of individuals) that did not document a wide variety of diets. In addition, some fundamental questions remained unsolved. Is microwear analysis applicable to any species of Carnivora? Can we use the same facets in any species of the order to make informative comparisons? Can the methodological approach applied to primates and ungulates also be applied to carnivorans, and if so, can microwear analysis be applied to fossil taxa and help to reconstruct their diet? The goal of the present study is to provide some answers to these questions and to assess the origin of microwear in carnivorans. We propose a precise methodological approach to test whether the microwear analysis can be applied to any carnivorans. The relationship between diet and dental microwear pattern is based here on an original database that is the most complete one ever published for carnivorans. Because this study aims to reconstruct the diet of extinct taxa, we also propose a reconstruction of the diet of two species of Amphicyonidae, an extinct family of generalist carnivorans, from the middle Miocene of France.

2. Material

2.1. Recent material

Extant species have been chosen with regard to their alimentary preferences. Each representative diet of Carnivora is illustrated by at least one extant species. The diet assigned to each extant species accounts for at least 70% of ingested food (Table 1). Our database contains 228 specimens belonging to 17 species (referred to the nine families of terrestrial carnivorans; Table 2). Only wild-caught and adult specimens are included to avoid biases resulting from artificial diet and lactation. See Table 2 for the condensed database and Appendix A for the complete one. This sample is chosen to be as representative as possible (without intrinsic bias) of the large range of diets, and therefore potential microwear patterns, within carnivorans.

2.2. Fossil material

There is little doubt that extinct hypercarnivorous taxa such as felids were meat eaters. In contrast, reconstructing the diet of an extinct taxon

Table 2
Observed sample (sorted by name)

Species	Vernacular name	Family	Number of specimens	Specimens analysed on the slicing facet	Specimens analysed on the grinding facet
Ailuropoda melanoleuca	Great panda	Ursidae	4	4	3
Ailurus fulgens	Lesser panda	Ailuridae	5	3	4
Crocuta crocuta	Spotted hyena	Hyaenidae	15	13	5
Enhydra lutris	Sea otter	Mustelidae	4	4	4
Eupleres goudotii	Falanouc	Eupleridae	9	7	0
Fossa fossana	Malagasy civet	Eupleridae	14	14	12
Galerella sanguinea	Slender mongoose	Herpestidae	21	17	11
Hyaena hyaena	Stripped hyena	Hyaenidae	6	5	3
Leptailurus serval	Serval	Felidae	12	11	9
Lutra lutra	European river otter	Mustelidae	20	20	18
Meles meles	European badger	Mustelidae	23	17	20
Melursus ursinus	Sloth bear	Ursidae	4	4	2
Mungos mungo	Stripped mongoose	Herpestidae	13	9	8
Potos flavus	Kinkajou	Procyonidae	21	14	10
Tremarctos ornatus	Spectacled bear	Ursidae	2	2	2
Ursus maritimus	Polar bear	Ursidae	19	16	18
Vulpes vulpes	Red fox	Canidae	25	25	25