A dental microwear texture analysis of the Mio-Pliocene hyaenids from Langebaanweg, South Africa

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Hyaenids reached their peak diversity during the Mio-Pliocene, when an array of carnivorous species emerged alongside dwindling civet-like and mongoose-like insectivorous/omnivorous taxa. Significantly, bone-cracking morphological adaptations were poorly developed in these newly-emerged species. This, their general canid-like morphology, and the absence/rarity of canids in Eurasia and Africa at the time, has led researchers to hypothesise that these carnivorous Mio-Pliocene hyaenas were ecological vicars to modern canids. To shed further light on their diets and foraging strategies, we examine and compare the dental microwear textures of *Hyaenictitherium namaquensis*, *Ikelohyaena abronia*, *Chasmaporthetes australis*, and *Hyaenictis hendeyi* from the South African Mio-Pliocene site of Langebaanweg with those of the extant feliforms *Crocuta crocuta*, *Acinonyx jubatus*, and *Panthera leo* (caniforms are not included because homologous wear facets are not directly comparable between the suborders). Sample sizes for individual fossil species are small, which limits confidence in assessments of variation between the extinct taxa; however, these Mio-Pliocene hyaenas exhibit surface complexity and textural fill volume values that are considerably lower than those exhibited by the living hyaena, *Crocuta crocuta*. Dental microwear texture analysis thus supports interpretations of craniodental evidence suggesting low bone consumption in carnivorous Mio-Pliocene hyaenas.

Key words: Mammalia, Hyaenidae, durophagy, dental microwear textures, Mio-Pliocene, South Africa.

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Introduction

Hyaenids, with the exception of the aardwolf, *Proteles cristatus*, are the most durophagous carnivorans alive today. While bone is a dominant component of the diets of extant hyaenids, durophagy probably only came to typify this family during the Plio-Pleistocene, when taxa with functional-morphological features suggestive of a bone-cracking specialisation rose to prominence (Werdelin and Solounias 1991; Werdelin 1996a; Turner et al. 2008). Levels of durophagy were presumably much lower during the earlier phases of hyaena evolution, when bone-cracking adaptations were less developed in the family. Most of our assumptions regarding the importance of bone in the diets of these early taxa, and their foraging behaviour, have been deduced from their craniodental morphologies (Werdelin and Solounias 1991, 1996; Ferretti 2007; Tseng et al. 2010, 2011; Tseng and Stynder 2011). Craniodental features do not necessarily reflect dietary preferences alone, though. It is well known that other factors, such as phyletic af-

finity, also play a role (Goillot et al. 2009; Popowics 2003; Sacco and Van Valkenburgh 2004). Furthermore, craniodental morphology only provides insights into the foods that an individual was capable of eating, not the foods that it actually ate on a daily basis.

Dental microwear analysis, the study of patterns of microscopic use-wear on teeth, can, in contrast, provide direct evidence of the diets and foraging strategies of animals over the course of days, weeks, or perhaps months before death. Because microwear signatures reflect the mechanical properties of foods actually eaten by individuals, dietary inferences are not greatly affected by adaptationist assumptions. Here we employ dental microwear texture analysis (RS Scott et al. 2005, 2006; Ungar et al. 2008, 2010; JR Scott et al. 2009; Merceron et al. 2010a; Schubert et al. 2010) to inform on durophagy levels in *Hyaenictitherium namaquensis*, *Ikelohyaena abronia*, *Chasmaporthetes australis*, and *Hyaenictis hendeyi* from the South African Mio-Pliocene fossil site of Langebaanweg (LBW) E Quarry (32˚582S, 18˚72E) (Hendey

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1981, 1982, 1984; Roberts 2006). These four taxa fall into three adaptive types or ecomorphologies (ecomorphs) (Werdelin and Solounias 1996; Turner et al. 2008) that dominated the hyaena evolutionary record immediately prior to the proliferation of developed bone-cracking taxa. Although none likely exhibited the levels of durophagy evident in developed bone crackers, varying degrees of morphological adaptation to bone cracking suggest that these taxa may have differed in their levels of bone consumption and thus in the degree and/or type of carcass utilisation.

The three extant bone-cracking hyaenas, *Parahyaena brunnea*, *Hyaena hyaena*, and *Crocuta crocuta*, are members of the crown group Hyaeninae (Koepfli et al. 2006). While all three taxa are efficient scavengers, *Crocuta crocuta* is also a proficient hunter (Kruuk 1972). Morphological adaptations for bone cracking in these taxa include large, robust crania with vaulted foreheads, short muzzles, wide palates, powerful jaw muscles, and large quadrangular premolars with pronounced central cusps and strengthened enamel (Ferretti 2007; Tseng et al. 2011). Post-carnassial teeth, which have a crushing role in carnivorans such as canids, are either absent or strongly reduced. For this reason, bone-cracking hyaenas typically use their premolars (particularly P3/p3) and carnassials to process bone. Post-carnassial teeth were, however, prominent in the jaws of the earliest fossil hyaenas (Werdelin and Solounias 1991, 1996; Werdelin 1996a; Ferretti 2007; Turner et al. 2008; Tseng et al. 2011). In these taxa, hard-brittle foods were likely processed using the post-carnassial teeth and not the premolars.

Hyaenidae evolved from stem feliforms sometime during the Late Oligocene (Werdelin and Solounias 1991; Koepfli et al. 2006). From that time until the present, the hyaenid bauplan has changed substantially and in a gradational manner. Many of the evolutionary changes that this family underwent reflect convergences on the morphologies of other carnivoran families. Werdelin and Solounias (1991, 1996) identified six ecomorph groups among the almost seventy recognised fossil hyaena species: (i) civet-like insectivores/omnivores; (ii) mongoose-like insectivores/omnivores; (iii) jackal- and wolf-like meat and bone eaters; (iv) cursorial meat and bone eaters; (v) transitional bone crackers; and (vi) fully-developed bone crackers. The very earliest forms of hyaena were the civet- and mongoose-like taxa (ecomorph groups 1 and 2) (Fig. 1). These had generalised dentitions including well-developed post-carnassial teeth, and none of the cranial specialisations associated with bone cracking seen in later taxa (Werdelin and Solounias 1991; Ferretti 2007). During the Middle to Late Miocene, Hyaenidae experienced a major radiation as a variety of canid-like ictitherines such as *Ictitherium*, *Thalassictis*, *Hyaenotherium*, *Miohyaenotherium*, and *Hyaenictitherium* (ecomorph group 3) began to appear and the earlier civet-like and mongoose-like taxa (ecomorph groups 1 and 2) went into decline (Fig. 1). While the earliest ictitherines differed only marginally from the civet- and mongoose-like taxa, the more derived members of this ecomorph group evinced some craniodental specialisations

for meat and bone eating (Werdelin and Solounias 1991; Werdelin 1996a). It has been suggested that, as a group, the ictitherines may have occupied the same ecological zone that wolves, wild dogs and jackals do today (Werdelin 1996a; Werdelin and Solounias 1996). The aridification and opening of environments during the Late Miocene and Early Pliocene evidently led to a significant increase in ungulate biomass (Cerling et al. 1997), providing new ecological niches for hyaenas. At this time, the subfamily Hyaeninae emerged and the Ictitheriinae declined and eventually disappeared, along with the few late-occurring civet-like and mongoose-like hyaenids (Fig. 1). The canid-like morphology seen in the Ictitheriinae persisted in some hyaenines, such as *Lycyaena*, *Chasmaporthetes*, and *Hyaenictis* (ecomorph group 4), though the group also began to trend towards greater craniodental specialisation in the direction of meat eating. In addition, the *Lycyaena–Chasmaporthetes– Hyaenictis* clade exhibited increased cursoriality (Werdelin and Solounias 1991; Werdelin 1996a), likely in response to an increasingly open habitat. At the same time, hyaenas exhibiting transitional bone-cracking morphologies emerged, likely to take advantage of increased scavenging opportunities. These early bone crackers, which include the genera *Metahyaena*, *Palinhyaena*, *Belbus*, and *Ikelohyaena* (ecomorph group 5), eventually paved the way for the second major hyaena radiation of well-developed bone-cracking genera such as *Parahyaena*, *Hyaena*, *Pachycrocuta*, *Adcrocuta*, and *Crocuta* (ecomorph group 6) during the Plio-Pleistocene (Werdelin and Solounias 1991; Werdelin 1996a) (Fig. 1).

Werdelin and Solounias' (1991, 1996) model provides an excellent structure within which we can further investigate the evolution of dietary specialisations within Hyaenidae using dental microwear analysis. More specifically, dental microwear texture analysis may help inform us on this model by providing an independent test for the evolution of durophagy in hyaenids.

The Langebaanweg hyaenas.—Langebaanweg E Quarry, which was uncovered during phosphate mining operations in 1958, has produced a large number of faunal taxa; among these are the four securely identified hyaena species considered in this study. The sheer variety of mammalian and non-mammalian taxa in evidence suggests that animals from a variety of habitats are represented. Some of these lived in the vicinity of the site, formerly a river estuary, and others lived further afield, in the catchment area of the palaeo-Berg River that fed into the estuary. Werdelin (2006) recorded two hyaena species (*Chasmaporthetes australis* and *Ikelohyaena abronia*) in both the estuarine (Langeberg Quartzose Sand Member or LQSM) and river sediments (Muishhondfontein Pelletal Phosphate Member or MPPM), and one each in the LQSM (*Hyaenictis hendeyi*) and MPPM (*Hyaenictitherium namaquensis*). It has nevertheless been suggested that all four species may have been sympatric (Werdelin 1996b; Stynder 2009), as terrestrial carnivores today are generally not as tied to specific environments as herbivores are. The absence of
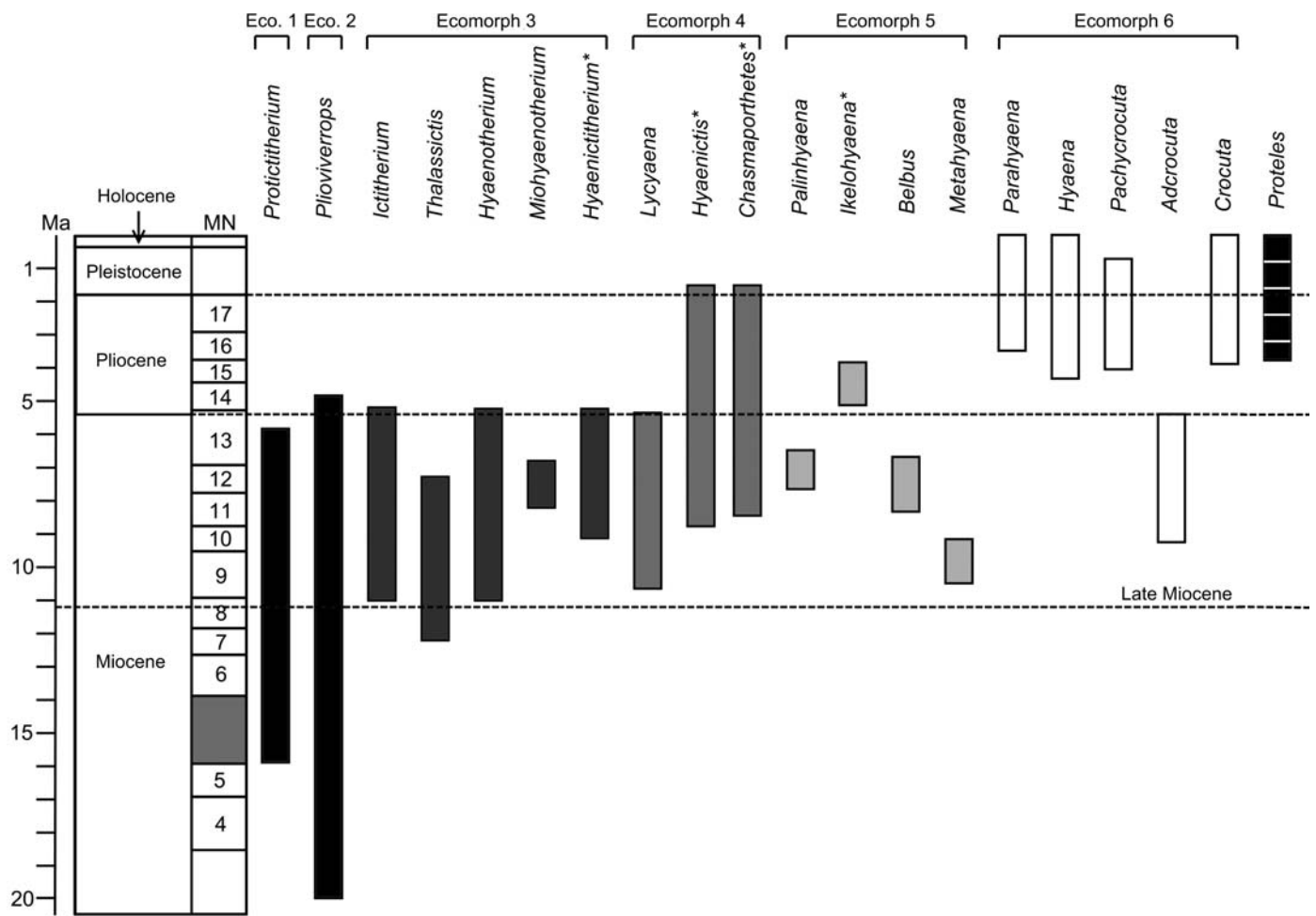
Fig. 1. Biochronology of species discussed in the text (based upon Werdelin and Solounias 1991; Turner et al. 2008). Asterisks refer to the genera analysed in this study. MN, Mammal Neogene Zone.

Hyaenictis hendeyi in the MPPM and *Hyaenictitherium namaquensis* in the LQSM may well be a sampling effect; most of the specimens recovered from this site were uncovered during mining rather than during controlled excavations, with an estimated 70% of the original fossil assemblage destroyed in the process.

The late-occurring ictitherine genus *Hyaenictitherium* was primarily of Eurasian origin. The three African representatives are *H. namaquensis*, *H. minimum*, and *H. barbarum* (Werdelin and Solounias 1991; Tseng and Wang 2007; Geraards et al. 2010). *Hyaenictitherium minimum*, which has been described as jackal-like in morphology and ecology, is one of the earliest known members of the genus (~7 Ma) (Tseng and Wang 2007; de Bonis et al. 2005). *Hyaenictitherium namaquensis* is not only more recent than *H. minimum*, but is also appreciably more derived. Compared to earlier ictitherines, *H. namaquensis* has a vaulted forehead, its mandible is more robust, its premolars (P2–P3 and p3–p4) are slightly larger, and its postcarnassial teeth are fewer and reduced in size. In addition, its dental enamel microstructure is characterised by zigzag Hunter-Schreger Bands (HSB), although angles are not

as acute as those seen in developed bone crackers (Ferretti 2007). These craniodental features, which are well-developed in extant bone-cracking hyaenas, suggest that *H. namaquensis* was a more capable bone cracker than earlier ictitherines, but not on the level of developed bone crackers or possibly even transitional bone crackers.

The transitional bone cracker *Ikelohyaena abronia*, which Hendey (1974, 1978) originally placed in the genus *Hyaena* (*Hyaena abronia*), is the only member of its genus. Shared characters between it and the extant *Hyaena* were later identified as plesiomorphic (Werdelin and Solounias 1991), resulting in *I. abronia* being placed in its own genus. Recently, Werdelin and Lewis (2005) questioned the generic distinctness of this species, suggesting it may be appropriate to sink it back into *Hyaena*. Morphologically, *I. abronia* is smaller than the extant hyaenines. Its postcranial features also point to a more canid-like posture and cursorial ability (Hendey 1974, 1978). Its forelimbs are more slender than those of extant hyaenines and its hindlimbs are proportionally longer (Hendey 1974). While its premolars exhibit a degree of buccolingual expansion, it does not exhibit the same degree of hypertrophied coni-

cal premolars as developed bone crackers. With its vaulted forehead, its skull shape does approach that of developed bone crackers, though it is less robust (Werdelin and Solounias 1991; Turner et al. 2008). *Ikelohyaena* also retains the first lower premolar and diminutive M2s, M3s and m2s. According to Krupandan (2010), *I. abronia* possessed zigzag HSB, although, as in *Hyaenictitherium namaquensis*, the angles are less acute than those of *Crocuta crocuta* and *Hyaena hyaena*. Recently, a finite element analysis of the holotype skull (SAM-PQL 14186) suggests that *I. abronia* already possessed derived features in skull stress distribution and levels of strain energy characteristic of *C. crocuta*, though bite force estimates were much lower than that of the extant taxon (Tseng and Stynder 2011). As a species considered morphologically intermediate between earlier canid-like hyaenas and more recent bone-cracking taxa, *I. abronia* is retrodicted to have had a level of durophagy intermediate between these groups.

The genera *Hyaenictis* and *Chasmaporthetes* fall into the clade of presumed canid-like cursorial meat and bone eaters including *Lycyaena*. The LBW fossil material currently attributed to *Hyaenictis* was originally attributed to *Euryboas* sp. (Hendey 1978); however, Werdelin et al. (1994) referred this species to *Hyaenictis* owing to similarities in dental morphology (especially in the case of the P4) with Eurasian *Hyaenictis* species. Although initially discovered in Europe and Asia, this genus is best known from African material dated to ~5.2–5.8 Ma (Haile-Selassie et al. 2004; Turner et al. 2008; Haile-Selassie and Howell 2009). The genus *Chasmaporthetes* was more widespread than *Hyaenictis*, and has been found at sites across Africa, Eurasia and North America. While it was initially thought to be a Plio-Pleistocene genus, fossil remains dated to ~7–6 Ma and identified as *Chasmaporthetes* cf. *C. australis* were recently discovered at Toros-Menalla, Chad (de Bonis et al. 2007).

A shift towards meat eating in the *Lycyaena–Chasmaporthetes–Hyaenictis* clade is implied by a general narrowing of the anterior premolars, loss of p1, m2 (in *Chasmaporthetes*) and M2, an increase in P2 and p2 size, a reduction of the posterolingual cingulum cusp on p4, the reduction (or loss) of the m1 metaconid, and the reduction of the m1 talonid (Werdelin et al. 1994). Be this as it may, derived members of this clade developed some craniodental characteristics associated with bone cracking, including vaulted foreheads and zigzag HSB (Ferretti 2007; Krupandan 2010). A recent finite element analysis of a *Chasmaporthetes lunensis* skull showed that it was well-adapted to withstand high stresses (Tseng et al. 2011). Given that the overall morphology of this skull is better suited to meat eating than bone cracking, Tseng et al. (2011) suggested that its high level of stress resistance was likely an aid for subduing prey during hunting rather than an adaptation for regular bone cracking. Durophagy levels are expected to be relatively low in the *Lycyaena–Chasmaporthetes–Hyaenictis* clade, particularly in comparison with transitional and developed bone crackers.

Based on gross craniodental morphology then, we expect that *Ikelohyaena abronia* was the most durophagous of the four LBW hyaena taxa and that *Chasmaporthetes australis* and *Hyaenictis hendeyi* were least durophagous. We also expect that *Hyaenictitherium namaquensis* was intermediate in its level of durophagy between *I. abronia* on the one hand, and *C. australis* and *H. hendeyi* on the other. If these retrodictions hold, it follows that *I. abronia* would have been the most complete processor of carcasses, followed by *H. namaquensis* and then *C. australis* and *H. hendeyi*.

Dental microwear analysis.—Dental microwear analysis has been widely used to examine aspects of diet and ecology in primates (Rafferty and Teaford 1992; Lucas and Teaford 1994; Teaford et al. 1996; Ungar 1996, 1998; Ungar and Teaford 1996; Ungar et al. 2004), artiodactyls (Solounias et al. 1988; Solounias and Moelleken 1993; Rivals and Deniaux 2003; Merceron et al. 2004, 2005b; Franz-Odendaal and Solounias, 2004; Semprebon et al. 2004; Merceron and Ungar 2005; Schubert et al. 2006; Ungar et al. 2007) and, to a lesser extent, other taxa, including carnivorans (see Taylor and Hannam 1987; Van Valkenburgh et al. 1990; Anyonge 1996; Goillot et al. 2009; Schubert et al. 2010; Ungar et al. 2010). Conventional techniques used to assess dental microwear image surfaces employ either a scanning electron microscope (Rensberger 1978; Teaford and Walker 1984; Grine et al. 2002) or a light stereomicroscope combined with image analysis software (Merceron et al. 2005a, 2010b; Calandra et al. 2008; Peigné et al. 2009) to count and measure individual features (pits and scratches) on occlusal surfaces. A technique where features are counted directly through a light stereomicroscope is also in use (Solounias and Semprebon 2002; Semprebon et al. 2004; Semprebon and Rivals 2007). These two-dimensional (2D) approaches are limited by observer measurement error and variation in instrument settings and specimen orientation (Gordon 1988; Grine et al. 2002; Scott et al. 2006; Schmidt 2010).

Recently, some researchers have begun to use dental microwear texture analysis, a new, 3D approach to microwear analysis free from observer measurement errors. Unlike feature-based microwear analyses, this approach does not depend on an observer to identify and measure individual microwear scratches and pits but, rather, characterises various attributes of wear surface textures across scales of observation (RS Scott et al. 2005, 2006; Ungar et al. 2008, 2010; JR Scott et al. 2009). For example, animals that feed on tough foods typically exhibit higher surface anisotropy (epLsar) and lower texture complexity (Asfc) than those that consume hard-brittle foods (Ungar et al. 2010).

Until relatively recently, microwear texture analysis had only been applied to primates (Merceron et al. 2006, 2009; RS Scott et al. 2005, 2006; Ungar et al. 2008; JR Scott et al. 2009), artiodactyls (Ungar et al. 2007; Merceron et. al. 2010; Schulz et al. 2010), and marsupials (Prideaux et al. 2009). In its first application to carnivorans, Schubert et al. (2010) compared carnassial microwear in three large feliforms, *Acinonyx jubatus* (the cheetah), *Panthera leo* (the lion), and *Crocuta crocuta* (the spotted hyaena). These authors demonstrated that in-

creased durophagy in feliform carnivorans results in an increase in microwear surface pittedness or complexity (higher Asfc), an increase in microwear surface feature size (higher Tfv) and a decrease in feature orientation (lower epLsar). The more durophagous *Crocuta crocuta* had the highest Asfc and Tfv means and the lowest epLsar mean in the study sample. *Acinonyx jubatus*, which normally avoids hard, brittle foods such as bone, had the lowest Asfc and Tfv means but the highest epLsar mean. The range of variation in values for *Panthera leo* reflects an average level of durophagy that falls on average between that of *A. jubatus* and *C. crocuta* (Schubert et al. 2010). Since a carnivore's level of durophagy reflects its degree and/or type of carcass utilisation, its microwear signature can be used as a general indicator of its niche position within its particular guild. This type of information makes dental microwear texture analysis well suited for reconstructing the diets and niche positions (given sufficiently large sample sizes) of species within carnivoran palaeoguilds.

Institutional abbreviations.—SAM, Iziko South African Museum, Cape Town, South Africa; AMNH, American Museum of Natural History, New York, USA.

Other abbreviations.—LBW, Langebaanweg E Quarry; LQSM, Langeberg Quartzose Sand Member; MPPM, Muishondfontein Pelletal Phosphate Member; HSB, Hunter-Schreger bands; epLsar, anisotropy; Asfc, complexity; Smc, scale of maximum complexity; Tfv, textural fill volume.

Material and methods

We compared the microwear patterns on the m1 carnassials of the four LBW hyaenas and three extant feliforms (from Schubert et al. 2010). Feliforms and caniforms differ markedly in the manner in which they use their carnassials (Ungar et al. 2010). Feliforms (and felids in particular), which have either no post-carnassial teeth or very rudimentary ones, generally use their carnassials for both meat-slicing and bone cracking. Hyaenids (and some other feliforms) differ from felids, in that the bone-cracking role is shared between the carnassials and pre-carnassials. While the pre-carnassials (particularly the P3/p3) carry much of the burden for crushing bone in hyaenids, our study is focused on the carnassials to maximise comparability with baseline taxa. We could not, however, include caniforms in our baseline, because these carnivorans tend to have well-developed post-carnassials, which are used for crushing (as opposed to the carnassials, which are used for slicing). Homologous facets on the carnassials of feliforms and caniforms are thus not functionally equivalent and cannot be compared directly (Ungar et al. 2010). While some very early hyaenids possessed a full set of post-carnassial teeth, these evidently played a decreasingly important role in the dietary behaviour of this family over time, as they were gradually lost and/or reduced in size. The four hyaenids analysed in our study either have no post-carnassial dentition or relict post-carnassial teeth that are diminutive and reduced in number.

Table 1 lists the fossil hyaena dental specimens included in this study. These are housed in the Cenozoic Palaeontology Collections of the Iziko South African Museum in Cape Town, South Africa (SAM-PQL). In addition to being relatively rare in the LBW assemblage, hyaena teeth also exhibit a high degree of wear and post-mortem damage. As a result, only 18 carnassial teeth from four hyaena taxa were found to be suitable for analysis: *Hyaenictitherium namaquensis* (n = 2), *I. abronia* (n = 8), *Chasmaporthetes australis* (n = 4), and *Hyaenictis hendeyi* (n = 4). While this sample is small, it is not

Table 1. Fossil hyaena dental specimens used in this study and their primary microwear data.

| Species	Specimen	Asfc	epLsar	Smc	Tfv	HAsfc9	HAsfc81
Chasmaporthetes australis	SAM-PQL50009	1.877	0.002	0.150	5889.602	0.552	1.324
	SAM-PQL22204	2.378	0.001	0.209	8239.073	0.777	1.130
	SAM-PQL46471	2.145	0.004	0.342	9603.436	0.667	0.600
	SAM-PQL21789	11.500	0.002	0.150	13288.956	0.843	1.548
Hyaenictis hendeyi	SAM-PQL50096	1.665	0.004	0.210	7759.931	0.812	1.063
	SAM-PQL21000	1.493	0.005	0.150	12395.555	0.438	1.043
	SAM-PQL20990	4.099	0.004	0.150	15142.653	0.312	0.797
	SAM-PQL40223	2.383	0.004	0.151	15643.813	0.549	1.035
Hyaenictitherium namaquensis	SAM-PQL25026	5.456	0.002	0.150	7747.657	0.440	0.954
	SAM-PQL12848	4.341	0.002	0.150	17806.294	0.766	0.974
Ikelohyaena abronia	SAM-PQL33046R	1.658	0.004	0.150	9473.360	0.306	0.577
	SAM-PQL45652	4.510	0.004	0.150	10749.153	0.673	1.348
	SAM-PQL46248	3.064	0.004	0.141	12395.574	0.410	0.849
	SAM-PQL20984	2.393	0.001	0.155	15617.477	0.315	0.580
	SAM-PQL46472	6.843	0.003	0.175	16625.684	0.407	0.889
	SAM-PQL41779	3.830	0.004	0.165	17309.016	0.509	0.942
	SAM-PQL22202L	3.820	0.002	0.145	17514.875	0.359	0.749
	SAM-PQL33520	4.898	0.004	0.155	17722.770	0.650	1.009
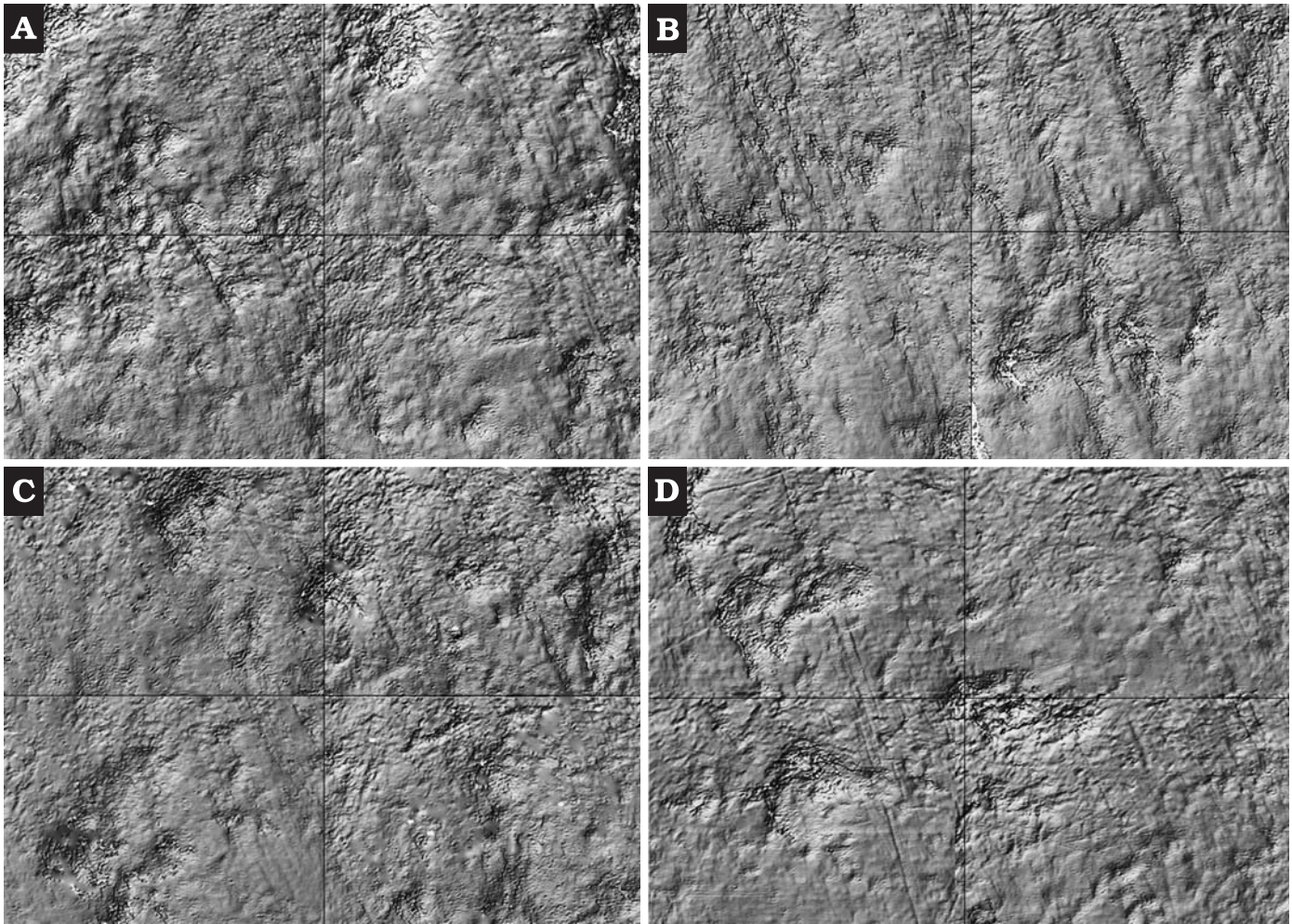
Fig. 2. Photosimulations of fossil hyaena microwear surfaces generated from point clouds. **A**. *Hyaenictitherium namaquensis* (Stromer, 1931), SAM-PQL 12848. **B**. *Hyaenictis hendeyi* (Werdelin, Turner, and Solounias, 1994), SAM-PQL 20990. **C**. *Ikelohyaena abronia* (Hendey, 1974), SAM-PQL 22202L. **D**. *Chasmaporthetes australis* (Hendey, 1974), SAM-PQL 22204. Each represents a field of view of 276 μm × 204 μm.

atypical for fossil microwear studies. Data reported here for the extant feliforms were taken from Schubert et al. (2010) and consist of adult, wild-caught individuals of *Crocuta crocuta* (n = 12), *Acinonyx jubatus* (n = 7), and *Panthera leo* (n = 10) housed in the American Museum of Natural History (AMNH) and the Iziko South African Museum (SAM-ZM). Prior to moulding, crown surfaces were cleaned with cotton-swabs soaked in acetone. Once they were clean, crown surfaces were moulded using President's Jet Microsystem regular body dental impression material (Coltène-Whaledent Corp.). Replicas were then prepared using Epotek 301 epoxy resin and hardener (Epoxy Technologies Corp.). These were examined by light microscopy and, where necessary, by white-light confocal profilometry to determine suitability for microwear analysis. Criteria for assessment of postmortem damage followed Teaford (1988) and King et al. (1999).

Specimens that preserved unobscured antemortem microwear were analysed using dental microwear texture analysis. A Plμ white-light confocal imaging profiler (Solarius, Inc.) was used to generate 3D point clouds representing the trigonid shearing facet of the m1 carnassial (following Van Valken-

burgh et al. 1990 and Schubert et al. 2010), with the surface sampled as close to the center of the facet as possible. Artifacts, such as adherent dust particles, were excluded by thresholding, erase operators and slope-filtering as necessary. Resulting point clouds had a lateral (x, y) sampling interval of 0.18 μm and vertical resolution of 0.005 μm. Four adjacent fields of 138 μm × 102 μm were sampled, for a total planimetric work envelop of 276 μm x 204 μm.

Each point cloud was analysed using scale-sensitive fractal analysis software (ToothFrax and SFrax, Surfract Corp.). Data were generated for area-scale fractal complexity (complexity, Asfc), exact proportion length-scale anisotropy of relief (anisotropy, epLsar), heterogeneity of area-scale fractal complexity (heterogeneity, HAsfc), the scale of maximum complexity (Smc), and textural fill volume (Tfv). Median values for each variable were then calculated for the four fields sampled from each individual. Each of the microwear texture attributes is described in detail elsewhere (Scott et al. 2006; Ungar et al. 2007). Taxa that consume more hard-brittle foods tend to have higher Asfc and lower epLsar values than closely related taxa that consume softer, tougher items (Scott et al. 2006; Ungar et

al. 2007, 2010; Prideaux et al. 2009; Schubert et al. 2010). Complexity reflects change in roughness across scales of observation. A surface with features of varying sizes has a high Asfc value. Anisotropy is a measure of orientation concentration of wear. A microwear surface dominated by scratches all running in a given direction has a high epLsar value.

Taxa have also been separated by scale of maximal complexity, textural fill volume and heterogeneity of complexity. Relationships between these variables and diet are not as well understood, though research is progressing to relate them to specific food properties. The scale of maximum complexity is the fine-scale limit of the steepest part of the curve describing Asfc. A surface that lacks features with small dimensions, for example, has a high Smc value. Textural fill volume is the difference in summed volume for fine and coarse square cuboids (in this case, 2 µm and 10 µm on a square side, respectively) that "fill" a surface. A surface with many mid-range scale features, for example, has a high Tfv value. Finally, heterogeneity reflects variation in complexity across a surface, and is measured as the quotient of the median absolute deviation of Asfc and the median of Asfc (in this case using nine cells, or a 3 × 3 matrix of subsampled areas).

Taxa were compared using a multivariate analysis of variance (MANOVA) model, with all five texture attributes included as variables. First, the raw data for each attribute were rank transformed to mitigate violation of assumptions inherent in parametric statistical analyses following usual procedures for microwear texture analyses (Conover et al. 1981). This conservative approach is used because microwear texture data are typically not normally distributed. Sources of significant variation were then assessed by ANOVAs for each variable, and multiple comparisons tests were conducted as necessary. Both Fisher's LSD and Tukey's HSD tests were used to balance risks of Type I and Type II errors (Cook and Farewell 1996). Results presented for which $p < 0.05$ for Fisher's LSD test but not Tukey's HSD test are here considered suggestive, but of marginal significance.

Results

Figure 2 illustrates representative microwear surfaces for each of the four fossil taxa. Table 1 presents the primary microwear data for each of the analysed fossil specimens. Statistical analyses suggest some differences between the fossil species for at least some of the tested texture variables, which is remarkable given the small sample sizes. The MANOVA comparing extant and fossil taxa demonstrates significant variation in microwear surface textures. Individual ANOVAs indicate that the sources of that variation are Asfc, epLsar, and Tfv (Table 2).

Surface complexity (Asfc).—As reported in Schubert et al. (2010), average microwear surface complexity varies with durophagy levels in the extant feliforms used in our analysis. *Crocuta crocuta* microwear surfaces are the most complex, those of *Acinonyx jubatus* are the least complex and those of
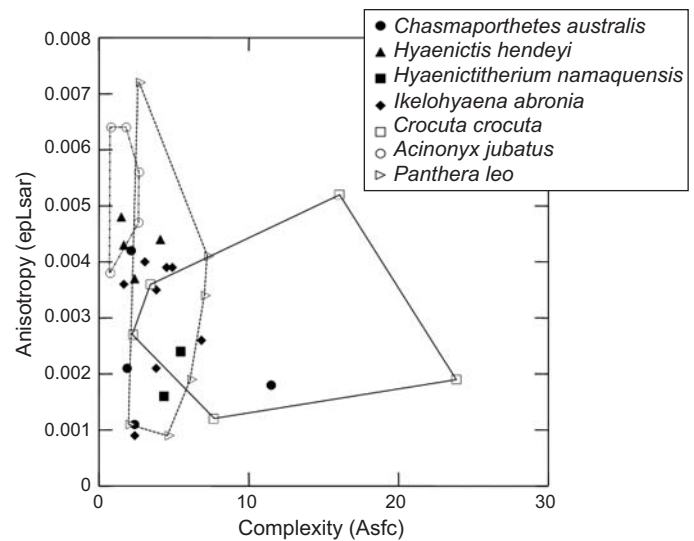

Fig. 3. Bivariate plot of fossil and extant feliform anisotropy and complexity. The lines on the graphs connect specimens with minimum and maximum values for each taxon, and indicate the ranges of variation for these attributes. The data for the extant species are from Schubert et al. (2010).

Panthera leo are intermediate (Table 3). The fossil hyaenas exhibit much smaller inter-specific differences in microwear surface complexity compared with one another; none of the species-pairs show significant differences (Tables 2 and 3). This is unsurprising given the small sample sizes for each. However, when individual fossil taxa are compared to the extant species, some variation is evident. Figure 3 indicates that *Hyaenictitherium namaquensis* values fall at the lower end of the Asfc range of variation of *C. crocuta*, where they also overlap with *P. leo*. While *H. namaquensis* does not differ from *C. crocuta* and *P. leo* with respect to surface complexity, Fisher's LSD test suggests a marginal difference from *A. jubatus* (Table 2). *Chasmaporthetes australis* exhibits the second highest mean Asfc value in the fossil sample after *H. namaquensis* (Table 3), though its mean Asfc value may be inflated by a single outlier. Exclusion of this outlier cuts its mean to less than half, giving it the lowest complexity average in the fossil sample (2.133). Neither Fisher's LSD nor Tukey's HSD tests indicate variation between *C. australis* and either *A. jubatus* or *P. leo* in complexity. However, Fisher's LSD test suggests a difference with *C. crocuta* (Table 2). *Ikelohyaena abronia*, like *H. namaquensis* and *C. australis*, does not differ significantly from *P. leo* with respect to complexity; however, Fisher's LSD test suggests a marginal difference between *I. abronia* on the one hand, and *C. crocuta* and *A. jubatus* on the other. *Hyaenictis hendeyi* exhibits the least complex microwear surfaces in the fossil sample (Table 3). Fisher's LSD and Tukey's HSD tests show no significant difference between *H. hendeyi* and *A. jubatus*, but the former does differ significantly from *C. crocuta* and *P. leo*.

Anisotropy (epLsar).—Anisotropy generally decreases with an increase in durophagy levels among the extant feliforms

Table 2. Results of statistical analyses; df, degrees of freedom.

A. Multivariate Nested Analysis of Variance

Between species	Test statistic	F	df	p
Wilk's Lambda	0.124	3.33	30.146	0.000
Pillai Trace	1.431	2.67	30.200	0.000
Hotelling-Lawley Trace	3.387	3.88	30.172	0.000

B. Nested ANOVAS

Microwear texture attributes	F	df	p
Asfc	7.569	6	0.000
epLsar	5.652	6	0.000
Smc	1.736	6	0.138
Tfv	3.671	6	0.005
HAsfc9	1.775	6	0.129

C. Matrices of pairwise differences (within family comparisons)

		Acinonyx jubatus	*Panthera leo*	*Crocuta crocuta*	*Chasmaporthetes australis*	*Hyaenictis hendeyi*	*Hyaenictitherium namaquensis*
Asfc	*Panthera leo*	-23.214***					
	Crocuta crocuta	-27.798***	4.583				
	Chasmaporthetes australis	-11.964	-11.250	15.833**			
	Hyaenictis hendeyi	-4.714	-18.5***	23.083***	7.250		
	Hyaenictitherium namaquensis	-20.214**	-3.000	7.583	-8.250	-15.500	
	Ikelohyaena abronia	-14.089**	-9.125	13.708**	-2.125	-9.375	6.125
epLsar	*Panthera leo*	23.107***					
	Crocuta crocuta	19.899***	3.208				
	Chasmaporthetes australis	27.107***	-4	7.208			
	Hyaenictis hendeyi	4.732	18.375**	-15.167**	-22.375**		
	Hyaenictitherium namaquensis	31.357***	-8.25	11.458	4.25	26.625**	
	Ikelohyaena abronia	19.482***	3.625	-0.417	-7.625	14.75**	-11.875
Tfv	*Panthera leo*	-13.814**					
	Crocuta crocuta	-19.798***	5.983				
	Chasmaporthetes australis	-9.214	-4.6	10.583			
	Hyaenictis hendeyi	-19.464**	5.65	0.333	-10.25		
	Hyaenictitherium namaquensis	-20.214**	6.4	-0.417	-11	-0.75	
	Ikelohyaena abronia	-25.964***	12.15**	-6.167	-16.75**	-6.5	-5.75

All analyses carried out on ranked data. Values represent differences between means. ** significant (p ≤ 0.05) with Fisher's Least Significance Test; ***significant (p ≤ 0.05) with both Fisher's Least Significance Test and Tukeys HSD Multiple Comparisons Test.

used in our analysis. *Crocuta crocuta* and *Panthera leo* exhibit the lowest epLsar values, while *Acinonyx jubatus* exhibits the highest (Table 3). With the exception of *Hyaenictis hendeyi*, which has a marginally higher mean than the other fossil taxa (and both *C. crocuta* and *P. leo*), the fossil sample varies little in epLsar (Table 3). *Hyaenictitherium namaquensis* does not differ significantly from *C. crocuta* or *P. leo* with respect to anisotropy; however, it does differ significantly from *A. jubatus* (Table 2). *Chasmaporthetes australis* and *Ikelohyaena abronia* also do not differ significantly from *C. crocuta* and *P. leo* with respect to anisotropy; however, these two fossil taxa do differ significantly from *A. jubatus*. *Hyaenictis hendeyi* on the other hand, does not differ significantly from *A. jubatus* in anisotropy, but Fisher's LSD tests suggest a marginal difference from *C. crocuta* and *P. leo*.

Textural fill volume (Tfv).—Textural fill volume generally increases with an increase in durophagy among the extant feliforms used in our analysis. *Crocuta crocuta* exhibits the highest average Tfv, followed by *Panthera leo* and *Acinonyx jubatus* (Table 3). With the exception of a marginal difference between *Ikelohyaena abronia* and *Chasmaporthetes australis*, the fossil taxa vary little from one another in Tfv (Tables 2 and 3). *Hyaenictitherium namaquensis* does not differ significantly from *C. crocuta* and *P. leo*, but differs marginally from *A. jubatus* (Table 2). *Hyaenictis hendeyi*, which differs significantly from *C. crocuta* and *P. leo* with respect to Asfc, does not differ significantly from these two extant species in Tfv (Table 2). Fisher's LSD test does however suggest a marginal difference in Tfv between *H. hendeyi* and *A. jubatus*. Finally, *C. australis* does not differ significantly from any of the three

Table 3. Descriptive microwear texture statistics for fossil and extant feliforms used in this study. Extant data are from Schubert et al. (2010).

Species	n		Asfc	epLsar	Tfv
Hyaenictis hendeyi	4	Mean	2.410	0.004	12735.487
		SD	1.190	0.000	3611.301
Ikelohyaena abronia	8	Mean	3.877	0.003	14675.988
		SD	1.605	0.001	3309.087
Chasmaporthetes australis	4	Mean	4.475	0.002	9255.268
		SD	4.688	0.001	3095.818
Hyaenictitherium namaquensis	2	Mean	4.899	0.002	12776.975
		SD	0.789	0.001	7112.525
Crocuta crocuta	12	Mean	9.315	0.003	12319.750
		SD	6.708	0.001	5665.799
Panthera leo	11	Mean	5.362	0.003	10741.331
		SD	1.526	0.001	3340.232
Acinonyx jubatus	7	Mean	1.537	0.005	4060.070
		SD	0.842	0.001	4582.274

extant taxa with respect to Tfv, while *I. abronia* differs significantly from *A. jubatus* and marginally from *P. leo*.

Discussion

Given the small fossil hyaena sample analysed, it is indeed remarkable that we found any significant variation in microwear textures between the extinct and extant taxa, let alone even marginal variation between fossil taxa. That said, we are hesitant to draw firm conclusions, given the small sample sizes. On the other hand, we believe that there is value in placing the fossil individuals in the context of the results for the baseline extant taxa.

The ictitherines have been likened to extant wild canids with respect to morphology and diet (Werdelin and Solounias 1991, 1996; Werdelin 1996a). This characterisation might fit the earlier ictitherines better than it does the later, more derived taxa such as *Hyaenictitherium namaquensis*. Early ictitherines had well-developed post-carnassial dentitions (Werdelin and Solounias 1991; Semenov 2008) that were probably used to crush hard-brittle bone, as is observed for extant canids. On the other hand, ictitherine carnassials, like those of canids, were probably used to slice tough foods (including meat). Early ictitherine craniodental resemblances to extant jackals and coyotes suggest diets similar to those of these extant canids. Jackals and coyotes are mesocarnivorous, meaning that their diets consist of 50% to 70% meat/bone, with the balance made up of nonvertebrate foods and plant matter (Van Valkenburgh 2007). By contrast, *H. namaquensis*, with its enlarged premolars and drastically reduced post-carnassials, may have been more of a hypercarnivore, i.e., its diet consisted of more than 70% meat/bone (Ferretti 2007; Tseng and Wang 2007; Van Valkenburgh 2007). Of the three extant baseline species used in this study, one would thus expect *H. namaquensis* to most closely resemble *Panthera leo* in microwear texture patterning. The *H.*

namaquensis dental specimens examined resembled both *P. leo* and *Crocuta crocuta* in having relatively high Asfc and Tfv values combined with low epLsar values, although average values were closer to *P. leo* than to *C. crocuta*. It is noteworthy that *H. namaquensis* was the only fossil species that did not differ significantly from *C. crocuta* in Asfc. While the *H. namaquensis* sample is admittedly much too small for any firm conclusions, microwear results for the two specimens available are consistent with this species being the most durophagous of the LBW hyaenas.

The craniofacial morphology of *Ikelohyaena abronia* suggests that it was adapted to consume substantial amounts of hard, brittle bone. We expected this taxon to approach *C. crocuta* with respect to microwear pattern. And indeed, it did not differ significantly from *C. crocuta* in epLsar and Tfv values, though neither did it differ from *P. leo* with respect to Asfc and epLsar. It did, however, differ from *Acinonyx jubatus* in Asfc, epLsar and Tfv values. *Ikelohyaena abronia*, also differed from *C. crocuta* in microwear texture complexity however, with a relatively low Asfc average suggesting that it was probably not as durophagous as the extant hyaena. This is consistent with its reconstruction as a transitional bone cracker. Its level of durophagy was closest to that of the occasional bone consumer, *P. leo*. Thus, while *I. abronia* very likely consumed some bone, it might have done so sporadically.

The craniofacial morphology of *Chasmaporthetes australis* suggests that it was a hypercarnivore that ate primarily meat. This species was expected to have a microwear pattern differing from those of both *Panthera leo* and *Crocuta crocuta*, perhaps most closely resembling that of *A. jubatus*. Surprisingly, the average epLsar of *C. australis* was significantly lower than that of *A. jubatus*, and its Asfc average was lower than that of *C. crocuta,* suggesting levels of durophagy and tough food consumption intermediate between these two extant feliforms. Instead, similarities between *C. australis* specimens and *P. leo* in Asfc, epLsar, and Tfv suggest that the diet of *C. australis* was more likely similar to that of living lions, including both meat and occasionally bone.

The craniofacial morphology of *Hyaenictis hendeyi* suggests that it was also a hypercarnivore that consumed mostly meat. It was therefore also expected to resemble *A. jubatus* with respect to microwear pattern. Indeed, the microwear textures of *H. hendeyi* resembled those of the obligate tough-soft-tissue feeder *A. jubatus* with respect to Asfc and epLsar. It displayed lower average Asfc and higher epLsar values than *P. leo* and *C. crocuta*. Interestingly, *H. hendeyi* exhibited higher Tfv values than *A. jubatus*. Our results, which are based on a very small sample, suggest that *H. hendeyi* might have actively avoided hard, brittle foods. On current evidence, its diet may have consisted mainly of tough foods such as meat, ligaments, and hide.

The expansion of open, often grass-dominated habitats at the end of the Miocene led to a significant increase in ungulate biomass. Among hyaenids, the decline of apparently mesocarnivorous canid-like taxa and the concurrent emergence of what appear to be meat- and bone-eating specialists,

suggest a shift in ecological focus, probably in response to the changing environmental conditions. At LBW, the inference of a late-occurring, canid-like meat and bone eater (*Hyaenictitherium namaquensis*), a transitional bone cracker (*Ikelohyaena abronia*), and two cursorial meat and bone eaters (*Chasmaporthetes australis* and *Hyaenictis hendeyi*) are consistent with the notion that this locality witnessed a shift in hyaena ecology. Given the morphological diversity evident among the LBW hyaenas, one would thus have expected to find significant inter-specific differences in microwear signatures in line with ecomorphological divisions. This, however, was not the case. While microwear results hint at differences in the frequency of bone consumption among the LBW hyaenas (i.e., differences in microwear surface texture complexity and anisotropy), these were marginal and, in certain cases, inconsistent with the ecomorphological evidence. This result is likely explained by small sample sizes, however, which are probably inadequate to distinguish the fossil taxa. We expect that an analysis of larger samples, if they were available, might well bring out inter-specific differences in durophagy in line with morphological indicators.

While nothing concrete can be said about inter-individual dietary variation among the LBW hyaenas, as a group, these hyaenas display some similarities in microwear patterning with *Acinonyx jubatus* and *Crocuta crocuta*; however, they are most like *Panthera leo*, a meat eater that occasionally consumes bone. This is in agreement with the suggestion that bone only came to dominate the hyaenid diet with the rise to prominence of fully-developed bone-cracking taxa (ecomorph 6) during the Plio-Pleistocene (Werdelin and Solounias 1991; Werdelin 1996a; Turner et al. 2008). While *Adcrocuta* was likely a bone cracker, it is currently the only known Miocene taxon to exhibit fully-developed bone-cracking adaptations (Werdelin and Solounias 1991; Turner et al. 2008).

Our results are consistent with Werdelin and Solounias' (1991, 1996) and Werdelin's (1996a) characterisation of carnivorous Mio-Pliocene hyaenas as active hunters, rather than bone-cracking scavengers. While they likely also scavenged on occasion, the microwear evidence is most consistent with meat eating and little more than sporadic bone consumption. A hunting lifestyle (probably group hunting in many cases) might well apply to ecomorph groups 3 and 4, given their general canid-like morphology (Werdelin and Solounias 1991, 1996; Werdelin 1996a); however, it might also have applied to transitional bone crackers. For instance, *I. abronia* had forelimbs and hindlimbs of similar lengths, which probably gave it a more dog-like cursorial gait, as opposed to the galloping gait typical of extant hyaenas. Thus, despite its relatively small size, *I. abronia* might well have been able to hunt small-to-medium-sized game animals (Tseng and Stynder 2011).

Based on our current knowledge of their diets, most carnivorous Mio-Pliocene hyaenas may have filled the ecological niches that hypercarnivorous canids occupy in modern Eurasian and African environments, given that canids only spread to Eurasia and Africa from North America about 7 million years ago (Wang and Tedford 2008). In light of their possible ecological similarity to extant canids, such as *Lycaon pictus* and *Canis lupus*, it is unsurprising that their decline and eventual replacement by bone-cracking specialists was paralleled by the rise in numbers and ecological importance of the family Canidae during the Plio-Pleistocene. While a single canid, *Eucyon* sp. (Hendey 1974; Rook 2009), was present at LBW, it was a small fox-like species that presumably did not compete substantively with the LBW hyaenas. Free of any meaningful competition from other ecologically similar carnivoran families, the LBW hyaenas were able to proliferate and diversify in the ungulate-rich LBW environment.

Summary and conclusion

- As a group, the four LBW hyaena species exhibited durophagy levels that were closest to *Panthera leo*, a carnivorous generalist that occasionally eats bone. This is consistent with the suggestion that bone did not come to dominate hyaenid diets until the rise to prominence of fully-developed bone-cracking taxa during the Plio-Pleistocene.
- Our results are in agreement with the notion that most carnivorous Mio-Pliocene hyaenas were active predators and not bone-cracking scavengers. As such, they likely occupied ecological niches similar to those of the large hypercarnivorous canids in modern African and Eurasian environments.

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