

Evolution of bone-cracking adaptations in hyaenids (Mammalia, Carnivora)

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Key words: Hyaenidae, Carnivora, feeding adaptations, enamel structure, evolution, palaeoecology

ABSTRACT

The Hyaenidae are one of the most diverse groups of carnivores in terms of body size and craniodental morphology, and as such they represent an ideal case to study the correlation between dental, and skeletal anatomy, and behavioral ecology in mammals. However, a comprehensive analysis, based on extant and fossil forms, including both gross-morphological and microstructural characters, is lacking. In this work, some representatives of the Hyaenidae were examined, in order to document the diversity of the masticatory apparatus, including enamel microstructure, and to trace the evolution of bone-cracking adaptations within this group. Primitive hyaenids lack bone-cracking modifications as compared to the generalized carnivore morphotype, in agreement with their insectivorous-omnivorous diet. A key innovation in hyaenid evolution was the acquisition of an enamel dominated by zig-zag Hunter-Schreger bands in the Middle Miocene, marking the transition of the group to the bone-eating niche. The observed morphological changes in hyaenids suggest an increasing degree of specialization towards bone-consumption.

RIASSUNTO

La famiglia degli Hyaenidae rappresenta un caso ideale per lo studio delle relazioni tra anatomia dentaria e scheletrica e comportamenti alimentari nei mammiferi. In questo lavoro, ienidi fossili ed attuali sono stati esaminati allo scopo di documentare la diversità dell'apparato masticatorio, compresa la microstruttura dello smalto, nella famiglia Hyaenidae e di tracciare l'evoluzione dell'adattamento alla dieta ossifaga all'interno del gruppo. Gli ienidi primitivi non possiedono nessuna delle modificazioni morfologiche legate al consumo di ossa, rispetto al morfotipo generalizzato dei carnivori in accordo con la loro dieta insettivora ed onnivora. Una innovazione chiave nell'evoluzione degli ienidi è rappresentata dalla comparsa di bande di Hunter-Schreger piegate (zig zag HSB) nello smalto dentario, che ha segnato l'occupazione di una nuova nicchia alimentare da parte di questo gruppo di carnivori a partire dal Miocene medio. Il cambiamento morfologico osservato suggerisce che l'evoluzione di questa famiglia sia stata caratterizzata da un progressivo aumento del grado di specializzazione dell'apparato masticatorio alla frantumazione e consumo di ossa.

Introduction

Extant hyaenas, with the exception of the termite-eating aardwolf (*Proteles*), are a specialized group of carnivores, displaying distinct craniodental adaptations to bone consumption (Werdelin 1989; Werdelin & Solounias 1991; Joeckel 1998; Rensberger 1999), in agreement with their scavenging feeding habits (Kruuk 1972, 1976). In contrast to modern species, the fossil Hyaenidae present a greater diversity of body sizes and craniodental morphologies, suggesting that they included a wider range of feeding types. This makes this family of carnivores an ideal case to study the correlation between dental and skeletal anatomy, and behavioral ecology in mammals (Berta 1981; Werdelin & Solounias 1991, 1996; Ferretti 1999; Stefen & Rensberger 1999). Dietary preferences are expected to be reflected in components of the masticatory system, such as the skull, mandible and teeth, which are directly concerned with the initial stages of food procurement and processing. Dental

specialization is also expected to affect the enamel, as its microstructure, in many cases, represents a selective response to stresses produced during the chewing process (Koenigswald & Pfretzschner 1991; Rensberger 1995).

The evolution of hyaenid anatomy, notably bone-cracking adaptations, has been discussed by various authors (Kurtén & Werdelin, 1988; Werdelin 1989; Werdelin & Solounias 1991; Joeckel 1998; Rensberger 1999). However, a comprehensive review and analysis of the morphological and microstructural correlates of durophagy, in extant and fossil Hyaenidae, is lacking. In this study, representatives of the major hyaenid clades recognized by Werdelin & Solounias (1991) have been described in terms of cranio-mandibular morphology, dentition, tooth shape, and enamel structure. The aim is to document the diversity of the masticatory apparatus in the Hyaenidae and to trace the evolution of bone-cracking adaptations within this family.

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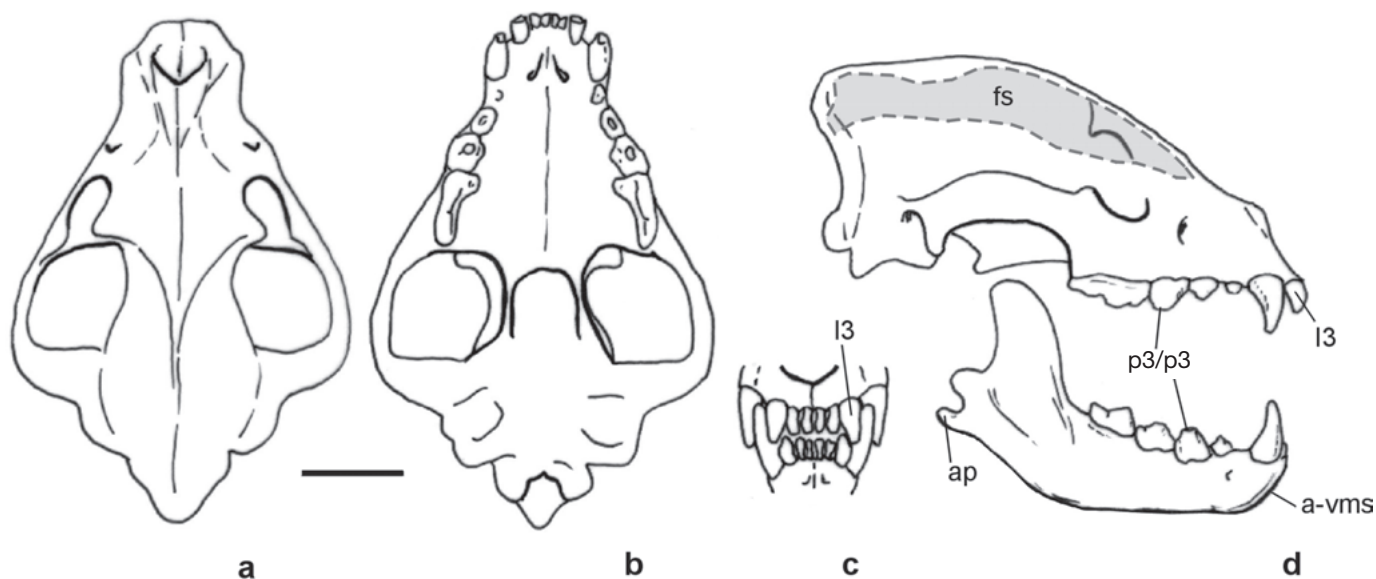


Fig. 1. Craniodental morphology of an extant bone-cracking hyaena (*Crocuta crocuta*, ZMF 2144). a) Skull in dorsal view. b) Skull in ventral view. c) Anterior dentition (incisors and canines) in anterior view. d) Skull and mandible in lateral view. The shadowed area indicates sagittal extension of frontal sinuses. Abbreviations: ap, angular process; a-vms, antero-ventral margin of the symphysis; fs, frontal sinuses; I3, upper third incisor; P3/p3, upper and lower third premolar. Scale bar: 5 cm.

Present diversity, feeding habits and adaptations of hyaenas

Extant hyaenids are represented by four species distributed across Africa and southwestern Asia, as far east as India (Hunt 1996). The diet of these species differs in the amount of meat, bones, invertebrates and plant material. *Proteles cristatus*, the aardwolf, is unique among extant hyaenas in feeding exclusively on social insects (Kruuk & Sands 1972). *Hyaena hyaena*, the striped hyaena, is a scavenger that also feeds on bones. Its feeding habits include also predation on small vertebrates and invertebrates, as well as frugivory (Kruuk 1976). *Parahyaena brunnea*, the brown hyaena, has a diet similar to that of the striped hyaena (Mills 1984). *Crocuta crocuta*, the spotted hyaena, is the species that most relies on active predation on large mammals (Kruuk 1972). Its diet also exhibits the highest proportion of bones among extant hyaenids. Comparisons of craniodental anatomy among extant bone-cracking hyaenas (*Hyaena*, *Parahyaena* and *Crocuta*), *Proteles*, and other carnivores, have highlighted several morphological modifications for bone consumption. Werdelin (1989), noted that bone-cracking forms have a shorter muzzle, a vaulted forehead, and a wider palate relative to more generalist carnivores (Fig. 1). Joeckel (1998), discussed the fact that in derived bone-cracking hyaenids, the frontal sinuses are anteriorly expanded, producing the characteristic stepped frontal profile of the skull. They are also caudally elongated, completely overlying the brain cavity (Fig. 1d). He concluded that, compared to other carnivores, the pneumatized skull roof of bone-cracking hyaenids would provide greater resistance to muscular load and compressive forces, generated by premolar biting during bone eat-

ing. This structure is absent in *Proteles*. Dental specializations of hyaenas for bone consumption include an imbricated and arched tooth row, enlarged distal premolars (P3/p3-p4; van Valkenburgh 1989), and carnassial blades that are not aligned with the mesial tooth row (Kurtén & Werdelin 1988; Fig. 1b). Modern bone-cracking hyaenas are also characterized by enlarged lateral incisors (especially the I3), which are also used in bone-cracking (Fig. 1c). The hyaenid mandible has received less attention as far as its functional adaptations are concerned. Nevertheless, the deep and stout mandibular body typical of extant bone-cracking hyaenas (Fig. 1d), is likely to be an adaptation to resist high bending stresses.

Enamel structure in carnivores

A major trend in mammalian enamel evolution is the development of a variety of structures aimed at reducing the risk of fracturing during occlusion. A very common solution to this problem is prism decussation (i.e. the crossing of enamel prisms; Pfretzschner 1988; Koenigswald 1997). The corresponding pattern, resulting from a regular decussation of prism organized into layers, is called Hunter-Schreger bands (HSB; Koenigswald & Sander 1997). All carnivores display HSB in most of their enamel (Stefen 1997). When observed from the outer enamel surface (i.e. in a tangential plane) by reflected light microscopy, HSB appear as alternating light and dark bands, depending on enamel prism direction within each band, with respect to the light source. The orientation of the HSB varies among taxa. The plesiomorphic condition for carnivores is of slightly undulating horizontal HSB (Stefen 1997). A de-

Tab. 1. Systematics, specimens, localities and ages of the hyaenid material.

Taxon	Specimen	Site	Age
Canidae			
<i>Vulpes vulpes</i>	ZMF 4141	Italy	Recent
<i>Canis aureus</i>	ZMF 2110	Somalia	Recent
	ZMF 1851	Somalia	Recent
<i>Canis lupus</i>	ZMF 11874	Italy	Recent
	ZMF 2033	Italy	Recent
<i>Lycaon pictus</i>	ZMF 22362	Kenya	Recent
	ZMF37597	Kenya	Recent
Herpestidae			
<i>Ichneumia albicauda</i>	ZMF 8956	Zaire	Recent
<i>Mungos mungo</i>	ZMF 3526	Somalia	Recent
<i>Herpestes sanguineus</i>	ZMF 480	Ethiopia	Recent
<i>Helogale undulata</i>	ZMF 4856	Africa	Recent
Viverridae			
<i>Civettictis civetta</i>	ZMF 8750	Somalia	Recent
<i>Genetta genetta</i>	ZMF 5531	Somalia	Recent
" <i>Viverra steinheimensis</i> "	IGF 4188V	La Grive, France	Middle Miocene (MN7-8)
" <i>Viverra angustidens</i> "	IGF 2163V	La Grive, France	Middle Miocene (MN7-8)
Hyaenidae			
<i>Plioviverrops faventinus</i>	BRS 5-367	Brisighella, Italy	Late Miocene (MN13)
	BRS 5-34	Brisighella, Italy	Late Miocene (MN13)
	BRS 5-169	Brisighella, Italy	Late Miocene (MN13)
	BRS 5	Brisighella, Italy	Late Miocene (MN13)
	BRS 5-30	Brisighella, Italy	Late Miocene (MN13)
<i>Ictitherium viverrinum</i>	MNH-PIK3006	Pikermi, Greece	Late Miocene (MN11-12)
<i>Hyaenotherium wongii</i>	KTB 90	Kemiklitepe B, Turkey	Late Miocene (MN12)
<i>Hyaenictitherium namaquensis</i>	MPR-VE2001	Sahabi, Lybia	Late Miocene (MN12-13)
<i>Lycyaena chaeretis</i>	BRS 27/17	Brisighella, Italy	Late Miocene (MN13)
	BRS 27/28	Brisighella, Italy	Late Miocene (MN13)
	NHM-M8979	Pikermi, Greece	Late Miocene (MN11-12)
<i>Chasmaporthetes lunensis</i>	IGF 4377	Olivola, Italy	Late Pliocene
	IGF 12461	Olivola, Italy	Late Pliocene
	NHMB-VA1822	Upper Valdarno, Italy	Late Pliocene/Early Pleistocene
	MGL-161818	St Vallier, France	Late Pliocene
	UCBL-211221	St Vallier, France	Late Pliocene
<i>Chasmaporthetes melei</i>	MAN 65729	Orosei, Italy	Late Pliocene/Early Pleistocene
<i>Parahyaena brunnea</i>	ZMF 35.9.1.288	South Africa	Recent
<i>Hyaena hyaena</i>	ZMF 2137	Somalia	Recent
<i>Pachycrocuta brevirostris</i>	IGF 494V	Upper Valdarno, Italy	Late Pliocene/Early Pleistocene
<i>Pachycrocuta brevirostris</i>	IGF 699V	Upper Valdarno, Italy	Late Pliocene/Early Pleistocene
<i>Pachycrocuta brevirostris</i>	IGF 839	Upper Valdarno, Italy	Late Pliocene/Early Pleistocene
<i>Pachycrocuta brevirostris</i>	IGF 12470	Upper Valdarno, Italy	Late Pliocene/Early Pleistocene
<i>Crocuta crocuta</i>	ZMF 2144	Somalia	Recent

rived HSB type is represented by the so-called zig zag HSB, also termed level II HSB (Rensberger 1999; Stefen & Rensberger 1999). The bands are steeply folded in zig zag HSB. The crests and troughs of adjacent waves of HSB are joined by vertical decussating prism bundles (Rensberger 1999). This very complex structure is supposed to represent an adaptation to withstand very high stresses during occlusion (Rensberger 1995, 1999; Rensberger & Wang, 2005), and has been related to bone-cracking. This particular type evolved convergently in various eutherian groups. Among carnivores, zig zag HSB are particularly developed in borophagine canids and hyaenids (Stefen 1997, 1999; Rensberger 1999; Stefen & Rensberger 1999; Rensberger & Wang 2005). A type of HSB with intermediate characters between undulating and zig zag HSB, has

been described as acute angled HSB (Stefen 1997, 1999). The occurrence of either one of the three HSB types, or a combination of them, bears relevant evidence on the species diet.

Abbreviations

Institutions and museums

BRS, Brisighella sample, Museo Civico di Scienze Naturali, Faenza (Italy); KTB, Kemiklitepe sample, Laboratoire de Géobiologie, Biochronologie et Paléontologie Humaine, Université de Poitiers (France); IGF, Museo di Storia Naturale (Sezione di Geologia e Paleontologia), University of Firenze (Italy); MAN, Museo Archeologico, Nuoro, Sardegna (Italy);

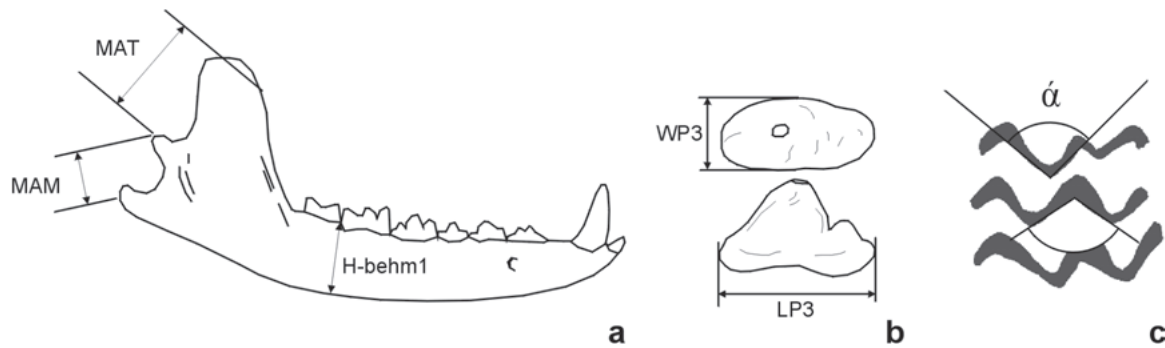


Fig. 2. Mandibular, dental and enamel (HSB) measurements. a) Mandible: H-behm1, height of body behind m1; MAT, moment arm of temporalis; MAM, moment arm of masseter. b) Upper third premolar (anterior is to the left): LP3, mesio-distal diameter of P3; WP3, bucco-lingual diameter of P3. c) Hunter-Schreger bands (HSB): α , folding angle at wave crests and troughs.

MGL, Musée Guimet, Lyon (France); MNHB, Naturhistorisches Museum, Basel (Swiss); MNH, Muséum d'Histoire naturelle, Lyon (France); MNHN, Muséum national d'Histoire naturelle, Paris (France). MPR, Museo di Paleontologia, Università La Sapienza, Roma (Italy); MZF, Museo di Storia Naturale (Sezione di Zoologia), Università di Firenze (Italy); NHM, Natural History Museum, London (UK); UCBL, Université Claude Bernard Lyon I, Lyon (France).

Dental nomenclature

C, upper canine; I, upper incisor; P, upper premolar; M, upper molar. Lower case is used for lower teeth.

Material and methods

Eleven hyaenid species were analyzed, represented by craniodental material (Table 1). Further data on dental and skeletal morphology and enamel structure of *Proteles*, *Ictitherium*, *Hyaenotherium*, *Hyaenictitherium*, *Parahyaena* and *Crocota* were taken from the following sources: Gaudry (1862–67); Werdelin (1988); Werdelin & Solounias (1991); Stefen & Rensberger (1999). The taxa examined here range from the Middle Miocene (ca. 15 Ma) to Recent times, and cover the major Hyaenidae clades recognized by Werdelin & Solounias (1991), as updated by Werdelin & Turner (1996a). Members of the Canidae, Herpestidae, and Viverridae (Table 1) were used for comparisons, to test the influence of phylogeny and dietary specialization on craniodental anatomy in the Hyaenidae. Canids belong to the Caniformia, the sister group of the Feloidae, the clade that includes Herpestidae, Viverridae, and Hyaenidae (Flynn et al. 1988).

External Hunter-Schreger Band (HSB) morphology and enamel outer surface features (perikymata, sculpturing), were observed by light microscopic methods. Analysis of enamel at this level of complexity, intermediate between prism type and tooth shape (Koenigswald & Clemens 1992), allows for a rapid survey of the whole dentition under reflected light microscope, without particular preparation of specimens.

Six metric characters of the mandible, third upper premolar and enamel microstructure (Fig. 2), have been either measured or obtained from published data (see above), in order to compare functionally significant features amongst taxa.

Craniodental measurements are according to Smith & Savage (1959), Radinsky (1981, 1982), and Werdelin & Solounias (1991), and include: 1) Moment arm of masseter (MAM), measured from the dorsal face of the mandibular condyle to the ventral margin of the angular process; 2) Moment arm of temporalis (MAT), measured from the condyle to the apex of the coronoid process; 3) Height of mandibular body behind the distal margin of the m1; 4) Length of third upper premolar (LP3); 5) Width of upper third premolar (WP3). In addition, the angle (α) surrounded by two consecutive HSB segments forming either a crest or a trough (Fig. 2), was considered. It was measured using light micrographs of the outer enamel surface (OES) of upper and lower third premolars, taken at about mid-crown eight.

Results

Canidae

Generalized, omnivorous canids (e.g., *Vulpes vulpes* and *Canis aureus*) possess elongated and narrow muzzles, a shallow mandible with a broad angular notch (MAT/MAM ratio in *V. vulpes* is 1.52), and an unreduced carnivoran dentition, comprising four premolars (P1-P4/p1-p4), and well developed crushing teeth (M1-M2; m1 talonid-m3). The premolars are well separated from one another, narrow, with poorly developed accessory cusps, and set in a straight line. All teeth display a smooth OES and undulating HSB throughout the dentition. Larger canid species (e.g. *Canis lupus* and *Lycan pictus*), that consume a greater quantity of bones (van Valkenburgh 1989, 1996; Stefen 1997), show more complex HSB in some places (e.g. canine, occlusal end of premolars), either transitional to, or fully comparable with, the zig zag type (Stefen 1999).

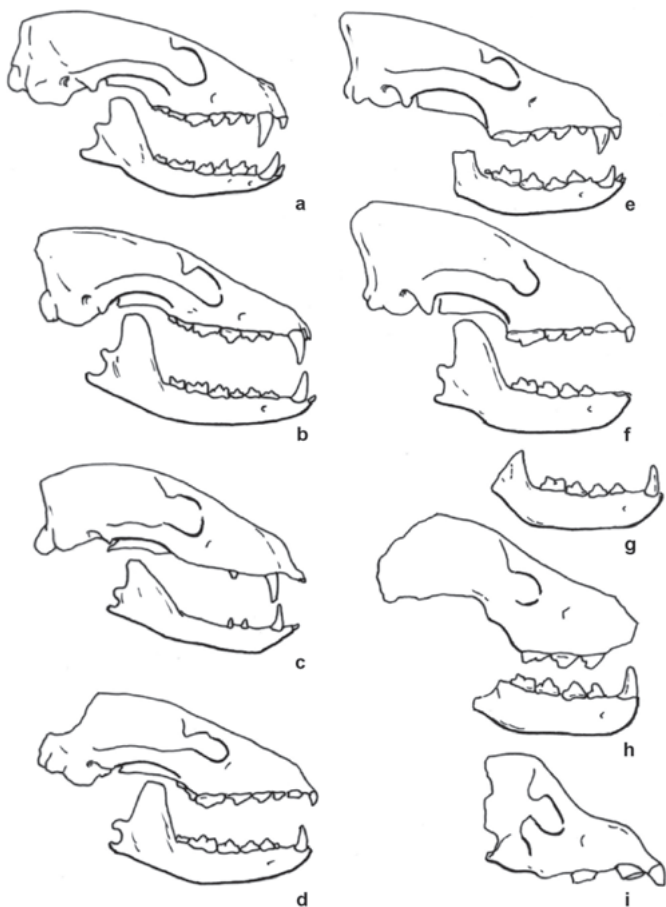


Fig. 3. Schematic drawings of the skull and mandible of a viverrid (a) and representative hyaenids (b-i), in lateral view. a) *Viverra tangalunga* (Recent; redrawn from Radinsky 1982). b) *Plioviverrops faventinus* (Late Miocene; reconstruction of the skull and mandible based on BRS 5 & 5-34). c) *Proteles cristatus* (Recent; redrawn from Werdelin & Solounias 1991). d) *Ictitherium viverrinum* (Late Miocene; redrawn from Gaudry 1862-67). e) *Hyaenotherium wongii* (Late Miocene; skull redrawn from Werdelin & Solounias 1991; mandible redrawn from Werdelin 1988). f) *Hyaenictitherium* (skull of *H. hyaenoides* redrawn from Werdelin & Solounias 1991; mandible of *H. namaquensis*, MPR A-2001). g) *Lycyaena chaeretis* (Late Miocene; mandible NHM M8979). h) *Chasmaporthetes lunensis* (Late Pliocene; skull IGF 4377; mandible UCBL 211221). i) *Pachycrocuta brevirostris* (Late Pliocene-Early Pleistocene; skull IGF 839). All skulls are drawn to the same basal length.

Herpestidae and Viverridae

Representatives of both the Herpestidae and Viverridae are characterized by relatively small to medium body size (0.2 to 20 kg). Feeding preferences of herpestids and viverrids include invertebrates, small vertebrates, as well as fruits (van Valkenburgh 1989; Nowak 1999). The overall cranial and dental morphology is similar within and between the two families. In general, the skull is low, with a flattened forehead and an elongated muzzle (Figs. 3a, 4a). The mandible (Fig. 3a), has a shallow body, while the ventral margin of the symphysis is slightly sloping. The ramus is low. The angular notch is wide and deep. In the studied herpestids, the average MAT/MAM ratio is 1.02.

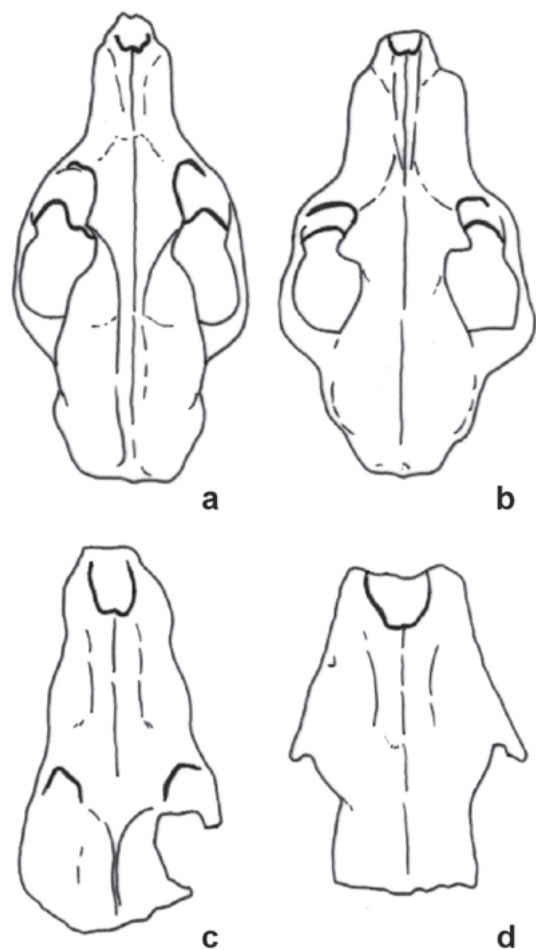


Fig. 4. Schematic drawings of the skull of a viverrid (a) and representative hyaenids (b-d), in dorsal view. a) *Viverra tangalunga* (Recent; redrawn from Radinsky 1982). b) *Proteles cristatus* (Recent; redrawn from Werdelin & Solounias 1991). c) *Lycyaena chaeretis* (Late Miocene; Skull BRS 27/17). d) *Chasmaporthetes lunensis* (Late Pliocene; Skull IGF 4377). Not to scale.

The dentition displays well developed puncture-crushing teeth (P1-P3/p1-p4; M1-M2/m1taloid-m2). The upper and lower third molars (M3/m3) are lost. In all the herpestid species examined in this study, the tooth enamel is characterized by a smooth OES and undulating HSB. The viverrid sample includes both fossil and modern taxa. The Miocene civet “*Viverra steinheimensis*” has teeth with a smooth OES and a predominance of undulating HSB. Acute-angled HSB are found, however, in some places in both the canine and the premolars. The teeth of “*Viverra angustidens*”, from the Miocene of La Grive, show only undulating HSB (Fig. 5a). The extant African civet (*Civettictis civetta*), the largest viverrid here examined (7 to 20 kg), is characterized by a rough OES, with marked perikymata. Almost all teeth of *C. civetta* have densely packed undulating HSB. Acute-angled HSB have been observed only in the lower canine. The genet, *Genetta genetta*, has a diet similar to that of the civets, but is markedly smaller (1 to 3 kg). It has a smooth OES and undulating HSB.

Hyaenidae

Plioviverrops faventinus TORRE 1994

P. faventinus, from the Late Miocene of Italy, is the youngest species of this fox-sized genus (Torre 1994). Its cranial features are rather generalized and resemble that of viverrids (Fig. 3b). The muzzle is, however, longer relative to the neural portion of the skull, than in the viverrid species analyzed. In this respect, the skull shape of *Plioviverrops* recalls that of *Vulpes*. The skull roof is flat, suggesting a poor development of the frontal sinuses (Joeckel 1998). The mandible is similar to that of viverrids, but the angular notch is relatively narrower (MAT/MAM is 1.6). The dentition of *Plioviverrops* is primitive in retaining four premolars (P1-P4/p1-p4) and two molars (M1-M2/m1-m2), a condition similar to that of viverrids. The third upper incisor is the largest of the three incisors, and has a pointed tip. The tooth row is straight. *Plioviverrops* displays a crushing-puncturing dentition, with well developed post-carnassial teeth (M1-M2/m2). The width to length ratio (%WP3/LP3) of the P3 is 46. All teeth are characterized by a smooth OES. Perikymata are present on premolars and molars (Fig. 5b). All teeth show slightly undulating HSB ($\alpha = 116^\circ$; Figs. 5c–d).

Proteles cristatus (SPARRMAN 1783)

The size of the aardwolf is comparable to that of civets (ca. 10 kg). The skull has a slightly convex dorsal profile, with no pronounced step between nasals and frontals (Figs. 3c, 4b). The frontal sinuses are not caudally enlarged (Joeckel 1998). The mandible has a slender body and a relatively low ramus, which is possibly related to the reduction of the masticatory muscles. The aardwolf has a reduced dentition, related to its diet of social insects (Kruuk & Sands 1972; Werdelin & Solounias 1991). The incisors are small, of sub-equal size, and with a flat occlusal edge. The canines are relatively long and slender. The post-canine dentition is rudimentary and tends to be lost during growth. The tooth enamel is very thin and characterized by undulating HSB (Stefen 1999).

Ictitherium viverrinum ROTH & WAGNER 1854

This Late Miocene hyaenid resembles jackals both in size and overall shape. Compared to *Plioviverrops*, it differs in its more sturdy cranial and dental morphology (Fig. 3d). Noteworthy is that the frontal sinuses are caudally developed, even though they are not as large as in extant bone-cracking hyaenas (Joeckel 1998). The angular notch of the mandible is large, even though it is relatively narrower than in *Plioviverrops* (MAT/MAM in *I. viverrinum* is 1.8). The dental formula is plesiomorphic. The lateral incisors are only slightly larger than the mesial ones. The premolars are markedly more robust than in *Plioviverrops* (%WP3/LP3 is 53), with clear apical wear, suggesting a more durophagous diet. Tooth OES displays a

shallow furrowing pattern (Fig. 5e). All examined teeth show zig zag HSB (Fig. 5f). By changing the direction of the incident light, vertical bands, connecting successive crests and troughs of the level I HSB, are visible. The mean value for angle α at mid crown height of P3 is 103° . The folding angles weaken toward the cervix, where undulating HSB occur.

Hyaenotherium wongii (ZDANSKY 1924)

Hyaenotherium wongii, from the Late Miocene of Eurasia, is a coyote-sized form. The skull is slightly more robust than that of *Ictitherium* and possesses a more stepped dorsal profile (Fig. 3e). The frontal sinuses are, however, similarly developed in the two taxa (Joeckel 1998). The mandible resembles that of *Ictitherium*. The dentition is more derived in having more reduced post-carnassial teeth and relatively larger crushing premolars (P2-P3 and p3-p4; %WP3/LP3 is 54). The OES is generally smooth and furrowed only at places. Zig zag HSB extended to all teeth (Fig. 5g). In this species as well, HSB change to the undulating type toward the tooth cervix. The average value for angle α in P3 is 92° , indicating a more derived condition than in *Ictitherium*.

Hyaenictitherium namaquensis (STROMER 1931) and *H. hyaenoides* (ZDANSKY 1924)

These late Miocene forms were larger than the hyaenid species described so far, reaching, in the case of *H. namaquensis*, the size of a modern brown hyaena. *Hyaenictitherium hyaenoides* shows a vaulted forehead, although less so than in extant hyaenas (Werdelin & Solounias 1991; Fig. 3f). The snout is relatively longer than in modern bone-cracking hyaenas. The I3 is not enlarged relative to the medial incisors. The mandible of *H. hyaenoides* is relatively more robust than that of both *Ictitherium* and *Hyaenotherium*, but the angular and symphyseal portions retain a primitive morphology. Compared to *H. hyaenoides*, *H. namaquensis* is markedly larger and characterized by a more stoutly built mandible. The mandible of *H. namaquensis* is derived in having a higher coronoid process. The angular notch, on the other hand, is primitively large (MAT/MAM is 1.52; Fig. 3f). The ventral margin of the mandibular symphysis of *H. namaquensis* is more ventrally inclined than in the hyaenid taxa described so far. The dentition in both *Hyaenictitherium* species is characterized by large premolars (P2-P3 and p3-p4), developing a large, flat, apical wear facet. The postcarnassial molars (M1-M2/m2) are reduced in size with respect to the condition in *Hyaenotherium*. The enamel is dominated by zig zag HSB, characterized by a mean α value similar to that observed in *Hyaenotherium*.

Lycyaena chaeretis (GAUDRY 1861)

L. chaeretis from the Late Miocene of Europe, was a wolf-sized species, with slender skeleton and elongated skull (Figs. 3g, 4c). The mandible is robust, with a more steeply slop-

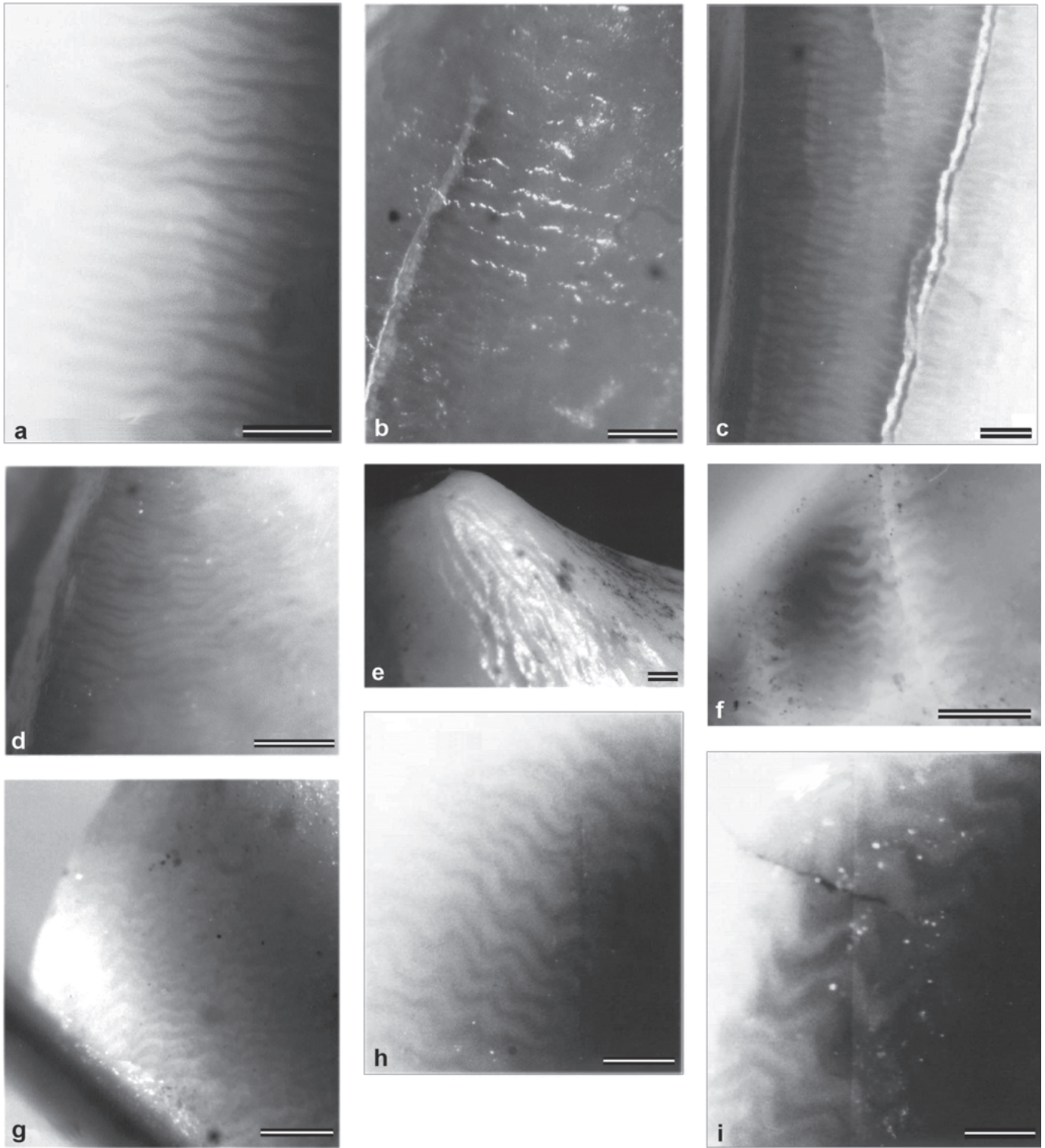


Fig. 5. Hunter-Schreger bands (HSB) and outer enamel features in viverrids and hyaenids, under reflected light. a) Labial side of P3 of “*Viverra angustidens*” (Middle Miocene), undulating HSB are visible. b) Lingual side of P3 of *Plioviverops faventinus* (Late Miocene), showing well marked perikymata. c) Labial side of upper canine of *P. faventinus*, showing undulating HSB. d) Lingual side of P3 of *P. faventinus*, enamel formed by undulating HSB. e) Labial side of P3 paracone of *Ictitherium viverrinum* (Late Miocene), OES presents shallow furrows, the worn tip of the paracone is visible (upper left). f) Lingual side of P3 of *I. viverrinum*, showing primitive zig zag HSB. g) Mesio-distal margin of p3 of *Hyaenotherium wongii* (Late Miocene), zig zag HSB are visible at mid crown. h) Labial side of P3 paracone of *Chasmaporthetes lunensis* (Late Pliocene), zig zag HSB are clearly visible. i) Labial side of P3 of *Pachyrocuta brevirostris* (Late Pliocene), highly folded zig zag HSB are a prominent feature of this large species. Scale bars: 0.25 mm (a & h, i); 0.5 mm (b–d, f, g); 1 mm (e).

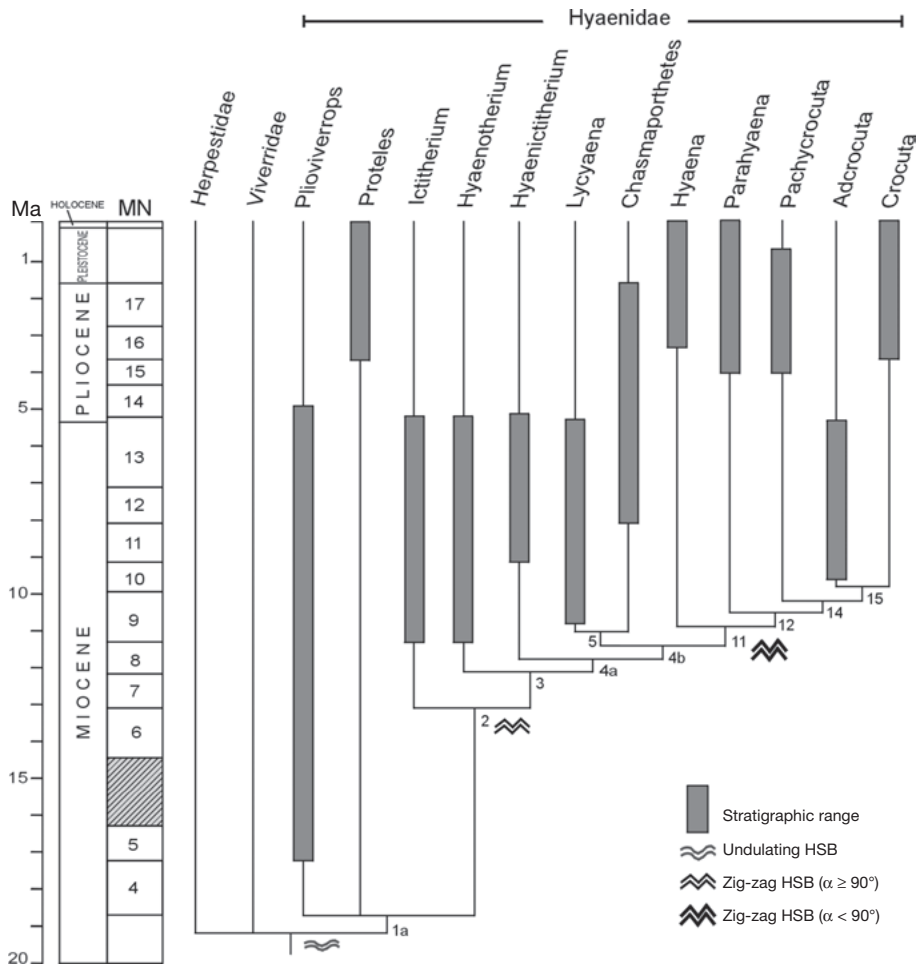


Fig. 6. Phylogeny and biochronology of the 11 hyaenid taxa analyzed in this study, with the addition of *Adcrocuta* (based on Werdelin & Solounias 1991, 1996). Numbers indicate the nodes discussed by Werdelin & Solounias (1991: fig. 38). Thick vertical lines show the known temporal range of the selected hyaenid genera. The distribution of HSB types is reported. Abbreviations: Ma, million years ago; MN, European Neogene mammal faunal zone.

ing symphysis than in *I. viverrinum* (Fig. 3g). *Lycyaena* has a straight and sectorial tooth row. The anterior premolars (P1/p1) tend to be lost during growth. P3 and p3 are relatively large, but more compressed laterally than in extant bone-cracking hyaenas (%WP3/LP3 is 59). The second upper molar is lost. In all studied teeth, the OES is rough, with well developed furrowing. Zig zag HSB are present in all teeth. In the P3, the average value for angle α is 90° , similar to the condition in *Hyaenotherium*.

Chasmaporthetes lunensis (DEL CAMPANA 1914)

This late Pliocene species is characterized by large size and elongated distal limb segments, evidence of a cursorial adaptation (Schaub 1941). It has a deep skull, with a short muzzle and a vaulted forehead (Figs. 3h, 4d), similar to the condition in *Hyaena*. The mandible is also deep, with a vertical symphysis (Fig. 3h). The tooth rows are straight with robust premolars, that develop a sub-horizontal apical wear facet (Fig. 3h). The p1 and m2 are lost. The outer enamel ornamentation is variable among the studied samples, ranging from the smooth OES of the Olivola and St. Vallier samples to the feebly fur-

rowed surface of the Upper Valdarno sample. All examined specimens display zig zag HSB (Fig. 5h). Though more advanced in its cranial features relative to *Hyaenictitherium* and *Lycyaena*, *Chasmaporthetes* is comparable to these taxa in the complexity of the HSB. In particular, the mean folding angle α in P3 is 90° . The closely related *C. melei*, from the Plio-Pleistocene of Sardinia (Rook et al. 2004), displays enamel microstructural features similar to those described in *C. lunensis*.

Pachycrocuta brevirostris (AYMARD 1846)

The Plio-Pleistocene Eurasian *P. brevirostris* is the largest known hyaena. It has a massive skeleton and a short and deep skull, with an extremely vaulted forehead (Fig. 3i). The mandible is morphologically similar to that of extant bone-cracking hyaenas. It is characterized by a deep body, with a subvertical, antero-ventral symphyseal margin. The ventral margin of the body is markedly angled. The angular notch is very narrow (MAT/MAM is 2.30). The coronoid process is massive and high. The lateral upper incisor (I3) is very robust and markedly larger than the mesial ones. In *Pachycrocuta* adults, the I3 develops and extensive wear facet. The distal

premolars (especially P3/p3) are extremely robust, with a broad, rounded base (%WP3/LP3 is 71). The outer enamel surface of the teeth of *Pachycrocuta* is deeply furrowed producing a wrinkled surface. All the examined teeth display well developed zig zag HSB (Fig. 5i). These are connected at wave troughs and crests by vertically directed bands. The mean angle (α) at wave troughs and crests in the studied sample is more acute than in all above mentioned taxa, ranging from 60° to 75°. Also, the amplitude of the waves in *Pachycrocuta* is higher than in the hyaenid taxa described above (Fig. 5i). Extant bone-cracking hyaenas (*Crocuta*, *Hyaena* and *Parahyaena*) are characterized by the same HSB morphology as described for *Pachycrocuta*.

Discussion

Distribution of bone-cracking adaptations among the Hyaenidae

Plioviverrops represents the most basal hyaenid taxon here analyzed and is placed at node 1a in the cladogram presented in Figure 6. It does not show any bone-cracking modifications when compared to the condition seen in members of the sister clades Viverridae and Herpestidae. As such, it may provide a suitable model for the primitive masticatory apparatus of Hyaenidae. Primitive features include: a flat skull (suggesting unexpanded frontal sinuses), a relatively longer muzzle, a narrower palate, a slender mandible (with a slightly sloping antero-ventral symphyseal margin), a wider angular notch, lateral incisors not enlarged, narrower premolars, well developed post-carnassial crushing molars, and tooth enamel with undulating HSB. With these characters, *Plioviverrops* resembles viverrids and small generalist canids (e.g. *Vulpes*), and likely occupied a similar feeding niche. The affinity of *Proteles* to other hyaenids has not been definitively established, even though a sister taxon relationship with *Plioviverrops* is strongly suggested (Thenius 1966; Werdelin & Solounias 1991). *Proteles*, while retaining most of the primitive hyaenid traits, is highly derived in its dental modification to feed on social insects (e.g. dentition reduction, incisors of equal size and with a flat occlusal edge), it has become a specialist in its own right. Bone-eating specializations are first found, in a phylogenetic sense, in *Ictitherium*, placed at node 2. These include caudally extended frontal sinuses, enlarged distal premolars and zig zag HSB. Except for the cervical portion, zig zag HSB are extended to the entire tooth crown. Relative to modern bone-cracking hyaenas, *Ictitherium* possesses HSB with a more open angle at wave troughs and crests (average α is 105°), suggesting a less specialized structure. In the same way, the skull profile and the mandible maintain a primitive shape. *Ictitherium* has been considered as a meat-eater species with bone-eating habits (Werdelin & Solounias 1996), an interpretation supported by the present analysis.

At node 3, is *Hyaenotherium*. This taxon is quite similar to *Ictitherium*, with further modified premolars and HSB, respec-

tively characterized by slightly broader crown and more closed folding angles (α). Nevertheless, the trophic specialization of *Hyaenotherium* is interpreted as similar to that of *Ictitherium*. At node 4, is *Hyaenictitherium*, which presents several more derived features. *Hyaenictitherium* is markedly larger than either *Hyaenotherium* and *Ictitherium*, its skull has a vaulted dorsal profile, the mandible, though retaining an overall primitive structure, is more robust, the tooth row forms an open arch, the distal premolars (P2-P3/p3-p4) are relatively larger and broader, and the post-carnassial teeth are more reduced in size. On the other hand, HSB morphology is similar to that of *Hyaenotherium*. Functional interpretation of the feeding apparatus of *Hyaenictitherium* suggests a greater emphasis on bone-eating relative to more primitive taxa, though not as important as in modern hyaenid species. The dichotomy at node 4b is characterized by a further modification of the feeding system: members of both the *Lycyaena-Chasmaporthetes* and modern bone-cracking hyaenas clades, possess a more robust mandible, with a steeply inclined anterior symphyseal margin and greatly reduced post-carnassial dentition. Species within the *Lycyaena-Chasmaporthetes* lineage (node 5), developed cursorial and hypercarnivorous adaptations (Berta 1981; Kurtén & Werdelin 1988; Werdelin & Solounias 1996). Nevertheless, derived *Chasmaporthetes* species (e.g. *C. lunensis*), paralleled the *Hyaena-Crocuta* clade in the development of some bone-cracking characteristics (e.g. a vaulted forehead, more enlarged premolars).

Node 11 represents the clade including all modern bone-cracking hyaenas. With respect to the masticatory system, this node is characterized by: the highest development of the frontal sinuses, resulting in an extremely vaulted skull profile, greatly enlarged lateral incisors, relatively broader distal premolars, markedly reduced mesial premolar and postcarnassial teeth, extremely folded zig zag HSB, with an average folding angle of less than 90°, and significantly higher wave amplitude. Remarkably, all teeth anterior to the carnassial blade (I3, C, P2, P3, P4 paracone) are used in bone-cracking, as demonstrated by the development of extensive wear facets. While most of these anatomical features (e.g. a thick mandible, very large and wide premolars) can be easily seen as mechanical adaptations to high stresses, generated during bone fracturing and consumption, others allow for a less straightforward functional interpretation. In particular, the configuration of the angular region of the mandible (either characterized by a wide or a narrow angular notch) is unclear. It could be related to the leverage of the masseter muscle, whose posterior fibers insert on the lateral side of the angular process. Indeed, a larger angular notch implies a greater distance between the angular process and the condyle and thus a higher moment arm of the masseter (see Smith & Savage 1959). Relative to primitive hyaenids, specialized bone-eaters have reduced the distance between the angular process and the mandibular condyle, possibly to further increase the mechanical advantage of the temporalis over the masseter. The present analysis shows that there is a high correlation between P3 robusticity and the intensity of HSB folding in hyaenids (Fig. 7). This is not surpris-

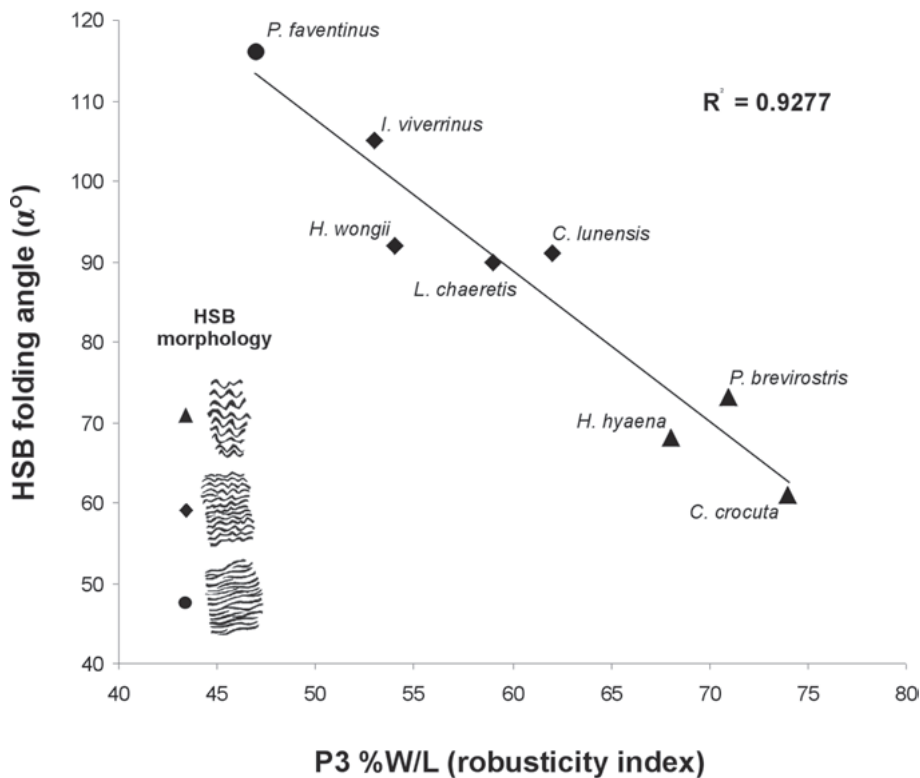


Fig. 7. Correlation between P3 robusticity and HSB morphology in hyaenids. P3 robusticity index corresponds to the percentage of width to length ratio and HSB (complexity) is expressed as a function of the folding angle α (see Fig. 2). Regression line and coefficient of determination (R^2) are indicated. See Table 1 for the systematics.

ing, as both characters have been shown to be adaptations to resist high stresses, produced during bone consumption (van Valkenburgh 1989; Rensberger 1995, 1999). Significantly, insectivorous-omnivorous hyaenids (such as *Plioviverrops* and *Proteles*), with no evidence of bone consumption, are characterized by undulating HSB with a wide folding angle (mean $\alpha = 116^\circ$), relatively narrow premolars (%W/L ranging from 45–50), and primitive (i.e. not expanded) frontal sinuses. In contrast, derived bone-cracking hyaenas have steeply folded HSB (α ranging from 61° to 73°), extremely broad premolars (%W/L ranging from 65 to 75), and greatly expanded frontal sinuses. Species such as *Ictitherium* and *Hyaenotherium*, with intermediate characters between these two extreme ecomorphs, probably represent an intermediate degree of specialization toward bone-consumption, reflecting differences in the relative amount of bone consumed.

Enamel structure and body size

Though the influence of body size on the evolution of zig zag HSB in hyaenids has not been especially addressed here, it should be noted that relatively large forms (e.g. *Hyaenotherium*), have usually a more complex enamel structure than smaller ones (e.g. *Ictitherium*). This may suggest the possibility that the development of zig zag HSB could be (at least in part) a size related phenomenon. Indeed, large bodied species possess more powerful masticatory muscles than similar but smaller forms, then their enamel require a more resistant structure.

However, the observed difference in the intensity of the HSB folding between hyaenids of similar size (e.g. between *Hyaenictitherium namaquensis* and *Parahyaena brunnea*), seems to confirm that HSB morphology is most related to feeding behaviour than merely to body size. This conclusion is also supported by the correlation between HSB subtypes and the amount of bone consumed among recent carnivores (Steffen 1997, 1999).

Phylogenetic aspects of enamel structure in the Hyaenidae

The results of the present study show that HSB morphology provides informative characters for hyaenid phylogeny. Based on structural features (Rensberger 1999) and their distribution among the studied taxa, the following transformation series is suggested for the decussation pattern of hyaenid outer enamel: 0, undulating HSB; 1, zig zag HSB with $\alpha \geq 90^\circ$; 2, zig zag HSB with $\alpha < 90^\circ$.

Outgroup comparison indicates that undulating HSB characterized the primitive condition in the Hyaenidae, and are retained in *Plioviverrops* and *Proteles*. Based on the cladogram of Werdelin & Solounias (1991: fig. 38; Fig. 6), the *Ictitherium-Crocota* clade (dichotomy 2) is characterized by zig zag HSB. These zig zag HSB, with wider folding angle ($\alpha \geq 90^\circ$), would define node 2 and are retained by *Ictitherium*, *Hyaenotherium*, *Hyaenictitherium*, *Lycyaena*, and *Chasmaporthetes*. Modern bone-cracking hyaenas (node 11), are characterized by zig zag HSB with a narrower folding angle ($\alpha < 90^\circ$). However,

the assignment of this derived zig zag HSB type to node 11 is uncertain. This character might equally define any of the nodes between 7 and 11 (not shown), corresponding to the so-called transitional bone-cracking hyaenas (Werdelin & Solounias 1991, 1996), not included in the present analysis. The lack of information about the condition in these forms precludes any definitive conclusion. Zig zag HSB are not exclusive to hyaenid enamel. This complex type of decussation evolved independently in several mammalian groups, as a mechanical response to a high occlusal stress (Stefen 1997; Rensberger 1999; Stefen & Rensberger 1999). However, the observed distribution pattern of the different HSB types among the reported hyaenids is consistent with the hypothesis that enamel dominated by zig zag HSB is a synapomorphy of the *Ictitherium-Crocota* clade.

Stefen & Rensberger (1999) observed a transition from undulating to zig zag HSB, in the teeth of *Protictitherium crassum* from the Early to Middle Miocene of Europe. All other *Protictitherium* species described by Stefen & Rensberger (1999), were characterized instead by undulating HSB. *Protictitherium* is considered as the most primitive hyaenid genus, even though its place among the Hyaenidae has not been definitively settled, based on available material (Werdelin & Solounias 1991). The present analysis suggests that the occurrence of zig zag HSB, limited to the tooth apex in *P. crassum*, is an autapomorphy of this species.

Conclusions

A key innovation in hyaenid evolution was the acquisition of enamel dominated by zig zag HSB. This marked the initial transition of the group to the bone-eating niche. Fossil evidence indicates this event likely took place in the Middle Miocene. Moreover, it could have triggered the rapid differentiation of the so-called type 3 hyaenids, including *Ictitherium*, *Hyaenotherium* and *Hyaenictitherium* (Werdelin & Solounias 1996), during Middle to Late Miocene times (Fig. 6). An important turnover in Old World hyaenid faunas, took place across the Miocene/Pliocene boundary (Werdelin & Solounias 1996; Werdelin & Turner 1996b), leading to the extinction of all type 3 hyaenids and the dispersal of modern bone-cracking hyaenas in Eurasia. The demise of type 3 hyaenids in Europe seems related to the gradual reduction of woodland habitats in the latest Miocene, which had a strong impact on herbivore communities (Bernor et al. 1996; Werdelin & Turner 1996b; Eronen & Rook 2004). During the same time interval, the first canid of modern-type (*Eucyon*) dispersed to the Old World (Rook 1993; Tedford & Qiu 1996). The *Chasmaporthetes* lineage, on the other hand, survived in Europe until the Pliocene-Pleistocene transition, giving rise to an endemic insular form in the Western Mediterranean (Rook et al. 2004). Note that the extinction of the European hunting hyaena was coeval with the dispersal of the large cursorial canid *Lycaon* into Western Europe (Martinez-Navarro & Rook 2003), suggesting a possible causal link between these two events.

Based on the phylogenetic reconstruction of Werdelin & Solounias (1991), bone-cracking hyenas of modern type were already differentiated in the early Late Miocene (MN10). However, they became widespread only in the Pliocene. In Europe, large scavenging bone-cracking hyaenas (e.g. *Pachycrocuta*; Ficarelli & Torre 1970) were particularly common in the Villafranchian (Late Pliocene–Early Pleistocene), maybe favored by the spread of open habitats, where the probability of tracking large carcasses was higher. Hyaenas belonged to the European large carnivore guild until the Last Glacial Age and disappeared at the end Pleistocene mega-mammal extinction.

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